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RESEARCH ARTICLE

Remotely sensed agricultural modification improves prediction of suitable habitat for a threatened lizard

David T. Y. Wong, William S. Osborne, Stephen D. Sarre and Bernd Gruber

Institute for Applied Ecology, University of Canberra, Canberra, Australia

ABSTRACT

The geographical distribution of a species is limited by factors such as climate, resources, disturbances and species interactions. Environmental niche models attempt to encapsulate these limits and represent them spatially but do not always incorporate disturbance factors. We constructed MaxEnt models derived from a remotely sensed vegetation classification with, and without, an agricultural modification variable. Including agricultural modification improved model performance and led to more sites with native vegetation and fewer sites with exotic or degraded native vegetation being predicted suitable for A. *parapulchella*. Analysis of a relatively well-surveyed sub-area indicated that including agricultural modification led to slightly higher omission rates but markedly fewer likely false positives. Expert assessment of the model based on mapped habitat also suggested that including agricultural modification improved predictions. We estimate that agricultural modification has led to the destruction or decline of approximately 30–35% of the most suitable habitat in the sub-area studied and approximately 20–25% of suitable habitat across the entire study area, located in the Australian Capital Territory, Australia. Environmental niche models for a range of species, particularly habitat specialists, are likely to benefit from incorporating agricultural modification. Our findings are therefore relevant to threatened species planning and management, particularly at finer spatial scales.

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Introduction

Environmental niche models (Guisan and Zimmermann 2000, Elith *et al*. 2006, Sillero 2011, Warren 2012, 2013) are commonly applied to predictions of the occurrence of species or communities to support conservation management and planning (Pearce and Lindenmayer 1998, Ferrier *et al*. 2002, Loiselle *et al*. 2003, Raxworthy *et al*. 2003, Guisan and Thuiller 2005, Pearson 2007). Such models usually incorporate limiting or scenopoetic factors that relate to the eco-physiology of a species (Hutchinson 1978); *bionomic* factors, such as food, water and shelter (Hutchinson 1978, Guisan and Thuiller 2005) or natural and human-caused disturbances, which can influence both limiting factors and availability of resources. Therefore, when dealing with species that are adversely affected

CONTACT David T. Y. Wong David.Wong@canberra.edu.au; Bernd.Gruber@canberra.edu.au
Supplemental data for this article can be accessed here.

by disturbance and/or species with low rates of dispersal or migration, incorporating disturbance is likely to be critical.

Anthropogenic disturbance such as the intensification of agriculture and land clearing threaten biodiversity (Perrings *et al*. 2006, Hoffmann *et al*. 2010) and therefore will affect species distribution in many parts of the world. The relative influence of key threatening processes may vary according to location and species of interest. For example, roads, hunting, recreational disturbance and pollution are key threatening processes for mammals, reptiles and amphibians in Canada (McCune *et al*. 2013). Habitat loss, inappropriate fire regimes and invasive species are the major threats to species in Australia, with much of this associated with habitat clearance for agriculture in southwestern, eastern and southeastern Australia (Evans *et al*. 2011). As agricultural modification increases, habitat specialists face a higher risk of extinction whilst generalists often benefit, leading to ecosystem homogenisation (Foufopoulos and Ives 1999, McKinney and Lockwood 1999). Agricultural disturbance has led to declines in many Australian taxa (Brown 2001, Hero and Morrison 2002, Benton *et al*. 2003, Maron and Lill 2005, Brown *et al*. 2008, Evans *et al*. 2011, Webb *et al*. 2014). Livestock grazing and the addition of fertiliser are two widespread forms of agricultural modification that have led to changes in plant species composition and richness as well as changes to habitat structure (Clarke 2003, McIntyre and Tongway 2005, Klimek *et al*. 2007, Dorrough and Scroggie 2008) with subsequent impacts on animal communities (Brown 2001, James 2003, McIntyre 2005). In particular, reptiles have been found to respond negatively to the addition of fertiliser as well as other key drivers such as land clearing and ploughing (Dorrough *et al*. 2012, Webb *et al*. 2014). It is evident that management interventions that address these issues are essential for effective conservation on agricultural land. Such interventions are therefore likely to play a key role in arresting species decline (Perrings *et al*. 2006, Pereira *et al*. 2010).

Given the importance of agricultural modification in Australia and many other parts of the world, environmental niche models that incorporate agricultural disturbance factors known to affect certain species should improve prediction of suitable habitat for those species. Nevertheless, disturbance variables are not always included in environmental niche models, partly because they are more difficult to incorporate into the modelling framework than bioclimatic variables (Guisan and Zimmermann 2000, Lippitt *et al*. 2008). The increasing availability of fine-scale land cover data derived from remote sensing offers the potential to improve existing models (Ferrier *et al*. 2002) and land cover or remotely sensed data have been successfully incorporated into environmental niche models using both coarse-grained data (Raxworthy *et al*. 2003, Pearson *et al*. 2004, Luoto *et al*. 2006, Heikkinen *et al*. 2007) and fine-grained data (Engler *et al*. 2004, Van Manen *et al*. 2005, Guisan *et al*. 2006, Marage *et al*. 2007, Le Lay *et al*. 2010, Gogol-Prokurat 2011, Messick and Hoagland 2013, Wilson *et al*. 2013).

Here, we test the prediction that incorporating fine-grain, remotely sensed vegetation-type data that is indicative of agricultural modification improves the performance of an environmental niche model for a disturbance-sensitive lizard, *Aprasia parapulchella*. We used MaxEnt models to test for the influence of agricultural modification on models predicting suitable habitat for this vulnerable species at a spatial scale of approximately 50 km $\times$ 50 km and grain size of 25 m. We find that incorporating agricultural disturbance into the model reduces the likelihood of errors of commission. Our findings and the methods we use could be applied to test the relative importance of agricultural vegetation modification versus other environmental factors for other threatened species in landscapes dominated by agricultural land-use.

Methods

To examine the effect of agricultural modification on the modelling, we took the following steps:

(1) Created MaxEnt models with and without the agricultural modification variable.
(2) Determined the differences between the models using a test area.
(3) Determined the differences in the models with respect to vegetation classes that were predicted as suitable.
(4) Assessed differences between areas predicted suitable in each of the models with reference to habitat mapped in the field.

Study area

This study was conducted in south-eastern Australia in the Australian Capital Territory (ACT) and New South Wales (NSW), Australia (centroid: −35.334167, 149.119167 DD) in an area of 52.2 km × 50.95 km which encompasses most of the known location records of *A. parapulchella* in the ACT and surrounding region (Figure 1). We built the environmental niche model for this entire 2660 km^2 study area (2088 rows × 2038 columns × 25m grid cells), and then designated two smaller sub-areas within it to further test the model. Sub-area 1 (Figure 1) is approximately 6 km × 7 km and exhibits varying levels of historical agricultural modification. This sub-area was chosen for testing as there was a good level of prior knowledge about habitat and occurrence over much of the site (Barrer 1992, Osborne and Wong 2010, Wong and Osborne, unpublished data) and because it represents a relatively large area of land with varying degrees of agricultural modification. Land in Sub-area 1 within the Molonglo River Corridor had undergone lower levels of modification through agricultural activities such as grazing and the addition of fertiliser when compared with the adjacent agricultural leases which comprised the remainder of Sub-area 1. Sub-area 2 (Figure 1), approximately 1.5 km to the southeast of Sub-area 1, was used to provide a second location where the model could be tested in an area where very detailed on-ground survey had been conducted for the lizards (Osborne and Wong 2010). This sub-area was chosen because of the detailed level of knowledge of the area and its occupancy by *A. parapulchella*.

Study species

The pink-tailed worm-lizard *(Aprasia parapulchella)* (Pygopodidae) Kluge 1974 is a threatened legless-lizard found in temperate south-eastern Australia. Most of the known records of occurrence of the species are in the ACT and adjacent areas of NSW with scattered disjunct occurrences in other locations in NSW and Victoria (see Wong *et al*. 2011 for a review of the life history and ecology of this species). *A. parapulchella* is a habitat specialist relying on native grass cover, lightly embedded rocks and a relatively small number of small ant species on which it preys (Osborne *et al*. 1991, Jones 1999).

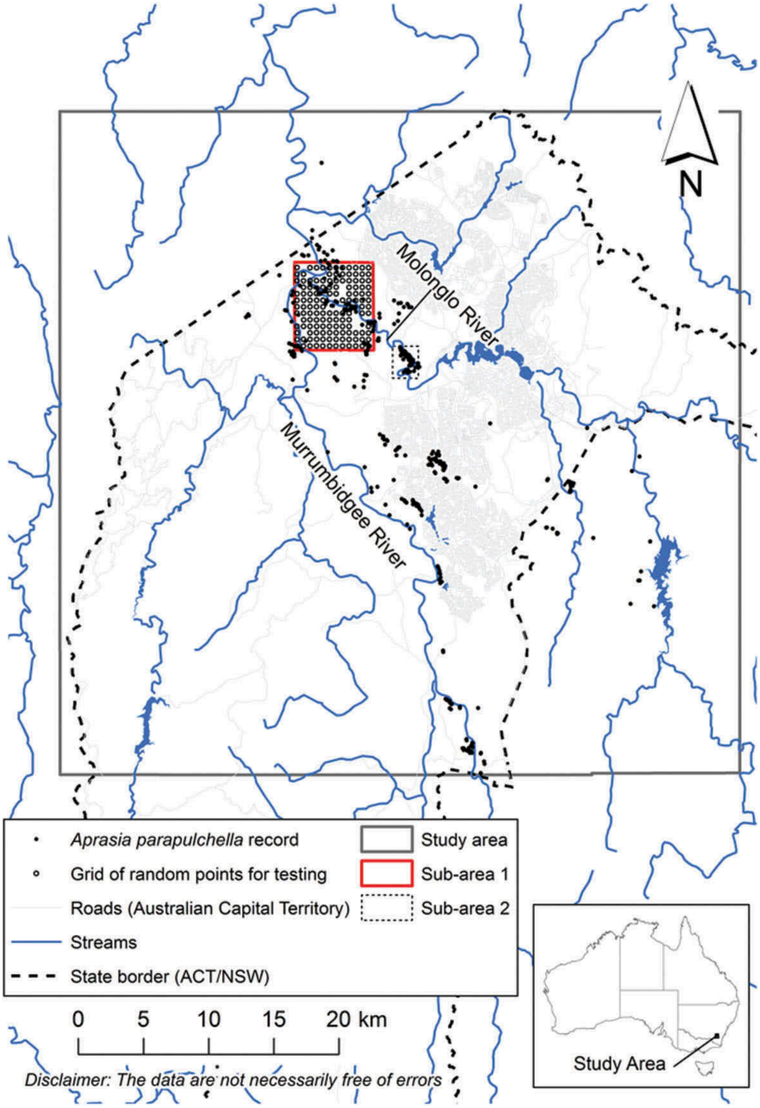

Figure 1. Map showing location of the study area and occurrence records used in MaxEnt modelling. The sub-area where the models were separately tested including the grid of points used for testing (Sub-area 1) is shown as is the second sub-area where habitat had been mapped in the field and extensively surveyed (Sub-area 2).

Previous studies (Osborne *et al*. 1991, Jones 1992, 1999, Osborne and McKergow 1993) have identified a number of habitat and environmental variables associated with the occurrence of the species. The species appears to prefer Silurian-age volcanic geology and the sandy-loam soils derived from this parent material (Osborne *et al*. 1991, Osborne and McKergow 1993, Wong *et al*. 2011), gentle to steep slopes (although it is most commonly on moderate slopes) and sites experiencing higher levels of solar radiation (Osborne *et al*. 1991, Jones 1992). In the ACT, *A. parapulchella* has been mostly linked to sites that include a relatively low cover of over-storey vegetation as well as native grasses (particularly *Themeda triandra*) (Osborne *et al*. 1991, Osborne and McKergow 1993, Jones 1999, Wong 2013), and is likely to be more abundant at sites that contain large-tussock forming species (Wong 2013). Such grasses decline with disturbance by agricultural practices that include fertiliser addition and overgrazing (Stuwe and Parsons 1977, Groves *et al*. 2003, McIntyre and Tongway 2005). Conversely, *A. parapulchella* is absent from rocky areas that exhibit exclusively exotic grass species as a result of grazing, fertiliser addition or the combination of these practices (Osborne and McKergow 1993, Jones 1999).

Data layer selection

Environmental layers and presence data for *A. parapulchella* were obtained from the ACT Government (Environmental Planning and Sustainable Development Directorate, Conservation Research). These data included ACT wildlife atlas records collected between 1990 and 1997 (107 records) which had mostly been digitised from grid references or maps from previous surveys (Barrer 1992, Jones 1992, 1999, Osborne and McKergow 1993) and which were supplemented by 308 records collected using GPS during extensive surveys conducted within the study area (Osborne and Coghlan 2004, Osborne and Wong 2010, Wong and Osborne 2010). To minimise sampling bias, we performed spatial filtering (Kramer-Schadt *et al*. 2013) by removing any records that were closer than 30 m from another record and excluding records that coincided with areas that had been masked out of the agricultural modification layer. This left 336 occurrence records for the modelling. We also included climate variables for rainfall and temperature in our model because, while the study area is small, there are significant changes in elevation (~400 m ASL–1850 m ASL), which affect local climate (Adomeit *et al*. 1987). We included mean October minimum temperature and mean monthly rainfall as variables because *A. parapulchella* is thought to disperse and breed in spring (Jones 1999). Minimum temperature was selected over maximum temperature because low temperatures are generally more limiting to Australian reptiles than high temperatures (Heatwole and Taylor 1987). The cell size for all environmental layers was 25 m.

Our initial set of environmental layers included topographical layers derived from a 25-m digital elevation model (DEM) of the ACT region and climatic layers for mean monthly maximum and minimum temperature and mean monthly rainfall calculated using ESOCLIM (Houlder *et al*. 2000, Xu and Hutchinson 2011), based on climate data between 1976 and 2005 and a 25-m DEM (see Xu and Hutchinson 2011 for a map of weather stations and for further details). Environmental layers were selected based on their ecological relevance for the species (Austin 2002). Variables that were very highly correlated ($r > 0.75$) (Figure S1) were removed.

As *A. parapulchella* is unlikely to be found in areas that have undergone very high levels of agricultural modification (Osborne and McKergow 1993, Jones 1999) or where grazing and fertiliser addition have increased the presence of exotic winter growing plants in place of native summer growing grasses (Stuwe and Parsons 1977, Groves *et al*. 2003), we used a vegetation classification provided by the New South Wales Office of Environment and Heritage (Environmental Research and Information Consortium 2001) as an agricultural modification variable. This classification uses the differences in spectral reflectance between remotely sensed images in spring and summer to discriminate between areas dominated by C4 (primarily summer growing native) and C3 (primarily winter growing exotic or degraded native) areas and was based on the methods developed by Langston (1996). The classification had been verified in the field (Environmental Research and Information Consortium 2001). We reclassified the original non-ordinal classification of 23 classes into four classes: native grassy areas (likely to be C4 dominated); woodland; exotic or degraded native grassy areas; and unknown (not extensively ground-truthed). It should be noted that all the areas that we visited that had been classified as unknown largely consisted of exotic or degraded native vegetation; so we consider that vegetation in this 'unknown' class to be largely exotic or degraded native vegetation. Some areas of the extent (forested areas of >30% tree cover, and urban area) had been masked out when the original classification was produced. However, we do not consider this to be a major limitation in the ACT because *A. parapulchella* appears to largely avoid forested areas in this region (Wong *et al*. 2011).

We included surficial geology, soil type and slope in the model as all have been described previously as being associated with the occurrence of *A. parapulchella* (Osborne *et al*. 1991, Jones 1999). The geology and soils layers (provided by the ACT Government) were derived from regional vector geology and soils maps and were converted to non-ordinal 25-m grid format. The geology layer was derived from a 1:100,000 scale map series (Richardson and Barron 1977, Owen and Wyborn 1979a, 1979b, Abell 1992). The soils layer was derived from a combination of a regional soils map and unpublished internal soils maps derived from surveys carried out by the ACT Government (G. Hirth pers. comm., Environment Planning and Sustainable Development Directorate, ACT Government, 2017 and M. Dunford, Geoscience Australia, 2017). Exploratory analyses revealed that solar radiation had a negligible influence on the model and so this variable was not included for reasons of parsimony.

Modelling

We used the MaxEnt package (Version 3.3.3e) (Phillips *et al*. 2004) to model the distribution of *A. parapulchella* because our data consisted of presence-only records and included categorical variables, both of which can be accommodated by the MaxEnt approach. A total of 10 replicate model runs were generated using 168 randomly selected records subsampled for training, with the remaining 168 records used for testing for each replicate. We used surficial geology, soil type, slope, minimum temperature in October, rainfall in October and agricultural modification as our environmental predictors. Of these, the surficial geology, soil type and agricultural modification variables were non-ordinal categorical variables and the remainder were continuous. We included all feature types in the modelling (linear, quadratic, product threshold and hinge). Regularisation values were: linear/quadratic/product: 0.050, categorical: 0.250, threshold: 1.000, hinge: 0.500. The logistic output was used, but treated as an index of habitat suitability rather than an actual probability of occurrence (Merow *et al*. 2013). For all other parameters we used the default settings. As we preselected a small number of predictor variables, we did not consider it necessary to increase the regularisation multiplier.

Field mapping

Detailed mapping of suitable habitat for *A. parapulchella* was available from previous surveys. In particular, Sub-area 2 (Figure 1) had been mapped and all rocky areas surveyed for lizards (Wong and Osborne 2010, Wong and Osborne, unpublished data) and therefore provided an area of detailed knowledge about potential habitat that could be used to compare model outputs. Parts of Sub-area 1 were mapped with some areas surveyed for lizards (Barrer 1992, Osborne and Wong 2010).

Where detailed mapping had been undertaken (Osborne and Wong 2010), areas of rocky habitat were digitised in a GIS using a fine resolution (10 cm resolution) orthophotograph layer provided by the Environment Planning and Sustainable Development Directorate, ACT Government. Digitised habitat patches were then field checked and classified into three categories: high, moderate or low quality potential habitat. We considered potential habitat to be high quality if it contained suitable rocky habitat and vegetation dominated by native large tussock species (e.g. *Aristida ramosa, Cymbopogon refractus, Dianella* spp., *Lomandra* spp., *Poa sieberiana, Sorghum leiocladum* or *Themeda triandra*) (McIntyre and Tongway 2005) or with a diverse range of disturbance-sensitive species (Rehwinkel 2007) both of which are characteristic of low levels of disturbance; moderate quality if it contained suitable rocky habitat but was dominated by more disturbance-tolerant C3 native grasses such as *Rytidosperma* spp. and *Austrostipa* spp. and contained little or no occurrence of disturbance-sensitive forb species; and low quality if it contained suitable rock but had very little or no evidence of native grass species (usually as a result of extreme levels of agricultural or forestry-related disturbance).

Testing the effect of agricultural modification

To test the contribution of agricultural modification data to the model, ten additional model replicates were run as described above with the agricultural modification layer omitted. From this point forward, the models are referred to as Model.ag (agricultural modification included) and Model.no.ag (agricultural modification omitted). We also ran ten null model replicates (Model.null) for testing, which used the same settings and inputs as Model.ag, but used 344 points (172 training; 172 testing) randomly generated in ArcGIS rather than records of occurrence.

We compared the area under the receiver operating curve (AUC) (Hanley and NcNeil 1982, Pearce and Ferrier 2000) and gain (Phillips 2017) values calculated by MaxEnt for Model.ag and Model.no.ag using two-sample Student's *t*-tests and compared values for Model.ag and Model.null using a Welch's unequal variances two-sample *t*-test. We also interpreted the variable contribution and jackknife analysis. The gain is a measure of the improvement in penalised average log likelihood compared to a null model (Elith *et al*. 2011). Higher values of AUC and gain indicate better model performance. The jackknife analysis creates models with all variables, but which exclude each variable in turn, as well as models of each variable in isolation in order to test their contribution to the models (Phillips 2017).

Within Sub-area 1, we compared the mean logistic value of Model.ag and Model.no.ag corresponding with known occurrence records of the species (74 records), using a two-sample Student's *t*-test. We then compared the mean logistic value of Model.ag and Model.no.ag corresponding with a regular grid of points within Sub-area 1 that excluded known occurrence locations and sites with known potential suitable habitat. As not all the habitat in the sub-area was mapped, the resulting regular grid represented a random sample of 133 points biased towards habitat that was likely to be unsuitable rather than habitat that was actually unsuitable. If the Model.ag performed better, we expected it to predict higher suitability at known occurrence sites and lower suitability at the points biased towards likely unsuitable habitat than Model.no.ag.

We then produced binary suitability models for Model.ag and Model.no.ag using the threshold suggested by MaxEnt that maximised specificity (equal training sensitivity and specificity) and a threshold of 0.5 (determined as providing a good approximation for the most suitable mapped habitat in Sub-area 2 when a range of thresholds were tested) to determine the cut-off for suitability, and generated confusion matrices for Sub-area 1 (Fielding and Bell 2002). MaxEnt suggests a range of possible thresholds that can be used. The most stringent of the thresholds suggested by MaxEnt was chosen because comparisons with mapped habitat suggested there was over-prediction associated with the thresholds suggested by MaxEnt and the 'equal training sensitivity and specificity' threshold was the one that minimised over-prediction. The threshold of 0.5 was used as it provided a better match of mapped suitable habitat within Sub-area 2 than those suggested by MaxEnt. These comparisons were achieved by examining predicted suitability of Model.ag at a range of thresholds (i.e. 0.35, 0.40, 0.45, 0.50, 0.55, 0.60 and 0.65). Between 0.35 and 0.5 changes to the output were substantial but beyond 0.5, changes to the output were negligible, so 0.5 was chosen as the threshold to represent the most suitable habitat. It should be noted that the species can still occur in less suitable habitat, but the threshold of 0.5 appeared to provide a good estimate for the best quality habitat in Sub-area 2. From the confusion matrices, we calculated the overall performance (correct classification rate), omission rate (proportion of known presences predicted as absent) and commission index (proportion of points from the regular grid biased towards likely absence predicted as presences) (Fielding and Bell 2002, Anderson *et al*. 2003).

To examine how Model.ag and Model.no.ag differed according to vegetation type across the ACT, we calculated the area of habitat predicted to be suitable by each model (using the equal training sensitivity and specificity threshold) within each of the four vegetation classes derived from the remotely sensed vegetation classification. Specifically, we multiplied the binary suitability layer for Model.ag and Model.no.ag by the vegetation classification layer using the Raster Calculator in ArcGIS to determine the distribution of vegetation classes corresponding with suitable habitat for Model.ag and Model.no.ag. We then subtracted one of the resulting layers from the other to determine where the models differed spatially and generated a difference plot of the two models.

To estimate how much of the habitat most suitable for *A. parapulchella* has declined through conversion to agriculture, we compared the outputs of the Model.ag and Model.no.ag using a threshold of 0.5 (as determined by comparison to known habitat). We used ArcGIS to map grid squares where the predictions of Model.ag and Model.no.ag differed and calculated the percentage of pixels in each of the four vegetation classes that were predicted to be suitable by Model.no.ag, but were predicted not suitable by Model.ag. If these pixels now characterised by exotic or degraded native vegetation were in fact suitable habitat before agricultural modification, then their area provides an estimate of the percentage of suitable habitat that has been lost. This estimate also depends on the assumption that current presence of introduced C3 vegetation is not correlated with some other important environmental predictor of lizard habitat suitability that was not included in the model. This issue is addressed further in the discussion.

Finally, we compared binary predictions of habitat suitability from Model.ag and Model.no.ag (calculated using both thresholds) with mapped habitat from previous surveys to assess how well each of the models predicted known habitat.

Results

All AUC and gain values were significantly higher ($p < 0.01$) for Model.ag (Mean training AUC: 0.935; Mean SD: 0.007; Mean regularised training gain: 1.453) compared with Model.no.ag (Mean training AUC: 0.928; Mean SD: 0.007; Mean regularised training gain: 1.361) indicating that Model.ag performed significantly better than Model.no.ag (Table 1). Model.ag had AUC and gain values much higher than Model.null (Mean training AUC: 0.621; Mean SD: 0.022; Mean regularised training gain: 0.050) with extremely high significance values ($p < 0.01$) (Table S1).

The estimates of variable contribution (Table 2) indicate that soil type (30.9%) had the greatest influence on the model followed by slope (19.8%), surficial geology (17.8%), average minimum temperature in October (16%) and rainfall in October (15.5%). The contribution of agricultural modification to the model was 7.8% when included. MaxEnt response curves for the variables are shown in Figure S2. The jackknife analysis (Figure S3) indicated that surficial geology contributed most to the gain in isolation from the other variables; however, omission of the soil variable led to the greatest decrease in gain, suggesting that the soils variable accounted for the highest amount of variation not explained by other variables. The jackknife analysis and the estimates of variable contribution showed some differences but both analyses showed that the most influential variables were geology, soils, slope and temperature, with rainfall having less influence and agricultural modification showing the least influence. The jackknife analysis and analysis of variable contribution can be affected by inter-correlation between predictor variables, so these results should be interpreted with caution, but shed light on broader patterns of variable contribution.

The mean logistic values of Model.ag and Model.no.ag at presence locations in Sub-area 1 were not significantly different. Conversely, the mean logistic value, at locations on the regular grid of points which were biased towards likely unsuitable habitat, was

Table 1. Area under the receiver operating curve (AUC) and gain values for MaxEnt models for *Aprasia parapulchella* in the Australian Capital Territory with (Model.ag) and without (Model.no.ag) the inclusion of an agricultural modification layer as well as two-sample *t*-test results comparing differences between the mean values.

	Mean value Model.ag	Mean value Model.no.ag	Two-sample *t*- test value
Regularised training gain	1.453	1.361	4.22**
Unregularised training gain	1.718	1.624	3.37**
Unregularised test gain	1.558	1.468	3.33**
Training AUC	0.935	0.928	3.03**
Test AUC	0.922	0.915	2.97**
AUC Standard deviation	0.007	0.0072	1.00 (ns)

** $p < 0.01$; ns: not significant.

Table 2. Estimates of relative contribution of variables in environmental niche models for *Aprasia parapulchella* with (Model.ag) and without (Model.no.ag) the inclusion of an agricultural modification variable. MaxEnt obtains the estimate by adding or subtracting (if the *lambda* value is negative) the absolute value of increase or decrease in regularised training gain to the contribution of the variable in each iteration of the training algorithm.

	Percentage contribution (Model.ag)	Percentage contribution (Model.no.ag)
Soils	30.9	28.9
Slope	19.8	17.3
Geology	17.8	17
Average minimum temp. (October)	16	15.3
Average rainfall (October)	15.5	13.7
Agricultural modification	7.8	N/A

significantly lower for Model.ag when compared with Model.no.ag (t = 2.32; p = 0.021), indicating a much lower likelihood of false positives associated with Model.ag (Table 3).

Examination of the confusion matrices for Model.ag and Model.no.ag using the equal sensitivity and specificity threshold and the threshold of 0.5 (Table 4) indicated that, whilst the omission rate was slightly lower for models without agricultural modification, the commission index was markedly higher. As a result, correct classification rates were higher for models with agricultural modification. When a threshold of 0.5 was applied to the model the omission rate increased, but the commission index decreased, particularly for Model.ag, leading to an increased correct classification rate. For the threshold of 0.5, the total area predicted by the model with agricultural modification was 71.7% of that predicted by the model without agricultural modification (Table 4).

When we applied the equal sensitivity and specificity threshold, Model.ag predicted a larger proportion of habitat corresponding with areas classed as native in the remotely sensed classification across the study area compared with Model.no.ag. Conversely, Model.no.ag predicted a higher proportion of habitat corresponding to areas classed as exotic or degraded native in the remotely sensed classification than did Model.ag (Figure 2). Where the models differed, Model.ag predicted pixels not predicted by Model.no.ag largely in the native class, while Model.no.ag predicted pixels not predicted by Model.ag largely in the exotic/degraded native class but also to some extent in the woodland and unknown classes (Figure 3).

When we analysed differences between Model.ag and Model.no.ag (using a threshold of 0.5) in Sub-area 1, we found that areas classed as exotic/degraded native vegetation and predicted as suitable by Model.ag, but not predicted as suitable by Model.no.ag,

Table 3. Results of the two-sample *t*-test comparing mean logistic suitability value for models with (Model.ag) and without (Model.no.ag) agricultural modification included using: (a) records from an area of approximately 6 km × 7 km area (Sub-area 1) which contained a range of levels of agricultural disturbance and (b) a regular grid of points from the same area biased towards locations that are likely to be unsuitable. Higher values indicate a higher likelihood that the area is predicted by the model as suitable.

	Mean logistic suitability value (Model.ag)	Mean logistic suitability value (Model.no.ag)	df	t -Value	p-Value
(a) Records	0.602	0.610	146	0.317	0.752 (ns)
(b) Regular grid biased towards likely unsuitable locations	0.324	0.383	264	2.317	0.021*

* $p < 0.05$.

Table 4. Model evaluation figures derived from confusion matrices for MaxEnt models with (Model.ag) and without (Model.no.ag) the agricultural modification variable included in Sub-area 1. The performance of the models was assessed based on 74 presence points and a regular grid of 133 points that was biased towards habitat likely to be unsuitable by excluding random points that coincided with mapped habitat in the study area. Values are given for models using the threshold for presence suggested by MaxEnt that maximised model specificity (equal training sensitivity and specificity) as well as for a threshold of 0.5 that predicted optimal habitat in an area of known mapped habitat (Sub-area 2) when used with Model.ag.

	Equal training sensitivity and specificity threshold		Threshold of 0.5	
	Model.ag (threshold: 0.341)	Model.no.ag (threshold: 0.32)	Model.ag	Model.no.ag
Overall performance (Correct classification rate)	0.70	0.61	0.75	0.71
Omission error (false negative rate)	0.04	0.08	0.26	0.23
Commission index (false positive rate)	0.45	0.56	0.24	0.32
Proportion of pixels predicted present	0.51	0.59	0.28	0.39
Area predicted present (ha) (Total area = 4076.5 ha)	2065.9	2394.7	1146.7	1598.8

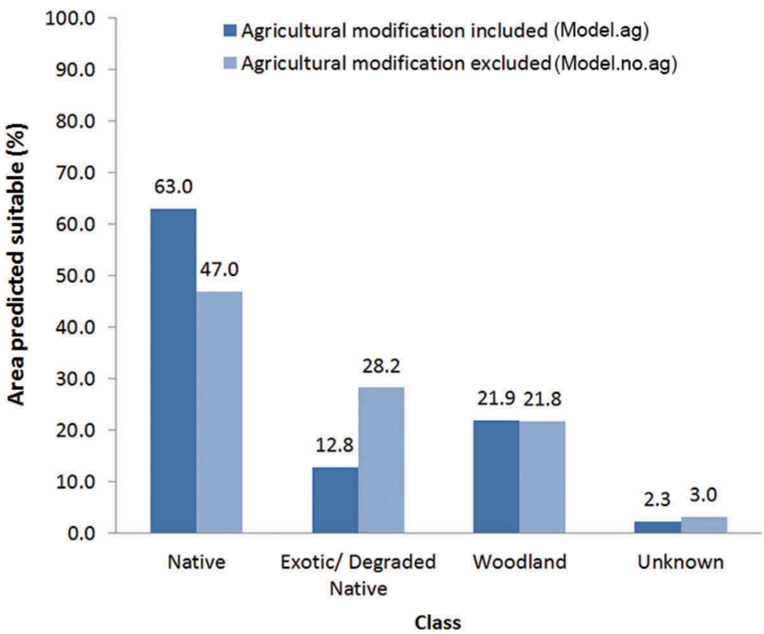

Figure 2. The percentage of the total area in each remotely sensed vegetation class derived from the remotely sensed classification predicted to be suitable by the two MaxEnt models Model.ag and Model.no.ag using the equal sensitivity and specificity threshold.

accounted for 31.5% of Sub-area 1. This figure increased to 35.2% when both the exotic/degraded native and unknown classes were considered together. When the calculation was applied across the whole modelling extent, the corresponding values were 21% (exotic) and 22.3% (exotic + unknown).

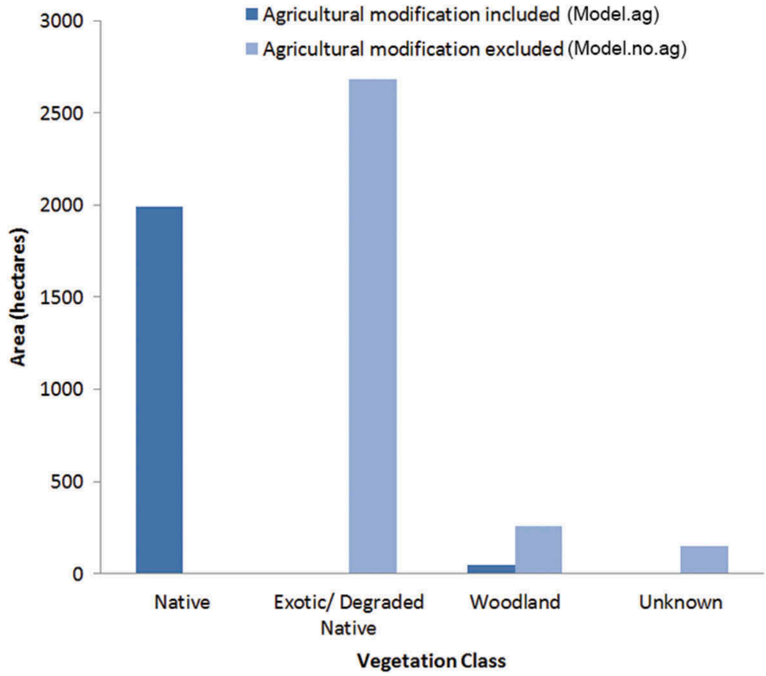

Figure 3. Difference plot showing total area within each of the remotely sensed vegetation classes predicted by one model but not the other. To generate the difference plot predicted suitability was determined based on the equal sensitivity and specificity threshold and each binary layer multiplied by the vegetation class layer using the Raster Calculator tool in GIS. The resulting layers were then subtracted to determine areas of difference so that areas in common between the models would have a zero value and unique areas would retain their vegetation class value.

By visually comparing the outputs of Model.ag and Model.no.ag to mapped habitat in Sub-area 2 (Figure 4), it was clear that the model with agricultural modification better characterised the actual extent of suitable habitat. The presence threshold suggested by MaxEnt led to models which over-predicted suitable habitat in Sub-area 2, whether agricultural modification was included or not. Using a threshold of 0.5 resulted in predictions that closely matched the higher quality habitat areas for Model.ag. By contrast, the changes to Model.no.ag were slight when a threshold of 0.5 was used (Figure 4).

Discussion

We demonstrate that including agricultural modification as a variable markedly improved the environmental niche model for the threatened, habitat specialist, the pink-tailed worm-lizard *(A. parapulchella),* particularly in areas that have undergone agricultural disturbance. This finding strengthens the argument that agricultural modification such as intensive grazing and pasture improvement are likely to promote contraction or loss of *A. parapulchella* across its range (Langston 1996, Jones 1999). It is possible that C3 vegetation may in some places be correlated with some unmeasured variable important to *A. parapulchella*, such as seasonal water abundance (Murphy and Bowman 2007) or rockiness. However, the effect of such variables is likely to be localised

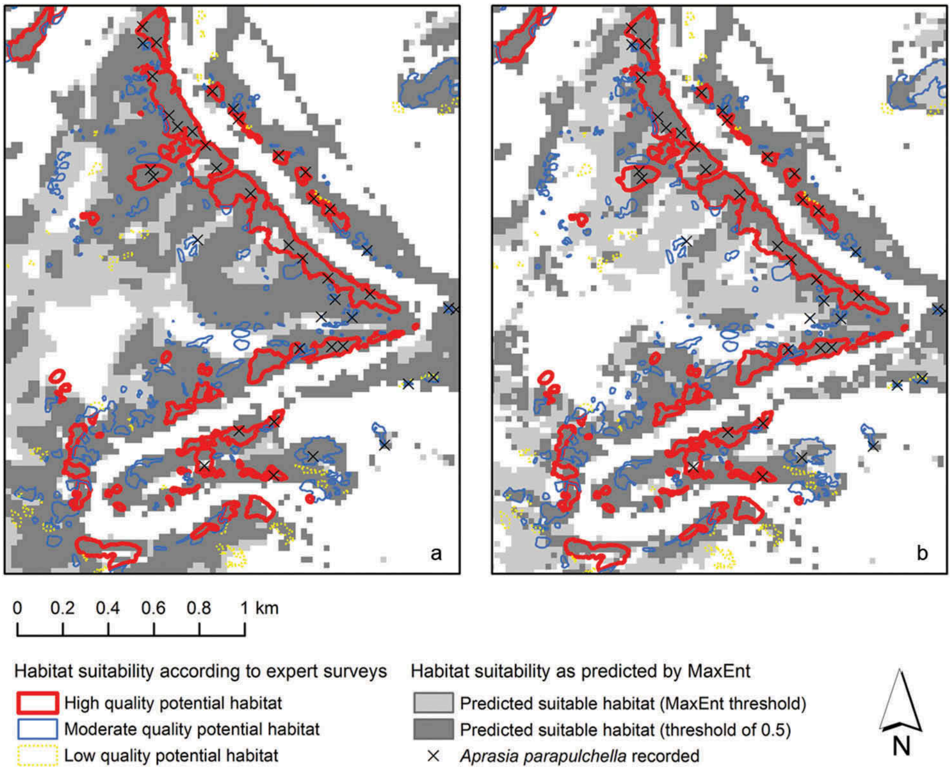

Figure 4. Comparison of thresholded MaxEnt model without (a) and with (b) the agricultural modification variable included within Sub-area 2 (see Figure 1), a location where potential habitat for *A. parapulchella* had been mapped in the field using expert knowledge of habitat requirements (see Field Mapping section in Methods for an explanation of how habitat was classified). The models were converted to presence/absence predictions by using the threshold selected by MaxEnt that maximised specificity (depicted in light grey) and a threshold of 0.5 (depicted in dark grey). White areas indicate areas not predicted as suitable by either of the models or had been masked out of one of the input layers (e.g. river).

compared with the extensive conversion of C4 grasses such as *Themeda triandra* to C3 species as a result of agricultural practices (Stuwe and Parsons 1977, Groves *et al*. 2003, McIntyre and Tongway 2005). The negative effect of this change in grassland community on the presence and abundance of *A. parapulchella* has been observed in a number of studies (Jones 1992, 1999, Osborne and McKergow 1993, Wong 2013). While the percentage contribution of the agricultural modification variable was lower than the contribution of other variables and the increase in AUC value was not large (Table 1), this is likely to be due to the influence of spatial scale. Variables that act on a broader spatial scale, such as climate, geology and topography, are likely to be the most influential variables over the whole study area, whilst disturbance is important at finer scales (Mackey and Lindenmayer 2001). Therefore, the changes to the model as a result of adding agricultural modification as a factor are likely to be in the form of refinements at the local scale rather than major changes to the model. Nonetheless, the analyses showed that the improvement to model specificity was marked at finer spatial scales (Table 3; Table 4; Figure 4). Such models are therefore likely to be of use to farmers, planners and conservation managers as this is often the scale at which farm or reserve management is planned and implemented.

Comparison of the models

Our finding that including agricultural modification improves model specificity (Table 3; Table 4) is consistent with our knowledge of the ecology of *A. parapulchella* and is likely to also apply to other species sensitive to agricultural disturbance. As agricultural disturbance reduces the amount of suitable habitat, it reduces the geographical range of potentially suitable habitat that can be exploited. Therefore, incorporation of agricultural modification should allow better prediction of the extent of this geographical distribution across landscapes that have been modified for over 100 years. Inspection of the model outputs in conjunction with the results of field mapping of potential habitat for *A. parapulchella* showed that the model with agricultural modification included was much more effective in predicting the actual extent of habitat (as mapped by experts in the field). However, the predicted presence/absence layer based on the threshold suggested by MaxEnt that maximised model specificity still appeared to over-estimate the amount of suitable habitat and the area predicted was almost double the area of the presence/absence model that used a threshold of 0.5 (Table 4). The findings indicate that neglecting to include agricultural modification data can lead to over-prediction of suitable habitat in areas that have undergone high levels of agricultural modification. This could lead to managers believing that unsuitable areas are in fact suitable for the species. Interestingly, MaxEnt is known for performing well with respect to errors of commission or over-prediction of suitable habitat (Elith *et al*. 2006, Swenson 2008) although some over-prediction, particularly at very fine spatial scales, is to be expected. However, the prevalence of a given species may influence prediction in methods (such as MaxEnt) which use the receiver operating curve to optimise thresholds (Manel *et al*. 2001) and prevalence may be difficult to determine.

The results of the modelling suggest that agricultural modification may have led to a decline or loss of at least 30–35% of the most suitable habitat in Sub-area 1 (Table 4). Applying this calculation across the ACT suggests a decline or loss of approximately 20% or more of the most suitable habitat across the ACT as a result of agricultural modification. These estimates incorporate the assumptions that: (1) based on the agreement between known mapped habitat with model predictions (Figure 4), using a suitability threshold of 0.5, Model.no.ag represents suitable areas of optimal habitat for *A. parapulchella*; and (2) that the remotely sensed vegetation classification used to indicate agricultural modification is not correlated with some other important environmental factor not included in the environmental niche model. It should be noted that both models are based on modern-day occurrence records (since 1974) and this is likely to have influenced the model. For example, the species may be completely absent from areas in the environmental space that have experienced long periods of intensive agricultural disturbance. Conversely, not all potentially suitable or predicted habitat is occupied, and if the proportion of degradation is higher in predicted habitat that is not occupied than in areas that are, the estimate may be higher than the actual loss or degradation of habitat. Therefore, the estimates of loss and degradation of habitat may be lower or higher than the actual loss and degradation that has occurred. Whilst this possibility should be considered, the findings of this study suggest there is potential for comparison of models with and without a disturbance variable to identify areas where a given species has declined as a result of disturbance as well as to monitor or document decline or improvement of the habitat of species or communities.

We found that Model.ag predicted a higher area of native grass cover (C4) and a lower area of exotic/degraded native (C3) grass cover as being suitable than did Model.no.ag (Figures 2, 3). Therefore, the predictions of the Model.ag are more consistent with findings that *A. parapulchella* requires areas dominated by native vegetation and cannot persist in areas that have undergone very high levels of agricultural modification, characterised by a cover of almost exclusively exotic grasses (Osborne and McKergow 1993, Jones 1999). Nonetheless, some of the areas classed as exotic may, in fact, be degraded native areas dominated by C3 species of grass (R. Rehwinkel, NSW Office Environment and Heritage, pers. comm.). Such areas may still support *A. parapulchella* (Jones 1999), so this should be considered when interpreting the model and when optimising thresholds against known habitat. It is likely that models including agricultural disturbance will be useful for identifying the highest quality potential habitat for the species as well as fine-scale differences in habitat suitability, thereby identifying the most ecologically intact areas that are critical for the conservation of the species. As the vegetation classification we used may not reflect recent changes in vegetation characteristics, determining the current disturbance status of the vegetation through remote sensing is likely to improve the model. Further refinement of the model may also be possible if spectral data or LiDAR data (Sillero and Gonçalves-Seco 2014) can be used to identify rocky areas as the species is dependent on areas of shallowly embedded rock in the ACT (Wong *et al*. 2011).

The limitations of using thresholds are well recognised and, increasingly, it is recommended that thresholds are not used at all (Merow *et al*. 2013). Still, there may be cases where thresholding is seen as necessary. The results indicate that the threshold used as a cut-off for predicting the presence of the species is important, and thresholds suggested by MaxEnt may over-predict suitable habitat in some situations (Figure 4). One of the possible reasons for this is that many users of modelling software such as MaxEnt are interested in the overall distribution of species, often at broad spatial scales (Pearson and Dawson 2004). Some research also indicates that using AUC to optimise thresholds for predicted occurrence can lead to overestimation of suitable habitat for species which have low prevalence in the landscape (Manel *et al*. 2001). However, the threshold used depends on the purpose. If the goal is to find all areas where a species may occur across the region (e.g. for impact assessment where a precautionary approach is desirable), a conservative threshold would be appropriate. If fine-scale prediction of high quality suitable habitat is the goal, higher thresholds may be favoured (Pearce and Ferrier 2000). In such cases, optimisation of thresholds to minimise commission error may be appropriate. However, for presence-only modelling, this may be a challenge if the rate of occurrence of the species in the landscape is unknown (Anderson *et al*. 2003, Elith *et al*. 2011). Optimisation using mapped habitat, as we have done in this study, is an effective way of addressing this problem.

Conclusion

There are clear implications of this modelling for the longer term conservation of *A. parapulchella*. With increased demands on land for agriculture, land managers may decide to increase the extent of pasture improvement on their properties. Our research shows that such actions are incompatible with the protection of habitat for this vulnerable species. Of concern is the situation in the Australian Capital Territory, which is considered to be the stronghold for *A. parapulchella* and where all land is leased from the government rather than privately owned. Indeed, this may explain, at least in part, its stronghold status (Langston 1996, Jones 1999). Since 1999, permitted lease terms in this jurisdiction have increased substantially to 99 years (previously 20 years or 50 years) (*Australian Capital Territory Planning and Development Act 2017*). This increase in certainty of tenure is likely to result in further pasture improvement. With demand for agricultural land increasing worldwide, many species will face similar threats. Incorporating agricultural disturbance into models that estimate the distribution of such species will therefore be increasingly important if managers wish to accurately predict their occurrence.

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ORCID

David T. Y. Wong http://orcid.org/0000-0003-3538-1854
Stephen D. Sarre http://orcid.org/0000-0002-7158-2517
Bernd Gruber http://orcid.org/0000-0003-0078-8179

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