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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.

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