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Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory

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Abstract

Pollination by bees is important for food production. Recent concerns about the declines of both domestic and wild bees, calls for measures to promote wild pollinator populations in farmland. However, to be able to efficiently promote and prioritize between measures that benefit pollinators, such as modified land use, agri-environment schemes, or specific conservation measures, it is important to have a tool that accurately predicts how bees use landscapes and respond to such measures. In this paper we compare an existing model for predicting pollination (the “Lonsdorf model”), with an extension of a general model for habitat use of central place foragers (the “CPF model”). The Lonsdorf model has been shown to perform relatively well in simple landscapes, but not in complex landscapes. We hypothesized that this was because it lacks a behavioral component, assuming instead that bees in essence diffuse out from the nest into the landscape. By adding a behavioral component, the CPF model in contrast assumes that bees only use those parts of the landscape that enhances their fitness, completely avoiding foraging in other parts of the landscape. Because foraging is directed towards the most rewarding foraging habitat patches as determined by quality and distance, foraging habitat will include a wide range of forage qualities close to the nest, but a much narrower range farther away. We generate predictions for both simple and complex hypothetical landscapes, to illustrate the effect of including the behavioral rule, and for real landscapes. In the real landscapes the models give similar predictions for visitation rates in simple landscapes, but more different predictions in heterogeneous landscapes. We also analyze the consequences of introducing hedgerows near a mass-flowering crop field under each model. The Lonsdorf model predicts that any habitat improvement will enhance pollination of the crop. In contrast, the CPF model predicts that the hedgerow must provide good nesting sites, and not just foraging opportunities, for it to benefit

35   pollination of the crop, because good forage quality alone may drain bees away from the field.

36   Our model can be used to optimize pollinator mitigation measures in real landscapes.

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38   **Keywords:** pollination; bee; bumblebee; optimality; central-place foraging; mass-flowering crop

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INTRODUCTION

More than one third of the global food production comes from crops partially or totally dependent on animal-mediated pollination (Klein et al. 2007). Pollination may also enhance crop quality (Klatt et al. 2014), and is particularly important for crops providing essential nutrients (Eilers et al. 2011). Bees, including both managed and wild ones, are the most important group of pollinators of crops (Delaplane and Mayer 2000). Although honey bees are frequently used to enhance crop pollination, recent declines of managed honey bees (National Research Council 2006, Potts et al. 2010a) have increased the focus on wild bees as important crop pollinators. Furthermore, a recent global meta-analysis demonstrated that increased abundance of wild pollinators increases fruit set of crops independent of the presence of honey bees (Garibaldi et al. 2013). However, land use changes and landscape modifications resulting from agricultural expansion and intensification have reduced the amount of habitat for wild pollinators, potentially compromising crop pollination (Kremen et al. 2002, Potts et al. 2010b). To be able to efficiently use managed pollinators and to benefit wild pollinator populations in contemporary agricultural landscapes, it is important to understand how they are affected by habitat quality and landscape composition in order to determine where to place managed bees and whether, where and what type of habitat management is required.

Since bees are central place foragers, bringing food to a nest to benefit offspring, the spatial association of nesting sites and foraging habitat is critical (Westrich 1996). Hence, pollinator abundance in a specific habitat such as a crop will not only depend on its quality to bees, but also on the distance to bee hives or potential nesting habitat for wild bees (Ricketts 2004, Öckinger and Smith 2007, Ricketts et al. 2008, Ekroos et al. 2013), with consequences for crop pollination.

Recently, Lonsdorf et al. (2009) presented a spatially-explicit model to evaluate bee relative abundance in landscapes, allowing consequences of crop placement and habitat management on pollination to be evaluated. The model is based on explicit knowledge about the spatial arrangement of bees' nesting and feeding habitats, which may be separated in space and vary in time. Because bees need to return to their nest with the nectar and pollen they collect, the bee visitation rate at a patch with flower resources depends on the distance from that patch to nesting habitat (Lonsdorf et al. 2009). That model can reasonably well predict pollination services at the landscape scale (Lonsdorf et al. 2009, Kennedy et al. 2013), and it can identify situations in which habitat restoration would potentially enhance the pollination service (Ricketts and Lonsdorf 2013). However, whereas the model (Lonsdorf et al. 2009) performs reasonably well in coarse grained, rather homogenous (simple), landscapes, it performs less well in more heterogeneous (complex) landscapes (Kennedy et al. 2013).

We argue that a major reason that the Lonsdorf et al. (2009) model performs less well in complex landscapes is that it is not based on central place foraging theory (Schoener 1979, Olsson et al. 2008), and thus does not assume that bees select foraging habitat to maximize fitness. In the model there is no behavioral mechanism by which bees can select foraging patches. Instead they simply "diffuse" out from the nest. This contrasts with empirical studies of foraging bees, that have demonstrated that bee densities in both crops and wild flowers depend on both local habitat quality (Carvell et al. 2007, Woodcock et al. 2014) and the quality of surrounding habitat (Steffan-Dewenter et al. 2002, Heard et al. 2007, Carvell et al. 2011, Holzschuh et al. 2011, Scheper et al. 2013), this limitation of the model may result in spatial variation in bee densities, and hence pollination, being less accurately predicted. A consequence

of assuming that visitation rates and the distance a bee is willing to travel in the model does not depend on floral patch quality or the quality around a patch will result in the model not capturing relatively fine-scale variation in habitat quality in a complex landscape. Furthermore, the model will not be able to predict changes in visitation rates in response to small-scale alterations in the landscape, such as the addition of a hedgerow or wildflower strip that change the spatial structure of resources within a field but have little effect on the total resources at a landscape scale. Hence, although, there is concern that flower strips or hedgerows might be “too attractive” and drain bees out of crop fields needing pollination (cf. Bartomeus and Winfree 2011, Lander et al. 2011), or that mass flowering crops might attract bees away from natural habitats, where pollination of the wild plants could be suffering (Holzschuh et al. 2011, Kovács-Hostyánszki et al. 2013), the Lonsdorf et al. (2009) model would predict that adding more flower resources and nesting habitat always leads to increased visitation rates.

We propose that integration of more complex foraging mechanisms, such as central place foraging theory (Schoener 1979, van Gils and Tijssen 2007, Olsson et al. 2008) into the Lonsdorf et al. (2009) modeling framework may solve some of the above mentioned shortcomings. Central place foraging theory (CPF) is based on the premise that animals forage for resources in patches dispersed in a landscape around a central place (nest, burrow, or refuge). They harvest resources in the patches, and then need to travel back to the central place either to unload the resources or to rest in safety. Travelling to and from patches takes time and also entails costs in terms of energy and mortality risk. Carrying a large load might additionally be more expensive (Olsson et al. 2008). Central place foraging theory has been applied to bees to determine the distance bees are willing to travel to forage and the amount of food they are willing to acquire during the

foraging trip (Schmid-Hempel et al. 1985, Kacelnik et al. 1986, Cresswell et al. 2000), but the theory has not been applied to describe habitat use for bees.

Recently, Olsson and Bolin (2014) built a habitat use model from CPF, demonstrating how to predict what patches foragers should use in a specific landscape. That model, which is general for any CPF forager and not specific to pollinators, shows how the marginal fitness value of patches depends on two variables: patch quality and distance to the central place. A key result of the model (Olsson and Bolin 2014) is that for any patch quality there will be a maximum distance that the forager would be willing to travel. Hence, near the nest patches of a large range of qualities should be used, but far from the nest only the best patches will be used. Patches of low quality might therefore be passed on the way to patches of higher quality. Using that model, landscape quality can be derived as the summed value of all useable patches in the landscape, i.e. all patches contributing positively to fitness if used.

In this paper we will address the limitations of the Lonsdorf et al. (2009) model by combining its general framework with the behavioral mechanism for central place foraging developed by Olsson and Bolin (2014). Our goal is to develop a spatially-explicit, central place foraging analysis of pollination service that better reflects the foraging behavior of bees. Such a model is likely to be able to generate improved predictions for the pollination service in complex landscapes and the consequences of habitat enhancement. We expect that a model with an added behavioral mechanism will have similar predictions as the Lonsdorf et al. model in relatively simple landscapes, but as the complexity of landscapes increases, the correspondence between the models would decrease. Similarly, we should be able to show that a model which

incorporates central place foraging theory can identify landscapes in which habitat enhancements would draw bees away from a patch that was once visited.

MODEL DESCRIPTION

We will compare the performance and predictions of the model by Lonsdorf et al. (2009; hereafter “the Lonsdorf model”) with our new model based on Olsson and Bolin (2014; hereafter “the CPF model”), by applying them in the same artificial or real landscapes. Both models are described in the previous work, and here we only present the minimal necessary theory from those papers, and the extensions we make to apply both models to the landscape context that we are considering here. Bees require nesting resources and fitness at the nest site depends on enough foraging resources within their flight range, and thus the input data for both models is one map of nest site qualities, and one map of floral resource qualities. For model coherency we do not consider temporal changes in floral qualities.

The Lonsdorf model first estimates relative fitness of a pollinator species nesting in each pixel, based on the available nesting resources in that patch and the quality of floral resources in surrounding pixels. In evaluating floral resources, nearby pixels are given more weight than more distant patches, based on a species’ expected foraging range. The result is a map that provides an index of nesting fitness (0 to 1) across a landscape. Given the fitness pattern of nesting bees in the landscape, the model then estimates the relative abundance of foraging bees visiting floral areas. It averages the relative bee fitness in neighboring patches, again giving more weight to nearby patches, based on average foraging ranges. This distance-weighted average is the relative index of abundance for each pollinator (Fig. 1A). Applied to a raster or

gridded land cover map, Lonsdorf et al. (2009) described an index of bee fitness within nest site i , G_i , as:

$$G_i = N_i \frac{\sum_{j=1}^M F_j e^{-\frac{D_{ij}}{\alpha}}}{\sum_{j=1}^M e^{-\frac{D_{ij}}{\alpha}}} , \quad (1)$$

where N_i is an indicator variable equal to 1 if the pixel i provides suitable nesting habitat and 0, otherwise. The ratio represents the distance-weighted average floral quality of the landscape surrounding nest site i . The numerator is distance weighted sum of all floral resources across all M pixels where F_j is the floral quality, scaled from 0 to 1, of site j , D_{ij} is the Euclidean distance between nest site i and floral site j and α is a distance-decay scalar representing the average distance the bee would travel to forage. The denominator is simply the distance weighted habitat availability. The fitness index is scaled from 0 to 1 and provides an indication of how many bees are supported by the landscape surrounding site i , i.e. P_i .

To determine the abundance of bees foraging or visiting a particular floral patch or crop, Lonsdorf et al. (2009) used the same framework to redistribute bees from nest sites onto the landscape. They assumed that bees foraged from nest sites to the surrounding foraging areas, such that forage areas that are surrounded by nests with relatively high fitness would have a higher abundance index than those with fewer nests or nests with lower fitness. Thus the index of abundance for bees foraging at site j , P_j , is equivalent to the distance-weighted average fitness of surrounding nests:

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$$P_j = \frac{\sum_{i=1}^M G_i e^{-\frac{D_{ij}}{\alpha}}}{\sum_{i=1}^M e^{-\frac{D_{ij}}{\alpha}}} , \quad (2)$$

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where G_i is the nest fitness index at site i , as described above.

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The CPF model uses an alternative way to model bee visitation rates by applying a general

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model for central place foraging (Olsson and Bolin 2014). That model is based on the

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assumption that the forager (thought of as a bee worker in the current case) goes from the nest to

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a resource (floral) patch, forages until it has filled its loading capacity, L , and then returns home

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with the collected food (pollen and/or nectar). Travel time, τ , is a linear function of distance to

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the patch. The quality of a patch is expressed as the harvest rate, A , attained while foraging in it.

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Assuming that harvest rate is constant throughout a patch visit, the time it takes to harvest the

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food in the patch will be an inverse function of patch quality, i.e. L/A . Harvesting food as well as

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travelling is associated with their respective metabolic costs and mortality risks. There is a fixed

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total length of time (breeding season) during which the foraging takes place, and the time not

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spent foraging will be spent at home at lower (but above zero) costs, but no rewards. Fitness is a

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decelerating function of the total amount of resources harvested until the end of the time period

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multiplied by the survival over the whole period. For full reference of the model, please refer to

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Olsson and Bolin (2014). One of their (Olsson and Bolin 2014) central results is that in order to

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maximize fitness a patch of quality A should only be used if it takes less than τ time units to

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travel there and back from the nest:

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$$\tau = \tau_{\max} + \frac{\omega}{A} . \quad (3)$$

While τ and A are the variables of the model, the parameters $\tau_{\max}$ and ω are results found at the solution which maximizes fitness. Here, $\tau_{\max}$ is the maximum travel time accepted to reach a patch of infinite quality and ω is a parameter ($\omega < 0$) that relates quality to travel time (distance) in a manner which is appropriate for the life-history of that organism (Fig. 1B). The ω is a composite parameter that depends on many of the different life-history parameters (Table 1; Olsson and Bolin 2014). It is effectively constant for any particular life-history strategy (such as a species), and nearly independent of the environment. However, $\tau_{\max}$ increases in poor environments meaning they are forced to select patches further away and of lower quality, and is typically negatively related to fitness (Olsson and Bolin 2014). The parameters used in the simulations (Table 1) were chosen with a relatively long-flying bumblebee species (e.g. *Bombus terrestris*) in mind, but have not been measured from empirical data.

The shading in figure 1 shows the marginal fitness value, Δ , to the bee (or bee colony) of using a patch at a given distance and of a particular quality. A patch falling on the curve separating the shaded area from the white area provides no value, and one above that curve should not be used as it would give a negative value. That is, floral patches that fall outside of the shaded area should not be visited, as their combination of qualities and distance to the nest make them unprofitable to use.

To develop Olsson and Bolin's (2014) model to one that predicts pollinator visitation rates, and pollinator fitness in landscapes we proceeded as follows. We calculated the bee visitation rates for the CPF-model, by assuming that the number of workers going from a nest to a resource

patch is proportional to the marginal fitness value of that patch to the nest. The total number of workers from all n nests visiting floral patch j is proportional to:

$$V_j = \sum_{i=1}^n \left[N_i \left(\Delta_{i,j} - \frac{kT}{M_i} \right) \right], \quad (4)$$

where $-kT$ is the fitness overhead cost of not using any patch, as k is the metabolic rate of spending time idle in the nest, T is the length of the breeding season, and M_i is the total number of floral patches visited by nest i . The fitness of a nest can then simply be expressed as the sum of the marginal values of each of the patches:

$$G_i = \left(\sum_{j=1}^{M_i} \Delta_{i,j} - kT \right) N_i. \quad (5)$$

The CPF model is consistent with a previous model by Cresswell et al. (2000). However, our model is more general, particularly in that it evaluates an entire landscape of foraging patches, rather than just a pair of two patches. It also incorporates predation risk in the fitness function, and under some conditions can be solved analytically (Olsson and Bolin 2014).

In both models there is a direct proportionality between the number of nests and the number of workers, as there is no competition for resources. Each nesting pixel can have only a single nest, but adjacent pixels can be inhabited. The more nests in an area, the more bee visits the surrounding landscape will get.

To determine if the different approaches would yield different projections regarding bee visitation rates, we made a number of comparisons to investigate the effects of landscape complexity and the potential to predict one high quality floral patch drawing bees away from nearby lower quality patches. First, to investigate if the models' different treatment of foraging

resulted in qualitatively different predictions regarding how bees distribute in the landscape, we compared how bees leaving from a single nest were distributed in contrasting synthetic landscapes. Second, to investigate if the models generate different predictions for bee distribution in real landscapes, we compared the two models' predictions for three different real landscapes that varied in the amount of pollinator-friendly habitat and landscape complexity. Finally, to specifically investigate the consequences of the two approaches for predicting the effect of adding pollinator friendly habitat (hedgerow or flower strip, which provides nesting and/or flowering resources) on crop pollination, we applied the models to a new set of synthetic landscapes with and without a hedgerow adjacent to a crop field. For simplicity we consider the same species throughout the paper, described with its life history in table 1.

MODEL PREDICTIONS

Landscape type I: single nest with contrasting forage patterns

To illustrate the consequences of different foraging functions for visitation, we created a simple landscape 750×750 m, with a 30×30 m pixel size (Fig 2; Code to produce the relevant calculations is supplied in the Supplementary information) with a single nest site along the western edge of the landscape (marked with a cross). The landscape has two fields, one adjacent to the nest and one in the east half of the landscape, relatively far from the nest site. Using this simple system, we model the distribution of foraging bees on the landscape resulting from four different scenarios of forage quality of the fields as shown in figure 2A, E, I, and M.

In all four landscapes (Fig 2) the Lonsdorf model predicts the same relative visitation rates, while the CPF model predicts different visitation patterns because bees direct their efforts to areas of higher qualities.

The Lonsdorf model predicts the number of workers produced, i.e. the nest fitness, to be higher in landscape 2 (Fig. 2E), compared to landscapes 1 and 3 (Fig. 2A and I), and higher in landscape 4 (Fig. 2M) compared to 3 (Fig. 2I). However, the relative distribution of those bees will be identical between landscapes, i.e. the same proportion of those bees will visit the same pixel in each case (Fig. 2C, G, K, and O). In contrast, the CPF model gives different predictions for the four different landscapes of type I. In the first, with homogeneous floral quality, and second, with slightly better forage near the nest site, the predictions are nearly identical to the Lonsdorf model. The only difference is that according to the CPF model the bees will not visit floral patches at all beyond a certain distance ($\tau_{\max}$) from the nest, whereas the Lonsdorf model predicts small fractions of the workers reaching these far-away patches. In the second landscape, the CPF model predicts no visitation at all in the far away, poor field. These differences between the models can also be seen from the curves of the visitation rates (Fig. 2B and F), which hits zero for the CPF bees, but for the Lonsdorf bees it only approaches zero asymptotically.

In the third and fourth landscapes, which both have higher quality forage far from the nest site (Fig. 2), there is a striking difference between the models, because the CPF bees reduce their visitation of the nearby field of poor quality to instead increase their foraging efforts to the far away high quality field (Fig 2L and P). This effect is even more accentuated in the fourth landscape, where the difference in floral quality between the rich and the poor landscapes are

stronger. Here, the CPF bees only visit the very near parts of the poor fields, right next to the nest; most of them will skip over that field entirely and devote their effort to the parts of rich field that are still close enough for them to use.

Landscape type II: real landscapes that differ in complexity

We applied the models to an analysis of three landscapes from the province of Scania, Sweden (Fig. 3). We assigned floral and nesting qualities to each of the land cover types, in a simple but more or less realistic manner, similar to previous studies (e.g. Kennedy et al. 2013). These landscapes are 3×3 km, with a pixel size of 25 m, and floral and nesting qualities for each of the land cover types are shown in figure 3. The simplest landscape consists mainly of non-flowering annual crops, a single large patch of a mass-flowering crop that does not provide nesting and a few smaller patches of land that provide nesting and moderate floral resources. In the moderately complex landscape, mass-flowering crop fields are slightly smaller and often next to small pasture fields and patches of forest, which provide nesting sites. The most complex landscape has a mix of forested land, small patches of mass-flowering crop and scattered patches of semi-natural land, pasture and other flowering crops that each provide some nesting and floral resources.

The differences in model predictions can be seen by comparing the panels of figure 3 (B vs C, E vs. F, and H vs. I, respectively). For example, there are two illustrative areas within the moderately complex landscape where the CPF model shows its strength (Fig. 3D). At coordinates (1500, 2000), a small forest patch is surrounded by a bit of “other farmland”. The forest is considered good nesting habitat only, and the only floral resources nearby is the “other

farmland” habitat, so these patches are predicted to have high visitation rates coming from those forest nests, with no visits to the forest. The Lonsdorf model predicts most visits in the forest (which has no floral value). South of this forested area at coordinates (1200, 1200) is a moderately-sized strip of mass-flowering crop with two patches of other farmland embedded. The mass flowering crop, which is a better floral resource but no nesting, draws visitors away from the other farmland. So visitation rates to the “other farmland” predicted by the CPF model vary from place to place, reflecting their relative attractiveness, which is not captured by the Lonsdorf model.

In figure 4 we show how the bee visitation rates (Fig. 4 A, C, and E) and fitness (Fig. 4B, D, and F) compares between the models. Each dot is a pixel from the landscapes shown in figure 3. Visitation rates are predicted differently by the models, and in particular the Lonsdorf model often predicts high visitation rates in areas where the CPF model predicts none. The correspondence between the models appears better in the simple landscape (Fig. 4A) than in the most complex (Fig. 4E). Particularly the mass-flowering crop fields (black dots) are very differently predicted by the two models. By contrast, the nest fitness of the bees is predicted very similarly between the models.

The inherent dynamics of the CPF model is shown in figure 5. In poor areas (pixels), where realized fitness is low, the maximum travel distance ($\tau_{\max}$) is nearly twice as high as in the best areas with high fitness.

Landscape type III: evaluating habitat enhancements

We again use a synthetic landscape to show how the approaches differ in their predictions of the consequences of planting a pollinator-friendly hedgerow for bee visitation in an adjacent field of pollinated crop (Fig. 6A). We generate the landscape using four components: a natural area that is highly suitable for pollinators, an agricultural field of a pollinator-dependent crop that has moderate quality forage for pollinators but provides no nesting, an agricultural crop that is unsuitable for pollinators and a hedgerow in which we vary the relative suitability for pollinators. Within the landscape, the natural area forms the southern border of the landscape, the pollinator-dependent crop is a 270-by-270 m (9 x 9 pixels) block of habitat to the north of the natural area, and if there is a hedgerow, it is a 9-by-1 pixel strip along the western border of pollinator-dependent crop. The remainder of the landscape is pollinator unfriendly crop. We create four scenarios to illustrate the effects of the hedgerow on visitation in the field of the pollinator-dependent crop: (1) no hedgerow, (2) the hedgerow provides good nesting only, (3) the hedgerow provides only high quality forage and (4) the hedgerow provides both good nesting and high quality forage (Fig. 6). We also investigate the effect of varying the hedgerow's forage quality continuously from none to very high, with and without nesting sites.

Our results from the type III landscape illustrate the mechanistic differences between the models (figures 6 and 7). Adding nest sites, or both nest sites and floral resources enhance pollination in the crop field according to the Lonsdorf model. That model predicts that adding nesting sites are more important for pollination than is floral resources, but that adding floral resources is always beneficial, as this increases the landscape bee population size (Fig. 6B – E, Fig. 7A). In contrast, the CPF model (Fig. 6F – I) predicts that, while adding nesting sites enhances pollination (Figure

7A – CPF, with nest), adding floral resources in the hedgerow might reduce bee visitation rates (Figure 7A – CPF, without nest). Still, adding both nesting and floral resources yields much higher visitation rates than having no hedge at all, as long as the distance to the hedgerow is not too far. But as the forage quality of the hedgerow increases, the number of bees supported in the landscape will increase, but the CPF model predicts that bees will be drawn towards the hedgerow instead of the crop (cf. Fig. 7A and B).

DISCUSSION

Incorporating a behavior into a model of crop refines and changes predictions in important ways. While the CPF and Lonsdorf models similarly predict the quality of a landscape to support bees, only the CPF model predicts visitation based on floral patch quality relative to the distance from the nest. The added behavioral mechanism importantly allows the CPF model to make fine-scale evaluations of potential farm management options such as hedgerow or floral plantings. The model bees respond to difference in local patch quality compared to the larger landscape, such that they fly farther for high quality patches, particularly when it is a relatively poor quality landscape (Steffan-Dewenter and Kuhn 2003, Westphal et al. 2006b, Heard et al. 2007, Jha and Kremen 2013). Specifically, the CPF model predicts a negative correlation between maximum travel distance and fitness (Fig. 5), such that travel distances from nest sites in a floral rich area are shorter than nest sites surrounded by poorer resources – a result consistent with recent findings by Carvell et al. (2012). Thus, long-distance traveling is an indication of resource limitation. This is consistent both with findings that fitness decreased when solitary bees were forced to fly longer distances (Zurbuchen et al. 2010), and that bumblebees in poor landscapes have longer trip durations (Westphal et al. 2006b).

The Lonsdorf et al. (2009) model only considers distance in determining foraging patterns, not the quality of the patch and so bees would potentially visit every part of the landscape regardless of its quality. In contrast, the CPF model's strength is its ability to weigh the costs vs. benefits of different patches in the landscape (Figure 2). It assumes that foragers only utilize patches where a combination of local quality and distance from the nest results in a positive contribution to fitness. This simple and elegant assumption allows for spatially-explicit foraging behavior, such that bees will fly over poor quality areas to get to higher quality patches. This results in distinctly different prediction on the distribution of bees in landscapes.

Under reasonable assumptions of foraging distances and differences in habitat qualities, the CPF model makes important predictions for real landscapes (type II, Fig. 3), which the Lonsdorf model is unable to make. These differences in model predictions for the type II landscapes further illustrate the ability of the CPF model to incorporate variation in configuration and quality distribution of forage resources in predicting visitation rates of bees in a real landscape (Figure 3). With the Lonsdorf model, the amount and location of bees is determined only by the general quality of landscape so fine-scale features do not matter, such that the abundance of bees in any given location is simply an indication of the average nest fitness in the surrounding pixels (Kennedy et al. 2013). In contrast, the CPF model would predict that the highest visitation rates would occur when forage resources are limited in the surrounding landscape (Fig. 3). Isolated patches with high forage values would thus concentrate the number of foraging bees.

The two models provide general agreement about the overall quality of a landscape for bees in terms of the number or fitness of bees that a landscape would support (Fig. 4) but, within a landscape, the models clearly differ in suggesting where and how many bees are foraging. As landscape complexity increases, the correspondence between the models declines (Figure 4). In the simplest landscapes, both models provide general agreement as to where bees are visiting floral resources. The simplest type II landscape is most like the first two scenarios in the type I landscape, in which nesting is next to high quality forage. As the patch sizes get smaller and landscape heterogeneity with respect to patterns of nesting and floral resources increases, the CPF model describes much more within-patch variation in visitation. In contrast, the Lonsdorf model creates weighted-average hot-spots representing locations that have good floral and nesting areas (cf. Fig. 3). However, it cannot pick up fine-scale nuances in the landscape like the CPF model.

The Lonsdorf model in essence estimates the quality of foraging resources to central-place foraging bees (Vos et al. 2001), but fails to show how bees *de facto* utilize the landscape since it lacks a behavioral habitat selection component. The CPF model provides this additional component, such that the relative attraction of any pixel for forage depends on the relative quality of other nearby pixels. Thus, the Lonsdorf model provides good insight into the evaluation of number of bees that could be supported by a landscape but cannot provide the type of guidance at a fine-scale important to predict e.g. crop pollination that the CPF model can.

The CPF model handles landscape heterogeneity within the bees' home range, which the Lonsdorf model does not. Therefore, in comparisons of the two models, the agreement between

418 them is high in simple landscapes but declines with increasing landscape complexity (Fig. 4). In
419 fact, the models begin to diverge strongly in complex landscapes where the size of high quality
420 patches is less than the foraging distance of the bees (figures 3 and 4). The Lonsdorf model
421 would predict relatively few bees in high quality patches that are somewhat isolated due to the
422 fact the nest fitness is low, whereas the CPF model would predict a high concentration of bees in
423 an isolated high quality patch because it would draw bees from all around. This is consistent with
424 the idea that finding a lot of pollinators foraging in one place does not necessarily indicate a high
425 quality landscape, but rather indicates that a forage patch is of higher value relative to the
426 surrounding landscape (Holzschuh et al. 2011, Kovács-Hostyánszki et al. 2013, but see Jönsson
427 et al. 2015).

428
429 Practically, the CPF model provides a method to support fine-scale decision-making, such as the
430 evaluation of hedgerow planting. Because the visitation predicted by the Lonsdorf model is only
431 a function of the landscape quality, it would always predict that adding a hedgerow would
432 improve the visitation rate. And that improvement in crop field visitation is positively correlated
433 with the quality of hedgerow (Fig. 7). In contrast, the predictions of the CPF should be context-
434 specific, such that effect of the hedgerow depends on relative differences between forage
435 qualities of the hedgerow and the adjacent crop field, as well as the relative distance to nearby
436 pollinator-friendly habitat.

437
438 The main insight from the model comparisons is that if the crop field provides some floral
439 resources but poor nesting habitat, then the main benefit of the hedgerow is to provide nesting
440 habitat. Indeed, hedgerows would potentially increase the fitness of bees nesting in the area but

unless the hedgerow provides nesting habitat, bees would preferentially visit the hedgerow over the crop (Holzschuh et al. 2011). As long as the hedgerow provides nesting and is close to a field, the hedgerow would be beneficial. The effect is similar to, and the model might provide a possible mechanism for, what Lander et al. (2011) termed the Circe principle (see also Bartomeus and Winfree 2011), i.e. that the pollinators are waylaid by super attractive habitats and therefore reduce visitation to other habitats. Jönsson et al. (2015) recently showed that bumblebees were more abundant in sown flower strips than in and adjacent crop field or in the wider landscape, but also more abundant in landscapes with sown flower strips than without. Those results {Jönsson 2015} seem to be best explained by the CPF-model.

In both models, adding floral resources will increase the number of bees. However, the difference between the models arises because the Lonsdorf model predicts visitation all over the landscape, whereas the CPF model predicts visitation based on the best areas to forage, i.e. the hedgerow itself (figures 6 and 7). Additionally, as the landscape quality is increased by adding floral resources, the maximum travel distance, $\tau_{\max}$, will decrease.

Both models have limitations as neither currently incorporate intra- or interspecific competition. Rather, we have assumed that each landscape pixel with a nesting site can have one active nest. The CPF model could be developed to incorporate intraspecific competition, which would likely refine predictions for how bee visitation varies with landscape quality and heterogeneity. It would also be possible to include interspecific competition between species with e.g. different flight ranges. Throughout the paper we have considered a generalist species with a fixed life history. Developing the model to incorporate competition between multiple species with varying

life histories could provide insight into coexistence and patterns of community assembly or disassembly with respect to foraging patterns (Amarasekare 2003, Westphal et al. 2006a, Diekötter et al. 2010). As high quality forage habitat becomes rare and fragmented, or even as floral resources change throughout a growing season, changes in visitation and fitness patterns are likely to be species-specific (Carvell et al. 2011). The CPF model provides indications of how far bees would be willing to travel and thus provides thresholds. Relatively small “islands” of forage may not be visited if nearby a relatively large patch because there are sufficient forage resources in a “mainland.” The definition of mainland vs. island will vary from species to species and the CPF model can identify thresholds like this, whereas the Lonsdorf et al. (2009) model cannot. The CPF model also takes us one step further in trying to estimate spill-over effects from more natural habitat to crops, and vice versa. In the type III landscapes we give predictions on how a hedgerow would affect visitation rates in agricultural field and these estimates could be tested empirically which Tscharnkte et al. (2012) call for.

A further limitation of the CPF model as used here, is that it does not account for intra- and inter-seasonal dynamics. Recent studies have shown mass-flowering crops, such as red-clover, oil seed rape or sunflowers, can have effects on the reproduction of bees and bumblebees, with consequences for population sizes later in the same year or even in the next year (Westphal et al. 2003, Riedinger et al. 2014, Rundlöf et al. 2014). Extending the CPF model to include such coupled dynamics is in principle straightforward, and should be done in the future. This will allow tailoring both placement and seasonal dynamics of measures to benefit pollinators such as wild flower strips (Scheper et al. 2013) in an optimal way to benefit crop pollination. This could

also give us interesting predictions for how bee's phenology could change and what effects this could have with climate change both on biodiversity and ecosystem services.

Conclusions

Overall, the CPF model presented here provides behaviorally rich, spatially explicit evaluation of habitat for pollinators. It fills a gap of predicting fine-scale movement patterns in more complex forage landscapes. Furthermore, it provides a mechanism to assess the costs and benefits in crop bee visitation as a function of hedgerow or wildflower plantings.

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TABLES

Table 1. Model parameters and their values used in all analyses. See Lonsdorf et al. (2009) and Olsson and Bolin (2014) for full description. Units for the parameters are kilometers (km), time units (tu), and energy units (eu). Those with no units shown are dimensionless. Time units and energy units are arbitrary, but balanced such that total foraging time and total travel time becomes approximately equal.

Parameter	Value	Description	Units
α	0.150	Distance-decay scalar representing the average distance the bee would travel	km
v	1	Flight speed	km/tu
L	4	Load size the forager may collect	eu
c	4	Metabolic rate while foraging	eu/tu
μ	0.002	Predation rate while foraging	tu ⁻¹
k	0	Metabolic rate multiplier while in the nest (α in the notation of Olsson and Bolin 2014)	
β	1.1	Metabolic rate multiplier of flying	
δ	0.1	Predation rate multiplier while sitting in the nest	
ε	1.1	Predation rate multiplier while flying	
x	0.75	Parameter describing diminishing returns of energy	
T	250	Length of the breeding season in time units	tu
ω	-0.49	Curvature of τ . The value given is a mean value given the above parameters, with a standard deviation of 0.003 among the population in the landscape in Fig. 3D.	

FIGURE LEGENDS

Figure 1. A. Distance decay function of the Lonsdorf model, showing how visitation rate is expected to decline with distance from the nest. **B.** Patch value (Δ) of the CPF model shown as a grey shading, as a function of patch quality and distance (travel time) from the nest. The solid curve indicates combinations of qualities and distances where patch value is zero, i.e. it is a fitness isocline. This isocline tends towards a finite maximum travel time ($\tau_{\max}$), shown by the dashed line.

Figure 2. Predictions of the two models in four different simple landscapes, as illustrated in by the maps in A, E, I, and M. Hot colors (dark red) indicates high forage quality, and cold (dark blue) low forage quality, of the two fields. The cross in each map shows the position of a single nest. Panels B, F, J, and N show the visitation rates predicted by the Lonsdorf model (dashed red curve) and CPF model (solid blue curves). Predicted visitation rates in each pixel in the landscapes is shown in C, G, K, and O for the Lonsdorf model and in D, H, L, and P for the CPF model.

Figure 3. Land use in three different real 3000×3000 m landscapes (simple: A; intermediate: D; and heterogeneous G) with 25 m pixel size. For each land use class the floral value (A) and nesting value (N) used in the model is given in the legend (printed as A/N). Floral values used in the Lonsdorf model are rescaled to values between 0 and 1 as $F=A/25$. Predictions for the Lonsdorf model are shown in B, E; and H, and for the CPF model in C, F, and I.

Figure 4. Predicted bee visitation rates from the Lonsdorf model (x-axis) plotted against predictions from the CPF model (y-axis) in the simple (A), intermediate (C), and heterogeneous (E) landscapes. Each symbol represents one pixel. The black solid circles are mass flowering crop fields, and the open circles are all other land use classes. In B, D, and F is shown the predicted nest fitness for all pixels with nesting quality 1. Note that the units of the values for visitation as well as fitness are arbitrary, and hence only statements about relations between models can be made, not about absolute magnitudes.

Figure 5. Maximum travel distance as a function of fitness for each nesting pixel in the real landscapes, as predicted by the CPF model. Black dots are for the simple landscape, medium grey for the intermediate landscape, and light grey for the heterogeneous landscape.

Figure 6. Panel A shows a map of a hypothetical landscape with semi-natural habitat (nesting and intermediate floral quality) along the southern edge, a mass-flowering crop field (no nesting, but high floral quality) in the center, with a hedgerow along its western edge. The remaining area (dark blue) is pollinator unfriendly habitat. Panels B-E show predicted bee visitation rates in the area enclosed by the dotted line in A, according to the Lonsdorf model for combinations of nesting quality (0 or 1) and floral quality (0 or 25) in the hedgerow. Panels F-I show the corresponding predictions according to the CPF model.

Figure 7. A. Visitation rates to the crop field shown in figure 6 according to the Lonsdorf model (thin curves) and CPF model (bold curves) as a function of the floral quality of the hedgerow,

- 689 when the hedgerow is nesting habitat (solid curves) and is not nesting habitat (dotted curves). **B.**
- 690 Visitation rates to the hedgerow for the same combinations as in A.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7