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

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LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

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

2

3 Ola Olsson¹, Arvid Bolin^{1,2}, Henrik G. Smith^{1,2}, and Eric V. Lonsdorf^{2,3}

4

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

40 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 Tijssen 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:

$$157 \quad G_i = N_i \frac{\sum_{j=1}^M F_j e^{-\frac{D_{ij}}{\alpha}}}{\sum_{j=1}^M e^{-\frac{D_{ij}}{\alpha}}}, \quad (1)$$

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:

174

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

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

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

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:

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

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:

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

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

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

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

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).

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394

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.

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 an 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

635 TABLES

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

645 FIGURE LEGENDS

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.

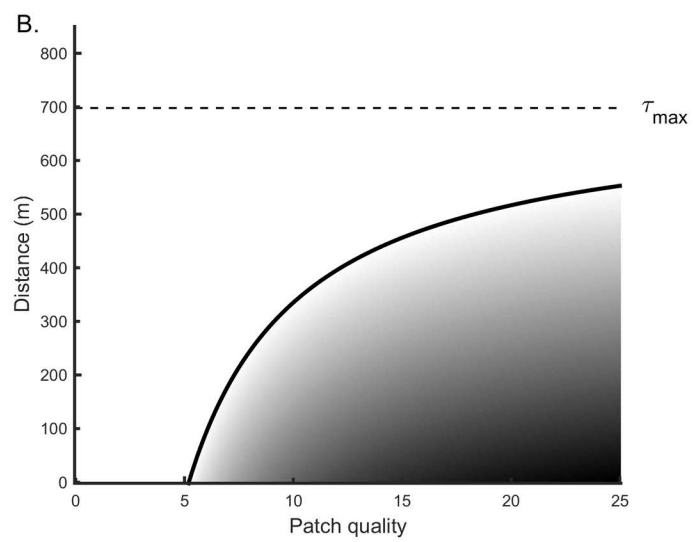
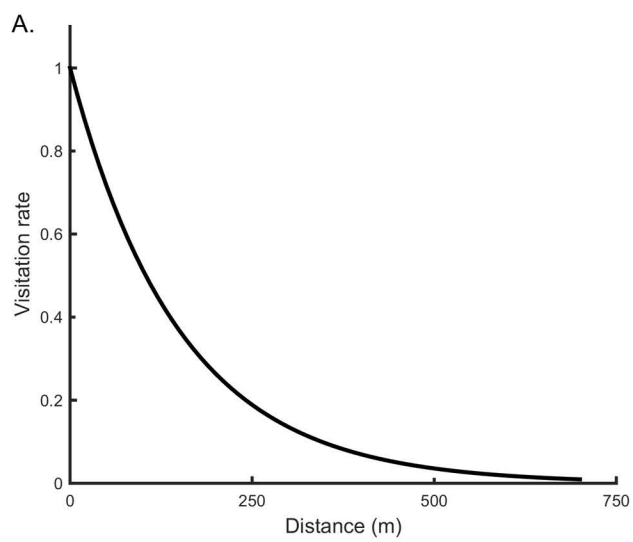


Fig. 1

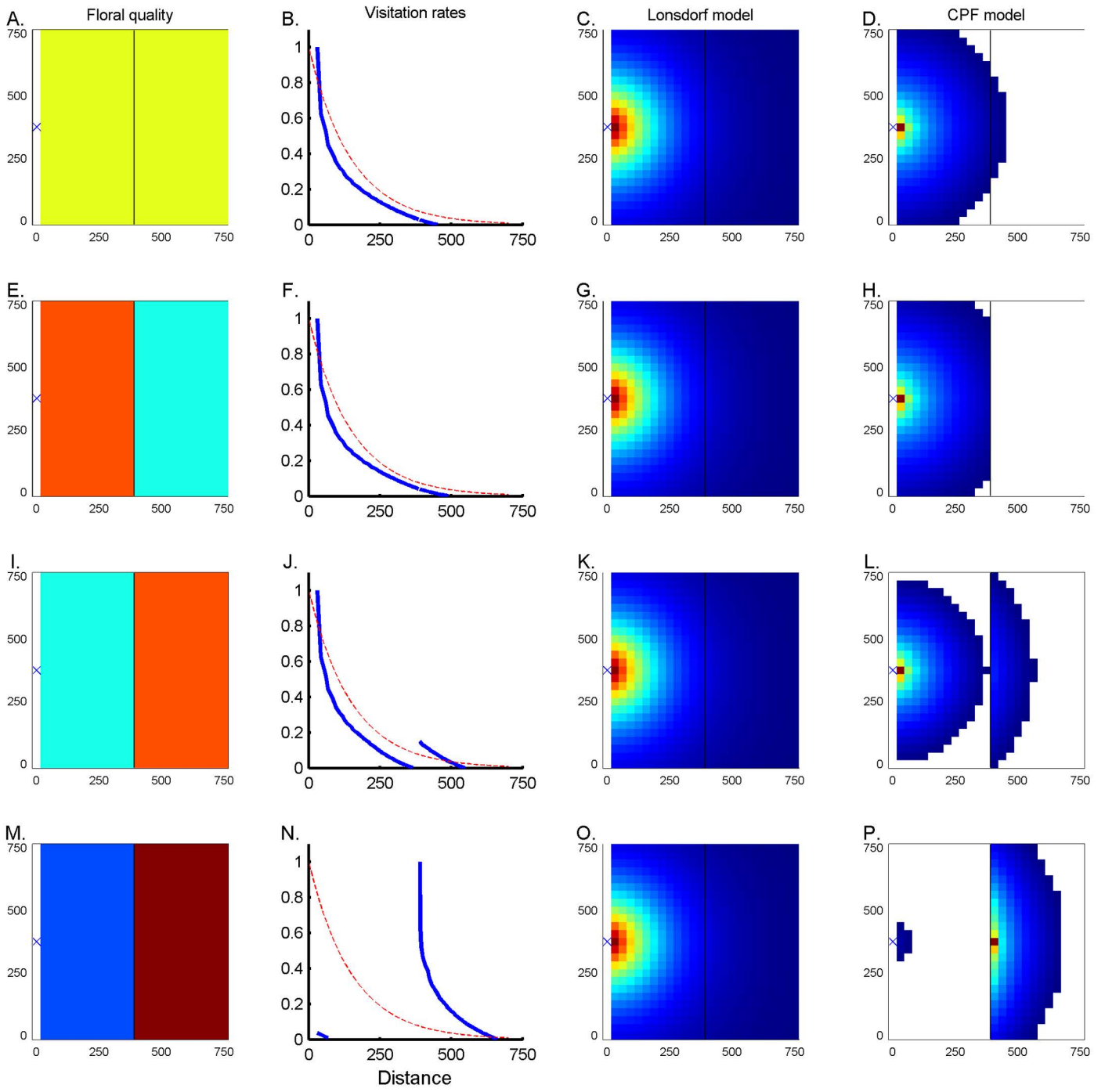


Fig. 2

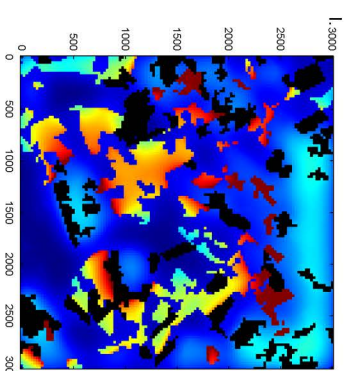
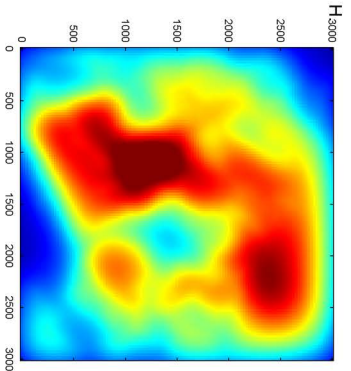
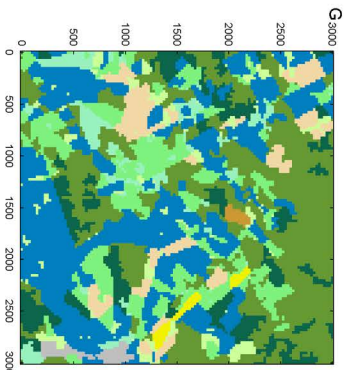
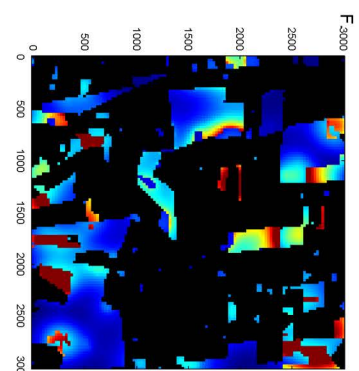
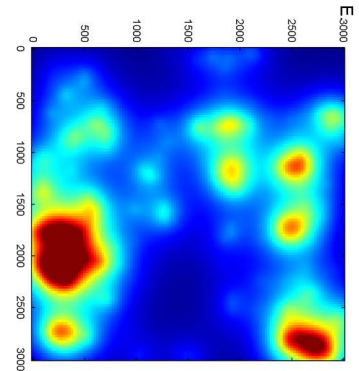
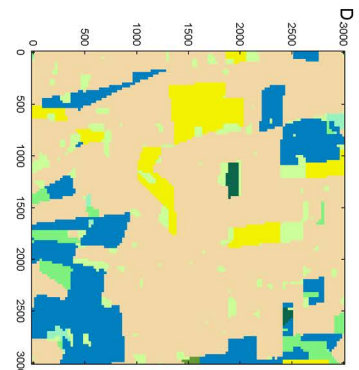
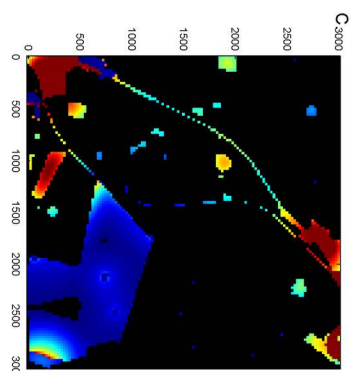
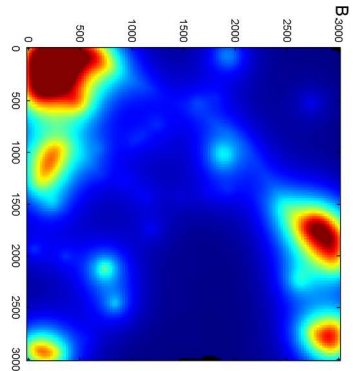
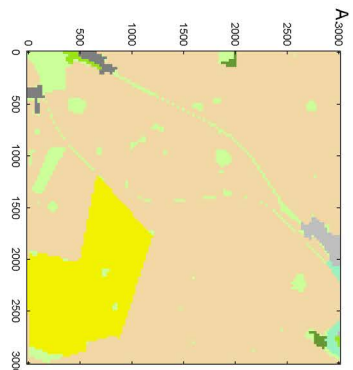
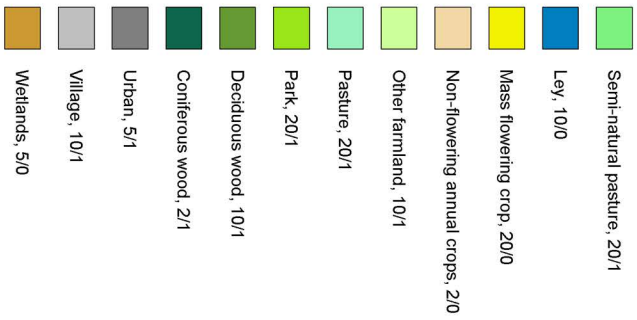


Fig. 3

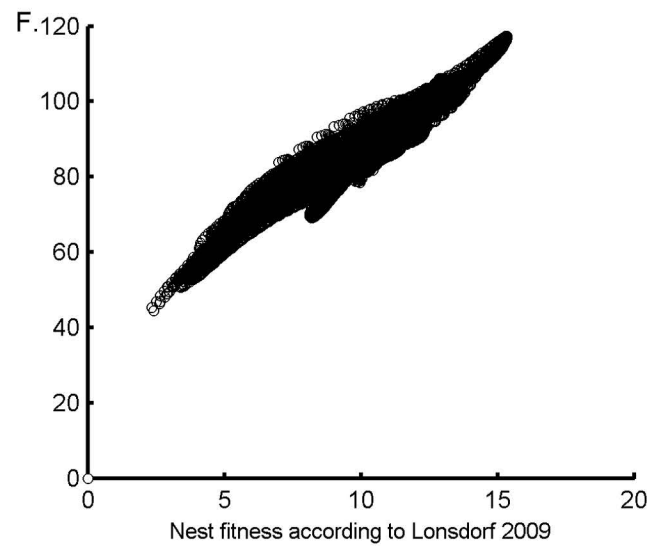
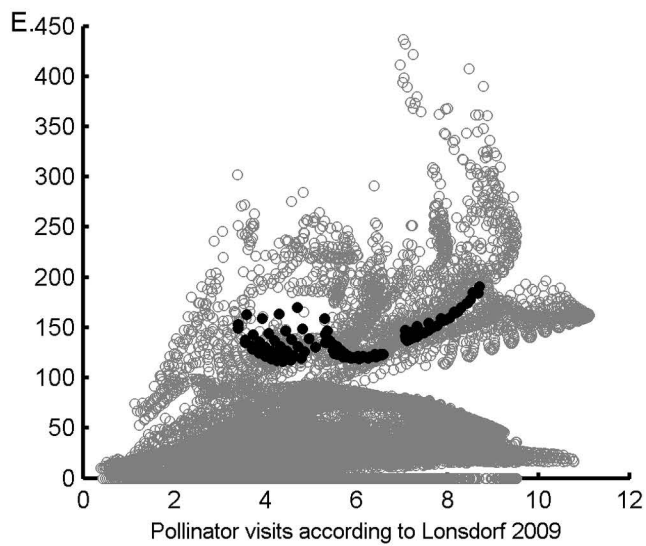
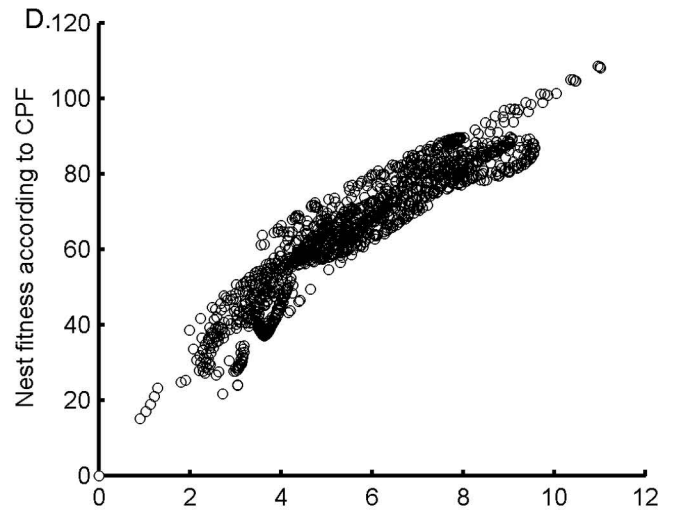
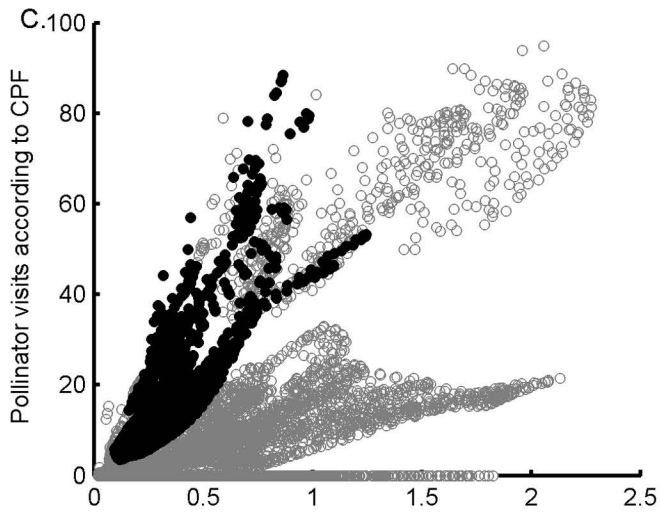
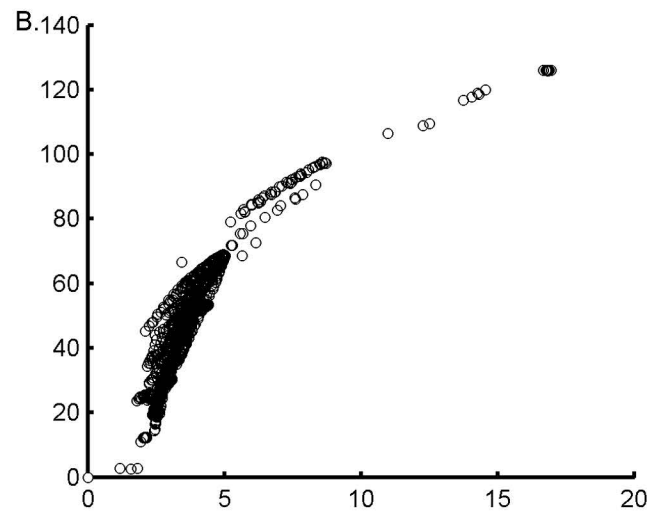
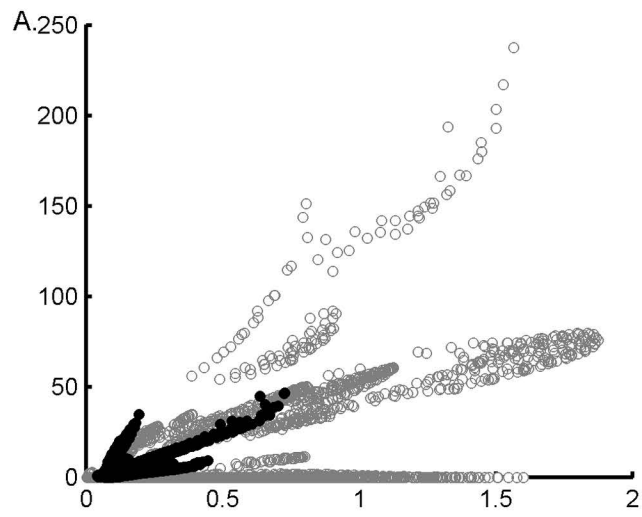


Fig. 4

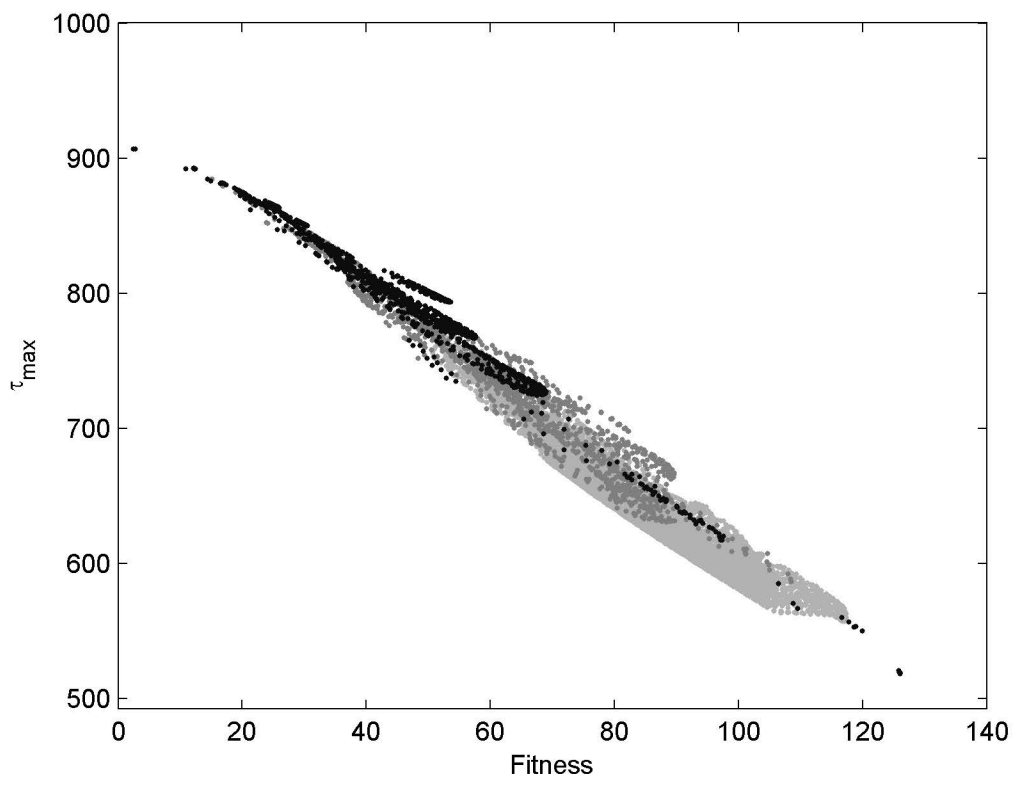


Fig. 5

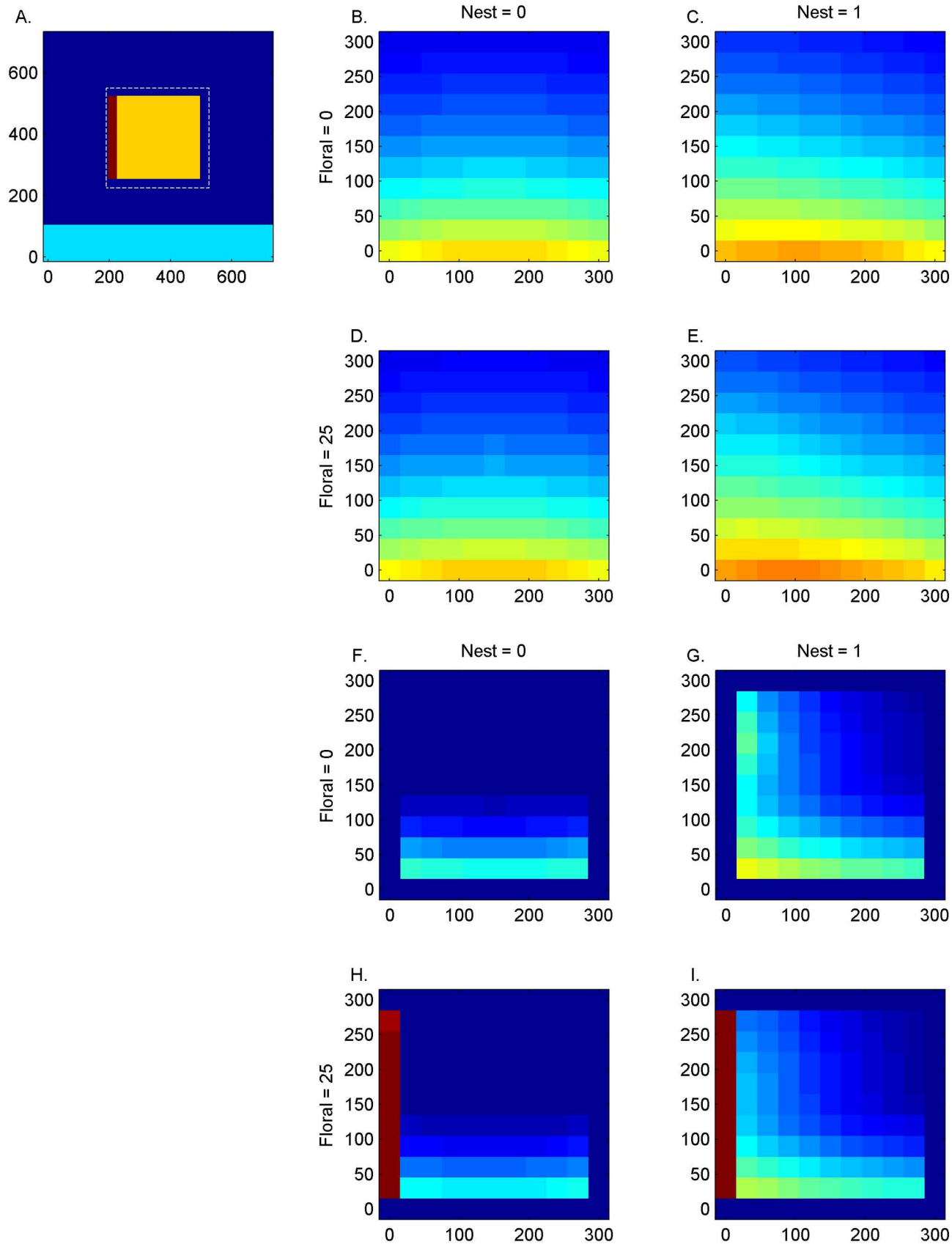


Fig. 6

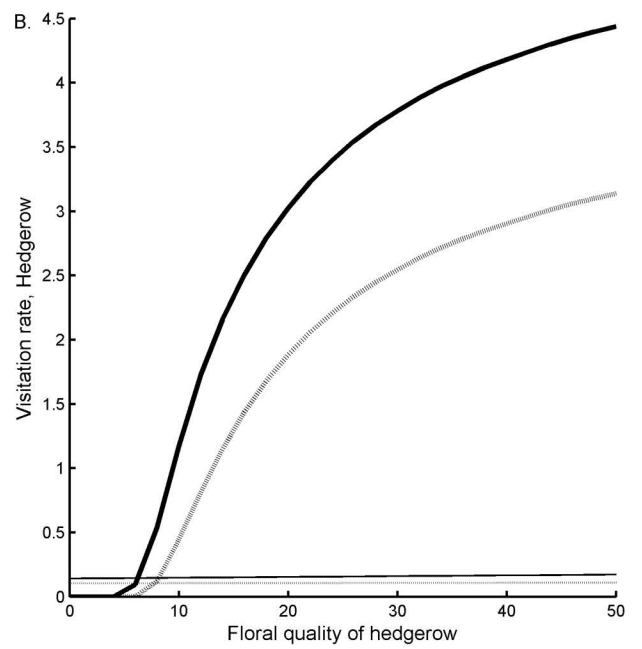
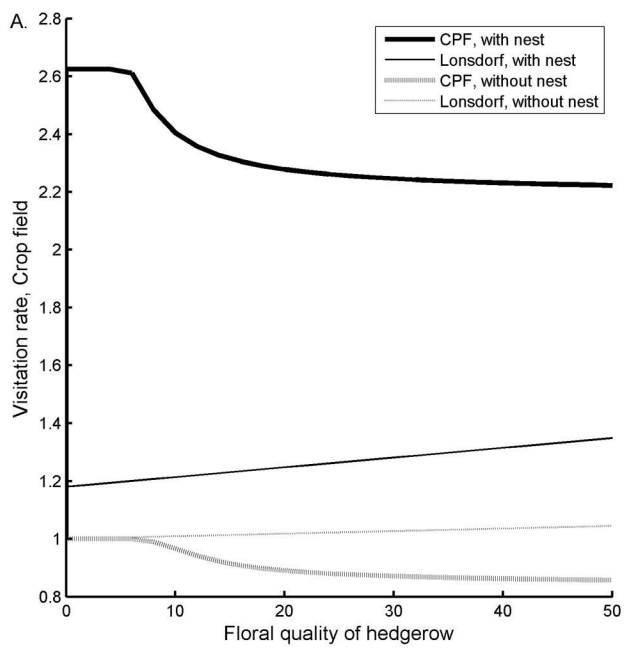


Fig. 7