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An energetics-based honeybee nectar-foraging model used to assess the potential for landscape-level pesticide exposure dilution

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Estimating the exposure of honeybees to pesticides on a landscape scale requires models of their spatial foraging behaviour. For this purpose, we developed a mechanistic, energetics-based model for a single day of nectar foraging in complex landscape mosaics. The hive population was assumed to select the resource patch with highest net energetic efficiency in perfect knowledge of its environment. During the day the optimal patch could change, due to resource depletion or related to the characteristics of the resource (i.e., the period flowers were open and provided nectar). By quantifying foraging costs and yield in terms of energy, we accounted for the impact of field distance and size, the occurrence of resource depletion and the characteristics of the resource type (crops and wild flowers), like seasonal and diurnal patterns in availability.From the model we derived simple rules for resource patch selection, e.g., for landscapes with mass-flowering crops, the net energetic efficiency would be proportional to the ratio of the energetic content of the nectar of the crop divided by distance of crop field to the hive. Also, we determined maximum distances at which resources like oilseed rape and clover could still be energetically attractive.We used the model to assess the potential for pesticide exposure dilution in landscapes of different composition and complexity. Dilution implied a lower average concentration in nectar arriving at the hive, resulting from foraging effort being diverted away from treated fields. Applying the model for all possible hive locations in a landscape, landscape-specific distributions of dilution values were obtained.For a case study area for which detailed spatial data were available, we tested three scenarios that were expected to lead to exposure dilution: the presence of i) equally attractive crop fields in the neighbourhood of a treated field, ii) highly attractive flowers strips of different widths at the edges of treated fields (off-crop in-field resources), and iii) highly attractive resources on off-field (semi-natural) habitats. The results indicated significant dilution at landscape scale only from flowers strips of more than 5 m wide and off-field habitats. On an area-base, flowers strips were approximately 10 times as effective as off-field habitats, the main reason being that the flowers strips had an optimal location, always at the edges of treated fields.

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INTRODUCTION

There is serious concern about the widespread decline of honeybees and wild pollinators in the agricultural landscape (Potts et al. 2010; Vanbergen et al. 2013). Combined stress from pesticides, parasites and lack of floral resources, is probably the main cause of the observed decline (Goulson et al. 2015). Honeybees, by exploiting mass-flowering crops, operating over long distances, and by being carefully managed by beekeepers, may be relatively insensitive to the disappearance and deterioration of semi-natural elements providing food and nesting opportunities (Sponsler & Johnson 2015). Their dependence on cropland for nectar and pollen acquisition, however, leads to high potential exposure to pesticides (Krupke et al. 2012).

To understand the role that each of the factors pesticides, parasites and lack of floral resources, may play in honeybee colony failure, multi-stress models are needed that deal with hive dynamics, parasitic infections as well as contaminants (Grimm et al. 2014). The BEEHAVE model is an example of such a model (Becher et al. 2014; Rumkee et al. 2015) that can be exploited to disentangle the multi-stress interactions.

Understanding to what extent pesticides may contribute to the decline, requires as an essential first step the quantification of potential exposure. Exposure at the hive is the outcome of honeybee foraging in the landscape surrounding the hive, as concentrations of pesticides in nectar and pollen brought by foraging bees will depend on the provenance of these food items, and thus on choice of forage and foraging locations (Garbuzov et al. 2015a). It is well known that honeybees may forage over long distances (Beekman & Ratnieks 2000), up to approximately 10 km away from the hive. However, when sufficient high quality resources are available nearby, most foraging will take place within a few kilometres. Decoding waggle dances of three colonies in an urban area, it appeared that about 90% of the foragers visited food sources within 1 km although further away also good food sources were available (Garbuzov et al. 2015c). Exposure assessment therefore needs to consider a spatial scale of at least 1 km, and address the choice of foraging locations in complex and heterogeneous landscapes, with multiple resources and resource patches.

Honeybee foraging models may thus be used to predict potential exposure on a landscape scale. They may also serve as a tool to test landscape management measures aimed at lowering exposure risk (mitigation) on their effectivity. Most of the published honeybee foraging models (Schmickl & Crailsheim 2007) focus on the role of social behaviour in foraging, like recruitment of scouts and foragers, rather than on the choice between numerous resources. Among the 12 models discussed in (Becher et al. 2013) were relatively complex individual-based models (de Vries & Biesmeijer 1998; de Vries & Biesmeijer 2002; Dornhaus et al. 2006; Johnson & Nieh 2010; Schmickl & Crailsheim 2004; Schmickl et al. 2012) and equation-based models (Beekman et al. 2007; Camazine & Sneyd 1991; Sumpter & Pratt 2003) that were developed to study emergent behaviour and self-organization at the colony level. Some models focussed more on the economics of foraging (Cresswell et al. 2000; Dukas & Edelstein-Keshet 1998; Schmid-Hempel et al. 1985). The majority of the models based the choice of foraging site or patch on energetic profitability, and used energetic efficiency as the optimized currency. None of these models were applied to realistic, heterogeneous landscapes, with variation in distance, size and quality of the food sources.

To obtain a landscape-level foraging model, we extend and adapt the energetics-based approach of (Cresswell et al. 2000; Dukas & Edelstein-Keshet 1998; Schmid-Hempel et al. 1985) to deal with honeybee foraging on a large spatial scale, in heterogeneous landscapes with multiple resources, including mass-flowering crops and wild flowers in semi-natural habitats. We derive how the choice of foraging patches affects pesticide concentration in the nectar arriving at the hive, when some of these patches represent crop fields treated with pesticides. Variability at landscape scales is accounted for by running the model in a probabilistic way for all possible locations of a bee hive and derive distributions of exposure concentrations and dilution factors. Dilution refers here to a lowered exposure of the beehive due to foraging effort being diverted away from pesticide-treated fields.

We apply the model to explore whether landscape management aimed at pollinator conservation may have the additional benefit of lowering the exposure of honeybees to pesticides. Three hypothetical scenarios were tested for their impact on exposure dilution, through the presence of i) attractive alternative crop fields, ii) flowers strips (off-crop in-field resources), and iii) attractive resources on off-field habitats.

MATERIAL & METHODS

Energetics-based foraging model

The model ignores in-hive colony dynamics and assumes the colony to be in equilibrium with its surrounding landscape, to have perfect knowledge of available resources and to adapt quickly to environmental fluctuations in food conditions (Beekman & Bin Lew 2008; Beekman et al. 2003). We assume that its (self-)organization ultimately allows it to focus on a single most-profitable food patch at a time, and in case of two or more approximately equally profitable sources, that mechanisms are present that reinforce the use of only one of them (e.g., symmetry breaking and cross inhibition (de Vries & Biesmeijer 2002)). So, unlike many of the published foraging models, our aim is *not* to model the mechanisms by which the colony is able to exploit the best available forage sources (Myerscough et al. 2014). Instead, we consider this ability as given. Field observations ((Beekman et al. 2004; Visscher & Seeley 1982)) indicate nonetheless that within a single day a colony may exploit several patches. For a colony in deciduous forest, on average 9.7 resource patches accounted for 90% of the daily forage (Visscher & Seeley 1982). A colony may indeed utilise mechanisms to deal with alternative resources that become profitable at different times of the day (Van Nest & Moore 2012). By applying hourly time steps, we allow resource conditions and thus the optimal resource patch to change during the day.

As in most energetics-based honeybee foraging models, a foraging trip comprises three components: travel from hive to nectar source patch, searching for flowers in the patch and extracting the nectar, and the travel back to the hive.

Within the field, floral resources are collected assuming a type II functional response (Holling 1959), so the number of flowers with nectar that are visited per time unit amounts to

(eq. 1) $$f = \frac{aF}{1 + ahF}$$

with F the density of open (nectar providing) flowers (m^{-2}), a the attack rate ($m^2\ s^{-1}$) and h the handling time per flower (s). Thus f is expressed in flowers handled per honeybee per second.

The density of open flowers is the product of the number of plants per m^2 and the average number of open flowers per plant.

The rate of nectar collection (mg s^{-1}) is given by fg, with g representing the average amount of nectar obtained from a flower (mg). When the specific energy content of the nectar (kJ mg^{-1}) is known, this factor can be converted into collected energy (kJ). The time t_L it takes to collect nectar to full capacity can then be calculated as

(eq. 2) $$t_L = \frac{\gamma}{fg}$$

where the capacity is given by γ (mg). Note that unlike e.g., (Schmid-Hempel et al. 1985) we assume that foragers always collect a full load.

Flight time and flight costs are assumed to be proportional to the distance from hive to the resource patch. The foraging time-budget (the duration of a foraging trip) is thus defined by the sum of travel time and the time spent at the patch:

(eq. 3) $$t_{trip} = 2\frac{D}{v} + \frac{\gamma}{fg}$$

with D being the distance from the hive to the field (m), and v the flight velocity (m s^{-1}).

The energy expenditure EE (in kJ, ignoring basic metabolism) can be calculated as the sum of the travel costs EE_{travel} (travel time * energetic costs per time unit) and the costs while loading nectar in the field EE_{field}. The latter term is made up by flight costs while searching for nectar flowers and costs while sitting on the flowers extracting the nectar. The latter is ignored, as it is approximately an order of magnitude smaller than flight costs (a value of 0.0042 J s^{-1}was applied in (Schmid-Hempel et al. 1985)). Energy expenditure at the field thus becomes:

(eq. 4) $$EE_{field} = \left(t_L - \frac{\gamma}{g}h\right)e_F = \frac{\gamma e_F}{gaF}$$

The equation is simplified by substituting equations 2 and 1, thus eliminating the handling time. NB, in the EE_{field} equation we use the average flight cost e_F (kJ s^{-1}), as during foraging in the field the individual state changes gradually from unloaded to loaded. The value of e_F is obtained from loaded $e_{F,L}$ and unloaded $e_{F,U}$ flight costs (Seeley 1986). The total travel costs are given by:

(eq. 5) $$EE_{travel} = \frac{D}{v}\left(e_{F,U} + e_{F,L}\right) = 2\frac{D}{v}e_F$$

If the same route is followed when heading for the field and when returning to the hive, the energy costs can be averaged.

The total energy expenditure EE_{total} (kJ) for a foraging bout sums to:

(eq. 6) $$EE_{total} = \left(t_L - \frac{\gamma}{g}h\right)e_F + 2\frac{D}{v}e_F = (t_L - \frac{\gamma}{g}h + 2\frac{D}{v})e_F = (\frac{\gamma}{gaF} + 2\frac{D}{v})e_F$$

The yield of a trip in terms of energy, energy intake EI (kJ), depends on the energy content of the collected nectar of resource type R, e_R (kJ mg^{-1}):

(eq. 7) $$EI = \gamma e_R$$

With t_{trip}, EE and EI, the basic ingredients for a “decision making process” for a colony are specified, and costs (both in energy and time) and yields for specific foraging locations in a landscape with multiple fields can be compared. In theory, there are different currencies that might be optimized (Stephens & Krebs 1987). For honeybees considerable effort has been invested in deciding whether the relevant currency is the net rate of energy delivery ((gain-cost)/time) or the net energetic efficiency ((gain-cost)/cost). Experimental data, e.g., (Seeley 1994) but see (de Vries & Biesmeijer 2002), and models fit to experimental data (Schmid-Hempel et al. 1985), as well as several of the other foraging models discussed by (Becher et al. 2013) indicate that net efficiency is the most appropriate currency.

We therefore assume that net energetic efficiency NEE

(eq. 8) $$NEE = \frac{EI - EE_{total}}{EE_{total}}$$

is maximized and determines floral patch selection.

Diurnal variation

By calculating optimal field selection with an hourly time-step we may account for, 1) any diurnal pattern in the anthesis of flowers, 2) possible depletion of floral resources occurring in small resource patches, and, 3) diurnal patterns in the number of active foragers in the hive.

We thus take into account the observation that crops (as well as each wild flower species) may have a specific time-window, during which flowers are actually open and nectar is available. For simplicity's sake we assume a binary pattern (all flowers open or closed). By calculating for each hour in the daylight period an optimal field, we are able to predict from the model the use of multiple fields within a day, matching the observation that the population of foragers in the hive does not seem to be restricted to foraging on one single field only.

We deal with depletion of floral resources within a day, by subtracting at the end of the hourly time step, the visited number of open flowers from the initially present number. The visited number of flowers is scaled to an hourly time step, to account for multiple trips when trips have a shorter duration than 1 hour (or less than 1 trip per forager in case trips have a longer than 1 hour duration):

(eq. 9)
$$F_{t+1} = F_t - \frac{n\gamma \quad \Delta t}{gA(t_{trip} + t_U)} = F_t - \frac{n\gamma}{gA} b$$

with A representing field size (m^2), n the number of active foragers and t_U the time needed for unloading the nectar at the hive and b represents the foraging trips per time step $\Delta t/(t_{trip} + t_U)$ an individual foragers can make. A fixed number of flowers γ/g is visited for a full load. Note that we need the *absolute* number of active foragers (n) at each time step, to be able to account for depletion. After lowering the open flower density, in the next time step another field may be identified as the optimal one, as the time to collect a full load will have increased with lower open flower density in the previously optimal field.

The model can be applied for a landscape containing different types of resource patches, e.g. fields with mass-flowering crops providing nectar, and semi-natural habitats constituting resource patches with a range of possible qualities depending on the dominant flower species or group. All resource patches are assumed to be internally homogeneous.

The model predicts the set of foraging patches that will be used during a single day. Its output also includes several quantities that could be compared to field observations for hives at a specific location in a specific landscape, e.g. the amount of sugar (mg) arriving at the hive, , exploited nectar sources weighted by the amount of collected sugar in each, or the distribution of foraging distances. Alternatively, the impact of the hive population on a crop can be quantified, e.g., as the number of flower visits per unit area, per flower or per patch (Eq. 9).

Exposure

When the model as described above is combined with information on fields being treated with a chemical, and/or off-field habitats being exposed to spray-drift, the model can be used to estimate the concentration of the chemical in the nectar brought into the hive.

From the sequence of optimal fields and the diurnal distribution of active foragers, we obtain the absolute amount of nectar (wet weight) brought into the hive over the whole foraging period, from each optimal field.

(eq. 10) $\sum_{i=1}^{L} n_i \gamma b_i$

Here, L represents the foraging time window, defined as the integer number of time steps (hours, indexed by i) in which foraging is possible, and n_i the number of active foragers at time step i. The exposure at the hive depends on the concentration of the chemical in the nectar of flowers in each resource patch i, C_i, expressed in e.g., µg mg^{-1}

(eq. 11) $\sum_{i=1}^{L} n_i \gamma b_i C_i$

Underlying assumption for equation 10 is that the full load of nectar collected in the field is transported to the hive. In reality, especially for longer distances, some of the sugar in the nectar might be consumed by the bees. The amount of energy in the nectar that will be used during the return flight, E_c, is obtained from the energetics model. It would be approximately equal to $e_L \frac{D}{v}$ in case the whole flight back is based on energy from the nectar load. The amount of nectar arriving at the hive decreases by consumption to $\gamma - \frac{E_c}{e_R}$ and thus becomes:

(eq. 12) $$\sum_{i=1}^{L} n_i\left(\gamma - \frac{E_{c,i}}{e_{R,i}}\right) b_i$$

When the chemical is metabolized together with the sugar, its concentration in the nectar remains the same but exposure (absolute amount) at the hive will be lower:

(eq. 13) $$\sum_{i=1}^{L} n_i\left(\gamma - \frac{E_{c,i}}{e_{R,i}}\right) b_i C_i$$

If the chemical is not metabolized, the absolute amount arriving at the hive is as defined by equation 11. The concentration of the chemical in nectar at arrival will however no longer equal C_i, but instead become $C_i/\left(1 - \frac{E_{c,i}}{\gamma e_{R,i}}\right)$, implying enrichment.

From the point of view of exposure risk inside the hive, the relevant chemical concentration should be expressed on a sugar base: nectar with a low sugar content will be concentrated until a minimum sugar content is reached. The exposure on a sugar-base is obtained by dividing the total amount of the chemical (μg) entering the hive by the total amount of sugar entering the hive (mg). When the chemical is metabolized with the sugar (no enrichment) we obtain as sugar-based daily averaged concentration of the chemical (μg mg^{-1}) entering the hive:

(eq. 14) $$X_m = \frac{\sum_{i=1}^{L} n_i\left(\gamma - \frac{E_{c,i}}{e_{R,i}}\right) b_i C_i}{\sum_{i=1}^{L} n_i \frac{(\gamma e_{R,i} - E_{c,i})}{e_{SUGAR}} b_i}$$

The denominator is obtained by multiplying each term in the summation (Eq. 12) with the sugar content of the nectar (g g^{-1}) given by e_R/e_{SUGAR}.

Without metabolization of the chemical (with enrichment) we obtain from equation 13:

(eq. 15) $$X_e = \frac{\sum_{i=1}^{L} n_i \gamma b_i C_i}{\sum_{i=1}^{L} n_i \frac{(\gamma e_{R,i} - E_{c,i})}{e_{SUGAR}} b_i}$$

Equations 14 and 15 quantify the contribution of each per time-step *i* selected resource patch to the sugar-based concentration of a chemical (μg chemical mg^{-1} sugar) entering the hive. Using this information together with the calculated amount of sugar having this concentration we can construct detailed distributions quantifying the relative composition of the nectar entering a particular hive, in terms of sugar-based concentrations.

Dilution

Exposure dilution at the landscape level is the extent to which exposure to a chemical is reduced by foraging on other resources than a treated resource. These other resources should be less contaminated, or not contaminated at all, to obtain lowered exposure (real dilution). Dilution is defined relative to a reference concentration, e.g., the sugar-based concentrations in the nectar of a treated field X_P with resource R:

(eq. 16) $$X_P = C_P \frac{e_{SUGAR}}{e_R}$$

where C_P refers to the concentration (on a wet-weight base) in nectar on the treated field, often referred to as the predicted environmental concentration (*PEC*) resulting from a certain application rate of the chemical. Dilution factors follow from actual X_m or X_e as:

(eq. 17) $$\varphi_m = X_m/X_P \text{ and } \varphi_e = X_e/X_P$$

Note that with a patch-specific C we can represent variability in the applied dose for the treated crop (setting for each a *PEC* from a probability density function), deal with a substance that is applied on different crops with different doses, or include patches representing off-crop or off-field habitats that are exposed through spray drift only.

Risk Assessment

In a risk assessment on landscape scale, the specific setting may allow for several simplifying assumptions. When dealing with a single resource that is being sprayed, further referred to as the 'target crop', a constant application rate on the target crop, and a landscape consisting only of fields with this target crop, the dilution factor (Eq. 14) becomes:

(eq. 18) $$\varphi_m = \frac{\sum_{i=1}^{L} \delta_i n_i (\gamma - \frac{E_{c,i}}{e_R}) b_i C_P \quad 1}{\sum_{i=1}^{L} n_i \frac{(\gamma e_R - E_{c,i})}{e_{SUGAR}} b_i \quad C_P \frac{e_{SUGAR}}{e_R}} = \frac{\sum_{i=1}^{L} \delta_i n_i (\gamma e_R - E_{c,i}) b_i}{\sum_{i=1}^{L} n_i (\gamma e_R - E_{c,i}) b_i}$$

with $\delta_i = 1$ in case the field selected in time step *i* is sprayed. Similarly, for the case with possible enrichment (Eq. 15) we obtain:

(eq. 19) $$\varphi_e = \frac{\sum_{i=1}^{L} n_i \gamma b_i C_P \quad 1}{\sum_{i=1}^{L} n_i \frac{(\gamma e_R - E_{c,i})}{e_{SUGAR}} b_i C_P \frac{e_{SUGAR}}{e_R}} = \frac{\sum_{i=1}^{L} \delta_i n_i \gamma b_i}{\sum_{i=1}^{L} n_i (\gamma e_R - E_{c,i}) b_i}$$

Equations 18 and 19 show that for this simplified case, dilution factors do not depend on C_P. Note that to a large extent the dilution factor will be determined by δ, the selected fields being treated or not. When all selected fields are treated φ_m will be one, while φ_e may even exceed one. In a probabilistic approach, with *p* representing the probability for a field of being treated, dilution will on average approximate *p*. When exposure from spray-drift on off-crop resource patches is expressed relative to the exposure in-crop, e.g., as a fraction of C_P, this exposure can be accounted for in the equations.

In a landscape-level risk assessment approach, as described by e.g., (Barmaz et al. 2010), the model is applied for all possible locations of an apiary. Following recent guidance (EFSA 2013), all sites at edges of target crop fields are considered to be potential locations and the target crop patch adjacent to the hive location is always assumed to be sprayed. Model coefficients will depend, among others, on substance, type of target crop and the timing of applications in the season. For example, the timing is linked to typical cycles of target crops and will affect the daily foraging time-window, the presence and state of alternative nectar sources in the landscape, as well as some of the colony characteristics (diurnal activity pattern, number of active foragers, etc.).

The general approach would thus be to run the model for all potential beehive locations, and to obtain for each location the set of patches exploited during a single day. This set may contain target crop patches that may be sprayed, and/or off-field habitat patches affected by spray drift. When no actual data on spraying are available, a probabilistic approach can be applied, assuming a probability of spraying for each target crop field. In such case, an average dilution factor can be calculated based on a large number of permutations of the set of sprayed fields. A cumulative frequency distribution of all dilution factors over all hive locations allows calculating statistical descriptors, e.g., the 90th percentile that quantifies the amount of exposure dilution predicted for 90% of all sites.

For a realistic risk assessment, all resource patches available in the considered landscape need to be specified. We used the model in simplified scenarios regarding the presence of resources, in order to explore whether landscape-based approaches to exposure mitigation can be effective.

Model Analysis & Application

Energetics-based model

From the energetics-based model (Eq. 6 and 7); we derived thresholds for the exploitation of resources depending on distance to the resource patch and resource characteristics, as done by (Cresswell et al. 2000). For extreme cases of landscape composition, we derived rules of thumb for the selection of foraging locations. For different resources we also estimated the relative importance of the two stages determining energy expenditure: traveling to and from the resource patch and foraging in the resource patch.

Landscape-level dilution

When it is assumed that nectar and/or pollen are collected from all resources in the landscape proportional to their attractiveness (defined by e.g., sugar content of the nectar) (EFSA 2013), considerable exposure dilution is always to be expected in landscape mosaics with multiple resource patches. In our model, and in all foraging models based on an assumption of optimality, at any time only the patch with highest net energetic efficiency will be exploited. As a consequence, dilution might be much harder to achieve. To explore whether landscape-level risk mitigation options are still viable, we tested three scenarios for exposure dilution.

i) **Alternative Fields**: Dilution can result from the presence of attractive but untreated fields, either with the target crop or with alternative attractive (mass-flowering) crops. For each potential hive location (site) at the boundary of these fields, the nearest crop field was always assumed to be treated, while for the other crop fields in the landscape, treatment occurred following a probability p. The average local dilution factor for a site was then calculated from 100 different random realizations of the series of treated fields. The analysis was done for a range of values for p (0 to 1, with an interval of 0.1). A variant of this mechanism would be the presence of fields with another, attractive, crop type. We tested this by defining another common crop in Flevoland as a hypothetical alternative mass-flowering crop, largely identical to oil-seed rape (Fig. 1). The energetic attractiveness of this crop was manipulated to range from less to more attractive than oil-seed rape, by adjusting its sugar content (0.8, 0.9, 1, 1.1 and 1.2 times oil-seed rape sugar content).

ii) **Flower Strips**: Dilution can result from the presence of highly attractive flower strips around target crop fields. This was simulated by adding to each target crop field up to 4 flower strips at the edge of the field. Flowers in the strips were assumed to be identical to oil-seed rape flowers, except for a higher energy content of their nectar (sugar content increased by 50%). Presence of each strip was randomly set, with a probability q (0 to 1, with an interval of 0.1). The area of a flower strip was set to a prescribed width w multiplied by strip length, by definition ¼ of field perimeter. Width values of 1, 2, 5 and 10 m were tested. The area contained in the strips was subtracted from the crop field area. Thus, strips were strictly in-field off-crop habitats.

iii) **Off-field Habitats**: dilution can result from the presence of off-field semi-natural habitats, the green-veining or green infra-structure of the landscape. Predominantly narrow, linear elements, e.g., ditches and ditch sides, road side verges, shores and other natural habitats, may offer nectar resources when managed in an appropriate way. We tested this using geo-data for fields (as above) and for semi-natural elements (Fig. 1). We assumed a single common flower species (white clover, *Trifolium repens*, table 2) to be representative for all off-field habitats. Clover is in the Netherlands, as in many other locations (Sponsler & Johnson 2015) an important floral resource, common along roadsides and field margins. As the presence and size of these habitats was fixed (defined by the geo-data), we tested their impact on dilution for a range of resource quality values. To allow these off-field resources to be selected at all, it was required that at equal distance the ratio between energy intake and expenditure for these resources could be higher than for oil-seed rape, at least in the high quality case. Therefore, the density of open clover flowers in high quality off-field habitat was increased to 9000 flowers m^{-2} (see results, first section). Medium and low quality habitats were characterised by 6000 and 3000 flowers m^{-2}, respectively. The three quality levels were tested for a range of values for q, here representing the probability that an off-field element was considered a nectar resource patch.

All mechanisms are based on the idea of providing alternative floral patches, diverting foraging effort away from the exposed sites. Flower strips and semi-natural habitats may contribute to the persistence of pollinator populations in the agricultural landscape (Garibaldi et al. 2014; Haaland et al. 2011; Wratten et al. 2012). Also the presence of different (early and late) mass-flowering crops has been suggested to enhance pollinator density (Riedinger et al. 2014).

Real-world GIS data

We assessed potential dilution under these scenarios, using the northern part of the Flevoland area in the Netherlands as a case study. Geo-referenced data for field crops were obtained from the spatial land-use database LGN6 (grid-based, 25 m resolution) (Hazeu et al. 2011). For “Off-field Habitats”, data on the presence of off-field habitats (road side verges, ditch sides, shores, other semi-natural elements) were required. These were obtained from the vector-based dataset TOP10NL (PDOK 2015). We focussed on oil-seed rape as the dominant mass-flowering nectar-providing crop in Flevoland. In LGN6 oil-seed rape was included under the land-use category “other crops”. For the scenario studies we assumed that all fields in this category represented oil-seed rape. For the “Alternative Fields” scenario, an alternative mass-flowering crop was assumed to be present in the landscape. We chose one randomly from the other crop categories in LGN6. The combined geographic data that were used are shown in figure 1. All sites (cells in the 25 m grid) that bordered target crop fields were considered as potential beehive locations (Supplemental Figure S1).

The area contained 1207 fields with presumed oil-seed rape, in total 7057 ha. The alternative crop representing another attractive nectar source was present on 454 fields, in total 3375 ha. Off-field habitat patches were small and numerous: 58137 patches representing in total 3410 ha.

The used model coefficients are shown in tables 1 and 2, with crop-specific values set for oil-seed rape and clover. Regarding phenology and anthesis of flowers, we simply assumed that all resources were completely available during the whole day (10 hours of foraging). A uniform diurnal activity pattern of foraging was assumed, with the number of active foragers set to 1000. Results refer to dilution without enrichment.

RESULTS

Energetics-based model

From the energetics-based model (Eq. 6 and 7) we derived thresholds for the exploitation of resources depending on distance to the resource patch and other resource characteristics. The energy balance (*EI* – *EE*) for a foraging trip has to be positive (Dukas & Edelstein-Keshet 1998), leading to the condition:

(eq. 20)
$$\gamma e_R - \left(\frac{\gamma}{gaF} + 2\frac{D}{v}\right)e_F > 0$$

The threshold distance at which a resource patch cannot be exploited any more amounts to

(eq. 21)
$$D = \frac{v\gamma}{2}\left[\frac{e_R}{e_F} - \frac{1}{g}\left(\frac{1}{f} - h\right)\right] = \frac{v\gamma}{2}\left[\frac{e_R}{e_F} - \frac{1}{gaF}\right]$$

Figure 2 shows how threshold distance depends on resource characteristics e_R (J mg^{-1} nectar) and gF (mg nectar m^{-2}). The attack-rate a is assumed to be constant there.

Resource patch selection based on net energetic efficiency implies selecting the patch for which the ratio between energy intake and expenditure *EI/EE* is largest:

(eq. 22) $$\frac{EI}{EE} = \frac{\gamma e_R}{\left(\frac{\gamma}{gaF} + 2\frac{D}{v}\right)e_F}$$

This can be rewritten to:

(eq. 22a) $$\frac{EI}{EE} = \frac{gaF}{\left(1 + \frac{2D}{\gamma v}gaF\right)}e_R/e_F$$

Or, substituting $\frac{2D}{\gamma v}$ by constant C:

(eq. 22b) $$\frac{EI}{EE} = \frac{gaF}{(1 + CgaF)}e_R/e_F$$

Figure 3 shows how this ratio depends on resource characteristics *gaF,* the nectar acquisition rate, and *gF*, the nectar density. At equal distance, *EI/EE* scales linearly with energetic content e_R and asymptotically with *gaF*. In a mass-flowering case, a further increase of *gaF* will not increase *EI/EE* much. For a “sparse-flowering” resource to compete in attractiveness with a mass-flowering crop, its energy content or flower density needs to be considerably higher.

An interesting ‘extreme’ case arises for landscapes consisting entirely of fields with mass-flowering crops. There, open flower density *F* will be (very) large, and the functional response *f* will approach 1/*h*. As a consequence, the energy spent in the field EE_{field} will become very small (approaching zero) and *EE* will thus be determined mostly by EE_{travel}. The threshold distance (Eq. 21) will simplify to a linear relationship with e_R, with steepness independent of other crop properties (the honeybee constants between brackets):

(eq. 23) $$D \approx \left[\frac{\gamma v}{2e_F}\right]e_R$$

Maximising the net energetic efficiency in the mass-flowering case means maximising

(eq. 24) $$\frac{EI}{EE} \approx \left[\frac{\gamma v}{2e_F}\right]\frac{e_R}{D}$$

For fields at equal distance, the selected field will thus be the one with the highest energy content e_R (J mg^{-1} nectar).

Landscape scenarios

“Alternative Fields”

For a landscape containing only fields with the target crop, less than 1% of the sites have a dilution factor smaller than unity (Supplemental Figures S2). Even when p is zero (none of the fields besides the nearest are treated) there is no site with a dilution factor of zero, indicating that for every site the nearest (by definition treated) field was always included in the set of 10 hourly optimal resource patches. Fields are large enough so no depletion occurred that would induce a switch to another optimal field.

For the variant of alternative, by definition untreated, crops, there will be a fraction of sites for which the alternative crop field is the optimal resource (Supplemental Figures S3). For these sites, dilution will be absolute (no exposure at all). The fraction of sites for which this is the case increases linearly with the sugar content, as predicted from the net energetic efficiency being proportional to e_R (Supplemental Figures S4). As depletion is not likely to occur on most fields, except for the very small ones, there are only few intermediate values: either the nearest oil-seed rape field or an alternative crop field is selected and remains optimal during the whole day. Intermediate values arise when the set of daily optimal fields includes both types of fields.

“Flower Strips”

The typical cumulative dilution factor distribution (Fig. 4, Supplemental Figures S5) for a single simulation (a single landscape configuration with randomly located flower strips) shows sites with absolute dilution (no exposure), sites with no dilution at all, and sites with intermediate values, in proportions depending on the probability of a flower strip being present at an edge of a target crop field, p_{strip}, and the width of the flower strips, w (Fig. 5). Intermediate values occur at a site when one or more, but not all, of the hourly selected foraging patches for this site are without exposure (thus, flower strips). With an increasing width of the flower strips, the sites with some dilution change into sites with absolute dilution (no exposure). This implies that with narrow strips the selected strips were depleted while with strips wider than 5 m, depletion in the strips was not intense enough to make the field more attractive for foraging as compared to the flower strip.

The proportion of sites with no dilution at all did not depend on the width of the flower strips, but only on the probability of strips being present (Fig. 5). With flower strips always present on all four sides of a target crop field (p=1), only few sites (approx. 5 %) did not show any dilution.

"Off-field Habitats"

Presence of high quality off-field resource patches affected the distributions of dilution factors in a similar way as flower strips of 2 m wide (Fig. 6, Supplemental Figures S6). For the situation that each off-field patch was a resource patch (p_{res} =1) there were still sites with no dilution at all. The number of such sites increased with decreasing quality of the off-field resource, approximately from 10 to 30 % (Fig. 6). The main difference as compared to the "Flower Strips" scenario was that flower strips were by definition on the area of the target crop field and thus for sure close to the considered bee hive site. With off-field resources patches, there was no guarantee that these were sufficiently close to all target crop fields and thus to the bee hive sites. In addition, in most cases off-field resources were not present on every side of a target crop field.

The results for the "Flower Strips" scenario with 2 m wide strips, and "Off-field Habitats" with high density (high quality) patches, appeared very similar. Plotting dilution factors for both scenarios as a function of the required managed area, it appeared that the "Flower Strips" approach was approximately 10 times as efficient as compared with the "Off-field habitat" (Fig. 7). With managed flower strips of 5 m width, it was in the simulations even possible to reduce the proportion of exposed sites to almost zero, when flower strips were located around each target crop field.

DISCUSSION & CONCLUSIONS

Conceptual model

In the model the selection of an optimal resource patch, was based on energetic efficiency. The duration of a foraging trip was not directly accounted for in the efficiency, though indirect it had large impact through flight costs. Our assumption that no energetic costs were associated with extracting the nectar also implied that handling time did not affect patch choice, neither directly or indirectly. This means that flowers with long handling time were treated as equally attractive as flowers with short handling times. The model could easily be adjusted to incorporate energetic costs for extracting nectar, e.g., proportional to sugar content (viscosity). With handling times assumed equal, however, this would not make a difference for the results of our scenario study .

Assuming perfect knowledge of resource patches implies that no effects of fragmentation (e.g. isolated small patches remaining undetected), as found by (Dauber et al. 2010) for small patches only, can occur. The size of a resource patch itself has in the model no direct effect on its attractiveness, only indirectly through faster depletion of smaller patches. The forager population of a hive is treated as single organism. Thus, all foragers are assumed to visit the same optimal resource patch. As a consequence, the model predicts a decreasing flower visiting rate with patch size. This seems in accordance with findings of (Garbuzov et al. 2015b). As a fixed number of foragers are distributed, forager dilution may occur at field scale, similar to the pollinator dilution effect (Holzschuh et al. 2011; Veddeler et al. 2006).

The assumption that per time step a single resource patch is selected may seem at odds with the observation that within a day a colony may exploit several nectar sources (Beekman et al. 2004; Visscher & Seeley 1982). However, on a daily base, the current model allows this to happen, e.g., when during the day different resource patches may become optimal, due to diurnal dynamics in nectar availability (anthesis of the flowers) or due to depletion taking place. A single selected patch is the obvious outcome when assuming optimality. In reality there may be several causes for why the observed foraging is ‘sub-optimal’: the rate of adaptation of the colony to fluctuating resources, involving individual and social behaviour, may be limiting. Such factors can be explored well in complex individual-based models, but not in our parsimonious modelling approach. Tests with field data are needed to determine whether the “single resource selected per hour” restriction needs to be relaxed, and e.g., be replaced by one allowing a (small) set of resources to be exploited simultaneously.

The current modelling approach is for nectar foraging only. It is well known, that besides nectar, bee colonies also need pollen to satisfy the needs for protein. For several reasons exposure via nectar may be more important. Based on the annual need of pollen and nectar of 25 and 125 kg respectively, an about equal load (weight) per foraging trip of nectar and pollen and the assumption that both pollen- and nectar collecting bees forage per day similarly frequent, 5 times more foragers will be nectar collectors (Seeley 1985). In the hive, the in-coming nectar is divided over the foragers to provide them with energy for the next foraging trip, via trophallaxis the nectar is divided over most of the in-hive bees and brood, e.g., (DeGrandi-Hoffman & Hagler 2000). Pollen is stored directly in the cells for the silage process and subsequently consumed mainly by young nurse bees. Overall, the sugar consumption of individual bees exceeds the protein consumption about 5 times (Rortais et al. 2005). To deal with pollen foraging, the current model can be simplified, as there appear to be no large differences in quality of pollen, between different sources.

Energetics-based model

The maximum distance at which nectar-providing resource patches can, ignoring depletion, be exploited is given by Equation 21. The distances that were estimated for oil-seed rape and clover fields, 5.6 km and 5 – 8 km (for clover they were very sensitive to changing values of functional response coefficients), are well within the range of maximum observed foraging distances. For these mass-flowering crops, the threshold distance is mainly defined by the energy content (sugar content) of their nectar (Eq. 23). For natural elements with much sparser flower distributions, maximum distances can be lower (Fig. 2), but, depending on sugar content, also higher. Searching times in the patch will be higher in any case, increasing the energetic costs of traveling between flowers.

In landscapes with predominantly mass-flowering crops, our results indicate that foraging field selection may be determined by the ratio of energy content (sugar content) of the crops and their distance from the hive (equation 24). For natural elements with a sparse flower distribution, more factors have to be taken into account to calculate net energetic efficiency (full equation 22). Differences in species composition may, due to subtle differences in nectar content of their flowers, in the energy content of nectar, or in the flower density, lead to different outcomes. Hence, more variation in dilution factors is to be expected when accounting for more diverse nectar producing plants.

Depletion of resource patches will depend on their absolute patch size but also on their resource density (flowers or amount of nectar per unit area). Mass-flowering crops are biased with respect to both factors. Fields tend to be considerably larger in size than off-field elements. Flower density is extremely high, leading to a saturated functional response that will hardly decrease when available flower density decreases. For semi-natural elements the reverse is true.

On a landscape level, in current agro-ecosystems, few high quality off-field resource patches will be available to honey bees (De la Rúa et al. 2009). The energetic model predicts that mass-flowering crops will be selected even when these are located at a large distance from the hive. Observations indeed indicate that in the period during which mass-flowering crops are available, these crops constitute the predominant nectar source (Requier et al. 2015). Depletion is not likely to play a large role in these systems, as most crop fields are large and flower densities in the saturating range of the functional response. The model thus suggests that in general there will be little potential for dilution of exposure in such landscapes, as the only resource that may beat a mass-flowering crop is another (potentially sprayed) mass-flowering crop.

Landscape level exposure dilution

We tested three mechanisms for exposure-reduction resulting from landscape-level foraging. Starting from the worst-case assumption that the nearest target crop field was always treated, all tests indicated that there were only perspectives for dilution when untreated patches were 1) of high quality (equally or more attractive than the target crop), 2) nearby, and 3) numerous and of sufficient size (to avoid depletion and back-switching to the target crop). In a landscape with only crop fields providing resources, dilution appeared unlikely. In such a coarse-grained landscape, the probability of having a more attractive (in the sense of higher sugar content or smaller distance) untreated field in the neighbourhood is simply too small, even though this neighbourhood becomes extended when sugar content is higher. High quality flowers strips had the highest potential for dilution at the beehive: when all target crop fields were surrounded by flowers strips of at least 5 m wide, dilution factors became zero for almost all sites. High quality off-field habitat patches were, on an area base, approximately 10 times less efficient as compared to flower strips: 10 times as much area managed for high quality resources was needed to achieve the same dilution as 2 m wide flower strips. Their maximum possible impact was also smaller: when all off-field landscape elements were considered as high quality resource patches, still a considerable number of sites experienced no dilution at all. The explanation for the better performance of flower strips is easy to find: by being located on the target crop field, they can optimally fulfil the 3 conditions stated above, if they are sufficiently wide. Nevertheless, the location in the target crop field has an additional associated risk. It is very likely that treatment of the crop will lead to non-zero exposure in the strips at the field edges, through e.g., spray drift. With spray drift, effectiveness in attracting foragers may trade off against higher exposure risk for flower strips, and it will be possible to achieve a higher dilution for off-field patches that are carefully chosen with respect to their location relative to crop fields.

We applied the energetics-based model in a theoretical analysis of landscape-level mitigation options, based to a large extent on real-landscape data. The results show the potential of using this model in a realistic spatially-explicit risk assessment. Realism in this context refers in the first place to mapping presence and status of all relevant sources of nectar in the landscape. Clearly, for concrete applications this will require considerable effort, taking advantage of detailed GIS data that are increasingly often becoming available, and focussing on obtaining resource-specific model coefficients in particular for the resources associated with semi-natural habitats.

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Table 1(on next page)

Fixed(energetic) coefficients for honeybee and nectar

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Table 1.

Coefficient	*Symbol*	*dimension*	*Value*	*source*
Maximum foraging distance	D_{max}	m	Max 13.5 km; 95% within 6 km; mean 2.3 km	Values cited in (Beekman & Ratnieks 2000)
Flying speed	v	$m\ s^{-1}$	250 / 60 = 4.17	(de Vries & Biesmeijer 1998)
		$m\ s^{-1}$	417 / 60 = 6.95	(Seeley 1995)
Flight cost (unloaded)	e_U	$J\ s^{-1}$	2.22 / 60 = 0.037[1]	(Van Nest & Moore 2012) (from (Seeley 1986))
Flight cost (loaded)	e_L	$J\ s^{-1}$	4.5 / 60 = 0.075	(Van Nest & Moore 2012) (from (Seeley 1986))
Capacity (maximum load)	γ	mg	32.5	(Winston 1987)
Energetic value sugar	e_{SUGAR}	$J\ mg^{-1}$ sugar	17.2	(Seeley 1985)
Time unloading nectar	t_U	s	116	(Seeley 1994)

[1] Other values: 0.0334 $J\ s^{-1}$ (Schmid-Hempel et al. 1985) and references therein.

Table 2(on next page)

Resource-specificcoefficients

Coefficient values for the two resources considered in the study, oil-seed rape and clover

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Table 2.

Crop specific parameters				*Oil-seed rape*	*Off-field (clover)*
	g	nectar per flower	mg flower^{-1}	**2.4**	**0.24**
	F	Open flowers per area	open flowers m^{-2}	**1173**	**1500, 3000**[1]
		share of sugar in nectar	g g^{-1}	**0.53**	**0.67**
	e_R	energetic content nectar	J mg^{-1}	**9.116**	**10.777**
	a	attack rate	m^2 s^{-1}	**0.001**	**0.001**
	h	handling time	s flower^{-1}	**4**	**4**[2]

[1] 20-40 flowers per flower-head (average 30) (Burdon, 1983), assuming 50 – 100 flower-heads per m^2. In the simulations, 3000 open flowers m^{-2} was used in the low density (low quality) scenario. Hypothetical medium and high quality values were 6000 and 9000 open flowers m^{-2}, respectively.

[2] no data specific for clover, therefore assumed to be identical

1

Map of the case-study area

Oil-seed rape fields (ochre), alternative crop fields (lilac) and off-field resource patches (green) as used in the simulations.

2

The maximum energetically-profitable foragingdistance depending on flower (crop) characteristics

Maximum distance increases linearly with energy content of the resource (e_R here referred to as e_{crop} , in J mg $^{-1}$) and asymptotically with resource density *gF* (mg nectar m $^{-2}$) or its ^{10} log as shown here

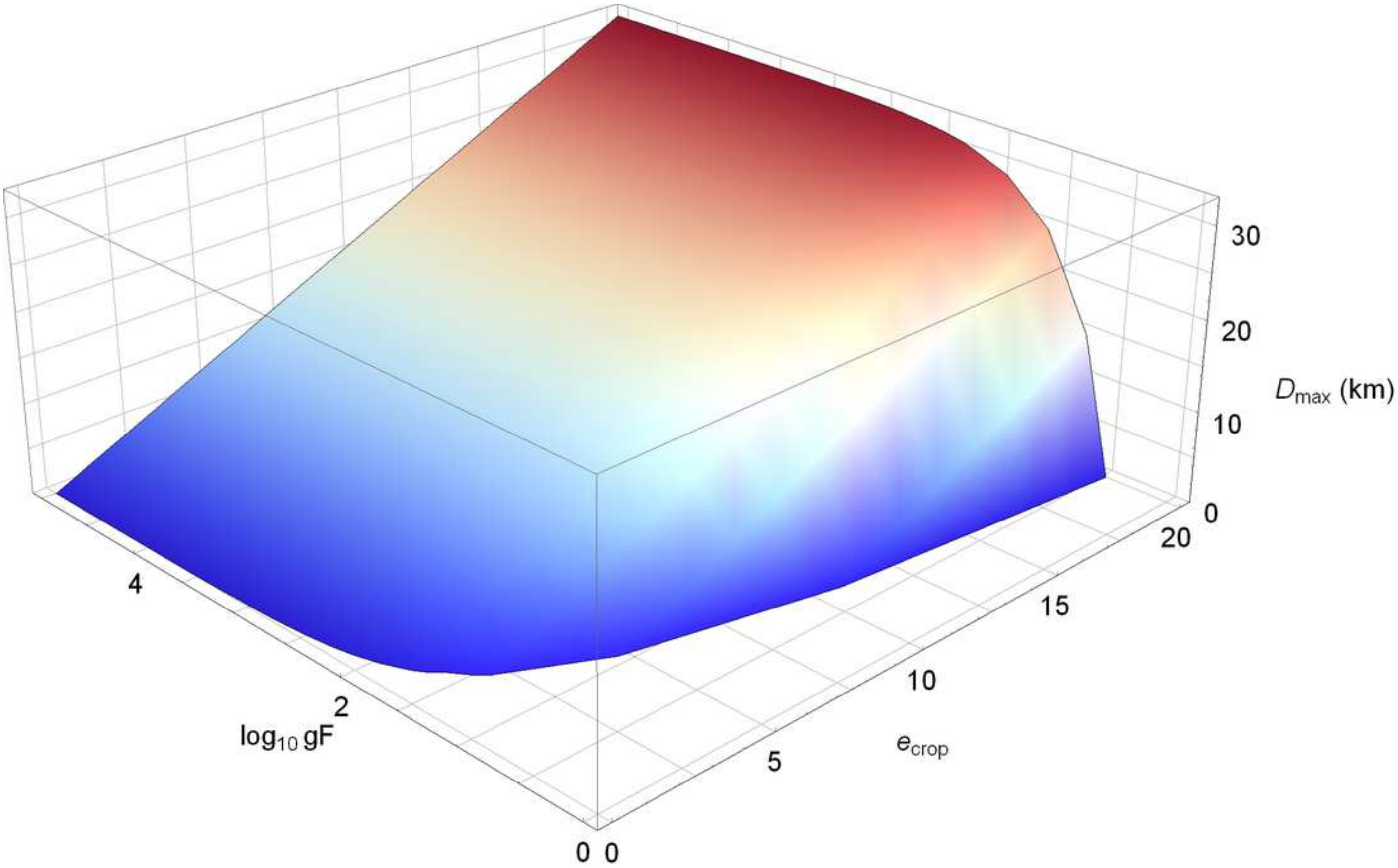

Figure 3(on next page)

Choice of resources depends on net energeticefficiency

The choice between resources at equal distance depends on their value for *EI/EE* (Eq. 22b). This ratio increases asymptotically with effective resource density *gaF* to the limit value 1/C × e_R / e_F. With larger e_R, e.g., for clover (dashed lines) compared to oil-seed rape (lines), *EI/EE* will level off at a higher value. When flower density is much higher, the resulting value of *EI/EE* may still be larger for the resource with the lower e_R (indicated points for clover and oil-seed rape).

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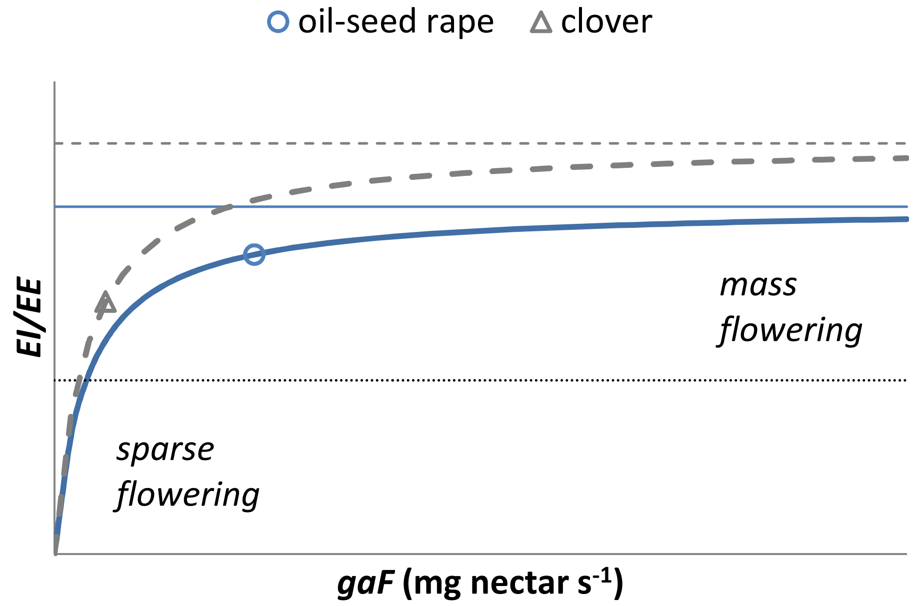

Figure 3

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Figure 4(on next page)

Flower strips may lead to exposure dilution

Individual simulations show that there are sites with no exposure, some dilution and no dilution. When averaging over multiple runs with different random assignment of flower strips, this information is lost.

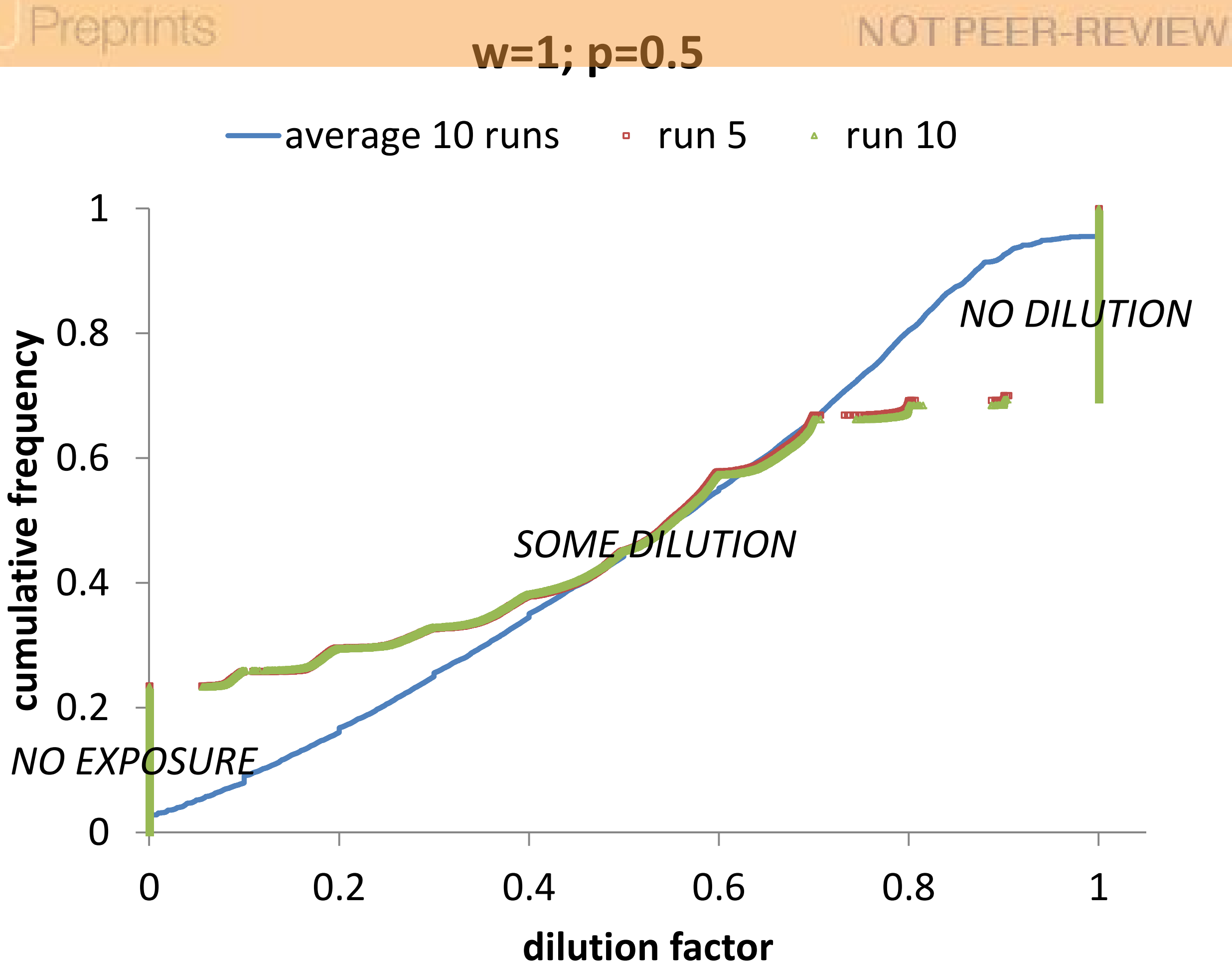

Figure 4

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Figure 5(on next page)

Probability of dilution depends on width andincidence of flower strips

The relative abundance of bee hive sites experiencing no dilution, some dilution or no exposure, depends on the probability *p* of a flower strip being present at a side of a target crop field, and on the flower strip width (*w*). Based on results from a single simulation (variation between simulations was small (Fig. 4)).

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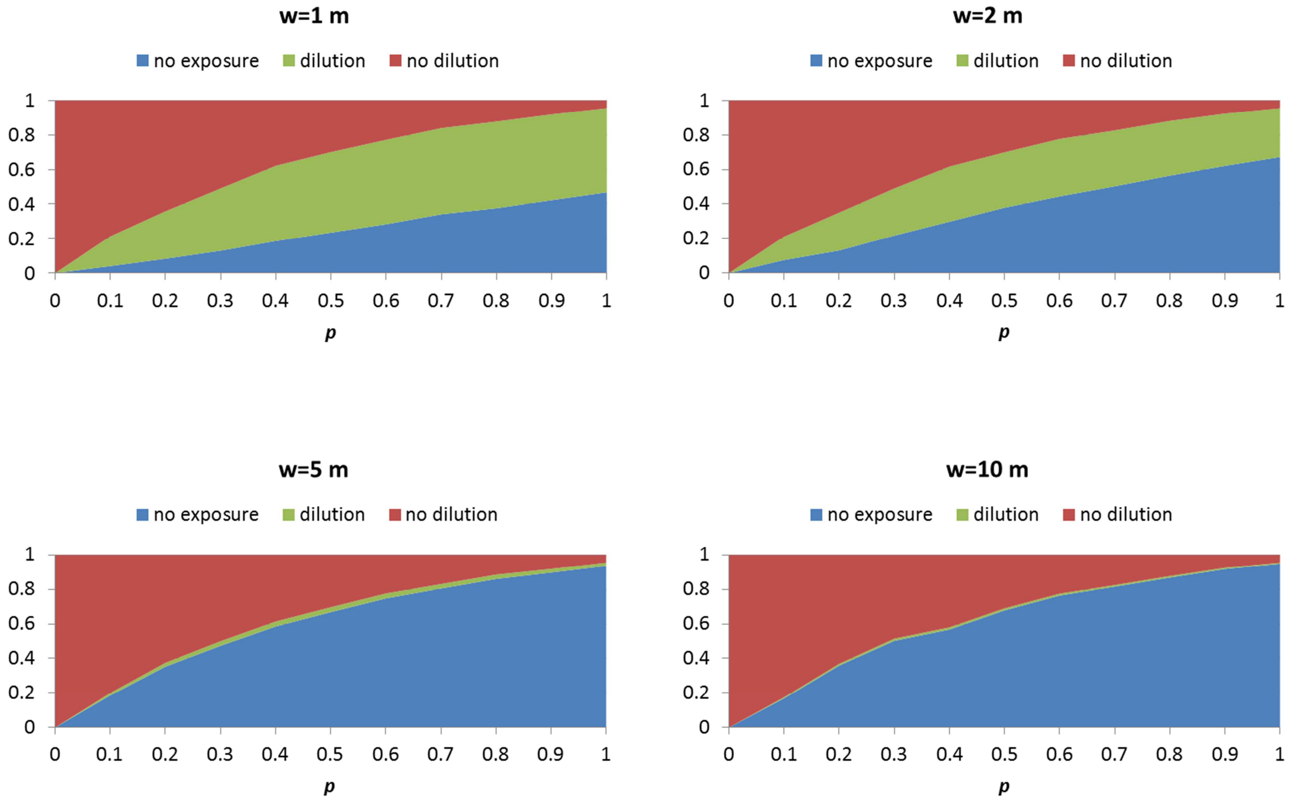

Figure 5

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Figure 6(on next page)

Probability of dilution depends on incidence andquality of managed off-field resource patches

The relative abundance of bee hive sites experiencing no dilution, some dilution or no exposure, depends on the probability p of an off-field patch being a managed resource patch, and on the quality of the off-field resource (represented by flower density). Based on results from a single simulation (variation between simulations was small).

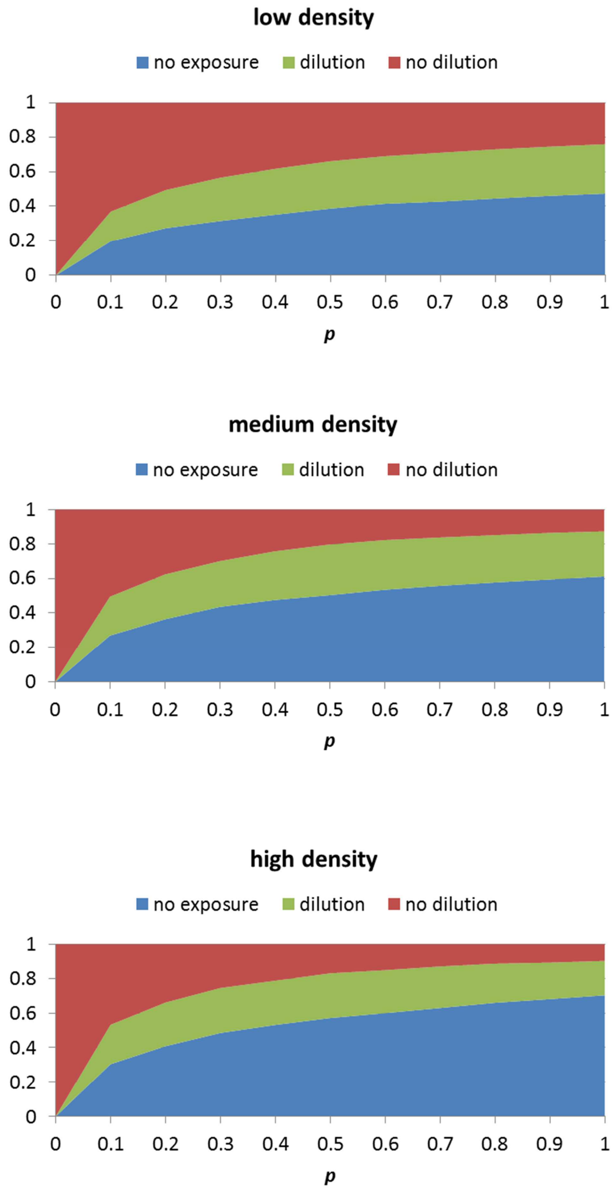
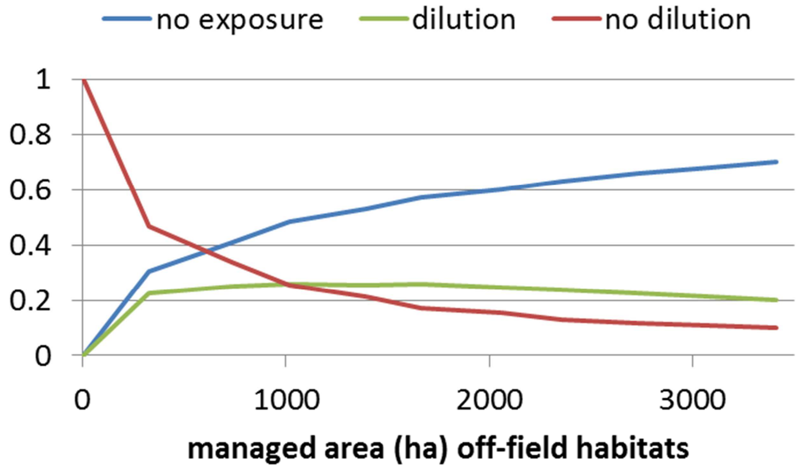

low density
🟦 no exposure 🟩 dilution 🟥 no dilution
1
0.8
0.6
0.4
0.2
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
p
medium density
🟦 no exposure 🟩 dilution 🟥 no dilution
1
0.8
0.6
0.4
0.2
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
p
high density
🟦 no exposure 🟩 dilution 🟥 no dilution
1
0.8
0.6
0.4
0.2
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
p

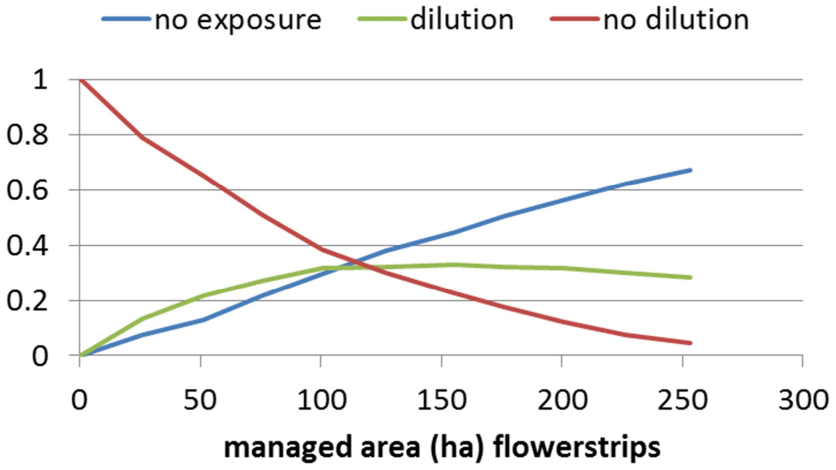
Figure 6

Figure 7(on next page)

Probability of dilution depends on managed area ofoff-field habitats or flower strips

The proportions of sites with no exposure, some dilution and no dilution depending on the managed area. Top: off-field habitats managed to provide high density (high quality) nectar resources. Middle: flower strips of 2 m wide. Bottom: flower strips of 5 m wide.





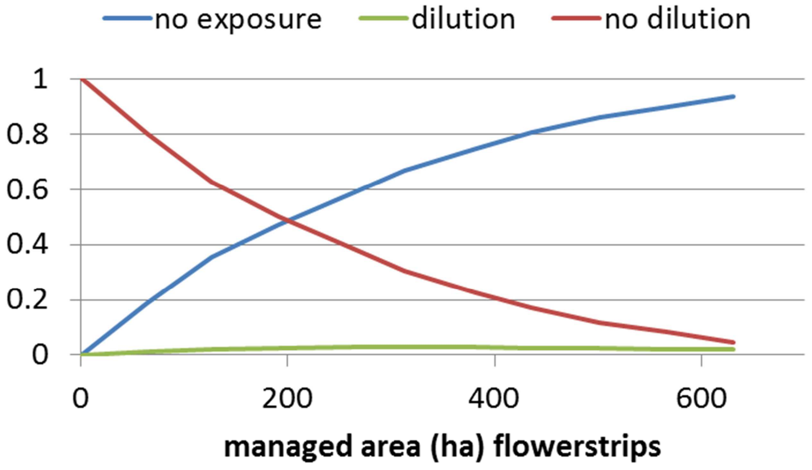


Figure 7

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