CHAPTER 10

Crop pollination services

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10.1 Introduction

10.1.1 Importance to agriculture and policy

Crop pollination by bees and other animals is an ecosystem service of enormous economic value (Losey and Vaughan 2006; Allsopp et al. 2008). Pollination can increase the yield, quality, and stability of crops as diverse as almond, cacao, canola, coffee, sunflower, tomato and watermelon. Indeed, Klein et al. (in press) found that 75% of globally important crops benefit from animal pollination. The value of this service, while difficult to quantify properly, has been estimated several times over the past decade (Southwick and Southwick 1992; Costanza et al. 1997; Losey and Vaughan 2006; Allsopp et al. 2008) with a recent estimate of 195 billion Euros (~$200 billion) worldwide (Box 10.1).

While much research and policy attention has focused on managed bees (especially the honey bee, Apis mellifera), wild bees and other insect species also contribute importantly to crop pollination. Our models focus on wild bees, because the pollination they deliver represents an ecosystem service from natural systems. In fact, for some crops (e.g., blueberry), wild bees are more efficient and effective pollinators than honey bees (Cane 1997). Diverse bee communities potentially provide more stable pollination services over time, compared to single (managed) species (Greenleaf and Kremen 2006; Hoehn et al., 2008). Finally, if alarming regional declines in honeybee populations continue (National Research Council of the National Academies 2006; Stokstad 2007; Klein et al., in press), wild pollinators may become increasingly important to farmers.

Maintaining pollinator habitats in agricultural landscapes, therefore, can help ensure food production, quality, and security. While other pollinators (e.g., bats and moths) also pollinate crops, bees are the most important crop pollinators (Free 1993) and are thus the focus of our models.

The pollination models aim to quantify and map scores for relative pollinator abundance across an entire landscape, including farms requiring pollination. The models use these results to indicate areas supplying pollinators that increase crop yields. Alternatively, intermediate results can be integrated into our agricultural model (see Chapter 9) to estimate the economic value of pollination services as an input to crop yields in a more sophisticated manner. Either way, these models can inform agricultural and land management policies in several ways. First, land-use planners could predict consequences of different policies on pollination services and income to farmers (Priess et al. 2007). Second, farmers could use these tools to locate crops in places where their pollination needs are most likely to be met. Third, conservation organizations that guide land management and restoration could use the tool to optimize conservation investments for both biodiversity and crop productivity. Finally, governments or others proposing payment schemes for ecosystem services could incorporate the results into plans for who should pay whom, and how much.

10.1.2 Scientific foundations and context

Our pollination models are founded on an increasing number of studies that have investigated the impacts of landscape structure and habitat-quality
Box 10.1 Assessing the monetary value of global crop pollination services

**Nicola Gallai, Bernard E. Vaissière, Simon G. Potts, and Jean-Michel Salles**

Most major crop species are pollinated by bees or other insect groups (Klein et al. 2007). As the abundance and diversity of bees are now declining in many parts of the world, there is a growing need for improved methods to: (1) adequately assess the potential loss in terms of economic value that may result from pollination shortfalls, and (2) link this value to the vulnerability of agriculture confronted with pollination shortages.

To evaluate the monetary value of crop pollination services worldwide, we used the FAO global crop production statistics (http://www.fao.org) coupled with the reported degree of dependency of each crop on biotic pollination (Klein et al. 2007). FAO statistics are available for direct crops (production data available) and commodity crops (individual crop production data is aggregated for each commodity). Although these aggregations of crop production may represent a significant part of the agricultural output of a given country or region, and some of these species depend heavily on biotic pollination (Klein et al. 2007), we excluded all aggregated crop complexes from our analysis as prices and production figures were not available for each individual crop.

Following Gallai et al. (2009), we defined the economic value of pollinators (EVP) as the value of the pollinator contribution to the total economic crop production value. This contribution was calculated based upon the dependence ratio of crop production on pollinators, defined as the proportion of the yield attributable to insect pollinators. The economic value of pollinators was thus calculated as

\[
EVP = \sum_{i=1}^{X} \sum_{x=1}^{i} P_{ix} Q_{ix} D_{ix} , \quad (10.A.1)
\]

where \( P \) is the producer price per production unit, \( Q \) is the quantity produced for each crop \( i \in [1; I] \) for each country \( x \in [1; X] \), and \( D \) is the dependence ratio for each crop \( i \in [1; I] \). For \( Q \), we used 2005 FAO production data expressed in metric tons. Producer prices, \( P_{ix} \), for 2005 were obtained using data from financial markets, USDA (http://www.fas.usda.gov) and Eurostat (http://epp.eurostat.ec.europa.eu), and actualization of FAO data and expressed in US$ per metric ton. The dependence ratios \( D_{ix} \) were calculated based upon the five dependency levels defined in the Appendix 2 of Klein et al. (2007). For each crop, we calculated an average dependence ratio based on the reported range of dependence on animal-mediated pollination. Based on this, the 2005 worldwide economic value of pollinators was US$190 billion compared to US$2,013 billion for the overall crop production value (Gallai et al. 2009).

Vulnerability is a function of three elements: exposure, sensitivity and adaptive capacity. For crops, the agricultural vulnerability to pollinator decline depends upon the crop dependency on pollinators and the capacity of farmers to adapt to pollinator decline. In this context, we used the ratio of the economic value of pollinators (EVP) to the total economic crop production value (EV) to calculate a level of vulnerability, which provides a measure of the potential relative production loss attributable solely to the lack of insect pollination. We evaluated the vulnerability in term of the proportion of the agricultural production value that depends on insect pollination (Gallai et al. 2009):

\[
VR = \frac{EVP}{EV} = \frac{\sum_{i=1}^{X} \sum_{x=1}^{i} P_{ix} Q_{ix} D_{ix}}{\sum_{i=1}^{X} \sum_{x=1}^{i} P_{ix} Q_{ix}} \% \quad (10.A.2)
\]

The vulnerability ratio of global agricultural production used for human food in 2005 was 9.5% (Gallai et al. 2009). The ratio varied considerably among different geographical areas, for example, at a national level, the vulnerability of European countries varied between 1% in Ireland to 19.5% in Austria (Figure 10.A.1). In Europe, there was a positive correlation between the vulnerability to pollinators of a crop category and its value per production unit \( r = 0.729 \) \( n = 10, \rho = 0.017 \), indicating that the more a crop is dependent on insect pollination, the higher its value per production unit.

However, our approach provides an incomplete picture of the value of insect pollinators to society because we did not take into account agricultural production not used directly for human food (e.g., fodder crops), seeds produced for plant breeding, and perhaps most importantly, natural vegetation and all its associated ecosystem services which would almost certainly be strongly impacted by pollinator decline. Our estimates are therefore conservative.
They have found that the availability of nesting substrates (e.g., suitable soils, tree cavities; Potts et al. 2005) as well as floral resources (i.e., both nectar and pollen) in both natural and semi-natural habitats can strongly influence the diversity (Hines and Hendrix 2005), abundance (Williams and Kremen 2007), and distributions of pollinators across a landscape (Tepedino and Stanton 1981; Potts et al. 2003). In addition, because bees forage from fixed nest sites with limited foraging ranges, their abundance and diversity on a farm, as well as their effect on crop pollination, can be influenced strongly by proximity to nesting habitats (Morandin and Winston 2006).

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 forest than in fields further away. On the other hand, other studies have found little effect of landscape pattern on pollinator visitation, such as Winfree et al.’s (2008) study of pollination services to vegetable crops in the northeastern USA. Despite this variation among studies, Ricketts et al. (2008) synthesize 23 case studies (including

Box 10.1 continued

Distribution of the vulnerability ratio across Europe

Vulnerability ratio (%):

- 1.0–5.7
- 5.7–8.0
- 8.0–9.4
- 9.4–12.1
- 12.1–19.5

Figure 10.A.1 Distribution of crop vulnerability to pollination service across Europe.
many of those cited above) and find a general “consensus” decline in pollination services with increasing isolation from natural or semi-natural habitat.

Building from these and many other studies, Kremen et al. (2007) have proposed a general framework for understanding how pollination services are delivered across landscapes, and how these services are affected by land-use change in agricultural regions (Figure 10.1). Here, we develop a simplified version of this general model (indicated in Figure 10.1), which uses simple landscape indices, governed by a few key parameters that can be estimated from field data or expert opinion, to predict relative pollinator abundances across a landscape and agricultural fields. Moreover, we use the framework that predicts abundance at crop field to attribute the pollinator-dependent gains in yield and crop value to the parcels supplying the pollinators.

10.1.3 Model intuition and difference between tiers

10.1.3.1 Overview of data requirements

Pollinators require two basic types of resources to persist on a landscape: nesting substrates and floral resources (Westrich 1996; Kremen et al. 2007). The model therefore requires estimates of availability of both of these resource types for each land-use and land cover type (LULC) in the map. These data can be derived from quantitative field estimates or from expert opinion. Pollinators move between nesting habitats and foraging habitats (Westrich 1996; Williams and Kremen 2007), and their foraging distances, in combination with arrangement of different habitats, affects their persistence, their abundance, and the level of service they deliver to farms. Our model therefore also requires a typical foraging distance for pollinators. These data can be supplied, e.g., from quantitative field estimates.

Figure 10.1  General conceptual model describing pollination services and their delivery across an agricultural landscape (full framework, reproduced from Kremen et al. (2007)).
Land-use practices (Box a) determine the pattern of habitats and management on the landscape (Box b). The quality and arrangement of these habitats affect both pollinator and plant communities (Boxes c and d). The value of pollination services (Box f) depends on the interaction between specific plants (e.g., crops) and their specific pollinators. Our pollination model is a simplified version of this full model, capturing the following arrows only: 3a, 3c, 6a, and with economic model 6b.
(Knight et al. 2005), from proxies such as body size (Gathmann and Tscharntke 2002; Greenleaf et al. 2007), or from expert opinion.

The ultimate level of pollination service provided to a farm depends on the crops grown, the ability of each modeled species to pollinate them effectively, the crop’s response to animal pollination and the abundance of pollinators at the crop. The model therefore incorporates data on location of farms of interest, the crops grown there, and how effective each species is as a pollinator for a given crop.

10.1.4 Model intuition

Using these data, the model first estimates a relative abundance score of each pollinator species in each parcel (hereafter, pollinator “supply” to follow the conventions in Chapter 3), based on the available nesting resources in that parcel and the floral resources in surrounding parcels. We define parcel as the analytical spatial unit on the landscape. In our case, it is a 90 meter by 90 meter grid cell that may have more than one land cover within it. In calculating floral resources, nearby parcels are given more weight than distant parcels, based on the species’ average foraging range. The result is a map of relative abundance scores (0–1) for each species in the model (the “supply map”).

Given this pattern of pollinator supply, the model then estimates the relative abundance of foraging bees arriving at each farm (“farm abundance”). It sums the relative bee abundances in neighboring parcels, again giving more weight to nearby parcels, based on average foraging ranges. This weighted sum is our relative index (0–1) of abundance for each pollinator in the farm. If the crop type at each parcel and its pollinators are known, the model will limit the weighted sum only to relevant pollinators.

We use a very simple yield function to translate farm abundance into relative crop yields. Alternatively,

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Tier 1</th>
<th>Tier 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>HN</td>
<td>Habitat suitability for nesting</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>HF</td>
<td>Habitat suitability for foraging</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>J</td>
<td>Number of land cover types (each indexed by j)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>N_j</td>
<td>Compatibility of habitat j for nesting</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>F_j</td>
<td>Compatibility of habitat j for foraging</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>M</td>
<td>Number of parcels in landscape (indexed by m)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>D</td>
<td>Distance between parcels</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>α</td>
<td>Expected pollinator foraging distance</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>P</td>
<td>Pollinator abundance score</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>O</td>
<td>Number of farm parcels (indexed by o)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>X</td>
<td>Pollinator source parcel</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>ψ</td>
<td>Farms’ average change in normalized scores (used for sensitivity analysis)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Y</td>
<td>Crop yield (indexed by o)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>V</td>
<td>Crop value based on agricultural production function (indexed by o)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>ν</td>
<td>Proportion of a crop’s yield attributed only to wild pollination (indexed by c)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>K</td>
<td>Pollinator abundance to achieve ½ of pollinator-dependent yield (indexed by c)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>PS</td>
<td>Pollinator service provided to crops (indexed by m)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>S</td>
<td>Number of species (indexed by s)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>I</td>
<td>Number of nesting types (indexed by i)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>W</td>
<td>Weight describing importance of floral season for pollinator</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>K</td>
<td>Number of floral seasons (indexed by k)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>C</td>
<td>Crops’ pollinator requirement</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>ε</td>
<td>Relative abundance of pollinator in landscape</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>

The last seven parameters are unique to tier 2. The model can be run with a mixture of tier 1 and tier 2 parameters, allowing a continuum of model complexity to match data availability.
one can use farm abundance as an input in the more sophisticated agricultural production model (Chapter 9) to determine the crop yield and value on each farm parcel. Finally, our model redistributes crop value back onto the landscape to estimate the service value provided from each parcel to surrounding farms (equivalent to the “use” and “value” in the parlance of this book, Chapter 3). It does so using the same foraging ranges, so that parcels that are sources of abundant pollinators and near to farms tend to have relatively high service value.

The pollination model has two tiers permitting use of different amounts of information. The tier 1 models are nested within tier 2 (i.e., tier 1 is a simpler version of tier 2). Both tiers are based on a LULC map, showing both natural and managed land types. Onto this landscape, tier 1 models a single pollinator that represents the overall pollinator community, while tier 2 considers multiple pollinator species or guilds, allowing them to differ in flight season, resource requirements, and foraging distance. Because the models are nested, tier 1 and tier 2 are actually endpoints of a continuum of potential model complexity (Table 10.1). For example, one can recognize multiple species and use a different foraging radius for each (Eq. (10.2)), but model only a single flowering season and nesting guild. This nestedness also allows easy comparisons of model outputs between tiers, as we explore in Chapter 15.

10.2 Tier 1 supply model

Pollinators require habitat for nesting and within some foraging distance they require floral resources for food. The first step of our model is to translate a LULC map (Figure 10.2a; Plate 5a) into a nesting suitability map and a floral resource availability map. Then based on the amount and location of nesting and floral resources, we calculate the pollinator supply map.

The first step in calculating the pollinator source score at each parcel is identifying the proportion of suitable pollinator nesting habitat in a parcel $x$ as a function of LULC $j$, $HN_x$:

$$HN_x = \sum_{j=1}^{N} p_j p_{jx},$$

where $N_j \in [0,1]$ represents compatibility of LULC $j$ for nesting and $p_{jx}$ is the proportion of parcel $x$ that is covered by LULC $j$. This provides a landscape map of nesting suitability where $HN_x \in [0,1]$ (Figure 10.2b; Plate 5b). A score of 1 would indicate that the entire area of the parcel provides habitat suitable for nesting (e.g., forest habitat in Supplemental Online Material (SOM) Table 10.S1) while a score of 0.2 would indicate 20% of the parcel’s area provides suitable nesting habitat (e.g., coffee/pasture habitat).

We calculate the proportion of suitable foraging habitat surrounding a parcel $x$, given by $HF_x \in [0,1]$. We assume that foraging frequency in parcel $m$ declines exponentially with distance (Cresswell et al. 2000), and that pollinators forage in all directions with equal probability. Therefore, parcels farther away from nest parcel $x$ contribute less to total resource availability than parcels nearby, and leads to the following prediction for the potential floral resources available to pollinators nesting in parcel $x$, $HF_x$:

$$HF_x = \frac{\sum_{n=1}^{M} \sum_{j=1}^{N} F_j p_{jx} e^{-\frac{D_{nx}}{a}}}{\sum_{m=1}^{M} e^{-\frac{D_{mx}}{a}}}$$

where $p_{jm}$ is the proportion of parcels $m$ in LULC $j$, $D_{nx}$ is the Euclidean distance between parcels $m$ and $x$, $a$ is the expected foraging distance for the pollinator (Greenleaf et al. 2007) and $F_j \in [0,1]$ represents relative amount of foraging resource in LULC $j$. The numerator is the distance-weighted resource summed across all $M$ parcels. The denominator represents the maximum possible amount of forage in the landscape. This equation generates a distance-weighted proportion of habitat providing floral resources within foraging range, normalized by the total forage available within that range (Winfree et al. 2005) (Figure 10.2c; Plate 5c).

Supply map: Since pollinator abundance is limited by both nesting and floral resources, the pollinator abundance score on parcel $x$ is simply the product of foraging and nesting such that $P_x = HF_x HN_x \in [0,1]$. This score represents the location and supply of pollinators available for crop pollination from
Figure 10.2  Example results of pollination model for watermelon in Yolo County, California. The model uses (a) land cover data as input and derives maps of (b) nesting habitat and (c) floral resources. From this, it generates (d) a pollinator supply map that describes an index of pollinator abundance on the landscape. Based on the supply map, the model generates (e) a pollinator abundance map on farm parcels (i.e., “farm abundance”). After using a simple yield function to translate farm abundance into relative yield the model distributes yield or economic value back onto the surrounding landscape to generate (f) the value map. All steps are the same for tier 1 and tier 2 models; results here are tier 2, based on data supplied in supplemental online appendix. (See Plate 5.)
parcel $x$ and results in the supply map. This map does not account for the location or type of crops present in the landscape, and as such has not adjusted pollination to show the actual service supplied to people, but rather all potential pollination on the landscape.

**10.3 Tier 1 farm abundance map**

For pollinators’ actions to provide crop pollination benefits to people, pollination must take place on a farm growing a crop that requires insect pollination. In the next modeling step, we identify farms on the landscape, and the relative abundance of wild pollinators on each farm.

Pollinators leave their nesting sites to forage in surrounding parcels, so farms surrounded by a higher abundance of nesting pollinators should experience higher abundances of pollinating visitors to their crops. We use the foraging framework described in Eq. (10.2) to determine the contribution to pollinator abundance from a single nest parcel $m$ to forage on a crop in farm $o$:

$$P_{om} = \frac{P_m e^{-\frac{D_{om}}{\alpha}}}{\sum_{m=1}^{M} e^{-\frac{D_{om}}{\alpha}}}$$

(10.3a)

where $P_m$ is the relative supply of pollinators on map unit $m$, $D_{om}$ is distance between source parcel $m$ and farm $o$, and $\alpha$ is species’ average foraging distance. $O$ can be used to index specific farms of interest or every agricultural parcel on the landscape. The numerator of Eq. (10.3a) represents the distance-weighted proportion of the pollinators supplied by parcel $m$ that forage within farm $o$ and the numerator is a scalar that normalizes this contribution by the total area within foraging distance to farm (Winfree et al. 2005). The total pollinator abundance on farm $o$, $P_o$, is simply the sum over all $M$ parcels,

$$P_o = \sum_{m=1}^{M} P_{om}.$$  

(10.3b)

**10.4 Tier 1 valuation model**

Pollination has economic value as an ecosystem service because it is an input to agriculture, from which people derive food and income. In formal terms, pollination can be an important factor in agricultural production functions, which relate yields of a given crop to the quantity and quality of various inputs (e.g., water, soil fertility, labor, chemicals). Production functions (or “yield functions”) are a well-established econometric technique used widely in agriculture and product manufacturing (Polasky et al. 2008). The agricultural models described in Chapter 9 take exactly this approach, so we do not repeat it here; instead, we offer an extremely simple alternative. Our “farm abundance” results above can be used as inputs to either one.

Using production functions in this way will result in an estimate of the economic value of pollinators at each farm. It is most likely of interest, however, to estimate the value of the habitats in the landscape that support these pollinators. For this we can use the ecological models described here, which model movement of pollinators from source parcels to farms, to attribute economic value realized on farms back to the pollinator-supporting habitats.

**10.4.1 Estimating crop yield and value**

The calculated pollinator abundance from Eq. (10.3b) will be an input into the agricultural production function to determine the crop yield and crop value on each parcel. In lieu of a more detailed agricultural production model (Chapter 9), we use a simple saturating yield function to translate the abundance of pollinators on farms into an expected yield. Yield should increase as pollinator abundance and diversity increase (Greenleaf and Kremen 2006), but crops vary in their dependence on pollinators, i.e., some crop species are self-compatible and yield is less dependent on pollination while other species obligately require pollination to generate any yield (Allsopp et al. 2008; Rickert et al. 2008). We account for both observations, and thus calculate the expected yield of a crop $c$ on farm $o$, $Y_o$, as

$$Y_o = 1 - \nu_c + \nu_c \frac{P_o}{P_o + K_c},$$

(10.4)
where \( v_c \) represents the proportion of total crop \( c \)'s yield attributed only to wild pollination (e.g., \( v_c \) would be equal to 1 if a crop is an obligately out-crossing species and equal to 0 if the crop species were wind-pollinated). In the denominator of the third term, \( k_c \) is a half-saturation constant and represents the abundance of pollinators required to reach 50% of pollinator-dependent yield. The monetary value of the crop on farm \( o \), \( V_o \), is simply the product of yield per hectare, \( Y_o \), the number of hectares of the crop and the price of the crop (Gallai et al. 2009).

### 10.4.2 Assigning value back to pollination sources: service value

We use the pollinator model here to redistribute each farm \( o \)'s value back onto the landscape based on the actual level of service supplied by each parcel \( m \). Recall Eqs. (10.3a) and (10.3b) that determined the total abundance on farm \( o \) by summing across all \( M \) supply parcels the proportion of pollinators foraging from each supply parcel to farm \( o \). Here, we instead attribute the pollinator-generated value from the \( O \) farms back to the \( M \) supply parcels. For each supply parcel \( m \), we sum across all \( O \) parcels, weighting the contribution from each farm \( o \) to parcel \( m \) by their proximity. Thus, supply parcels close by crops (or guild) differences in habitat suitability so that the proportion of suitable nesting habitat in a parcel \( x \) for pollinator species \( s \) as a function LULC \( j \), \( HN_{sx} \) is

\[
HN_{sx} = \sum_{j=1}^{J} N_{js} p_{js},
\]

where \( N_{js} = [0,1] \) represents compatibility of LULC \( j \) for nesting by species \( s \).

Some LULC classes can provide habitat suitable for multiple nesting types. For example, in California, we scored oak woodland habitat as providing good habitat for wood-nesting, ground-nesting and cavity-nesting bees, but scored agricultural habitat as providing poorer habitat for ground-nesting bees, and non-habitat for wood or cavity nesters (see Section 10.4.1).

For bee species or groups that span nesting types (e.g., species that nest in the ground and in hollow stems) we assigned the habitat type according to the nest type that maximized its suitability for that bee species. In other words, if there are \( I \) nesting types, then \( N_j = \max\{NS \times N_{ps}, \ldots, NS \times N_{ps}\} \), where \( NS \times N_{ps} \) is the nesting suitability of nesting type \( i \) for species \( s \) and \( N_j \) is the suitability of LULC \( j \) for nesting type \( i \). This analysis provides a map of nesting suitability (Figure 10.2b; Plate 5B).

As in Tier 1, we calculate the proportion of suitable foraging habitat for pollinator species \( s \) nesting in parcel \( x \) given by \( HF_{sx} \in [0,1] \). In tier 2, though, we allow for production of floral resources to vary among \( K \) seasons. We also use data or expert opinion to assess flight period and account for variation among pollinators in their \( K \) flight seasons, e.g., some are present in summer only, while others are present in multiple seasons. We calculate the overall floral resources available as a
weighted sum across $K$ seasons where the weight $(w_{sk}) \in [0,1]$ represents the relative importance of floral production in season $k$ for species $s$. We constrain each $w_{sk}$ value such that $\sum_{k=1}^{K} w_{sk} = 1$. This leads to the following prediction for the potential floral resources available to species $s$ parcel $x$ across $K$ seasons, $HF_{os}$

$$HF_{os} = \sum_{s=1}^{S} \sum_{m=1}^{M} \sum_{j=1}^{J} F_{m,s} P_{m,s} e^{-D_{om} / \alpha_{s}},$$

(10.7)

where $P_{m,s}$ is the proportion of parcel $m$ in LULC $j$, $D_{om}$ is the Euclidean distance between parcels $m$ and $x$, $\alpha_{s}$ is the typical foraging distance for species $s$ and $F_{m,s} \in [0,1]$ represents suitability for foraging of LULC $j$ for species $s$ during season $k$. The use of $F_{m,s}$ permits attributing different resource levels to the same LULC type for different bee species or guilds. The weights for each species can be determined by expert opinion or with observed data. Additional species-by-crop weights could be added to Eq. (10.9b) in the same fashion as $\epsilon_{s}$ to account for differences among pollinators in their effectiveness on a given crop (Greenleaf and Kremen 2006).

### 10.6 Tier 2 farm abundance map

To calculate the abundance of each pollinator species on a crop in parcel $o$, we use the framework described in Eqs. (10.3a) and (10.3b). First to calculate pollinator visitation by species $s$ from nest parcel $m$ to farm parcel $o$, $P_{\text{o}mn}$

$$P_{\text{osmn}} = \frac{P_{os} e^{-D_{os} / \alpha_{s}}}{\sum_{m=1}^{M} e^{-D_{om} / \alpha_{s}}},$$

(10.8a)

where $P_{os}$ represents the supply of pollinator $s$ on map unit $m$, $D_{os}$ is distance between map unit $m$ and farm $o$ and $\alpha_{s}$ is species $s$' typical foraging distance. The total pollinator abundance of species $s$ on farm $o$, $P_{os}$, is simply the sum of $P_{\text{osmn}}$ over all $M$ parcels at each farm $o$,

$$P_{os} = \sum_{m=1}^{M} P_{\text{osmn}}.$$  

(10.8b)

This score represents the relative abundance of pollinators visiting farm and results in the farm abundance map (Figure 10.2e; Plate 5E).

To calculate the total pollinator score for farm $o$ from all pollinators, $P_{o}$, we calculate the normalized pollinator score for all pollinator guilds or species, such that

$$P_{o} = \frac{\sum_{s=1}^{S} C_{s} P_{os}}{\sum_{s=1}^{S} C_{s}}.$$  

(10.9a)

where $C_{s} \in [0,1]$ if the crop requires pollinator $s$ and 0 otherwise. This unweighted summation assumes that all pollinators are equally abundant. However, if some pollinators have higher background abundance than others, then a weighted average may be more appropriate such that

$$P_{o} = \frac{\sum_{s=1}^{S} \epsilon_{s} C_{s} P_{os}}{\sum_{s=1}^{S} C_{s}},$$  

(10.9b)

where $\epsilon_{s}$ represents the abundance of pollinator $s$ in the landscape, relative to other pollinator species or guilds. The weights for each species can be determined by expert opinion or with observed data. Additional species-by-crop weights could be added to Eq. (10.9b) in the same fashion as $\epsilon_{s}$ to account for differences among pollinators in their effectiveness on a given crop (Greenleaf and Kremen 2006).

### 10.7 Tier 2 valuation model

As in tier 1, the calculated tier 2 abundance from Eq. (10.9b) will be an input into a simplified agricultural production model to determine the crop yield and crop value on each farm parcel. The description in Section 10.4.1 and Eq. (10.4) are the same for tier 2. It follows we again use the ecological model to redistribute the value from all $O$ farms onto each supply parcel $m$ for each species $s$. The resulting score represents the available supply weighted by
the relevant demand, each species’ relative abundance in the landscape, effectiveness ($e_s$) and the crop value within foraging distance. Thus we calculate pollinator service value from parcel $m$ to other $O$ parcels, $PS_{mO}$ as

$$PS_{mO} = V_m \sum_{s=1}^{S} e_s C_s V_s \frac{P_m}{P_o}.$$ (10.10)

This score generates the tier 2 pollinator service value map (Figure 10.2f; Plate 5F) and represents the location and pollination service value based on relative abundance of pollinators that provide crop pollination from parcel $m$ to farm $o$.

### 10.8 Sensitivity analysis and model validation

We first compare model predictions against field data in two contrasting landscapes in California, USA, and San Isidro, Costa Rica. We then illustrate a sensitivity analysis with the Costa Rican data to determine the extent to which our results depend on the precision and accuracy of our parameter estimates.

#### 10.8.1 Model validation

To validate our model, we compare its predictions of total (community-wide) abundance against total observed abundance in farms of crops in two landscapes: coffee in Costa Rica and watermelon in California. The Californian and Costa Rican examples use different levels of model complexity and differing mixes of field- and expert-derived parameters. In all cases, model parameters were derived independently of field validation data (e.g., estimates of typical foraging ranges ($\alpha$), were derived from bee body size; floral availability was estimated through expert assessment based on other studies, not from field measurements taken simultaneously with pollinator abundances).

**10.8.1.1 Costa Rica**

We applied the model to an agricultural landscape in the Valle del General, Costa Rica, one of that country’s major agriculture regions. The landscape is dominated by coffee, sugar cane, and cattle pasture, all of which surround hundreds of remnants of tropical/premontane moist forests (Janzen 1983). Studies were conducted on 12 sites in a large coffee farm (approx. 1100 ha) in the center of this landscape.

High-resolution (1 m) aerial photos, supplied by CATIE (Centro Agronómico Tropical de Investigación y Enseñanza), were classified into six major classes of LULC and resampled to 30m spatial resolution. These classes were then assigned values of nesting and floral resources (assuming a single flowering season) based on expert opinion (see SOM Table 10.S1), informed by field work in the area (Ricketts 2004; Brosi et al. 2008). The most common visitors to coffee in this region are 11 species of native stingless bees (Meliponini) and the introduced, feral honey bee, *Apis mellifera*. For the model, these 12 species were assigned to two nesting guilds based on expert opinion (SOM Table 10.S2). All 11 species were observed during the period of study, but sampling did not continue year-round. Lacking this information on seasonality, we assumed a single flight season for all species. To estimate typical foraging ranges for each species (Table 10.2), we used intertegular spans for 10 museum specimens and the statistical relationship presented by Greenleaf et al. (2007).

During the flowering seasons of 2001 and 2002, Ricketts and colleagues (Ricketts 2004) measured bee activity, pollen deposition, and pollen limitation in 12 sites, varying from 10 to 1600 m from the nearest major forest patch. We used these observations to compare against our model. Our models predict at least 80% of the variance in observed pollinator abundance (Figure 10.3a).

The model’s predictions for farm abundance scores were not as strongly related to field measurements of pollen deposition on coffee stigmas (Figure 10.3b), which is a closer correlate to actual pollination service (Ricketts 2004). Modeled abundance scores do not predict pollen limitation of coffee well (Figure 10.3c). Pollen limitation is the degree to which coffee production (seed number and mass) is reduced due to insufficient pollination, and is a close measure of actual pollination services. Pollen limitation does decline with increased modeled service scores, but the fit is weak. Variation in pollen deposition and pollination limitation also
depends on pollination efficiency of each bee species, on resource limitation of the coffee plant itself, and other factors not captured in a prediction of pollinator abundance, which likely contributes to the poor fit.

10.8.1.2 California
We applied the model to an agricultural landscape in the Central Valley of California, across a strong gradient in isolation of farms from large tracts of natural habitats (oak woodland, chaparral scrub
and riparian deciduous forest). Studies were conducted on watermelon (Kremen et al. 2002b, Kremen et al. 2004) across this landscape.

The LULC data were simplified from a 13-class supervised classification of Landsat TM data at 30 × 30 m resolution (described in detail in Kremen et al. 2004) into six classes. Four additional cover classes were hand drawn on the landscape using ArcGIS to account for nesting and floral resources that come from edges of roads, agricultural parcels, residential areas and irrigation ditches (Figure 10.2a; Plate 5A). These classes were then assigned values of nesting and floral resources based on expert opinion values (SOM Table 10.S3), informed by studies of bee-plant networks (Kremen et al. 2002a, Williams and Kremen 2007, Kremen et al., unpublished; Williams and Kremen, unpublished) and bee-nesting densities (Kim et al. 2006) in the same landscape.

During the flowering season of 2001, bee visits were recorded at 12 sites, and median species-specific pollen deposition per visit was estimated (Kremen et al. 2002b). Each bee species in the study was characterized by its nesting habit based on expert opinion and the length of its flight period, based on over 12000 bee specimens collected from 1999 to 2004 by pan-trapping and netting at flowers in this landscape (Kremen and Thorp, unpublished; Williams et al., unpublished) (SOM Table 10.S4). Typical foraging distances were calculated from measurements of intertegular span, using the regression in Greenleaf et al. (2007). For nearly all bee species, at least five individuals were measured but for a few species, only one measurement was used. Data on *Apis mellifera*, which are managed for pollination in this landscape, were removed prior to analysis.

The model provided a reasonable fit to the observed data on total abundance of native bees on watermelon, although with considerable scatter (Figure 10.3b). Model predictions were strongly related to estimated pollen deposition from native bees (Figure 10.3d), a more direct measure of pollination services that has been used to assess the contributions of wild bees to pollination services (Kremen et al. 2002b; Kremen et al. 2004; Winfree et al. 2007). However, we caution against interpreting the model’s ability to predict pollen deposition since pollen deposition is calculated from visitation data, not direct observations (Kremen et al. 2002b).

### 10.8.2 Sensitivity analysis

Sensitivity analysis should identify the model parameters that have the greatest influence on model results. This allows the scientist to focus on improving accuracy and precision of parameters to which the model is most sensitive, and allows managers to determine the major sources of uncertainty affecting model predictions. In our case, we are interested in how estimates of nesting suitability, floral resource availability and bee dispersal distance influence our predicted pollinator abundance scores. If we find them to be quite sensitive, then further research is required to reduce this uncertainty before the model can be used with confidence.

Our model predicts a parcel’s pollinator abundance relative to other parcels on a landscape, so our sensitivity analysis focuses on these relative scores. We let \( \hat{P}_o \) represent a normalized pollinator score on farm \( o \) from Eq. (10.3) or (10.9) based on the original parameter estimates such that

\[
\hat{P}_o = \frac{P_o - P_{\text{min}}}{P_{\text{max}} - P_{\text{min}}}
\]

where \( P_{\text{min}} \) and \( P_{\text{max}} \) are the minimum and maximum pollinator service scores for all farms on the landscape. We let \( \hat{P}_{oc} \) represent the analogous normalized score on farm \( o \) resulting from modified parameter combination \( c \), and let \( \hat{\psi}_c \) be the average change in normalized scores from combination \( c \) such that

\[
\hat{\psi}_c = \sum_{o=1}^{O} \frac{\hat{P}_o - \hat{P}_{oc}}{O}
\]

where \( O \) is the number of farms in the analysis.

We use regression analysis to determine sensitivity, similar to McCarthy et al.’s (1995) logistic regression approach used in population viability analyses. Our goal is to calculate how variation in each parameter affects estimates of a parcels’ pollinator abundance, independent of all other parameters in the model. Given the number of parameters, exploring every combination is impractical. Instead, we create a sample of parameter combinations by selecting parameter values randomly from a uniform distribution, each within its range of uncer-
tainty and then generate an estimated pollinator score $\hat{P}_o$ for each parcel.

To generate parameter combinations, we set a minimum and maximum for the range of parameter values and drew a random number from a uniform distribution with this range (Table 10.2). For floral and nesting resources we set the range as ±0.1 around the estimate, and we did not allow the max-

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Max</th>
<th>Min</th>
<th>$\delta$ (Slope)</th>
<th>SE</th>
<th>Standardized regression coefficient (t-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>1</td>
<td>1</td>
<td>0.9</td>
<td>4.550</td>
<td>1.303</td>
<td>3.493*</td>
</tr>
<tr>
<td>Coffee</td>
<td>0.5</td>
<td>0.6</td>
<td>0.4</td>
<td>7.758</td>
<td>0.666</td>
<td>11.643*</td>
</tr>
<tr>
<td>Cane</td>
<td>0</td>
<td>0.1</td>
<td>0</td>
<td>0.027</td>
<td>1.356</td>
<td>0.020</td>
</tr>
<tr>
<td>Pasture/grass</td>
<td>0.2</td>
<td>0.3</td>
<td>0.1</td>
<td>0.144</td>
<td>0.652</td>
<td>0.221</td>
</tr>
<tr>
<td>Scrub</td>
<td>0.3</td>
<td>0.4</td>
<td>0.2</td>
<td>0.553</td>
<td>0.657</td>
<td>0.842</td>
</tr>
<tr>
<td>Bare</td>
<td>0.1</td>
<td>0.2</td>
<td>0</td>
<td>0.300</td>
<td>0.663</td>
<td>0.453</td>
</tr>
<tr>
<td>Built-up</td>
<td>0.3</td>
<td>0.4</td>
<td>0.2</td>
<td>0.450</td>
<td>0.676</td>
<td>0.666</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Apis nesting suitability (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
</tr>
<tr>
<td>Coffee</td>
</tr>
<tr>
<td>Cane</td>
</tr>
<tr>
<td>Pasture/grass</td>
</tr>
<tr>
<td>Scrub</td>
</tr>
<tr>
<td>Bare</td>
</tr>
<tr>
<td>Built-up</td>
</tr>
<tr>
<td>Aapis melifera</td>
</tr>
<tr>
<td>Huge Black 2002**</td>
</tr>
<tr>
<td>Melipona fasciata</td>
</tr>
<tr>
<td>Nannotrigona mellaria</td>
</tr>
<tr>
<td>Partamona cupira/Trigona fussipennis/Trigona corvina***</td>
</tr>
</tbody>
</table>

Foraging range (m) for each species

<table>
<thead>
<tr>
<th>Species</th>
<th>Min</th>
<th>Max</th>
<th>SE</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plebeia jatiformis</td>
<td>25</td>
<td>30</td>
<td>0.027</td>
<td>0.024</td>
</tr>
<tr>
<td>Plebeia frontalis</td>
<td>33</td>
<td>36</td>
<td>0.005</td>
<td>0.051</td>
</tr>
<tr>
<td>Trigona (Tetragonid) clavipes</td>
<td>48</td>
<td>63</td>
<td>0.004</td>
<td>0.009</td>
</tr>
<tr>
<td>Trigona (Tetragonid) angustula</td>
<td>20</td>
<td>24</td>
<td>0.013</td>
<td>0.029</td>
</tr>
<tr>
<td>Trigona dorsalis</td>
<td>54</td>
<td>66</td>
<td>0.006</td>
<td>0.011</td>
</tr>
<tr>
<td>Trigona fulviventris</td>
<td>73</td>
<td>82</td>
<td>0.046</td>
<td>0.015</td>
</tr>
<tr>
<td>Trigona sp.</td>
<td>20</td>
<td>23</td>
<td>0.043</td>
<td>0.051</td>
</tr>
</tbody>
</table>

* $p < 0.05$.
** Unidentified species.
*** These species were indistinguishable during field observations and lumped together.

The strength of the model’s sensitivity is given by the standardized regression coefficients in the final column. These coefficients result from a multiple regression of the parameter value combinations on the average change in normalized pollination score, $\hat{\psi}_c$. 

---

Table 10.2 Results of sensitivity analysis for Costa Rican study
imum to exceed 1 or the minimum to drop below 0. For foraging ranges, we set the range using the minimum and maximum of the 10+ measurements of intertlegular span.

By iterating this parameter draw process 1000 times, and then regressing the change in scores, \( \hat{\psi} \), against randomly varying parameters, we can estimate sensitivity to each parameter while accounting for variation in the others. The sensitivity of each predictor variable is indicated by its standardized regression coefficient (t-value), calculated from the best fit of a multiple linear regression model: 

\[
\hat{\psi} = \delta_0 + \delta_1 x_1 + \ldots + \delta_n x_n,
\]

where \( x_n \) are predictor variables (foraging distance, nesting suitability values, etc) and \( \delta_n \) are the regression coefficients. The standardized regression coefficient is the regression coefficient (slope of a line) divided by its standard error (Cross and Beissinger 2001). This is a unitless quantity that allows one to directly compare the sensitivity among parameters, and because our parameter combinations were created randomly, also accounts for potential interactions among model parameters (Cross and Beissinger 2001). The standard error for one model parameter is caused by the dependence of \( \hat{\psi} \) on other parameters and the significance of the slope is calculated using a two-tailed t-distribution (a t-value greater than 1.9 or less than -1.9 is significant at \( p < 0.05 \)).

We illustrate the sensitivity analysis using our Costa Rica data set (Table 10.2). The results indicate that a farm’s normalized pollinator score, \( \hat{P} \), is most sensitive to foraging resources present in coffee (t-value = 11.65; \( p < 0.05 \)) and forest (t-value = 3.50; \( p < 0.05 \)) habitats. Interestingly, \( \hat{P} \) is also sensitive to uncertainty in a group of species’ foraging distances, which ranged between 77 and 214 m. Pollinator service scores were not sensitive to species with smaller or greater estimated foraging ranges. These sensitivities are likely due to the variation in forest composition surrounding farms sites at these moderate scales. The implication for conservation is that additional effort to estimate and manage the floral resources within coffee farms, and bee-pollinated crops in general, would be of highest priority for understanding the response of pollination to landscape change.

10.9 Limitations and next steps

10.9.1 Limitations

Despite the promising results, there are several limitations to our model. First, our models estimate the benefits of wild pollinators to agricultural crop production, but pollinators contribute to a much broader set of social benefits that need to be modeled separately (Box 10.2). Second, our models are limited to predicting relative pollinator abundance, which is only one of many potential contributors to crop yield (see Chapter 9). Translating from pollinator abundance to pollinator influence on crop yield will be limited in many cases by gaps in our understanding of pollinator-yield effects. First, we often do not know the functional form of the relationship between increased number or quality of pollen grains deposited and yield, and the functional form may further vary with crop variety as well as water and nutrient availability. In addition to the relationship between pollinator abundance and the amount and quality of pollen delivered, pollination is influenced by pollinator foraging behavior and effectiveness, across scales from within flower, inflorescence, patch and landscape (Klein et al. 2007; Kremen et al. 2007; Ricketts et al. 2008).

The uncertainty in the relationship between the model’s output, a relative score, and quantitative pollinator abundance currently limits the models application to land-use planning. Without a quantified relationship between the model score and abundance, it is difficult to determine the precise yield, crop value and subsequent service value of supply parcels. And without these precise values, decisions about land management, often based on a cost-benefit analysis, would be difficult because the benefits are thus uncertain. In other words, the model can determine that one landscape will provide qualitatively more pollinators to a farm, but it cannot determine if the cost of management or habitat restoration is outweighed by the benefits. Parameterizing the model to facilitate this type of cost-benefit analysis is an obvious next research priority.

LULC data are often only available at resolutions coarser than the scale at which they influence pollinator behavior. Thus, while our model predicts the
At the other end of the spectrum, services that are ecologically distal to pollination have the opposite set of characteristics (right side of Figure 10.B.1):

- Many pollination events, integrated over large scales of space and time, are needed to support the service

- The role of pollination for the value of the service in any given small scale of space and time is relatively minor

- There is relatively high resilience of the service to pollination losses over short scales of space and time; but if pollination losses were to be sustained over larger
spatiotemporal scales, these functions and services could greatly suffer

Animal-mediated pollination is ultimately derived from the actions of single pollinators moving between a few plants over small spatial scales. Thus, the services that are most proximal to pollination are typically tangible, plant-derived products, while those more distal to pollination are produced by the aggregate actions of countless pollinators at scales larger than that of individual plants (from several square meters to the globe).

There is considerable middle ground in this spectrum. The aforementioned Amazon freshwater fishery is relatively proximal to pollination (disruptions in flooded forest pollination would have major consequences for the fishery over short timescales). The pollination of mahogany (*Swietenia macrophylla*), which provides valuable tropical timber, has fewer ecological linkages than the Amazon fishery example. Yet mahogany timber production could be considered more distal to pollination, because pollination disruptions in any given year would be unlikely to have a strong effect on the value of the mahogany harvest that year. Continued pollination disruptions, however, would eventually damage the mahogany timber industry since the trees could no longer reproduce in the absence of pollination.

Pollination affects ecosystem services in interdependent ways. For example, the weevil-mediated pollination of *Bactris gasipaes*, the peach palm, is a regulating service. But that service allows for the production of peach palm fruits (a provisioning service), which in turn are a cultural necessity in parts of Latin America—providing important cultural services.

Because plants are central to all of the primary supporting services in the terrestrial biosphere—such as primary production, nutrient cycling, and preservation of options (e.g., genetic diversity for future use in pharmaceuticals)—this is perhaps the most important functional role of non-agricultural pollination services. Just as one example, a large proportion of plants in the bean family (legumes) are animal-pollinated; this family is critical for its fixation of atmospheric nitrogen to the soil. If legumes were to suffer pollination reductions, even plant species that are wind-pollinated or self-pollinated would be greatly affected by reductions in available soil nitrogen over timescales as short as a few years.

Flowering plants are also central to a host of climate regulation functions (oxygen production, carbon sequestration, etc.) and hydrological functions (water filtration and flow regulation) that yield vital services. As with supporting services, pollination is important, but ecologically distal, to many of these regulating functions.

The benefits of pollination are most tangible in the production of provisioning services, such as products from non-managed ecosystems, including wild food (e.g., Brazil nuts), fiber (e.g., rattan), and fuelwood resources. Many animals hunted as food for people (not just the tambaqui fish) in turn feed on pollination-dependent fruits and other plant parts. Such products can have a high economic value, particularly when considered in the aggregate (Peters et al. 1989). Pollination is key for the population persistence of a number of valuable timber trees as well, not just mahogany.

Pollination interactions are invaluable in the varied roles they play in providing ecosystem services beyond agriculture. Yet we still know little about how ongoing anthropogenic environmental changes will affect communities of pollinators or the pollination functions they perform. For example, there is serious concern in the scientific community that global climate change will lead to changes in the timing of flowering and of pollinator foraging behavior, disrupting pollination interactions worldwide (e.g., Memmott et al. 2007). Such disruptions would have major impacts on global ecological functioning and thus on a huge range of non-agricultural pollination services. This makes the need for understanding and ameliorating the effects of environmental change on pollination all the more pressing.

Finally, our model, while quantitative, is essentially a statistical evaluation of the landscape so it cannot project pollinator abundance over time. Rather it assumes population stasis given a particular landscape configuration. In other words, our model does not provide an estimate of pollinator population viability or predict pollinator tem-
poral dynamics or interaction of time and space through meta-population dynamics. As such, it does not incorporate stochastic events, which may influence long-term population dynamics and yield.

**10.9.2 Next steps**

While new ecological data are needed to gain a better understanding of the relationship between crop pollination and yield, we can use this current model framework to advance our understanding in a number of ways. First, we can apply this model to a much larger set of crop studies conducted at the landscape scale (viz, studies in Ricketts *et al.* 2008). Second, using statistical techniques, we can relate the landscape-level outputs of the model (pollinator supply) to the observed measure of pollination services in each study (e.g., pollen deposition, pollen limitation) to attempt to develop a direct relationship between landscape and yield effects via pollinator abundances. Third, by manipulating modeled landscapes (e.g., by increasing floral or nesting resources in different spatial configurations), we can estimate the effects on pollinator abundances and pollination services across a range of changes in resources, and look for generalities across landscapes in the density and arrangement of resources needed to provide adequate pollinators and pollination services. This would inform efforts to preserve existing habitats within degraded landscape and also guide planning of habitat restoration. Similar to our sensitivity analysis of model parameters, we also envision analyses exploring the sensitivity of modeled pollination services to resource patchiness at different grain sizes or to different landscape configurations.

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**References**


