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 toward 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 pollination of the crop, because good forage quality alone may drain bees away from the field. Our model can be used to optimize pollinator mitigation measures in real landscapes.
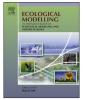
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1. Introduction

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.

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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 Tijsen, 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. (2009) 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.

2. 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