

Spatial autocorrelation in honeybee foraging activity reveals optimal focus scale for predicting agro-environmental scheme efficiency

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ABSTRACT

A substantial honeybee decline is being observed worldwide. Agricultural intensification and loss of wild floral resources rank among the main factors contributing to this decline. Landscape enhancement of floral resources has been proposed as an agro-environmental scheme intended to provide honeybees with compensatory food sources in intensive agrosystems. Floral scheme efficiency has rarely been evaluated with respect to landscape context. In this study, we developed and validated a modeling tool to delineate the landscape areas likely to be associated with higher efficiency of floral enhancement schemes. In particular, the proximity of some landscape elements used by honeybees, either as foraging habitat or as visual landmark for orientation, may partly determine floral scheme efficiency. We investigated this issue using resource selection functions (RSFs), i.e. models that aim to predict the occurrence of foraging honeybees at floral patches as a function of the presence of keystone landscape elements in their proximity. However, deciding which landscape elements are effectively *in the proximity* or not is mostly a matter of subjectivity. The novelty of our approach resides in its use of a distance-weighting function to explicitly account for the spatial location of surrounding landscape elements. In that respect, a distance function should be scaled on movement patterns of foraging organisms. Herein, we inferred movement patterns from the autocorrelative properties of honeybee foraging activity. This modeling approach was developed on *Phacelia (Phacelia tanacetifolia)* field margin strips, a typical “honeybee-friendly” floral scheme. A foraging survey conducted on 170 *Phacelia* plots (2 m × 2 m) from 17 *Phacelia* strips, all positioned within the foraging range of an experimental apiary, revealed that (i) the floral scheme efficiency is positively influenced by the presence of linear landscape elements such as hedgerows and forest edges, but negatively affected by the presence of alternative floral resources, and that (ii) weighting the relative importance of those landscape elements by incorporating a distance function into models considerably improved their predictive power. This modeling tool has the potential to help land managers optimizing their financial investment by avoiding low-efficiency landscape areas, or favoring high-efficiency ones, at the time of planning floral enhancement schemes.

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1. Introduction

Agricultural intensification leads to the degradation and loss of natural habitats as well as food sources for bees. This is now

recognized as one of the major threats to these important pollinators, as reviewed by a growing body of literature (Steffan-Dewenter and Tscharntke, 1999; Kremen et al., 2002; Biesmeijer et al., 2006; Murray et al., 2009; Potts et al., 2010). To counteract the decline of honeybees, *Apis mellifera* L., as well as that of wild bees in intensive agrosystems, various agro-environmental schemes have been proposed and evaluated (Dicks et al., 2010). Among them, bee conservation may be promoted through landscape enhancement of floral resources (Decourtye et al., 2010). These include the use and management of some flowering crops, floral cover plants and fallows or sown field margins and roadsides. Agro-environmental schemes in general (Kleijn et al., 2006), and those for bees in

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particular (Dicks et al., 2010), have shown variable levels of efficiency per se. However, their efficiencies have seldom been evaluated with respect to landscape context (Heard et al., 2007).

Landscape context typically refers to the degree of landscape structural complexity, ranging from intensive, simplified, crop monoculture areas to complex areas with greater amounts of semi-natural habitats (e.g. Steffan-Dewenter and Kuhn, 2003). Theory predicts that environmental schemes may have a greater impact in simple landscapes than in complex ones (Tscharntke et al., 2005) but empiric evidence are still scarce. Assessing the effect of landscape context on the efficiency of environmental schemes requires thorough modeling approaches capable of simulating animals' distribution under different landscape management scenarios. Among the large array of landscape modeling approaches being currently developed (Gaucherel and Houet, 2009; Buckley et al., 2010; Ferrier and Drielsma, 2010), resource selection functions (RSF) are particularly well suited for that purpose. RSFs are functions returning predictive values proportional to the probability of resource use by an organism (Manly et al., 2002; Boyce et al., 2002). Resource units may be either discrete elements or more generally map pixels. As an artificial resource unit, floral enhancement schemes for honeybees can be analyzed within the frame of a RSF approach, and this is the focus of our study.

RSFs may be obtained by modeling resource use as a function of landscape predictors by the mean of generalized linear models (GLMs) or related models (Boyce et al., 2002). Determining a priori relevant landscape predictors is one critical step in the procedure. Current literature on bee landscape ecology indicates that various landscape elements have the potential to influence bee foraging activity at a given resource patch. In particular, hedgerows, forest margins and other linear landscape elements may be used as visual landmarks by bees to direct their flight path and to relocate food sources (Chittka and Geiger, 1995; Dyer, 1996; Dyer et al., 2008). As such, linear landscape elements are generally considered to promote landscape connectivity (Taylor et al., 1993), i.e. to facilitate movement of organisms among their resource patches by forming flight corridors (Townsend and Levey, 2005; Van Geert et al., 2010). Accordingly, wild bee abundance and diversity in agricultural areas is locally enhanced by the presence of high-quality natural habitats in the close vicinity (<150 m to about 1 km, Kohler et al., 2008; Ricketts et al., 2008; Krewenka et al., 2011) and those areas are probably more suited for introducing floral enhancement schemes.

Yet, these expected patterns are not always supported by empiric observations made on particular bee species. Bumblebees, for instance, tended to be more abundant at floral enhancement schemes located in areas with high proportions of arable land (Heard et al., 2007). Likewise, experimental flower patches attracted fewer honeybees when implanted in landscapes characterized by a higher amount of semi-natural habitats (field and forest margins, hedgerows, fallows and extensive grasslands) within a 3-km radius (Steffan-Dewenter et al., 2002). This suggests honeybees and bumblebees actually compensate for the lack of natural resources in simplified landscapes by making a disproportionate use of floral schemes.

Bee foraging activity at floral schemes thus appears to be driven by a complex interplay between behavioral processes acting at different spatial scales. While navigation skills are influenced by visual landmarks at the perception scale (several tens of meters) resource selection may vary at the home range scale (hundreds of meters or more, Zurbuchen et al., 2010) depending on spatial patterns of resource availability. Therefore, any RSF aiming at predicting the efficiency of floral schemes as a function of landscape context should take into account possible scale dependency effects. By scale dependency, we refer to situations where RSFs return different predictions depending on the focus scale at which landscape predictors are calculated.

Scale is considered as a major issue in the context of RSFs and should be explicitly explored or taken into account in models (Boyce, 2006). Following current landscape modeling practices, scale dependency may be fixed simply by focusing on a functional scale, i.e. a scale that makes sense from an ecological perspective (e.g. home range size, movement abilities, foraging or dispersal distances). This however implies a subjective prior guess of the optimal scale. For that reason, landscape ecologists often choose a suite of spatial scales to figure out the optimal one. To do so, landscape predictors are calculated over a series of concentric buffers or rings (Rhodes et al., 2009), and the corresponding candidate models are further selected using criteria derived from information theory (e.g. Akaike Information Criterion AIC, Anderson et al., 2001). This, however, requires the handling of large quantities of non-independent candidate predictors or models. By doing so, investigators go against model parsimony requirements and expose themselves to increased risks of misleading statistical inference.

Recently, Forester et al. (2009) have proposed to incorporate models of individual movement into RSFs in order to explicitly account for scale dependency, while keeping models as parsimonious as possible. The basic reasoning behind is that the probability of an animal moving from one location to another decreases with distance between those locations. This decreasing function of distance can be used to attribute a greater weight to landscape elements located close to a given resource patch, relative to those located farther away, when measuring landscape predictors (Henry et al., 2007). Such distance-weighting functions scaled on animals' movements have been actually used in a variety of spatial modeling contexts and under different names, but with fundamentally similar meaning. Analogous terminology includes *dispersal kernel* (Moilanen, 2004), *patch accessibility function* (Heinz et al., 2005), *movement distance probability* (Rhodes et al., 2005), *individual dispersal function* (Klein et al., 2006) or *neighboring function* (Henry et al., 2007).

The main objective of our study was to develop a RSF for honeybees with the aim of delineating landscape contexts likely to be associated with higher efficiency of floral schemes in an intensive agricultural system. By floral scheme efficiency, we refer to the amount of honeybees foraging at floral schemes. Specific objectives where (i) to derive a distance-weighting function scaled on honeybee movements, and (ii) to test whether incorporating the distance-weighting function in a RSF effectively delivered better predictions than unweighted RSFs – i.e. RSFs assuming the probability of movement between resource patches is independent from distance.

In practice, data on movement patterns are needed to set distance functions. However, due to their small size and high mobility, flying insects are extremely difficult to track while foraging. Therefore, we explored and compared two analytic alternatives to infer on honeybee probability of movement among resource patches. First, we modeled the spatial autocorrelation in honeybee foraging activity as a proxy of movement probability. Indeed, the use of a given resource patch by honeybees is likely to be influenced by the foraging activity generated at neighboring patches. For instance, scouting honeybees may have greater chance to find new food sources close to already known foraging patches. Likewise, recruited foragers may expand their foraging activity around the target patch initially indicated by scouting honeybees, either through spatial drift of foraging activity, imprecision in patch relocation, or trap-lining behavior (Lihoreau et al., 2010, 2011). Such inter-patch movements actually lead to spatial dependency among neighboring resource patches, i.e. spatial autocorrelation in honeybee foraging activity. Therefore, we assumed that the autocorrelative properties of foraging activity would give back insights on how inter-patch movements relate with distance. In a

second approach, we derived a distance function from literature data on honeybee orientation flights (Capaldi et al., 2000). Orientation flights are the first flights processed by honeybees before they become foragers. They permit honeybees to learn the relative position of the hive and surrounding landscape elements under the form of a mental map (e.g. Menzel et al., 2005). Therefore, we thought orientation flights would merely reveal the spatial extent over which honeybees may perceive and move among surrounding landscape elements while foraging, including resource patches.

To investigate these spatial issues, we used field margin strips of Phacelia (*Phacelia tanacetifolia*) as experimental resource patches, and we measured honeybee foraging activity at those patches. Phacelia is one of the most attractive plants used in honeybee compensatory floral resource schemes (Carreck and Williams, 2002; Decourtye et al., 2010).

2. Method

2.1. Modeling approach and data collection

We used an empiric modeling approach whereby a response variable, honeybee foraging activity on Phacelia, was modeled as a function of landscape predictors. Following previous RSF studies (Boyce et al., 2002), we used estimates of resource availability within a given radius as landscape predictors of the occurrence of honeybees in a Phacelia patch located at a particular point of the space (or map pixel). The novelty of our approach actually resides in its use of distance-weighted landscape predictors, whereby the relative importance of surrounding resource units is weighted against distance to the considered Phacelia patch. The modeling procedure was achieved in three main steps (Fig. 1), further detailed thereafter.

2.1.1. Study area and experimental setup

The study was carried out in a 150-ha area managed by the ARVALIS Institute for applied research on agriculture (48°19'39"N, 2°22'58"E, Boigneville, France). This site is characterized by intensively managed agricultural land with annual crops and patchily distributed fragments of forest and semi-natural habitats, representing a typical land use system of Northern France. Two components were required in the experimental setup: an apiary to ensure an adequate honeybee activity in the environment, and field margins sown with Phacelia to provide honeybees with a rich nectar and pollen source.

The apiary was made up of 10 honeybee colonies (*A. mellifera* L.) of approximately 30,000 individuals. Colonies were raised in spring from artificial swarms and 2-year-old, mated queens obtained from a professional beekeeper. All queens had the same mother and were mated at the same queen mating station. Colonies were in 10-comb Dadant hives (five brood combs, three honeycombs and two empty combs). Hive entrances were facing south and placed downwind from a woodlot edge. Honeybee activity at colonies was monitored daily before the experiment started to ensure no abnormal mortality occurred. Additionally, colony health conditions were monitored monthly by a routine check of a professional beekeeper several times during the study (June–July).

All experimental Phacelia strips were sown within a 2-km radius from the apiary. This distance potentially covers most of honeybee foraging ranges (Steffan-Dewenter and Kuhn, 2003). To support colonies, a total of 600-m long × 2-m wide Phacelia strips was sown (seed density = 10 kg/ha), but honeybee foraging activity was actually monitored over seventeen 20-m long strips, i.e. a subset of about 57% of the total sown surface (see below). Monitored strips were located about 20–1700 m apart from each other. This large

range was chosen so that we could adequately cover the spatial autocorrelative properties of honeybee foraging activity.

2.1.2. Response variable: honeybee foraging activity on Phacelia

Phacelia RSF was assessed using honeybee foraging activity. To this end, honeybees were counted twice a day – weather permitting (10–13 h and 14–17 h) on 10 adjacent, 2m-long, fragments on each of the 17 Phacelia strips. This led to 26 series of 170 honeybee counts (17 strips × 10 plots per strip) realized during 16 days and covering the whole flowering period (10 June to 6 July 2010). No count was made during windy, rainy or cold days (maximum temperature <15 °C). Counts on Phacelia strips were performed by the same observer over the whole study, and in an order randomized everyday.

The response variable was the mean number of honeybees counted on a per Phacelia plant basis during the whole study period. This was calculated as the ratio of all honeybees counted on a given plot over the whole study period, divided by the number of Phacelia plants occurring in that plot. The resulting foraging activity values, expressed in honeybees × plant⁻¹, were treated as an indicator of the efficiency of Phacelia strips as a compensatory floral resource for honeybees.

2.2. Modeling step 1: attributing resource availability scores to land cover classes

2.2.1. Land cover characterization

All landscape elements were mapped within a 2-km radius around the apiary, using a GIS program (ArcView 9.3.1, ESRI Inc.). We distinguished seven different land cover classes: (i) Phacelia strips, (ii) flowering crops visited by honeybees during the study period, (iii) flowered grasslands and fallows, (iv) hedgerows, (v) woodlots and forested habitats, (vi) woodlot and forest edges, (vii) the remaining agricultural matrix, supposedly unfavorable to bees, mainly cereal fields. There was no other Phacelia strip than the experimental ones in the area.

For the need of the modeling, the study map was exported as an ASCII raster map of 10 m × 10 m resolution. In the rasterization process, landscape units (i.e. map pixels), were assigned to the dominant habitat they covered (*flowering crop, flowered grassland and fallow, forested habitat or agricultural matrix*) or to the dominant linear element they intersected (*Phacelia strip, hedgerow or forest edge*).

2.2.2. Estimating land cover resource scores

The computation of RSF landscape predictors required we attribute resource scores to each of the seven land cover classes defined previously. Resources were interpreted in three ways. First, we scored land cover classes based on food resource availability for honeybees, as defined by food occurrence probability in map pixels. By definition, flowered land cover classes (*Phacelia strip, flowering crop, flowered grassland and fallow*) were coded “1”. The *agricultural matrix* class (cereals and non-flowering crops) was coded “0”. The other land cover classes (*hedgerow, woodlot and forested habitat, and woodlot and forest edge*) received intermediary scores based on field surveys of wild flowering plants used by honeybees, according to expert knowledge (Odoux et al., 2005). For that purpose, large flowering plants (trees and shrubs) or flowering patches of at least 2-m in diameter were censused within large parts of the study area during two whole days. Those surveys indicated, for instance, that 26% of *hedgerow* map pixels contained flowering resources (see Table 1 in results).

Second, we thought after an alternative land cover score for food resource availability, scaled on honeybee foraging preference, i.e. the effective contribution of land cover classes to colony diet. Diet composition was assessed from the pollen brought by colonies. The

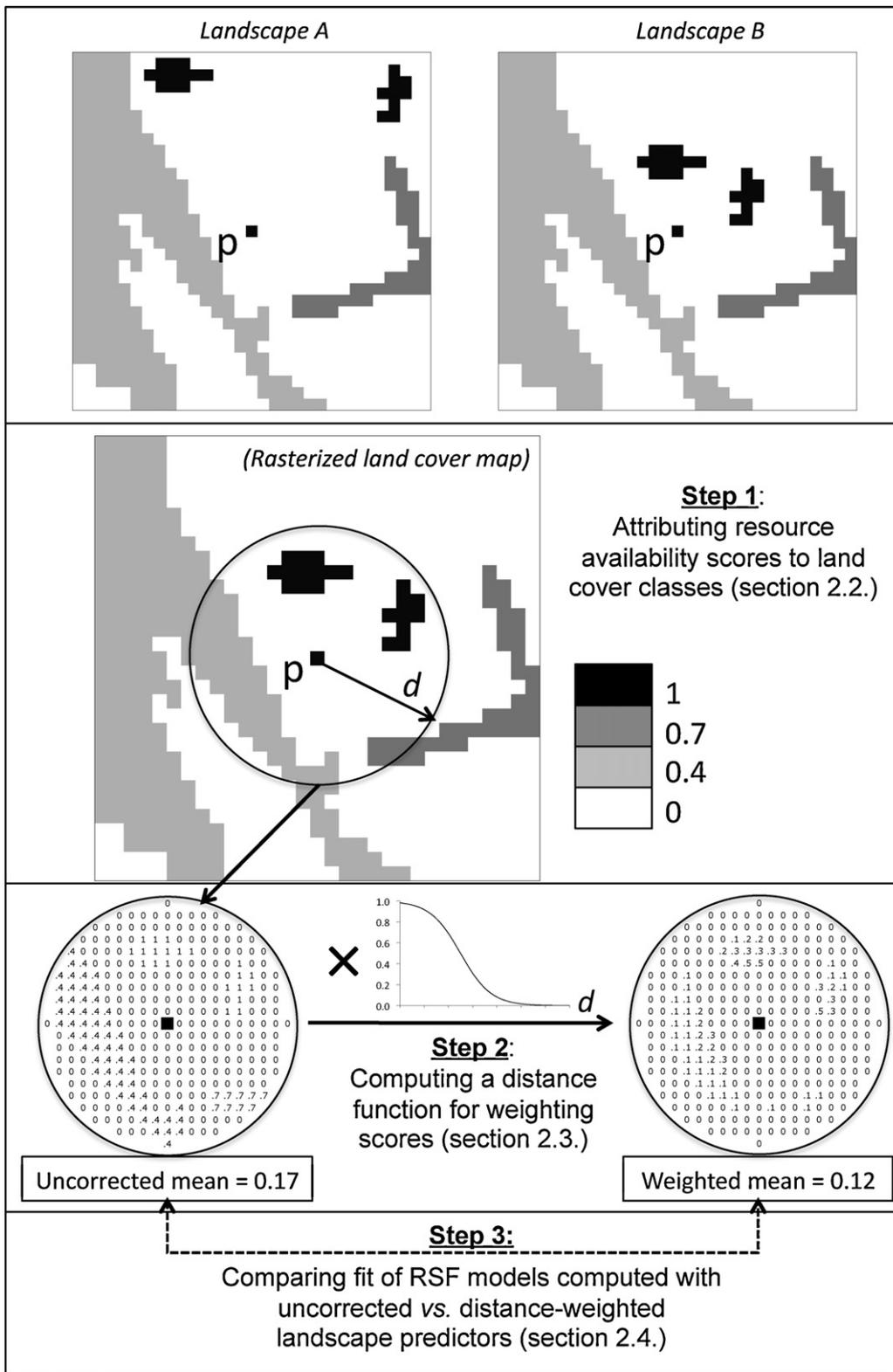


Fig. 1. Conceptual diagram of the modeling procedure. Virtual landscapes A and B have equal habitat composition, but high quality habitats in black are more likely to influence honeybee foraging activity at a Phacelia patch p in landscape B due to their closer position. A modeling procedure was developed in three steps to account for position effect. In a first step, land cover classes were mapped over the study area and assigned a score describing the quality of the resource they provide. Second, a distance function $C(d)$ was computed to weight resource scores as a function of their proximity to monitored Phacelia patches. For a given Phacelia patch p , the weighted mean gave the value of the landscape predictor we used in RSF models. Notice the distance function may return rather large adjustments of predictor values (in this example, 0.12 vs. 0.17). Third, we applied usual model selection procedures to assess whether landscape predictors delivered better fit to data when they incorporate a distance-weighting function.

Table 1
Resource scores attributed to each land cover class for the calculation of landscape predictors.

Land cover class	Food resource availability based on probability of occurrence within map pixels	Food resource availability based on percentage contribution to pollen diet volume ^a	Visual landmark resource
Phacelia strips	1	0.14	0
Flowering crops	1	0.20	0
Flowered grasslands and fallows	1	0.30	0
Hedgerows/woodlot and forest edges	0.26/0.91	0.25 ^b	1
Woodlots and forests	0.05	0.11	0
Agricultural matrix	0	0	0

^a See Appendix C for percentage contributions detailed by pollen species, as well as species assignments to land cover classes.

^b Hedgerow class and woodlot and forest edge class received the same food resource score because they held the same flowering plant resources – though these plants were about three times less abundant in hedgerows.

entrance of three beehives was fitted with pollen traps. This device is composed of a series of small openings through which returning foragers are forced to crawl. A portion of honeybees loses pollen loads while entering the beehive. Pollen traps were left for three complete weeks covering the Phacelia full bloom. Their contents were collected every week and mixed among colonies (see Appendix C for an illustration). The species composition of homogenized pollen mixtures was then established following a pollen identification routine developed by JFO and colleagues (Odoux et al., 2005). A 1-g sample was taken from each pollen mixture and diluted in distilled water. One droplet per sample was then colored and mounted on a microscope slide for pollen identification based on shape, size and texture. Species composition was calculated from subsets of 600 to >1300 pollen grains per sample, and later averaged among the three sampling dates. To set land cover scores, pollen species were assigned to land cover classes using the following rules: Phacelia pollen was assigned to the *Phacelia* land cover class, pollen from trees to the *woodlot and forest* class, pollen from flowering crop species to the *flowering crop* class, pollen from wild herbaceous plants to the *flowered grassland and fallow* class, pollen from shrubs and climbing plants to the *hedgerow* class and to the *woodlot and forest edge* class. The two later classes shared the same score because field surveys have shown they held the same plant resources (though in different abundance). The percentage contributions of pollen species to total diet were summed within land cover classes to get the final land cover scores. Percentages based on pollen grain numbers are subject to strong biases because pollen grain size, and therefore the amount of grains contained in a single pollen load, may vary substantially among species (10–60 μm in diameter), leading to an overrepresentation of flower species producing many small grains compared to large-grained species. Therefore, we preferred expressing species composition in percentage of total pollen volume, using pollen grain dimensions.

In a third approach, we scored land cover classes based on the availability of visual landmarks as resources for orientation by honeybees (Chittka and Geiger, 1995; Dyer, 1996). Structurally homogeneous landscape elements were coded as “0”, while hedgerows and forest edges were coded as “1” because we assumed these were the only elements honeybees could use as visual cues for orientation in the study area. Indeed, these were the only elements ensuring structural breaks in the openfield system.

Once resource scores had been attributed to each land cover class, landscape predictors could be calculated for each Phacelia plot. For a given plot, the landscape predictor was calculated as the mean resource score among all landscape units located within a given radius. For those predictors assuming uniform accessibility of resources within the radius, we used a simple arithmetic mean. For those predictors assuming distance-dependant accessibility of food resources, we used a weighted mean whereby the score of a given pixel was weighted as a function of its distance to the focal Phacelia plot. We called the later values “distance-weighted”

landscape predictors. The challenge resides now in the definition of the distance-weighting function.

2.3. Modeling step 2: computing a distance function for weighting scores

2.3.1. Distance function computed from spatial autocorrelation structure

By definition, the distance function sets the probability of movement between resource patches as a function of distance between these patches. It may also be interpreted as an indication of the accessibility of a given landscape unit as a function its distance to the current location of the animal (Henry et al., 2007; Forester et al., 2009). We based our distance function on the autocorrelation structure of honeybee foraging activity. Herein, autocorrelation measures the extent to which honeybee foraging activity at one particular Phacelia plot was influenced by other plots located at a given distance. As such it merely reveals the ability of honeybees to move among landscape units or resource patches as a function of the distance to cover.

To reduce as much as possible field biases at this stage, we used a simple marking technique that specifically identified honeybees from our apiary. We used honeybee mass-marking devices (Frankie, 1973; Howpage et al., 1998) disposed at the entrance of seven of our 10 experimental hives (see Appendix C for an illustration). At each passage through the marking device, individuals received a small amount of red fluorescent powder. The bright color allowed for a rapid, unambiguous, identification of individuals originating from the experimental apiary during foraging surveys. The autocorrelation analysis was performed on *marked* foraging honeybees only for two reasons: (i) it ensured all bees counted on the field actually originated from the same place, and therefore it fixed any statistical noise possibly generated by other undetected apiaries in the environment, (ii) it ensured greater independence between the foraging datasets used for calibrating the distance function on one hand (marked honeybees only), and for the final landscape models on the other hand (all honeybees).

The spatial autocorrelation structure of *marked* honeybee foraging activity was modeled using the generalized least square (GLS) function available in the *Linear and Nonlinear Mixed Effects Models* package (NLME) of the R statistical software (R Development Core Team, 2008; Pinheiro et al., 2010). GLS allows to fit models with autocorrelation error structure. To isolate autocorrelation per se in foraging activity data, no landscape predictor was specified in the GLS model, but only a null model formula and a spatial correlation structure. Then, following Zuur et al. (2009), we tried different correlation structures (Gaussian, spherical, exponential or rational quadratic), computed either with or without nugget effect. In spatial modeling jargon, a nugget effect occurs when the variance among theoretic measurements taken at the same location (zero distance) remains positive due to statistical noise. We used the AIC to figure out which spatial model would best account for spatial

autocorrelation (Anderson et al., 2001; Burnham and Anderson, 2002). AIC is a model selection criterion derived from information theory. Its calculation is based on likelihood and is intended to help model selection based on a tradeoff between model fit to data and model complexity. Models with the lowest AIC receive the greatest statistical support given fit to data. Complex models that incorporate many predictors have penalized AIC. Additionally, model selection uncertainty was assessed using AIC weights W_i , i.e. the probability that a given model i is the best candidate in the model set. Foraging activity data were normalized using a log-transformation prior to analyses.

2.3.2. Distance function computed from literature data

We sought after an alternative manner of computing a distance function, completely independent from our field data. For that purpose, we used orientation flight distances provided by Capaldi et al. (2000) as an indicator of the most relevant spatial scale for honeybee orientation, and thus for scaling the distance function that describes movement probabilities among resource patches or landscape units. Orientation flights range from 9 to 314 m with a median at 58 m (Capaldi et al., 2000). Therefore, we set the distance function to reach a maximal value, a minimal value, and an intermediate value at these three distances, respectively. For that purpose, we fitted a distribution function to these three distances values (see Appendix A for calculation details).

2.3.3. Uncorrected landscape predictors

To assess whether distance-weighted predictors perform better than predictors assuming uniform resource accessibility, we produced a series of uncorrected landscape predictors. Landscape predictors were calculated around Phacelia plots as simple (unweighted) means of resource scores within a fixed radius. We selected two radius values that we thought could be most relevant from a functional perspective. First, 60 m as an estimation of maximal distance over which a flying honeybee may detect landscape elements. Second, 600 m as the distance over which autocorrelation of foraging activity fell to zero (see Section 3).

2.4. Modeling step 3: computation and comparison of RSF models

RSFs consisted in modeling total honeybee foraging activity at Phacelia plots as a function of landscape predictors, i.e. visual landmark and food resource scores around plots. For that purpose, we computed an autoregressive GLS models, as described above, and introduced a combination of landscape predictors as explanatory variables.

In order to keep models parsimonious and ecologically relevant, we favored simple model structures with only one or two landscape predictors introduced at a time. Three models were computed with each of the three landscape predictors taken separately, namely (i) the availability of visual landmark resources, (ii) the availability of food resources scaled on probability of occurrence in map pixels or (iii) the availability of food resources scaled on the percentage contribution to pollen diet volume. Additionally, two models were set to combine the visual landmark predictor on one hand, and one of the two food resource predictors on the other hand.

These five basic model structures were reiterated with the two series of distance-weighted landscape predictors (distance function scaled on autocorrelation data or on literature data) and with the two series of uncorrected landscape predictors (60 and 600 m radii). The resulting 20 candidate models were sorted based on fit and complexity using AIC (Anderson et al., 2001; Burnham and Anderson, 2002). The AIC-based selection allowed determining whether distance-weighted predictors perform better than uncorrected predictors in predicting honeybee foraging activity at Phacelia strips. We also computed a null model, i.e. a model with

an autocorrelative structure maintained but without any landscape predictor specified. The null model was intended to further grade candidate models against the scenario of random foraging activity.

3. Results

3.1. Honeybee foraging activity on Phacelia

A total of 8976 foraging honeybees were counted on the field, among which 2540 (28.3%) were marked honeybees from the experimental apiary. Foraging activity in a given plot ranged from 6 to 130 honeybees per ten Phacelia plants (median = 38.8). Bumblebees were also abundant, but they mostly occurred during the second half of the blooming period, while honeybee foraging activity decreased in Phacelia strips.

3.2. Land cover resource scores

Final resource scores attributed to the seven land cover classes are summarized in Table 1. Flowered classes set apart, *woodlot and forest edge* was the class offering the greatest amount of food resources, with on average 91% of map pixels containing flowering plants or patches according to field surveys. Similar plant species assemblages were found in the *hedgerow* class, but at a rate about three times lower (26%), while *woodlot and forested habitat* class was estimated to offer resources in only 5% of the map pixels. Resource availability scores scaled on percentage contribution to pollen diet volume delivered much more balanced scores, ranging from 11% (*woodlot and forest habitat* class) to 30% (*flowered grassland and fallow* class). On average, Phacelia accounted for 14% of total pollen volume brought by colonies, but its contribution peaked at 32% during the third pollen sampling period (Appendix B).

3.3. Distance function computed from spatial autocorrelation structure

Bee foraging activity values expressed a strong spatial autocorrelation. All GLS models computed with an autocorrelation error structure returned much greater fit to data than the null model (Table 2). None of the candidate models attained an AIC weight convincingly higher than the others (all $W_i < 50%$), meaning that we are not quite sure about which one is the best model in the set. Therefore, we defined a 95% confidence set, i.e. the model set that totalizes 95% of probability of including the best candidate model, as indicated by accumulated AIC weights W_i . The three

Table 2

AIC-based selection of the best candidate autoregressive models of honeybee foraging activity. Models are ranked by order of decreasing AIC. The best candidate models, i.e. models delivering the best tradeoff between fit and complexity, have the smallest AIC values and a $\Delta_{AIC} < 2$ (AIC difference with the best model). AIC weight W_i gives the probability that model i is the best model in the set. The null model (no spatial autocorrelation assumed) is far less supported than all other models. Models without nugget effects received much less support than complete models ($\Delta_{AIC} \gg 4$). The first three models totaled altogether an AIC weight of about 95%, and therefore were taken to constitute the 95% confidence set of best models.

Rank	Autocorrelation function	Nugget effect	df	AIC	Δ_{AIC}	W_i
1	Spherical	Yes	4	-19.32	0.00	0.497
2	Exponential	Yes	4	-18.95	0.37	0.413
3	Ratio	Yes	4	-14.90	4.42	0.054
4	Gaussian	Yes	4	-14.03	5.29	0.035
5	Exponential	No	3	37.34	56.66	0.000
6	Spherical	No	3	45.33	64.65	0.000
7	Ratio	No	3	104.96	124.28	0.000
8	Gaussian	No	3	167.08	186.40	0.000
9	No (null model)	No	2	299.03	318.35	0.000

models retained in the 95% confidence set were, by order of decreasing fit to data: the spherical, the exponential and the rational quadratic error—all including a nugget effect. The level of spatial autocorrelation predicted by these three models is given by Eq. (1), Eq. (2) and Eq. (3), respectively (Pinheiro et al., 2010):

$$C_{sph.}(d) = (1 - n) \times \left(1 - 1.5 \times \left(\frac{r}{d} \right) + 0.5 \times \left(\frac{r}{d} \right)^3 \right) \quad (1)$$

$$C_{exp.}(d) = (1 - n) \times e^{-(r/d)} \quad (2)$$

$$C_{rat.}(d) = \frac{1 - n}{1 + (r/d)^2} \quad (3)$$

where d is the distance (m) among observation plots, n is the nugget effect ($n = 0.102, 0.098$ and 0.139 , for $C_{sph.}$, $C_{exp.}$ and $C_{rat.}$, respectively), and r is the spatial autocorrelation range (403, 261 and 83 m, respectively). As each of these three models bears a certain degree of uncertainty, we actually derived an average autocorrelation function from their uncertainty-weighted mean, following a multi-model inference procedure:

$$C_{av.}(d) = \frac{W_{sph.}C_{sph.}(d) + W_{exp.}C_{exp.}(d) + W_{rat.}C_{rat.}(d)}{W_{sph.} + W_{exp.} + W_{rat.}} \quad (4)$$

where W_i is the AIC weight of model i (Table 2) and C_i the autocorrelation function of model i , as given by Eqs. (1–3). The resulting $C_{av.}(d)$ distance function (Fig. 2) returns high weighting coefficients for landscape elements located within a 100-m radius, intermediate coefficients within a 100- to 200-m radius, and minimal coefficients beyond 400–600 m.

3.4. Distance function computed from literature data

Our attempt to derive a distance function from literature data (Capaldi et al., 2000) led to slightly different values, though spanning over approximately the same range of distances (Fig. 2). Compared with the autocorrelation-based function, the literature-based function attributes a greater importance to landscape elements located close to the plots (<100 m) relatively to those located farther away (>100 m). Nevertheless, both functions returned minimal values for distances >400 m.

Table 3

AIC-based selection of the best candidate RSF models. Models are ranked by order of decreasing AIC. Each model is given with the corresponding estimates of landscape predictor effects – either obtained from uncorrected mean resource scores within fixed radius or from distance-weighted means. Method indicates whether autocorrelation curve or literature-derived curve was used for distance-weighted models. Null model (no landscape predictor specified, foraging activity assumed to be random) received less support than distance-weighted models ($\Delta_{AIC} > 2$). Abbreviations follow Table 2.

Rank	Focal scale	Method	Intercept	Visual landmark resources	Food resource availability (occurrence probability)	Food resource availability (pollen contribution)	df	AIC	Δ_{AIC}	W_i
1	Distance-weighted	Autocorrelation	-0.40	23.01	-	-5.41	6	7.56	0.00	0.174
2	Distance-weighted	Literature	0.53	9.69	-	-3.84	6	7.75	0.19	0.158
3	Distance-weighted	Literature	0.12	10.18	-	-	5	8.09	0.53	0.134
4	Distance-weighted	Autocorrelation	-0.59	24.67	-6.23	-	6	8.78	1.22	0.095
5	Distance-weighted	Autocorrelation	-0.79	21.27	-	-	5	8.78	1.22	0.095
6	Distance-weighted	Literature	0.30	10.52	-1.91	-	6	9.44	1.88	0.068
7	Distance-weighted	Literature	1.70	-	-	-4.14	5	10.06	2.50	0.050
8	Distance-weighted	Autocorrelation	1.80	-	-	-4.45	5	10.73	3.17	0.036
9	null model	-	1.30	-	-	-	4	10.96	3.40	0.032
10	Distance-weighted	Autocorrelation	1.62	-	-3.37	-	5	11.94	4.39	0.019
11	Uncorrected (60 m)	-	1.41	-	-0.50	-	5	12.05	4.50	0.018
12	Uncorrected (600 m)	-	1.75	-	-5.65	-	5	12.06	4.51	0.018
13	Uncorrected (60 m)	-	1.39	-	-	-0.89	5	12.08	4.52	0.018
14	Uncorrected (600 m)	-	1.50	-	-	-1.49	5	12.15	4.59	0.018
15	Uncorrected (60 m)	-	1.28	0.30	-	-	5	12.17	4.62	0.017
16	Uncorrected (600 m)	-	1.51	-2.31	-	-	5	12.40	4.85	0.015
17	Uncorrected (60 m)	-	1.39	0.73	-0.98	-	6	13.71	6.15	0.008
18	Uncorrected (60 m)	-	1.28	0.82	-	-1.21	6	13.83	6.28	0.008
19	Distance-weighted	Literature	0.96	-	3.22	-	5	13.90	6.34	0.007
20	Uncorrected (600 m)	-	1.95	-4.41	-	-2.21	6	14.07	6.51	0.007
21	Uncorrected (600 m)	-	1.86	4.47	-11.93	-	6	14.33	6.77	0.006

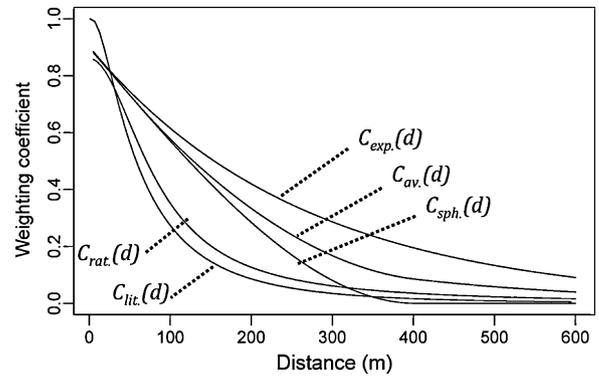


Fig. 2. Distance-weighting functions scaled (i) on exponential, ratio and spherical autoregressive functions ($C_{exp.}$, $C_{rat.}$ and $C_{sph.}$, respectively), (ii) on the weighted average of the three later functions ($C_{av.}$) and (iii) on literature data ($C_{lit.}$).

3.5. Computation and comparison of RSF models

The series of models using distance-weighted landscape predictors, either scaled on autocorrelation or literature data, performed better than those using uncorrected predictors (Table 3). All but one distance-weighted models ranked before uncorrected models. Furthermore, all uncorrected models had an $\Delta_{AIC} > 2$, suggesting that none of them actually received sufficient support to rank among the best candidate models in the set (Anderson et al., 2001; Burnham and Anderson, 2002). Most strikingly, all uncorrected models ranked after the null model, i.e. the scenario of random honeybee activity, while most distance-weighted models ranked before the null model. This clear-cut dichotomy between uncorrected and distance-weighted models is further illustrated by the large evidence ratios in favor of the latter models. Evidence ratios measure the probability that a given model performs better than another one. They can be assessed by the ratio of the corresponding AIC weights W_i . Herein, evidence ratios indicate that distance-weighted models are 5–20 times more likely than uncorrected models.

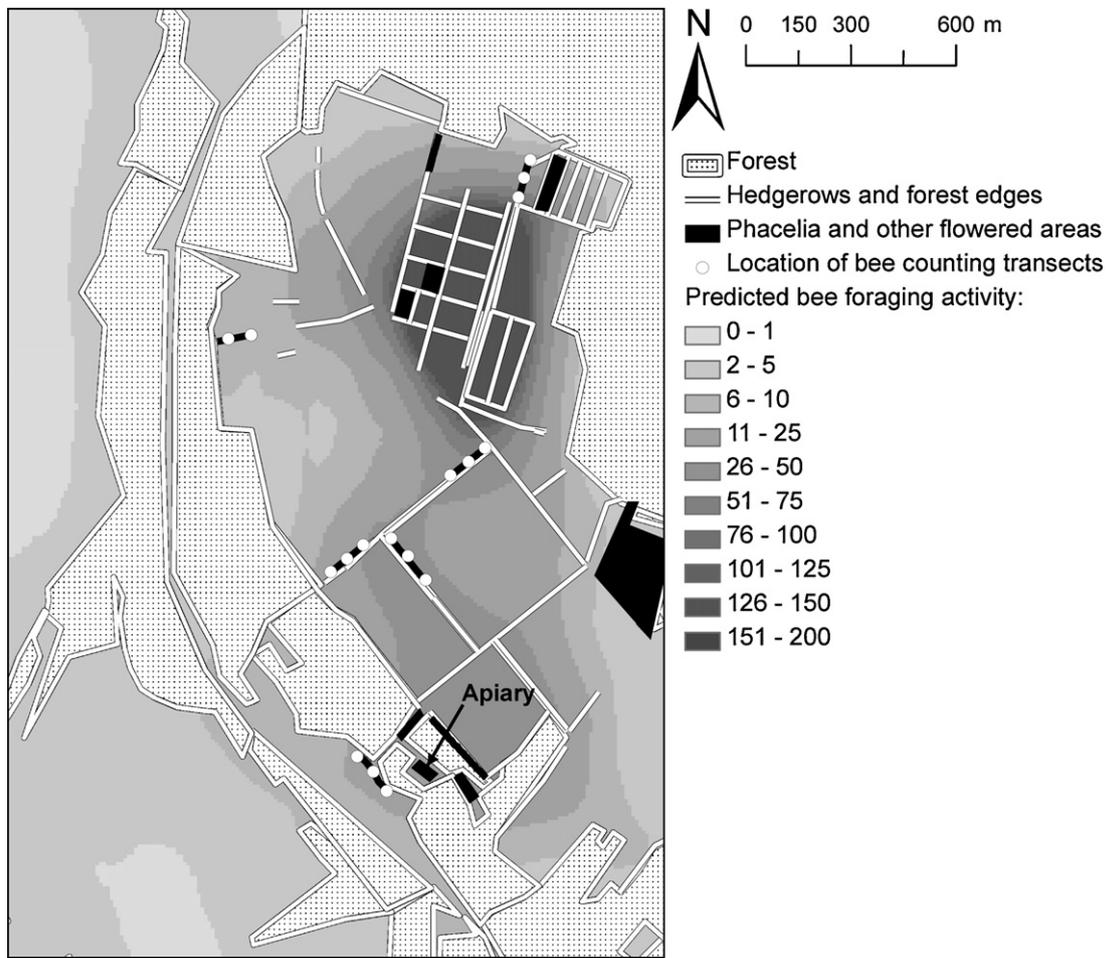


Fig. 3. Spatialization of the best candidate RSF model that predicts honeybee foraging activity on potential Phacelia sowing areas (total honeybee counts per 10 Phacelia plants, following our counting protocol). Notice the non-linear color scale: predictions vary across two orders of magnitude. Experimental Phacelia strips are indicated by narrow black strips; other flowering crops (broad beans, peas) and flowered grasslands and fallows are indicated by large black surfaces.

Model selection results (Table 3) reveal a clear relationship between honeybee foraging activity and distance-weighted landscape predictors. First and foremost, the null model of random foraging activity does not rank among the best candidate models as its Δ_{AIC} falls below the critical limit of 2. Conversely, the six best candidate models ($\Delta_{AIC} < 2$) were about 2–5.5 more likely than the null model, as revealed by evidence ratios of the corresponding AIC weights. Finally, estimates of landscape predictor effects are congruent among the six best candidate models in terms of effect sign. Visual landmark resources had a positive effect on local honeybee activity, while food resources availability had a negative effect.

The best model predictions were mapped over the studied territory (Fig. 3). The resulting map delineates the hot-spot areas where Phacelia strips are supposed to reach their maximal efficiency regarding honeybee foraging activity. Predictions vary across two orders of magnitude, indicating that there is still place for substantial improvement to optimize floral scheme efficiency. To further illustrate this, we compared the outcome of two landscape planning scenarios, namely a random landscape planning vs. a model-based landscape planning. In the random scenario, we randomly positioned Phacelia strips within the landscape (except forested areas). In the model-based scenario, we specifically targeted high-foraging activity areas with predicted foraging activity scores = 100–200 (see Fig. 3). We simulated 100 times the random and model-based scenarios and found average foraging activity scores of 11.1 ± 8.3 and 124.4 ± 17.2 , respectively. In other words, a model-based planning of floral scheme location would be on average 11.2 times

(=124.4/11.1) more efficient than a random planning with no prior guess about the best scheme locations in the landscape.

4. Discussion

First and foremost, it is noteworthy that honeybees effectively used Phacelia strips intensively, which supports the effectiveness of Phacelia strips as an agro-environmental scheme. About 28% of honeybees found foraging on Phacelia were marked individuals from the experimental apiary. Furthermore, up to 32% of pollen volume brought by colonies originated from Phacelia strips (Appendix B). Therefore, Phacelia was among the keystone food resources at that time of the season, while few other mass flowering crops or wild plants were available to bees. Nevertheless, Phacelia plots did vary greatly in their propensity to attract honeybees, with foraging activity spanning an order of magnitude (6–130 honeybees $\times 10 \text{ plant}^{-1}$, mean = 38.8). This variability was partly explained by landscape context. Therefore, model-based landscape planning may efficiently optimize floral enhancement schemes.

The modeling procedure we developed in this study is not a RSF *sensu stricto*. RSFs are intended to produce values proportional to the probability of resource use by an organism (Manly et al., 2002). Resource use is a binary variable (presence/absence) and is usually treated using binomial family models (Boyce et al., 2002). However, all monitored plots in our study were indeed used by honeybees (no absence data) making binomial models inapplicable. Conversely, honeybee foraging activity varied greatly among plots,

and therefore was a more appropriate entry for modeling resource use.

Our results indicate that the use of distance functions substantially improved the quality of models aiming to predict honeybee foraging activity at the Phacelia strips. From an ecological perspective, the distance function can be seen as an economic component that helps accounting for honeybees' foraging decisions when confronted to foraging optimization problems. Honeybees are central place foragers and must return to the colony after each foraging bout. As such, they must maximize their rate of energy intake relatively to the energy expended for reaching foraging sites (Cresswell et al., 2000). As energy expenditure is a linear function of flight distance, the distance function we used is a straightforward way to assign landscape elements a biologically relevant economic value.

When fixing this economic optimization issue by a distance function, the models supported congruent conclusions regarding the efficiency of Phacelia schemes: (i) Phacelia was more attractive when salient visual landmarks were available in the vicinity, but (ii) tended to be less attractive when concurrent floral resources were also present. Salient landscape elements may be used as visual landmarks by honeybees to direct their flight path and to relocate food sources (Chittka and Geiger, 1995; Dyer, 1996; Dyer et al., 2008). Another, not mutually exclusive, explanation may invoke the notion of landscape connectivity. Connectivity measures the extent to which landscape facilitates or impedes the movement of organisms among resource patches (Taylor et al., 1993). Bees in general and honeybees in particular are known to use linear landscape elements as flight corridors (Townsend and Levey, 2005; Van Geert et al., 2010). Therefore, these elements are important components of the landscape and are likely to influence the probability honeybees would use nearby resource patches. The presence of other nearby mass-flowering resources, however, reduced honeybee foraging activity at Phacelia plots. This may be interpreted as a dilution effect, with overall honeybee activity at the local scale being shared among concurrent resources. At the time of the recordings, the main concurrent resources were restricted to several trees and shrubby plants and some small fallows and lots planted with broad beans and peas.

Beyond the gain in model fit per se, the use of a distance function allowed for a more impartial modeling procedure. It actually ruled out the subjectivity one normally introduces when choosing a spatial scale for analyses. Indeed, in our study, the failure of uncorrected models (radius fixed at 60 m or 600 m) illustrates the difficulty of choosing an appropriate spatial scale. Likewise, Steffan-Dewenter et al. (2002) found little effect of landscape context (amount of semi-natural habitats) on honeybee foraging activity in experimental flower patches, with focus scales ranging from 250 m to 3 km. It is possible that an effect of landscape context would have been actually visible at shorter scales. All the distance functions shown in Fig. 2 predict a critical range at about 80–200 m for expecting an effect of neighboring resources or other landscape elements. All distance curves expressed their steepest decreasing slope at this distance range, with weighting coefficients falling below 50% of their initial value. In other words, honeybee foraging activity measured at a given flower patch is expected to be poorly influenced by landscape elements located beyond that distance threshold of 80–200 m.

There is no evidence in favor of one or the other of the two distance functions we used. The best candidate model was obtained with the distance function scaled on autocorrelation data, while the analogous model scaled on literature data ranked second in the list (Table 3). Both received equal statistical support, with very similar AIC and AIC weights. Yet, the two distance functions used in the algorithm differed substantially in their shape (Fig. 2). The literature-based function assigned more weight to landscape

elements located at rather short distances (<60 m) while the autocorrelation-based function assigned more weight to landscape elements located up to 160 m away. Our opinion is that the distance function based on autocorrelation is probably most adapted to our context as it originates from our own field data. Some authors plead for the use of spatial autocorrelation as a tool to derive information on ecological processes and to help setting model parameters (Boyce, 2006). We do share this point of view and encourage the use of spatial autocorrelation data as a paradigm to set the most appropriate focus scale in landscape models.

The distance-weighting approach has nevertheless some limits. First, it is probably sensitive to inaccurate assessment of food resource availability values in semi-natural areas (Table 1). This should be further explored using sensitivity analyses (see Lonsdorf et al., 2009 for a sensitivity analysis in a similar context). In particular, the assessment of food resource availability based on pollen composition is probably subject to strong instability. Composition of collected pollen is known to vary substantially among colonies and weeks. As a consequence, the pollen identification effort required to achieve accurate pollen-based predictors appears somehow prohibitive given the trivial gain in model goodness of fit over simpler predictors (see model ranks 1 and 2 vs. 3 and 4 in Table 1). Second, the distance-weighted models are computationally more intensive and return landscape predictors that may appear difficult to interpret at first glance. A simplified version of this approach may be preferred, whereby the distance function would be replaced by a two-stage weighting strategy. Assuming the median weighting coefficient corresponds to a distance of about 160 m (C_{av} curve in Fig. 2), one may simply assign twice as much weight to landscape elements located close (<160 m) compared to those located farther away (160–600 m). In that respect, the critical inflection point of 160 m actually segregates the area referred to as *local context* from that referred to as *landscape context*.

Regardless the behavioral processes behind, it appeared that the efficacy of the flower enhancement scheme varies substantially with local and landscape context. This issue has been poorly explored to date (Heard et al., 2007). Yet, enhancement of set-aside land may require disproportionate financial investments in some areas – generally where farming practices are intensive (Van Buskirk and Willi, 2004; Kleijn et al., 2009). Therefore, it appears critical to gain a prior knowledge about where in the landscape enhancement schemes are likely to reach maximal efficiency. As an illustration of this, simulations of model-based landscape planning scenarios returned efficiency values 11.2 times greater than simulations of random landscape planning scenarios (see Section 3). Similarly, the overall efficiency of our 600m-long Phacelia sowing scheme could have been increased by a factor of 9–12 simply by moving Phacelia strips by several hundreds of meters each. In other words, one could have reached the same efficiency by expending 9–12 times less financial investments in that floral scheme.

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Appendix A. Computation of a distance-weighting function based on literature data, $C_{lit.}(d)$.

In ecological modeling studies, the accessibility of a given resource patch by an organism located at a particular point in space is usually depicted as a decreasing function of the distance the organism has to cover to reach that patch. Such a function has to be approximated by behavioral data such as movement abilities or perception skills. In the distance-weighting approach as developed by Henry et al. (2007) for frugivorous bats, real flight distance data were used and converted into a decreasing probabilistic form to set the distance function. Herein, we have developed an analogous distance-weighting function, $C_{lit.}(d)$, based on a probability distribution function of flight distances:

$$C_{lit.}(d) = 1 - P(d) \quad (B.1)$$

where $P(d)$ is the cumulative probability distribution function of flight distances. Under this form, $C_{lit.}(d)$ is a decreasing function of distance that returns a value between 0 and 1, giving the probability that an organism will reach *at least* a certain distance d during a given flight. As a cumulative probability function, $P(d)$ can be written as:

$$P(d) = \int_{-\infty}^d p(t) dt \quad (B.2)$$

where $p(d)$ is the probability distribution function of flight distances d . The advantage of this approach over the original method developed in Henry et al. (2007) is that one do not need any complete flight distance dataset, but only simple estimates of flight distance parameters to define $p(d)$ (e.g. mean, standard deviation).

In our study, we used parameters of honeybee orientation flights obtained by harmonic radar technology (Capaldi et al., 2000). Orientation flights are the first flights processed by honeybees. They allow honeybees to learn the relative position of the hive and landscape features. Therefore, we thought orientation flights would merely reveal the spatial extent over which honeybees may perceive and move among surrounding landscape features while foraging.

Orientation flight distances range from 9 to 314 m, with a median of 58 m (Capaldi et al., 2000). We noticed that these flight statistics are compatible with the properties of a log-normal distribution: the logarithm of the median (Eq. (B.3)) approaches the averaged logarithms of maximum and minimum values (Eq. (B.4)).

$$\log(58) \approx 1.76 \quad (B.3)$$

$$\frac{\log(314) + \log(9)}{2} \approx 1.73 \quad (B.4)$$

Therefore, we assumed $p(d)$ is a log-normal probability function of distance d . A log-normal probability function is written as a normal probability function (Sokal and Rohlf, 1994), except that values are log-transformed – see $\log(d)$ within the following formula:

$$p(d) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(1/2)[(\log(d)-\mu)/\sigma]^2} \quad (B.5)$$

where μ and σ are the mean and standard deviation of the log-transformed flight distances d , respectively. The latter parameters were calculated from the log-transformed minimal (9 m), median (58 m) and maximal (314 m) flight distances reported by Capaldi et al. (2000), as follows:

$$\mu = \log(58) \approx 1.76 \quad (B.6)$$

$$\sigma = \frac{CI_{95\%}}{1.960} \approx 0.394 \quad (B.7)$$

where $CI_{95\%}$ is the 95% confidence interval of log-transformed flights distances, and 1.960 is the coefficient linking $CI_{95\%}$ and σ in normally distributed datasets. We considered that the minimal (9 m) and maximal (314 m) distances observed in the field actually set the lower and upper 95% confidence boundaries. Therefore, we approximated $CI_{95\%}$ using a simple difference average between μ and the upper and lower boundaries:

$$CI_{95\%} = \frac{[\log(314) - \mu] + [\mu - \log(9)]}{2} \approx 0.771 \quad (B.8)$$

Once the μ and σ parameters of the probability function $p(d)$ have been established, we used the *pnorm* function of the *stats* package of R software to calculate $P(d)$ (Eq. (B.2)). The resulting distance-weighting function $C_{lit.}(d)$ is graphically represented in Fig. 2. Conformingly to the above-described parameterization, the curve returns a 95% and a 5% score for minimal (9 m) and maximal (315 m) distances, respectively, and an intermediate score of 50% for the median (58 m) distance.

Appendix B. Percentage contributions to pollen diet volume detailed by pollen species, and pollen species assignment to land cover classes. Pollen samples covered 1 week each, evenly distributed during the Phacelia flowering period (June 15–22, June 22–29, June 29–July 06). Averaged volume contributions within land cover classes were used to score food resource availability (Table 1).

Land cover class	Pollen species	Week 1	Week 2	Week 3	Average
Flowering crops	<i>Vicia faba</i>	44.90%	9.05%		
	<i>Pisum sativum</i>	4.12%			
	<i>Sinapis</i> sp.	1.21%	<0.10%	<0.10%	
	<i>Heliantus annuus</i> L.			<0.10%	
Flowered grasslands and fallows	<i>Heracleum spondylium</i>	<0.10%			
	<i>Papaver rhoeas</i>	1.00%	0.12%	0.73%	
	<i>Plantago</i> sp.	5.87%	16.02%	0.59%	
	<i>Reseda lutea</i>	0.40%	0.41%		
	<i>Capsella</i> sp.	0.57%	6.39%	16.74%	
	<i>Carduaceae</i>		0.57%	0.60%	
	<i>Chelidonium</i> sp.		<0.10%		
	<i>Helianthemum</i> sp.	1.43%	0.62%	<0.10%	
	<i>Magnolia</i> sp.	<0.10%			
	<i>Hypericum</i> sp.	0.14%	2.60%	15.43%	
	<i>Ornithogalum</i> sp.	8.30%			
	<i>Potentilla</i> sp.	2.81%	1.06%		
	<i>Rosa</i> sp.		0.26%	0.81%	
	<i>Trifolium</i> sp.	4.70%	<0.10%	1.19%	
	<i>Veronica</i> sp.	0.60%		<0.10%	
	<i>Echium vulgare</i> L.	0.30%	<0.10%		
Woodlots and forested habitats	<i>Castanea sativa</i>		23.77%	8.84%	
	<i>Tilia</i> sp.	0.12%		0.16%	
Hedgerows/forest edges	<i>Bryonia dioica</i> Jacq.	<0.10%			
	<i>Clematis vitalba</i>			0.18%	
	<i>Cornus sanguinea</i> L.	2.35%			
	<i>Sambucus nigra</i> L.	1.87%			
	<i>Rubus</i> sp.	18.19%	22.48%	17.27%	
	<i>Rhus</i> sp.		3.44%	3.05%	
	<i>Ligustrum</i> sp.	0.35%	3.48%	1.10%	
<i>Parthenocissus</i> sp.			1.18%		
Phacelia strips	<i>P. tanacetifolia</i>	0.54%	9.67%	32.12%	
Total contribution per land cover class					
flowering crops		50.23%	9.06%	<0.10%	19.8%
flowered grasslands and fallows		26.14%	28.13%	36.11%	30.1%
woodlots and forested habitats		0.12%	23.77%	9.00%	11.0%
hedgerows/forest edges		22.77%	29.40%	22.78%	25.0%
Phacelia strips		0.54%	9.67%	32.12%	14.1%
Total number of pollen grains counted		614	1389	1228	

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.11.015.

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