Research Article

Climate, human influence and the distribution limits of the invasive European earwig, *Forficula auricularia*, in Australia

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Abstract

BACKGROUND: By modelling species–environment relationships of pest species, it is possible to understand potential limits to their distributions when they invade new regions, and their likely continued spread. The European earwig, *Forficula auricularia*, is a non-native invasive species in Australia that has been in the country for over 170 years. However, in the last few decades it has invaded new areas. Unlike in other countries, *F. auricularia* is a pest species of grain production in Australia. In this study we detail the Australian distribution of this species, adding new samples focused around grain-growing regions. Using this information, we build global species distribution models for *F. auricularia* to better understand species–environment relationships.

RESULTS: Our models indicate that the distribution of *F. auricularia* is strongly associated with temperate through to semi-arid environments, a high winter rainfall and pronounced temperature seasonality. We identified regions that hold suitable, but as yet vacant, niche space for Australian populations, suggesting further potential for range expansion. Beyond climate, an index describing human influence on the landscape was important to understand the distribution limits of this pest. We identified regions where there was suitable climate space, but which *F. auricularia* has not occupied, probably due to low levels of human impact.

CONCLUSION: Modelling the global distribution of a non-native pest species aided understanding of the regional distribution limits within Australia and highlighted the usefulness of human impact measures for modelling globally invasive insect species. © 2018 Society of Chemical Industry

Supporting information may be found in the online version of this article.

Keywords: European earwig; human influence; species distribution modelling; grain production; niche analysis

1 INTRODUCTION

The global costs of invasive insects are estimated at US$70 billion annually,[1] and new introductions continue to occur.[2] Predicting the distribution, spread and potential impacts of non-native insects is an important, ongoing and challenging task.[3] Effective management and policy formation require accurate predictions of potential distribution, especially for non-native economic pests, and species that are ecologically disruptive or impact human health.[4] Building predictive models for mapping pest distributions not only helps to communicate risks to industry, but also increases understanding of ecological limits to species distributions and identification of processes that may promote invasiveness.

Climate suitability is a major predictor of establishment success and subsequent spread for insects that has been exploited to produce distribution maps for use in management for close to 100 years (dating back to WC Cook[5–7]). The ability to translate species climatic or environmental tolerances into geographical prediction relates to the *niche*. If there is enough information on the direct physiological requirements of a species, obtained through experimental evidence and field-testing, it is possible to

estimate components of the *fundamental niche* of a species (e.g. Kearney *et al.*[8]; Gutierrez *et al.*[9]). Presence/absence points for a species represent a physical expression of the niche, and theoretically approach the fundamental niche given complete sampling and no biotic interactions or constraints to dispersal. However, biotic interactions and barriers to movement are common and further restrict distributions, thus the *realised niche* describes the proportion of the fundamental niche that is expressed by a population.[10–12] Nevertheless, for predicting establishment and potential distributions of many globally invasive insect species,

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using climatic suitability to characterise the realised niche is often a useful first approximation, unless there are substantial evolutionary shifts that facilitate niche change in an invaded region (e.g. Rey *et al.*[13]; Egizi *et al.*[14]).

There are several approaches to characterise a niche and link a species to its environmental requirements. Species distribution models (SDMs) (or ecological niche models) are the most commonly applied technique. These characterise species–environment relationships by correlating observations of species occurrence with covariates, typically in the form of interpolated climate or environmental indices generated through Geographical Information Systems (GIS). Species distribution models in this sense attempt to characterise something close to the realised niche. The accuracy of SDMs depends on all factors defining the niche boundaries, and hence distribution, being included at the appropriate modelled scale.[15] This requirement means that any predictor variables included in the models and the availability of occurrence records are both critical to producing meaningful predictions. While applying the same set of predictor variables across a range of species can give insight into general patterns of invasion,[16] predicting the distributions of invasive species is not a 'one size fits all' approach.[17] Predictor variables should ideally be chosen based on how directly they relate to a species' physiology and based on a low level of correlation between variables across ranges (see Petitpierre *et al.*[18]). Whilst climatic predictor variables are generally employed, responses to modified environments are also likely to contribute to the invasion success of non-native insect species.[19,20]

Typically, the only occurrence data available are *ad hoc* observations of species presence, rather than rigorous and systematic sampling strategies that yield both presence and absence information. There will also be biases in occurrence records, depending on the status of the species in a region, and resources used for monitoring. For example, more observations are likely in regions where the species is a pest, however many species are not pests in their native range. Species distribution models constructed from the native range alone (with potentially limited observations) may then be poor predictors of invasive ranges.[16,21] The inclusion of all known populations across the entire distribution can provide better characterisation of species–environment relationships. Additionally, a well-sampled species distribution across ranges allows SDMs to investigate which variables are relevant (proximal) in defining current distributions and to identify changes between native and invaded environments.[22]

The European earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae), is a species with a broad native range extending across northern Africa, Europe and eastern Asia,[23] with many non-native populations (e.g. the USA and New Zealand), and was introduced to Australia over 170 years ago.[24] *Forficula auricularia* has been common throughout south-eastern Australia since the 1900s; despite only being first recorded in Western Australia 24 years ago, it is now common throughout south-western parts of this state.[24] *Forficula auricularia* is often found in disturbed locations[23,25] and can be an important predator in apple,[26] pear[27] and kiwifruit[28] orchards, but is regarded as a plant-feeding pest in softer fruits such as stonefruit,[29] and sometimes as a contaminant during harvest.[30] In Australia, *F. auricularia* is a pest in grain crops,[31,32] although internationally it is more typically considered a beneficial predator in grain systems.[33–36] *Forficula auricularia* is generally found in locations with pronounced summer/winter seasonality. Populations can survive cold winters where total annual rainfall exceeds 500 mm.[37] The overall development of *F. auricularia* depends on temperature,[38] with upper development temperature limits around 23–28 °C.[38] Temperatures above 24 °C may reduce population size.[37] Two reproductively isolated clades have been identified in Europe and North America, though they often coexist. Clade A is typically thought to produce one brood per year, while clade B can produce two broods per year.[25] While the life history of *F. auricularia* is thought to be linked to lineage, individuals are also able to change their life-history traits to suit local environmental conditions.[39] As far as we know, all Australian earwigs are from clade B.[24] A better understanding of environmental factors that affect the spatial distribution of this species can help predict distribution limits in Australia and aid targeted management strategies across local grain production areas.

In this study, we combine published records, field data, and pest reports to construct global species distribution models for *F. auricularia*. Using these models, we characterise species–environment relationships to predict the distribution of *F. auricularia* in Australia. We assess if this species occupies a different niche to populations elsewhere in the world, both native and introduced. Additionally, we test whether or not the species is in climatic equilibrium, if it has expanded its niche and if there is potential for future range expansion. Given a putative association with human-impacted environments, we also assess how such impacts might change species–environment relationships and distributional limits, particularly with respect to Australian grain regions.

2 MATERIALS AND METHODS
2.1 Global spatial information
To compile a complete distribution dataset for *F. auricularia*, we obtained data from a variety of local and global sources. We collated georeferenced distribution records to construct a dataset of locations where *F. auricularia* has been recorded. The Global Biodiversity Information Facility (GBIF) is an open database that provides records from several sources to aid research. We used the R (version 3.4.4[40]) package rgbif[41] to download all records for *F. auricularia*, which provided 26 012 records. The Atlas of Living Australia (ALA) is an open database for reports of any species found in Australia. We used the R package ALA4R[42] to download occurrence data for *F. auricularia*, which gave 24 records. The Australian Pest Plant Database (APPD; Plant Health Australia 2001) is a closed database that contains records of pests and diseases of economically important plants in Australia. This yielded 238 records. All databases were accessed on 27 February 2018. In addition to these databases, we added further Australian data from a published field dataset,[24] which yielded another 33 records. The data collected through field sampling and pest reporting services (up to 2014; see below) were included in this larger dataset to construct the SDMs. From these datasets we had a total of 294 localities for *F. auricularia* in Australia.

We examined the entire dataset and removed geographical outliers to restrict the distribution to points that came from well-sampled regions, corresponding to Europe, North America, New Zealand and Australia (the first three comprising our 'global' dataset). While *F. auricularia* is reported in Africa (as a native, except for South Africa where it is reported as invasive) and South America (Chile and the Falkland Islands), there was too little information on its distribution within these regions to enable their incorporation into this global dataset.

2.2 Targeted field sampling in grains

To enhance the distribution dataset, we conducted targeted sampling of *F. auricula* over 2016–2017, specifically focusing on grain crops throughout Australia (see Supplementary Material 1.1 for map). Samples were taken in crops (canola, wheat, barley) using cardboard rolls that encourage earwigs to take refuge.[23,43] The cardboard rolls consisted of single-sided corrugated cardboard 250 mm in width rolled to form 50 mm diameter cylinders with longitudinal corrugations. The rolls were inserted into a 200 mm length of 50 mm diameter polyvinyl chloride (PVC) pipe and were left out for 7 days at each location. As earwigs are also ground-active,[44] we additionally used pitfall traps at the same sites.[45] Each trap consisted of a PVC sleeve placed in the ground, flush with the soil surface. Vials 45 mm in diameter and 120 mL in volume, containing 60 mL of 100% propylene glycol, were placed inside the sleeves and left open for 7 days.

In addition to field samples, we obtained data from three Australian pest-reporting services for the major grain-growing regions of Australia up to 2014. These reporting services collate incidences of pest outbreaks and reports from farmers, farm advisors and other industry personnel in the respective regions (Western Australia, South Australia, New South Wales and Victoria). They involve PestFacts south-eastern (cesar; http://cesaraustralia.com/sustainable-agriculture/pestfacts-south-eastern), PestFacts South Australia (SARDI; http://www.pir.sa.gov.au/research/services/reports_and_newsletters/pestfacts_newsletter) and PestFax Western Australia (DAFWA; https://www.agric.wa.gov.au/newsletters/pestfax). These services yielded 17, 7 and 53 localities with coordinates, respectively.

## 2.3 Environmental predictors and geographic extent

To characterise species–environment relationships of *F. auricularia* with broad scale variables, we employed the 19 bioclimatic variables from WorldClim 2.0[46] at a 10′ resolution. These variables describe means, patterns and trends for temperature and precipitation observations in the interval 1970–2000. They are part of the BIOCLIM package[47] and are widely employed in species distribution modelling. The scale of 10′ (roughly 20 km² at the equator) is also relevant to the model construction and transferability for broadly distributed species between large, distinct, geographical regions.[16,48,49] To address different resolutions of reported coordinates and repeated local observations across datasets (and provide data at the same resolution as the predictor variables) we rescaled all observations to this grid cell level, which resulted in 3304 unique points, 162 in Australia. We included a global aridity index from the CGIAR-CSI (Consortium for Spatial Information – Consultative Group for International Agriculture Research) database[50,51] (http://www.cgiar-csi.org: accessed February 2018), as it correlates with the limit of the distribution of *Halotydeus destructor*, an invertebrate pest with a broadly similar Australian distribution.[22] Within Australia, *F. auricularia* is rare in undisturbed habitats,[24] so we also included a non-climatic environmental predictor that describes the impact of human influence (HII[52]) to examine how the global distribution may be associated with factors such as human population density, roads, agriculture and urban development. We consider this variable to indicate anthropogenic disturbance at a grid cell. The index ranges from 0 to 72, with higher scores indicating greater human influence.[52] We also examined a soil classification layer, however this was not included in the modelling process but in examining model output (see Supplementary Material 2).

Prior to SDM and niche analyses, the geographic extent of the analysis was defined. The modelling extent, or background, is typically defined by restricting the geographic extent to environmental conditions similar to the environments held across the presence points, but that have not been occupied for a number of reasons. To achieve this, we selected the backgrounds for this study by using the Biome definitions of Olson *et al.*[53] This approach has been applied successfully to other invasive species (e.g. Mateo *et al.*;[54] Hill *et al.*[16]) and provides a workable and repeatable background selection procedure. All biomes per continent that held a presence point were retained and used to create a single surface to extract background information.

As fewer variables are likely to result in models with better transferability, we examined which predictor may be more closely associated with the distribution of this species. We calibrated a principal components analysis (PCA) across all available predictors for the entire study area, which provides an effective method for choosing variables to aid transferability when the best predictive variables are unknown.[18] Using R, we performed a PCA across all presence points to examine the variance and loadings of the different climatic predictor variables. This method identified aridity as explaining 99.8% of the total variance on the first axis, and seven bioclimatic variables on the second axis: temperature seasonality (bio04), annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of wettest quarter (bio16), precipitation of driest quarter (bio17), precipitation of warmest quarter (bio18) and precipitation of coldest quarter (bio19). We performed another PCA, this time removing aridity, to examine variance explained by just the bioclimatic variables, and the first two axes of the PCA explained 84.4% and 13% of the total variance, respectively, with the same seven variables identified. While it was likely masked by the climatic variables and appeared not important in terms of PCA loadings, the density of the HII across occurrences versus a null distribution indicated a clear positive association of *F. auricularia* with human impact (Fig. 1(B)), warranting its inclusion to create a dataset of nine predictor variables. We then generated 40 000 random points across the entire training background (global distribution) of *F. auricularia* and extracted predictor information for the eight variables. Correlations between the nine predictor variables were assessed using Kendall's τ (tau) within the corrplot[55] package in R before inclusion in the initial models (Supplementary Material 1.3).

2.4 Species distribution modelling

Our approach to species distribution modelling employed an iterative approach across five models (see Table 1). First, a model was developed based on our predictor set of eight variables using default settings of Maxent as implemented through the dismo[56] package in R. Maxent has been widely used for SDM purposes and provides a suitable framework for modelling when the data is presence-only (i.e. true absence data is not available, typical of insects[57]). Second, we changed the settings of Maxent to those of a point process model.[58] While regression models examine the relationship between a random variable and covariates, point-process models work on the principal that the spatial location of the observed points is driven by the covariates, and investigate this by jointly modelling the location of the points with the expected intensity per unit area.[58] An advantage over default Maxent settings here is that the predicted intensities from point-process models are scale invariant. Third, we repeated the second model, but without the inclusion of the HII variable, to
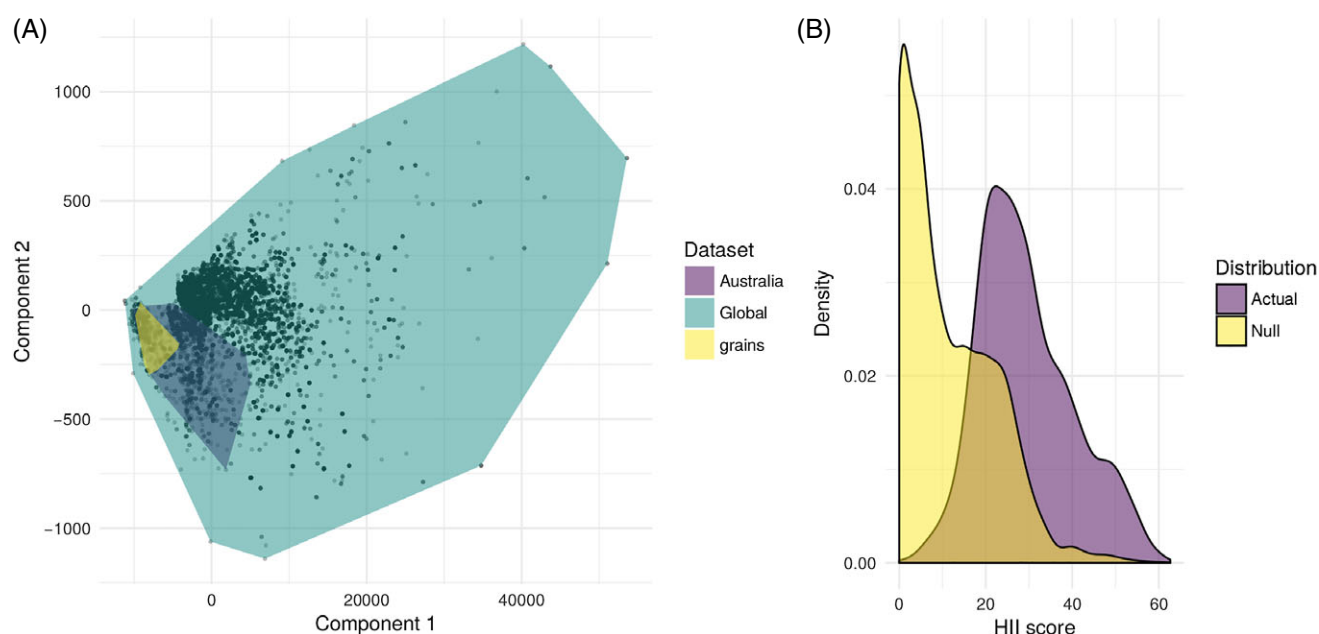
Figure 1. (A) The first two axes of a Principal Components Analysis (PCA) using eight climatic variables for the entire distribution of *F. auricularia*. Component 1 is solely the aridity index. Component 2 represents the seven other climatic variables used in this study. (B) Density of values for the impact of human influence (HII) extracted at each point for the global distribution of *F. auricularia* versus a null distribution of the same number of points. All points were rescaled to the grid cell (10′) level ($n = 3113$).

examine how a model with only climate variables performs. Following these initial three models, model selection was achieved through the corrected Akaike Information Criterion (AICc) and the Bayesian Information Criterion (BIC) using all data for training and the R package rmaxent[59], and by examining the area under the curve of the receiver–operator characteristic (AUC) across ten cross-validated replicates, using a 70:30 training:testing split.

We then sought to create a further subset of predictor variables by determining which of the nine variables contributed most, and where, in Australia. We examined the modelled responses of the individual variables (percentage contribution and permutation importance) alongside the limiting factor analysis, and from these results (and examining the amount of correlation between variables ($\tau < 0.7$)) removed an additional four climatic variables (bio12, bio16, bio17, bio18; Table 2). We then ran a fourth Maxent model on the reduced number of variables and compared this with the previous models to examine if any important information had been discarded. Finally, for the fifth model, we again excluded the HII and compared this back to the other models to examine the influence of the non-climatic variable within the reduced predictor set.

2.5 Reciprocal distribution modelling

To examine how the geographical representation of the niche may differ between Australian and non-Australian populations of *F. auricularia* we constructed SDMs based on subsets of the data (corresponding to different ranges) and reciprocally projected these models between ranges.[22,49] We aimed to determine how well the species–environment relationships of the global distribution can be characterised from the populations in Australia, and vice versa. To perform the reciprocal distribution models, we used the same predictor variables and model settings as found through the SDM process, but only trained the model on a subset of the data, corresponding to either the 'global' (North America, Europe and

New Zealand) or 'Australia' ranges. Once the models were constructed, we projected them to the reciprocal background: 'Australia' to 'global', 'global' to 'Australia'. We then calculated a measure of niche overlap, Schoener's *D*, and used the corresponding range point data to perform an AUC test.

2.6 Niche change analysis

To further understand how the niche of Australian populations may be different from the non-Australian populations in environmental space, we measured amounts of niche change as detailed elsewhere,[47,16,60] which involves a PCA across the combined backgrounds (global and Australia) and the respective ranges. All PCAs were rescaled to 100 × 100 cells and the densities of occurrence (the native and non-native ranges, respectively) were projected onto these surfaces. This procedure is undertaken to reduce bias from the different sizes of the two ranges and the relative amount of sampling undertaken. The two rescaled surfaces were then overlaid and the amount of niche change measured. The main components measured were the amount of overlap (again through Schoeners' *D*), niche expansion (climates available in both ranges that have not been exploited in the native range) and niche unfilling (climates available in both ranges that have not been exploited in non-native range). We then examined these three components of niche change with and without the inclusion of HII to test how much climate versus other abiotic factors (encapsulated in the HII) affect niche change and hence potential distribution.

3 RESULTS

3.1 Distribution information

The study contributed 39 new distribution localities from grain production systems in Australia through field surveys, adding to those from the pest-reporting services to create a novel dataset of 100 (92 at the 10′ grid cell level) *F. auricularia* distribution points (Supplementary Material 1.1). Nineteen sampled localities

Table 1. Model selection process

Model/ Setting	Variables	*n*	*k*	*ll*	AIC	AICc	BIC	AUC
1/Default	arid bio04 bio12 bio13 bio16 bio17 bio18 bio19 hii	3113	156	−31858.68	64029.35	64045.92	64972.11	0.94
2/Point process	arid bio04 bio12 bio13 bio16 bio17 bio18 bio19 hii	3113	52	−31445.68	62995.35	62997.15	63309.61	0.96
3/Point process	arid bio04 bio12 bio13 bio16 bio17 bio18 bio19	3272	221	−34412.12	69266.24	69298.41	70612.83	0.95
4/Point process	arid bio04 bio19 bio13 hii	3113	164	−31381.26	63090.53	63108.89	64081.64	0.96
5/Point process	arid bio04 bio19 bio13	3272	163	−34998.17	70322.34	70339.55	71315.53	0.94

Columns give the variables used for each Maxent model: *n* (the number of occurrence records used for model training), *k* (the number of features with non-zero weights), *ll* (the negative log likelihood of the model), AIC (Akaike Information Criterion), AICc (sample size corrected AIC), and BIC (Bayesian Information Criterion) and AUC (Area Under Curve of the Receiver-Operator Characteristic).
Variables: arid = aridity index; bio04 = temperature seasonality (standard deviation × 100); bio12 = annual precipitation; bio13 = precipitation of wettest month; bio16 = precipitation of wettest quarter; bio17 = precipitation of driest quarter; bio18 = precipitation of warmest quarter; bio19 = precipitation of coldest quarter; hii = Human Influence Index (HII).

Table 2. Niche change metrics for populations *Forficula auricularia* in Australia *versus* the 'global' distribution (see Fig. 4 for descriptions)

Variables	Expansion	Stability	Unfilling	Overlap (*D*)
Final set	0.01	0.99	0.17	0.29
Climate only	0.01	0.99	0.34	0.16

The overlap is Schoeners' *D*.

did not yield any *F. auricularia*. As these sites may indicate seasonal absence rather than complete absence, they were not included in our modelling.

3.2 Environmental variables and model selection

The predictor variables identified as being important and model selection criteria are shown in Table 1. Two models stand out as best performing: models 2 and 4. Model 2 has nine predictor variables, whereas model 4 has only five. The slight decrease in AUC and increase in AICc for selecting model 4 over model 2 can be justified in the lower dimensionality, which is important to model transferability[61] (i.e. the subsequent reciprocal distribution modelling and niche analysis use only subsets of the data and project across ranges). Our final predictor variable set, in order of importance as determined by Maxent, consisted of the human influence index (HII), bio04 (temperature seasonality (standard deviation × 100), bio19 (precipitation of the coldest quarter), aridity index and bio13 (precipitation of the wettest month). The variable response curves of model 4 are presented in Supplementary Material 1.4. As the aridity index is defined as mean annual precipitation divided by mean annual potential evapotranspiration, it represents precipitation availability over atmospheric water demand. Aridity values at around 0.2 (semi-arid) resulted in higher probabilities (for this variable), with arid (<0.1) and humid (>0.65) locations being much less suitable. Beyond aridity, this predictor set indicates a strong association with winter rainfall (200–800 mm) and defined seasons (standard deviation of 3–4 °C over 1970–2000, based on the standard deviation of monthly temperature averages) (Supplementary Material 1.4). Based on

the PCA constructed on climatic information (Fig. 1(A)), the Australian distribution is nested with the global distribution, and the distribution from the grain-growing regions of Australia is nested within the Australian distribution (Supplementary Material 1.2). The density of species occurrence across the HII layer (Fig. 1(B)) shows that the global distribution of *F. auricularia* is associated with higher levels of human impact than expected at random. The modelled response for HII shows that higher values for this variable resulted in higher probabilities (Supplementary Material 1.4).

3.3 Model prediction

The model prediction in Australia shows that habitat suitability for *F. auricularia* is mainly restricted to southern regions, corresponding to areas of strong seasonal differences in temperature and a predominantly winter rainfall (Fig. 2). These areas also correspond to the main grain cropping regions (and temperate horticultural regions) of southern Australia. In Western Australia, there is suitable habitat to the north of the currently observed distribution. The limiting factor analysis that accompanies this model prediction (Supplementary Material 1.5) shows that HII often restricts the distribution more than climatic variables, and aridity limits the distribution around the occurrence points. Areas such as south-west Tasmania and parts of eastern Victoria highlight regions where the climate is expected to be suitable (Supplementary Material 1.5), but perhaps these regions are not sufficiently disturbed to facilitate population establishment.

3.4 Reciprocal distribution modelling

For the reciprocal distribution modelling (RDM) (Fig. 3), the model projected globally is the predicted distribution of *F. auricularia* given our dataset (Fig. 3(A)). This global model projected well to the Australian background with an AUC of 0.83 and a Schoener's *D* score of 0.89 (Fig. 3(B)), indicating high transferability and overlap in geographical space. The Australian model projected to the global background with an AUC of 0.94 and a Schoener's *D* score of 0.82 (Fig. 3(C)). These overlap scores indicate that there is little change in niche dimensions between the global and Australian distributions. The Australian-trained model does give a much denser prediction for Australia than the globally trained one,
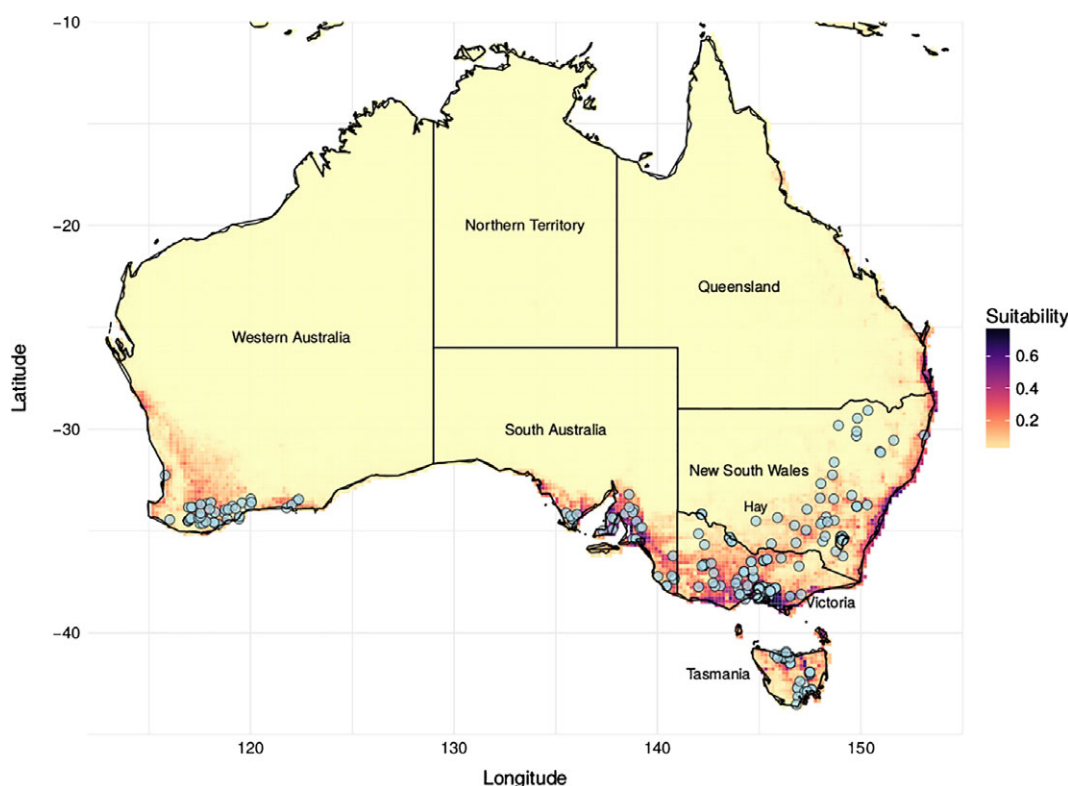
Figure 2. Modelled distribution of *Forficula auricularia* trained on all available data, predicted in Australia. This prediction is the final model selected for optimal settings and variables (see text). The scale ranges from 0 to 1, with 1 indicating high suitability and 0 indicating not suitable. Points indicate localities where *F. auricularia* has been found.

indicating that the species–environment relationships are characterised slightly differently on this data subset (Fig. 3(D)).

3.5 Niche change

The niche change analysis shows low amounts of overlap in the environmental space occupied by the Australian and global distributions ($D = 0.16$), suggesting that the global distribution is broader and the Australian distribution occupies a subset of the total range of environments of *F. auricularia* (Fig. 4). There is no evidence for niche expansion in Australia, again suggesting that the Australian populations occupy a subset of the global niche, rather than any new environments (Table 2). Both niche change analyses also show high amounts of unfilling, which suggests that *F. auricularia* is not currently found in all possible environments in Australia (Table 2). Importantly, the niche change score for unfilling was much lower when the HII was included. In summary, the reciprocal distribution modelling and niche change analysis demonstrate that the Australian distribution falls within the environmental ranges expected from the global distribution (Fig. 4, Table 2).

4 DISCUSSION AND CONCLUSIONS

Forficula auricularia is widely distributed across southern Australia. By using a comprehensive global dataset to characterise species–environment relationships and examining niche dynamics, we provide evidence that the distribution limits are not met and there is potential for future spread. *Forficula auricularia* displays relationships with climate that align with current knowledge of its physiology and result in spatial overlap with the temperate horticultural and major grain-growing regions of

Australia. Furthermore, *F. auricularia* has a strong association with human-influenced habitat, an obvious attribute of broad-acre agricultural landscapes. Whether or not this is related to the pest status in Australian grains remains an interesting question, however the association of *F. auricularia* with human-influenced habitat appears linked to the species' ability to occupy certain environments, as we identified regions where there was suitable climate space, but which *F. auricularia* has not occupied, probably due to a low level of human impact.

Aridity is the most important variable in limiting the distribution of *F. auricularia*. As for many invertebrate species, humidity is critical to prevent desiccation of *F. auricularia* eggs and nymphs.[38] The other important predictors identified, winter rainfall and temperature seasonality, are typical attributes of the main regions where grains and other agricultural crops are grown in southern Australia. Winter rainfall is a critical component to successful grain cropping, supporting the initial growth of several economically important crops that are typically harvested in spring and summer. Temperature seasonality further reflects components of the lifecycle. *Forficula auricularia* is likely to occupy below-ground nests when crops are sown (winter) and then emerge around the same time the crop is maturing (late spring–summer). Our study highlights the importance of using covariates beyond climate; in particular, human-impacted environments seem important for a number of non-native invasive insect species.[16] Human influence may contribute to the distribution of *F. auricularia*, either directly, such as by reducing the heterogeneity of habitat (e.g. biotic homogenization through agricultural monocultures) and providing new host plants, or indirectly by reducing species that they may compete with or predate.[62,63]
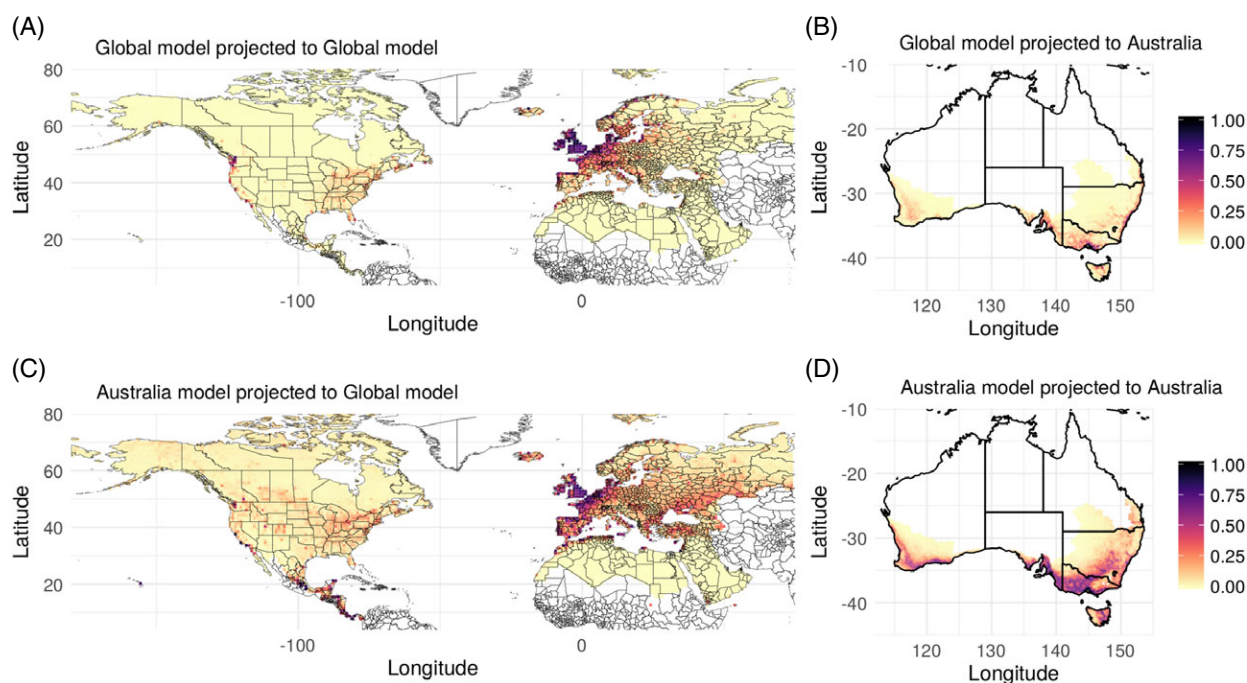
Figure 3. Reciprocal distribution modelling of *F. auricularia* between the 'global' distribution and Australia. For mapping purposes, only the Northern Hemisphere is shown; the New Zealand data was, however, included in these analyses. The scale ranges from 0 to 1, with 1 indicating high suitability and 0 indicating not suitable. The top two panels (A and B) show the projections made from a model trained only on the data from outside Australia. (A) The projection into the 'global' range. (B) The projection into Australia. The bottom two panels (C and D) are the projections made from a model trained only on the data from Australia. (C) The projection from Australia to the 'global' range, (D) The projection to Australia. The overlap (Schoeners' D) between panels A and C is $D = 0.9$ and the overlap between panels B and D is $D = 0.84$.

For a few regions in Australia our models predict suitable habitat where *F. auricularia* has not been observed. The largest of these is in Western Australia (WA) to the north of current observations (Fig. 2). Interestingly, this was found to be suitable regardless of whether or not the human influence index was included. Quarrell

et al.[24] speculated that inland populations at Hay in New South Wales (Fig. 2) (where our models predicted marginal suitability) are indicative of a species that can exist in a variety of environments, and therefore is able to spread into new regions like those in WA. As *F. auricularia* has only been in WA for 24 years
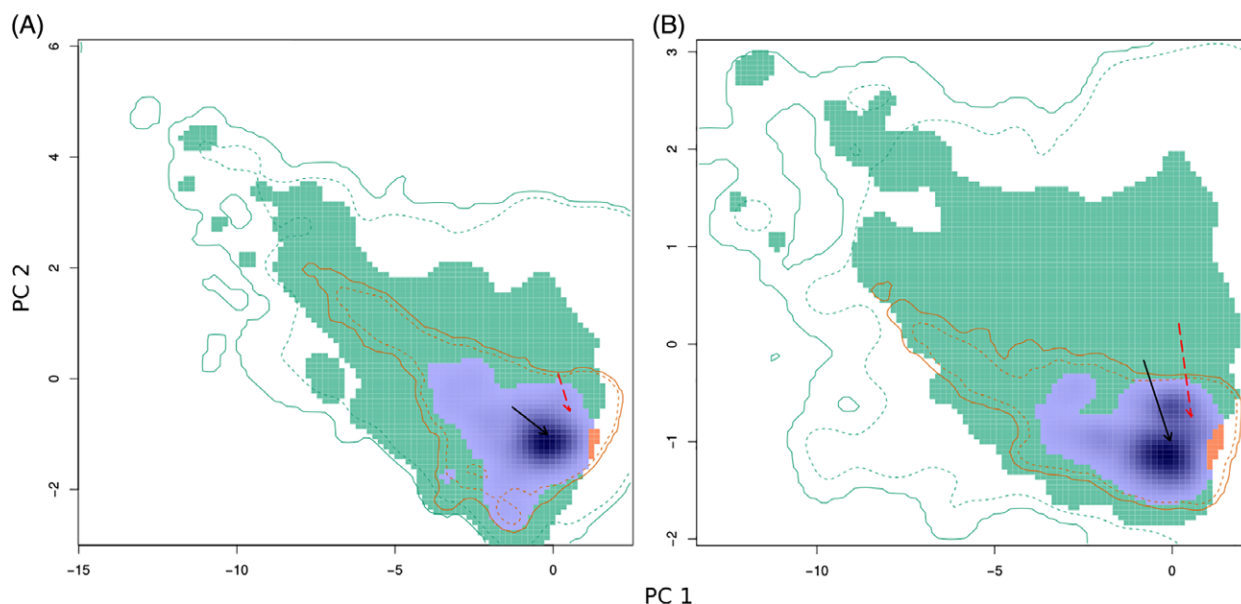
Figure 4. Niche change analysis for *F. auricularia* in Australia compared to its global distribution. The green region indicates the amount of niche unfilling, the orange the amount of niche expansion and the blue the niche stability. The solid red line indicates the climates available in the non-native range (Australia) and the dashed line represents the climates at the 75th percentile. The solid green line indicates the climates available in the native (global) range. (A) Final climate dataset with the HII included. (B) Final climate dataset without HII. See Table 2 for scores of the different niche change components.

it may still be in the process of spreading to its limits (see Quarrell *et al.*[24]). Alternatively, there could be soil properties or other abiotic components not included here limiting its distribution. However, we found no evidence for soil-related effects in that region (Supplementary Material 2). Finally, our models are calibrated on a global dataset that encompasses diverse populations across a broad range of climates; while this helps determine the species–environment relationships, it may identify regions suitable for a species as a whole, but not for a local population. Quarrell *et al.*[24] found that, unlike for the rest of Australia, populations in WA were started by only a few individuals, perhaps limiting adaptive capacity and the ability of this population to expand further.

The broad distribution of *F. auricularia* across a range of agricultural environments suggests that the species either has a generalist nature or that it has undergone adaptive shifts to allow it to move onto new hosts and landscapes, including grains, during its invasion.[64] Some invasive insects, for example *Wasmannia auropunctata* and *Leptinotarsa decemlineata*, likely adapted to anthropogenic landscape changes in their home ranges (forests replaced with plantations, provision of new agricultural hosts) before becoming highly invasive species.[65] Other species, particularly agricultural pests like *Ostrinia nubilalis* and *Daktulosphaira vitifoliae*, have undergone 'bridgehead' scenarios, enabling a single evolutionary shift towards invasiveness in an intermediate invaded region to facilitate subsequent invasions.[64] Given the strong association of *F. auricularia* with human-impacted environments, comparisons of *F. auricularia* populations from different landscapes should provide insights into this issue.

To better understand species–environment relationships in *F. auricularia*, additional occurrence information from places like South Africa, Chile and the Middle East is needed. Consistent reporting across ranges is an issue with many globally invasive species,[66] as surveying and reporting efforts between countries vary due to the regional impact of the pest, reporting incentive and resources available.[67] Reporting bias is further complicated by the fact that *F. auricularia* is not considered a pest in some agricultural contexts. While the scale of predictors used in this study is suited to developing a range of hypotheses, some of the fine-scale behaviour and interactions with other species and environmental parameters could not be tested. For instance, predators such as ants or spiders, as well as competitors, may limit the distribution of this species. Other earwigs are found throughout the grain-growing regions of Australia,[68,69] although their abundance and pest/beneficial status is not well understood. These include earwigs from the family Anisolabididae and the genera *Labidura* and *Nala*.[32,69] To our knowledge, *F. auricularia* is the only confirmed non-native species in these systems, although other species (e.g. cryptic Anisolabididae and Nala spp.) may have been introduced. Further work is required to understand the distributional limits of these other earwig species, along with potential niche overlap and competitive interactions.

We have shown that species–environment relationships characterized using SDMs provide insight into potential factors that limit distributions. While it was possible to map the potential distribution of *F. auricularia*, predictions around population abundance and pest status require empirical research and different models. Mechanistic models, including temperature-based day-degree models, can help predict the timing and emergence of *F. auricularia* in grains and other agricultural systems. Furthermore, while the HII affected the predicted distribution of *F. auricularia*, additional work is required to understand the components of human impact critical to the distribution of *F. auricularia*. This information in turn may indicate whether the species is an opportunistic pest of grain crops or if grain-production systems have facilitated its spread.

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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