Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory

Olsson, Ola; Bolin, Arvid; Smith, Henrik; Lonsdorf, Eric V.

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1 **Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory**

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3 Ola Olsson[1], Arvid Bolin[1,2], Henrik G. Smith[1,2], and Eric V. Lonsdorf [2,3]

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5 [1]. Biodiversity unit, Department of Biology, Lund University, Sweden

6 [2]. Centre for Environment and Climate Research, Lund University, Sweden

7 [3]. Biology Department, Franklin and Marshall College, United States

8

9 Address for correspondence: Ola Olsson, Ecology Building, SE-223 62 Lund, Sweden

10 ola.olsson@biol.lu.se, Tel.: +46 46 2223774

11

12   *Abstract*

13   Pollination by bees is important for food production. Recent concerns about the declines of both

14   domestic and wild bees, calls for measures to promote wild pollinator populations in farmland.

15   However, to be able to efficiently promote and prioritize between measures that benefit

16   pollinators, such as modified land use, agri-environment schemes, or specific conservation

17   measures, it is important to have a tool that accurately predicts how bees use landscapes and

18   respond to such measures. In this paper we compare an existing model for predicting pollination

19   (the "Lonsdorf model"), with an extension of a general model for habitat use of central place

20   foragers (the "CPF model"). The Lonsdorf model has been shown to perform relatively well in

21   simple landscapes, but not in complex landscapes. We hypothesized that this was because it

22   lacks a behavioral component, assuming instead that bees in essence diffuse out from the nest

23   into the landscape. By adding a behavioral component, the CPF model in contrast assumes that

24   bees only use those parts of the landscape that enhances their fitness, completely avoiding

25   foraging in other parts of the landscape. Because foraging is directed towards the most rewarding

26   foraging habitat patches as determined by quality and distance, foraging habitat will include a

27   wide range of forage qualities close to the nest, but a much narrower range farther away. We

28   generate predictions for both simple and complex hypothetical landscapes, to illustrate the effect

29   of including the behavioral rule, and for real landscapes. In the real landscapes the models give

30   similar predictions for visitation rates in simple landscapes, but more different predictions in

31   heterogeneous landscapes. We also analyze the consequences of introducing hedgerows near a

32   mass-flowering crop field under each model. The Lonsdorf model predicts that any habitat

33   improvement will enhance pollination of the crop. In contrast, the CPF model predicts that the

34   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.

37

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

39

INTRODUCTION

41   More than one third of the global food production comes from crops partially or totally

42   dependent on animal-mediated pollination (Klein et al. 2007). Pollination may also enhance crop

43   quality (Klatt et al. 2014), and is particularly important for crops providing essential nutrients

44   (Eilers et al. 2011). Bees, including both managed and wild ones, are the most important group

45   of pollinators of crops (Delaplane and Mayer 2000). Although honey bees are frequently used to

46   enhance crop pollination, recent declines of managed honey bees (National Research Council

47   2006, Potts et al. 2010a) have increased the focus on wild bees as important crop pollinators.

48   Furthermore, a recent global meta-analysis demonstrated that increased abundance of wild

49   pollinators increases fruit set of crops independent of the presence of honey bees (Garibaldi et al.

50   2013). However, land use changes and landscape modifications resulting from agricultural

51   expansion and intensification have reduced the amount of habitat for wild pollinators, potentially

52   compromising crop pollination (Kremen et al. 2002, Potts et al. 2010b). To be able to efficiently

53   use managed pollinators and to benefit wild pollinator populations in contemporary agricultural

54   landscapes, it is important to understand how they are affected by habitat quality and landscape

55   composition in order to determine where to place managed bees and whether, where and what

56   type of habitat management is required.

57

58   Since bees are central place foragers, bringing food to a nest to benefit offspring, the spatial

59   association of nesting sites and foraging habitat is critical (Westrich 1996). Hence, pollinator

60   abundance in a specific habitat such as a crop will not only depend on its quality to bees, but also

61   on the distance to bee hives or potential nesting habitat for wild bees (Ricketts 2004, Öckinger

62   and Smith 2007, Ricketts et al. 2008, Ekroos et al. 2013), with consequences for crop pollination.

63   Recently, Lonsdorf et al. (2009) presented a spatially-explicit model to evaluate bee relative

64   abundance in landscapes, allowing consequences of crop placement and habitat management on

65   pollination to be evaluated. The model is based on explicit knowledge about the spatial

66   arrangement of bees' nesting and feeding habitats, which may be separated in space and vary in

67   time. Because bees need to return to their nest with the nectar and pollen they collect, the bee

68   visitation rate at a patch with flower resources depends on the distance from that patch to nesting

69   habitat (Lonsdorf et al. 2009). That model can reasonably well predict pollination services at the

70   landscape scale (Lonsdorf et al. 2009, Kennedy et al. 2013), and it can identify situations in

71   which habitat restoration would potentially enhance the pollination service (Ricketts and

72   Lonsdorf 2013). However, whereas the model (Lonsdorf et al. 2009) performs reasonably well in

73   coarse grained, rather homogenous (simple), landscapes, it performs less well in more

74   heterogeneous (complex) landscapes (Kennedy et al. 2013).

75

76   We argue that a major reason that the Lonsdorf et al. (2009) model performs less well in

77   complex landscapes is that it is not based on central place foraging theory (Schoener 1979,

78   Olsson et al. 2008), and thus does not assume that bees select foraging habitat to maximize

79   fitness. In the model there is no behavioral mechanism by which bees can select foraging

80   patches. Instead they simply "diffuse" out from the nest. This contrasts with empirical studies of

81   foraging bees, that have demonstrated that bee densities in both crops and wild flowers depend

82   on both local habitat quality (Carvell et al. 2007, Woodcock et al. 2014) and the quality of

83   surrounding habitat (Steffan-Dewenter et al. 2002, Heard et al. 2007, Carvell et al. 2011,

84   Holzschuh et al. 2011, Scheper et al. 2013), this limitation of the model may result in spatial

85   variation in bee densities, and hence pollination, being less accurately predicted. A consequence

86   of assuming that visitation rates and the distance a bee is willing to travel in the model does not

87   depend on floral patch quality or the quality around a patch will result in the model not capturing

88   relatively fine-scale variation in habitat quality in a complex landscape. Furthermore, the model

89   will not be able to predict changes in visitation rates in response to small-scale alterations in the

90   landscape, such as the addition of a hedgerow or wildflower strip that change the spatial structure

91   of resources within a field but have little effect on the total resources at a landscape scale. Hence,

92   although, there is concern that flower strips or hedgerows might be "too attractive" and drain

93   bees out of crop fields needing pollination (cf. Bartomeus and Winfree 2011, Lander et al. 2011),

94   or that mass flowering crops might attract bees away from natural habitats, where pollination of

95   the wild plants could be suffering (Holzschuh et al. 2011, Kovács-Hostyánszki et al. 2013), the

96   Lonsdorf et al. (2009) model would predict that adding more flower resources and nesting

97   habitat always leads to increased visitation rates.

98

99   We propose that integration of more complex foraging mechanisms, such as central place

100   foraging theory (Schoener 1979, van Gils and Tijsen 2007, Olsson et al. 2008) into the Lonsdorf

101   et al. (2009) modeling framework may solve some of the above mentioned shortcomings. Central

102   place foraging theory (CPF) is based on the premise that animals forage for resources in patches

103   dispersed in a landscape around a central place (nest, burrow, or refuge). They harvest resources

104   in the patches, and then need to travel back to the central place either to unload the resources or

105   to rest in safety. Travelling to and from patches takes time and also entails costs in terms of

106   energy and mortality risk. Carrying a large load might additionally be more expensive (Olsson et

107   al. 2008). Central place foraging theory has been applied to bees to determine the distance bees

108   are willing to travel to forage and the amount of food they are willing to acquire during the

109   foraging trip (Schmid-Hempel et al. 1985, Kacelnik et al. 1986, Cresswell et al. 2000), but the

110   theory has not been applied to describe habitat use for bees.

111

112   Recently, Olsson and Bolin (2014) built a habitat use model from CPF, demonstrating how to

113   predict what patches foragers should use in a specific landscape. That model, which is general

114   for any CPF forager and not specific to pollinators, shows how the marginal fitness value of

115   patches depends on two variables: patch quality and distance to the central place. A key result of

116   the model (Olsson and Bolin 2014) is that for any patch quality there will be a maximum

117   distance that the forager would be willing to travel. Hence, near the nest patches of a large range

118   of qualities should be used, but far from the nest only the best patches will be used. Patches of

119   low quality might therefore be passed on the way to patches of higher quality. Using that model,

120   landscape quality can be derived as the summed value of all useable patches in the landscape, i.e.

121   all patches contributing positively to fitness if used.

122

123   In this paper we will address the limitations of the Lonsdorf et al. (2009) model by combining its

124   general framework with the behavioral mechanism for central place foraging developed by

125   Olsson and Bolin (2014). Our goal is to develop a spatially-explicit, central place foraging

126   analysis of pollination service that better reflects the foraging behavior of bees. Such a model is

127   likely to be able to generate improved predictions for the pollination service in complex

128   landscapes and the consequences of habitat enhancement. We expect that a model with an added

129   behavioral mechanism will have similar predictions as the Lonsdorf et al. model in relatively

130   simple landscapes, but as the complexity of landscapes increases, the correspondence between

131   the models would decrease. Similarly, we should be able to show that a model which

132   incorporates central place foraging theory can identify landscapes in which habitat enhancements

133   would draw bees away from a patch that was once visited.

134

135   MODEL DESCRIPTION

136   We will compare the performance and predictions of the model by Lonsdorf et al. (2009;

137   hereafter "the Lonsdorf model") with our new model based on Olsson and Bolin (2014; hereafter

138   "the CPF model"), by applying them in the same artificial or real landscapes. Both models are

139   described in the previous work, and here we only present the minimal necessary theory from

140   those papers, and the extensions we make to apply both models to the landscape context that we

141   are considering here. Bees require nesting resources and fitness at the nest site depends on

142   enough foraging resources within their flight range, and thus the input data for both models is

143   one map of nest site qualities, and one map of floral resource qualities. For model coherency we

144   do not consider temporal changes in floral qualities.

145

146   *The Lonsdorf model* first estimates relative fitness of a pollinator species nesting in each pixel,

147   based on the available nesting resources in that patch and the quality of floral resources in

148   surrounding pixels. In evaluating floral resources, nearby pixels are given more weight than

149   more distant patches, based on a species' expected foraging range. The result is a map that

150   provides an index of nesting fitness (0 to 1) across a landscape. Given the fitness pattern of

151   nesting bees in the landscape, the model then estimates the relative abundance of foraging bees

152   visiting floral areas. It averages the relative bee fitness in neighboring patches, again giving

153   more weight to nearby patches, based on average foraging ranges. This distance-weighted

154   average is the relative index of abundance for each pollinator (Fig. 1A). Applied to a raster or

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

156   i, G_i, as:

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

158   where N_i is an indicator variable equal to 1 if the pixel i provides suitable nesting habitat and 0,

159   otherwise. The ratio represents the distance-weighted average floral quality of the landscape

160   surrounding nest site i. The numerator is distance weighted sum of all floral resources across all

161   M pixels where F_j is the floral quality, scaled from 0 to 1, of site j, D_{ij} is the Euclidean distance

162   between nest site i and floral site j and α is a distance-decay scalar representing the average

163   distance the bee would travel to forage. The denominator is simply the distance weighted habitat

164   availability. The fitness index is scaled from 0 to 1 and provides an indication of how many bees

165   are supported by the landscape surrounding site i, i.e. P_i.

166

167   To determine the abundance of bees foraging or visiting a particular floral patch or crop,

168   Lonsdorf et al. (2009) used the same framework to redistribute bees from nest sites onto the

169   landscape. They assumed that bees foraged from nest sites to the surrounding foraging areas,

170   such that forage areas that are surrounded by nests with relatively high fitness would have a

171   higher abundance index than those with fewer nests or nests with lower fitness. Thus the index of

172   abundance for bees foraging at site j, P_j, is equivalent to the distance-weighted average fitness of

173   surrounding nests:

9

$$P_j = \frac{\sum_{j=1}^{M} G_i e^{-\frac{D_{ij}}{\alpha}}}{\sum_{j=1}^{M} e^{-\frac{D_{ij}}{\alpha}}} \ , \tag{2}$$

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

176

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

192   travel there and back from the nest:

193
$$\tau = \tau_{\max} + \frac{\omega}{A} \ . \tag{3}$$

194 While τ and *A* are the variables of the model, the parameters τ_{max} and ω are results found at the

195 solution which maximizes fitness. Here, τ_{max} is the maximum travel time accepted to reach a

196 patch of infinite quality and ω is a parameter ($\omega<0$) that relates quality to travel time (distance) in

197 a manner which is appropriate for the life-history of that organism (Fig. 1B). The ω is a

198 composite parameter that depends on many of the different life-history parameters (Table 1;

199 Olsson and Bolin 2014). It is effectively constant for any particular life-history strategy (such as

200 a species), and nearly independent of the environment. However, τ_{max} increases in poor

201 environments meaning they are forced to select patches further away and of lower quality, and is

202 typically negatively related to fitness (Olsson and Bolin 2014). The parameters used in the

203 simulations (Table 1) were chosen with a relatively long-flying bumblebee species (e.g. *Bombus*

204 *terrestris*) in mind, but have not been measured from empirical data.

205

206 The shading in figure 1 shows the marginal fitness value, Δ, to the bee (or bee colony) of using a

207 patch at a given distance and of a particular quality. A patch falling on the curve separating the

208 shaded area from the white area provides no value, and one above that curve should not be used

209 as it would give a negative value. That is, floral patches that fall outside of the shaded area

210 should not be visited, as their combination of qualities and distance to the nest make them

211 unprofitable to use.

212

213 To develop Olsson and Bolin's (2014) model to one that predicts pollinator visitation rates, and

214 pollinator fitness in landscapes we proceeded as follows. We calculated the bee visitation rates

215 for the CPF-model, by assuming that the number of workers going from a nest to a resource

216　patch is proportional to the marginal fitness value of that patch to the nest. The total number of

217　workers from all n nests visiting floral patch j is proportional to:

218
$$V_j = \sum_{i=1}^{n} \left[N_i \left(\Delta_{i,j} - \frac{kT}{M_i} \right) \right],$$
(4)

219　where $-kT$ is the fitness overhead cost of not using any patch, as k is the metabolic rate of

220　spending time idle in the nest, T is the length of the breeding season, and M_i is the total number

221　of floral patches visited by nest i. The fitness of a nest can then simply be expressed as the sum

222　of the marginal values of each of the patches:

223
$$G_i = \left(\sum_{j=1}^{M_i} \Delta_{i,j} - kT \right) N_i.$$
(5)

224　The CPF model is consistent with a previous model by Cresswell et al. (2000). However, our

225　model is more general, particularly in that it evaluates an entire landscape of foraging patches,

226　rather than just a pair of two patches. It also incorporates predation risk in the fitness function,

227　and under some conditions can be solved analytically (Olsson and Bolin 2014).

228

229　In both models there is a direct proportionality between the number of nests and the number of

230　workers, as there is no competition for resources. Each nesting pixel can have only a single nest,

231　but adjacent pixels can be inhabited. The more nests in an area, the more bee visits the

232　surrounding landscape will get.

233

234　To determine if the different approaches would yield different projections regarding bee

235　visitation rates, we made a number of comparisons to investigate the effects of landscape

236　complexity and the potential to predict one high quality floral patch drawing bees away from

237　nearby lower quality patches. First, to investigate if the models' different treatment of foraging

238   resulted in qualitatively different predictions regarding how bees distribute in the landscape, we

239   compared how bees leaving from a single nest were distributed in contrasting synthetic

240   landscapes. Second, to investigate if the models generate different predictions for bee

241   distribution in real landscapes, we compared the two models' predictions for three different real

242   landscapes that varied in the amount of pollinator-friendly habitat and landscape complexity.

243   Finally, to specifically investigate the consequences of the two approaches for predicting the

244   effect of adding pollinator friendly habitat (hedgerow or flower strip, which provides nesting

245   and/or flowering resources) on crop pollination, we applied the models to a new set of synthetic

246   landscapes with and without a hedgerow adjacent to a crop field. For simplicity we consider the

247   same species throughout the paper, described with its life history in table 1.

248

249   MODEL PREDICTIONS

250   *Landscape type I: single nest with contrasting forage patterns*

251   To illustrate the consequences of different foraging functions for visitation, we created a simple

252   landscape 750×750 m, with a 30×30 m pixel size (Fig 2; Code to produce the relevant

253   calculations is supplied in the Supplementary information) with a single nest site along the

254   western edge of the landscape (marked with a cross). The landscape has two fields, one adjacent

255   to the nest and one in the east half of the landscape, relatively far from the nest site. Using this

256   simple system, we model the distribution of foraging bees on the landscape resulting from four

257   different scenarios of forage quality of the fields as shown in figure 2A, E, I, and M.

258

259   In all four landscapes (Fig 2) the Lonsdorf model predicts the same relative visitation rates, while

260   the CPF model predicts different visitation patterns because bees direct their efforts to areas of

261   higher qualities.

262

263   The Lonsdorf model predicts the number of workers produced, i.e. the nest fitness, to be higher

264   in landscape 2 (Fig. 2E), compared to landscapes 1 and 3 (Fig. 2A and I), and higher in

265   landscape 4 (Fig. 2M) compared to 3 (Fig. 2I). However, the relative distribution of those bees

266   will be identical between landscapes, i.e. the same proportion of those bees will visit the same

267   pixel in each case (Fig. 2C, G, K, and O). In contrast, the CPF model gives different predictions

268   for the four different landscapes of type I. In the first, with homogeneous floral quality, and

269   second, with slightly better forage near the nest site, the predictions are nearly identical to the

270   Lonsdorf model. The only difference is that according to the CPF model the bees will not visit

271   floral patches at all beyond a certain distance (τ_{max}) from the nest, whereas the Lonsdorf model

272   predicts small fractions of the workers reaching these far-away patches. In the second landscape,

273   the CPF model predicts no visitation at all in the far away, poor field. These differences between

274   the models can also be seen from the curves of the visitation rates (Fig. 2B and F), which hits

275   zero for the CPF bees, but for the Lonsdorf bees it only approaches zero asymptotically.

276

277   In the third and fourth landscapes, which both have higher quality forage far from the nest site

278   (Fig. 2), there is a striking difference between the models, because the CPF bees reduce their

279   visitation of the nearby field of poor quality to instead increase their foraging efforts to the far

280   away high quality field (Fig 2L and P). This effect is even more accentuated in the fourth

281   landscape, where the difference in floral quality between the rich and the poor landscapes are

14

282 stronger. Here, the CPF bees only visit the very near parts of the poor fields, right next to the

283 nest; most of them will skip over that field entirely and devote their effort to the parts of rich

284 field that are still close enough for them to use.

285

286 *Landscape type II: real landscapes that differ in complexity*

287 We applied the models to an analysis of three landscapes from the province of Scania, Sweden

288 (Fig. 3). We assigned floral and nesting qualities to each of the land cover types, in a simple but

289 more or less realistic manner, similar to previous studies (e.g. Kennedy et al. 2013). These

290 landscapes are 3×3 km, with a pixel size of 25 m, and floral and nesting qualities for each of the

291 land cover types are shown in figure 3. The simplest landscape consists mainly of non-flowering

292 annual crops, a single large patch of a mass-flowering crop that does not provide nesting and a

293 few smaller patches of land that provide nesting and moderate floral resources. In the moderately

294 complex landscape, mass-flowering crop fields are slightly smaller and often next to small

295 pasture fields and patches of forest, which provide nesting sites. The most complex landscape

296 has a mix of forested land, small patches of mass-flowering crop and scattered patches of semi-

297 natural land, pasture and other flowering crops that each provide some nesting and floral

298 resources.

299

300 The differences in model predictions can be seen by comparing the panels of figure 3 (B vs C, E

301 vs. F, and H vs. I, respectively). For example, there are two illustrative areas within the

302 moderately complex landscape where the CPF model shows its strength (Fig. 3D). At

303 coordinates (1500, 2000), a small forest patch is surrounded by a bit of "other farmland". The

304 forest is considered good nesting habitat only, and the only floral resources nearby is the "other

305   farmland" habitat, so these patches are predicted to have high visitation rates coming from those

306   forest nests, with no visits to the forest. The Lonsdorf model predicts most visits in the forest

307   (which has no floral value). South of this forested area at coordinates (1200, 1200) is a

308   moderately-sized strip of mass-flowering crop with two patches of other farmland embedded.

309   The mass flowering crop, which is a better floral resource but no nesting, draws visitors away

310   from the other farmland. So visitation rates to the "other farmland" predicted by the CPF model

311   vary from place to place, reflecting their relative attractiveness, which is not captured by the

312   Lonsdorf model.

313

314   In figure 4 we show how the bee visitation rates (Fig. 4 A, C, and E) and fitness (Fig. 4B, D, and

315   F) compares between the models. Each dot is a pixel from the landscapes shown in figure 3.

316   Visitation rates are predicted differently by the models, and in particular the Lonsdorf model

317   often predicts high visitation rates in areas where the CPF model predicts none. The

318   correspondence between the models appears better in the simple landscape (Fig. 4A) than in the

319   most complex (Fig. 4E). Particularly the mass-flowering crop fields (black dots) are very

320   differently predicted by the two models. By contrast, the nest fitness of the bees is predicted very

321   similarly between the models.

322

323   The inherent dynamics of the CPF model is shown in figure 5. In poor areas (pixels), where

324   realized fitness is low, the maximum travel distance (τ_{max}) is nearly twice as high as in the best

325   areas with high fitness.

326

16

327 *Landscape type III: evaluating habitat enhancements*

328 We again use a synthetic landscape to show how the approaches differ in their predictions of the

329 consequences of planting a pollinator-friendly hedgerow for bee visitation in an adjacent field of

330 pollinated crop (Fig. 6A). We generate the landscape using four components: a natural area that

331 is highly suitable for pollinators, an agricultural field of a pollinator-dependent crop that has

332 moderate quality forage for pollinators but provides no nesting, an agricultural crop that is

333 unsuitable for pollinators and a hedgerow in which we vary the relative suitability for pollinators.

334 Within the landscape, the natural area forms the southern border of the landscape, the pollinator-

335 dependent crop is a 270-by-270 m (9 x 9 pixels) block of habitat to the north of the natural area,

336 and if there is a hedgerow, it is a 9-by-1 pixel strip along the western border of pollinator-

337 dependent crop. The remainder of the landscape is pollinator unfriendly crop. We create four

338 scenarios to illustrate the effects of the hedgerow on visitation in the field of the pollinator-

339 dependent crop: (1) no hedgerow, (2) the hedgerow provides good nesting only, (3) the

340 hedgerow provides only high quality forage and (4) the hedgerow provides both good nesting

341 and high quality forage (Fig. 6). We also investigate the effect of varying the hedgerow's forage

342 quality continuously from none to very high, with and without nesting sites.

343

344 Our results from the type III landscape illustrate the mechanistic differences between the models

345 (figures 6 and 7). Adding nest sites, or both nest sites and floral resources enhance pollination in

346 the crop field according to the Lonsdorf model. That model predicts that adding nesting sites are

347 more important for pollination than is floral resources, but that adding floral resources is always

348 beneficial, as this increases the landscape bee population size (Fig. 6B – E, Fig. 7A). In contrast,

349 the CPF model (Fig. 6F – I) predicts that, while adding nesting sites enhances pollination (Figure

17

350   7A – CPF, with nest), adding floral resources in the hedgerow might reduce bee visitation rates

351   (Figure 7A – CPF, without nest). Still, adding both nesting and floral resources yields much

352   higher visitation rates than having no hedge at all, as long as the distance to the hedgerow is not

353   too far. But as the forage quality of the hedgerow increases, the number of bees supported in the

354   landscape will increase, but the CPF model predicts that bees will be drawn towards the

355   hedgerow instead of the crop (cf. Fig. 7A and B).

356

357   DISCUSSION

358   Incorporating a behavior into a model of crop refines and changes predictions in important ways.

359   While the CPF and Lonsdorf models similarly predict the quality of a landscape to support bees,

360   only the CPF model predicts visitation based on floral patch quality relative to the distance from

361   the nest. The added behavioral mechanism importantly allows the CPF model to make fine-scale

362   evaluations of potential farm management options such as hedgerow or floral plantings. The

363   model bees respond to difference in local patch quality compared to the larger landscape, such

364   that they fly farther for high quality patches, particularly when it is a relatively poor quality

365   landscape (Steffan-Dewenter and Kuhn 2003, Westphal et al. 2006b, Heard et al. 2007, Jha and

366   Kremen 2013). Specifically, the CPF model predicts a negative correlation between maximum

367   travel distance and fitness (Fig. 5), such that travel distances from nest sites in a floral rich area

368   are shorter than nest sites surrounded by poorer resources – a result consistent with recent

369   findings by Carvell et al. (2012). Thus, long-distance traveling is an indication of resource

370   limitation. This is consistent both with findings that fitness decreased when solitary bees were

371   forced to fly longer distances (Zurbuchen et al. 2010), and that bumblebees in poor landscapes

372   have longer trip durations (Westphal et al. 2006b).

373

374   The Lonsdorf et al. (2009) model only considers distance in determining foraging patterns, not

375   the quality of the patch and so bees would potentially visit every part of the landscape regardless

376   of its quality. In contrast, the CPF model's strength is its ability to weigh the costs vs. benefits of

377   different patches in the landscape (Figure 2). It assumes that foragers only utilize patches where

378   a combination of local quality and distance from the nest results in a positive contribution to

379   fitness. This simple and elegant assumption allows for spatially-explicit foraging behavior, such

380   that bees will fly over poor quality areas to get to higher quality patches. This results in distinctly

381   different prediction on the distribution of bees in landscapes.

382

383   Under reasonable assumptions of foraging distances and differences in habitat qualities, the CPF

384   model makes important predictions for real landscapes (type II, Fig. 3), which the Lonsdorf

385   model is unable to make. These differences in model predictions for the type II landscapes

386   further illustrate the ability of the CPF model to incorporate variation in configuration and

387   quality distribution of forage resources in predicting visitation rates of bees in a real landscape

388   (Figure 3). With the Lonsdorf model, the amount and location of bees is determined only by the

389   general quality of landscape so fine-scale features do not matter, such that the abundance of bees

390   in any given location is simply an indication of the average nest fitness in the surrounding pixels

391   (Kennedy et al. 2013). In contrast, the CPF model would predict that the highest visitation rates

392   would occur when forage resources are limited in the surrounding landscape (Fig. 3). Isolated

393   patches with high forage values would thus concentrate the number of foraging bees.

394

395   The two models provide general agreement about the overall quality of a landscape for bees in

396   terms of the number or fitness of bees that a landscape would support (Fig. 4) but, within a

397   landscape, the models clearly differ in suggesting where and how many bees are foraging. As

398   landscape complexity increases, the correspondence between the models declines (Figure 4). In

399   the simplest landscapes, both models provide general agreement as to where bees are visiting

400   floral resources. The simplest type II landscape is most like the first two scenarios in the type I

401   landscape, in which nesting is next to high quality forage. As the patch sizes get smaller and

402   landscape heterogeneity with respect to patterns of nesting and floral resources increases, the

403   CPF model describes much more within-patch variation in visitation. In contrast, the Lonsdorf

404   model creates weighted-average hot-spots representing locations that have good floral and

405   nesting areas (cf. Fig. 3). However, it cannot pick up fine-scale nuances in the landscape like the

406   CPF model.

407

408   The Lonsdorf model in essence estimates the quality of foraging resources to central-place

409   foraging bees (Vos et al. 2001), but fails to show how bees *de facto* utilize the landscape since it

410   lacks a behavioral habitat selection component. The CPF model provides this additional

411   component, such that the relative attraction of any pixel for forage depends on the relative

412   quality of other nearby pixels. Thus, the Lonsdorf model provides good insight into the

413   evaluation of number of bees that could be supported by a landscape but cannot provide the type

414   of guidance at a fine-scale important to predict e.g. crop pollination that the CPF model can.

415

416   The CPF model handles landscape heterogeneity within the bees' home range, which the

417   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

441   unless the hedgerow provides nesting habitat, bees would preferentially visit the hedgerow over

442   the crop (Holzschuh et al. 2011). As long as the hedgerow provides nesting and is close to a

443   field, the hedgerow would be beneficial. The effect is similar to, and the model might provide a

444   possible mechanism for, what Lander et al. (2011) termed the Circe principle (see also

445   Bartomeus and Winfree 2011), i.e. that the pollinators are waylaid by super attractive habitats

446   and therefore reduce visitation to other habitats. Jönsson et al. (2015) recently showed that

447   bumblebees were more abundant in sown flower strips than in and adjacent crop field or in the

448   wider landscape, but also more abundant in landscapes with sown flower strips than without.

449   Those results {Jönsson 2015} seem to be best explained by the CPF-model.

450

451   In both models, adding floral resources will increase the number of bees. However, the

452   difference between the models arises because the Lonsdorf model predicts visitation all over the

453   landscape, whereas the CPF model predicts visitation based on the best areas to forage, i.e. the

454   hedgerow itself (figures 6 and 7). Additionally, as the landscape quality is increased by adding

455   floral resources, the maximum travel distance, τ_{max}, will decrease.

456

457   Both models have limitations as neither currently incorporate intra- or interspecific competition.

458   Rather, we have assumed that each landscape pixel with a nesting site can have one active nest.

459   The CPF model could be developed to incorporate intraspecific competition, which would likely

460   refine predictions for how bee visitation varies with landscape quality and heterogeneity. It

461   would also be possible to include interspecific competition between species with e.g. different

462   flight ranges. Throughout the paper we have considered a generalist species with a fixed life

463   history. Developing the model to incorporate competition between multiple species with varying

464   life histories could provide insight into coexistence and patterns of community assembly or

465   disassembly with respect to foraging patterns (Amarasekare 2003, Westphal et al. 2006a,

466   Diekötter et al. 2010). As high quality forage habitat becomes rare and fragmented, or even as

467   floral resources change throughout a growing season, changes in visitation and fitness patterns

468   are likely to be species-specific (Carvell et al. 2011). The CPF model provides indications of

469   how far bees would be willing to travel and thus provides thresholds. Relatively small "islands"

470   of forage may not be visited if nearby a relatively large patch because there are sufficient forage

471   resources in a "mainland." The definition of mainland vs. island will vary from species to species

472   and the CPF model can identify thresholds like this, whereas the Lonsdorf et al. (2009) model

473   cannot. The CPF model also takes us one step further in trying to estimate spill-over effects from

474   more natural habitat to crops, and vice versa. In the type III landscapes we give predictions on

475   how a hedgerow would affect visitation rates in agricultural field and these estimates could be

476   tested empirically which Tscharnkte et al. (2012) call for.

477

478   A further limitation of the CPF model as used here, is that it does not account for intra- and inter-

479   seasonal dynamics. Recent studies have shown mass-flowering crops, such as red-clover, oil

480   seed rape or sunflowers, can have effects on the reproduction of bees and bumblebees, with

481   consequences for population sizes later in the same year or even in the next year (Westphal et al.

482   2003, Riedinger et al. 2014, Rundlöf et al. 2014). Extending the CPF model to include such

483   coupled dynamics is in principle straightforward, and should be done in the future. This will

484   allow tailoring both placement and seasonal dynamics of measures to benefit pollinators such as

485   wild flower strips (Scheper et al. 2013) in an optimal way to benefit crop pollination. This could

486 also give us interesting predictions for how bee's phenology could change and what effects this

487 could have with climate change both on biodiversity and ecosystem services.

488

489 *Conclusions*

490 Overall, the CPF model presented here provides behaviorally rich, spatially explicit evaluation of

491 habitat for pollinators. It fills a gap of predicting fine-scale movement patterns in more complex

492 forage landscapes. Furthermore, it provides a mechanism to assess the costs and benefits in crop

493 bee visitation as a function of hedgerow or wildflower plantings.

494

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634

636 **Table 1.** Model parameters and their values used in all analyses. See Lonsdorf et al. (2009) and

637 Olsson and Bolin (2014) for full description. Units for the parameters are kilometers (km), time

638 units (tu), and energy units (eu). Those with no units shown are dimensionless. Time units and

639 energy units are arbitrary, but balanced such that total foraging time and total travel time

640 becomes approximately equal.

641

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.	

642

643

644

646 **Figure 1. A.** Distance decay function of the Lonsdorf model, showing how visitation rate is

647 expected to decline with distance from the nest. **B.** Patch value (Δ) of the CPF model shown as a

648 grey shading, as a function of patch quality and distance (travel time) from the nest. The solid

649 curve indicates combinations of qualities and distances where patch value is zero, i.e. it is a

650 fitness isocline. This isocline tends towards a finite maximum travel time (τ_{max}), shown by the

651 dashed line.

652

653 **Figure 2.** Predictions of the two models in four different simple landscapes, as illustrated in by

654 the maps in A, E, I, and M. Hot colors (dark red) indicates high forage quality, and cold (dark

655 blue) low forage quality, of the two fields. The cross in each map shows the position of a single

656 nest. Panels B, F, J, and N show the visitation rates predicted by the Lonsdorf model (dashed red

657 curve) and CPF model (solid blue curves). Predicted visitation rates in each pixel in the

658 landscapes is shown in C, G, K, and O for the Lonsdorf model and in D, H, L, and P for the CPF

659 model.

660

661 **Figure 3.** Land use in three different real 3000×3000 m landscapes (simple: A; intermediate: D;

662 and heterogeneous G) with 25 m pixel size. For each land use class the floral value (A) and

663 nesting value (N) used in the model is given in the legend (printed as A/N). Floral values used in

664 the Lonsdorf model are rescaled to values between 0 and 1 as $F=A/25$. Predictions for the

665 Lonsdorf model are shown in B, E; and H, and for the CPF model in C, F, and I.

666

667   **Figure 4.** Predicted bee visitation rates from the Lonsdorf model (x-axis) plotted against

668   predictions from the CPF model (y-axis) in the simple (A), intermediate (C), and heterogeneous

669   (E) landscapes. Each symbol represents one pixel. The black solid circles are mass flowering

670   crop fields, and the open circles are all other land use classes. In B, D, and F is shown the

671   predicted nest fitness for all pixels with nesting quality 1. Note that the units of the values for

672   visitation as well as fitness are arbitrary, and hence only statements about relations between

673   models can be made, not about absolute magnitudes.

674

675   **Figure 5.** Maximum travel distance as a function of fitness for each nesting pixel in the real

676   landscapes, as predicted by the CPF model. Black dots are for the simple landscape, medium

677   grey for the intermediate landscape, and light grey for the heterogeneous landscape.

678

679   **Figure 6.** Panel A shows a map of a hypothetical landscape with semi-natural habitat (nesting

680   and intermediate floral quality) along the southern edge, a mass-flowering crop field (no nesting,

681   but high floral quality) in the center, with a hedgerow along its western edge. The remaining area

682   (dark blue) is pollinator unfriendly habitat. Panels B-E show predicted bee visitation rates in the

683   area enclosed by the dotted line in A, according to the Lonsdorf model for combinations of

684   nesting quality (0 or 1) and floral quality (0 or 25) in the hedgerow. Panels F-I show the

685   corresponding predictions according to the CPF model.

686

687   **Figure 7. A.** Visitation rates to the crop field shown in figure 6 according to the Lonsdorf model

688   (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.

A.

B.

τ_{max}

Fig. 1

	Floral quality	Visitation rates	Lonsdorf model	CPF model

A. B. C. D.
E. F. G. H.
I. J. K. L.
M. N. O. P.

Distance

Fig. 2

Fig. 3

Semi-natural pasture, 20/1
Ley, 10/0
Mass flowering crop, 20/0
Non-flowering annual crops, 2/0
Other farmland, 10/1
Pasture, 20/1
Park, 20/1
Deciduous wood, 10/1
Coniferous wood, 2/1
Urban, 5/1
Village, 10/1
Wetlands, 5/0

Fig. 4

Fig. 5

Fig. 6

A.

CPF, with nest
Lonsdorf, with nest
CPF, without nest
Lonsdorf, without nest

Visitation rate, Crop field

Floral quality of hedgerow

B.

Visitation rate, Hedgerow

Floral quality of hedgerow

Fig. 7