

Climate contributes to the evolution of pesticide resistance

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Abstract

Aim: The evolution of pesticide resistance through space and time is of great economic significance to modern agricultural production systems, and consequently, is often well documented. It can thus be used to dissect the evolutionary and ecological processes that underpin large-scale evolutionary responses. There are now nearly 600 documented cases of pesticide resistance in arthropod pests. Although the evolution of resistance is often attributed to the persistent use of chemicals for pest suppression, the rate of development of resistance should also depend on other factors, including climatic conditions that influence population size and generation time. Here, we test whether climatic variables are linked to evolution of resistance by examining the spatial pattern of pyrethroid resistance in an important agricultural pest.

Location: Southern, agricultural regions of Australia.

Time period: 2007–2015.

Major taxa studied: The redlegged earth mite, *Halotydeus destructor*.

Methods: We quantified patterns of chemical usage based on paddock histories and collated long-term climatic data. These data were then compared against presence–absence data on resistance using a boosted regression-tree approach, applied here for the first time to the spatial categorization of pesticide resistance.

Results: Although chemical usage was a key driver of resistance, our analysis revealed climate-based signals in the spatial distribution of resistance, linked to regional variation in aridity, temperature seasonality and precipitation patterns. Climatic regions supporting increased voltinism were positively correlated with resistance, in line with expectations that increased voltinism should accelerate evolutionary responses to selection pressures.

Main conclusions: Our findings suggest that the prediction of rapid evolutionary processes at continental scales, such as pesticide resistance, will be improved through methods that incorporate climate and ecology, in addition to more immediate selection pressures, such as chemical usage. Boosted regression trees present a powerful tool in the management of resistance issues that has hitherto not been used.

KEYWORDS

boosted regression tree, evolutionary ecology, gradient boosting, *Halotydeus destructor*, pyrethroid, selection pressure, species distribution

1 | INTRODUCTION

Despite ongoing challenges with pesticide resistance in agricultural systems (Sparks & Nauen, 2015), the evolutionary ecology of field resistance remains poorly understood. Laboratory-based experiments

are able to demonstrate evolutionary responses to pesticide applications (Feng & Isman, 1995), but it is difficult to extend results to the field, where a complex network of biotic and abiotic factors interact to influence selection pressures for resistance (Kimball & Levin, 1985). Models of resistance normally focus on factors that determine the

selection of alleles that confer pesticide resistance (resistance alleles) in populations and how these are affected by species biology and environmental factors (Georghiu & Taylor, 1977; REX Consortium, 2013). However, it is often difficult to capture the level of complexity required for meaningful predictions to be made except in specific situations dealing with specific pests (Stratonovitch et al., 2014).

The evolution of resistance in agricultural pests is likely to depend not only on the number of chemical applications in crops, but also on climatic factors that influence resistance evolution in several ways. Resistance alleles are usually exceedingly rare (Roush & Tabashnik, 1990) and therefore more likely to appear in large populations; climatic variables driving long-term abundance of pest species might help to explain patterns of field resistance. Climate can influence the evolution of resistance by affecting the generation time of multivoltine pests (Tobin, Nagarkatti, Loeb, & Saunders, 2008), with shorter generation times expected to speed up the rate of resistance evolution. Climatic conditions can also influence selection pressures on resistance alleles by influencing the rate of breakdown of chemicals in the environment (Khodaverdi, Fowles, Bick, & Nansen, 2016), increasing selection when cross-resistance occurs between chemicals and climatic extremes (Patil, Lole, & Deobagkar, 1996), and increasing the susceptibility of organisms to chemicals when they are exposed to climatically stressful conditions (Polson, Brogdon, Rawlins, & Chadee, 2012).

To evaluate the overall impact of climatic factors on patterns of resistance development, well-studied cases of resistance are needed that vary spatially and/or temporally. Here, we take advantage of the documented spatial spread of pyrethroid resistance in the redlegged earth mite (RLEM), *Halotydeus destructor* (Acari: Penthalidae). This species was first detected in Australia in 1917 after it arrived from its native range in the Western Cape of South Africa. Since introduction, this polyphagous mite has emerged as one of the most important invertebrate pests affecting Australia's grain and pastoral industries (Murray, Clarke, & Ronning, 2013; Ridsdill-Smith, 1997; Sloane Cook & King PTY LTD, 1989). The suppression of RLEM below damaging threshold levels is heavily reliant on chemical control methods, such as applications of synthetic pyrethroids and organophosphates. Resistance to pyrethroid chemicals in RLEM was first reported at a single location in 2007 (Umina, 2007). It has since been detected in > 50 locations across Western Australia (Figure 1), and genetic analyses indicate that resistance has likely evolved independently several times (Q. Yang, G. Rasic, P. Umina, and A. Hoffmann, unpublished observations).

Redlegged earth mites spend > 90% of the time on or near to the soil surface, generally moving onto a plant only to feed, which they do by lacerating the epidermis and consuming the exposed cell contents (Ridsdill-Smith, 1997). The life cycle of RLEM, as well as changes in the distribution and abundance of this pest, are closely tied to climatic factors (Ridsdill-Smith & Annells, 1997; Ridsdill-Smith et al., 2008). The mite usually has three or four generations from autumn to early spring, depending on local climatic conditions, and then enters a summer diapausing period, with diapause broken and egg hatch triggered by a combination of rainfall and low temperature the following autumn (McDonald, Umina, Macfadyen, Mangano, & Hoffmann, 2015; Wallace & Mahon, 1971). Long-distance wind-assisted dispersal of mites can

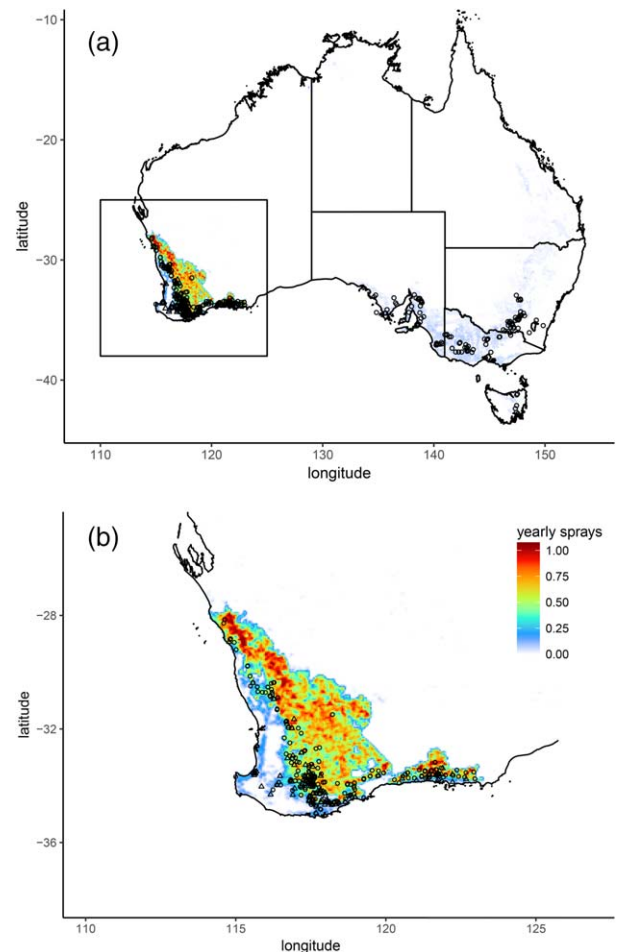


FIGURE 1 Estimated mean annual application rate of pyrethroids across Australia derived from 2010–2011 and 2005–2006 land usage and 2005–2014 paddock history data. Usage rates are estimated at (a) a resolution of 0.05° (c. 5 km) for Australia and (b) a magnified Western Australia region where resistance has been detected. The magnified region is defined by the rectangle in (a). Populations resistant to pyrethroids are shown as triangles, with circles indicating susceptible mite populations

occur when cadavers containing diapause eggs are blown (or otherwise transported, e.g., with silage) across the landscape. The life cycle of RLEM restricts suitable areas to parts of southern Australia, South Africa and New Zealand. Within Australia, Hill, Hoffmann, MacFadyen, Umina, and Elith (2012) found that the occurrence of RLEM was favoured in locations of high temperature seasonality, intermediately moist winter conditions with temperatures between 10 and 25 °C, and dry summer conditions.

Redlegged earth mites prefer certain host plants, such as legumes and pastures, over grasses, which has consequences for their abundance in crops (Ridsdill-Smith, 1997). Mite abundance is further modulated by crop condition (e.g., short pasture is less favourable than long pasture, presumably owing to the associated warmer, dryer microclimate; Grimm, Hyder, Doyle, & Michael, 1994). RLEM are well known to prefer moist, vegetated habitats (Ridsdill-Smith, 1997), with mites exhibiting lowest mortality at 100% relative humidity (Solomon, 1937). Mites develop most rapidly at a temperature of c. 28 °C, with the rate

of development decreasing towards both higher and lower temperatures (James & O'Malley, 1991). There have been numerous published studies on RLEM plant hosts (Gaul & Ridsdill-Smith, 1997; Umina & Hoffmann, 2004), with no significant impacts on mite development times reported. Competitive interactions between RLEM and other earth mites also change with climatic conditions (Weeks & Hoffmann, 2000).

The aim of this study was to assess whether regional differences in chemical usage, and climatic conditions affecting voltinism and the distribution/abundance of RLEM, could explain spatial patterns in the occurrence of pyrethroid resistance. Specifically, we hypothesized that: (a) chemicals applied during the periods when mites are active (i.e., outside of the summer diapause period) would be positively associated with resistance; (b) climatic conditions more suitable for RLEM (cooler, wetter regions) would be associated with a greater abundance of mites and thus more genetic variation for resistance to develop; (c) likewise, differences in land usage and associated host plants would affect abundance because of known host-plant preferences; and (d) conditions favouring faster generation turnover (optimal development temperatures) and a longer RLEM active season (early season rain and long growing season) would speed up the evolution of resistance. These hypotheses cannot be considered in isolation, because the underpinning processes are linked. For example, pesticide usage is likely to be linked to climatic factors that increase abundance and voltinism. This is an inherent weakness of correlational studies; however, we attempt to minimize the effect of potentially interacting processes by ensuring that predictor variables are not highly correlated, and through the inclusion of land usage data, likely to be a more important driver of pesticide usage than climate (recognizing that higher value crops experience higher pesticide inputs to mitigate the risk of pest damage). In this study, we apply an increasingly used method for the analysis of complex categorization problems: boosted regression-tree (BRT) models (a special case of generalized boosted models). Boosted regression-tree models have been applied to other areas of high economic importance, such as in the fields of epidemiology (Dhingra et al., 2014; Friedman & Meulman, 2003) and biosecurity (Catford, Vesk, White, & Wintle, 2011; Compton, De Winton, Leathwick, & Wadhwa, 2012), but, to our knowledge, this is the first application to resistance management issues.

2 | METHODS

2.1 | Pyrethroid resistance occurrence data

Joint resistance monitoring efforts supported by the Australian Grains Research and Development Corporation have resulted in a data set of 722 unique RLEM populations spanning 2007–2015 for which field resistance has been measured. This spans the distribution of RLEM across southern Australia. Pyrethroid-resistant individuals are c. 250,000 times more resistant to bifenthrin when compared with susceptible mites (Umina, 2007). This high degree of resistance allows for the separation of resistant individuals from susceptible ones through exposure to a range of discriminating doses of bifenthrin (e.g., 0.1 or

100 mg L⁻¹). In this study, we used distribution data of resistance previously published by Umina et al. (2012) and Umina, Lord, Micic, and Edwards (2017), as well as unpublished data gathered over multiple years (P. A. Umina, unpublished data). These data have been obtained by undertaking pesticide laboratory bioassays using a glass vial technique, as described in detail by Hoffmann, Porter, and Kovacs (1997). Of the 722 data points included in this study, 659 resulted from screening *H. destructor* populations at either 0.1 mg a.i. L⁻¹ (which is roughly the LC₉₀ (90% lethal concentration) value multiplied by 2) or a higher rate (100 mg a.i. L⁻¹), according to the approach used by Umina et al. (2012). In all bioassays, a control of water was used, and a known susceptible mite population was included as a comparison. The remaining 63 mite populations were screened using a molecular diagnostic designed to detect a modification at the *kdr* gene that is tightly associated with bioassay survival and known to confer resistance to pyrethroid chemicals (O. R. Edwards, T. K. Walsh, S. Metcalfe, W. T. Tay, A. Hoffmann, P. Mangano, A. Lord, S. Micic, & P. Umina, unpublished observations; see Figure S12 in Supporting Information). Approximately 100 mites were used in both the pesticide bioassay and genetic screening approaches.

For the purposes of this analysis, any detection of resistance has been defined as 'field-evolved resistance', a genetically based decrease in the susceptibility to a pesticide in a population caused by exposure to the pesticide in the field (following Tabashnik, Mota-Sanchez, Whalon, Hollingworth, & Carrière, 2014). Thus, a mite population was deemed to be 'resistant' if there was some level of pyrethroid resistance detected, regardless of the proportion of individual mites found to have resistance (i.e., even 1 in 100 screened individuals). The analysis was conducted at the 0.05° resolution (c. 5 km). If any survey within each 0.05° grid cell detected resistance, then pyrethroid resistance was considered present within that grid cell. This resulted in a total of 413 cells with resistance information (101 resistant and 312 susceptible cells) being included in the analysis.

2.2 | Land usage data

The spatial distribution of agricultural land use at the 0.01° resolution for the 2005–2006 and 2010–2011 periods was derived from Advanced Very High Resolution Radiometer (AVHRR) satellite imagery [Australian Bureau of Agricultural & Resource Economics – Bureau of Rural Sciences (ABARE–BRS), 2014]. Older available data on land usage was not used (e.g., 2000–2001) because of incongruities in land use categories, which were specified at a coarser level (e.g., no distinction between summer or winter cereals). The estimated type and abundance of agricultural land use was further restricted by agricultural census data [Australian Bureau of Statistics (ABS), 2012]. Land use was reported as falling into one of 26 categories as specified by the Australian Land Use and Management (ALUM) Classification (Bureau of Agricultural & Resource Economics & Sciences, 2010). The most common land usage within each 0.05° grid cell (of the 25 constituent 0.01° grid cells) was used in the analysis. Details of the land usage data can be found in Figure S9 in Supporting Information.

2.3 | Chemical usage data

Chemical usage across Australia (Figure 1) was estimated through the combination of two data sets: (a) gridded data on estimated land usage in Australia for the periods 2010–2011 and 2005–2006; and (b) survey data detailing the paddock histories and chemical applications of Australian growers (c. 1,000 spray histories from nearly 200 unique locations, spanning years 2009–2014). As land use categories for gridded data and survey data did not correspond exactly, remapping of categories was required. We used mean chemical application rates from paddocks labelled in the survey data as 'pasture', 'vetch', 'lucerne' and 'ryegrass' to estimate usage for the ALUM category 'grazing sown pastures' and 'pasture for hay or seed', paddocks labelled 'wheat', 'barley', 'cereal' and 'oats' in the survey data to estimate usage for the ALUM category 'winter cereals', and paddocks labelled 'lupin' and 'canola' to estimate usage for the ALUM categories 'winter legumes' and 'winter oilseeds', respectively. Owing to insufficient chemical data on other ALUM land usage categories, pyrethroid usage was assumed negligible in other land usage types. As farming practices differed between regions, Western Australian survey data on chemical usage were analysed separately from other Australian states, which were pooled owing to data availability. Land usage data (available at the 0.01° resolution) allowed the estimate of pesticide usage to be an aggregated approximation of usage across a region (i.e., 25 cells aggregated per 0.05° cell), which captured the effect of multiple land uses within a region (i.e., prevailing crop rotations).

2.4 | Climatic data

As a proxy for processes affecting long-term abundance and distribution of RLEM, climatic variables were chosen based on a recent study on RLEM niche shifts using a MaxEnt modelling approach (Hill, Chown,

& Hoffmann, 2013). Hill et al. (2013) used a subset (temperature seasonality, winter temperature and the amount of rainfall in the warmest and coolest quarter of the year) of the 19 primary BIOCLIM variables (Booth, Nix, Busby, & Hutchinson, 2014) in combination with a CGIAR-CSI global aridity index (Zomer, Trabucco, Bossio, & Verchot, 2008), successfully to describe past and present distributions of RLEM in both Australia and their native range of South Africa. The BIOCLIM variables were obtained from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), which are derived from average monthly (1950–2000) temperature and precipitation data. The variables describe means, trends and seasonal variations of temperature and precipitation, which are more likely to represent physiological limits for species (Graham & Hijmans, 2006). The global aridity index was calculated as the mean annual precipitation divided by the mean annual potential evapotranspiration and therefore represents precipitation availability over atmospheric water demand (Zomer et al., 2008). These environmental correlates (Table 1) conform with what is known about the biology of RLEM, which prefer cool, moist environments while active (Solomon, 1937), but are able to tolerate hot, dry summer conditions as diapause eggs (Wallace, 1970).

2.5 | Voltinism

To estimate voltinism (number of generations per year), we applied general methods initially to calculate: (a) the cessation of diapause in autumn; (b) the commencement of diapause in spring; and (c) the temperature response of life cycle duration so that the number of generations can be predicted between these two time points. The onset of diapause was estimated using a model developed in 2005, which predicts the date of 90% diapause from daylength and long-term growing season (Ridsdill-Smith, Pavri, De Boer, & Kriticos, 2005). This tool is

TABLE 1 Definitions and relative contributions to model performance (%) of variables tested as predictors of pyrethroid resistance in red-legged earth mites using boosted regression-tree models

Predictor variables	Description	Relative contribution (%)
Summer precipitation (bio_18)	Mean precipitation of warmest quarter determined to the nearest month in millimetres of rain	24.9
Selection	Mean annual number of synthetic pyrethroid applications based on land usage (ALUM data set) and chemical usage (grower surveys)	17.8
Aridity	Mean annual precipitation divided by the mean annual potential evapotranspiration	17.1
Seasonality (bio_4)	Temperature seasonality expressed as the standard deviation of the monthly mean temperatures divided by mean of those temperatures in kelvin	17.0
Generations	Number of generations per year, based on estimated development rate, autumn hatch date and spring diapause date	12.7
Winter precipitation (bio_19)	Mean precipitation of coolest quarter determined to the nearest month in millimetres of rain	10.5
Rainy season temperature (bio_8) ^a	Mean temperature of wettest quarter determined to the nearest month in degrees Celsius	NA
Land usage 2005–06 ^a	Most common land usage for each grid cell during 2005–2006 period	NA
Land usage 2010–11 ^a	Most common land usage for each grid cell during 2010–2011 period	NA

^aRemoved from the model after the tree was simplified following Elith et al. (2008).

widely used across Australia to time chemical applications effectively in spring (i.e., before mites have laid diapause eggs). The cessation of diapause was estimated using a recently developed model for predicting the timing of RLEM egg hatches across Australia from a combination of cumulative rainfall and cold temperatures (McDonald et al., 2015). Finally, life cycle duration was estimated to require 5 weeks to complete at a temperature cycle of 10 hr at 18 °C, 14 h at 11 °C (Ridsdill-Smith & Gaull, 1995), which was adjusted for temperature using the Boltzmann–Arrhenius equation, with inhibition at temperatures < 4 and > 30 °C based on developmental rate data (James & O'Malley, 1991). Gridded data on daily climatic conditions was derived from 20 year averages of climatic data from the Australian Bureau of Meteorology.

2.6 | Modelling approach

The BRT approach is a machine learning technique used for classification problems that produces a prediction from an ensemble (boosting) of many weaker models (decision trees) (Elith, Leathwick, & Hastie, 2008; Friedman, 2002). Models are added to the ensemble iteratively based on the optimization of a loss function, which is usually some measure of predictive deviance. Overfitting is reduced by a process called bagging, whereby each model added to the ensemble is fitted to a randomly sampled (with replacement) subset of data. Predictions based on an ensemble of many simple models with a probabilistic component are usually more stable and accurate than those based on single decision trees (Elith et al., 2008). We chose a bagging size of 0.5, which is appropriate for smaller data sets (Friedman, 2002), and implemented the model in R using code provided by Elith et al. (2008). A *k*-fold cross-validation procedure was used to train (90%) and test (10%) each model, whereby the data are randomly divided into 10 subsets, with each subset sequentially omitted from the training process and used to test the model predictions. A learning rate of 0.001 was used, resulting in a model with 2,450 trees. The relative contribution of each predictor variable to the model was estimated using a standard practice (Elith et al., 2008; Friedman, 2002) whereby the importance is proportional to the frequency with which a variable is selected for splitting, weighted by the squared improvement to the individual tree as a result of each split, and averaged over all trees. Following Elith et al., 2008, if the omission of a predictor variable did not significantly impact the model (predictive deviance \pm SE from 10-fold cross-validation interval included the predictive deviance of the full model), it was excluded. Pairwise Pearson's correlation coefficients of predictor variables were evaluated to ensure that no predictor variables were collinear. Coefficients > 0.8 were considered to indicate high correlation (Hill et al., 2013; Lozier & Mills, 2009). Interactions between predictors are automatically captured in a BRT model if supported by the data, with the dimension of the interaction set by the depth of the tree (e.g., a tree with five branches can theoretically capture a five-dimensional interaction). Pairwise interaction strength can be examined by estimating model predictions for a grid of values for each pair of predictors (with all other predictors held at their mean level) and linearly regressing this grid against the two predictors (treated as categorical

variables without interaction). This method essentially identifies deviations of the BRT model predictions from linear combinations of each predictor pair, which can be used as a measure of interaction strength. No significant interactions were identified in the data set, with the relative strength of interactions detailed in Table S2 in Supporting Information.

3 | RESULTS

Our spatial model accurately predicted the evolution of pyrethroid resistance, achieving a receiver operating characteristic (ROC) score of 0.96 for the training data and 0.83 for the cross-validation (cv) data set. The mean total deviance and residual deviance of the model was 1.11 and 0.56, respectively. Although there was some correspondence between estimated chemical usage and the occurrence of resistance (Figure 2), the importance of climatic variables in the model suggests that climate, in addition to chemical usage, must be considered in explaining the evolution of resistance in RLEM. In particular, summer precipitation contributed the most to the model performance (24.9%), with selection pressure contributing 17.8% (Table 1). The analysis identified conditions and locations associated with a high certainty of resistance (Figures 2 and 3). A threshold effect was observed for rainfall in the warmest quarter, whereby rainfall > 60 mm per quarter was associated with a lower risk of resistance. Temperature seasonality contributed 17.0% to the model, with resistance associated with low seasonality (i.e., small variation in monthly mean temperatures). As expected, low selection pressure was associated with the lowest risk of resistance, but the risk did not increase in a positive monotonic relationship, as shown in the multimodal partial dependence plot (Figure 2). The aridity index contributed 17.1% to model performance, with intermediate values of *c.* 0.8 most associated with resistance. Voltinism contributed 12.7% to the model, with a positive functional response as expected, and winter precipitation contributed 10.5%, with resistance associated with moderate rainfalls. After fitting a model with all predictor variables described in Table 1, model simplification eliminated predictor variables for rainy season temperature and both land usage variables.

To identify other areas of high predicted risk of pyrethroid resistance, the fitted model was projected across Australia to areas without observations (Figure 3). Within Western Australia, the south-western region was identified as a location not presently known to contain resistant populations, but estimated as highly suitable for resistance evolution. Outside of Western Australia, where resistance has not been observed, the model predicts some coastal areas of south-eastern Australia to be most at risk.

4 | DISCUSSION

In contrast to a decade ago, pyrethroid resistance in RLEM is now found across many regions in Western Australia (cf. Umina, 2007). However, these locations are not a random subset of the occupied species range. Our findings indicate that there is a strong environmental signature in the spatial pattern of resistance; this can be related to

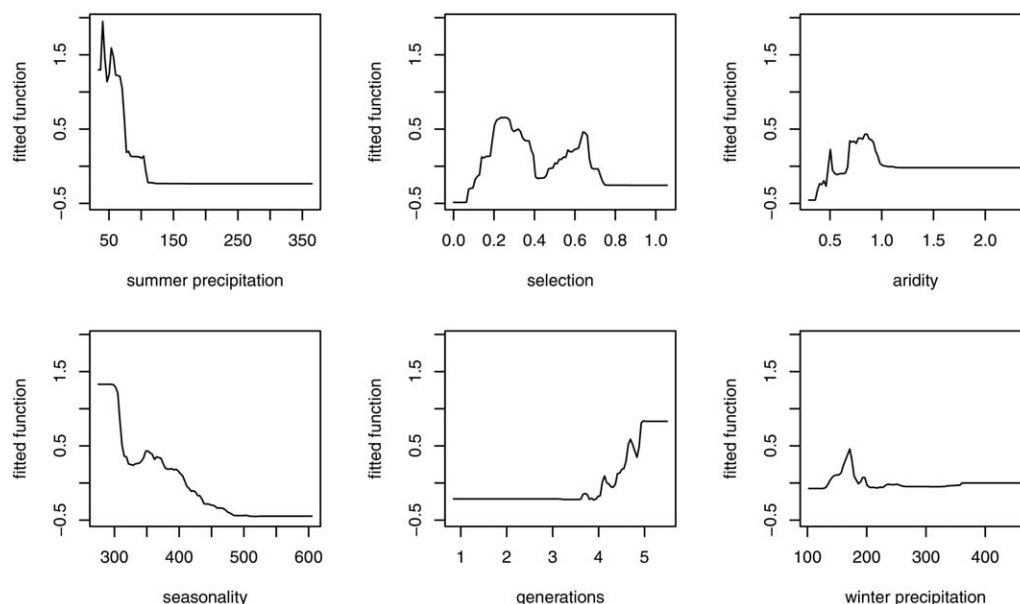


FIGURE 2 Partial dependency plots for six predictors of resistance as determined from a boosted-regression tree model (other variables fixed at their average values). See Table 1 for a description of predictor variables and their relative contributions. The y axes are logit scale, scaled to have zero mean over the data range

variables associated with selection pressure, voltinism and abundance. In addition to increasing our understanding of the potential drivers in the evolution of resistance, our approach highlights regions with conditions most favourable to the future evolution of resistance. Our findings suggest that management of resistance in other pest species might be improved through methods that incorporate climate and ecology, in addition to pesticide usage. Boosted regression-tree models are an established tool in ecology, having made large contributions to difficult presence-absence problems, such as understanding species distributions. We have shown here that these models have the potential to contribute significantly to understanding the distribution and drivers of pesticide resistance, which is an increasingly important problem in agricultural systems.

Selection pressure was estimated from land usage patterns and corresponding average chemical practices. The resulting pyrethroid usage layer accounted for broad regional differences in application rates (owing to differences in land usage and prevailing chemical practices), which might help to explain why pyrethroid resistance in RLEM has not yet been detected in eastern states. However, within Western Australia, areas of the highest estimated chemical application rates did not necessarily correspond to areas where resistance is most prevalent (Figure 1). This finding is also evident in the predicted functional response of pyrethroid usage (Figure 2), which counter-intuitively declines at higher rates. This may be attributable to several factors. Firstly, chemical application rate was estimated at a coarse resolution (land usage at 0.01° aggregated to 0.05° grid cells), reflecting limitations in satellite-derived data. Secondly, chemical usage was assumed to depend only on the land usage type and broad geographical region (i.e., Western Australia and eastern Australia) and did not take into account fine-scale regional variation, as would be expected to exist because of individual management decisions and cultural

factors determining local practices (Pannell et al., 2006). Thirdly, the chemical layer alone does not reflect how environmental variables will affect mite numbers, and thus the requirement for chemical control, which is discretionary. Fourthly, the rate of development of resistance is not necessarily related to chemical usage directly given that intermediate levels of chemical usage can lead to more rapid evolution of resistance than high or low levels (Shaw, 2000). Despite these limitations, estimated chemical application was found to be a strong contributor to the model (Table 1), with higher levels of chemical application, in general, leading to more resistance compared with low levels. But the large contribution of climatic variables to the model highlights the importance of considering other environmental drivers in the evolution of resistance.

Despite resistance currently being restricted to Western Australia, our model predicted areas within eastern Australia that are at highest risk of developing pyrethroid resistance. As many of these locations have not yet been screened for insecticide resistance (Figure 1), it is possible that resistance has already developed, but remains at levels lower than that required for chemical control failures to be detected. These predictions will be useful to ongoing monitoring and extension efforts surrounding the prioritization of future resistance surveillance and education programmes.

The shapes of the response curves of climatic predictors in this study were broadly similar to that found in a study that modelled the distribution of RLEM (Hill et al., 2012), despite being based on a unique data set (resistance data, rather than species distribution data). Similarity in response curves may be unsurprising given that variables associated with higher habitat suitability are consistent with ecophysiological knowledge on RLEM (Ridsdill-Smith, 1997) and are also likely to be associated with both a higher requirement for chemical control and a higher standing genetic variation.

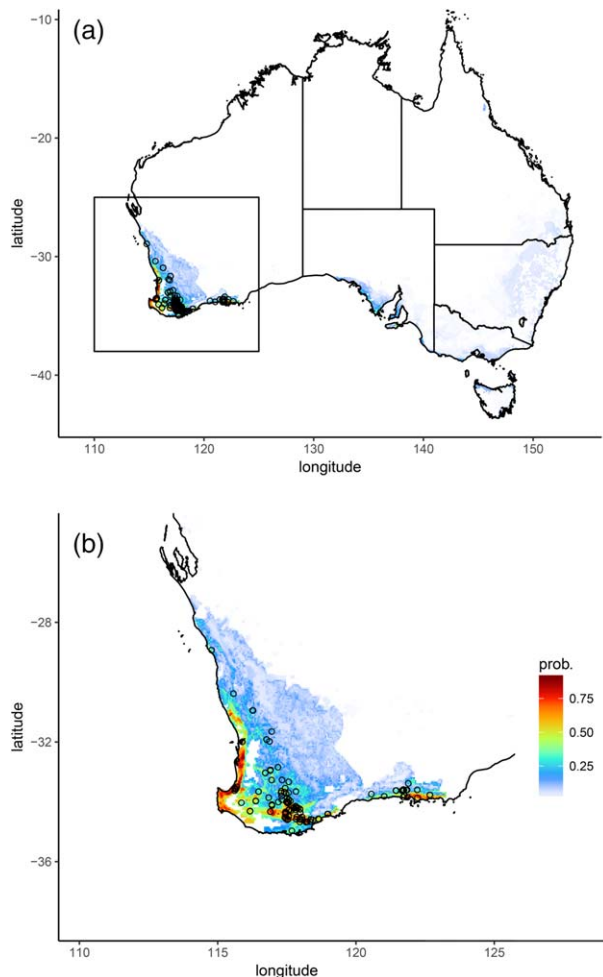


FIGURE 3 Fitted probability of pyrethroid resistance estimated at (a) a resolution of 0.05° (c. 5 km) for Australia and (b) a magnified region of Western Australia where resistance has been detected. The magnified region is defined by the rectangle in (a). Populations resistant to pyrethroids are shown as open circles. Regions estimated to have no chemical usage and < 1% occurrence probability were masked

Although there are similarities between the climatic responses of resistance and distribution models, the exception to this was the effect of temperature seasonality. In the distribution model of Hill et al. (2012), increased temperature seasonality was associated with a higher presence of mites, whereas the opposite was found here for resistance. This may relate to the increased ability to control mites with a single chemical application in more seasonal environments (Gower, Hoffmann, & Weeks, 2008; Ridsdill-Smith & Pavri, 2015; Ridsdill-Smith et al., 2005). Ridsdill-Smith et al. (2015) hypothesized that chemical control was less effective in eastern Australian populations of RLEM because of the more variable spring and early summer conditions, compared with the more mediterranean climate of Western Australia. If correct, this implies that more variable climatic conditions lead to less synchronized mite populations and less control per pesticide application, which may result in higher chemical doses to achieve a given level of control and, consequently, greater selection pressure. Indeed, as part of a recently developed national resistance management strategy for

RLEM, multiple applications of a single chemical class within a season were strongly advised against owing to the associated increase in selection pressure for resistance, in part attributable to overlapping generations (Umina et al., 2016).

In this study, we hypothesized that differences in land usage would be an important predictor of resistance because of potential effects on mite abundance and management practices (e.g., mites prefer, and are more abundant, in pasture compared with canola, but canola tends to receive more frequent pesticide applications than pasture because of its higher value per unit land area). However, land usage contributed little to the model and was subsequently removed in the process of model simplification. This may be because of the effect of climate being relatively more important in determining properties of mite populations. However, as detailed in Figure S9 Supporting Information, land usage categories are coarse (e.g., winter cereals include oats, barley and wheat), and in some cases, are incomplete (e.g., 37 of 412 cells were classed as 'non-agricultural land or no data'). Finer variation within categories might lead to a stronger signature of land use on resistance.

The modelling approach used did not include migration processes because of the limited ability of RLEM to disperse (Weeks, Turelli, & Hoffmann, 2000) and the discovery of multiple resistance evolution events. However, when dealing with pests where dispersal is clearly very important to evolution of resistance (e.g., Bass et al., 2014), the model would benefit from the explicit inclusion of migration processes. Furthermore, our approach is based on correlation between variables, and thus only links indirectly to processes driving resistance evolution. An attempt was made to ensure that more proximate variables affecting the evolution of resistance were derived from less proximate variables (e.g., voltinism rather than daily temperatures). A more mechanistic approach could be undertaken to gain greater understanding of the processes leading to evolution of resistance. Mechanistic models tend to outperform correlative approaches when predicting in new scenarios (Maino, Kong, Hoffmann, Barton, & Kearney, 2016). This minimizes the risk of unrealistic predictions, such as when resistance is predicted to occur in locations with no estimated chemical usage but owing to the correlative contribution of other variables in the model. The main trade-off with mechanistic approaches is that they require an in-depth knowledge of the components relevant to predicting a particular system. In the case of RLEM, important biological knowledge, such as the drivers of seasonal abundance (Ridsdill-Smith & Annells, 1997) and the mechanisms conferring resistance (e.g., acquired insensitivity to a chemical or enhanced detoxification; Roush & Tabashnik, 1990), has only been resolved in part. This highlights a key strength of the approach used here, which allows for imperfect biological knowledge to formulate predictions and to generate hypotheses of the drivers of resistance. Such predictions can be tested in more controlled conditions, such as through simulation or experimental approaches, and should ultimately lead to improved pest management practices.

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DATA ACCESSIBILITY

Sensitive information such as GPS points of properties with resistance are not able to be made publicly accessible, however, all other data is publicly available and can be accessed as specified in the supplementary information.

AUTHOR CONTRIBUTIONS

J.L.M., P.A.U. and A.A.H. conceived and designed the study. J.L.M. and P.A.U. compiled the resistance data. J.L.M. compiled the covariate layers, performed modelling work and analysed output data. J.L.M., P.A.U. and A.A.H. contributed to writing and revising the manuscript.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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