A Generic Individual-Based Spatially Explicit Model as a Novel Tool for Investigating Insect-Plant Interactions: A Case Study of the Behavioural Ecology of Frugivorous Tephritidae

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Abstract

Computational modelling of mechanisms underlying processes in the real world can be of great value in understanding complex biological behaviours. Uptake in general biology and ecology has been rapid. However, it often requires specific data sets that are overly costly in time and resources to collect. The aim of the current study was to test whether a generic behavioural ecology model constructed using published data could give realistic outputs for individual species. An individual-based model was developed using the Pattern-Oriented Modelling (POM) strategy and protocol, based on behavioural rules associated with insect movement choices. Frugivorous Tephritidae (fruit flies) were chosen because of economic significance in global agriculture and the multiple published data sets available for a range of species. The Queensland fruit fly (Qfly), Bactrocera tryoni, was identified as a suitable individual species for testing. Plant canopies with modified architecture were used to run predictive simulations. A field study was then conducted to validate our model predictions on how plant architecture affects fruit flies’ behaviours. Characteristics of plant architecture such as different shapes, e.g., closed-canopy and vase-shaped, affected fly movement patterns and time spent on host fruit. The number of visits to host fruit also differed between the edge and centre in closed-canopy plants. Compared to plant architecture, host fruit has less contribution to effects on flies’ movement patterns. The results from this model, combined with our field study and published empirical data suggest that placing fly traps in the upper canopy at the edge should work best. Such a modelling approach allows rapid testing of ideas about organismal interactions with environmental substrates in silico rather than in vivo, to generate new perspectives. Using published data provides a saving in time and resources. Adjustments for specific questions can be achieved by refinement of parameters based on targeted experiments.
Introduction

Computational modelling is playing an increasingly significant role in understanding complex biological behaviours. Over a decade ago medical molecular and cell biologists found that computational models, used to simulate hypothesised mechanisms underlying processes in the real world, could be of great value in understanding the systems they study [1]. Such endeavours have also grown in general biology and ecology [2–5].

Individual-based models (IBMs) are a type of computational model that uses simple rules to simulate individual behaviour, the interactions among and between individuals, and the interactions between individuals and their abiotic environment [6]. IBMs simulating individual behaviour have been found to be a valuable tool to analyse the complicated interactions and emergent outcomes observed in behavioural ecology [7–10]. However, IBMs often focus on specific interactions, and require large, specialised biological data sets to derive individual behaviour rules, which can make them difficult to be developed [6].

In cancer research, generic computational models have been constructed using existing data to define foundations for design of patient specific cancer therapy [11, 12]. This idea of using generic models seems not to have been promoted in ecology. In general, IBMs focus on specific questions for which datasets need to be generated [13]. Instead of generating new data before beginning to develop a computational model, biologists or ecologists could be looking at published data and divining commonalities in that data to create generic models; only undertaking additional targeted data-gathering where such models do not match outcomes in specific cases.

To test the feasibility of the above idea, this study focuses on individual-based modelling of the within canopy movement patterns of frugivorous Tephritidae, the ‘true fruit flies’. Because they are pests of economic significance to global agriculture [14], there are multiple data sets available in the published literature on the behaviour of these flies, e.g. for the apple maggot fly, Rhagoletis pomonella (Walsh) [15–18], the Chinese citrus fruit fly, Bactrocera minax (Enderlein) [19], the European cherry fruit fly, Rhagoletis cerasi (Linnaeus) [20], the Queensland fruit fly (Qfly), Bactrocera tryoni (Froggatt) [21–25], and others like the Mexican fruit fly, Anastrepha ludens (Loew), the melon fruit fly, Bactrocera cucurbitae (Coquillett), the oriental fruit fly, Bactrocera dorsalis (Hendel), the olive fruit fly, Bactrocera oleae (Gmelin), and the Mediterranean fruit fly, Ceratitis capitata (Wiedemann) [18].

The success of a generic individual-based spatially explicit model rests on commonality of behavioural rules across the organisms being considered. There is evidence that underlying rules for generating insect movement behaviour patterns in plant canopies may be simple and generic, based largely on plant architecture and some simple insect behavioural rules [26–29]. The same drivers may follow a common pattern for frugivorous fruit flies. Raghu et al. [30] showed that host plant structure has significant effects on the abundance and behaviour of the wild tobacco fruit fly, Bactrocera cacuminata (Hering). For the Queensland fruit fly, B. tryoni, Balagawi et al. [24] and Balagawi et al. [23] argued that traits of plant architecture influence the insect’s interactions with their host plants: most flies were caught in the mid to upper canopy on fruiting plants. The apple maggot fly, Rhagoletis pomonella (Walsh) [31], the Mexican fruit fly, Anastrepha ludens (Loew) [32], and the Mediterranean fruit fly, Ceratitis capitata (Wiedemann) [33], have also been found to have a different abundance at different canopy heights. Although there is evidence showing a significant relationship between host plant architectural characteristics and behaviour of fruit flies, the fundamental scientific questions of how fruit flies optimise their search patterns and limit competition through movement choices and how these movement patterns are affected by plant architecture are still not well understood.

In this paper we hypothesize that spatial patterns of insect abundance in plant canopies emerge from the behaviour of individual insects, so an individual-based model should be able
to be used to simulate the studied system [34]. The overall aim of the paper was to develop a generic individual-based spatially explicit model of tephritid within-canopy foraging using published data from many tephritid species, and to determine whether it could then accurately predict the behaviours of a single species (in this case B. tryoni). Our goal is to determine if IBMs in biology and ecology can only be developed after the generation of unique and targeted data sets, or if at least initial IBMs can be developed using pre-existing data which may or may not be directly related to the particular focus system.

Materials and Methods

A generic 3D individual-based spatially explicit model was developed, tested and parameterized in terms of the Pattern-Oriented Modelling (POM) strategy [35] and protocol [36]. The generic model was built using published frugivorous tephritid data for multiple species, and aims (1) to predict fruit fly movement and spatial distribution patterns in plant canopies to be compared with the observed patterns in experiments on the behaviour of B. tryoni in Valencia orange trees, conducted by Dalby-Ball and Meats [22], and (2) to conduct different simulation experiments after being verified. The model description is written in terms of the ODD (Overview, Design concepts, Details) protocol for describing individual and agent-based models [37, 38]. NetLogo [39] has been used to develop the generic 3D individual-based spatially explicit model (for NetLogo 3D 5.1.0 code; see S1 Appendix).

ODD protocol

Overview.

1. **Purpose:** The purpose of the model is to simulate movement patterns and spatial distributions of visits (e.g. across canopy regions and across trees) of the frugivorous Tephritidae on foliage and fruits within fruiting plant canopies with different architectures.

2. **Entities, state variables, and scales:** The entities in the model are female fruit flies and the spatial units are cubes composing the fruiting tree and the ground. One unit distance in the model is equal to 4cm in reality. The tree is about 1 m in height and 1.5 m in width. The average leaf area of Valencia orange trees is around 20 cm² [40]. We assume that a green cube represents two leaves with the average leaf area of around 20 cm². A red cube represents host fruit. Individual female flies forage for host fruit in the tree canopy and are characterized by the state variables of identification number, location, and orientation. Foliage and fruit cubes are characterized by the state variables of component type (represented as colour), location and visits counter. The extent of the model worlds are 64 × 64 × 50 cubes. The simulation will stop when the time step reaches 15 (equivalent to 15 minutes in reality).

3. **Process overview and scheduling:** The processes are executed as described in Fig 1. At the beginning of the simulation, a tree is created and female fruit flies are randomly located in green vegetation cubes in the lower third part of tree. In each movement step, if there is any host fruit within the sensing volume, the fruit fly will move in the direction of the fruit landing on the first intervening green cube or on the fruit if there are no cubes between the fruit and itself. If not, the fruit fly will then move to the nearest vegetation cube in a randomly selected direction within the sensing volume. During the simulation the following main processes are executed:

   - **move-flies:** fruit fly undertakes short hops and tends to move upwards by a short distance between vegetation cubes, while foraging for host fruit.

   - **count-visits:** vegetation cubes will show how many times a visit by a fruit fly has occurred.
• **display-output**: is run when the simulation stops to show the movement patterns as well as spatial distributions of visits on the canopy.

**Design concepts.**

4. **Design concepts:**

• **Basic principles**

The basic principle of the model is that spatial patterns of insect abundance in plant canopies emerge from the local behaviour of individual insects. Fundamental fruit fly behaviours were derived from the literature for multiple species. Fruit flies tend to move upward by short hops, e.g. the apple maggot fly, *R. pomonella* [15], and prefer moving in the inner region of canopy e.g. the Mediterranean fruit fly, *C. capitata* and Qfly, *B. tryoni* presumably because the intervening foliage can provide flies with some protection from predation [22, 41, 42]. The wild tobacco fruit fly, *B. cacuminata* also prefer moving toward denser foliage volumes in the host plant canopy, for the same reason [30], while adjacent foliage increases the probability of finding host fruit for Qfly, *B. tryoni* in the tree canopy [25].
We make the simplifying assumption that local movement to nearest leaves is driving the process. Therefore, the rationale underlying the model is biased random movement, based on environmental inputs including plant component location relative to the fly’s position at any time.

• Emergence
The movement patterns and spatial distributions of visits (on foliage and fruit) emerge from mechanistic representation of the behaviours of individual fruit flies, which are not imposed by rules that force the model to produce certain patterns. These patterns are at the population scale.

• Sensing
Frugivorous Tephritidae (fruit flies) evaluate the surrounding space for sensory information using principally their eyes and the olfactory hairs and pegs found on the antennae that act as a nose. There is a limit, however, to how far a fly can see both in the forward direction and in an arc around the head (‘field of view’). This also depends on what is being viewed, such as near-by foliage, or the edge of a tree canopy. Each sensory system has a limit to the linear effective range over which it can be active, resulting in a ‘detection radius’ (sensory range). For example, a fly may not be able to see a fruit because of foliage blocking the view, but if the fruit is within a certain distance—the olfactory range—it will be able to smell that a fruit is nearby and move in the direction of the odour. The area within which a fly effectively uses its senses is a volume described by linear distance and arc (degrees from horizontal) that describes a ‘sensing volume’. Fruit flies are potentially aware of the vegetation cubes or fruit within a sensory range in their field of view. Lack or low number of vegetation cubes will indicate when they are within the top or edge of the canopy.

• Interaction
There are no interactions between fruit fly individuals in this model. Flies can sense fruit and vegetation components and move towards them. The number of visits on vegetation and fruit components is recorded.

• Stochasticity
  • Fruit flies are randomly positioned in the lower third part of tree using a uniform distribution at the beginning.
  • If flies reach the edge of the canopy, there is a probability (20%) that flies will leave the tree, because the experiments conducted by Dalby-Ball and Meats [22] have shown that some B. tryoni depart from the fruiting tree before reaching the top of the canopy.
  • To define their orientation, flies will randomly select a target leaf from those within the sensing volume with equal probability.
  • The probability of detecting fruit is defined as a function of distance (see Submodel section).
  • If there is no vegetation cube or fruit within the sensing volume, fruit flies will randomly hop upwards using uniform random numbers to generate hop length and direction within user-defined ranges.

• Observation
The number of visits to each vegetation cube and movement trails among vegetation cubes can be displayed numerically, or visually in the model. This provides output for
comparisons between runs of the model using different parameter settings for testing, understanding and analysing fly movement patterns. Data are also written to files for further analysis.

**Details.**

5. **Initialization:** The extent of the model world is $64 \times 64 \times 50$ cubes. The model world has a tree (tree architecture can be modified for simulation requirements) and a ground made up of cubes (patches in the spatial units of the NetLogo world). A green cube represents two leaves, while a red cube represents host fruit. The tree has a closed-canopy (cylinder volume—height: 1 m and width: 1.5 m) containing 300 green vegetation cubes (equivalent to 600 leaves in reality) and 6 host fruit to be consistent with the experiments conducted by Dalby-Ball and Meats [22]. The foliage density of closed-canopy is 339.53 leaves per cubic meter. The canopy is considered to consist of lower, middle and upper parts, each approximately one-third the height of the canopy and containing 100 green vegetation cubes and 2 host fruit. The canopy is also considered to consist of inner and outer parts (Fig 2), with 150 green vegetation cubes in each. Female flies are randomly placed in green vegetation cubes in the lower third of the tree. The number of visits for all green vegetation cubes and host fruit is set to zero.

6. **Input data:** No input data.

7. **Submodels:** All model parameters are listed in [Table 1](#).

![Fig 2. The inner and outer parts of the tree.](#)

Concentric circles represent an aerial view of a cross section through the canopy of the simulated tree, divided into two sections, the outer and the inner part of the tree with the same number of vegetation cubes in each of the two sections. The grey-coloured area represents the inner part of the tree.

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**move-flies**: The following rules are applied by the individual fruit fly in the simulation (Fig 3):

- A fly moves by short hops (a limited distance movement between vegetation cubes within the sensing volume)
- A short hop ends with the fly finding host fruit or the nearest vegetation cube in the previously selected random direction.
- If flies reach the edge of the canopy, there is a fixed probability of leaving.
- If not at the top of the canopy, the hopping process is repeated.
- When the top of the canopy is reached, the fly will leave the tree [22].

A sensing volume is defined by two parameters, the detection radius (sensory range) and sensing angle (field of view). In the current study, we used 40 cm and 220 degrees as detection radius and sensing angle for the sensing volume (Fig 4). The reason for using these values is that:

- The distance threshold of the sphere of attraction for the apple maggot fly, *Rhagoletis pomonella* (Walsh), is around 80 cm in an apple tree canopy [17]. However, when 80 cm was used in the model, a pattern was produced with too many flies remaining in the tree, which did not match with published experimental outcomes, where according to Dalby-Ball and Meats [22], most *B. tryoni* left the tree within 15 minutes. The model identified that the distance threshold of the sphere of attraction is a key parameter in simulating fruit flies’ search for host fruit, therefore additional targeted experiments will need to be conducted for *B. tryoni*. We followed the POM strategy [35] and protocol [36], and employed a sensitivity analysis for the detection radius parameter and used three
different patterns to reduce the uncertainty in the model structure and parameters [43]. After the sensitivity analysis, the distance threshold of the sphere of attraction was modified to 40 cm, because this distance resulted in a better match to all three observed experimental patterns (S2 Appendix).

- The flies have a probability of locating fruit that is a function of distance, generated by curve fitting using observed probabilities of visiting the stimulus source in Fig 4(a) from Verdeny-Vilalta et al. [17]. Flies do not have a 100% chance, as there may be intervening objects. After logistic curve fitting (adjusted $R^2 = 0.879$, $P < 0.001$), a mathematical function was obtained:

$$y = \frac{a}{b \ln(x + c)}$$

where $y$ is the probability of locating fruit and $x$ is the distance between fly and host. 

![Fig 3. Simulation of individual fly movement through a closed-canopy.](image)
Simulation experiment 3: different entry point of *B. tryoni*

The use of two different entry points for *B. tryoni* into the tree canopy (closed-canopy type) allowed an investigation of the importance of this factor on movement and visitation within the canopy. In the tree with the new entry point (upper region entry rather than lower), the visits (742) on host fruit in the upper region was four times greater than in the middle region (162). There were no visits on host fruit in the lower region. The visits on host fruit among three regions in the tree with the new higher entry point or with lower entry point, were significantly different (Fig 8).

For comparison of visits on host fruit among the two treatments, the visits (742) in the upper part of the tree with the higher entry point was 1.5 times as many as the visits (487) in the upper part of the closed-canopy. Not surprisingly, less visits were found on fruit in middle or lower parts in the tree with the new entry point. The visits (904) on total fruit in tree with the new entry point were half that (1899) of the initial lower entry point closed-canopy tree. The visits among three regions on both treatments were significantly different (Fig 8).

Model output corroboration

Our model predictions were compared to independently generated findings of other studies, after running simulation experiments. Three independent patterns (Table 5) have been used for the model output corroboration.

The model predictions show:

- Pattern4: fewer *B. tryoni* are found in the lower canopy compared with the middle and upper canopy in the closed-canopy tree (Fig 6).

- Pattern5: significant differences for movement patterns of *B. tryoni* among different types of tree architecture (closed-canopy vs. vase-shaped) (Table 3).

- Pattern6: *B. tryoni* spend more time on host fruit (in total) in vase-shaped canopies (Table 3).

These model predictions are consistent with the three independent patterns.

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Table 3. The comparison of mean time (min) spent by 30 *Bactrocera tryoni* on the vegetation volume and host fruit in each part of the two types of tree canopy.

|                  | Closed-canopy | Vase-shaped | t    | df | P       |
|------------------|---------------|-------------|------|----|---------|
| Mean time        |               |             |      |    |         |
| Upper            | 103.7         | 62.32       | 11.975 | 84.412 | < 0.001 |
| Middle           | 97.24         | 71.1        | 9.761  | 96.58  | < 0.001 |
| Lower            | 55.58         | 70.44       | -5.864 | 92.094 | < 0.001 |
| Fruit in upper   | 9.74          | 10.84       | -1.133 | 97.868 | 0.26    |
| Fruit in middle  | 16.6          | 10.5        | 5.804  | 97.9   | < 0.001 |
| Fruit in lower   | 11.64         | 24.62       | -12.271 | 90.198 | < 0.001 |
| Total fruit      | 37.98         | 45.96       | -4.753 | 96.75  | < 0.001 |

Note: the data sets for time spent on green vegetation cubes and host fruit in each part of two types of tree architecture were normally distributed (Shapiro-Wilk normality test). An independent samples t-test was used to compare time spent on the green vegetation cubes and host fruit in the same parts of the canopy but between different architectures (e.g. the upper part of closed-canopy vs. the upper part of the vase-shaped tree).

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Discussion

The generic individual-based spatially explicit model, built here from published data on frugivorous tephritids and operating on a simple set of behavioural rules, predicted fruit fly movement and spatial distribution patterns consistent with published literature. Such patterns, secondary or independent predictions, discussed below can be strong indicators that the model is structurally realistic [43]. Our generic model worked for a specific tephritid species against which it was tested, namely *B. tryoni*. There is general agreement that the abundance of

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*Fig 7. The results of fruit-centralized tree treatment. Median time (min) spent by 30 *Bactrocera tryoni* on host fruit in each part of the fruit-centralized tree (Kruskal-Wallis test: Median = 11|12|9, H = 5.43, df = 2, P = 0.066, n = 50 simulations).*
The comparison of mean/median time (min) spent by 30 *Bactrocera tryoni* on host fruit in each part of two treatments.

|                | Closed-canopy | Fruit centralized tree | Closed-canopy | Fruit centralized tree | t    | W     | df | P     |
|----------------|---------------|------------------------|---------------|------------------------|------|-------|----|-------|
| Fruit in upper | 9.74          | 11.52                  | -             | -                      | -1.692 | -     | 96.695 | 0.094 |
| Fruit in middle| 16.6          | 12.46                  | -             | -                      | 3.925  | -     | 97.851 | < 0.001 |
| Fruit in lower | -             | -                      | 12            | 9                      | -      | 1559  | -     | 0.033 |
| Total fruit    | 37.98         | 34.14                  | -             | -                      | 1.999  | -     | 88.749 | 0.049 |

Note: an independent samples t-test was used to compare time spent on host fruit in the same parts of the canopy but between two treatments (e.g. the upper part of closed-canopy vs. the upper part of the fruit centralized tree), while the Mann-Whitney-Wilcoxon Test that is the non-parametric equivalent of the independent samples (or two-sample) t-test, was used when the data sets are not normally distributed.

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Frugivorous fruit flies at different canopy heights is varied, and the increasing height is generally associated with greater abundance of frugivorous fruit flies [24]. This argument can be supported by data from the wild tobacco fruit fly, *Bactrocera cacuminata* (Hering) [30], the apple maggot fly, *Rhagoletis pomonella* (Walsh) [31], the Mexican fruit fly, *Anastrepha ludens* (Loew) [32], and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) [33]. In particular, the model predictions match with the findings by Balagawi et al. [24] in terms of the patterns of abundance of *B. tryoni* in different heights of canopy, in which fewer *B. tryoni* are

Fig 8. The results of simulation experiment 3: different entry point of *B. tryoni*. Visits on host fruit in a divided plant canopy for different entry points by *B. tryoni*: data displayed as proportion. A one-way tables Chi-square test and a two-way tables Chi-square test were used to look at the differences in visits per canopy region within the canopy and among treatments respectively: $X^2 = 99.093$, df = 2, $P < 0.001$, n = 50 simulations for the lower entry point; $X^2 = 1010.19$, df = 2, $P < 0.001$, n = 50 simulations for the upper entry point; the two treatments differed significantly: $X^2 = 836.998$, df = 2, $P < 0.001$, n = 50 simulations.

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found in the lower canopy compared with the middle and upper canopy. Furthermore, our model predicts that *B. tryoni* spend more time in the inner region of canopy. There is evidence that fruit flies prefer moving in the inner region of canopy e.g. the Mediterranean fruit fly, *C. capitata* and Qfly, *B. tryoni* presumably because the intervening foliage can provide flies with some protection from predation [22, 41, 42]. The wild tobacco fruit fly, *B. cacuminata* also prefer moving toward denser foliage volumes in the host plant canopy, for the same reason [30].

The model also generated specific predictions of behaviour. Orchardists modify tree architecture for a number of reasons such as to increase fruit-yield and reduce occurrence of some pests and diseases [48, 50] but impact on tephritid movement and host-finding success does not appear to have been investigated specifically. To investigate differences in movement patterns of *B. tryoni*, predictive simulations were run with plant canopies whose architecture had been modified. The output suggests significant differences for movement patterns of *B. tryoni* among different types of tree architecture. For example, *B. tryoni* were predicted to spend more time on host fruit (in total) in vase-shaped canopies. Changes in canopy architecture also result in *B. tryoni* leaving the tree either earlier or later and therefore affect likelihood of fruit-finding. In support of these predictions, Balagawi et al. [23] found that *B. tryoni* prefer a more open and branched canopy over a denser and closed canopy. The vase-shaped canopy may be presenting architecture more in accordance with such an open and branched canopy. In addition, our field study demonstrated that host fruit (in total) were more often visited by *B. tryoni* in the vase-shaped canopy, in contrast to in the closed-canopy. As a result, *B. tryoni* spent more time on host fruit (in total) in the vase-shaped canopy (S3 Appendix).

Raghu et al. [30] suggested that host plant architecture, e.g. density of foliage, and microclimate, e.g. temperature and light intensity, can significantly affect the abundance and behaviour of the wild tobacco fruit fly, *Bactrocera cacuminata*. An increase in numbers of wild tobacco fruit flies at the host plant is associated with increasing temperature and light intensity, and more wild tobacco fruit flies were found in host plants with dense foliage. The data output from the model can be understood from the perspective that a vase-shaped canopy could get more sunlight due to its shape, and fruit flies could therefore spend more time in the vase-shaped tree and this would increase the chance of finding host fruit for flies. So the generic model has generated outcomes that relate to microclimate from simple behavioural movement rules. A more complex model constructed from data integrating multiple environmental factors was not found to be necessary. This outcome supports our hypothesis that initial IBMs can be built successfully from existing data focussed on fundamental behavioural rules without the need for generating dedicated and complex data sets that can take many years to achieve.

As another example, the model identified that the position of host fruit in the canopy and the entry point of *B. tryoni* to a tree canopy may be crucial in terms of fruit finding and number of visits, which would translate to infestation of a crop. The prediction is that *B. tryoni* will spend more time on host fruit in the edge region of a canopy, as well as on host fruit in the

| Patterns | Description | Source |
|----------|-------------|--------|
| Pattern4 | Fewer *B. tryoni* are found in the lower canopy compared with the middle and upper canopy in the closed-canopy tree | [24] (pp. 284) |
| Pattern5 | Different plant architectures (denser, closed canopy vs. open, branched canopy) affect *B. tryoni* resting behaviours on foliage and host fruit | [23] (pp. 515) and our field study (S3 Appendix) |
| Pattern6 | *B. tryoni* spend more time on host fruit (in total) in vase-shaped canopies | Our field study (S3 Appendix) |

Table 5. The overview of three independent patterns used for the model output corroboration.
upper canopy. An application of this model output would be to place traps in fruiting trees in the upper canopy at the edge in closed-canopy trees, and mid to upper parts in vase-shaped architecture in order to maximise fly-catch. This prediction is supported by a study that looked at positioning of protein bait sprays for *B. tryoni* management to maximise efficacy and came to the conclusion that they should be applied as high in the canopy as is mechanically possible [24].

Although unique predictions require validation in the real world, the strength of the modelling approach is that trust-worthy predictions can be achieved in a timely fashion from current data. Additionally, such pattern-oriented models can produce comparative predictions that can be tested in the field [35, 36]. As a result, time and resources can be better focussed on experimentation that shows the greatest likelihood of success. For instance, we conducted our field study based on our model predictions, and the findings of our field study are consistent with model predictions ([S3 Appendix].

Once a generic model is constructed, however, there may be cause to adjust it further to study particular interactions, and for particular species. In our case, the detection radius of the sphere of attraction is an example of this. Data for how close a fly needs to be to a host-fruit to respond to it is only available for *Rhagoletis pomonella* (Walsh), where it appears to be associated with the density of the tree canopy [17]. The generic model has identified these data as important for future research efforts to better adjust the model to individual species for exploration of foliage density effects. Studies have suggested that animals tend to optimize their foraging activities (e.g. strategies of movement) [51, 52]. Our model also suggested that detection radius for fruit flies in trees with the same foliage density may vary, largely based on relative tree size. In our study, the closed-canopy tree is about 1.5 m diameter by 1 m height and the use of 40 cm (medium short distance compared to the tree height) for fruit flies allows them to find more fruit in the tree ([S2 Appendix]. However, Verdeny-Vilalta et al. [17] found that detection radius for *Rhagoletis pomonella* (Walsh) is approximately 80 cm in a tree with about 2.8 m diameter by 3 m height. Thus, the distance for short hops of fruit flies during searching for host fruit in trees with same foliage density but different height, may vary, largely based on the relative host plant size. Future research will need to be conducted to look at this.

Other adjustments are also possible. In the current model, a volume is used to represent vegetation. A finer resolution was not needed because the analysis focused on outputs involving abundance and spatial distribution within architectural canopies. To involve movement patterns at individual leaf or branch level, more detailed modelling of plant architecture can be achieved using the Lindenmayer system (L-system) formalism [53, 54], which can provide an explicit and detailed model of the 3D structure [55–57].

In summary, this study has demonstrated that it is feasible to build an individual-based model from generic published data from multiple species that utilise similar behavioural rules, to explore behavioural ecology of an individual species. Species that hold economic importance generally have multiple published data sets to draw from, in comparison to those that do not. Given this distinction, the generic individual-based spatially explicit model is best suited to driving innovation in ecological studies that have direct application to management issues. For other species, targeted data generation would be necessary, informed by the data sets that have proven most useful for the generation of the current model. Such a model allows rapid testing of ideas about organismal interactions with environmental substrates *in silico* rather than *in vivo*, to generate new perspectives. Since published data are used, there is a saving in time and resources. Adjustments for specific questions can be achieved by tuning parameters based on targeted experimentally obtained data or utilisation of different modelling platforms such as the L-system to simulate at a more detailed level.
Supporting Information

S1 Appendix. NetLogo 3D 5.1.0 Code. (DOCX)

S2 Appendix. Model Analysis. (DOCX)

S3 Appendix. Field Study. (DOCX)

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Author Contributions

Conceived and designed the experiments: MW BC ARC JH. Performed the experiments: MW. Analyzed the data: MW BC. Contributed reagents/materials/analysis tools: BC ARC. Wrote the paper: MW BC ARC JH. Designed and developed the model: MW JH.

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