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Understanding niche shifts: using current and historical data to model the invasive redlegged earth mite, *Halotydeus destructor*

Matthew P. Hill[1]*, Ary A. Hoffmann[1,2], Sarina Macfadyen[3], Paul A. Umina[1,4] and Jane Elith[5]

[1]*Department of Zoology, The University of Melbourne, Parkville, Victoria 3010, Australia,* [2]*Department of Genetics, The University of Melbourne, Parkville, Victoria 3010, Australia,* [3]*CSIRO Ecosystem Sciences, Black Mountain, ACT 2601, Australia,* [4]*cesar, 293 Royal Parade, Parkville, Victoria 3052, Australia,* [5]*Department of Botany, The University of Melbourne, Parkville, Victoria 3010, Australia*

ABSTRACT

Aim Niche conservatism is key to understanding species responses to environmental stress such as climate change or arriving in new geographical space such as biological invasion. *Halotydeus destructor* is an important agricultural pest in Australia and has been the focus of extensive surveys that suggest this species has undergone a niche shift to expand its invasive range inland to hotter and drier environments. We employ modern correlative modelling methods to examine niche conservatism in *H. destructor* and highlight ecological differences between historical and current distributions.

Location Australia and South Africa.

Methods We compile comprehensive distribution data sets for *H. destructor*, representing the native range in South Africa, its invasive range in Australia in the 1960s (40 yr post-introduction) and its current range in Australia. Using MAXENT, we build correlative models and reciprocally project them between South Africa and Australia and investigate range expansion with models constructed for historical and current data sets. We use several recently developed model exploration tools to examine the climate similarity between native and invasive ranges and subsequently examine climatic variables that limit distributions.

Results The invasive niche of *H. destructor* in Australia transgresses the native niche in South Africa, and the species has expanded in Australia beyond what is predicted from the native distribution. Our models support the notion that *H. destructor* has undergone a more recent range shift into hotter and drier inland areas of Australia since establishing a stable distribution in the 1960s.

Main conclusions Our use of historical and current data highlights that invasion is an ongoing dynamic process and demonstrates that once a species has reached an established range, it may still expand at a later stage. We also show that model exploration tools help understand factors influencing the range of invasive species. The models generate hypotheses about adaptive shifts in *H. destructor*.

Keywords

Biological invasions, *Halotydeus destructor*, invasive species, MAXENT, niche conservatism, niche shift, reciprocal distribution modelling.

*Correspondence: Matthew P. Hill, Department of Zoology, The University of Melbourne, Parkville, Victoria 3010, Australia.
E-mail: hillmp@unimelb.edu.au

INTRODUCTION

Invasive species lead to significant losses of biodiversity and are harmful to agricultural production, but may serve as valuable model organisms for investigating mechanisms underlying ecological and evolutionary processes over relatively short time-scales (Sax *et al.*, 2007). Central to the understanding of invasive species is the concept of the niche (Alexander & Edwards, 2010). Through defining the niche in the sense of G. E. Hutchinson as a suite of species–environment relationships within physical (environmental) and geographical (biotope) space (Colwell & Rangel, 2009; Wiens *et al.*, 2009), it is

possible to investigate ecological processes such as biological invasion across large geographic scales. The Hutchinsonian idea of the niche may take the form of the *fundamental* niche – the direct physiological requirements of a species, or the *realized* niche – the proportion of the fundamental niche actually exhibited by the species at a point in time, because of limits set by both biotic and abiotic interactions (Wiens *et al.*, 2009). When this interpretation of the niche is applied to invasive species, it is apparent that climatic similarity of both native and invasive ranges of a species is crucial to invasion success (Ficetola *et al.*, 2007; Thomas, 2010) and that the native range of a species is often able to predict its potential invasive range (Sutherst & Maywald, 2005; Venette & Cohen, 2006).

In an invasive range, a species encounters a geographically isolated set of environments that may or may not allow persistence because of limitations of the fundamental niche that evolved within its native range. An invasive species that occupies geographical regions corresponding to regions of niche space set by the fundamental niche is said to have displayed niche conservatism (Colwell & Rangel, 2009). Conversely, niche shifts describe transgression between species–environment relationships across ranges (e.g. Fitzpatrick *et al.*, 2007; Broennimann *et al.*, 2007), or over time (e.g. Kharouba *et al.*, 2009). Niche conservatism is key to understanding species response to environmental stress such as climate change or arriving in new geographical space as in biological invasion (Wiens *et al.*, 2009). However, it is difficult to test for niche conservatism, as it is impossible to characterize the complete fundamental niche (Kearney *et al.*, 2008; Jiménez-Valverde *et al.*, 2011). To describe niche conservatism, species distribution models (SDM) are commonly employed tools (e.g. Broennimann *et al.*, 2007; Kharouba *et al.*, 2009; Beaumont *et al.*, 2009) that characterize something much closer to the realized niche (Jiménez-Valverde *et al.*, 2011). Therefore, when SDMs are used to measure niche conservatism, they inherently encompass a broad range of factors and include the possibility that 'shifts' are not a result of change in the fundamental niche. Niche shifts may occur if the native range only holds a subset of the full range of the fundamental niche because of interspecific competition (the presence of predators and pathogens) or a geographical barrier, or a limited set of possible environments – the species in its invasive range might simply be expressing other parts of the fundamental niche (Broennimann *et al.*, 2007; Rödder & Lötters, 2009; Alexander & Edwards, 2010; Medley, 2010). Alternatively, the species may have adapted, resulting in a change in a species' response to environmental variables over time (Broennimann *et al.*, 2007; Ficetola *et al.*, 2010). A niche shift may also arise through species dispersal and colonization, driving expansion geographically into new environmental habitats (Alexander & Edwards, 2010). These processes of range expansion may be facilitated by changes in climatic conditions, land use or through evolutionary adaptation.

Species distribution modelling methods such as MAXENT (Phillips *et al.*, 2004, 2006) can model presence-only data within a presence-background modelling framework to pro-duce biologically relevant models for distributions of species in their native range. These can be useful for exploring suitability of habitats in invaded ranges (e.g. Fitzpatrick *et al.*, 2007; Rödder & Lötters, 2009). Reciprocal distribution modelling (RDM; Fitzpatrick *et al.*, 2007) is a method of testing for niche conservatism through constructing SDMs for both native and invasive ranges and reciprocally projecting them onto the alternate range (Fitzpatrick *et al.*, 2007; Medley, 2010). To be effective, a RDM must assume that distributions in both ranges are broad enough to characterize species–environment relationships (Fitzpatrick *et al.*, 2007). This is achieved through comprehensive sampling and establishing that the species has dispersed to all possible environments within the invasive range. Using RDMs, niche shifts have been described for various species such as the fire-ant, *Solenopsis invicta* (Fitzpatrick *et al.*, 2007), spotted knapweed, *Centaurea maculosa* (Broennimann *et al.*, 2007), the Mediterranean house gecko, *Hemidactylus turcicus* (Rödder & Lötters, 2009), and the mosquito, *Aedes albopictus* (Medley, 2010). However, such models need to be applied carefully because they often require extrapolation into unsampled environments (Elith & Leathwick, 2009). Model exploration tools extend RDM methods to encourage scrutiny, reduce uncertainty associated with correlative model projections and allow for predictor variables to be examined spatially across distribution data sets. These tools can demonstrate areas of range shift and important variables associated with niche shifts (Elith *et al.*, 2010).

The redlegged earth mite, *Halotydeus destructor* Tucker (Acari: Penthaleidae), is a polyphagous mite native to the Western Cape of South Africa. *Halotydeus destructor* was first reported in Western Australia in 1917 and was recorded in Victoria by 1921 (Newman, 1923). In Australia, it is unlikely to be limited by host plant availability, as it is commonly associated with a wide range of plants, grain crops and pasture species such as subterranean clover, *Trifolium subterraneum*, and the South African-introduced *Arctotheca calendula* (capeweed) (Ridsdill-Smith, 1997). It is now a major winter-active pest across southern Australia, completing three generations between May and October with an obligate summer diapause (Ridsdill-Smith *et al.*, 2005). The species has also been reported from New Zealand, although it is not presently a significant pest (Ridsdill-Smith, 1997).

An extensive survey of *H. destructor* in Australia was carried out in the 1960s to accurately describe the distribution of this species (Wallace & Mahon, 1971). This survey covered areas far beyond the known distribution of *H. destructor* and included the Northern Territory, northern Western Australia, south-eastern Queensland and inland New South Wales. Given that ample time for full dispersal had elapsed since colonization, and because host plants were widely distributed, the range limits of *H. destructor* established at that time were thought to be dictated by climate and particularly moisture; distribution limits coincided closely with the 205-mm rainfall isohyet (Wallace & Mahon, 1971). However, 30 yr later, further sampling efforts in eastern Australia show that *H. destructor* existed further north and inland than earlier reported (Weeks

& Hoffmann, 1999; Robinson & Hoffmann, 2001). More recently, distribution data from pest outbreaks, control failures and field observations indicate that *H. destructor* occurs in hotter and drier areas, well beyond the long-term average 205-mm rainfall isohyet (Arthur *et al.*, 2011). If the 1960s range of this species represented an equilibrium distribution, these data suggest a recent range expansion, perhaps because of climatic changes (in particular rainfall), changes in agricultural practice and/or an adaptive shift in physiology.

The apparent niche shift and range expansion in *H. destructor* provide an opportunity to investigate niche conservation during invasion through new modelling tools. In this paper, we build robust models for *H. destructor* by combining data on distribution shifts with correlative modelling techniques. These approaches can provide insights into climatic influences driving species range expansions and potential adaptive physiological shifts now and into the future. We present current distribution information for *H. destructor* in Australia and South Africa and then investigate climatic variables associated with any niche shift for *H. destructor* by building RDM methods and expanding on these with recently developed model exploration tools. We identify niche shift for *H. destructor* in Australia by combining historical and current distribution information with long-term averaged climate data sets. Finally, our models are used to form hypotheses and point to future experiments to test them.

METHODS

Species data

Species locality data for *H. destructor* were obtained from a variety of sources. The majority of the distribution information was taken from published literature, extracted as an electronic image and then assigned geographical coordinates in ArcGIS (version 9.2; ESRI 2005, Redlands, California, USA). We used this technique to extract data for a historical data set from sampling conducted in the 1960s (Wallace & Mahon, 1971), which yielded 583 points for Australia. We also constructed a current distribution data set by extracting point data from Robinson & Hoffmann (2001), which included points from Qin (1997) and Weeks & Hoffmann (1999). This provided 271 locality points. To allow for error in this technique, we created a buffer of 25 km around each location assigned to literature records and randomly sampled a new point in each buffer. This was repeated 10 times for both data sets. All models (described below) were run with the originally assigned location and the ten randomly jittered locations. The resulting mapped predictions were compared using ENMtools (version 1.3, Warren *et al.*, 2008) niche overlap analysis (Schoener's D statistics). We then performed a one-tailed t test to determine whether the actual data set was producing models different than those with random error incorporated.

Additional distribution points for *H. destructor* were obtained through surveys undertaken in 2006–2007 across southern Australia. This yielded 174 points from Western

Australia, 19 from South Australia, seven from New South Wales and 24 from Victoria. Samples were collected using a Stihl SH55 blower vacuum (Andreas Stihl AG & Co. KG, Waiblingen, Germany), mostly focussing on vegetation along roadsides. Exact localities were recorded with using a Navman global positioning system (Model iCN 320; MiTAC International Corp., Taipei, Taiwan). Data from pest outbreak surveys were also included (see Arthur *et al.*, 2011). *Halotydeus destructor* specimens were identified from samples provided by agricultural workers following outbreaks or control failures from 2005 to 2007, contributing another 29 points.

The South African distribution of *H. destructor* is reported in Halliday & Paull (2004). Detailed locality data were obtained for 16 localities from specimens held in the Australian National Insect Collection (Canberra, Australian Capital Territory). We added to this an additional 15 records for *H. destructor* in South Africa from Eddie Ueckermann (pers. comm.).

Climate variables

We used two distinct sets of climate variables that are most appropriate for our two questions and to take advantage of access to a finer temporal resolution for a subset of our area of interest (Australia). For the RDM, bioclimatic variables were obtained from Worldclim (http://www.worldclim.org accessed September 2010); (Hijmans *et al.*, 2005) to use as predictor variables. These variables are based on average monthly (1950–2000) temperature and precipitation data and describe means that define trends, seasonal variations of temperature and precipitation (Graham & Hijmans, 2006). Grid cells were at a resolution of 5 arc minutes, *c.* 9.3×9.3 km = 86 km^2 at the equator. A global aridity index from the CGIAR-CSI (Consortium for Spatial Information – Consultative Group for International Agriculture Research) database (Zomer et al., 2007;2008; http://www.cgiar-csi.org accessed December 2010) was also included because we expect aridity to limit *H. destructor*. The aridity index was calculated as the mean annual precipitation divided by the mean annual potential evapotranspiration (multiplied by 10,000, for memory management) and therefore represents precipitation availability over atmospheric water demand.

To investigate range shift in Australia, we built bioclimatic variables with 10×10 km grid cells for the two time periods (historical: 1921–1995 and current: 1975–2010) available in the ANUCLIM program (Version 6.1; The Fenner School of Environment and Society, Australian National University; Mike Hutchinson pers. comm.). Whilst these time frames overlap, no distribution records in our historical data set were collected after 1970, and no distribution records for our current data set were collected before 1995, meaning that the data sets could only fall within one of these time frames. To make an aridity layer for the two time periods of interest in Australia, we followed the methods used by CGIAR-CSI (Zomer et al. 2007;2008). Because of data availability, a rainfall-adjusted radiation instead of a clear-sky measure was used and an estimate of the ratio of actual to possible hours of

sunshine through the effect of clouds on radiation. Our final aridity layers for Australia were highly correlated ($r = 0.97$) with the coarser CGIAR-CSI layer used in the RDM.

MAXENT modelling

There is a range of methods for invasive species modelling [see Venette *et al.* (2010)]. We constructed *H. destructor* distribution models using MAXENT (Version 3.3.3i, AT&T Labs, Florham Park, New Jersey, USA), a method specifically designed for presence-only data and shown to have good predictive performance across various applications (Elith *et al.*, 2010; Kearney *et al.*, 2010; Medley, 2010). MAXENT has been described elsewhere (Phillips *et al.*, 2004, 2006; Elith *et al.*, 2011), so we only mention those settings and considerations important for this application. MAXENT uses information on the conditions in the region of interest as a basis for comparison with conditions at known presence sites. This means that the regions (or 'background') need to be defined. We set the background for the native range to the borders of South Africa, and for the remaining models, the whole continent of Australia was used. The rationale here was to select regions that represented the areas potentially available to the species (i.e. to which it might have dispersed if environments were suitable) that were also within the areas that could be considered surveyed given the methods and data available. All our climatic data were 'unprojected' and hence had varying cell areas. By default, MAXENT samples background points at the level of the grid cell and assumes equal cell area. To account for this, we created our own background sample using the raster package in R (version 2.10.1; R Development Core Team 2009) and methods presented in Elith *et al.* (2011). For the Australian background, we sampled 20,000 points that were weighted to reflect a random sample of area, not grid cells. We similarly sampled 10,000 points across South Africa. As considerable sampling for the species was performed along roadsides, we also tested for collection bias. Given no evidence of collection bias in environmental space (see Appendix S1, Suppoting information), the only bias that we deal with is that resulting from unprojected data.

Because climatic variables are often highly correlated and predictors need to be as proximal as possible, we reduced the initial variable set. We performed Pearson's *r* correlation tests across all pairwise combinations of the 20 predictor layers for Australia and South Africa in R. Variable pairs were considered highly correlated if $r \geq 0.80$, and in such pairs, only the variable that was more relevant to the winter-active life history of *H. destructor* was retained. To further select variables, the jackknife feature in MAXENT was used to assess performance of each variable in terms of AUC (area under the curve of receiver-operator characteristic) gain on both test and training data. The AUC score reflects the probability that a randomly chosen presence site will rank above a randomly chosen background site. An AUC score of 0.5 indicates randomness, whilst a ranking of 1.0 indicates perfect model performance [although with presence-background data, as used in MAXENT,

the achievable maximum is < 1 (Phillips & Dudík, 2008)]. As we are comparing models on a constant set of data, with constant background (i.e. no change in background extent), the use of AUC is reasonable here. Our use of AUC was to assess which variables added least to predictive performance of the model, rather than assess overall model performance. Variables that added little to model performance were omitted from the analyses, and the model was run again. Each iteration was compared to the initial model that employed all 20 variables to ensure that models with fewer variables were not under- or over-predicting distributions. Final models were run with 10-fold cross-validation and the AUC score examined to assess each model's predictive performance across the held-out folds.

The complexity of MAXENT models can be controlled through choice of feature classes and regularization parameters (Elith *et al.*, 2011). For this paper, model names follow a 'training-projection' convention, where S.Africa = South Africa; Aust.hist = historical Australian; and Aust.curr = current Australian. For the S.Africa-S.Africa and Aust.curr-Aust.curr models, we left MAXENT settings as default, apart from turning off threshold features. For the Aust.hist-Aust.hist model, we explored how complexity may influence model output, because we were interested in exploring whether our perception of suitable habitat was influenced by model tuning. We turned off threshold features and increased the regularization multiplier at various increments.

Reciprocal distribution modelling

To explore niche conservatism across ranges, we built S.Africa-Aust.curr and Aust.curr-S.Africa models. We tried various regularization increases for the S.Africa-S.Africa model to subsequently apply to the S.Africa-Aust.curr model, in an attempt to even out variable response curves. The aim here was to relax model fitting as much as possible in the projected range – to try and match model projections with the current distribution in Australia. We calculated two presence/absence thresholds for the projected ranges by calculating the least training presence (LTP; Pearson *et al.*, 2007) and a modified least training presence – E (error that was set at 5%) in the training range (Donalisio & Peterson, 2011). The first of these provides a conservative estimate of habitat suitability, and the second allows for a percentage of localities to be geographical and ecological outliers, which for *H. destructor* are likely to be microclimate refuges. To investigate variable differences between ranges, we used multivariate environmental similarity surfaces (MESS) and the most dissimilar variable (MoD) of these MESS maps [Elith *et al.* (2010), Supporting information)], both within MAXENT. Some studies use principle component analysis (PCA) to elucidate predictor variable contributions across ranges (Broennimann *et al.*, 2007; Beaumont *et al.*, 2009; Medley, 2010), but these are not spatially explicit. The MESS feature allows for a pixel-by-pixel analysis of the relatedness of a given point to a reference set of climate layers, whether spatial or temporal, to give a scale of similarity, including negative values (Elith *et al.*, 2010). Its value is driven

by the variable for which that pixel is most dissimilar from the reference set and reported as its distance (in percentiles) from the core of the distribution of values for that variable. The MoD maps report the variable with the smallest similarity at each point (Elith *et al.*, 2010).

### Range expansion in Australia

To explore the possibility of recent range expansion for *H. destructor* in Australia, we constructed Aust.hist-Aust.curr and Aust.curr-Aust.hist models and then examined differences between them. First, we subtracted the logistic output of the Aust.hist-Aust.hist from the output of the Aust.curr-Aust.curr to identify which regions held more suitable climate space between models. Second, we used ENMtools to quantify niche overlap between Aust.hist and Aust.curr models with Aust.hist-Aust.curr and Aust.curr-Aust.hist projections. For this, mapped outputs from the ten 'replicate' models generated during the 10-fold cross-validation were compared with each of the replicates of whichever other model was of interest, and the pairwise differences across these were examined using a generalized linear model. Finally, to examine how variable importance may have changed for both historical and current models, we applied limiting factor analysis in MAXENT to each model (Elith *et al.*, 2010). At each pixel, the limiting factor is determined as the variable that, when changed to its average value at occupied sites, results in the largest positive model value change (Elith *et al.*, 2010).

RESULTS

Distribution fits

The South African native distribution (Fig. 1a) is within the Western Cape and western Northern Cape Provinces of South Africa. The historical distribution for *H. destructor* in its introduced range in Australia (Fig. 1b) is taken from the comprehensive survey of Wallace & Mahon (1971). The current distribution records for *H. destructor* provide the most comprehensive information in Australia (Fig. 1c); however, there are no recent data for Tasmania. All new data points added in this study fell within the distribution described by Robinson & Hoffmann (2001), showing an inland, northward expansion into New South Wales since the 1960s.

From 20 predictor variables, we ended up with a final suite of five variables (Table 1), with three consistently important across all three models. In our South African model, the aridity index was highly correlated with 'Precipitation of Warmest Quarter' (bio18; $r = 0.827$) and did not add to model performance. Instead, model performance was increased by incorporating 'Temperature Seasonality (Coefficient of Variation)' (bio4). To maintain consistency [and as MAXENT can fit stable models even with highly correlated variables (Elith *et al.*, 2011)], we used both bio4 and aridity for all models. 'Precipitation of Coldest Quarter' (bio19) was the most influential variable in all three models. Figure 2 shows the
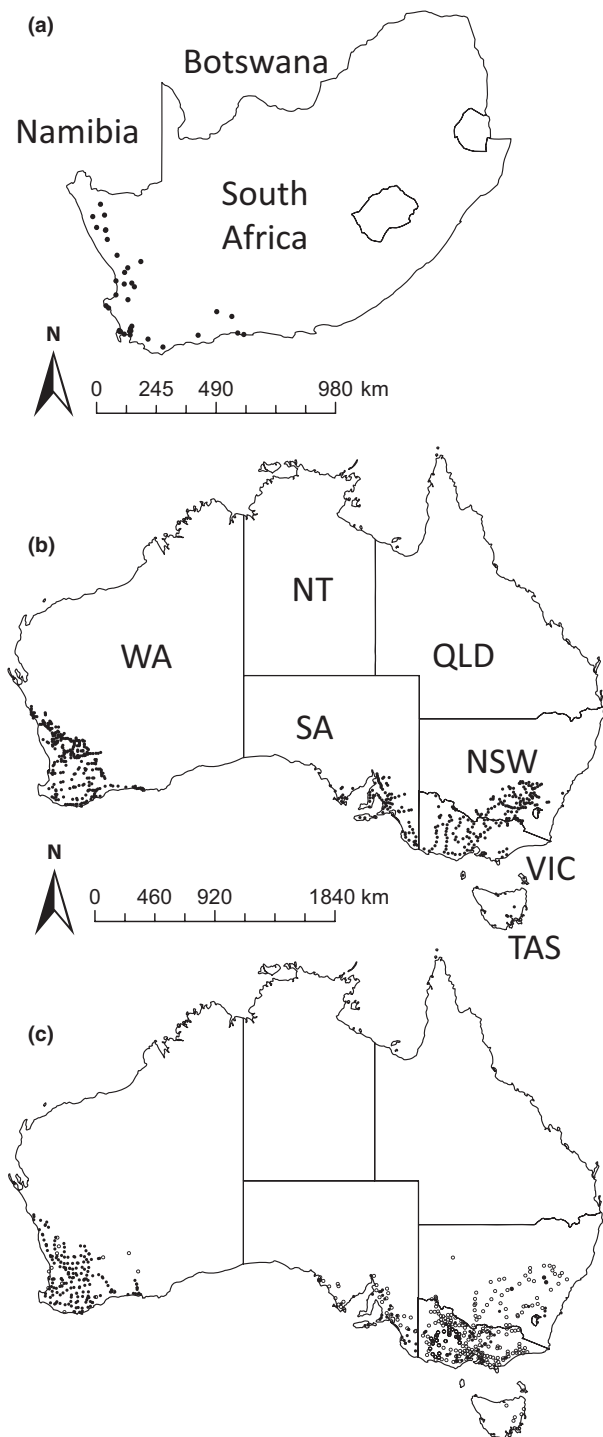
Figure 1 (a) Distribution of *Halotydeus destructor* in South Africa (●), sources are Halliday & Paull (2004) and Eddie Ueckermann, pers. comm. (b) Historical distribution of *H. destructor* from the 1960s, as described in Wallace & Mahon (1971) and denoted as (●). State names: WA, Western Australia; SA, South Australia; NT, Northern Territory; QLD, Queensland; NSW, New South Wales; VIC, Victoria; ACT, Australian Capital Territory; TAS, Tasmania. (c) Current distribution of *Halotydeus destructor* in Australia. Distribution described in Robinson & Hoffmann (2001) (including data from Qin (1997) and Weeks & Hoffmann (1999)) and denoted by (○). Points added in this study are indicated by (●).

Table 1 Percentage contribution of predictor variables to each model. Percentage based on mean area under the curve of receiver-operator characteristic (AUC) test gain across 10 MAXENT cross-validation replicates.

			Variable contribution				
	n	AUC	arid	bio4	bio8	bio18	bio19
S.Africa	31	0.972	0	6.9	11.6	31.1	50.3
Aust.hist	583	0.941	3.9	3.9	45.7	6.2	41.6
Aust.curr	505	0.930	6.4	2.6	60.0	4.0	27.0

Arid, aridity index; bio4, Temperature Seasonality (Coefficient of Variation); bio8, Mean Temperature of Wettest Quarter; bio18, Precipitation of Warmest Quarter; bio19, Precipitation of Coldest Quarter.

response curves for the variables used in our models. As environmental space is multivariate, and these represent the response to one variable with others held constant, interpretation must be made cautiously. Nevertheless, these responses can provide testable ecological insights. The responses indicate that *H. destructor* is associated with winter temperatures (bio8) in the range 7–23 °C (Fig. 2), within areas that are not too dry (as shown by higher aridity index [∼> 20,000 = semi-arid and above) and winter rainfall around ∼100–300 mm (bio19)]. The modest importance of the declining response to 'Precipitation of the Warmest Quarter' (bio 18) reflects the unsuitability of tropical summer wet areas of Australia. Overall, the shape of the response curves is similar between Aust.hist-Aust.hist and Aust.curr.Aust.curr models, although both models have different response curves to the S.Africa-S.Africa model. This reflects both the differing environmental conditions in the two areas and the different relative importance of variables across these ranges/models (Table 1). Comparison of the historical and current responses suggests that *H. destructor* currently occurs in more arid areas than historically. This is reflected in the more gradual current decline in suitability at low values of the aridity index, the weakening of the strong historic decline at higher values of 'Temperature of Wettest Quarter' (bio8) and higher arch of the curve for drier areas (< 200 mm) in the current response for 'Precipitation of Wettest Quarter' (bio19; Fig. 2).

The three cross-validated models for historical, current and South African distributions all performed strongly in terms of high AUC scores (> 0.9) estimated on held-out cross-validation data within the training areas (Table 1). Testing of the extraction method from the literature confirmed model stability in the face of uncertainty. Variations in locations of up to 25 km did not significantly change model predictions (see Appendix S1).

Reciprocal distribution model

For the S.Africa-S.Africa model (Fig. 3a, left side), there is little prediction outside the convex hull surrounding the known distribution points, even when regularization was increased > 1.0. The S.Africa-Aust.curr (Fig. 3a) model considerably under-projects to the invasive range, including eastern Victoria, although over-projects across the Great Australian Bight (the central area along the southern coast of Australia). The S.Africa-Aust.curr projection does encompass the Australian point of invasion, Fremantle, in southwest Western Australia (Swan, 1934). Increasing the regularization of the S.Africa-Aust.curr model to 3.0 relaxed the model in the projected range; however, we were still unable to find congruence with either the historical or current Australian distributions. The Aust.curr-S.Africa model also under-projects suitable climate space in the native range (Fig. 3b), successfully predicting the southern half of the native range, but not its northern half.

Range expansion in Australia

Apart from the highland areas in the Victoria Alps, the Aust.hist-Aust.hist model (Fig. 4a) predicts continuous suitable climate space over south-eastern Australia, including the eastern half of Tasmania. The model also predicts that Western Australia has suitable habitat across the entire south-west corner. The Aust.curr-Aust.curr model (Fig. 4b) is broadly congruent with the Aust.hist-Aust.hist model. The predictions are similar for Western Australia, although slightly broader in the southern parts of the range. In eastern Australia, the distribution extends further inland and northwards, but also more suitable habitat towards the south-eastern corner of Victoria. Subtracting the Aust.hist-Aust.hist from the Aust.-curr-Aust.curr models highlights the areas of range expansion for *H. destructor* in Australia (Fig. 4c). This is mostly into the New South Wales Riverina area and the Victorian Mallee in the eastern half of the range, inland and north of the historical distribution. Increasing the regularization parameter in MAXENT from 1 to > 3 allowed us to smooth out the variable response curves. However, we were unable to 'relax' the Aust.hist-Aust.hist model and push predictions into the range of the Aust.curr-Aust.curr model, suggesting that model complexity is not responsible for under-prediction. The comparison of niche overlap scores within and between models and model projections is shown in Fig. 4d. Within the cross-validated replicates of both models (A and B), there is high overlap as expected (Fig 4d.). The replicates within the models overlap significantly more with each other than they do with models built on the reciprocal time series then projected to comparable data (D and E). The least overlap is between current models (fitted and predicted to current data) with historic models (C). The niche overlap values of the two latter model comparisons (D and E) suggest that based on our climate predictors, there may be some facilitation of range expansion through climate, although it is not enough for reciprocal projections between time series to be congruent.

Model exploration

The MESS map for South Africa (Fig. 5b) shows that the northern part of the native distribution is found in dissimilar
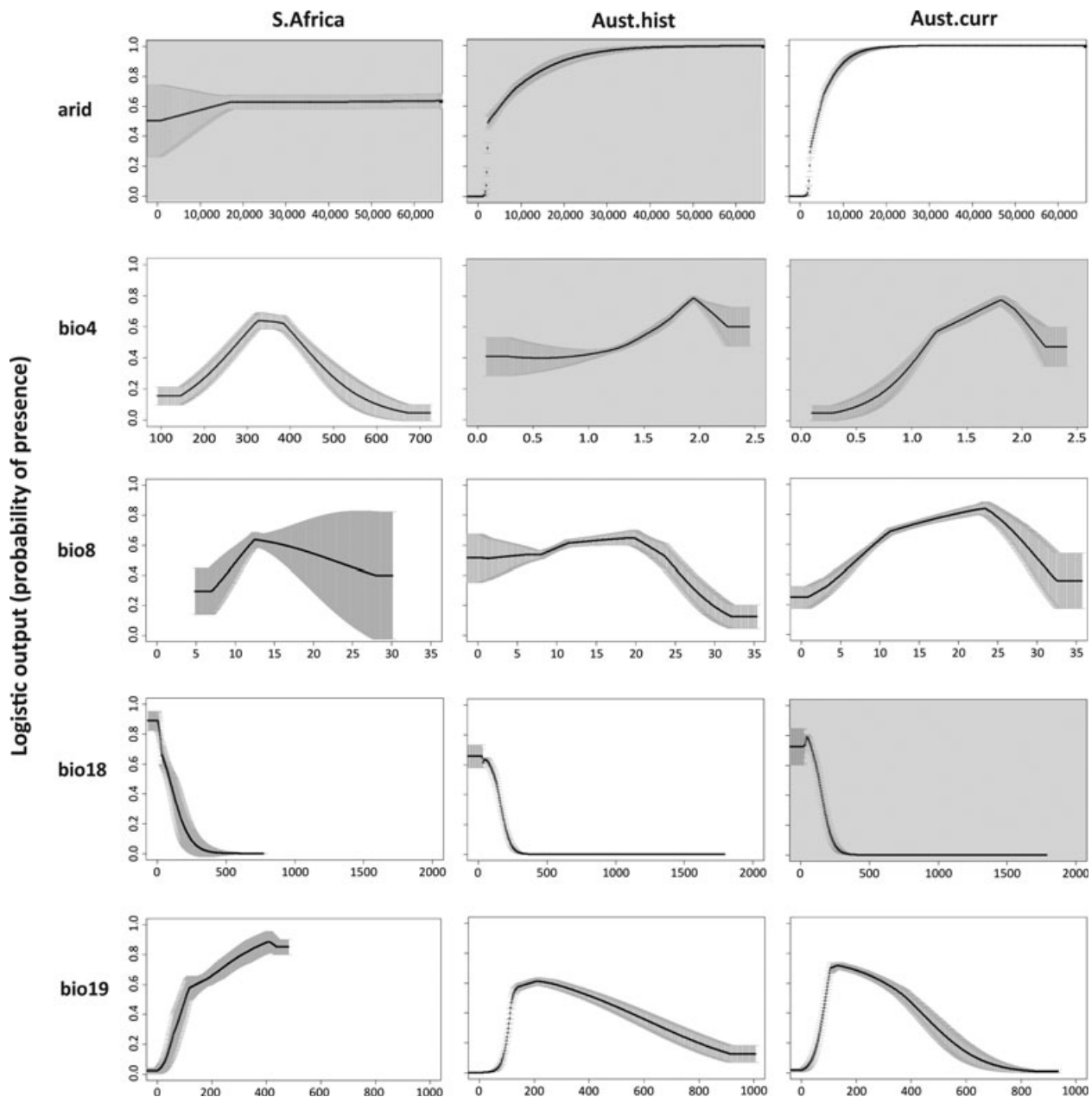
Figure 2 Variable response curves for five predictor variables across three models of *Halotydeus destructor* built in MAXENT. Variables that contributed < 5% predictive power to the respective model are shaded grey. The black line on the graphs is the mean of 10 cross-validation replicates, and the light grey is the standard deviation across these replicates. arid, aridity index (mean annual precipitation divided by the mean annual potential evapotranspiration, multiplied by 10,000); bio4 = Temperature Seasonality (Coefficient of Variation); bio8 = Mean Temperature of Wettest Quarter (°C); bio18 = Precipitation of Warmest Quarter (mm); bio19 = Precipitation of Coldest Quarter (mm). The variable 'bio4' is calculated differently in WORLDCLIM and ANUCLIM data sets so that is plotted on different scales.

climate space than encountered in the Australian background. Likewise, The MESS map for Australia (Fig. 5a) indicates several areas with predictor variables values outside the range encountered across the South African background. These areas identified as dissimilar climate space were not shown to be climatically suitable in the RDMs (Fig 3). The MoD maps (Fig. 5c,d) show variables that are most limiting and driving dissimilarity across the MESS maps. For South Africa, 'Precipitation of the Warmest Quarter' (bio18) is most

dissimilar across the native distribution area. In Australia, 'Precipitation of Coldest Quarter' (bio19) is most dissimilar from the South African background across much of the distribution of *H. destructor*. The limiting factor maps (Fig. 5e,f) suggest – for each grid cell – which variable is limiting the species' distribution for the two data sets and models. The climate space that is largely unsuitable for *H. destructor* in the historical map (Fig. 5e) is limited by the variable 'Precipitation of Coldest Quarter' (bio19). In the

(a)

(b)
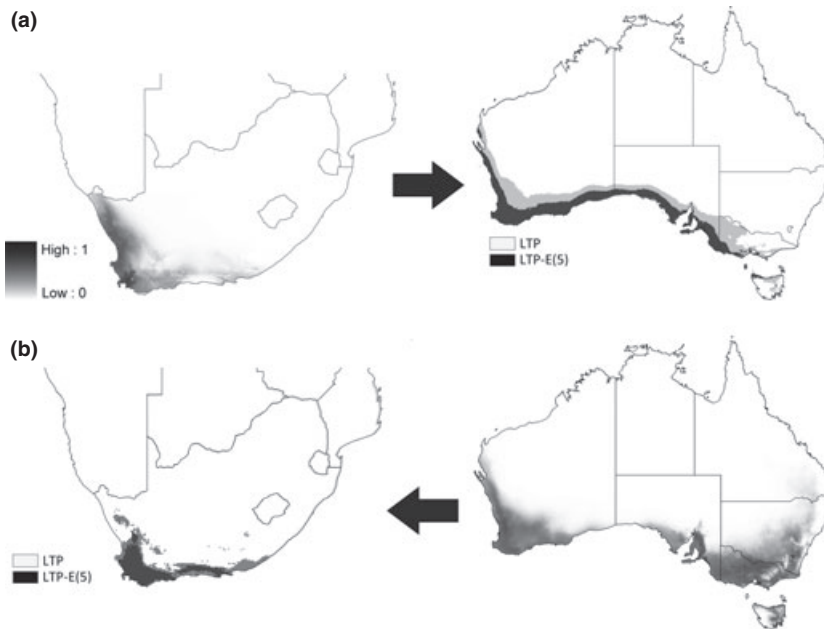
Figure 3 Reciprocal distribution models between South Africa and current Australian distribution built on WORLDCLIM data sets. (a) S.Africa-Aust.curr: South Africa shows the MAXENT logistic output as a continuous suitability (0–1) layer, and darker shading indicates higher climate space suitability. In Australia, the presence thresholds are least training presence (LTP) and least training presence omitting the lower 5% of records [LPT-E (5)]. (b) Aust.curr-S.Africa: Australia shows the MAXENT logistic output as a continuous suitability (0–1) layer, and darker shading indicates higher climate space suitability. In South Africa, the presence thresholds are LTP and least training presence omitting the lower 5% of records [LPT-E (5)].

(a) **(b)**

(c) **(d)**
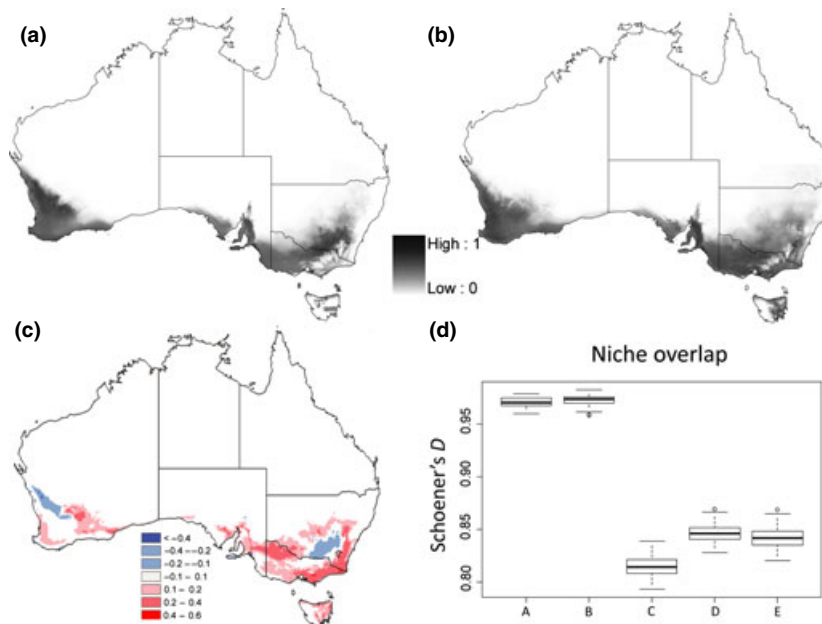
Figure 4 Range expansion in Australia. (a) MAXENT logistic output for *Halotydeus destructor* modelled on Aust.hist data, darker shading indicates more suitable climate space. (b) MAXENT logistic output for *H. destructor* modelled on Aust.curr data, darker shading indicates more suitable climate space. (c) Aust.hist logistic MAXENT output subtracted from Aust.curr MAXENT logistic output. Red areas indicate where more suitable climate space was predicted in the Aust.curr model than Aust.hist. Blue areas indicate where more suitable climate space was predicted in the Aust.hist model than the Aust.curr. (d) Distribution of niche overlap scores (Schoener's *D*) across replicates of the models and model projections; A = Aust.curr-Aust.curr/Aust.curr-Aust.curr; B = Aust.hist-Aust.hist/Aust.hist-Aust.hist; C = Aust.curr-Aust.curr/Aust.hist-Aust.hist; D = Aust.curr-Aust.curr/Aust.hist-Aust.curr; E = Aust.hist-Aust.hist/Aust.curr-Aust.hist. All paired replicate comparisons were significantly different from one another (*P* < 0.001 in all cases), except for the comparison of replicates between A and B (*P* = 0.625).

current map (Fig. 5f), aridity is restricting the northern expanse of the distribution. These results reflect observed changes in the response curves (Fig. 2). For both limiting factor maps, 'Precipitation of the Warmest Quarter' (bio18) is restrictive down the east coast of Australia.

DISCUSSION

Although niche conservatism between ranges is common for invasive species, species distribution modelling (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Medley, 2010) points
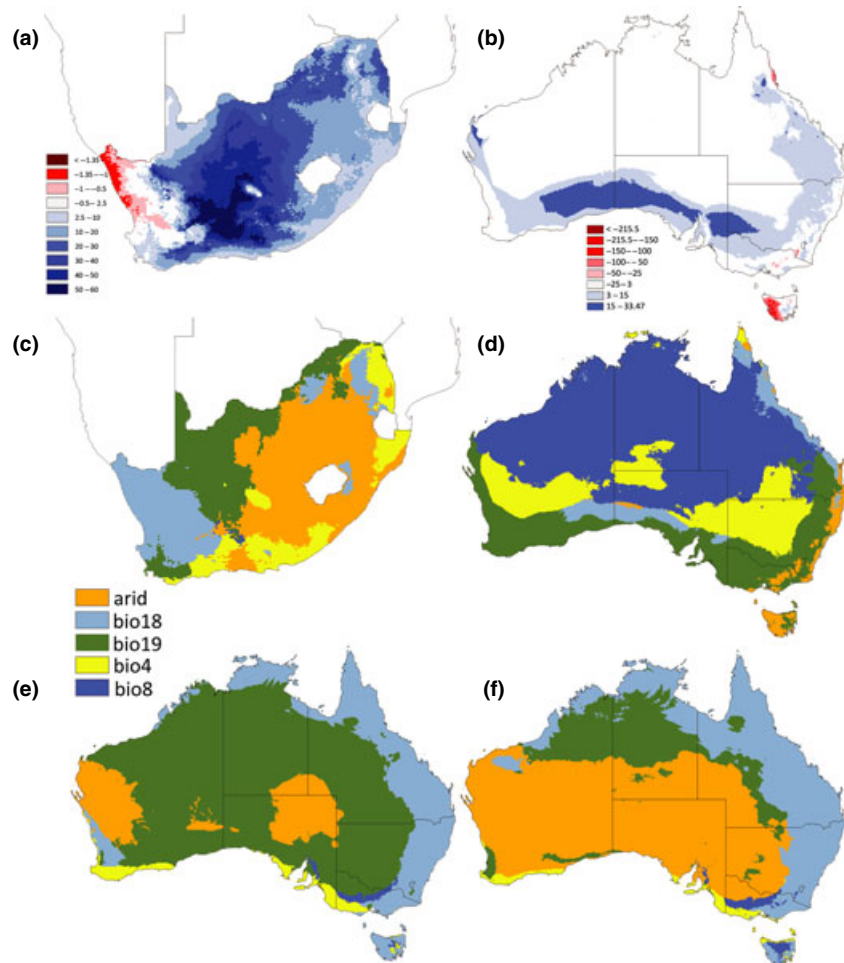
Figure 5 Model exploration maps. (a) Multivariate environmental similarity surfaces (MESS) map for South Africa compared to Australia. Scale on MESS maps shows analogous areas (blue), negative values correlate to novel environments from the calibration layers (red) and areas around zero (white). (b) MESS map for Australia compared to South Africa. (c) Most dissimilar variables (MoD) map for South Africa [from (a)]. MoD maps show which variable influences MESS maps at each given pixel on map. (d) MoD map for Australia [from (b)]. (e) Limiting factor map for Aust.hist MAXENT model. A limiting factor map shows the importance of each of the five predictor variables in terms of model performance (positive or negative relationship) at each pixel. (f) Limiting factor map for Aust.curr MAXENT model.

to several cases where niche shifts may have occurred (Alexander & Edwards, 2010). In the present study, models point to niche shift in *H. destructor*. The species occupies a broader range as an invasive species in Australia than predicted from its native South African range, as well as shifting its niche through range expansion in the last few decades. Whilst the models imply potential shifts in the fundamental niche, a range of factors needs to be considered. Biological constraints such as predation and competition, or other ecological and abiotic factors, may influence the realized niche in the native range (Fitzpatrick *et al.*, 2007; Alexander & Edwards, 2010). Australia lacks significant predators of *H. destructor* (Halliday & Paull, 2004), and competition is restricted to *Penthaleus* mites and perhaps the lucerne flea, *Sminthurus viridus* (Weeks & Hoffmann, 2000; Umina & Hoffmann, 2005). It is unlikely that *H. destructor* is excluded from large areas via competition given that competitive success varies temporally and spatially (Umina & Hoffmann, 2005). Such fine-scale interactions are also unlikely to influence broad-scale spatial patterns (Pearson & Dawson, 2003).

Our Aust.curr-S.Africa model under-predicted the native range in South Africa. Two factors might contribute to this difference. First, molecular work suggests that populations of *H. destructor* in Australia originated from near Cape Town

(Qin, 1997), and our model may reflect the fact that southern populations of South African *H. destructor* near this origin express different physiological limits than northern populations. The Australian populations of *H. destructor* represent one gene pool (Weeks *et al.*, 1995), which may encompass only a subset of the South African gene pool; under-projection may therefore reflect founder effects (e.g. Medley, 2010). Second, under-prediction may be due to an artefact of correlative modelling. Values for the predictor variables in parts of the South African landscape suitable for *H. destructor* population persistence were outside the training (invasive distribution) values encountered in Australia. This, combined with the shapes of the modelled responses, resulted in the Aust.curr-S.Africa model not predicting an area above Cape Town as holding suitable climate space, even though native populations exist there. Whilst analyses such as PCA can determine whether two or more distribution data sets cover similar environments (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007), unencountered ranges of variables may result in reciprocal under-projection. We suspect that this second factor needs to be considered in other studies examining niche conservatism through SDMs.

The inward range expansion of *H. destructor* in Australia since the 1960s may reflect one or more drivers: (1) a change in

farming practices, (2) a shift in climate or (3) adaptation. New farming practices in Australia since the 1960s have resulted in arable agriculture expanding into remote areas, and areas under irrigation have increased in the eastern states. *Halotydeus destructor* is prone to desiccation (Solomon, 1937; Ridsdill-Smith, 1997), so water availability could directly or indirectly (through host plants) buffer against desiccation. Conversely, much of the area in Western Australia beyond the distribution is not used for extensive agriculture and contains few suitable host plants (Wallace & Mahon, 1971; M.P. Hill pers. observ.), which may explain why the expansion had been more limited in this region. Conditions across most of the area where *H. destructor* is found have become warmer (mean annual temperature up to 1 °C) and drier (mean annual rainfall down by 100 mm) between our historical and current data sets (see Appendix S2). However, winter rainfall has increased marginally across the areas where *H. destructor* has expanded (see Appendix S2), which may have facilitated a range expansion by providing higher moisture levels within the microclimate of *H. destructor*. The shift in variable importance between historical and current models suggests that winter rain is less limiting in the inland parts of the current distribution. Finally, *H. destructor* may have responded to climatic variables following evolutionary changes in physiological traits. The increase in the importance of the aridity variable moving from the Aust.hist-Aust.hist to Aust.curr-Aust.curr models could reflect an adaptive shift to allow persistence in hotter and drier conditions. Adaptive genetic change can occur rapidly in invasive populations (Alexander & Edwards, 2010). Australian populations of *H. destructor* have recently evolved resistance to several commonly used pesticides (Umina, 2007). The relative importance of these drivers could be elucidated through experimental tests (Rödder & Lötters, 2009; Medley, 2010). For example, if adaptation is important, populations from inland/drier locations and populations from wetter/cooler areas would be expected to differ physiologically when reared in a common environment.

An issue when describing niche conservatism through SDMs is that during invasion, species are not in a state of equilibrium with their climate and thus correlative methods may not reflect physiological limits (Hartley *et al.*, 2010). Whether species are in equilibrium depends on factors such as time since arrival and human-aided dispersal (Thomas, 2010). *Halotydeus destructor* has been in Australia for almost 100 yr (Ridsdill-Smith, 1997), providing ample time for the species to establish across suitable habitat. Further, *H. destructor* has a relatively short generation time and is able to complete three generations per year (Ridsdill-Smith, 1997). Movement is easily facilitated by wind dispersal and anthropogenic mediation along road-sides, where both *H. destructor* and host plants are often found. This suggests sufficient time and opportunity for the species to occupy all potentially available space in the invasive range.

Sporadic or biased data collection limits the power of inference from models (Fitzpatrick *et al.*, 2007; Hartley *et al.*, 2010) and may give false indication of niche conservatism. *Halotydeus destructor* is a major pest in Australia (Ridsdill-

Smith, 1997; Umina & Hoffmann, 2005) and so has been the focus of extensive sampling across geographical space and environmental gradients. These data provide a range of environmental combinations for testing variables associated with distributions (Phillips *et al.*, 2006; Beaumont *et al.*, 2009). Despite good distribution data, correlative models are unable to encapsulate the fine-scale interactions of an organism with its microclimate (Buckley *et al.*, 2010; Hartley *et al.*, 2010; Kearney *et al.*, 2010), but instead capture a range of ecological processes between the relatedness of distribution and spatial information (Kearney *et al.*, 2010). Mechanistic models that examine limiting physiological processes of a species have been compared with correlative models to identify areas of model congruence and strengthen hypotheses of niche conservatism (Buckley *et al.*, 2010; Kearney *et al.*, 2010). Our models form a comparison for any future mechanistic modelling of *H. destructor*.

Halotydeus destructor has potentially increased in outbreak frequency and prevalence within Australia over the last decade (Hoffmann *et al.*, 2008), making it important to understand factors determining the distribution of this species. Our models of *H. destructor* support the use of correlative models as valuable tools to investigate niche conservatism spatially and temporally, and for understanding niche shifts in biological invasions (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Medley, 2010). It was particularly useful to visualize non-analogue environmental space and identify the model-based limiting factors. Whilst a complete understanding of niche conservatism in invasive species requires combining species distribution modelling, physiological and genetic approaches (Alexander & Edwards, 2010), the results herein identify niche shift in *H. destructor* and provide clear, testable hypotheses as to how range shifts may occur.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Testing data collection bias.

Appendix S2 Differences between climate datasets.

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BIOSKETCH

Matt Hill is a PhD candidate at the University of Melbourne, Australia. His research focusses on building distribution models for pest invertebrate species in Australia. These distribution models are incorporated into a predictive framework and used in concert with experimental data on physiological responses and population genetics to help inform management decisions under future climate change.

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