

A spatio-temporal modelling approach to understand the effect of urban fruit fly outbreaks on peri-urban orchards

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ABSTRACT

Urban areas are well-known sources of fruit fly introduction and unmanaged populations pose a high risk of dispersal to surrounding agricultural areas. Although management of urban fruit fly populations is recognised as being important for area-wide control programmes, its relative importance is rarely quantified. Identifying possible sources of fruit fly populations is important to the success of area-wide programs, as well as to on-farm management. We developed a modelling approach to analyse the spatio-temporal connectivity of fruit fly across urban-agriculture boundaries. For a case study, we examine Mediterranean fruit fly, *Ceratitis capitata*, outbreaks in two fruit growing regions in south-west Western Australia. Connectivity between population sources was defined using a dispersal kernel and routinely collected surveillance data from traps located across urban and agricultural areas. Spatio-temporal Bayesian models were then developed to quantify the extent to which unmanaged urban populations contribute to commercial orchards across each region. Our model results from two fruit growing regions indicate that population connectivity is a strong predictor of urban and commercial orchard Mediterranean fruit fly density. Models demonstrate that unmanaged urban outbreaks can contribute to increased pest pressure in surrounding orchards up to 2 km, but the urban contribution quickly declines over this distance. We also demonstrated that our models provide a means of predicting changes in Mediterranean fruit fly density across a region. Regional scale inference from our models may be particularly useful for sites where surveillance trapping data is unavailable. With an increasing risk of fruit fly incursions from expanding urban areas into agricultural regions, it is important to understand the processes driving population connectivity to target pest management strategies. By modelling surveillance trapping data and population connectivity, we can quantify how unmanaged urban pest infestations can contribute to pest pressure in nearby commercial orchards. Such information can help pest managers quantify the risk posed by unmanaged urban infestations when designing and implementing area-wide management.

1. Introduction

Managing outbreaks of pest species such as fruit flies (Diptera, Tephritidae) is one of the major challenges in agriculture (Papadopoulos, 2014). Agricultural regions at the edge of urban areas face added challenges, because they are not only points of entry for many invasive pest species, they can also provide fruit flies with a continuous supply of unmanaged host fruit in urban residences (Carey et al., 2017; Economopoulos and Rempoulakis, 2018). The presence of unmanaged hosts can lead to strong population growth across urban areas (Economopoulos and Rempoulakis, 2018). While urban areas are potential

sources of unmanaged populations, they can be costly and logistically challenging to include in area-wide pest management programs (Mumford, 2021; Papadopoulos, 2014). Area-wide programs can include the systematic application of bait sprays, mass trapping or sterile insect releases over large areas (Klassen and Vreysen, 2021). However, program managers are often confronted with balancing the economic and social risks of controlling unmanaged population sources, like those found in urban areas (Kruger, 2021; Mumford, 2021). In such cases, it is important to assess the risk posed by unmanaged urban infestations and their effect on surrounding orchards.

One of the main difficulties implementing area-wide programs is

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limited information on fruit fly population dynamics across regions (Klassen and Vreysen, 2021). Programs often rely on surveillance trapping networks to provide estimates of relative abundance and distribution, but it is difficult to determine which orchards will benefit most from urban control (Barclay et al., 2021; Lance, 2014). A further difficulty in understanding the effects of unmanaged populations is caused by changes in habitat within fruit growing regions (Klassen and Vreysen, 2021; Mumford, 2021). Agricultural practices at the farm, such as the type and rotation of crops, application of chemicals and time of harvest can affect habitat conditions and the distribution of fruit fly populations (Krasnov et al., 2021). As such, regional scale population dynamics are influenced by landscape heterogeneity and biological processes, such as population connectivity and dispersal (Hanski, 1998). The interplay between landscape, connectivity and dispersal processes can result in source-sink dynamics, where orchards in proximity to unmanaged population sources may exhibit more favourable population dynamics than anticipated solely based on local recruitment (de Godoy et al., 2023; van Langevelde, 2015).

Area-wide surveillance trapping can provide valuable insights into how an outbreak of urban fruit flies may spread through dispersal processes (Economopoulos and Rempoulakis, 2018; Weldon et al., 2014). Surveillance trap catch may be very low or delayed when fruit flies disperse in small numbers to colonise new areas (Meats et al., 2003). In contrast, dispersal from larger established populations is more likely to directly affect trap catch (Lance and Gates, 1994). The extent and frequency of dispersal events often leads to a patchy distribution of fruit fly populations, where some areas experience higher infestation levels compared to others (Weldon et al., 2014). Despite the importance of dispersal to population dynamics it is often difficult to measure how individuals move throughout landscapes (Papadopoulos, 2014). The dispersal ability of some economically important species of fruit fly have been investigated using mark-release-recapture (MRR) experiments (Weldon et al., 2014). The estimated dispersal distances from MRR studies vary among individual species, but short-range dispersal (< 1 km) is more common for many species (Meats and Smallridge, 2007; Weldon et al., 2014). Similar experiments have also found the direction and range of dispersal is influenced by landscape features such as mountain ranges, areas of open land or water (Copeland et al., 2006; Moreno et al., 2022). Though MRR experiments are often effective, they can be costly and resource intensive to implement (Weldon et al., 2014). For that reason, alternative approaches are needed to infer the likely extent of urban outbreaks from routinely collected surveillance trapping data using spatial models.

Statistical models play a crucial role in analysing the distribution of fruit fly outbreaks (Szyniszewska and Tatem, 2014; Watts and Worner, 2008). However, complications can arise in modelling fruit fly not only because surveillance trap catch are often overdispersed and have a high frequency of zero-values, but importantly spatial variation can manifest over short temporal scales (Sciarretta et al., 2018; Vanoye-Eligio et al., 2019). Fortunately, advances in the development and application of hierarchical spatial models provide a framework to link surveillance information and ecological processes to estimate how populations vary over space and time (e.g. Cressie and Wikle, 2011; Latimer et al., 2009). By accounting for spatial differences that change through time, hierarchical models can better estimate how populations are related to the proximity of areas experiencing outbreaks (Castrignano et al., 2012; Papadopoulos et al., 2003).

This study introduces a spatio-temporal modelling approach to quantify the contribution of unmanaged urban populations to regional pest pressure using surveillance trapping data. For a case study, we examine outbreaks of the globally important Mediterranean fruit fly, *Ceratitis capitata*, in two fruit growing regions in south-west Western Australia. Since it was first introduced to Western Australia around 1890 the Mediterranean fruit fly has become a major pest attacking many commercial fruit species (Rahman and Broughton, 2019). Despite commercial growers employing various strategies to control populations

within orchards, such as bait and cover sprays, seasonal outbreaks are common within fruit growing regions (Rahman and Broughton, 2019). Considering these consistent seasonal outbreaks, we hypothesise that unmanaged urban populations are contributing to pest pressure in surrounding agriculture regions (De Lima, 2008).

In our approach, we first relate dispersal of Mediterranean fruit fly to surveillance data from traps located across urban areas and surrounding orchards by modelling population connectivity. Connectivity is defined as the level of the potential exchange of individuals through dispersal between populations within each region (Kool et al., 2012). Bayesian hierarchical models were developed to estimate flies per trap per day (FTD) across each region. Once validated against observations we: 1) explore how distance from urban population sources affects FTD in the surrounding orchards; and 2) evaluate which orchards are most likely to benefit from the control of urban outbreaks. We present results from different model configurations, including variations in landscape by incorporating a non-stationary spatial effect (Bakka et al., 2019). Here, we assume large areas of open land or water may impede connectivity of Mediterranean fruit fly populations (Barclay et al., 2021; Copeland et al., 2006; Moreno et al., 2022). We then discuss implications of results for area-wide management and provide important information to help understand the negative effects of unmanaged urban Mediterranean fruit fly populations.

2. Materials and methods

2.1. Case study areas and species

This study is focused on the Donnybrook (−33.58, 115.82) and Manjimup (−34.24, 116.14) fruit growing regions in the south-west of Western Australia (Fig. 1). The urban centre of Manjimup has a population of 4279 and covers an area of 993 Ha, and Donnybrook has a population of 3035 and area of 536 Ha (Australian Bureau of Statistics, 2021). The south-west region has a Mediterranean climate that is characterised by cool-wet winters (June–August) and hot-dry summers (December–February) (Belda et al., 2014). The urban centres within each region provide an opportunity to evaluate how Mediterranean fruit fly populations in unmanaged urban sites affect commercial orchards. The Mediterranean fruit fly is a polyphagous species capable of infesting a wide range host fruit (Papadopoulos, 2008). Commercial fruit production in both regions mainly includes varieties and cultivars of pome fruit, stone fruit, avocados, grapes and citrus (Supplementary Fig. S1). Fruit species grown in orchards can also be found in urban areas with the addition many other species such as fig, loquat and tamarillo. Importantly, the fruit grown in urban areas can provide Mediterranean fruit fly with hosts that are available throughout the year (De Lima, 2008).

The life cycle of the Mediterranean fruit fly has four main stages: 1) after mating females lay eggs near the surface of maturing and ripe host fruit; 2) after a few days the eggs hatch to produce larvae that develop inside host fruit before exiting and falling to the ground; 3) the mature larvae burrow into the soil and pupate; and 4) after a period time they emerge from the soil as adults (Christenson and Foote, 1960). Development time of each life stage is strongly correlated with air temperature. Under warm conditions development time from eggs to adult stages can be as little as 30 days and in cooler temperatures over 90 days (De Lima, 2008). The shorter developmental time over the warmer months means multiple generations are possible over a single growing season (Papadopoulos, 2008).

2.2. Monitoring data

Trapping data were analysed from a monitoring and surveillance program carried out as part of a larger study by the Department of Primary Industries and Regional Development (DPIRD) in Western Australia. For this study we focus on trap data from commercial orchards located within 10 km from each urban centre, and urban sites within a

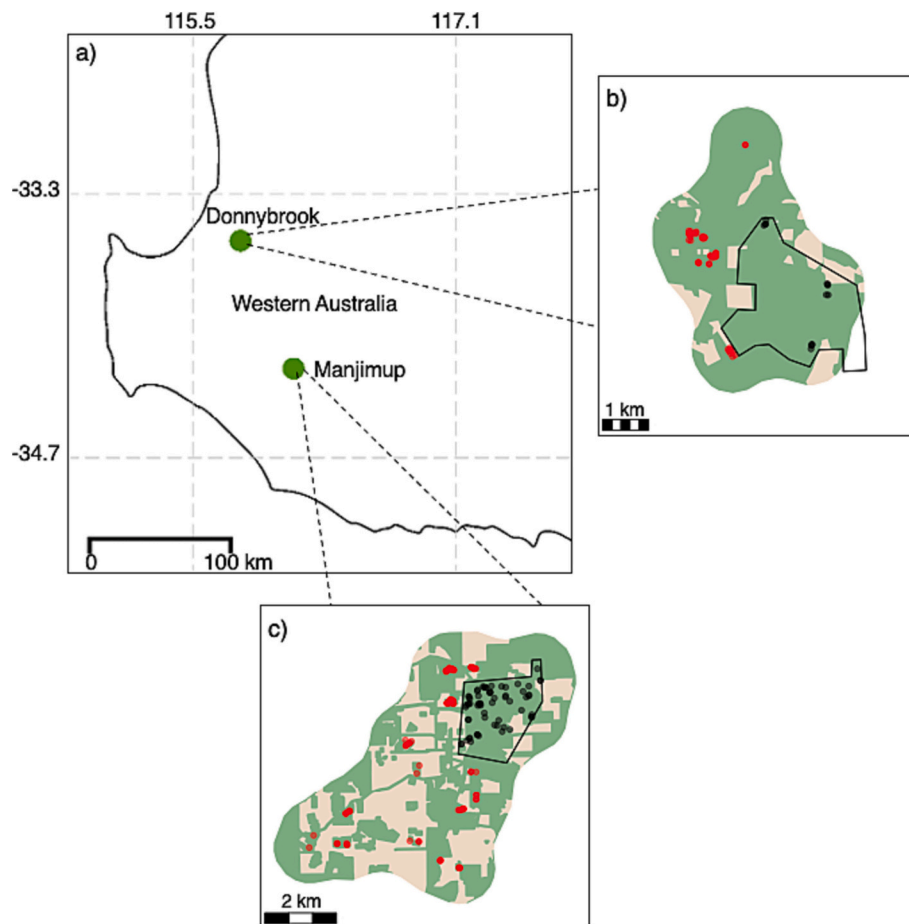


Fig. 1. Map of a) the south-west of Western Australia with b) Donnybrook and c) Manjimup fruit growing regions. In b) and c) the black line shows the boundary of each urban area, and the red and black circles indicate trap locations. The tan coloured areas represent open spaces with little or no tree cover, and the green colour indicates areas occupied by host or non-host trees. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

defined urban boundary that were collected over four years from October 2017 to September 2021. In the Manjimup region, traps were deployed at 12 orchards and 51 urban sites. At Donnybrook, traps were set in 3 orchards and 5 urban sites.

Adult Mediterranean fruit fly trapping was carried out using Biotrap® Globe traps (Biotrap®, Victoria, Australia) or Maxi® traps (Pro-bodelt, Amposta, Spain) baited with TMA Plus® Unipack lures (Süßbin, Mendoza, Argentina). All traps contained a single Biotrap® DDVP (Dichlorvos, 1.47 g) insecticide cube as the kill agent. The lures and kill agent were replaced every 3 months. The number of traps deployed varied among orchards and traps were placed up to 30 m from the edge of crops at each orchard. All urban and orchard traps were placed at least 50 m apart and mounted on the tree canopy at a height of around 1.8 m. Traps were checked monthly and the contents collected and brought back to a laboratory for identification and counting (Howse et al., Unpublished data).

For the purpose of this study, the number of flies per trap per day (FTD) was calculated by dividing the total number of flies caught in a trap by the number of days between collecting the contents of each trap.

2.3. Modelling approach

Our modelling approach aims to quantify how unmanaged urban populations can affect FTD in surrounding commercial orchards. To describe the approach, we outline each of its major components: explanatory variables, statistical models, model comparison and

evaluation, and predictions. The modelling and analyses were carried out within the R statistical computing software (R Core Team, 2021).

2.3.1. Explanatory variables

We consider explanatory variables that both help evaluate the hypothesis of this study and are important to the life cycle of the Mediterranean fruit fly. Given these factors we specify the following variables:

Population connectivity – A connectivity measure that is based on average Mediterranean fruit fly dispersal distance, population size (relative to trap catch) and distance between populations (trap distance). The population connectivity at a specific location, i , for a given month, t , is the sum of all population source locations (trap locations), j , excluding the specified location itself, $i \neq j$. Here, positive values of urban and orchard FTD represent the relative size of source populations, K_j . We assume source populations are mature Mediterranean fruit fly of which only a small proportion (10%) are likely to disperse beyond 400 m (Meats and Smallridge, 2007). The average dispersal distance, $\alpha_j = 1/\sqrt{D/\pi}$, is based on a diffusion coefficient, $D = 1241.9 \text{ m}^2 \text{ day}^{-1}$ (Caton et al., 2022; Weldon et al., 2014). Dispersal is assumed to be isotropic (equal in all directions), and the density of dispersers decreases with distance from a population source j to location i . The decline in density follows a negative exponential function where d_j is the distance between trap locations (Hanski, 1994):

$$PC_{it} = \sum_{j \neq i} \exp\left(-\frac{d_{ji}}{\alpha_{ji}}\right) K_{ji}$$

Degree days – Temperature is a key factor in Mediterranean fruit fly development. Here, we use the monthly accumulated degree days where the average temperature for a single day is one degree above a threshold, c , for each life stage: egg, 9.3 °C; larvae, 11.1 °C; pupae, 8.4 °C and adult, 12.8 °C, calculated as (De Lima, 2008):

$$DegDay_i = \sum_{t=1}^{\text{month}} \left(\frac{\min_t - \max \text{temperature}_t}{2} \right) - \text{threshold}_c + DegDay_{t-1}$$

with interpolated temperature data from the Queensland Government SILO database (Queensland Government, 2021). Given the geographical distance between each region we sourced temperature data separately for Manjimup and Donnybrook (Supplementary Fig. S2).

Generation number – The predicted generation number was based on the cumulative number of life cycles completed, from egg to adult, each month from October to September as estimated by the degree day model (Supplementary Fig. S2).

Month – The month of year defined as a categorical variable to account for changes in seasonality.

Host fruit status – A categorical variable that states whether host fruit are available or unavailable to female Mediterranean fruit fly at each orchard or urban site. The status reflects when individual fruit varieties are ripe and ready for harvest, which is an ideal fruit condition for female Mediterranean fruit fly to oviposit (Christenson and Foote, 1960).

2.3.2. Statistical models

Spatio-temporal Bayesian models were developed to quantitatively evaluate the extent to which unmanaged urban populations contribute to pest pressure in each agriculture region.

The models were developed using the integrated nested Laplace approximation (INLA) framework (Lindgren et al., 2011; Rue et al., 2009). The model building process included testing the effects of explanatory variables in spatial and spatio-temporal model configurations. To account for the large number of zero trap observations and reduce potential bias in FTD predictions we applied a hurdle gamma model. The hurdle model was executed in two stages: 1) a Bernoulli model to predict the presence or absence of Mediterranean fruit fly using all available data; and 2) a gamma model using zero truncated data because when Mediterranean fruit fly are present, we are interested in what is driving their distribution across the region.

The Bernoulli model, where z_{it} is the presence or absence of Mediterranean fruit fly at location i in month t that depends on an unobserved process λ_{ij} with hyperparameters θ :

$$z_{it} | \lambda_{it}, \theta \sim \text{Bernoulli}(\lambda_{it})$$

$$\text{logit}(\lambda_{it}) = \gamma_0 + \gamma_1 PC_{it} + \gamma_2 GenNr_{it} + \gamma_3 Month_{it} + \gamma_4 DegDay_{it} + \gamma_5 HostStatus_{it} + x_{iy}$$

a logistic link was used to estimate the probability of λ_{it} , γ_0 is the intercept, γ_1 to γ_5 are coefficients used to quantify the effect of covariates and x_{iy} is the spatio-temporal effect for each year y . It should be noted the spatio-temporal effect was trialled at monthly intervals but was found to be overfitting the model to available data.

The gamma model was applied on non-zero data where y_{it} represents FTD that depends on the unobserved process μ_{it} with hyperparameters θ . The gamma function was parameterised in terms of its mean μ , a scale parameter $s > 0$, and hyperparameter ϕ :

$$y_{it} | \mu_{it}, \theta \sim \text{Gamma}(\mu_{it}, s\phi)$$

$$\begin{aligned} \log(\mu_{it}) = & \beta_0 + \beta_1 PC_{it} + \beta_2 GenNr_{it} + \beta_3 Month_{it} + \beta_4 DegDay_{it} \\ & + \beta_5 HostStatus_{it} + x_{iy} \end{aligned}$$

a log link was used to estimate μ_{it} , β_0 is the intercept, β_1 to β_5 are coefficients used to quantify the effect of covariates and x_{iy} is the spatio-temporal effect.

Results from Bernoulli and gamma models were then combined to calculate the expected mean value and variance in FTD, ftd_{it} :

$$Expected(ftd_{it}) = \lambda_{it} \times \mu_{it}$$

$$variance(ftd_{it}) = \frac{\lambda_{it} \times r + \lambda_{it} - \lambda_{it}^2 \times r}{r} \times \mu_{it}^2$$

where r is the variance parameter from the gamma model.

The spatio-temporal effect x_{iy} in both the Bernoulli and gamma models were estimated using a Gaussian Markov random field (GMRF). The GMRF is assumed to follow a multivariate normal distribution with a zero mean and Matérn covariance function, $x_{iy} \sim \text{MVN}(0, \Sigma)$. The GMRF accounts for spatial autocorrelation by assuming nearby traps are more correlated and correlation between traps decreases by distance (Lindgren et al., 2011). In addition, any latent factors not explained by covariates, such as the availability of hosts or habitat that could influence the spatial distribution of Mediterranean fruit fly can also be accounted for by the GMRF.

Given there is some evidence that Mediterranean fruit fly dispersal is impeded by open water or land with minimal tree cover we evaluate non-stationary and stationary spatial effects (Copeland et al., 2006; Moreno et al., 2022). The stationary effect assumes spatial dependence is uniform throughout each region and does not vary according to direction, which represents a simple model of landscape with unobstructed connectivity between populations (Lindgren et al., 2011). In contrast, a non-stationary effect increases model complexity and adds realism by assuming spatial dependence can vary direction and be altered by different land-use types (Bakka et al., 2019). To model the non-stationary effect land-use maps were created from OpenStreetMap (OSM) using the osmdata package in R (Padgham et al., 2017). In this study, we are particularly interested in OSM groups 'landuse' and 'natural' having key values that indicate open spaces with little or no tree cover. The maps generated in R were then verified using satellite imagery from OSM and manually adjusted to ensure observations were not inside areas identified as open landscape. The non-stationary and stationary spatial effects were modelled using INLA's stochastic partial differential equation (SPDE) approximation based on the GMRF (Bakka et al., 2019; Lindgren et al., 2011). Here, the GMRF represents a mesh constructed from the triangulation of the spatial domain within each fruit growing region. The smoothness, range, and marginal variance of the GMRF were parameterised for use with the penalised complexity (PC) prior framework (see Fuglstad et al., 2019).

2.3.3. Priors

Priors were assigned to regression coefficients and hyperparameters of the Bernoulli and gamma model components. Gaussian prior distributions with 0 mean and precision 0.0001 were assigned to the coefficients γ and β of the continuous covariates. PC priors were used to set prior values for the gamma distribution and the GMRF (Fuglstad et al., 2019; Simpson et al., 2017). PC priors can help avoid model over-fitting by creating informative priors that shrink model components from more flexible to simpler base models (Simpson et al., 2017). The amount of flexibility allowed in model components is controlled by setting parameters using probability statements. For example, the gamma distribution was set to have a high probability the standard deviation would be between 0 and 1, $P(\sigma > 0.5) = 0.01$. Similarly, a joint PC prior for the range and variance was used to shrink the GMRF toward a base model of infinite range and zero marginal variance (Fuglstad et al., 2019). This

approach avoids overfitting of the GMRF by using the range and variance parameters to control the magnitude of spatial variation. In this setting and because long distance dispersal in Mediterranean fruit fly is rare, we assumed there was a high probability the spatial range parameter would be smaller than 3 km, $P(\rho < 3 \text{ km}) = 0.6$ (Caton et al., 2022; Meats and Smallridge, 2007; Weldon et al., 2014). We set the standard deviation of the spatial field so it was unlikely to exceed 2, $P(\sigma > 2) = 0.05$.

2.3.4. Model comparison and evaluation

The fit and predictive quality of models were evaluated separately for the Manjimup and Donnybrook regions using the deviance information criterion (DIC) and out-of-sample cross-validation. All models included the same fixed effect predictors. To determine whether differences in spatial processes influence model performance we compared models: a) with no spatial or spatio-temporal effect, b) spatial only, and c) a spatio-temporal effect that changes each year.

The DIC was calculated by INLA during model runs with lower values indicating improved model performance. We performed out-of-sample cross-validation by randomly partitioning data into training (80% of data) and test (20% of data) sets. Randomisation was stratified by trap locations and month to evaluate the ability of the models to predict FTD. Each model was initially fitted to the training set only. The fitted model was then used to predict FTD from the test set. Cross-validation was repeated 100 times for each model and results were compared to observations by calculating the root mean square error (RMSE) of FTD. Smaller RMSE values indicate a better fit and predictive quality, calculated as:

$$RMSE = \sqrt{\frac{1}{n_{obs}} \sum_{i=1}^{n_{obs}} (y_i - \hat{y}_i)^2}$$

The models with lower DIC and RMSE values suggest better performance and were used to investigate relationships between urban and orchard connectivity.

2.3.5. Model predictions and analyses

Once models were validated, we explored two scenarios to quantify the contribution of unmanaged urban populations to surrounding orchards, one with urban connectivity by including all trap data, and the other a simulation without urban connectivity by removing urban traps and recalculating the population connectivity explanatory variable. We then ran models through each scenario to predict mean values and associated variances in FTD for locations across each region. By comparing model results with and without urban connectivity we could evaluate the extent to which unmanaged urban populations may contribute to pest pressure in each region. Furthermore, by analysing model results we determine: 1) how distance from urban population sources affects pest pressure in the surrounding orchards; and 2) which orchards are most likely to benefit from the control of urban outbreaks. Prediction maps and figures were generated using the INLA and ggplot2 packages in R (Lindgren et al., 2011; Rue et al., 2009; Wickham, 2016).

3. Results

3.1. Explanatory variables

The posterior means and 95% credible intervals for model parameters are summarised in Tables S1 to S4 in the supplementary material. The effect of an explanatory variable was considered statistically important (Bayesian inference uses the term important rather than significant) when the 95% credible intervals of the estimated model coefficients did not include zero. The explanatory variable 'population connectivity' had a statistically important positive effect on FTD and presence-absence across all models and growing regions. In addition, 'host fruit status = unavailable' had an important negative association

with FTD and presence-absence for some Manjimup models. For Donnybrook models, 'host fruit status = available' had an important positive effect on presence-absence in some models. The remaining variables did not have a statistically important impact on modelled results. As a result of the consistent positive association of population connectivity with model responses we summarise the data generated in the following sections.

Population connectivity in the Manjimup region revealed strong spatial patterns with and without urban connectivity (Fig. 2). During the pome fruit peak harvest months (January – April) the average population connectivity at urban sites increased from 0.12 ± 0.03 to 1.60 ± 0.18 . At the same time, the average population connectivity at orchard sites ranged from <0.01 to 0.15 ± 0.01 . Suggesting Mediterranean fruit fly connectivity is higher within the urban area compared to orchard sites. When population connectivity was recalculated to simulate no urban connectivity the orchard sites across the region remained below 0.10 (Fig. 2b).

In the Donnybrook region, population connectivity was low (< 0.08) from mid-summer (January) and then increased at urban sites from 0.18 ± 0.06 to 0.80 ± 0.18 in late summer (February – March) (Fig. 3). Population connectivity values in orchards were on average lower ranging from 0.08 ± 0.01 in February to a peak of 0.47 ± 0.04 in April. In the absence of urban connectivity, the average population connectivity in orchards ranged from 0.07 ± 0.01 in February to 0.39 ± 0.04 in April (Fig. 3b).

3.2. Model evaluation and performance

The quality of fit between our five candidate models were evaluated to identify the best overall performing models (Table 1). Overall, the spatio-temporal models with stationary and non-stationary spatial effects (M3 and M5) performed well compared to other models having the lowest DIC scores and variance in the quality of fit. Of the Bernoulli and gamma models fitted to the Manjimup data the model with no spatial effect (M1) had higher (worse) DIC values. The addition of spatial (M2) and spatio-temporal (M3) effects improved model fit. There was little difference in DIC values between models with stationary (M2 and M3) compared to non-stationary (M4 and M5) spatial effects. The spatio-temporal models (M3 and M5) had the smallest difference between observed FTD and the fitted data (0.32 FTD). The models fitted to the Donnybrook data exhibited similar patterns in the quality of fit. However, there were greater differences in DIC values and RMSE between the model with no spatial effect (M1) and the other models. For models M2 to M5 there was little difference in DIC values or between observed FTD and the fitted data.

The predictive performance of models was compared using out-of-sample cross-validation (Supplementary Fig. S3). For Manjimup, the spatio-temporal models (M3 and M5) had the best predictive accuracy (0.25 FTD) and lowest variance in $RMSE_{Test}$ predictions (0.15 to 0.48 FTD). The mean predictive accuracy of $RMSE_{Test}$ data for Donnybrook was best for spatio-temporal models, ranging from 0.49 to 1.26 FTD. However, the range in variance of Donnybrook $RMSE_{Test}$ predictions was 47% greater than Manjimup, because excluding 20% of orchard traps from the smaller Donnybrook training data meant models were extrapolating predictions beyond limited observations.

The posterior mean spatial range obtained from each model was used to estimate spatial correlation as a function of distance where trap catch can be considered independent (Supplementary Fig. S4). The estimated spatial correlation in Manjimup and Donnybrook stationary models gradually decreased over 2.5 to 3.0 km. Spatial correlation for the Manjimup non-stationary models were lower, from 1 to 1.5 km, and in Donnybrook spatial correlation declined quickly in the first to 0.9 km.

3.3. Model predictions

Comparing FTD as a function of distance showed variation in model

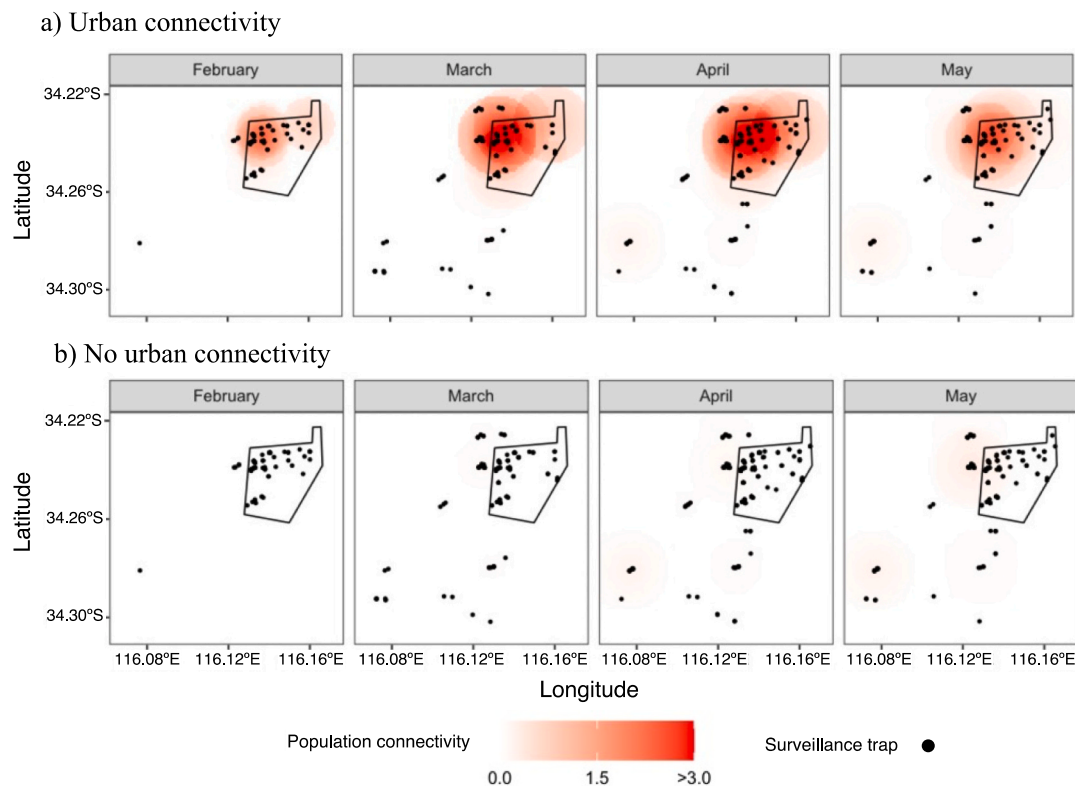


Fig. 2. Population connectivity in the Manjimup region calculated a) with urban connectivity and b) without urban connectivity, from surveillance trap catches during peak harvest, from February to May, averaged across years from 2017 to 2021.

predictions and their uncertainty between urban and no urban connectivity scenarios (Fig. 4). For Manjimup, the stationary spatio-temporal model (M3) with urban connectivity predicted a decline in FTD from 0.37 FTD (95% PI, 0.07 to 1.16 FTD) to around 0.03 FTD (95% PI, 0 to 0.11 FTD) at 2 km from the urban boundary. Model predictions without urban connectivity were consistently low at 0.01 FTD (95% PI, 0 to 0.04 FTD) up to 4 km. Similarly, model predictions for Donnybrook showed a decline in FTD from 0.60 (95% PI, 0.26 to 1.23 FTD) at the urban boundary to 0.06 (95% PI, 0 to 0.25 FTD) at 2.5 km (Fig. 4c,d). Predictions of FTD without urban connectivity were also consistently lower, < 0.11 (95% PI, 0 to 0.29 FTD). Despite potential differences in modelled stationary and non-stationary spatial effects, predictions were similar across all models (Supplementary Fig. S5).

The modelled (M3) spatial maps for the Manjimup and Donnybrook regions show contrasting changes in the density distribution of Mediterranean fruit fly with and without urban connectivity (Fig. 5). In the Manjimup region with urban connectivity, FTD was relatively high (> 0.2 FTD) within and around the urban boundary with a small patch (0.1 FTD) present around 5.5 km south-west. Spatial predictions without urban connectivity indicate a decline in pest pressure to < 0.05 FTD within 2 km of the urban boundary. The isolated patch toward the south-west remains unchanged, indicating urban connectivity has little effect on FTD at this location. In the Donnybrook region, predictions of FTD with urban connectivity resulted in higher, > 0.25 FTD, across most of the region with some patches > 0.5 FTD for up to 1 km from the urban boundary. The predicted spatial distribution without urban connectivity shows lower levels of FTD across most of the region with a single patch, < 0.25 FTD, up to 1 km from the urban boundary. Additionally, only small differences, < \pm 0.1 FTD, were evident between stationary (M3) and non-stationary (M5) models (Supplementary Fig. S7 and S8).

4. Discussion

In this study, we inferred a relationship between changes in the

density of Mediterranean fruit fly and population connectivity using routinely collected surveillance trap data. We used this relationship along with other explanatory variables to fit spatial-temporal models to assess how unmanaged urban Mediterranean fruit fly populations may affect nearby commercial orchards. Applying models in two fruit growing regions as case studies, our results highlight that unmanaged urban outbreaks can contribute to increased pest pressure in surrounding orchards up to 2 km, but the urban contribution quickly declines over this distance. We also demonstrated that our models provide a means of predicting changes in Mediterranean fruit fly density across a region, even with relatively sparse trapping networks. Regional scale inference from our models may be particularly useful for sites where surveillance trapping data is unavailable. In addition, our study provides a modelling framework that could be widely applied to other regions and area-wide programs to predict changes in the distribution of pest species from the application of pest control treatments.

We hypothesised that unmanaged urban populations contribute to pest pressure in surrounding agriculture regions. Our findings show significant changes in spatial patterns of pest pressure with and without urban connectivity, which suggest unmanaged urban populations do affect nearby commercial orchards. However, while the exact mechanism for this relationship remains unclear there are at least three possible mechanisms that could explain our results. First, direct dispersal of urban populations into orchard traps up to 2 km away is possible but seems unlikely as it would require high levels of constant migration throughout the season. Constant migration is less likely for Mediterranean fruit fly because short-range dispersal < 1 km is more common (Meats and Smallridge, 2007; Weldon et al., 2014). Second, urban immigrants may contribute to the reproductive potential of nearby orchard populations, which over generations may result in population growth and therefore larger trap catches (Weldon et al., 2014). Third, the observed effect of urban connectivity could be the result of there being more, and greater diversity, of fruit hosts immediately surrounding urban areas. This can be due to smaller block sizes,

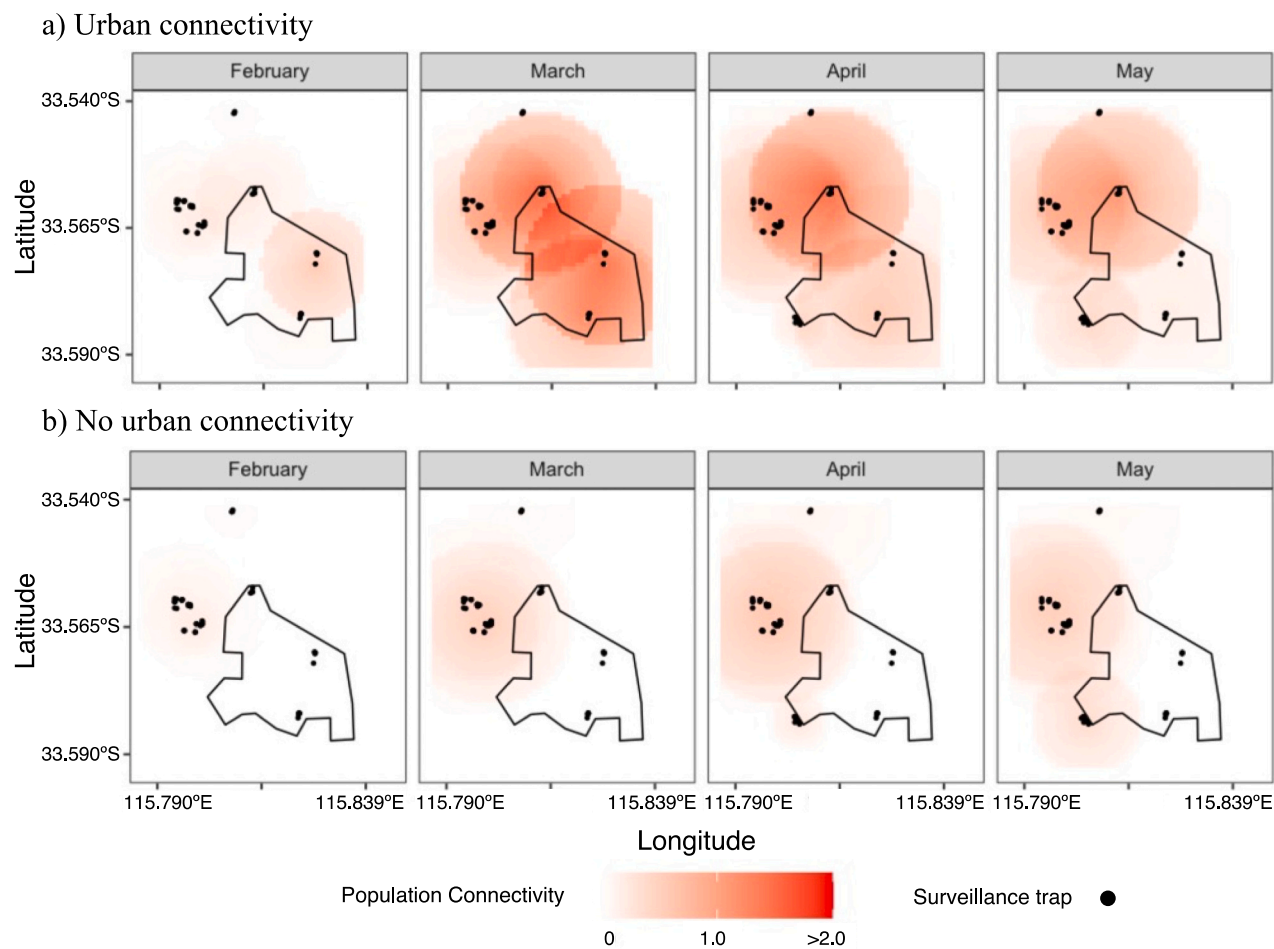


Fig. 3. Population connectivity in the Donnybrook region calculated a) with urban connectivity and b) without urban connectivity, from surveillance trap catches during peak harvest, from February to May, averaged across years from 2017 to 2021.

Table 1
Comparison of model fit of different candidate models with stationary and non-stationary spatial effects, using the deviance information criterion (DIC) and root mean square error (RMSE) of flies per trap per day (FTD).

Region	Model	Description	Spatial effect	Bernoulli	Gamma	Combined (FTD)
				DIC	DIC	RMSE
Manjimup	1	No spatial effect	None	234.18	−402.23	0.35
	2	Spatial	Stationary	156.44	−486.13	0.26
	3	Spatio-temporal	Stationary	162.49	−497.27	0.25
	4	Spatial	Non-stationary	156.28	−486.75	0.26
	5	Spatio-temporal	Non-stationary	156.21	−497.39	0.25
Donnybrook	1	No spatial effect	None	344.03	−96.18	0.98
	2	Spatial	Stationary	296.86	−281.59	0.67
	3	Spatio-temporal	Stationary	299.91	−288.09	0.61
	4	Spatial	Non-stationary	296.45	−281.35	0.66
	5	Spatio-temporal	Non-stationary	299.92	−288.92	0.61

more hobby farms that are less well managed, and more fruit-bearing weeds. The presence of unmanaged hosts could potentially also explain hot spots that we identified away from urban areas. Overall, our results support previous research that raised the importance of controlling urban outbreaks to reduce infestation from unmanaged sites at the edge of urban areas to nearby commercial orchards (De Lima, 2008; Economopoulos and Rempoulakis, 2018).

It has been previously suggested that areas with larger populations are more likely to serve as sources for propagules, contributing to higher propagule pressure in neighbouring areas (Drake and Lodge, 2006). In this framework, higher propagule pressure, characterised by increased numbers of dispersing individuals and frequent introduction events,

enhances the likelihood of successful establishment in new areas (Lockwood et al., 2005). While our results clearly show an unmanaged urban population effect, a rapid decline in FTD over short distance (< 1 km) suggest other dynamics may be at play. For instance, many Mediterranean fruit fly may choose to remain within urban environments where there are abundant resources and minimal disturbance, leading to lower propagule pressure in orchards. As a result, there are fewer individuals available in orchards to establish viable populations. In these low-density orchard populations, Allee effects can further impede population growth and more extensive spread across the region due to reduced mating opportunities or heightened vulnerability to environmental stochasticity (Drake and Lodge, 2006; Meats and Smallridge,

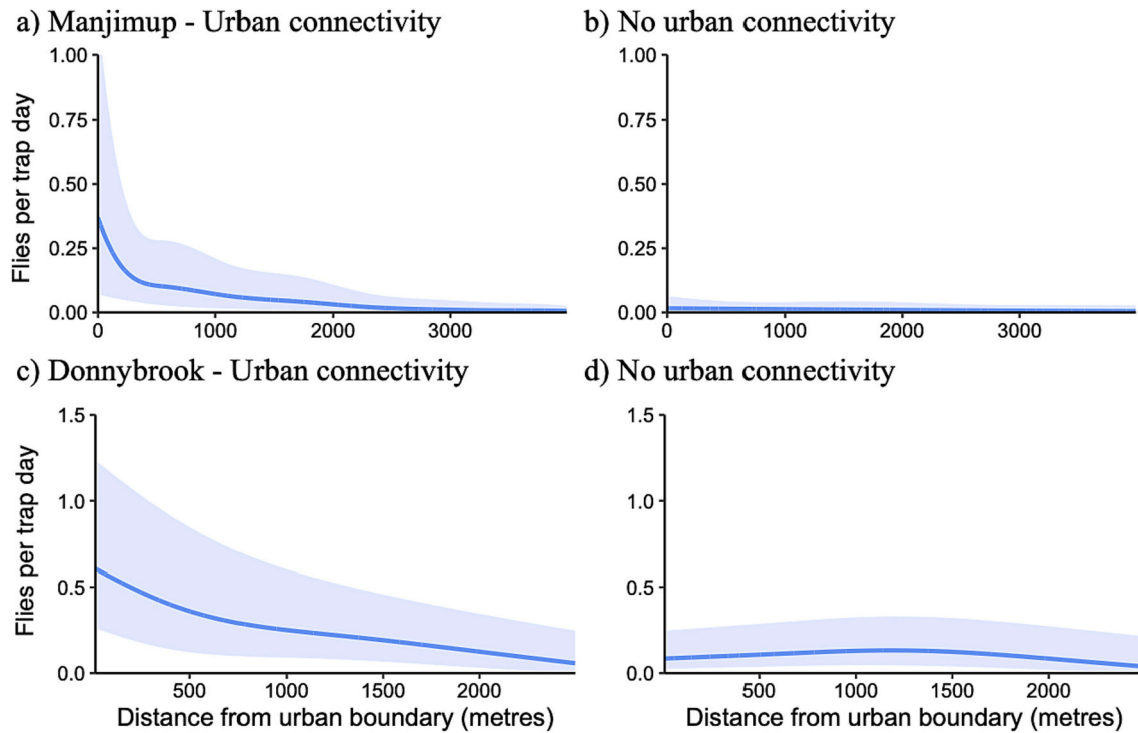


Fig. 4. Stationary model (M3) predictions of the contribution of urban populations to flies per trap day (FTD) as a function of distance from the urban boundary in a, b) Manjimup and c, d) Donnybrook regions with a, c) urban connectivity and b, d) no urban connectivity, averaged across years from 2017 to 2021. Shaded areas show 95% prediction intervals.

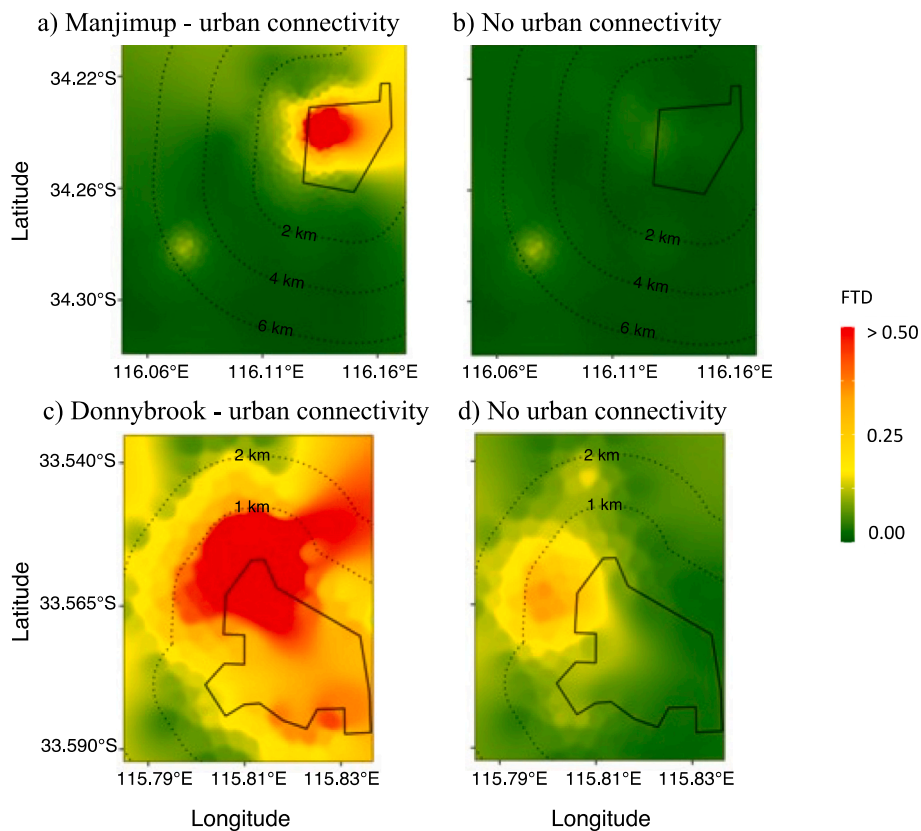


Fig. 5. Predicted spatial distribution of flies per trap day (FTD) from stationary spatio-temporal models (M3) in the a, b) Manjimup and c, d) Donnybrook regions with a, c) urban connectivity and b, d) no urban connectivity. Mean predictions from February to May across years 2017 to 2021.

2007). While this scenario may reduce the risk to orchards, more research on understanding these dynamics is essential for developing effective management strategies to mitigate the impact of Mediterranean fruit fly.

We also evaluated the effect of stationary (a uniform landscape with unrestricted dispersal) and non-stationary (dispersal is impeded by open land and water) spatial processes on the distribution of Mediterranean fruit fly. Here, our main objective was to determine if results from a more realistic model configuration such as the non-stationary model were different. The non-stationary model was considered more realistic because we assume large areas of open land or water represent areas that lack tree cover and host fruit (Barclay et al., 2021). Although this could be considered a strong assumption, we believe it is closer to reality than a landscape with unobstructed dispersal in the stationary model (Copeland et al., 2006; Moreno et al., 2022). However, there was little difference in the quality of fit and predictive performance between stationary and non-stationary models. The lack of pronounced differences between stationary and non-stationary models may be attributed to spatial dependencies in the data being adequately captured by the stationary model (Fig. S4). The predicted spatial maps were also quite similar, suggesting the more parsimonious stationary model with fewer parameters is preferred. The application of stationary and non-stationary spatial processes to assess the habitat used by Mediterranean fruit fly requires further investigation, because due to the lack of studies we used quite a coarse division of land use types: open and not. A clearer understanding of the range of habitats used by dispersing Mediterranean fruit fly would help. The resulting information could also be used by managers to determine the effectiveness of potential dispersal barriers that may be beneficial to pest control interventions.

The use of surveillance trapping data in statistical models can offer valuable insights to help manage pest outbreaks (Papadopoulos et al., 2003). However, while surveillance trapping is a key source of data for our models, it is important to acknowledge some limitations. The surveillance traps used in our study were placed at specific locations, which may not be representative of the entire population distribution. Despite the coarse and irregular trap placement in both Manjimup and Donnybrook there was sufficient data to make inferences with acceptable levels of uncertainty. Nonetheless, there were notable differences in DIC, RMSE and out-of-sample cross-validation values between Manjimup and Donnybrook models. The increased information availability in the larger Manjimup dataset led to more accurate parameter estimates and reduced uncertainty. Greater trap coverage would only improve modelled predictions and uncertainty estimates in the Donnybrook model. Despite some limitations, surveillance trap data can provide valuable insights when used cautiously by accounting for uncertainty to ensure accurate and reliable predictions.

5. Conclusions

Our modelling approach can be used to provide quantitative advice to effectively manage Mediterranean fruit fly outbreaks and minimise their impact on agricultural regions.

For example, commercial orchards <1–2 km from the edge of urban boundaries would immediately benefit from an effective area wide management or community baiting scheme. Furthermore, our modelling framework could be extended to assess the effectiveness of different area-wide control measures, such as sterile insect technique or pesticide application, by comparing reductions in population densities based on the efficacy of control interventions.

CRediT authorship contribution statement

Andrew Broadley: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Rieks D. van Klinken:** Writing – review & editing, Supervision, Methodology, Investigation, Funding

acquisition. **Dean R. Paini:** Writing – review & editing, Supervision, Methodology. **Matt Hill:** Writing – original draft, Supervision, Conceptualization. **Elliot Howse:** Writing – review & editing, Data curation.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2024.102536>.

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