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Intercropping Broccoli-Basil Reduces Aphid Growth: Spatio-Temporal Modelling Across Scales and Lab Experiments

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ABSTRACT

Shifting from conventional to sustainable agriculture demands well-designed experiments and robust analytical models to evaluate agroecological system performance and resilience. We modelled aphid population dynamics in broccoli monocultures and broccoli-basil intercrops using spatio-temporal approaches, informed by laboratory experiments on aphid avoidance behaviour. These experiments compared conventional, intensive crop production with sustainable plant protection practices, such as the impact of intercropping on aphid population growth rates. The results revealed that aphids significantly avoided broccoli leaves intercropped with basil, preferring monoculture broccoli. The presence of basil significantly reduced aphid population growth rates, leading to population decline. These findings informed mathematical models integrating plant-herbivore interactions, aphid movement, diffusion, and repellency. The models employed deterministic approaches, including non-spatial coupled population dynamics and spatial (1D and 2D) reaction-diffusion frameworks, simulating aphid dispersal and plant-aphid interactions over 50 and 100 m domains. Numerical simulations demonstrated that aphids avoid broccoli intercropped with basil, with models capturing basil's repellent effect in a spatio-temporal context. Simulations revealed cyclic oscillations in plant and aphid populations, stabilising to a steady equilibrium due to spatial population coupling. The spatially explicit approach highlighted how population growth rates, diffusion coefficients, aphid mortality, and spatial domain size influence aphid movement and repellency. Higher diffusion coefficients and lower aphid mortality from other causes amplified the repellent effect of the intercrop system, significantly reducing aphid populations. Our results suggest that broccoli-basil intercropping enhances pest regulation, offering a sustainable alternative to chemical pest control, although aphid dispersal rates and spatial domain size significantly affect its efficacy.

1 | Introduction

Sustainability is an increasingly common objective in modern agriculture, given the urgent need to promote environmental protection and ensure human health without compromising food security (Sharma et al. 2024). With rapidly rising global food production needs, agricultural systems should minimise pesticide use, especially as climate change alters pest-natural enemy dynamics (Wyckhuys et al. 2024). Therefore, there is a pressing need for innovative, eco-friendly strategies to maintain crop yields while minimising environmental impacts.

Intercropping, the practice of growing multiple crop species together, is a promising agroecological strategy that naturally regulates pests by repelling them, attracting natural enemies, and disrupting pest-host interactions (Letourneau et al. 2011). Aromatic plants such as basil (*Ocimum basilicum* L.) are especially effective, as their volatile organic compounds (VOCs) repel pests or mask host plant odours (Basedow et al. 2006). Basil's repellent properties have recently gained attention, with studies demonstrating reduced pest abundance in agroecosystems. Carvalho et al. (2017) observed reduced oviposition by *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) in basil intercropped with tomato. Integrating *O. basilicum* with faba bean (*Vicia faba* L.) significantly reduces infestation levels of the black bean aphid (*Aphis fabae* Scopoli) (Basedow et al. 2006). Other pest populations also decrease in cabbage when intercropped with *Ocimum* species (Yarou et al. 2017). Despite these findings, the underlying mechanisms, particularly spatio-temporal dynamics, remain underexplored.

Aphids are significant pests due to their sap-feeding behaviour and role as vectors of plant pathogens; their high reproductive rates enable rapid population growth, threatening crop yields (Ali et al. 2023; Stef et al. 2024). Although pesticides remain the primary pest control strategy, they can lead to resistance in pest populations and contribute to human and environmental contamination (Zhou et al. 2025). Modifying agroecosystems offers a suitable approach to suppress pests (Liu et al. 2020). Diversifying plant species creates physical and chemical barriers that disrupt aphids' ability to locate host plants (Hatt and Döring 2023).

Integrating experiments on the diffusive behaviour of agriculturally significant insects, particularly aphids, with mathematical models of repellent plant-induced movement patterns offers a powerful approach to modelling dynamic insect-plant systems (Byers and Levi-Zada 2022). This framework abstracts essential biological processes, integrating temporal and spatial dimensions to address key questions in insect-plant dynamics. Such insights are fundamental for designing and implementing effective integrated pest management (IPM) strategies.

This study examines the avoidance behaviour of the green peach aphid (*Myzus persicae* Sulzer) towards broccoli *(Brassica oleracea* var. italica) in broccoli-basil intercrop systems. Through controlled laboratory experiments, we quantified the effects of this intercropping arrangement on aphid population growth rates. We used these empirical findings to parameterise a continuous-time mathematical model simulating aphid population dynamics. The observed aphid avoidance behaviour motivated us to investigate how this repellency influences the spatio-temporal distribution of aphids across spatial scales.

2 | Materials and Methods

2.1 | Plants and Insects

We obtained broccoli (*B. oleracea* var. italica) and basil (*O. basilicum* L.) seedlings from a commercial nursery (IBS Mudas, Piracicaba, São Paulo, Brazil) and transplanted the seedlings into pots (2 L for broccoli, 350 mL for basil) filled with Forth Floreiras Substrate. Plants were grown under greenhouse conditions at the Department of Entomology and Acarology, ESALQ/USP, Piracicaba, São Paulo. Growth conditions maintained a mean temperature of 28°C ± 4°C under natural light. Plants received biweekly fertilisation with Forth Orchids NPK (9-45-15) and daily watering.

We maintained a colony of the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), at the Insect Interactions Laboratory, ESALQ/USP, Piracicaba, Brazil, rearing aphids on surface-sterilised cabbage (*B. oleracea* var. capitata) leaf discs (10.5 cm diameter) placed in Petri dishes containing a 5 mm layer of 10% water agar to maintain turgidity. Leaves were sterilised using neutral detergent, rinsed thoroughly with distilled water, and dried with sterile absorbent paper before use. Each dish contained 100 aphids maintained in a climate-controlled chamber (20°C ± 1°C, 70% ± 10% RH, 14:10 h light: dark photoperiod). We replaced the rearing medium (leaf discs and agar) twice weekly.

2.2 | Experiment 1: Dual-Choice Tests

We conducted experiments at the Laboratory of Insect Ecology and Forest Entomology, ESALQ/USP, Piracicaba, São Paulo, Brazil, with a randomised block design and 15 replicates *per* experimental period using three experimental periods: 27–30 October 2022; 8–12 November 2023; 21–25 November 2023 (total $n = 45$). Petri dishes (15 cm diameter) served as experimental units. We designed treatments with two aphid feeding options in Petri dishes, placed at opposite ends, as follows: Choice 1: One broccoli leaf disc (3 cm^2, *B. oleracea* var. italica), Choice 2: One broccoli leaf disc (1 cm^2) and one basil leaf disc (2 cm^2, *O. basilicum* L.) ensuring equal total leaf area (3 cm^2) for comparison.

We introduced 10 adult apterous *M. persicae* at the centre of each dish, and dishes were maintained in a biochemical oxygen demand chamber at 25°C ± 1°C, 70% ± 10% RH, and a 12:12 h L:D photoperiod. After 24 h, we recorded the number of aphids on each leaf disc (broccoli monoculture vs. broccoli-basil). Aphids not on either disc were counted as 'none'.

The current methodology was adapted from Jhou et al. (2021).

2.3 | Experiment 2: Impact of Basil on Aphid Population Growth

Experiments were conducted in a greenhouse at the Department of Entomology and Acarology, ESALQ/USP, Piracicaba, São Paulo, Brazil, in February 2023 with a randomised block design with two treatments: (i) broccoli monoculture and (ii) broccoli-basil intercrop. Each broccoli plant served as a sampling unit. Ten replicates *per* treatment *per* experimental period were used, with two periods (21–24 February and 25–28 February, 2023; total $n = 20$ per treatment). The experimental period determined the blocks, and the plant arrangement featured broccoli plants (25 cm tall) in a straight line with 5 cm spacing between plants. Intercropping a row of basil plants (spaced 5 cm apart) parallel to and behind the broccoli row, separated by 2 m, we introduced three adult apterous *M. persicae* onto each broccoli plant in greenhouse conditions. The average maximum/minimum temperatures were 32.5°C/21°C, and the average maximum/minimum relative humidities 96%/40%. After 72 h, we recorded the total number of aphids (adults and nymphs) on each broccoli plant and estimated the intrinsic rate of increase (r) for each replicate using Equation (1) (Culliney and Pimentel 1985):

$$r = \frac{\ln\left(\frac{N_{x+1}}{N_x}\right)}{t}, \tag{1}$$

where:

$\boldsymbol{N_x}$ = Initial aphid population size (three apterous adults), $\boldsymbol{N_{x+1}}$ = Final aphid population size (total aphids after 72 h), $\boldsymbol{t}$ = Time interval (3 days), ***Ln*** = Natural logarithm. $r > 0$ indicates population increase; $r = 0$ indicates stability; $r < 0$ indicates decrease.

2.4 | Statistical Analysis

The data analysis involved a three-option analysis of dual-choice tests:

A multinomial goodness-of-fit test to assess if the distribution of aphids across the three categories (broccoli alone (***br***), broccoli+basil (***brba***) and *none*) deviated significantly from an expected uniform distribution (1/3 probability for each category), and a chi-square goodness-of-fit test specifically to compare the distribution of aphids found on plants (i.e., excluding 'none') between the ***br*** and ***brba*** choices against an expected 1:1 ratio.

2.5 | Population Growth Rate Estimate

Differences in the intrinsic rate of increase ($\boldsymbol{r}$) between the broccoli monoculture (***br***) and broccoli-basil intercrop (***brba***) treatments were analysed using a linear mixed model with blocks (experimental period) as a random effect. We performed the analysis using R software version 4.3.1 (R Core Team 2023), primarily utilising functions from the stats package.

3 | Mathematical Modelling

3.1 | Plant-Herbivore Mathematical Model

We developed a model to simulate the dynamics of two plant populations—broccoli (*B. oleracea* var. italica) in monoculture (*br*) and broccoli intercropped with basil (*O. basilicum*) (*brba*)—and two aphid populations (*Myzus persicae*; A_1 and A_2) feeding on these plants. The model incorporates coupled population dynamics through the movement of aphids between two patches. We begin with a model using ordinary differential equations (ODEs) to describe the plant population dynamics. The dynamics of the broccoli (*br*) and broccoli-basil intercrop (*brba*) populations are described by:

$$\frac{dbr}{dt} = r_{br}br - CbrA_1 \tag{2}$$

$$\frac{dbrba}{dt} = r_{brba}brba - CbrbaA_2 \tag{3}$$

where r_{br} and r_{brba} are the intrinsic growth rates of *br* and *brba*, respectively, and *Cbr* and *Cbrba* are the consumption rates of *br* by aphid population A_1 and *brba* by A_2, respectively. These equations model exponential plant growth in the absence of aphids. In this model, we assume that plant growth is limited only by aphid feeding when aphids are present. We chose not to include a logistic function to focus exclusively on aphid herbivory as the limiting factor, following a Lotka-Volterra-like herbivory framework (Holt and Barfield 2013). The dynamics of aphid populations A_1 (feeding on *br*) and A_2 (feeding on *brba*) are described by:

$$\frac{dA_1}{dt} = (r_{A_1} - d)A_1 + gCbrA_1 + m(A_2 - A_1) \tag{4}$$

$$\frac{dA_2}{dt} = (r_{A_2} - d)A_2 + gCbrbaA_2 + m(A_1 - A_2) \tag{5}$$

where r_{A_1} and r_{A_2} are the intrinsic growth rates of A_1 and A_2, d is the aphid mortality rate, g is the conversion efficiency of consumed plant into new aphids and m is the term modelling the bidirectional aphid movement between the patches *br* and *brba*. The movement term $m(A_2 - A_1)$ in Equation (4) represents the net flux into the *br* patch, with positive values indicating movement from *brba* to *br* when $A_2 > A_1$ (more aphids on *brba*). Similarly, $m(A_1 - A_2)$ in Equation (5) represents the net flux into the *brba* patch, with positive values indicating movement from *br* to *brba* when $A_1 > A_2$. These terms model dispersal as a diffusion-like process, where aphids move from the patch with higher population density to the patch with lower density, capturing implicit spatial dynamics between the patches.

The model, based on the greenhouse experiment examining *M. persicae* feeding on broccoli (*B. oleracea* var. italica) in monoculture (*br*) and intercropped with basil (*O. basilicum*; *brba*), incorporates basil's repellent effect, which influences the aphid growth rate, supported by our experiments and a prior study (Yarou et al. 2021). The ODEs were solved numerically using the *deSolve* package (Soetaert et al. 2010) in R software. We derived parameter values, including mean aphid growth rates ($r_{A_1} = 0.31$ day^{-1} for A_1 on *br*; $r_{A_2} = -0.16$ day^{-1} for A_2 on *brba*), from experimental data (Table 1, Figure 1). Simulations explored two scenarios: no movement between patches ($m = 0$) and movement ($m = 0.1$), with m values selected based on prior sensitivity analysis identifying dispersal strengths that stabilise plant and aphid population dynamics.

3.2 | Spatially Explicit Reaction-Diffusion Model

A system of partial differential equations (PDEs) governs the spatially explicit reaction-diffusion model, describing the

TABLE 1 | Parameter values used in the Equations (1–4).

Parameters	Values	Source
C (plant consumption)	0.1	Costello and Altieri (1995)
d (aphid mortality)	0.42 and 0.3	Fidelis et al. 2018, and theoretically derived based on population dynamics models for sustainability
m (movement)	0.1	Exploratory but based on Kang, and Armbruster 2011
g (conversion efficiency from plant to aphids)	0.5	Theoretically derived based on population dynamics models for sustainability
$^*r_{A_1}$ (aphid growth rates)	0.31	Experimentally obtained
$^*r_{A_2}$ (aphid growth rates)	−0.16	Experimentally obtained
r_{br} (broccoli growth rate)	0.7	Theoretically derived based on population dynamics models for sustainability, and to give small differences at initial conditions
r_{brba} (broccoli-basil growth rate)	0.65	Theoretically derived based on population dynamics models for sustainability, and to give small differences at initial conditions

dynamics of broccoli (*br*), broccoli intercropped with basil (*brba*), and aphid density (A_1, A_2). PDEs characterise the relationships between the rates of change of functions concerning multiple independent variables—here, time and space—often discretised over spatial grids (Borthwick 2016). In this study, the model investigates these dynamics within a spatial domain. For each point in space, Equations (2)–(5) govern the reaction processes, describing the local population dynamics of plants and aphids. To incorporate spatial spread, the model includes diffusion terms in the aphid equations. The diffusion terms $D\frac{\partial^2 A_1}{\partial x^2}$ and $D\frac{\partial^2 A_2}{\partial x^2}$ model the spatial spread of aphids A_1 and A_2, respectively, where D is the diffusion coefficient, determining in this study the aphid dispersal speed (e.g., $D = 0.5$ and $D = 5\,\text{m}^2/\text{day}$). Incorporating these terms into the aphid equations results in:

$$\frac{\partial A_1}{\partial t} = (r_{A_1} - d)A_1 + gCbrA_1 + D\frac{\partial^2 A_1}{\partial x^2} \tag{6}$$

and

$$\frac{\partial A_2}{\partial t} = (r_{A_2} - d)A_2 + gCbrbaA_2 + D\frac{\partial^2 A_2}{\partial x^2} \tag{7}$$

Note that the plant equations remain as in Equations (2) and (3), without diffusion terms, assuming plants are stationary.

3.3 | Spatial Grid Setup

The model simulates aphid population dynamics across one-dimensional (1D) and two-dimensional (2D) spatial domains. The 1D domains span 50 and 100 m, discretised into 6 and 11 grid points, respectively, with a spatial step size of 10 m (i.e., $x = [0, 10, 20, 30, 40, 50]$ for 50 m; $x = [0, 10, 20, \ldots, 90, 100]$ for 100 m). The 2D domains are square, covering 50 m x 50 m (discretised into a 6 × 6 grid, 36 points) and 100 × 100 m (discretised into an 11 × 11 grid, 121 points), with a 10-m step size in both x and y directions. We visualise the results as heatmaps: 1D models show aphid density over time (0–50 days) and space in a single plane, while 2D models display aphid density across a plane at specific time points ($t = 0, 25, 50$ days).

3.4 | Numerical Implementation of the 1D Structure

We implemented the reaction-diffusion equations in two functions: (1) reaction-diffusion-*br*, which computes the time derivatives for broccoli and aphid population A_1, and (2) reaction-diffusion-*brba*, which computes the time derivatives for broccoli-basil intercropped and aphid population A_2. We used the Reac Tran R package (Soetaert and Meysman 2012) to handle the diffusion term and implemented it in R software version 4.3.1 (R Core Team 2023), which approximates the second spatial derivative using finite differences on 6- and 11-point grids. The model explicitly computes the reaction terms based on the previously described equations.

3.5 | Solving the PDE

We solved the PDE systems using the *ode 1D* function from the R deSolve package (Soetaert et al. 2010), and implemented it in R software, with a design for 1D PDEs. We employed the lsodes method, which is suitable for reaction-diffusion models due to the interplay of reaction and diffusion timescales, and specified initial conditions $yini_{br}$ and $yini_{brba}$. The model includes two species, representing plant and aphid densities, across spatial grids of 6 and 11 points. The solutions (out_{br} and out_{brba}) are matrices where rows correspond to time points and columns represent plant and aphid densities at each grid point.

3.6 | Output Matrix Structure and Data Processing for Visualisation

In the output matrices for a grid (e.g., out_{br} or out_{brba}), the aphid densities (A_1 for *br*, A_2 for *brba*) at the (N) spatial grid points are stored in columns $N + 2$ to $2N + 1$, where N is the number of grid points. For the broccoli (*br*) grid ($N = 6$), Columns 8–13 correspond to $x = [0, 10, 20, 30, 40, 50]$ or $x = [0, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100]$ for a 100 m spatial domain. These columns are extracted for visualisation to show aphid population dynamics over time and space. The offset, starting at column $N + 2$, indicates that the first $(N + 1)$ columns contain data such as time (Column 1) and plant density (Columns 2 to $N + 1$), before the aphid density data begins. We used the *melt function* from the R reshape2 package (Wickham 2007). It converts the aphid density matrices into long-format data frames ($u_{df_{br}}$ and $u_{df_{brba}}$).

3.7 | 2D Reaction-Diffusion Model

A key component of this model is the implementation of the 2D Laplacian operator (Borthwick 2016), which models the diffusion of aphids across the spatial domain, describing how aphids spread in both the x and y directions across the 50 m x 50 m and 100 m x 100 m domains.

We describe the aphid dynamics for the six-point grid (A_1) as follows:

$$\frac{\partial A_1}{\partial t} = (r_{A_1} - d)A_1 + gCbrA_1 + D\left(\frac{\partial^2 A_1}{\partial x^2} + \frac{\partial^2 A_1}{\partial y^2}\right) \tag{8}$$

and

similarly, for the *brba* grid (A_2):

$$\frac{\partial A_2}{\partial t} = (r_{A_2} - d)A_2 + gCbrbaA_2 + D\left(\frac{\partial^2 A_2}{\partial x^2} + \frac{\partial^2 A_2}{\partial y^2}\right) \tag{9}$$

The terms $D\left(\frac{\partial^2 A_1}{\partial x^2} + \frac{\partial^2 A_1}{\partial y^2}\right)$ and $D\left(\frac{\partial^2 A_2}{\partial x^2} + \frac{\partial^2 A_2}{\partial y^2}\right)$ represent the 2D Laplacian scaled by the diffusion coefficient ($D = 0.5\ \mathrm{m}^2$/day or $D = 5\ \mathrm{m}^2$/day) used to contrast different diffusion scales capturing the spatial diffusion of aphids in the 2D plane.

3.8 | Numerical Implementation of the 2D Laplacian

$$\nabla^2 A_{i,j} \approx \frac{A_{i+1,j} - 2A_{i,j} + A_{i-1,j}}{\Delta x^2} + \frac{A_{i,j+1} - 2A_{i,j} + A_{i,j-1}}{\Delta y^2} \tag{10}$$

since $\Delta x = \Delta y = 10$, and assuming a uniform grid, this simplifies to:

$$\nabla^2 A_{i,j} \approx \frac{A_{i+1,j} + A_{i-1,j} + A_{i,j+1} + A_{i,j-1} - 4A_{i,j}}{\Delta x^2}.$$

The diffusion term is then:

$$D\nabla^2 A_{i,j} \approx D\bullet \frac{A_{i+1,j} + A_{i-1,j} + A_{i,j+1} + A_{i,j-1} - 4A_{i,j}}{\Delta x^2} \tag{11}$$

We computed this approximation for each grid point. The *tran 2D* handles boundary conditions (typically no-flux, meaning aphids do not leave the domain), ensuring the matrix output matches the input dimensions.

3.9 | Laplacian Movement in Aphids and Numerical Simulations

We modelled aphid diffusion as a random walk, spreading aphids from high-density to low-density areas, modulated by the basil's repellency. Aphids move randomly across a 2D spatial grid, with their density at each grid point (i, j) denoted by $A_{i,j}$. The Laplacian $\nabla^2 A_{i,j}$ quantifies the net rate at which aphids enter or leave the grid point due to density differences between the point and its neighbours. The diffusion term $D.\ \nabla^2 A_{i,j}$ scales this rate by the diffusion coefficient D. The Laplacian approximation arises from discretising the second derivatives $\frac{\partial^2 A}{\partial x^2} + \frac{\partial^2 A}{\partial y^2}$. It involves aphid densities at the central grid point $A_{i,j}$ and its four immediate neighbours (right, left, up, down).

We define the aphid density values at the neighbouring grid points as:

$A_{i+1,j}$, $A_{i-1,j}$: determining aphid densities to the right and left, driving horizontal movement.

$A_{i,j+1}$, $A_{i,j-1}$: representing aphid densities above and below, driving vertical movement.

$-4A_{i,j}$: estimating the aphid potential of leaving the central point in four directions.

$\frac{1}{\Delta x^2}$: normalising the spatial gradient for grid resolution.

The combination $A_{i+1,j} + A_{i-1,j} + A_{i,j+1} + A_{i,j-1} - 4A_{i,j}$ measures the net aphid flux, with D scaling the speed of dispersal.

We conduct simulations for both 1D and 2D models with varying diffusion coefficients ($D = 0.\ 5\ \mathrm{m}^2$/day or $D = 5\ \mathrm{m}^2$/day) and aphid mortality rates ($d = 0.42$ or $d = 0.30$) to represent different levels of spatial expansion and mortality, respectively.

4 | Results

4.1 | Experiments

In the three-choice test, we evaluated aphid avoidance behaviour towards broccoli leaves paired with basil. Of the 450 aphids tested, 397 (88.2%) selected a leaf disc. Specifically, 228 aphids (50.7%) preferred broccoli alone (*br*), avoiding the broccoli-basil combination (*brba*), while 169 (37.5%) chose the broccoli-basil combination. The remaining 53 aphids (11.8%) showed no preference, staying in the centre of the Petri dish. The three-way multinomial test revealed a significant difference among the broccoli (*br*), broccoli-basil (*brba*), and no-preference (none) groups ($\chi^2 = 105.69$, $df = 2$, $p = 2.2e^{-16}$). In addition, a pairwise multinomial test revealed a significant

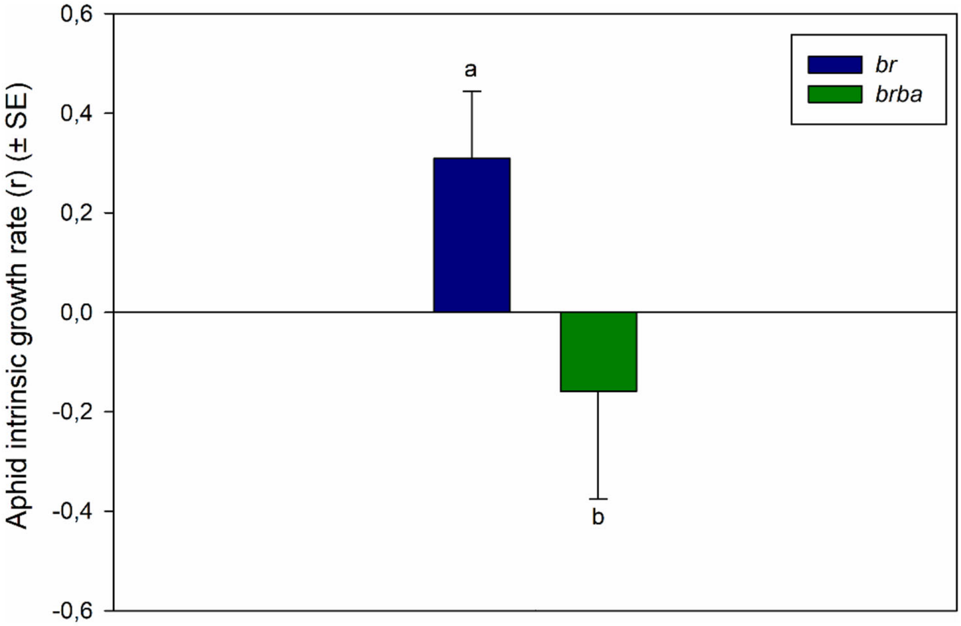

FIGURE 1 | Intrinsic growth rates of *Myzus persicae* feeding on broccoli (*br*, blue) and broccoli-basil intercrop (*brba*, green). Bars show means ± standard errors with different letters indicating significant differences ($p < 0.05$).

difference between the broccoli (*br*) and broccoli-basil (*brba*) groups ($\chi^2 = 8.77$, $df = 1$, $p = 0.003$).

The broccoli-basil intercrop had a significant effect on the intrinsic population growth rate of *M. persicae* (Figure 1). A mixed linear model revealed that the presence of basil significantly reduced the intrinsic population growth rate ($p = 0.0375$). Estimated means indicated a lower aphid population growth rate in the broccoli-basil intercrop ($r_{A_2} = -0.16$) compared to the broccoli-alone ($r_{A_1} = 0.31$).

4.2 | Mathematical Model

4.2.1 | Plant-Herbivore Mathematical Model

Plant dynamics in the broccoli-basil intercrop (*brba*) resulted in higher, cycling populations (Figure 2A, orange curve) compared to the broccoli-alone treatment (*br*), which exhibited cycling populations with dips near zero (Figure 2A, green curve). Aphid populations mirrored these plant dynamics, with narrower cycles and lower values in the intercrop (*brba*; A_2, Figure 2B, magenta curve) compared to wider cycles driven by consumption of unprotected plants in the broccoli-alone treatment (*br*; A_1, Figure 2B, blue curve). Figure 2C,D illustrates the stabilising effect of aphid movement ($m = 0.1$) on plant and aphid populations, with asymptotic dynamics converging to a stable equilibrium.

In Figure 2E–H, the population dynamics show a simulated decrease in aphid mortality from $d = 0.42$ to $d = 0.3$, leading to the complete extinction of broccoli (Figure 2E) due to increased aphid population growth (A_1, Figure 2F). The broccoli-basil intercrop (*brba*) persists because aphids feeding on it (A_2) maintain low population densities (Figure 2E,F). With aphid movement ($m = 0.1$), Figure 2G,H demonstrate a stabilising effect on plant and aphid populations, where both aphid populations (A_1 and A_2) persist at lower densities than in simulations without movement ($m = 0$, Figure 2F).

4.2.2 | Spatially Explicit Reaction-Diffusion Model

4.2.2.1 | 1D 50-m Domain. Figures 3 and 4 illustrate simulations of 1D aphid diffusion, where insect movement follows a linear pattern across 50 (Figure 3) and 100-m (Figure 4) domains. Figure 3 depicts plant grids comparing two aphid mortality rates: an experimentally derived mortality rate ($d = 0.42$, Figure 3A,B) and a simulated lower mortality rate ($d = 0.3$, Figure 3C,D). These simulations highlight the influence of intercropping broccoli with basil (*brba*) compared to broccoli alone (*br*) on aphid diffusion. Figure 3A shows high aphid density (A_1) during an initial period ($t < 10$ days), reaching up to 75 aphids per square metre on the left side of the graph (see horizontal gradient bar), interspersed with areas of lower density (< 25 aphids per square metre). Aphids are distributed horizontally in the broccoli grid (*br*) with a diffusion coefficient of $D = 0.5\ \mathrm{m}^2/\mathrm{day}$. After $t > 10$ days, aphid density (A_1) decreases significantly, approaching zero between 40 and 50 days. In the broccoli-basil intercrop (*brba*), aphids (A_2) show a similar interspersed density with transient low-density peaks, indicating reduced spread of high-density areas. Subsequently, aphid density (A_2) remains below 25 aphids per square metre, spanning the 50-m domain.

Figure 3B ($D = 5$) shows aphid density across broccoli (*br*) and broccoli-basil (*brba*) grids, with a pattern similar to Figure 3A but lower densities, particularly for A_1 in *br* (see horizontal gradient bar). Aphid density (A_1) in *br* declines over time, with a sharper decrease after 20 days, while A_2 in *brba* decreases continuously throughout the simulation. Figure 3C ($D = 0.5$) and D ($D = 5$) illustrate simulations with a reduced aphid

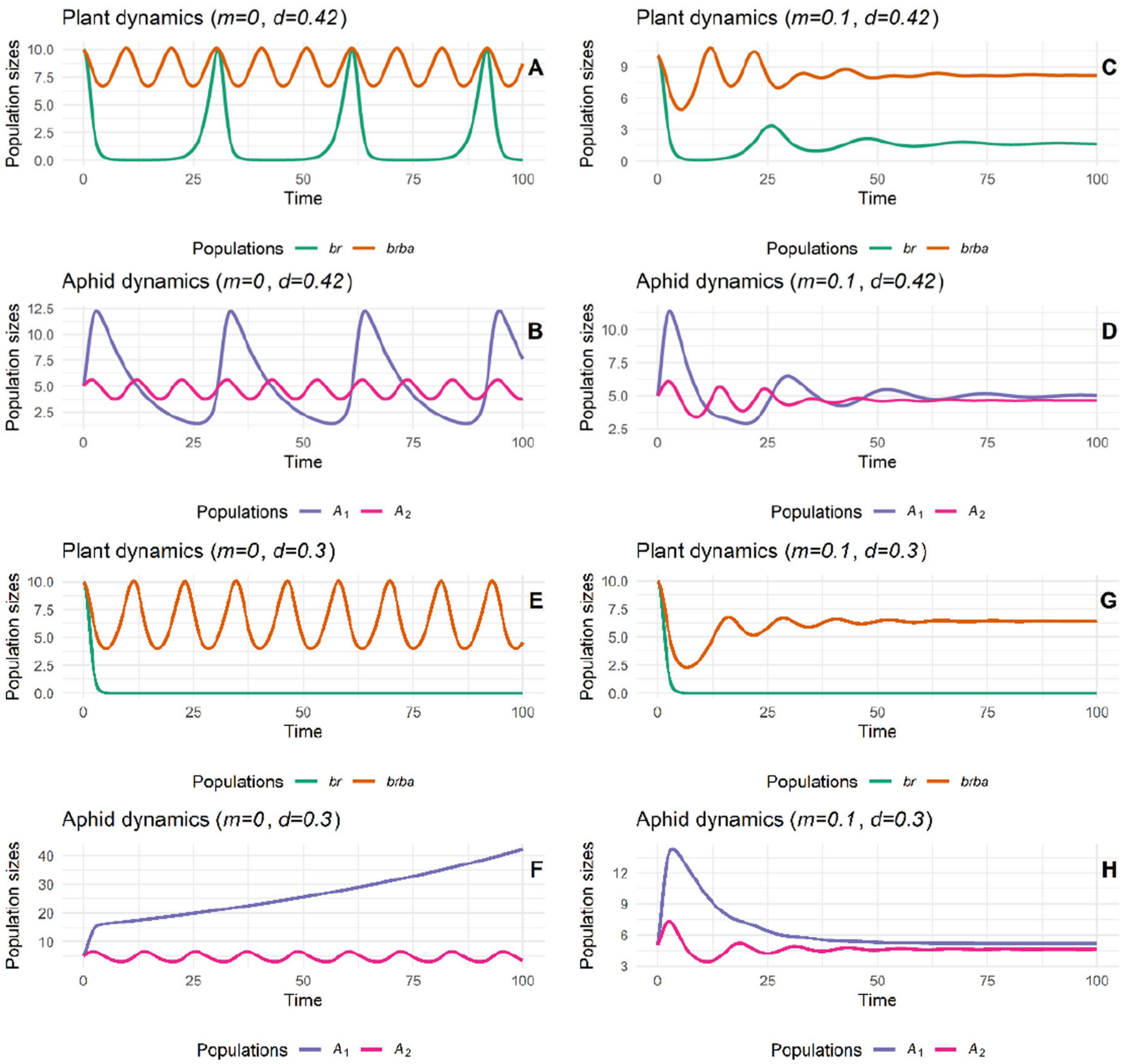

FIGURE 2 | Population dynamics of broccoli alone (*br*), broccoli-basil intercrop (*brba*), and aphid populations feeding on them (A_1 and A_2, respectively), simulated with growth rates $r_{A_1} = 0.31$ and $r_{A_2} = -0.16$. Experimental mortality rate of $d = 0.42$ for panels A, B, C, and D, and a simulated mortality rate of $d = 0.3$ for panels E–H in the model for both aphid populations. Panels A, B, E, and F depict dynamics without aphid movement ($m = 0$), whereas panels C, D, G, and H include aphid movement ($m = 0.1$).

mortality rate ($d = 0.3$) compared to the experimentally derived value ($d = 0.42$; Figure 3A,B). This reduction minimises other mortality factors included when $d = 0.42$, thereby increasing aphid density in simulated plant grids. In addition, increasing the diffusion coefficient from $D = 0.5$ to $D = 5$ m^2/day intensifies aphid dispersal, resulting in broader distribution patterns across the 50-m domain.

4.2.2.2 | 1D 100-m Domain. In the 100-m domain, aphid dispersal patterns in Figure 4A,B were similar to those in Figure 3A,B, but with more interspersed horizontal density bands due to the larger spatial scale. Comparisons between broccoli (*br*) and broccoli-basil intercrop (*brba*) grids reveal differences in aphid distribution at varying diffusion coefficients. Figure 4A ($D = 0.5$) exhibits higher maximum aphid densities than Figure 4B ($D = 5$), as indicated by the horizontal gradient bars below the figures, suggesting that the diffusion coefficient influences aphid dispersal at these and potentially intermediate values.

Figure 4C,D show aphid dispersion patterns similar to those in Figure 3C,D, but with more horizontal density bands alternating high and low densities due to the larger 100-m domain. The density gradient bars below Figure 4C ($D = 0.5$ m^2/day) and D ($D = 5$ m^2/day) indicate a wider aphid density range in Figure 4C compared to Figure 4D for both the broccoli (*br*) and broccoli-basil intercrop (*brba*) grids. However, maximum aphid density (A_1) in *br* is twice that (A_2) in *brba*, due to the repellent effect of the broccoli-basil intercrop. Additionally, simulations in Figure 4C,D, using a reduced aphid mortality rate ($d = 0.3$ vs. $d = 0.42$), highlight the aphid-repellent effect of the broccoli-basil intercrop (*brba*) but also influence lower mortality.

4.2.2.3 | 2D 50-m Domain. Figures 5 and 6 depict simulations of 2D aphid diffusion, with the horizontal and vertical axes representing aphid spatial positions (x and y coordinates). Time (t) is not an independent variable as previously viewed in the 1D diffusion, but is indicated by annotations above the

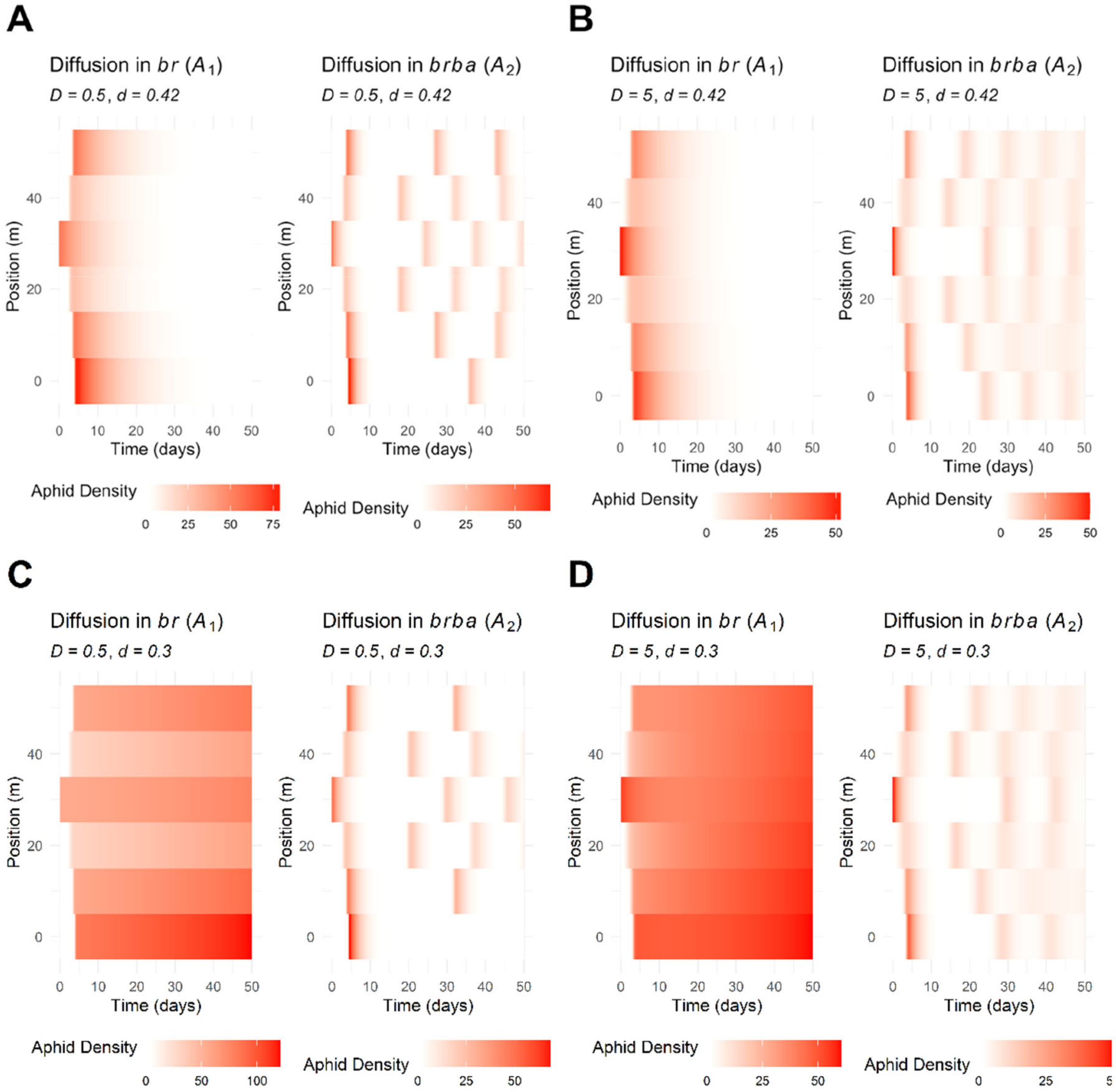

FIGURE 3 | Heatmap showing one-dimensional aphid diffusion (A_1 and A_2) in broccoli (*br*), and broccoli-basil intercrop (*brba*) with diffusion rates of $D =$ 0.5 (panels A and C), and $D =$ 5 (panels B and D), a mortality rate of $d =$ 0.42 (panels A and B) and a mortality of $d =$ 0.3 (panels C and D), in a 50-m-long domain.

figures (e.g., $t = 0$, $t = 25$, $t = 50$). In Figure 5A,B, the aphid density is high at $t = 0$ (represented by small, densely red rectangles), but spatially restricted, with the diffusion effect becoming evident over time. For $D = 0.5$ (Figure 5A), the repellent effect of broccoli-basil intercrop (*brba*) is pronounced at $t = 25$, with reduced aphid density (A_2) compared to the broccoli grid (*br*; A_1). By $t = 50$, the intercrop produces an unexpected result, with aphids (A_2) persisting, while A_1 trends to zero. For $D =$ 5 (Figure 5B), a similar pattern emerges, but with a broader aphid distribution across the 50 m × 50 m grid. These different patterns of diffusion on aphid density are likely attributable to the 2D insect movement, which differs from the 1D simulations in Figures 3,4.

The aphid diffusion patterns in Figure 5A and B ($d = 0.42$) are altered significantly with a reduced aphid mortality rate ($d = 0.3$) in Figure 5C and D in a 50 × 50 m^2 domain. For diffusion coefficients $D = 0.5$ m^2/day (Figure 5A) and $D = 5$ m^2/day (Figure 5B), the repellent effect of *brba* reduces aphid density (A_2) more than in *br* (A_1). This effect is visually stronger with $D =$ 0.5 m^2/day (Figure 5A) than $D = 5$ m^2/day (Figure 5B), as A_2 density is lower at $t = 25$ and $t =$ 50 days. On the other hand, the density gradient bar below Figure 5C shows a wider A_1 density range in the broccoli grid (*br*) in Figure 5C compared to Figure 5D, contributing to the stronger repellency effect at lower diffusion coefficients.

4.2.2.4 | 2D 100-m Domain.

The results in the 100 × 100 m^2 domain (Figure 6A–D) mirror those in the 50 × 50 m^2 domain (Figure 5A–D). The primary differences arise from the aphid mortality rates ($d =$ 0.42 and $d =$ 0.3), which affect aphid density (A_1) in the broccoli grid (*br*; Figure 6C,D) and aphid density (A_2) in the broccoli-basil intercrop (*brba*), as indicated by the density gradient bars below the figures. Nevertheless, the repellent effect of intercropping on A_2 density remains consistent across these systems, with a more pronounced effect when the aphid mortality rate is reduced to $d =$ 0.3. Notably, Figure 6A ($D =$ 0.5 m^2/day, $d =$ 0.3)

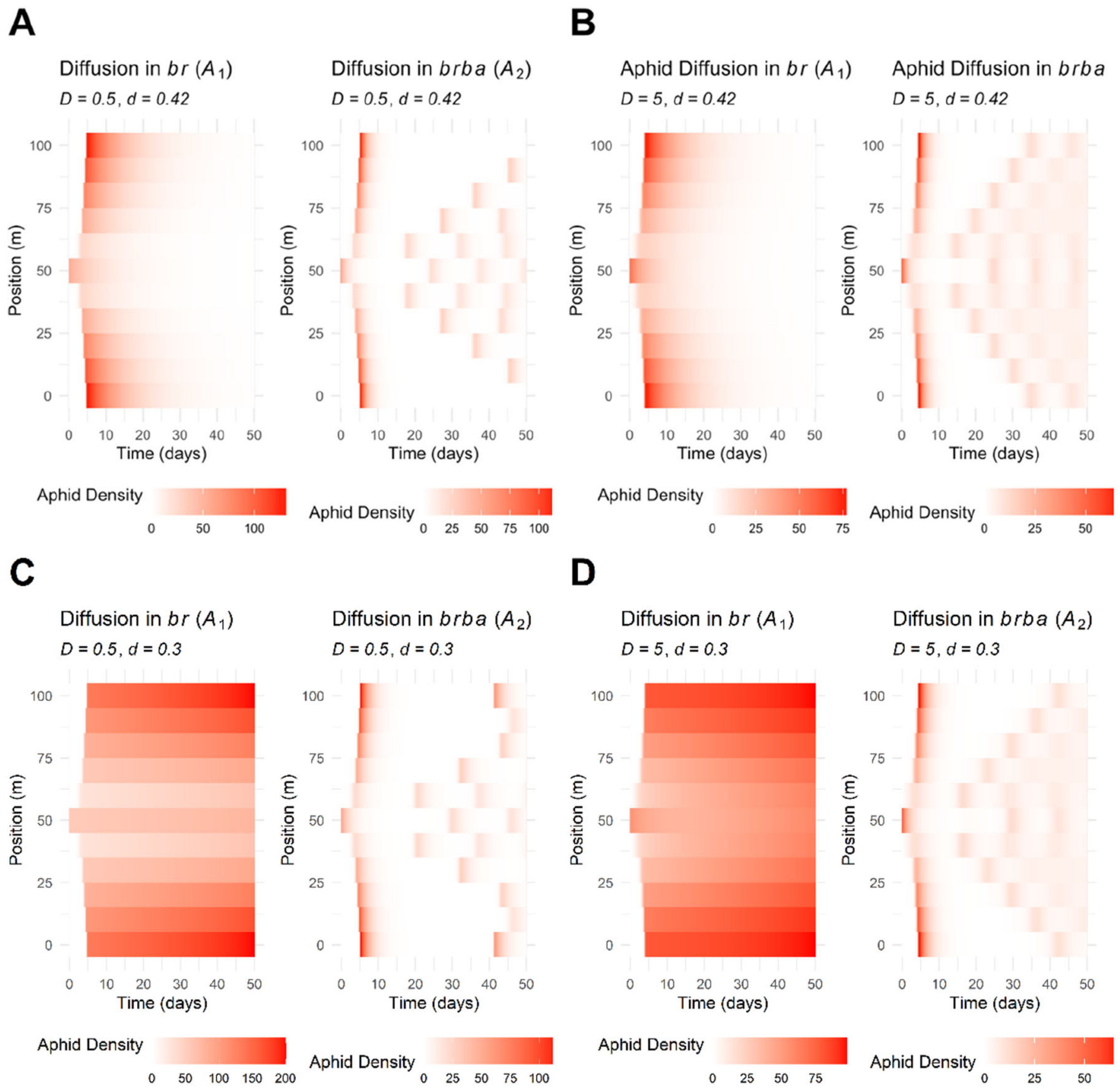

FIGURE 4 | Heatmap showing one-dimensional aphid diffusion ($A_1$and A_2) in broccoli (*br*), and broccoli-basil intercrop (*brba*) with diffusion rates of $D = 0.5$, (panels A and C) and $D = 5$ (panels B and D), a mortality rate of $d = 0.42$ (panels A and B), and a mortality of $d = 0.3$ (panels C and D), in a 100-m-long domain.

exhibits the highest aphid population density (A_1) among all 1D (Figure 3,4) and 2D (Figure 5,6) simulations, as indicated by the horizontal gradient bar (up to 300 aphids per square metre). Comparisons between A_1 (*br*) and A_2 (*brba*) reveal a marked difference in density, driven by the intercrop's repellent effect (Figure 6C, D).

5 | Discussion

5.1 | Choice Experiments

The experiments demonstrated that *M. persicae* significantly preferred broccoli over broccoli-basil intercrop, indicating avoidance of the latter due to basil's repellent properties. This repellency is likely driven by VOCs, such as linalool and estragole, emitted by basil, which alter the chemical environment and impair aphid host-plant recognition (Webster et al. 2010). Basil can mask target crop odours or emit repellent VOCs, complicating pest host location and indirectly influencing the foraging behaviour of natural enemies (Koschier et al. 2017). Aphids detect these VOCs through their antennal sensilla, enhancing the deterrent effect, repelling aphid populations, hindering their settlement, and reducing their reproductive performance, thereby inhibiting population development (Döring 2014).

5.2 | Impact of Basil on Aphid Population Growth

Our results showed a negative intrinsic growth rate of *M. persicae* in the broccoli-basil intercrop system, indicating that basil's repellent properties suppress aphid population growth as observed previously (Y. Zhang et al. 2025). There is robust evidence that basil, a non-host plant of *M. persicae*, modifies the chemical environment of neighbouring broccoli plants in the *brba* treatment, reducing aphid density (Deletre et al. 2016; Yarou et al. 2021), highlighting its value for biological control in intercropping systems.

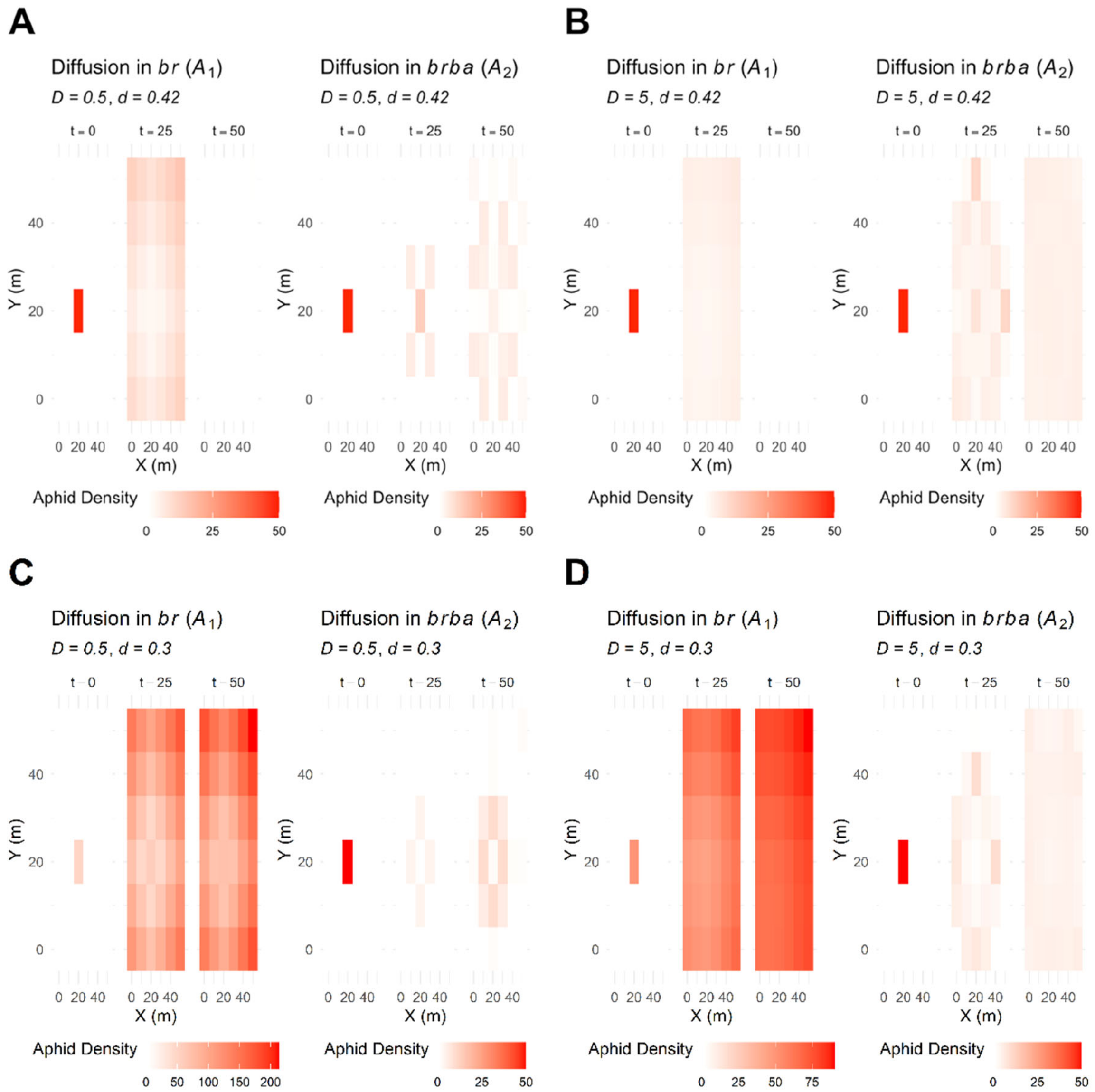

FIGURE 5 | Heatmap showing two-dimensional aphid diffusion (A_1 and A_2) in broccoli (*br*), and broccoli-basil intercrop (*brba*) with diffusion rates of $D = 0.5$ (panels A and C) and $D = 5$ (panels B and D), a mortality rate of $d = 0.42$ (panels A and B), and $d = 0.3$ (panels C and D) in a 50 m spatial domain.

5.3 | Plant-Herbivore Mathematical Model

Model simulations showed the repellent effect of the broccoli-basil intercrop, with reduced aphid density compared to oscillatory cycles in broccoli alone, where aphid (A_1) and plant populations periodically approached zero. This protective effect of *brba* consistently reduced aphid density across simulations. The analysis of the coupled aphid-plant dynamics using a spatially implicit model revealed populations trending to stable behaviours, depending on the aphid movement rate between patches. With no aphid movement, the *br* and *brba* patches operated independently, showing sustained oscillatory cycles in aphid and plant populations, with *brba* significantly reducing A_2 density.

This suggests that aphid movement stabilises dynamics by coupling the *br* and *brba* patches, balancing population growth and reducing extreme oscillations seen with no movement. Stable aphid populations, particularly those below the economic injury level, facilitate predictable and effective management strategies, including biological and cultural control methods (Rafikov and Balthazar 2005). In contrast, fluctuating pest populations may lead to unpredictable outbreaks and rapid growth, posing significant management challenges (Palma et al. 2023).

5.4 | Spatially Explicit Reaction-Diffusion Model

The repellent effect of the broccoli-basil intercrop was also evident in spatially explicit dispersal simulations, which showed pronounced impacts on *M. persicae* populations and plant dynamics at varying dispersal levels. Aphid mortality and intercropped plants synergistically influenced insect density, reducing aphid populations to low levels. The simulated reduction in aphid mortality from $d = 0.42$ to $d = 0.3$ enhanced visualisation of the repellent role of intercropped plants, highlighting their potential for IPM implementation. The

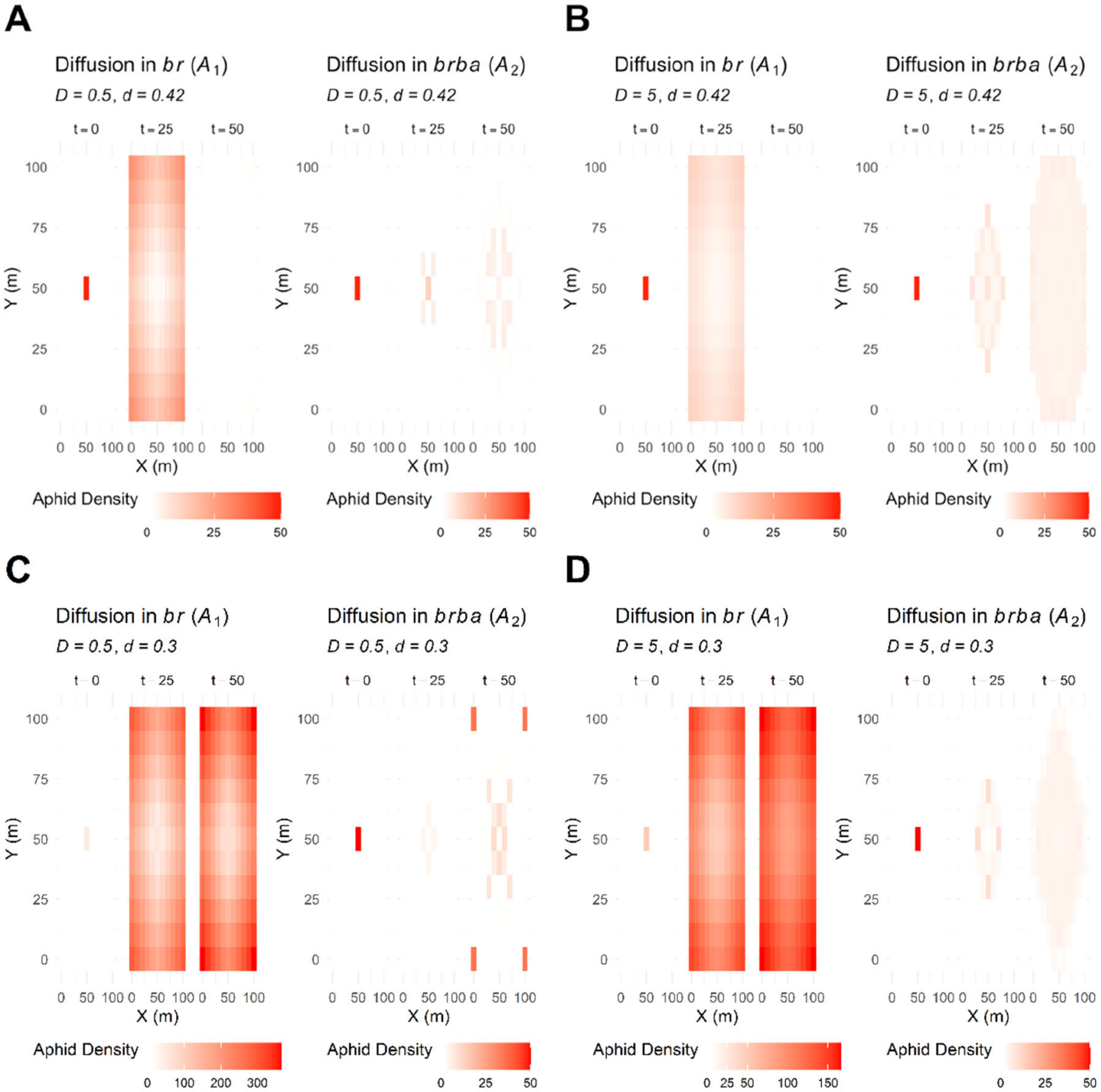

FIGURE 6 | Heatmap showing two-dimensional aphid diffusion ($A_1$and A_2) in broccoli (*br*), and broccoli-basil intercrop (*brba*) with diffusion rates of $D = 0.5$ (panels A and C) and $D = 5$ (panels B and D), mortality rate of $d = 0.42$ (panels A and B), and $d = 0.3$ (panels C and D) in a 100 m spatial domain.

mortality rate of $d = 0.42$, derived from real systems (Fidelis et al. 2018), was used in our simulations to contextualise IPM, indicating that multiple causes of aphid mortality should be considered in pest control programs. Conversely, the mortality reduction indirectly increased aphid population size, thereby amplifying the repellency effect. Simulations varying the diffusion coefficient at two levels ($D = 0.5$ and $D = 5\,\mathrm{m}^2/\mathrm{day}$) provided critical insights into the effectiveness of repellent plants in maintaining low aphid densities and spatial separation, offering valuable perspectives on their practical application in crop protection.

5.5 | Spatial Domain Sizes, Dimensions, and Diffusion-Based Spatiality

The investigation of varying domain sizes (50 and 100 m), and movement directions (1D and 2D) indicates that aphid diffusion patterns may shift based on the available dispersal distances and directions. While some similarities exist across different domain sizes, the diffusive demand alters the relationship with the occupied area. The domains examined introduce a critical scale dimension to the methodology (Lombaert et al. 2006), enabling comparisons of aphid diffusion across different scales. This suggests that neglecting this aspect could undermine the success of pest management programs (Petrovskii et al. 2014).

The implicit and explicit spatial approaches in our simulations complemented each other effectively. The implicit spatial model (e.g., movement rate, *m*) demonstrated dispersal's stabilising effect on *M. persicae* and plant dynamics in *br* and *brba*, mitigating population fluctuations and outbreaks for improved pest control. In contrast, the explicit spatial model examined the interplay of aphid mortality, diffusion coefficients, and grid domain size, revealing that *brba* repellency depends on multiple interacting factors.

5.6 | Modelling and Experimentation Integration

This study integrates modelling and experimentation, with data collected in controlled environments, such as chambers or greenhouses, simplifying model development by limiting *M. persicae* mobility. Despite these conditions, observed spatial heterogeneity in aphid distribution and plant interactions in the *brba* treatment supports the use of spatially explicit models, as explored by Lopes et al. (2010). While spatially explicit models effectively capture spatial dynamics, they typically do not emphasise movement triggered by repellency, such as that induced by the broccoli-basil intercrop on *M. persicae*. Such models have been extensively applied to study aphid population dynamics, often focusing on individual-based approaches. A notable example modelled the population dynamics of the aphid *Rhopalosiphum padi* in agricultural landscapes (Parry et al. 2006). This model accounted for individual-level effects while incorporating landscape properties, and environmental factors, such as wind speed and direction, within a spatio-temporal framework (Parry et al. 2006). In addition to Parry et al. (2006), studies have investigated aphid movement spatio-temporally, incorporating landscape structure, environmental conditions, and crop dimensions to inform pest management strategies (Thierry et al. 2017). These models highlight associations between initial population sizes and outbreaks, providing valuable predictions at landscape scales for pest management, complementing our patch-scale models for *M. persicae* in *brba*.

5.7 | Final Remarks

Although several models of aphid population dynamics have been documented (Klueken et al. 2009), most focus on immigration, movement, or migrant timing in crops. Our study, integrating repellent-driven behavioural responses and population dynamics of *M. persicae* in the *brba* treatment, provides a novel contribution by enhancing databases for analysing associations between plant repellency and aphid movement. This approach could enhance information for planning IPM programs for aphids and potentially other insects.

Plant-herbivore theory has evolved from viewing plants as passive victims to recognising them as dynamic players employing sophisticated defences against herbivory (War et al. 2012). Early ecological models, such as the Lotka-Volterra equations adapted from predator-prey dynamics, provided a framework for understanding plant-herbivore interactions. These models assume uniform plant vulnerability, but empirical evidence shows that plants, such as the *brba* intercrop, have evolved diverse defences, primarily chemical (e.g., VOCs like linalool and estragole), to deter herbivores like *M. persicae* (Ehrlich and Raven 1964).

Spatially explicit models have been widely used to study pest dispersal in crops and refuge areas, addressing movement and management for polyphagous species in intercropping and Bt resistance contexts (Ferreira et al. 2014; Caprio et al. 2016; Malaquias et al. 2017; Garcia et al. 2024). These models provide valuable insights into spatial dynamics, complementing our study's investigation of *M. persicae* dispersal and the repellent effect of *brba* in spatially explicit models.

This study addressed the complexity of agroecosystems through a mathematical model using parameters derived from experimental data to investigate the repellent effect of the broccoli-basil intercrop on *M. persicae* population growth compared to broccoli alone. Our study aligns with modern agroecological research emphasising the need to restore and maintain heterogeneity in agricultural systems to prevent pest outbreaks and enhance biological pest control (You et al. 2017). One effective strategy to mitigate pest threats is to identify key companion plants, such as basil in *brba*, that repel herbivorous pests like *M. persicae* (Morley et al. 2005).

6 | Conclusions

Aphids visibly exhibit an avoidance response to broccoli leaves when intercropped with basil, preferring broccoli grown in monocultures. Intercropping broccoli with basil significantly reduces aphid population growth rates, leading to a measurable decline in aphid infestations. The study employed deterministic models, including non-spatial population dynamics and spatial (1D and 2D) reaction-diffusion frameworks, to simulate aphid dispersal and interactions with plants. These models incorporated plant-herbivore dynamics, aphid movement, diffusion, and basil's repellent properties. Simulations from mathematical models demonstrated that basil repels aphids in broccoli-basil intercrops, with the effect observable in both spatial and temporal dimensions. The models revealed cyclic oscillations in plant and aphid populations, ultimately stabilising at a steady equilibrium driven by spatial population coupling.

The repellent effect of intercropping strongly depends on diffusion and mortality rate values, dispersal rates, and the size of spatial domains influence the system's efficacy. Broccoli-basil intercropping results in eco-friendly alternatives to chemical pest control, though its success depends on aphid dispersal behaviour and field size.

Author Contributions

All listed authors have made substantial contributions to the development and writing of this paper.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available on request.

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