

## RESEARCH ARTICLE

# Modelling agricultural landscape complementation for natural pest control

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**Abstract**

1. Pest-regulating natural enemies often require crop and non-crop habitats to persist and be effective. These habitats offer hibernation sites, alternative prey or floral resources but can also be complementary in when they provide resources. The relative contribution of these different habitats to the performance of pest-regulating insects is largely unknown, since it is difficult to study empirically. Landscape-based population-dynamical modelling can fill this research gap.
2. In this study, we modelled the dynamics of predatory hoverflies (Diptera: Syrphinae) and their aphid prey in a collection of habitats. These hoverflies are dependent on different habitats for different reasons. While their larvae predate on aphids, adult hoverflies require floral resources. Resources are often segregated in different habitats. In addition, they are only temporarily available in any habitat type. In our model, hoverflies move between different habitats and select where to feed and where to produce off-spring based on optimal foraging considerations. The model represents habitats common in arable landscapes and their temporal availability of resources is parameterized based on field observations.
3. The model shows that effective pest suppression will only occur in the presence of at least three different habitats, including two crops that provide prey resources at different times of the year. A woody habitat with shrubs and trees provide aphid prey very early and late in the season, whereas an early crop and a late crop cover the period in between. In addition, these habitats need to provide floral resources in the same period as aphids, for example by flower strips in the margins of crop fields or blossoming trees or shrubs in the woody habitat. Under the model assumptions, the best pest suppression is obtained when the woody habitats take up 6% to 10% of the landscape. In addition to yearly population fluctuations, also bi- or multi-yearly cycles may occur, depending on the composition of the landscape.
4. *Synthesis and applications.* Our model shows when an agricultural landscape is 'complete' for natural enemies (and for effective pest control). For this, it needs to

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contain multiple habitats that supply floral and prey resources in different periods of the year.

#### KEYWORDS

aphids, complementary habitats, conservation biological control, landscape composition, landscape management, population-dynamical modelling, predatory hoverflies, semi-natural habitats

## 1 | INTRODUCTION

Organisms typically require a range of conditions and resources throughout their life in order to survive and reproduce, and all these conditions and resources are not always available (at the right moment) within a single habitat. To overcome this limitation, organisms move among various habitats, each providing different necessities, such as sites for feeding, hibernation, roosting, breeding and predator and parasitoid free refuges (Dunning et al., 1992; Ouin et al., 2004). Habitats may not only differ in the type of necessities they provide but also in the time they provide them. Due to the spatial segregation of types and timing of resources, an organism might need to visit several habitats to obtain all its essentials throughout its lifetime. Ideally, these habitats with complementary conditions and resources for the organism can be found at distances that can be overcome by the organism without too many costs; a condition that has been labelled 'landscape complementation' by Dunning et al. (1992).

The post-World War II Green Revolution led to the expansion of intensively managed agricultural landscapes composed of large monocrop fields and few and impoverished (semi-)natural areas, resulting in an increased homogeneity of agricultural landscapes (Raven & Wagner, 2021). Biodiversity and the related ecosystem services have suffered from this process (Benton et al., 2003; Sirami et al., 2019). This is likely due to species having difficulties in finding all their essential conditions and resources within one habitat and, therefore, depending on multiple different habitats, between which they have to move to find them all. This is also true for organisms providing ecosystem services, such as pollination and natural pest control (Zhang et al., 2007).

Natural pest control is provided by natural enemies of crop pests and is important in reducing pesticide use and promoting sustainable food production (Losey & Vaughan, 2006; Rusch et al., 2013). Conservation biological control aims to enhance pest suppression through improving the environmental conditions for the natural enemies of the pests (Jonsson et al., 2008). Landscape management plays a key role in conservation biological control by increasing resource availability for natural enemies (Gurr et al., 2017; Landis et al., 2000). Research indicates that landscape composition, which refers to the proportion of habitats and defines the distribution of resources, strongly influences natural enemy richness and abundance (Bianchi et al., 2006; Dainese et al., 2019; Rusch et al., 2013; Tschamtko et al., 2007). Many arthropod predators and parasitoids of pests do not only require prey but also floral resources (nectar

and pollen) during part of their life cycle (Jervis et al., 1993; Landis et al., 2000; van Rijn et al., 2013; Wäckers & Van Rijn, 2012). In agricultural landscapes, floral food and pest prey generally occur spatially separated. However, it is largely unclear how landscape composition affects natural enemy dynamics and pest control through time and space, as many studies show substantial variation in the response of pests, natural enemies and crop damage to spatial variation in habitats (Grab et al., 2018). Based on landscape complementation theory we expect that the relative contribution of specific habitats to natural pest control will depend on the distribution of resources among the habitats within the landscape (van Rijn, 2017).

Understanding how the agricultural landscape can better support natural pest control is paramount. However, experimental studies at the landscape scale are notoriously difficult to perform and can be extremely time consuming, as new landscape elements sometimes need years to develop into suitable resource patches. Additionally, when in existing landscapes natural pest control is related to specific landscape elements, confounding factors are difficult to exclude (Karp et al., 2018; Rusch et al., 2010) and cause and effect are often difficult to separate. Landscape-based population-dynamical modelling offers an alternative approach (Bianchi et al., 2007; van Rijn et al., 2002). Both the process of formulating such a model, based on the natural history of key species, and the results from model simulations can serve to gain better understanding of the system and to identify key processes and their possible bottlenecks. Furthermore, the quantitative results from model simulations can help to predict the landscape configurations that maximize natural pest control.

We designed a model to capture the dynamics of predatory hoverflies (Diptera: Syrphinae) and its aphid prey (Homoptera: Aphididae) in a multi-habitat environment. Various aphid species are important pests in different arable crops, while other aphids are common in non-crop habitats as well (Dixon & Thieme, 2007; van Rijn, 2014). Predatory hoverflies are common and important natural enemies of aphid pests in arable crops (Jauker et al., 2012; van Rijn & Wäckers, 2010). Our population-dynamical model is based on work by van Rijn (2017), but is adapted to better fit the resource dynamics observed in North-Western European arable crops and semi-natural habitats (van Rijn et al., 2024). The model is spatially implicit and is framed in a set of ordinary and delay differential equations, similar to other population-dynamical models (Banks et al., 2017; Cushing, 2013; McCauley et al., 1993; van Baalen et al., 2001; van Rijn, 2017; van Rijn et al., 2002). Our model uniquely combines (1)

predator–prey interactions, (2) detailed seasonal forcing, (3) stage structure and (4) habitat structure, whereas other models combine only 2 or 3 of these attributes (Ellner et al., 2001; McCauley et al., 1993; Sauve et al., 2020).

This modelling study aims to explore how landscape composition influences natural enemy and pest dynamics and how it can be altered to enhance natural pest control. At a theoretical level, the focus is on two research questions: (1) Given a common North-Western European combination of arable agricultural habitats, what patterns of predator–pest dynamics may occur? (2) What is the effect of seasonal resource availability and landscape composition on predator–pest dynamics? At a more practical level, the research questions are: (3) What combination of habitats is essential for effective natural pest control? (4) What proportion of habitats in the agricultural landscape maximizes natural pest control?

## 2 | MATERIALS AND METHODS

### 2.1 | Model description

Here, we give a short overview of the main model components; see the [Supporting Information](#) for an in-depth model description. The model was inspired by the agricultural landscape of the Hoeksche Waard and similar areas dominated by arable crop production in the Netherlands. The main crops are winter wheat and potato, followed by sugar beet and a number of minor crops. Apart from residential areas, non-crop (semi-natural) habitats make up less than 5%, partly planted with trees and shrubs partly herbaceous. Flowers, essential for hoverflies, are especially available in field margins at the edges of arable fields (van Rijn et al., 2024). To create a simple model that still captures all aspects of the landscape that are important for predatory hoverflies, we defined the following habitat types: (a) woody habitat (providing prey and floral resources in spring), (b) flower-rich herbaceous habitat (providing floral resources especially in summer), (c) an early arable crop (typically winter wheat) and (d) a late arable crop (typically potato).

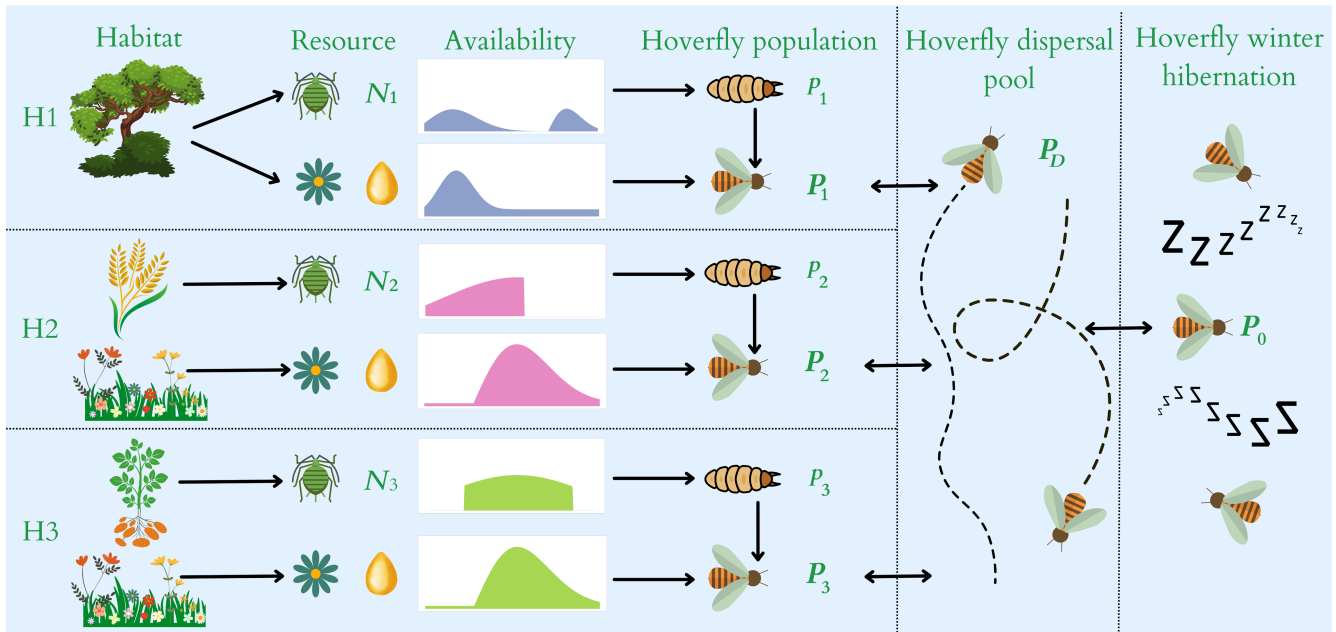
Since we know that predatory hoverflies are only able to produce offspring in colonies of aphids when floral resources are available as well (van Rijn et al., 2013), the flower-rich herbaceous habitats are represented by flower strips connected to each of the crops. The flower strips and the crop fields are therefore considered sub-habitats within the crop habitats. For consistency, all habitats (the woody habitat, the early crop and the late crop) are assumed to consist of two sub-habitats, one providing aphid prey and one providing floral resources. In the woody habitat, this distinction between sub-habitats can be seen as woody aphid host species and flower bearing woody species. Thus, the main habitats defined in our model are: (1) a woody habitat, (2) an early crop (winter wheat) and its flower rich field margin and (3) a late crop (potato) and its flower rich field margin (Figure 1). Movement between the main habitats ('dispersal') was considered to be a slower process than movement between the aphid and flower sub-habitat ('foraging', Box 2).

The habitats are characterized by the type and timing of the resources they provide for the hoverflies (Figure 1). The seasonal forcing functions used to describe the resource availability per habitat are all based on observations made in the field (van Rijn, 2014; van Rijn et al., 2024; Sections S1.1.1 and S1). A year is represented by a cycle of 210 days, the period in which the populations of hoverflies and aphids are expected to interact: early April until the end of October. In the remaining part of the year, the aphids and hoverflies are assumed to hibernate during which they experience mortality only.

The model has no explicit spatial dimensions but is formulated as a set of (delay-)differential equations with subsets for the different habitats. The state variables of the model represent the densities of the aphids (all life stages together) in habitat 1 ( $N_1$ ), 2 ( $N_2$ ), and 3 ( $N_3$ ); hibernating adult hoverflies ( $P_0$ ); adult hoverflies in habitat 1 ( $P_1$ ), 2 ( $P_2$ ) and 3 ( $P_3$ ); juvenile hoverflies in habitat 1 ( $p_1$ ), 2 ( $p_2$ ) and 3 ( $p_3$ ); and finally dispersing adult hoverflies ( $P_D$ ) (Box 1). The hoverflies are assumed to comprise one population because the adults can move among the habitats. However, the aphid populations are assumed habitat and host plant specific, hence, have separate populations in each habitat. Parameters for growth, death and development rates are based on data observed at 22°C but are corrected for daily temperature variation over the year, based on an approximately linear temperature–rate relationship with 4°C as lower threshold temperature. Daily temperature changes over the season are modelled by multiplying the rates with a temperature correction function ( $t_c$ ) (Figure 2b).

Aphid population densities are determined by intrinsic growth rate, carrying capacity, mortality rate, predation rate of hoverfly larvae and winter/harvest mortality (Box 1, equations 1 and 2). At the start of simulations, aphids enter the woody habitat and remain there the entire year; at the end of the year these aphids go into hibernation and a fixed proportion survives until the next year ( $m_i$ ). In the crop habitats, every year a fixed number of aphids enter the habitat shortly after crop emergence (late crop) or when temperatures allow aphids to become active (early crop) at an infestation rate that is carried out over 1 day ( $\text{in}N_{i,j}$ ); this process is repeated every year. The seasonal variation of the aphid growth rate (Figure 2c) and carrying capacity (Figure 2d, Weibull distribution) is characteristic for the different habitats. Predation on aphids is assumed to level off at higher aphid densities (type II functional response), described by the Michaelis–Menten equation ( $f(t)$ ). At crop removal, all aphids and juvenile hoverflies are assumed to die in the habitat within 1 day ( $m_m$ ).

Juvenile hoverfly densities are the result of adult female reproduction, daily mortality, development and harvest mortality (Box 1, equation 3). Hoverfly reproduction ( $G$ ) is positively affected by aphid density, because females produce eggs only when (cues of) aphids are detected. Only a proportion of adult hoverflies reproduce ( $sa_f$ , Box 2), which depends on floral resource availability ( $B_i$ ) as only females that have consumed enough pollen and nectar are assumed to search for prey and oviposit. The larval development rate ( $e$ ) is directly related to their feeding (predation) rate and their mortality ( $\mu_j$ ) is inversely related to it.



**FIGURE 1** Simplified diagram of the spatially implicit population-dynamical model for predatory hoverflies and their aphid prey in three habitats: A woody habitat (H1), an early crop (winter wheat) with adjacent flower margins (H2) and a late crop (potato) with adjacent flower margins (H3). In the crop habitats (H2 and H3), the crop provides aphid prey and the flower margin provides floral resources, whereas the woody habitat (H1) provides both but are in the model split up into sub-habitats. Timing of resource availability is indicated for every resource that a habitat provides per year, in the absence of predators, showing that every habitat provides the two resources during different times of the simulated year (210 days). The populations of hoverflies and aphids are assumed to interact from April until October (210 days). Adult hoverflies ( $P_h$ , with  $h$  indicating the habitat) feed on nectar and pollen but nectar is assumed to be limiting, so pollen availability is not modelled. Hoverfly larvae ( $p_h$ ) feed on aphids ( $N_h$ ) that are available in different habitats during different times of the year. Adult hoverflies move between habitats through the hoverfly dispersal pool ( $P_D$ ). At the end of the year, adult hoverflies hibernate ( $P_0$ ). In March, hoverflies emerge from hibernation and enter the dispersal pool ( $P_D$ ).

Adult hoverfly densities within the habitats are the result of development, mortality, dispersal, hibernation and winter mortality (Box 1, equation 5). Predator life-cycle stages that do not consume aphids and do not reproduce, such as the pupal stage, the female pre-reproductive stage and the egg stage, were not modelled explicitly but included as a time delay ( $\tau_h$ ) in the larval-to-adult transition. Upon completing their development ( $ep_h$ ), juveniles join the adult population after a delay of  $\tau_h$  days. Adult mortality rate  $\mu_{p_h}$  depends on floral resource level ( $B_h$ ) by affecting the proportion of ill-fed adult hoverflies in the flower sub-habitat ( $s_{b_i} \mu_{p_h}$ , Box 2).

Dispersal of adult hoverflies among habitats is modelled with a dispersal pool ( $P_D$ , Box 1, equation 6). The number of hoverflies that move from a habitat into the dispersal pool is proportional to habitat size and inversely related to their expected fitness in the current habitat, determined by flower ( $B_h$ ) and aphid ( $N_h$ ) availability. As a result, the distribution of hoverflies among the habitats is close to the distribution of fitness values (van Rijn et al., 2002). It is assumed that the females can only base their decision where to go on the value of the current resource densities for themselves and their offspring, and that the resource densities their offspring will experience are sufficiently correlated with the current values. The expected fitness can then be defined as the net reproduction rate ( $R_0$ ), which equals the product of daily oviposition rate ( $G(N_h)$ ), mean oviposition period ( $1/\text{adult mortality rate } \mu_{p_h}$ ) and juvenile survival, with the current

resource levels as input. We assumed that dispersing hoverflies do not know the quality of a habitat from a distance and redistribute themselves randomly among habitats proportional to their relative sizes ( $\alpha_h D_0 P_D$ ). So the influx into a habitat is proportional to its size, but the impact of the influx on population density is inversely proportional to habitat size and thus here, habitat size cancels out. Additionally, the dispersing population experienced daily mortality ( $\mu_{p_D}$ ), but do not survive the winter period ( $m_m$ , Box 1, equation 6). Hoverfly movement between the two sub-habitats within a habitat is described by a satiation-driven distribution model (Box 2).

In autumn, the hoverflies in the dispersal pool go into hibernation (Box 1, equation 4). This hibernating population ( $P_0$ ) survives into the next year but experience some winter mortality ( $m_i$ ). The rate at which hoverfly populations enter hibernation and the gradual emergence from hibernation in spring are modelled with a normal distribution as a function of time ( $h_1(t)$  and  $h_0(t)$ , respectively).

## 2.2 | Model analyses

The model dynamics were simulated with the package DeSolve in R, using the multi-step integration method lsoda (Soetaert et al., 2010). Simulations were run for multiple years until relatively stable patterns emerged to yield results that were independent from arbitrarily

## BOX 1 Differential equations

All state variables and many parameters are dependent on time. Functions can depend on state variables and other parameters, which is indicated between brackets in the differential equations. A brief explanation of all parameters and functions can be found in [Table 1](#). See [Supporting Information](#) for more detailed explanation.

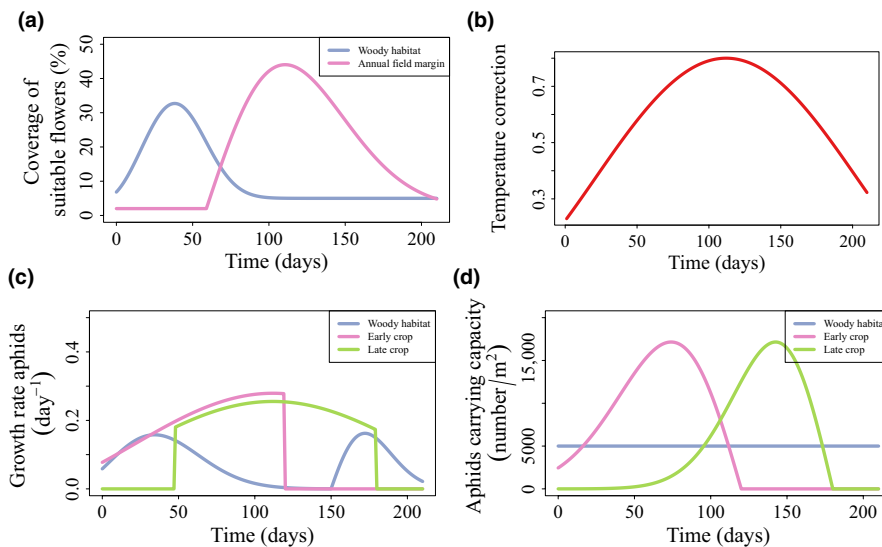
$$\left. \begin{array}{l} \text{Aphids in the woody habitat} \\ \frac{dN_1}{dt} = r_1(t)(1 - N_1/K_1)N_1 - \mu_1(t)N_1 - p_1f(N_1, t) - m_l(t)N_1 \quad (1) \\ \text{Aphids in crop habitat } h \\ \frac{dN_h}{dt} = \text{in}N_h(t) + r_h(t)(1 - N_h/K_h(t))N_h - \mu_h(t)N_h - p_hf(N_h, t) - m_m(t)N_h \quad (2) \\ \text{Juvenile hoverflies in habitat } h \\ \frac{dp_h}{dt} = G(N_h, t)s_{a_r}(B_h(t))P_h - \mu_j(N_h, t)p_h - e(N_h, t)p_h - m_m(t)p_h \quad (3) \\ \text{Hibernating adult hoverflies} \\ \frac{dP_0}{dt} = s_1(t)P_0 - s_0(t)P_0 - m_l(t)P_0 \quad (4) \\ \text{Adult hoverflies in habitat } h \\ \frac{dP_h}{dt} = e(N_h((t - \tau_1), t - \tau_1))p_h(t - \tau_1, t) + D_0P_D - \mu_{p_h}(t)s_{p_h}(B_h(t))P_h - D(N_h, B_h)P_h - m_m(t)P_h \quad (5) \\ \text{Dispersing adult hoverflies} \\ \frac{dP_D}{dt} = s_0(t)P_0 + \sum_{h=1}^3 \alpha_h D(N_h, B_h(t))P_h - s_1(t)P_D - D_0P_D - \mu_{P_D}(t)P_D - m_m(t)P_D \quad (6) \end{array} \right\}$$

TABLE 1 Brief explanation of parameters and functions found in the differential equations ([Box 1](#)). A more elaborate explanation of all parameters and functions can be found in the [Appendix S1](#) and [S2](#).

Function or parameter	Description
$\alpha_h$	Proportion of habitat $h$ in the landscape
$t_c(t)$	Temperature correction for growth, mortality and development rates, as a function of time of the year ( <a href="#">Figure 2b</a> )
$\text{in}N_h(t)$	Infestation rate of aphids in the crop habitat $h$ . A couple of days after the emergence of the crop ( $T_{hi}$ ), the crop is infested with $N_{hi}$ aphids/m <sup>2</sup> in 1 day
$r_h(t)$	Intrinsic growth rate of aphids in habitat $h$ as a function of time of the year ( <a href="#">Figure 2c</a> ). It is obtained by multiplying the intrinsic growth rate ( $r_{mh}$ ) by the habitat-specific resource availability ( $n_h(t)$ ) and the temperature correction ( $t_c(t)$ )
$K_h(t)$	Carrying capacity of aphids in habitat $h$ , as a function of time of the year ( <a href="#">Figure 2d</a> )
$\mu_h(t)$	Constant mortality rate of aphids in habitat $h$ , corrected for temperature with $t_c(t)$ , including all abiotic factors plus predation by natural enemies other than hoverflies (the dynamics of these other natural enemies are not included)
$f(N_h, t)$	Per capita predation rate of aphids by juvenile hoverflies, as function of local aphid density, levelling off at higher prey densities (type II functional response) and corrected for temperature with $t_c(t)$
$m_l(t)$	Low winter mortality of the hibernating aphids (H1) and adult hoverfly populations, modelled over a single day
$m_m(t)$	Maximum mortality of a population due to the onset of winter or crop plant removal, killing all the individuals in the population, modelled over a single day
$h_1(t)$	Rate of entering hibernation by adult hoverflies, as function of time of the year, modelled with a normal distribution function
$h_0(t)$	Rate of leaving hibernation by adult hoverflies in spring, as function of time of the year, modelled with a normal distribution function
$\tau_h$	Developmental delay for hoverflies that represents all non-predatory and non-reproductive stages in between larva and adult, included as an influx into the adult hoverfly population in habitat $h$

## BOX 1 Continued

Function or parameter	Description
$e(N_h, t)$	Developmental rate of hoverfly larvae as a function of their predation rate, corrected for temperature with $t_c(t)$
$\mu_p(t)$	Mortality rate of adult hoverflies in habitat $h$ , corrected for temperature with $t_c(t)$
$s_b$	Proportion of adult hoverflies that are ill-fed and in floral (sub-)habitat
$G_h(N_1, t)$	Reproduction rate of hoverflies in habitat $h$ , modelled as a type-II numerical response to prey density and corrected for temperature with $t_c(t)$ . Hoverfly reproduction is also affected by availability of floral resources because the proportion of females that will reproduce ( $s_a(B)$ ) is a function of floral resources availability
$B_h(t)$	Floral resource availability in habitat $h$ , as a function of time of the year, based on the cover of flowers with nectar accessible for hoverflies
$s_a(B_h(t))$	Proportion of adult hoverflies that is well-fed and in an aphid (sub-)habitat, which depends on the amount of floral resources present ( $B_h$ ), as described by the satiation-driven distribution model (Box 2)
$\mu_j(N_h, t)$	Mortality rate of juvenile hoverflies, inversely related to their predation rate and corrected for temperature with $t_c(t)$
$D_0$	Maximum dispersal rate of adult hoverflies
$D(N_h, B_h(t))$	Dispersal rate of adult hoverflies, inversely related to the net reproduction rate ( $R_0$ ) that is expected under current resource levels within the current habitat



**FIGURE 2** Seasonal forcing functions, defining how rates and resources change with the time of the year: (a) Density of floral resources suitable for hoverflies ( $B_h$ ) in woody habitats (habitat 1) and in annual field margins of the crop habitats (habitat 2 and 3). (b) Temperature correction for growth, mortality and development rates, as a function of time of the year ( $t_c$ ). (c) Aphid intrinsic growth rate in the three different habitats ( $r_h(1 - N_h/K_h)N_h$ ). In the woody habitat, the aphid intrinsic growth rate shows two peaks, one in spring and one in autumn, depending on the availability of phloem resources ( $n_h$ ). In crop habitats, the intrinsic growth rates are constant as long as the crop is present but corrected for temperature. (d) Aphid carrying capacity in three different habitats ( $K_h$ ). In the woody habitat (habitat 1), the carrying capacity is assumed to be constant. In the crop habitats (habitat 2 and 3), carrying capacity is determined by leaf surface area. It gradually increases with the growth of the crop plants and shows a rapid decline at the end of the growing season when the leaves of the crops start deteriorating.

chosen initial densities. Model dynamics were analysed by comparing multi-year simulations with default parameters to those with modified values.

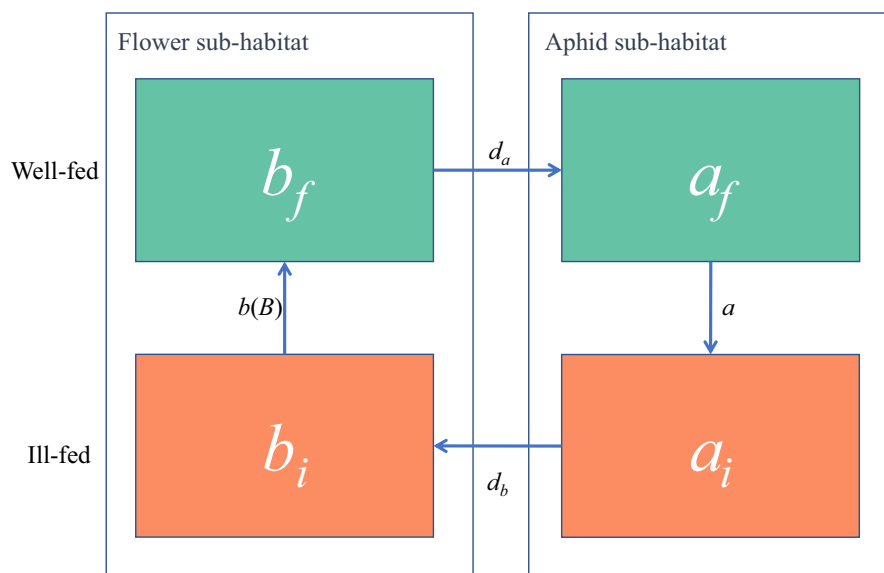
First, the importance of each habitat or sub-habitat within the landscape composition was studied by removing it from the model.

If a crop habitat was removed, the space it occupied was assigned to the other crop, while the proportion of the woody habitat remained the same. When the woody habitat was removed, the crop habitats each took up 50% of its area. Second, the effect of the amount of floral resources in the field margins was assessed by varying the

## BOX 2 Novel satiation-driven distribution model

Foraging movements between a sub-habitat with aphid prey and a sub-habitat with floral resources are assumed to be driven by the internal state of the adult female hoverfly, as hoverflies are expected to search for flowers when ill-fed and for prey when well-fed (Lewis et al., 1998; van Rijn et al., 2013). We created a sub-model based on this theory to predict the hoverfly distribution among the two sub-habitats in response to floral resource levels. When the hoverflies can be in two feeding states (ill- and well-fed) in two sub-habitats, the hoverflies can be in four different states (Figure 3). When in the flower sub-habitat and ill-fed ( $b_i$ ), hoverflies will feed and become well-fed ( $b_f$ ) at a rate  $b$ , which depends on the proportion of suitable flowers ( $B$ ) in this sub-habitat. When well-fed, hoverflies will move into the aphid sub-habitat ( $a_i$ ) at a rate  $d_a$ , where they will forage for plants with aphids to oviposit. In doing so, they use energy and will become ill-fed ( $a_i$ ) again at a rate  $a$ . When ill-fed, they will return to the flower sub-habitat with rate  $d_b$ . Neglecting mortality, hoverflies can move from one state to only one other state, thereby creating a cycle of states (Figure 3). The dynamics of the number of hoverflies in for example state  $a_f$  are now described by the differential equation:

$$\frac{dP_{a_f}}{dt} = d_a P_{b_f} - a P_{a_f}. \quad (1)$$



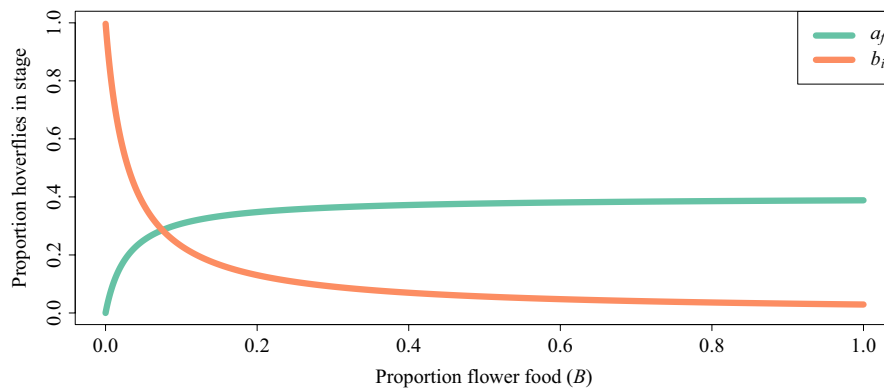
**FIGURE 3** The four states of a hoverfly depending on her feeding state (well-fed vs. ill-fed) and sub-habitat (flower vs. aphid), and their transition rates due to feeding ( $b$ ), using energy ( $a$ ), moving to the aphid sub-habitat ( $d_a$ ), and moving to the flower sub-habitat ( $d_b$ ). With no immigration or mortality, the proportion in each state depends on only two other states and the equilibrium distribution among the four states can be calculated explicitly from their transition rates. While all other rates are assumed to be constant, the feeding rate  $b$  is affected by the floral resource availability  $B$ .

Rather than expressing this sub-system with four differential equations for each habitat, we assumed that this foraging process is fast relative to other processes (population dynamics and dispersal among main habitats), so that the distribution among the four states is close to equilibrium. At equilibrium, equation (1) and the other three differential equations are equal to zero. Due to its circular dependence, the number of hoverflies in each state is proportional to the reverse of the outgoing relative transition rate, for example the number in  $a_f$  is proportional to  $a^{-1}$ , which means that the proportions  $s$  of hoverflies in each of the four states  $a_f$ ,  $a_i$ ,  $b_i$  and  $b_f$  can be described by:

$$\begin{cases} s_{a_f}(B) = \frac{a^{-1}}{a^{-1} + d_b^{-1} + b(B)^{-1} + d_a^{-1}} \\ s_{a_i}(B) = \frac{d_b^{-1}}{a^{-1} + d_b^{-1} + b(B)^{-1} + d_a^{-1}} \\ s_{b_i}(B) = \frac{b(B)^{-1}}{a^{-1} + d_b^{-1} + b(B)^{-1} + d_a^{-1}} \\ s_{b_f}(B) = \frac{d_a^{-1}}{a^{-1} + d_b^{-1} + b(B)^{-1} + d_a^{-1}} \end{cases}. \quad (2)$$

## BOX 2 Continued

The spatial proximity between flower and aphid sub-habitat is reflected in the values of  $d_a$  and  $d_b$ , which describe the movement rate of adult hoverflies between both sub-habitats. Reproduction was assumed to relate to the proportion well-fed hoverflies in the aphid sub-habitat ( $s_a$ ), and adult mortality was assumed to relate to the proportion ill-fed hoverflies searching for flowers ( $s_b$ ), due to starvation. In this way, population-level reproduction increases and mortality decreases with flower availability  $B_h$  within the habitat (Figure 4). Although the distribution is derived based on the assumptions of zero mortality, simulations with the sub-system of differential equations show that including mortality in  $b_i$  of for example 0.3/day changes the proportions with 20% at most, without changing the shape of the relationships with  $B$ .



**FIGURE 4** The proportion of hoverflies that can reproduce ( $a_f$ ) is an increasing function of flower availability ( $B$ ) and the proportion that experiences mortality ( $b_i$ ) due to starvation is a decreasing function of flower availability ( $B$ ) within each habitat.

maximum level of floral resources ( $B_{2m}$  and  $B_{3m}$ ) for natural enemies, between 0% and 100%. Finally, the effect of the percentage of woody habitat in the landscape was assessed by varying it stepwise between 0% and 12%, assuming that the early and late crop took up equal parts of the remaining landscape. Additionally, the possibility of compensating for the lack of one (sub-)habitats with increasing another was assessed by varying the percentage woody habitat both in the presence and absence of other (sub-)habitats. The results were summarized by the yearly average densities of aphids within each habitat and adult hoverflies in all habitats together. To explain multi-year population cycles, phase planes of aphid and predator densities were studied as well (further explained in Appendix 4).

## 3 | RESULTS

### 3.1 | Population dynamics

Due to seasonal forcing and predator-prey interactions, hoverfly (predator) and aphid (pest) populations showed strong seasonal cycles in all habitats within each yearly 210day interaction period. Adult hoverflies aggregate in the habitat that has the highest aphid and flower densities, in which, after a short delay, hoverfly larvae emerge. At some point, these larvae reduce the aphid densities in that habitat (Figure 5). During the year, adult hoverflies initially move to the woody habitat after emerging from hibernation, move to early

crop around June, and then, after having reduced the aphid numbers there to low levels, move to the late crop around July. After reducing the aphid numbers there as well, hoverflies return to the woody habitat and subsequently enter hibernation.

With the standard parameter set, the model exhibited both seasonal cycles within a year and stable bi-yearly population cycles of predator and aphid densities (Figure 6): years with higher predator and prey densities are consistently alternated with years with lower densities. Years with initial high aphid densities resulted in high predator densities that strongly reduced aphid densities later in the year, which ultimately (in the woody habitat) reduced the density of predators going into hibernation (Figure 6, years 2 and 4). The consequently lower initial predator densities in the next year caused higher aphid numbers in the crop habitats, which resulted in higher densities of predators going into hibernation (Figure 6, years 1 and 3).

### 3.2 | Effect of landscape composition

Removing any (sub-)habitats increased aphid densities in both crop habitats when averaged over the multi-year cycle (Figure 7: all dots are above the red line), indicating that all included landscape elements contribute to pest suppression. Removing the flower sub-habitat from the woody habitat resulted in a sixfold increase of the aphid density in the early crop and a threefold increase in the late crop (Figure 7). Removing the entire woody habitat raised average



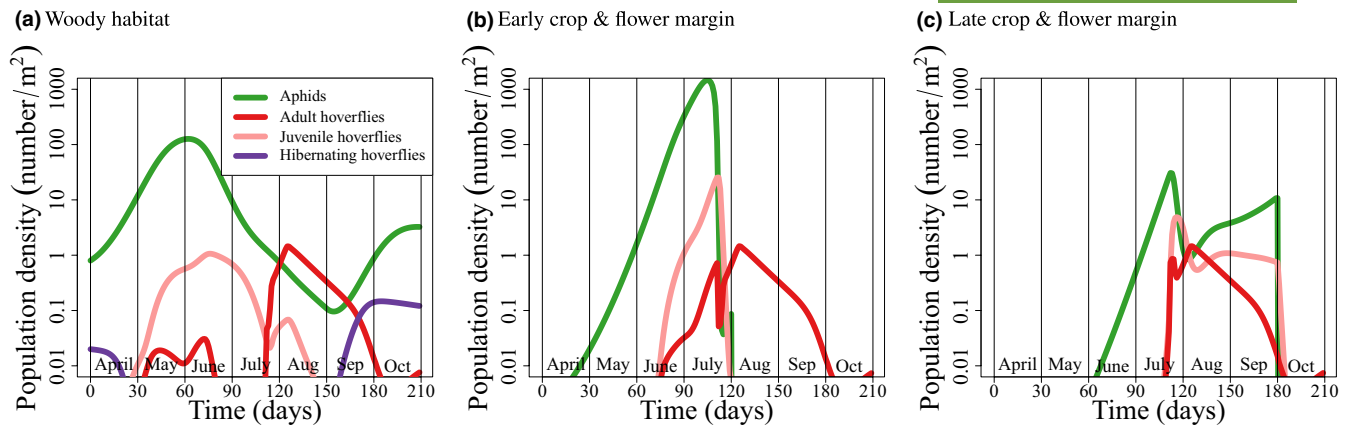


FIGURE 5 Seasonal population dynamics of hoverflies and aphids in three habitats: (a) woody habitat (H1), (b) early crop with flower margin (H2) and (c) late crop with flower margin (H3) within a 7-month period from early April until the end of October.

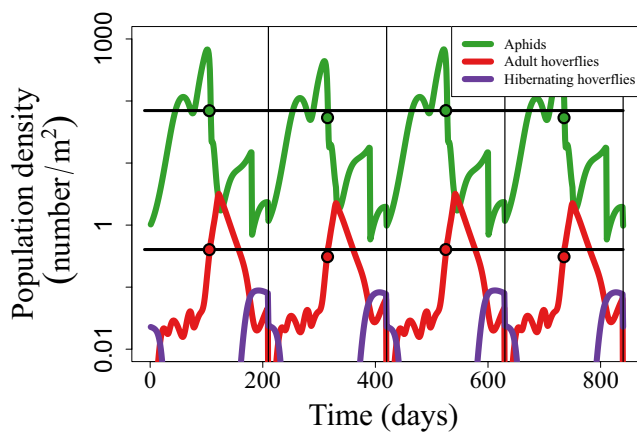


FIGURE 6 Population dynamics over 4 years of aphids and hoverflies of all habitats combined, as well as hibernating hoverflies. Dots show average yearly densities of aphids (green) and non-hibernating hoverflies (red). The black lines show the highest yearly average densities of aphids and hoverflies, to visualize that every other year the yearly average densities are lower, indicating bi-yearly cycles.

aphid density twelvefold in the early crop, which is similar to the level in the absence of predators and fivefold in the late crop (Figure 7). Clearly, the woody habitat plays a crucial role in sustaining predator populations before resources become available in the early crop.

Removing the flower margin of the early crop habitat (H2) increased the average aphid density in the early crop elevenfold, which is similar to the level in the absence of predators and fourfold in the late crop (Figure 7). Removing the entire early crop habitat (H2) increased the average aphid density in the late crop more than 300-fold (Figure 7b). Initially, we hypothesized that a landscape combining a woody habitat and a late crop with its flower margin, based on the overlap in resource availability functions (Figure 1), would provide sufficient resources year-round. However, our results revealed that a landscape without the early crop habitat did not sustain hoverflies throughout the year because the hoverflies quickly suppressed the aphid populations in the woody habitat, leading to a period without prey.

Removing the flower margin of the late crop (H3) increased the average aphid density fourfold in both the early and late crop (Figure 7). Removing the late crop habitat (H3) entirely increased the average aphid density in the early crop sevenfold (Figure 7a). Here, the absence of the late crop reduced the predator population that went into hibernation, resulting in lower predator densities in spring when the aphids in the early crop emerged.

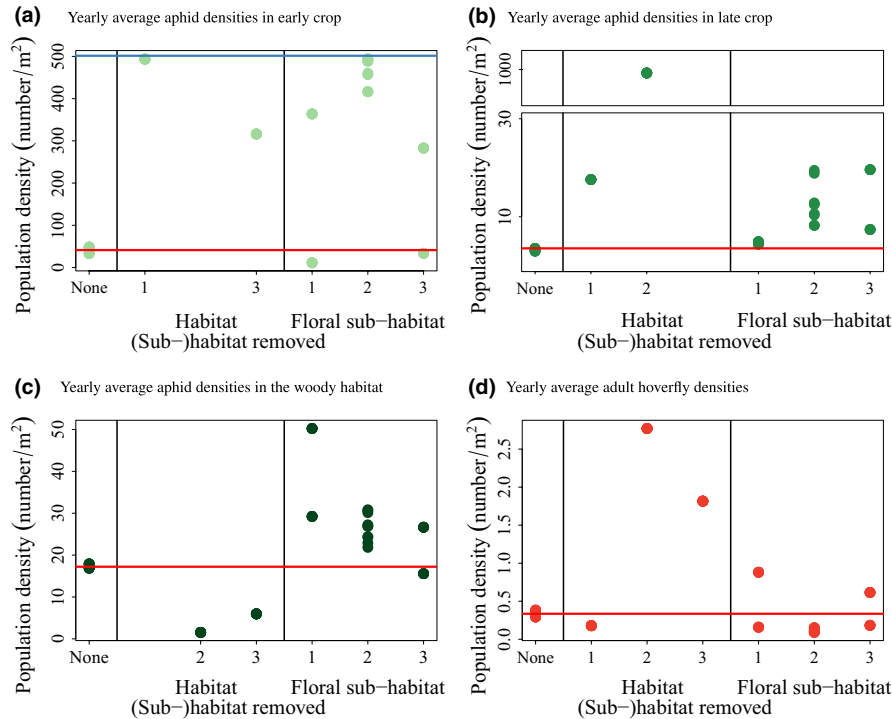
Whereas average aphid densities were consistently higher when removing one of the landscape elements, average predator densities were sometimes higher and sometimes lower (Figure 7d), implying that the average predator density is not a good indicator of pest control.

### 3.3 | Effect of floral resource levels

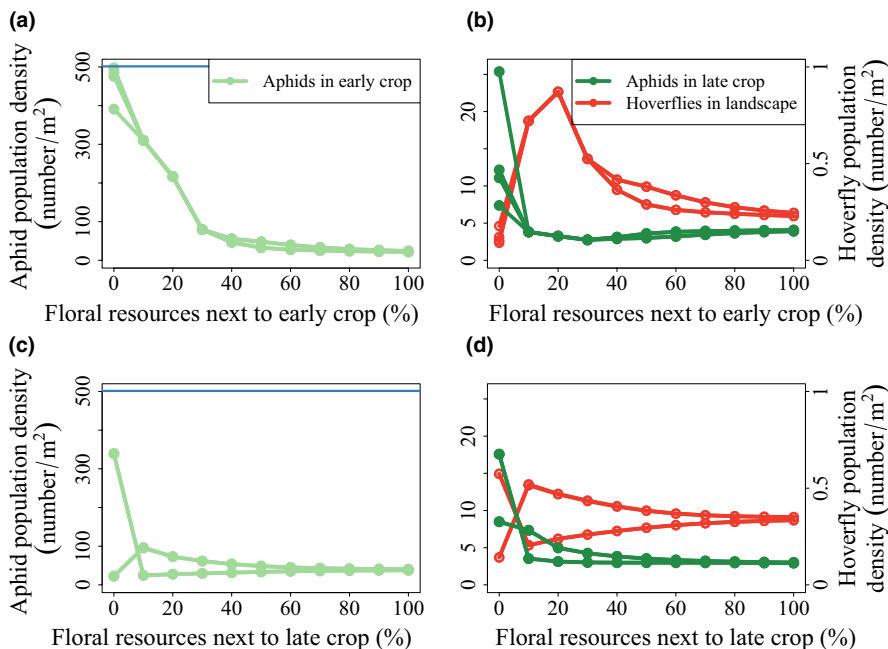
Increasing floral resource levels in the early crop habitat from 0% to 100% (with 49% as default value) reduced average pest densities in the early crop by 95% (Figure 8a) and (indirectly) by 70% in the late crop (Figure 8b). Even an increase to just 50% reduced average pest densities in the early crop to only 10% of the aphid densities observed when predators are absent (Figure 8a). Interestingly, a substantial reduction of aphid densities in the late crop was already achieved with a floral resource level in the early crop of 10% (Figure 8b). In the late crop, increasing floral resource levels resulted in an 80% reduction in the local pest density and the pest density in the early crop (Figure 8c,d). Beyond some minimal level, higher floral resource levels had only minor effects on average predator and pest densities, as the resulting reduction of pest densities ultimately limits predator numbers.

### 3.4 | Effect of proportion woody habitat in landscape

Increasing the percentage woody habitat in the landscape from 0% to 12% resulted in lower average aphid densities in both crop habitats, irrespective of the presence of other landscape elements



**FIGURE 7** Yearly average population densities of aphids in (a) the early crop, (b) the late crop, (c) the woody habitat and (d) hoverfly densities landscape-wide when specific (sub-)habitats are excluded, compared to the complete landscape. The x-axis indicates which (sub-)habitats are removed: 1 = woody habitat, 2 = early crop habitat, 3 = late crop habitat. When a full habitat is removed both sub-habitats are removed. Every dot represents the average population density over one year. When average population densities differed between years (due to multi-year cycles) multiple dots are indicated. The red line marks the multi-year average for the complete landscape. The blue line indicates the average aphid density in the absence of predators; in the late crop (b) this value is 1693 and in the woody habitat (c) 2515 aphids/m<sup>2</sup> (outside the graph range).

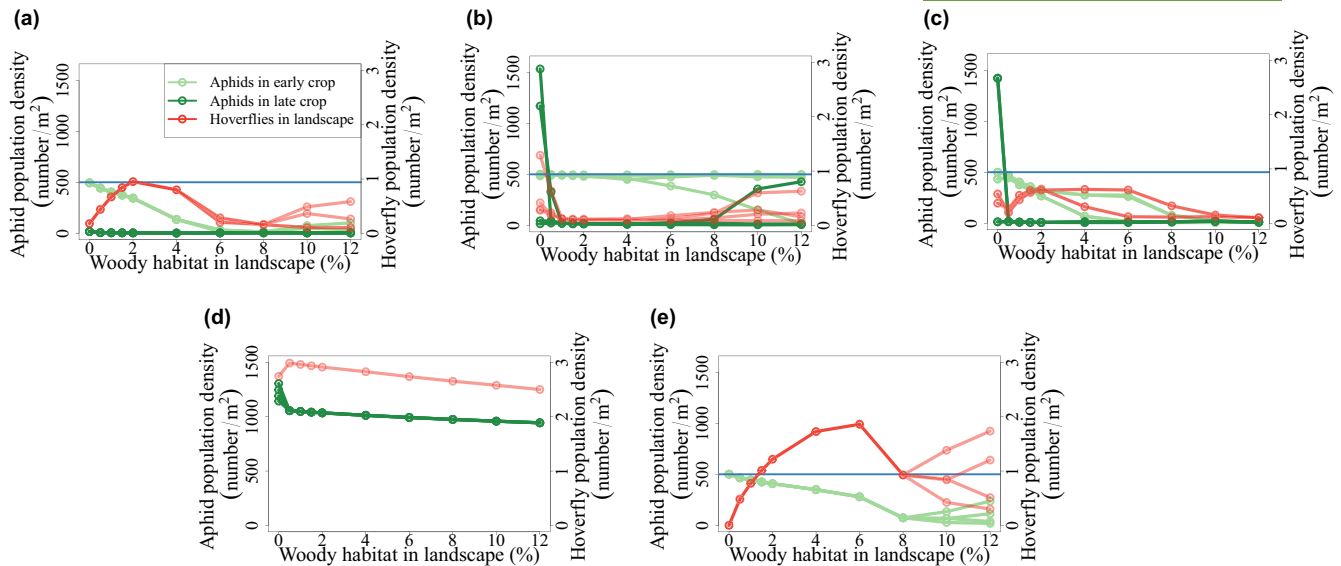


**FIGURE 8** Yearly average population densities of aphids in the early crop (a, c) and of aphids in the late crop (left axis) and of hoverflies (landscape-wide, right axis) (b, d) in response to floral resource levels in the flower margins of the early crop (a, b) and of the late crop (c, d). Floral resources of the other crop habitat was fixed at 49% (Appendix S2). When average population densities differed between years (due to multi-year cycles) multiple dots and lines of the same colour are indicated. The blue line indicates the average aphid density in the absence of predators; in the late crop (b, d), this value is 1693 (outside the graph range).

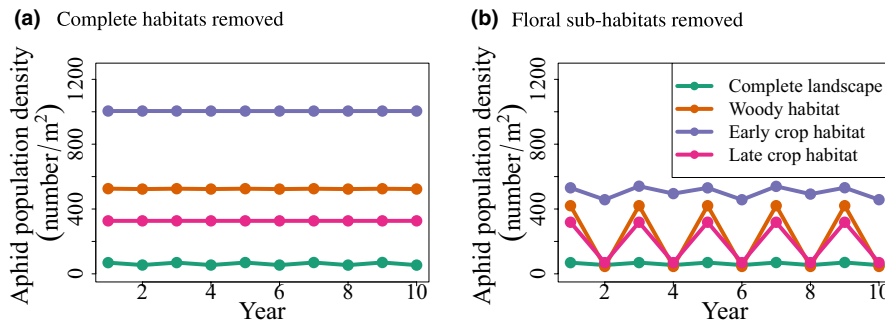
(Figure 9). Specifically, raising the percentage woody habitat in an otherwise complete landscape resulted in a 95% reduction in average aphid densities in the early crop and a 75% reduction in the late crop (Figure 9a). Aphid densities in the early crop were lowest with

circa 8% woody habitat (reduction of 95%) and in the late crop with circa 4% woody habitat (reduction of 85%).

Without the flower margin of the early crop habitat, pest suppression was severely limited by a lack of floral resources, and



**FIGURE 9** Yearly average densities of aphids in the early and late crop (left axis), and landscape-wide hoverfly densities (right axis) in response to the percentage of woody habitat in the landscape (ranging from 0.1% to 12%) for (a) a complete landscape or a landscape with (b) no early crop flower margin, (c) no late crop flower margin, (d) no early crop habitat (H2) and (e) no late crop habitat (H3). When average population densities differed between years (due to multi-year cycles) multiple dots and lines of the same colour are indicated. The blue line indicates the average aphid density in the early crop in the absence of predators; in the late crop, this value is 1693 (outside the graph range). The red lines showing the predator densities are made made slightly see through to make the lines under them more clear.



**FIGURE 10** Yearly average aphid densities in the whole landscape during 10 years (a) when full habitats are removed and (b) when floral sub-habitat are removed, and the green line in both panels shows the case of the complete landscape (no (sub-)habitats removed). The model with the complete landscape showed bi-yearly cycles. When whole habitats were removed no multi-year cycle in any of the other populations were observed. Removal of floral sub-habitat from the woody or late crop habitat resulted in bi-yearly cycles with large amplitudes. Removal of a floral sub-habitat from the early crop habitat resulted in four-yearly cycles.

increasing the woody habitat percentage to 12% resulted in only a 25% reduction in pest density in the early crop (Figure 9b). This average reduction was caused by one low aphid density year in a cycle of 4 years, while aphid densities remained high in the other 3 years (Figure 9b). In the late crop, aphid densities were better suppressed by increasing the woody habitat, with a maximum pest reduction of 98%, compared to the high densities in absence of the woody habitat.

Removing the flower margin of the late crop habitat hampered effective aphid control, but increasing the woody habitat percentage could still reduce aphid densities to very low levels in both habitats (Figure 9c), albeit higher compared to scenarios with the flower margin (Figure 9a).

In a landscape without the early crop, lack of pest suppression in the late crop could not be compensated by increasing the proportion woody habitat (Figure 9d). In a landscape without the late crop,

however, an increase in woody habitat resulted in a considerable increase in pest suppression in the early crop (Figure 9e), but not to the same level as with a complete landscape. Overall, aphid densities were higher when (sub-)habitats were missing, and this could, in some landscape configurations, only partially be compensated by increasing the percentage woody habitat in the landscape (Figure 9).

### 3.5 | Yearly and multi-year cycles

With changes in landscape composition or resource levels, the bi-yearly cycles altered into yearly, bi-yearly cycles with larger between-year differences, or even longer multi-year cycles of 3 years or longer (Figure 10). Removing (most of) the floral resources from one habitat

resulted in larger differences between years and sometimes also in longer multi-year cycles of 3 years or longer (Figures 8 and 10). This can be explained by the slower numerical response of the predators under these conditions (see Appendix S4 for phase planes visualising the predator-prey interactions). Removing one habitat altogether resulted in single-year cycles only and high aphid levels (Figure 10). This can be explained by the absence of sufficient top-down control and consequently of the predator-prey feedback that caused the bi-yearly cycles.

## 4 | DISCUSSION

This study aimed to explore the impact of landscape composition on natural enemy population dynamics and pest control. The model exemplifies the principle of landscape complementation (Dunning et al., 1992) as it shows that the combination of woody habitat, two different crops and flower margins results in the lowest pest densities and removal of any of these cannot be compensated by an increase of another.

An emergent property of the model is that the abundance of predators and pests showed bi-yearly cycles. Interestingly, similar biennial cycles have been observed for aphid populations in trees (Dixon et al., 1998), potatoes (Bagnall, 1992; Lambers, 1955) and soybean (Bahlai et al., 2015), which have also been explained by predator-prey cycles (Kirchner et al., 2013; Lambers, 1955). The explanation is that high pest abundance early in the year enhances predator abundance, reducing both pest and predator abundance before hibernation. Subsequently, lower predator abundance in the next year causes pest resurgence later in the year, followed by increased abundance of predators entering hibernation. Our model shows that this effect intensifies when certain resources for the predator are absent. Yearly average aphid densities can oscillate tenfold or more between years or the multi-year cycle can become longer (spanning over more than 2 years), especially when floral resources are missing in one of the habitats. Removing complete habitats disrupts the effect of predators on pest control, which results in single-year cycles with very high aphid densities. Multi-year cycles, quasi-periodicity or chaos can be induced in a predator-prey system due to seasonal forcing when the unforced system exhibits limit cycles or a sufficient level of oscillatory decay (Gragani & Rinaldi, 1995; Rinaldi et al., 1993; Rinaldi & Muratori, 1993; Taylor et al., 2013). In our case, these multi-year cycles occur due to seasonal forcing of floral resources, as limit cycles occur in the unforced system when floral resources are below a certain level (Appendix S5) and the floral resources in the forced system are often below this level. Long-term empirical datasets of pest and predator densities are scarce and often lack the resolution needed to confidently detect multi-year cycles or chaos under variable field conditions (Leslie et al., 2009; Welch & Harwood, 2014).

Our model illustrates that not only semi-natural habitats but also other crop fields can support natural pest control. Crops show to be major resource habitats and breeding grounds for natural enemies

and result in substantial increases in population numbers, eventually leading to dispersal into adjoining habitats (such as other crops), which is a classic example of a spill-over effect (Bianchi et al., 2007; Rand et al., 2006). Various empirical studies have included crop diversity in their analysis and showed a positive effect on natural pest control at small and large spatial scales (Croijmans et al., 2024; Redlich et al., 2018; Tamburini et al., 2020). Crop diversity can be achieved at three different scales: (1) at the field scale (such as intercropping or rotation schemes), (2) at the farm scale and (3) at the landscape scale (Thomine et al., 2022). On the one hand, crop diversity is often viewed at field or farm scale but is often difficult to implement on these smaller scales due to social or technical difficulties, such as lack of space or logistical constraints to harvest many different crops (Meynard et al., 2018; Morel et al., 2020; Thomine et al., 2022). On the other hand, landscape scale diversity management would require effective planning and coordination among different farms, but all farmers would benefit (Haan et al., 2021; Landis, 2017; Thomine et al., 2022).

Our model illustrates how flower margins, providing sufficient resources, can significantly reduce pest densities, both in the adjacent crop field, as well as in other fields. In empirical studies, flower strips have been proven effective for natural pest control in some studies, but insignificant or negative effects on natural pest control have been recorded as well (Albrecht et al., 2020; Crowther et al., 2023). Our model analyses show that the surrounding landscape can affect the potential positive effects of certain habitats on natural pest control. Additionally, not all flower strips are expected to be effective because some do not provide enough flowers with accessible nectar resources for natural enemies (van Rijn & Wäckers, 2016). Flower strips tailored for natural enemies are likely more effective in decreasing aphid and other pest densities in adjacent crops, compared to flower strips created for other aims (Campbell et al., 2017; Tschumi et al., 2016).

In our model, natural pest control increased in both crops with increased cover of woody habitat, but only up to a certain level. This suggests that woody habitats are vital for year-round predator persistence and pest suppression because they provide resources when other habitats do not. This is confirmed by empirical studies showing the importance of woody habitats for pest suppression in crops (Alignier et al., 2014; Ammann et al., 2022). In addition to providing food for predators, woody habitats may provide hibernation sites and physical protection against harsh weather conditions year-round (Bianchi et al., 2006; Sarthou et al., 2005).

Currently, many studies explore the relationship between landscape composition and natural pest control, attempting to link predefined habitat types, such as woody habitats and flowering field margins, to improved pest control (Albrecht et al., 2020; Alignier et al., 2014; Grab et al., 2018). A major limitation of this approach is that the timing and availability of resources can vary within a habitat type throughout the entire season, depending partly on predator-prey population dynamics in the landscape. Also within habitat types there can be a large variability in resource quality, quantity and timing and this variability might not reflect the specific

resource requirements of the focal species (Schellhorn et al., 2015). Additionally, empirical studies often rely on snapshot surveys during the main crop-growing season, hindering the identification of resource bottlenecks outside this period (Schellhorn et al., 2015). This might explain that reviews highlight the positive link between landscape heterogeneity and natural pest control (Aguilera et al., 2020; Bianchi et al., 2006; Kheirodin et al., 2020; Martin et al., 2019; Ouyang et al., 2020; Tschardt et al., 2007), but they also reveal that empirical studies oftentimes show inconsistent results (Albrecht et al., 2020; Chaplin-Kramer et al., 2011; Costamagna et al., 2015; Grab et al., 2018; Karp et al., 2018; Rusch et al., 2016). In our study, we modelled resource changes in habitats across all seasons and linked these to the actual requirements of natural enemies, revealing resource discontinuities as bottlenecks. We recommend adopting this approach to better understand and improve natural pest control. In conclusion, we highlight that landscape complementation is crucial when interpreting the results of empirical studies, as it explains the specific role a habitat plays in the life cycle of the natural enemy.

Many empirical studies use natural enemy abundance as proxies for natural pest control (Albrecht et al., 2020; Chaplin-Kramer & Kremen, 2012; Crowther et al., 2023; Karp et al., 2018; Martínez-Uña et al., 2013). However, our model shows that the average predator density is not a reliable indicator for pest control, as low pest densities do not always coincide with high average predator numbers. The reason is that when a predator is more effective, it is ultimately limited by the reduction of its own (prey) resources. This should be taken into account when interpreting the results of field studies. When designing new studies, resource levels and especially pest dynamics should always be included in the sampling program (Janssen & van Rijn, 2021).

In our model, the landscape is represented by a collection of habitats without defining space explicitly, that is landscape configuration is not included in this model. While spatially explicit models offer insights into specific landscapes, their results are often hard to generalize (DeAngelis & Yurek, 2017; Pichancourt et al., 2006). In contrast, spatially implicit models are simpler and help identify general patterns linking population dynamics and landscape (Pichancourt et al., 2006). By using a spatially implicit model, we assume that hoverflies can freely move among all habitats and are not limited by dispersal distance. Studies indicate that aphidophagous hoverfly densities are more influenced by landscape composition within a radius of 1000m than within 500 or 1500m (Kleijn & van Langevelde, 2006; Meyer et al., 2009), suggesting that the landscape at a distance between 500 and 1000m still affects local hoverfly densities. Therefore, we expect the model to be valid for landscapes where the woody and the crop habitats co-occur within a range of approximately 1km. Movement between floral and aphid sub-habitats is assumed to occur even at a smaller spatial scale. Experimental data (van Rijn et al., 2024; Woodcock et al., 2016) indicate that flower strips still provide effective aphid control at distances up to 50–80m, while individual-based modelling (including energy budgets, van Rijn unpublished

results) suggests that hoverflies will forage for aphid colonies over distances of 50–150m from a field margin, depending on the aphid density in the field. We assumed that the presence of these different habitats within the movement ranges of hoverflies in agricultural landscapes is feasible, for example in the Hoeksche Waard and other areas in the Netherlands fields are typically 200–400m wide (van Rijn et al., 2024). In very large monoculture fields, we expect less natural pest control further into the field, even with high landscape diversity surrounding the field, as natural enemies cannot migrate far enough into the field. Here, creating flower strips within the fields, for example in spraying tracts, can mitigate this limitation.

As with many predator–prey models, we included only one predator population, representing an important group of natural enemies, the predatory hoverflies, but in the field various other predators and parasitoids may influence aphid populations as well (Crowder et al., 2010; Hassell, 1978). Many of these predators and parasitoids, such as lacewings and parasitoid wasps, depend on floral resources in a similar way (Alcalá Herrera et al., 2022; Russell, 2015). Therefore, we expect that changing the predator identity will not have large impacts on the conclusions of the study. In the future, we will likely incorporate more predator types in the model to assess the robustness of this assumption and to test how interspecific competition and interference may affect the results. Overall, a dynamic model has to be based on many (simplifying) assumptions and parameter estimations, of which the rationale has been explained in other parts of this paper (and more extensively in the Appendix S1 and S2). We hope that the knowledge gaps identified will inspire other researchers to study and test these assumptions in more detail.

In conclusion, our model shows that an effective landscape for natural pest control of aphids by hoverflies consists of a woody habitat, an early and late crop and flower margins along each crop. In practice, various habitat combinations (including crops and (semi-) natural habitats) can support natural pest control, provided they are complementary in the timing and quality of the resources they offer to the natural enemies.

#### AUTHOR CONTRIBUTIONS

Paul C. J. van Rijn conceived the ideas and created the first version of the model; Laura Mansier and Paul C. J. van Rijn made updates on the model; Laura Mansier analysed the model; Laura Mansier led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The full model description and the parameter value determination can be found in the [Supporting Information](#). The model script is available via the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.13736744> (Mansier & van Rijn, 2024). Additionally, the model and analyses scripts will be made available on the Github page (<https://github.com/LauraMansier/ArableLandscape-PestControl>) of Laura Mansier under the name of ArableLandscape-PestControl (<https://github.com/LauraMansier/ArableLandscape-PestControl>) after publication and will remain updated.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Model description.

**Appendix S2.** Parameter value determination.

**Appendix S3.** Weibull distribution and time delays.

**Appendix S4.** Phase planes.

**Appendix S5.** Unforced model systems.

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