Effects of pollinator density-dependent preferences on field margin visitations in the midst of agricultural monocultures: a modelling approach

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ABSTRACT

Managed field margins offer a means of reducing the impact of agricultural monocultures within intensively-managed environments. By providing refuge for wild plants and the pollinators associated with them, field margins can also contribute to enhancing the pollination services within the monoculture. However, the effects of the monoculture on pollinator behaviour needs to be carefully considered. It is known that pollinators may show density-dependent preferences such as neophobia (an avoidance of unfamiliar items) when different types of flower are available within their environment, and the dominance of monoculture crops within the environment may consequently have adverse effects upon the preferences shown by pollinators living in the field margins within them. In order to examine how pollinator preferences for wild flowers are affected by monocultures, we modelled the effects of density-dependent preferences, flower densities, and the geometry of field margins within a monoculture landscape using numerical simulations. This was done by considering how the placement of pollinator nests within a simple, spatially explicit landscape consisting of fields of monoculture crops separated by margins containing wild flowers affected the ratio of wild and monoculture crops experienced by the pollinator, given that it could only forage within a limited distance from its nest. Increasing field margin width and decreasing monoculture field width both led to an increase in pollinators visiting wild flowers (which levelled off as width increased). The size of the monoculture fields had little additional effect once they had passed an intermediate width. Increasing wild flower density within the margins led to a shift away from preferring monocultures. When wild flowers were at low densities compared to the monoculture, even the addition of small amounts of extra wild flowers had a large effect in shifting foraging preferences away from the monoculture. The distance which pollinators normally forage over only has an effect upon preferences for wild flowers when the travel distance is small. This suggests that careful consideration of margin design might be extremely important for those species which do not travel far. Innate preferences for density-dependence and particular crop types may also have an effect on preference behaviour. We demonstrate that the way in which resources are presented to indigenous pollinators may be extremely important in influencing where they choose to forage within agricultural landscapes. Careful margin design, as well as increasing the density of wild flowers (such as by enhancing the wild seed bank within the margins), may lead to overall improvements in ecosystem function within intensively-farmed monocultures.

1. INTRODUCTION

It is widely acknowledged that landscape modification has severe effects upon the ecology and survival of those organisms living within the affected area (Fischer and Lindenmayer, 2007; Hobbs and Yates, 2003), and many tools and strategies have been developed to combat these effects (Farina, 2006). Within modern intensively-managed agricultural systems, vast uninterrupted monocultures of crop species dominate landscapes, and refuge for wild species is often relegated to small areas of untreated or specially set-aside land within the monoculture, such as the arable field margins legislated within the United Kingdom under its Countryside Stewardship and Environmental Stewardship Schemes (DEFRA, 2007; Little et al., 1998), and similar agricultural systems found throughout northern Europe (Marshall, 2002; Marshall and Moonen, 2002). Field margins separate monoculture fields by providing a semi-managed area of uncultivated land around field edges, and may include hedgerows and other more permanent landscape features (Marshall and Moonen, 2002). The margins act as miniature reserves within the mosaic of agricultural land, and can act as a valuable resource, offering both differing degrees of refuge for wild species and resources for them to use, as well as acting as a potential green corridor. Therefore, margins can contribute to increasing and maintaining regional biodiversity, and can act as a means of enhancing ecosystem services such as pollination within the agricultural landscape (Kremen et al., 2007).

Evidence suggests that insect pollinators are in decline (Biesmeijer et al., 2006; Fitzpatrick et al., 2006; Memmott et al., 2007), and blame for this decline has been laid on a wide range of possible causal factors (Goulson et al., 2008), many of which are connected with intensive agricultural practices. Urgent action to reverse this trend in decline is being called for (Brown and Paxton, 2009), as pollinator extinctions could have very marked effects upon modern, intensive agricultural practices (Aizen et al., 2009; Klein et al., 2007), which could in turn lead to a further increase in land use thus putting further pressure on already fragile ecosystems. Landscape fragmentation has a major effect upon the abundance and density of pollinator faunas (Aizen and Feinsinger, 2003; Rathcke and Jules, 1993), as well as a negative impact upon pollination and the reproductive success of plants (Aguilar et al., 2006). To some extent, these effects can be mitigated by treatments such as providing field margins, which are known to have a positive effect on pollinator abundance (Kells et al., 2001; Meek et al., 2002), and mass-flowering crops may in part be beneficial to supporting pollinators during their flowering periods (Herrmann et al., 2007; Westphal et al., 2003; 2009). However, it has been argued that we need a greater understanding of how pollinator behaviour is affected by agricultural practices in order to counteract some of the underlying problems faced by pollinators (Aizen and Feinsinger, 2003).

Pollinator services are required for many agricultural monocultures, where the pollinators receive a nectar or pollen food reward for their services. If a pollinator has a range of food rewards available to it from both the monoculture crop and the wild plants contained within field margins, its flower visitations are unlikely to be evenly distributed across all the resources available within its immediate foraging environment. The behaviour of the pollinator may well be affected by the density of the flower-types within its foraging environment, showing some sort of density-dependent choice behaviour (Greenwood and Elton, 1979; Smithson and MacNair, 1997). (Note that pollinator behaviour is also likely to be affected by many features of the environment such as nectar quality, environmental temperature, accessibility of resources, the presence of environmental risks, etc., as well as the behaviour of other pollinators present in the environment, but this study focuses specifically on the density of resources within the pollinator's environment, using a simple density-dependent preference based upon the ratio of floral types within the pollinator's foraging range). Bumblebees *Bombus impatiens* are also known to show 'neophobia' (the avoidance of unfamiliar objects) to novel flowers that they have not encountered before (Forrest and Thomson, 2009b), which suggests that they are likely to show density-dependent preferences for common flowers within their environment (Smithson and MacNair, 1996; 1997). Here, we explore the effects that density-dependent neophobia may have upon pollinator behaviour within intensive monoculture environments. We assume that the pollinators crucial to an ecosystem will be those nesting (or at least growing

through some part of their lifecycle) within the relatively protected field margins, which suggests that margin design will have repercussions on both the composition and success of the pollinator community, and therefore an effect on the composition of the wild flower community found in the green spaces within the monoculture. Assuming that the choice of foraging source made by these pollinators will be largely influenced by the dense monoculture crop around them, we explore the effects that both the degree of density dependence and the geometry of the landscape will have upon the likelihood of the pollinators visiting non-monoculture flowers within the field margins. Landscape geometry is known to have effects upon the movements of pollinators (Brosi et al., 2008) and other dispersing animals (e.g. Chapman et al., 2007; Dover and Settele, 2009; Hannunen, 2002; Johnson et al., 1992; King and With, 2002; Nonaka and Holme, 2007; Sibly et al., 2009) at many different scales, but the model we present here is the first to consider the effects of density-dependent preferences on foraging behaviour in a non-dispersing species. By using a modelling perspective, we are therefore able to examine the interactions between smaller-scale processes (pollinator movement) and larger-scale landscape processes (in this case, the design of field systems, and agricultural practices), and their effects upon pollination behaviour.

This model considers a landscape formed from a simplified grid of square fields, each of which is separated by a uniform field margin (figure 1a). The fields are assumed to contain a monoculture crop, and the margins contain wild flowers. Pollinators are free to nest anywhere in the field margins, but not within the monoculture fields. The pollinators are assumed to forage over the area within a set radius of the nest (figure 1b, where a randomly located nest is represented by the cross), and their preference for the monoculture crops relative to the wild flowers available is determined not just by the relative proportions of both flower types within their foraging area, but also by a density-dependent 'neophobia' effect determined by the relative proportions of these crops. This simplified model of floral preference is therefore determined by six variables: monoculture field width, field margin width, foraging radius, the relative ratio of wild to monoculture flowers, and the shape of the density-dependence function (which is characterised by two parameters). We use these simplifying assumptions to explore the effects that the fragmentation of an agricultural landscape could have upon the visitation behaviour of the pollinators to the wild and the monoculture flowers.

2. METHODS

The foraging landscape was modelled as a two-dimensional lattice of discrete unit squares. The landscape consisted of a grid of square fields of monoculture crop, separated by regularly-sized field margins. The density of wild flowers within the field-margins, denoted f, was assumed to be proportional to a set density of the monoculture crop (such that $f = 0.2$ indicates that the density of wild flowers within a unit of space of the field margin would be 20% of that of the monoculture crop when encountered within a unit space of the monoculture field: by using this ratio of wild to monoculture, we can therefore consider the effects of changing the densities of either without having to make further assumptions about their actual densities). For ease of calculation, the widths of fields and margins were assumed to take integer multiples of unit length. We also assumed that there were only two floral types to visit (monoculture flowers and wild flowers).

Forager nests were assumed to only occur within the field margins, and never within the monoculture fields. The foragers associated with a nest were assumed to be able to forage throughout the area occurring within a given maximum foraging radius of their home nest. Figure 1 gives a schematic diagram of the assumptions made, but for ease of calculation, we used a discretised framework here, based on a grid of integer unit squares (demonstrated in the conversion of figure 1b to figure 1c). Each nest considered was assumed to occur at the centre of a unit square, and a monoculture or field margin square was considered to occur within the foraging radius if the straight-line distance from its centre to the nest was equal to or less than the nest's maximum foraging radius.

Density-dependent preference for the monoculture D was modelled based upon an elaboration of the relationship considered by Greenwood and Elton (1979) (also used by Forrest and Thomson, 2009b; Smithson and MacNair, 1997), using the following relationship

$$D = \left(\frac{Vm}{m+fw}\right)^b \Big/ \left(\left(\frac{Vm}{m+fw}\right)^b + \left(1 - \frac{m}{m+fw}\right)^b\right) \qquad (1)$$

where b determines the shape of the density dependence function, where a larger value of b means a greater preference for the commoner flower type present. V controls the amount of density-dependence-free preference for the monoculture, where increasing the value of V gives an underlying greater preference for monoculture. m and w were the numbers of monoculture and wild-flower margin squares respectively that fell within the foraging area considered for a nest.

For each of the six variables, 10,000 independent sets of simulations were conducted where the target variable was varied systematically against a fixed set of the other five variables, which were randomly chosen from uniform distributions bounded by the ranges described in Table 1. Note that the extreme values of b and V used when exploring the specific effects of these two parameters fell outside the values used within the range that these values were taken from when generating random variable sets. The range of these two value was reduced when generating the random variables in order to reduce the amount of noise seen in the results. For each systematic variation of the target variable, a nest was randomly placed within a square in the field margin of a landscape determined by the fixed set of variables, and the overall preference for the monoculture described by the density dependence term D in eqn. 1 was recorded. Results were then explored and visualized with R 2.9.1 (R Development Core Team, 2009).

3. RESULTS

Changing the width of the field margin led to a shift in preference, with less bias towards monocultures as margin width increased (fig. 2a). Small increases in the margin width when the margin itself was small led to a greater shift in preference than for similar margin width enlargements when the margin was already fairly wide. Similarly, increasing the width of the monoculture fields led to a shift towards preferring monoculture crops (fig. 2b), which levelled off quickly as fields increased beyond an intermediate width.

Increasing the radius over which pollinator preference was influenced led to a mild increase in preference for monoculture crops (fig. 2c), but this increase quickly levelled out. The model parameters were set so that the maximum radius of influence could be much wider than the maximum field width, and this levelling out of preference demonstrates that shifts in preference are possibly going to occur when pollinators only forage over a relatively small distance away from their nest.

As would be predicted, the density of wild flowers in the field margin relative to the density of the monoculture affected preference for the monoculture, where sparse wild flower densities gave really high preferences for the monoculture (fig. 2d). This preference fell with an increase in wild flower density, and the greatest shifts in preference occurred when wild flowers were relatively rare compared to the monoculture density.

The density-dependence parameters also had predictable effects on monoculture preferences: both an increase in the density-dependent strength of preference parameter b and an increase in the density-independent preference parameter V gave an increase in the preference for the monoculture (figs. 2e and 2f). When b was small (meaning that there was little effect of density-dependence on preference), the preference for monocultures *versus* wild flowers was close to 50:50 for all the parameter sets

considered. When *b* was increased to a high value (meaning that the preference for the most common flower type was close to being a step-function), the median preference for the simulation sets was a 100% preference for the monoculture, but with a large spread of all the simulated preferences (see the right-hand box of fig. 2e). It should be remembered here that nests can only be found within the field margins, and at least some portion of a pollinator's circle of influence will contain field margin. Therefore, this wide tail of preferences is likely to come from those simulations where the radius of influence was small, and the field margin width was relatively large.

4. DISCUSSION

With these results, we demonstrate that simple density-dependence in flower preference can have varying effects upon the degree of preference shown by pollinating visitors, and that these effects can be altered by the composition of the landscape that the pollinator experiences. This density-dependence could be mediated through some form of neophobia by the pollinator (Forrest and Thomson, 2009b). Coupled with traplining behaviour driving a pollinator to faithfully revisit earlier choices (Ohashi and Thomson, 2009; Saleh and Chittka, 2007; Thomson, 1996) and preference for visiting common forms of flower in the environment through flower constancy mechanisms (Chittka et al., 1999; Darwin, 1876; Goulson and Wright, 1998; Waser, 1986), density-dependence is likely to have a large effect upon the likelihood that a pollinator visits rarer species when it is foraging within a dominant monoculture. This effect is demonstrated in the model with respect to the power of density-dependence, as mediated by the *b* parameter (fig. 2e): a high value of *b* (meaning a stronger preference for the common flower type) led to the forager tending to visit the common flower type much more.

If we are interested in encouraging pollinators to visit wild species, the power of the pollinators' density-dependence preference is something we are unlikely to be able to control, so we must act to counteract this preference in other ways. One way would be by supplementing wild populations in such a way that the ratio of wild to monoculture densities is affected, demonstrated in the model in the effects of changing the wild flower density parameter (fig. 2d): this suggests that if the wild population is rare, a small increase in density will lead to a relatively large shift away from solely visiting the monoculture. This in turn suggests that in cultivated wild flower margins, re-supplementing the wild seed bank at regular intervals in order to maintain wild flower levels may be the most viable strategy to maintain pollinator visits to wild flowers (as demonstrated by Carvell et al., 2004). Furthermore, supplementation of species may be a way of increasing those plant species that play an important role in ecosystem functioning, depending upon the processes by which biodiversity contributes to ecosystem function (Tscharntke et al., 2005), and careful choice of the correct supplemented crops could have a positive influence on the abundance of pollinators within the field margin (Carvell et al., 2004). The simple model proposed here only looks at the effects of the densities of one species of wild flower against a monoculture, but within field margins, there are likely to be many species present. We would tentatively suggest here that the supplementation of any alternative wild flower species might perhaps act to dilute the overwhelming effect of the monoculture on pollinator preferences, but whether this is true (as well as the exact details of how the presence of many different choices affects density dependence) would have to be investigated both experimentally and theoretically before firm predictions could be made. Furthermore, whether density-dependence is affected equally by all the resources available within the foraging range (as is modelled here) or whether there are other weightings on the degree of preference (such as proximity to the nest) requires further experimental and theoretical attention.

However, the pollinators may show an innate preference for the monoculture irrespective of its relative density to the wild flower population. For example, bumblebees may show distinct preferences for one particular flower type over another regardless of whether they have encountered particular flower types beforehand (Forrest and Thomson, 2009a; Gumbert, 2000; Ings et al., 2009; Raine and Chittka, 2007), and potential floral resource quality may also affect choice (Osborne et al.,

2007). Furthermore, the pollinator may be choosing to forage on different flowers for different reasons, as different species may offer alternative sorts of reward for visitation. For example, the nutritional quality (including amino acid differences and digestibility) of pollen varies between species (Roulston and Cane, 2000), and there may also be toxic compounds present (Praz et al., 2008). There may also be differences between plant species in the levels of essential micronutrients such as the rare earth metals that are available in the pollen and nectar, which could have impacts on the developmental success of pollinators nesting within the monoculture matrix. A mixed diet may therefore be essential for harvesting sufficient quantities of the micronutrients required, as is recognised in other non-pollinating invertebrates (Patt et al., 2003; Sigsgaard et al., 2001) as well as in polylectic (pollen generalist) honeybee larvae which may need pollen from several sources to reach maturity (Herbert et al., 1970) or to maximise their immunocompetence (Alaux et al., in press). Obviously, attention needs to be paid to the narrow range of flower species that are used by oligolectic (pollen specialist) species of bee (Wcislo and Cane, 1996), where building a nest within a matrix of a monoculture that is not used for foraging will have severe repercussions on the bees' survival and success. It may even be the case that the pollinators are receiving additional non-nutritional rewards such as heat from the species that they are visiting (Dyer et al., 2006; Rands and Whitney, 2008; Whitney et al., 2008), which could have confounding effects upon their foraging preferences. Therefore, a diet based on a monoculture crop may not provide suitable resources to successfully sustain pollinators that live within the monoculture environment. We acknowledge that monocultures may only be present in the pollinators' environment for a small proportion of the year (e.g. oil seed rape flowers for about four weeks Diepenbrock, 2000), but monoculture effects could be magnified if the flowering period ties in with a critical developmental phase in the pollinators' life history.

The model investigates the effects of landscape geometry on pollinator visitation rates to wild flowers, relative to field margin size, field size, and the distance over which pollinators forage. Within the simple geometry that we consider, we demonstrate that small changes in field margin size can have large effects upon pollinator visitation rates to wild flowers (fig. 2a), whilst the size of the monoculture is less important (fig. 2b): once the fields have reached an intermediate level of size, further increases have little effect. This suggests that large well-considered margins interspersed within large fields might actually be better for ensuring the pollination of the wild species present, rather than filling the monoculture landscape with lots of small and ineffective margins. The distance the pollinators are travelling over is also going to be an important factor to consider here (fig. 2c). Pollinators use widely different amounts of land for foraging within. Different species of *Bombus* use different scales (Westphal et al., 2006), and many pollinating bee species forage over relatively small distances of several hundred meters from the nest (Greenleaf et al., 2007; Knight et al., 2005; Walter-Hellwig and Frankl, 2000), which could potentially be affected by resource availability within foraging range from the nest (Knight et al., 2009). Studies suggest that *B. terrestris* and *A. mellifera* may forage between 1 and 10km from their nests (Beekman and Ratnieks, 2000; Goulson and Stout, 2001; Osborne et al., 2007; Visscher and Seeley, 1982; Walter-Hellwig and Frankl, 2000). These differences in scale may be a contributory factor to the success of *B. terrestris* and *A. mellifera* in outcompeting native species (Goulson, 2003; Nagamitsu et al., in press; Paini, 2004; Roubik and Wolda, 2001; Thomson, 2004). Monoculture crops and the arrangement of landscape to support these crops may well favour those species with long foraging ranges: natives with short ranges are unable to gain sufficient quantities of essential dietary components to develop successfully, whilst aliens with longer ranges are able to access nutrients from species other than monoculture, simply through being able to travel over longer distances in order to access them. Furthermore, features of the field edges themselves may be a barrier to the area visited by shorter-range pollinators (Wratten et al., 2003), where, for example, hedges may provide considerable barriers in movement between fields. The effects of different pollinator species' movement behaviour could be combined with the geometrical approach we consider here by including agent-based movement rules within the simulation (e.g. Rands et al., 2004; 2006).

Therefore, we suggest that careful consideration is given to the organisation of field margins in landscapes, if the intention of these is to maintain wild flower and pollinator populations within a landscape. The results presented by this model are novel, and as yet haven't been tested empirically,

and we are unaware of any studies that have explored the questions we address. Density-dependent pollinator behaviour may mean that fewer but wider margins are preferable to many small margins, and flower density may be an important contributory factor to the performance of the pollinator (although if crops are mostly pollinated by pollinators with short foraging ranges, the plants at the middle of the monocultures which are furthest from the field margins may consequently suffer from a reduced amount of pollinator visitation). Following on from the findings of Forrest and Thomson (2009b), investigation of how density dependence behaviour manifests itself in the field, as well as further investigation of the effects of exact field geometry (Kohler et al., 2007), would further improve our knowledge of the contribution of field margins to conserving biodiversity and providing pollination service within heavily-managed agricultural landscapes (Lonsdorf et al., 2009; Ricketts et al., 2008).

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Table 1: Description of the variables considered in models, and the ranges used for randomized variable sets within each of the simulations.

Variable	Range used in simulations
Width of field margins	1 – 25 length units
Width of square monoculture fields	1 – 100 length units
Radius over which foragers travel	1 – 1000 length units
f: Proportional floral density per unit area of wild flowers in margin, relative to monoculture density	0.01 – 1.0
b: Power term influencing density dependent preference for monoculture	0 – 2
V: Density-independent preference for monoculture	0 – 2
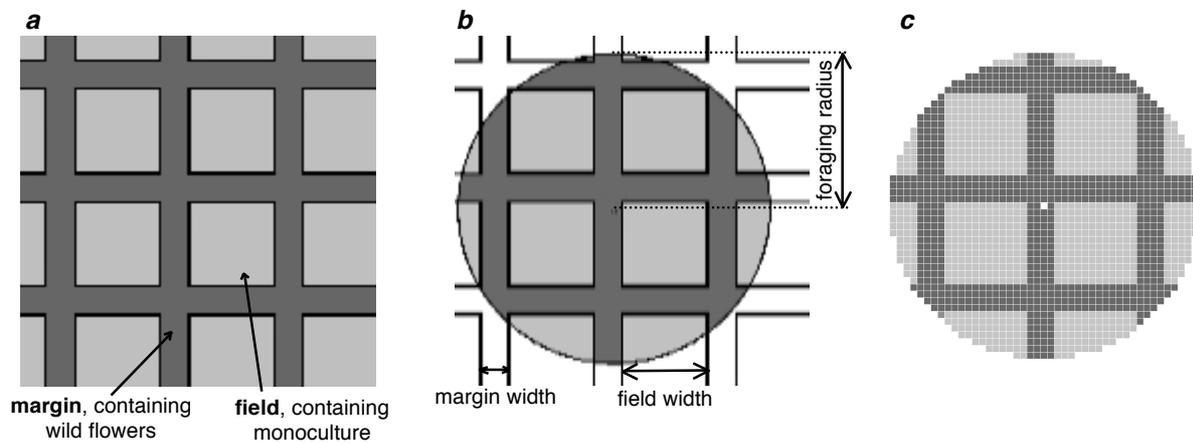
FIGURE 1: Schematic diagrams of field geometry. *a)* The landscape is composed of a grid of square fields of monoculture crop, separated by regular field margins. *b)* '×' marks the location of a randomly selected pollinator nest site, within the field margin area of the landscape. The circle edge illustrates the area over which the pollinator can forage, with the monoculture field and margin areas marked in gray contributing to the nest's potential foraging options. *c)* This geometry is then translated to a square grid.
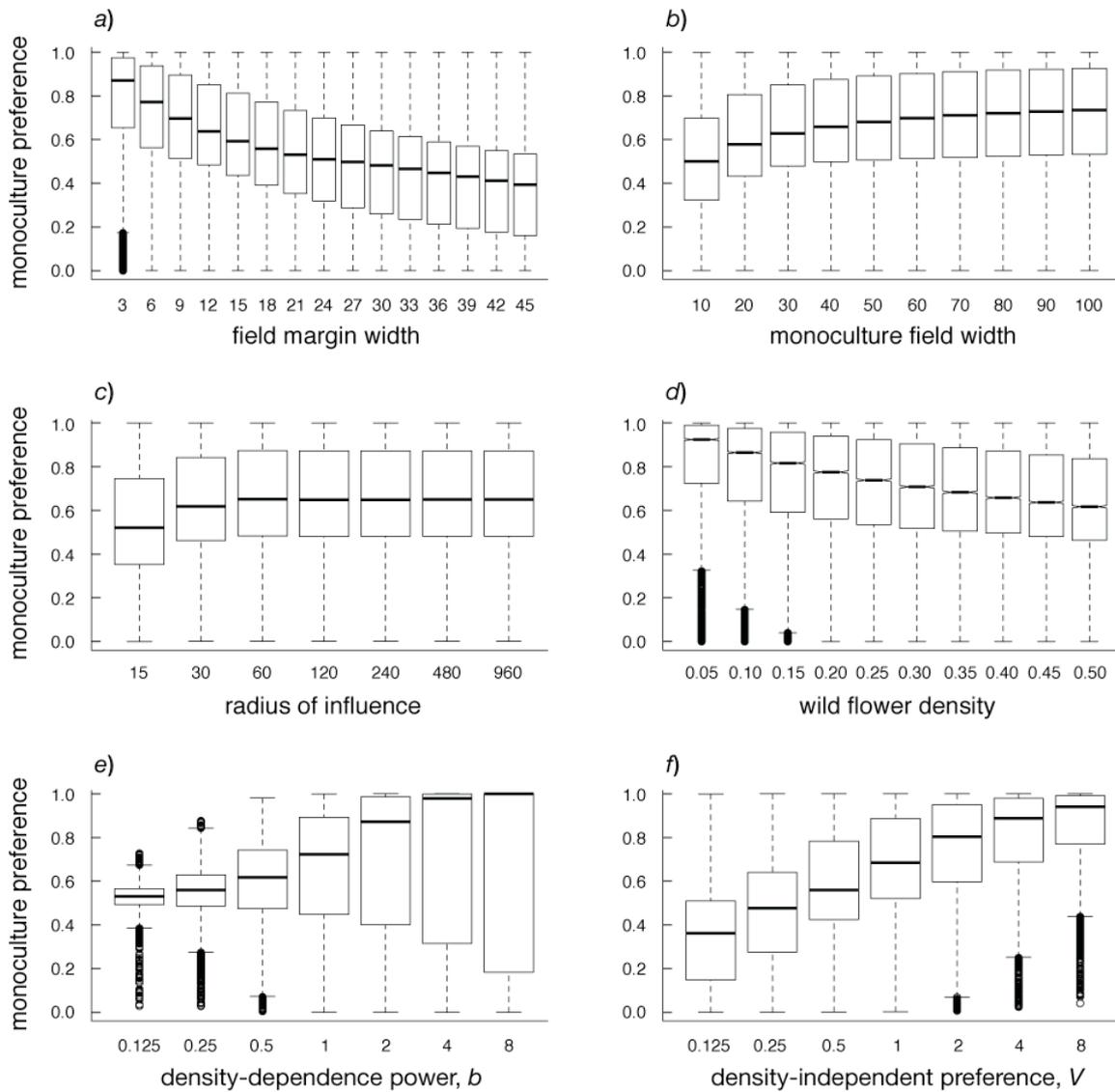
FIGURE 2: Boxplots showing the effects on preference for the monoculture crop when systematically changing: (*a*) the width of the field margin; (*b*) the width of the monoculture field; (*c*) the radius over which pollinator choice is influenced; (*d*) the density of wild flowers in a unit area of the field margin relative to the density of the monoculture crop in a unit area of field; (*e*) *b*, the parameter controlling the steepness of the density-dependence function; and (*f*) *V*, the parameter controlling the density-independent preference for the monoculture crop. Note that all the figures are drawn with notches, but these are only visible in panel *d*. Outliers are represented with the solid symbols.