# Distribution of cryptic blue oat mite species in Australia: current and future climate conditions

**Matthew P. Hill, Ary A. Hoffmann∗, Stuart A. McColl† and Paul A. Umina†**

*Department of Zoology, The University of Melbourne, Parkville, Victoria 3010, Australia, ∗Department of Genetics, The University of Melbourne, Parkville, Victoria 3010, Australia, and †CESAR Consultants, 293 Royal Parade, Parkville, Victoria 3052, Australia*

**Abstract**

1 Invertebrate pests, such as blue oat mites *Penthaleus* spp., cause significant economic damage to agricultural crops in Australia. Climate is a major driver of invertebrate species distributions and climate change is expected to shift pest assemblages and pest prevalence across Australia. At this stage, little is known of how individual species will respond to climate change.

2 We have mapped the current distribution for each of the three pest *Penthaleus* spp. in Australia and built ecological niche models for each species using the correlative modelling software, MAXENT. Predictor variables useful for describing the climate space of each species were determined and the models were projected into a range of future climate change scenarios to assess how climate change may alter species-specific distribution patterns in Australia.

3 The distributions of the three cryptic *Penthaleus* spp. are best described with different sets of climatic variables. Suitable climate space for all species decreases under the climate change scenarios investigated in the present study. The models also indicate that the assemblage of *Penthaleus* spp. is likely to change across Australia, particularly in Western Australia, South Australia and Victoria.

4 These results show the distributions of the three *Penthaleus* spp. are correlated with different climatic variables, and that regional control of mite pests is likely to change in the future. A further understanding of ecological and physiological processes that may influence the distribution and pest status of mites is required.

**Keywords** Blue oat mites, climate change, cryptic species, ecological niche modelling, MAXENT, *Penthaleus* spp., species distribution modelling.

## Introduction

Globally, invertebrate pests cause significant economic losses to agriculture. Blue oat mites *Penthaleus* spp. (Acari: Penthaleidae) are widespread pests of a variety of crops and are found across the circumpolar regions in both hemispheres of the world, including Australia (Umina & Hoffmann, 1999; Umina *et al*., 2004). *Penthaleus* spp. were first reported in Australia in 1921 (Froggat, 1921) and, by 1934, were recognized as an important agricultural pest (Swan, 1934). They feed on pastures and a variety of crops by penetrating the epidermal cells of plants and removing the cellular contents. This can lead to decreases in crop yields and the feed available for livestock (Umina *et al*., 2004). The *Penthaleus* complex currently

consists of three recognized pest species in southern Australia: *Penthaleus major* (Dugés), *Penthaleus falcatus* (Qin & Halliday) and *Penthaleus tectus* (Halliday) (Robinson & Hoffmann, 2001). The latter two were only recently discovered (Weeks *et al*., 1995; Qin & Halliday, 1996a; Weeks & Hoffmann, 1999), with studies before this considering the *Penthaleus* complex as a single species, referred to as *Penthaleus major*. The three species are morphologically cryptic and reproduce via obligate parthenogenesis (Weeks *et al*., 1995; Weeks & Hoffmann, 1999). Despite the morphological similarities, there are clear differences in the biology and ecology of each species. These include differences in host plants (Umina & Hoffmann, 2004), the timing of diapause egg production (Umina & Hoffmann, 2003) and tolerance levels to chemicals (Umina & Hoffmann, 1999; Weeks & Hoffmann, 1999). Such differences are important to consider when developing targeted control strategies (Halliday, 2005).

Correspondence: Matthew P. Hill. Tel.: +61 3 8344 2491; fax: +61 3 8344 2279; e-mail: m.hill2@pgrad.unimelb.edu.au

Although often occurring sympatrically, *Penthaleus* spp. differ in their distributions within Australia (Robinson & Hoffmann, 2001). Wallace and Mahon (1971) first mapped the distribution of *Penthaleus* spp. and concluded that the inland distribution was determined by a 190-mm minimum rainfall isohyet during the active season (May to October). This finding, however, preceded the separation of the three species. The distributions of the species in eastern Australia have subsequently been mapped (Weeks & Hoffmann, 1999; Robinson & Hoffmann, 2001). Both *P. major* and *P. falcatus* were found to occupy approximately the same area, although the former was far more abundant. *Penthaleus tectus* was found only in two disjunct regions; one in north-western Victoria and the other in north-eastern New South Wales. Weeks and Hoffmann (1999) also found that the distribution of *P. major* and *P. falcatus* extends further inland than previously recorded for *Penthaleus* spp. by Wallace and Mahon (1971). Expansion inland may indicate a range expansion, a shift in climate or an adaptive shift in mite physiology. The distribution for *Penthaleus* spp. in Western Australia has not been mapped, although *P. major* has been collected in the State (Qin & Halliday, 1996b).

Climate records for southern agricultural regions of Australia already show rising temperatures and reduced precipitation, and future climate projections suggest warmer and drier conditions (Australian Bureau of Meteorology & CSIRO, 2010). Climate change operating over a global scale greatly influences life-history traits (Jaramillo *et al.*, 2009), pest phenology (Harrington *et al.*, 2007; Parmesan, 2007) and species distributions (i.e. range shifts) (Karban & Strauss, 2004; Hoffmann *et al.*, 2008) through changing temperature and precipitation regimes. Although distributions are ultimately driven by a range of abiotic and biotic factors, climate (particularly temperature) is one of the major drivers shaping distribution patterns in most invertebrate species (Bale *et al.*, 2002). Climate has been shown to broadly influence distributions of *Penthaleus* spp. (Robinson & Hoffmann, 2001), as well as other pest mites within Australia, such as *Aceria tosichella* (Carew *et al.*, 2008), *Balaustium medicagoense* (Arthur *et al.*, 2010) and *Halotydeus destructor* (Robinson & Hoffmann, 2001). Although a full understanding of factors such as physiological mechanisms and land use is required to predict seasonality and fine-scale distributions, predictions of broad climatic patterns that influence species distributions can be made by combining well sampled distributions with long-term averaged climate data (Graham & Hijmans, 2006; Arthur *et al.*, 2010).

Species distribution modelling in the form of ecological niche models allows for distribution patterns to be correlated with broad predictor variables such as climate (Phillips *et al.*, 2004, 2006; Elith *et al.*, 2006). Climate space is closely related to suitable habitat, although fine-scale and biotic interactions will ultimately define local distributions for pest species of agriculture. Such modelling can identify species-specific climate space that can help elucidate ecological processes (Beaumont *et al.*, 2009). Ecological niche models can be projected into future climate change scenarios to examine how climate space may change (Pearson & Dawson, 2003; Thuiller *et al.*, 2004; Elith & Leathwick, 2009; Yates *et al.*, 2010), ultimately identifying areas that will be suitable for

population growth. In terms of management, this process can assist in targeting surveys of pests and in preparing growers for emerging problems. Robinson and Hoffmann (2001) used a process-based model, CLIMEX, to elucidate key responses of *Penthaleus* spp. to climate. This modelling method provided some insight into different climate variables that may be associated with *P. major* and *P. falcatus* (but not for *P. tectus*) though the method was also unable to separate the distribution for *P. falcatus* from the more widespread *P. major*.

In the present study, we provide comprehensive distribution maps for all three pest *Penthaleus* spp. in Australia that extend maps provided by Weeks and Hoffmann (1999) and Robinson and Hoffmann (2001). This information is used to develop correlative models describing suitable climate space, and to identify variables that are correlated with broad distribution patterns. We then project models of mite distributions into future climate space to assess the likely effects of climate change on the broader distribution and pest status of *Penthaleus* spp.

## Materials and methods

### Distribution mapping of Penthaleus *species*

Because of previous confusion over the taxonomy and distribution of *Penthaleus* spp. (Umina *et al.*, 2004), we only considered data from within Australia in the present study. To compile accurate distributions of *Penthaleus* spp. across Australia, we combined historical data with a comprehensive field survey in Western Australia where information was lacking. In July 2006, a total of 202 sites were sampled across the south-western agricultural region of Western Australia, an area considered to cover the distribution of earth mites based on findings by Wallace and Mahon (1971). The exact location of each site was recorded using a Global Positioning System (GPS) (Model iCN 320; Navman, Australia). Collection of samples took place during the active season of the mites from roadside vegetation and adjacent paddocks every 20–50 km. Samples were collected by vacuum using a blower-vac (Model SH 55; Stihl International, Germany) with a fine gauze sieve (200 μm) attached. They were placed directly into 70% ethanol and later sorted to species by observing dorsal setae morphology under × 40 magnification. Mites were obtained from a variety of plant types at each site to maximize the likelihood of collecting all species present.

Additional *Penthaleus* spp. distribution points were obtained from sampling that targeted other pest mite species (Arthur *et al.*, 2010). These samples were collected from 2005 to 2007 and included Victoria, South Australia and New South Wales. A few of these sites yielded *Penthaleus* spp. and, from 901 samples, we obtained 68 points (*P. major* = 57; *P. falcatus* = 4; *P. tectus* = 7). Distribution data were also included from pest outbreak surveys conducted from 2007 to 2009 (Arthur *et al.*, 2010). These were samples received from agricultural industry personnel after mite outbreaks or chemical control failures, and contributed 34 distribution points (*P. major* = 26; *P. falcatus* = 3; *P. tectus* = 5). Participants were asked to include the location of the property where the mites were collected and this was used to determine GPS coordinates

through Google Earth (Google Inc., 2009). All mites were identified under × 40 magnification.

Other distribution data for the three *Penthaleus* spp. was taken from Robinson and Hoffmann (2001), which describes distributions for the *Penthaleus* spp. across eastern Australia by combining survey data and distribution points taken from Weeks and Hoffmann (1999). Maps from Robinson and Hoffmann (2001) were overlayed in ARCMAP, version 9.2 (ESRI, 2005) and point data were plotted to extract GPS coordinates.

### Climate variables

To use as predictor variables, BIOCLIM variables were obtained from WorldClim (http://www.worldclim.org; Hijmans *et al.*, 2005), which offers high-resolution layers of averaged monthly climate data (1950–2000) from globally distributed weather stations. The primary 19 BIOCLIM variables are derived from averaged monthly temperature and precipitation data (Nix & Busby, 1986) and describe means, trends and seasonal variations of temperature and precipitation, which are more likely to represent physiological limits for species (Graham & Hijmans, 2006). These variables have been used widely for climate modelling over different temporal periods and for a range of different species' distributions (Giovanelli *et al.*, 2008; Lozier & Mills, 2009; Murienne *et al.*, 2009; Wang *et al.*, 2010), including pest mites (Arthur *et al.*, 2010). Grid cells were at a resolution of 30 arc seconds, approximately 0.83 km$^2$ at the equator.

### Distribution modelling

MAXENT, version 3.3.2i (Phillips *et al.*, 2004, 2006) was used for modelling the *Penthaleus* spp. distributions. MAXENT is a presence-only based method that correlates known distributions with predictor variables such as environmental variables, and gives model output in terms of habitat suitability. MAXENT has been applied to a variety of ecological modelling applications (Ficetola *et al.*, 2007; Giovanelli *et al.*, 2008; Lozier & Mills, 2009) and has also been used to project models into future climate space (Penman *et al.*, 2010; Yates *et al.*, 2010).

Although some studies use all 19 BIOCLIM variables as a 'complete' dataset (Giovanelli *et al.*, 2008; Evans *et al.*, 2009), we selected a more informative subset (Rödder *et al.*, 2009). Accordingly, each *Penthaleus* species was considered independently. To test for spatial correlation, values of each BIOCLIM layer for each species locality were extracted and Pearson's coefficient tests were performed between each pair of variables using R software (R Development Core Team, 2009). Any pair where $R \geq 0.80$ were considered correlated (Lozier & Mills, 2009). After correlated variables were identified, preliminary models were constructed and the MAXENT jackknife test was used to examine the importance of each variable and its relationship to each species (Ficetola *et al.*, 2007). For pairs of variables that were correlated, the variable that added the least unique information and least to model performance was omitted. The models were run again on the reduced dataset in a stepwise fashion. To ensure that reducing the

number of predictor variables was not compromising model performance, area under the curve (AUC) for the receiver-operator characteristic values were examined for each run of the model (Elith *et al.*, 2006; Ficetola *et al.*, 2007; Lozier & Mills, 2009). The output for each run was examined to ensure that the model was not over-predicting habitat suitability. This process was repeated until the model was built on a subset of the most informative predictor variables, without compromising AUC. An advantage of this method is that a reduced number of predictor variables can help avoid multicollinearity issues (Heikkinen *et al.*, 2006; Ficetola *et al.*, 2007). For each model with a final predictor variable set, MAXENT was run with 25% of the training dataset randomly chosen as a test dataset. Each final run of the model was run with ten-fold cross-validation. The remainder of the MAXENT modelling parameters were left at the default values (Phillips & Dudík, 2008).

### Future climate scenarios

The A1FI (fossil-intensive) Special Reports on Emission Scenarios (SRES) (Solomon *et al.*, 2007) future climate change scenario was used in the present study. The SRES reflect different societal responses and emission rates at the same time as accounting for population growth (Solomon *et al.*, 2007). This particular scenario incorporates a 'fossil intensive' projection of emissions incorporated with alternative directions of technological change. BIOCLIM variables were constructed for an ensemble of 23 general circulation models from the Intergovernmental Panel on Climate Change fourth Assessment Report, for three time periods, 2030, 2050 and 2070 (Solomon *et al.*, 2007). These were built on a national 9 s DIGITAL ELEVATION MODEL, version 3 (GeoScience, Australia) aggregated to 36 s (approximately 1 km), and the change grids and downscaling methods supplied in ANUCLIM, version 6.1 (Fenner School of Environment and Society, Australian National University). An ensemble of multiple general circulation models filters out individual model bias and allows for greater confidence to be placed on outcomes for future projections (Beaumont *et al.*, 2008). We set a presence/absence threshold at 10% of habitat suitability values from the original models for each species.

## Results

### Current distributions of Penthaleus *spp. in Australia*

We now have 537 distribution points (236 from the present study; 301 from the literature) for *P. major* (Fig. 1a); 170 distribution points (16 from the present study; 154 from the literature) for *P. falcatus* (Fig. 1b); and 66 distribution points (12 from the present study; 54 from the literature) for *P. tectus* (Fig. 1c). The distribution of *P. major* is widespread across the southern regions of Australia, with the species prominent in Western Australia, South Australia, Victoria, New South Wales and Tasmania (Fig. 1a). New distribution points from the present study fell within the expected range of previous work. *Penthaleus major* was the most common species collected and is the only *Penthaleus* species previously confirmed in

**Figure 1** Current distributions of *Penthaleus* spp. within Australia. Closed circles indicate points new from the present study; open circles indicate distribution points reported in Weeks and Hoffmann (1999) and Robinson and Hoffmann (2001). (a) Distribution for *Penthaleus major*, *n* = 537. (b) Distribution for *Penthaleus falcatus* *n* = 170. (c) Distribution for *Penthaleus tectus*, *n* = 66. Inset shows the names of Australian States and the major regions where grain crops are grown (source: Australian Collaborative Land Use Mapping Programme. Available at: http://adl.brs.gov.au/mapserv/landuse/). NSW, New South Wales; Vic, Victoria; Tas, Tasmania.

Western Australia (Robinson & Hoffmann, 2001). In Western Australia, the distribution of *P. major* extended as far as Northampton, approximately 50 km north of Geraldton, and as far inland as Southern Cross, approximately 370 km east of Perth. *Penthaleus major* was found at 153 out of 202 sites sampled in Western Australia.

For the first time, *P. falcatus* and *P. tectus* were reported from Western Australia. *Penthaleus falcatus* was found at seven sites across the sampled area in Western Australia (Fig. 1b), three sites in Victoria and a single site in New South Wales. *Penthaleus falcatus* was generally collected from the weed *Hypochaeris glabra* and some grasses that occurred infrequently in paddocks and roadside vegetation. As found previously in eastern Australia, the distribution of *P. falcatus* does not extend as far north as *P. major* in Western Australia. *Penthaleus tectus* was found at seven sites in a restricted area in the south-east of Western Australia (Fig. 1c). This area is approximately 250 × 150 km, and adds to the two disjunct populations previously found in eastern Australia. *Penthaleus tectus* was collected from wild oats and thick-bladed grasses in pasture paddocks, roadside vegetation and adjacent to cereal crops. As well as being reported for the first time in Western Australia, *P. tectus* was recorded from South Australia for the first time. All of the points added for Victoria and New South Wales from the present study fell within the disjunct distributions described by Robinson and Hoffmann (2001) (Fig. 1c). The new data for *P. tectus* now indicates that the species has disjunct distributions in Western Australia, Victoria and New South Wales, with a single population recorded from South Australia. *Penthaleus tectus* has not been detected in Tasmania.

*Climatic factors influencing species distributions*

Using MAXENT, we were able to determine three climatic variables for each of *P. major*, *P. falcatus* and *P. tectus* that

describe the different distributions within Australia (Table 1). These variables displayed little to no spatial correlation with each other and the combination of variables for each given species was unique. For all three species, distributions were influenced by 'Precipitation of Coldest Quarter (bio19)' and this variable contributed highly to the *P. major* and *P. tectus* models (57.9% and 74.1%, respectively), whereas it only contributed 7% to the *P. falcatus* model. *Penthaleus major* was influenced by 'Mean Temperature of Warmest Quarter (bio10)' and 'Mean Temperature of Coldest Quarter (bio11)'. The distribution of *P. falcatus* was influenced by 'Annual Mean Temperature (bio1)' and 'Precipitation of Driest Quarter (bio17)'. The model for *P. tectus* incorporated 'Temperature Seasonality (STDEV × 100) (bio4)' and 'Precipitation Seasonality (Coefficient of Variation) (bio15)'. The AUC values for the final model for all three species were very close to 1, with 1 indicating optimal model performance (*P. major* = 0.900; *P. falcatus* = 0.919; *P. tectus* = 0.957).

The predicted range for each species is shown in Figs 2–4. The model for *P. major* (Fig. 2) shows that the species has suitable climate space to occupy much of the southern regions of Australia. Known distribution points all fall within the predicted suitable habitat. The model also shows an area in southern Queensland as being moderately suitable, although this area is yet to be surveyed extensively. King Island, north of Tasmania, appears to be highly suitable for *P. major*; this area has not been sampled. In South Australia, there is an area of suitable habitat extending north from Adelaide. The model for *P. falcatus* predicts an expansive range in eastern Australia, extending further inland than *P. major* in New South Wales (Fig. 3). Although not as widespread as *P. major*, highly suitable habitat for *P. falcatus* is also predicted to extend into southern Queensland. This model also predicts suitable climate space in Western Australia, extending further along the southern coastline than known localities. As for *P. major*, South Australia holds suitable climate space for *P. falcatus*, extending north of Adelaide. The eastern half of Tasmania is also shown as having highly suitable climate space for *P. falcatus*. Predicted climate space for *P. tectus* is tightly associated with the known distribution points in Victoria, New South Wales and Western Australia (Fig. 4). Suitable climate space is predicted for southern Queensland, although not as far north or inland as either *P. major* or *P. falcatus*. The model also predicts that a large area of South Australia has suitable climate space, although there is only one record of *P. tectus* in this state. The model does not predict suitable climate space for *P. tectus* in Tasmania.

*Future distributions of species under climate change*

Under climate change projections, the climate space for all *Penthaleus* species tends to decrease over time and become fragmented at the southern borders. For *P. major*, the climate space within inland New South Wales decreases by 2030 and continues for each time period thereafter (Fig. 5a–c). The northern border is predicted to retreat from southern Queensland over time. In Victoria, the climate space for *P. major* remains similar, although it retreats somewhat south in western Victoria. In South Australia, the climate space of *P. major* becomes fragmented over time, becoming disjunct from the Victorian climate space by 2070. In Western Australia, the suitable climate space for *P. major* becomes smaller by retreating towards the south-western corner, separating from the other two species (Fig. 5a–c). The climate space for *P. major* in Tasmania is predicted to remain the same for the time period investigated.

Although remaining further inland than *P. major,* the Victorian–New South Wales climate space for *P. falcatus* is predicted to retreat both southward and towards the eastern coast of Australia (Fig. 5d–f). In South Australia, the *P. falcatus* climate space is significantly reduced to small fragments within a narrow band by 2070. The climate space in Western Australia is also predicted to retreat substantially into two small fragments in the south (Fig. 5d–f). Within Tasmania, the climate space changes very little for *P. falcatus* over the next 60 years.

The future climate space for *P. tectus* is predicted to broadly encompass the present area, although over time become smaller and further fragmented (Fig. 5g–i). This means that in areas such as South Australia and western Victoria, the climate space of *P. tectus* will occupy a different area from that of *P. major* and *P. falcatus*. Similar to the other species, the future climate space of *P. tectus* in New South Wales is expected to retreat southwards and towards the east coast. The position of suitable climate space for *P. tectus* in Western Australia remains similar to the current one, although it diminishes through time under each future climate projection (Fig. 5g–i). In Western Australia, the future climate space for *P. tectus* is further east than for *P. major* and further north of *P. falcatus*, resulting in non-overlapping climate space projections. There is only a very small amount of suitable climate space for *P. tectus* in Tasmania under future projections.

**Table 1** BIOCLIM variables identified and used for climate modelling for each *Penthaleus* species

| | BIOCLIM variable | *Penthaleus major* | *Penthaleus falcatus* | *Penthaleus tectus* |
|---|---|---|---|---|
| bio1 | Annual mean temperature | — | 54.9 | — |
| bio4 | Temperature seasonality | — | — | 12.6 |
| bio10 | Mean temperature of warmest quarter | 31.5 | — | — |
| bio11 | Mean temperature of coldest quarter | 16.9 | — | — |
| bio15 | Precipitation seasonality | — | — | 11.7 |
| bio17 | Precipitation of driest quarter | — | 40.5 | — |
| bio19 | Precipitation of coldest quarter | 51.6 | 4.7 | 75.7 |

Values represent the percentage contribution of each variable to species models after Pearson's and jack-knifing tests.
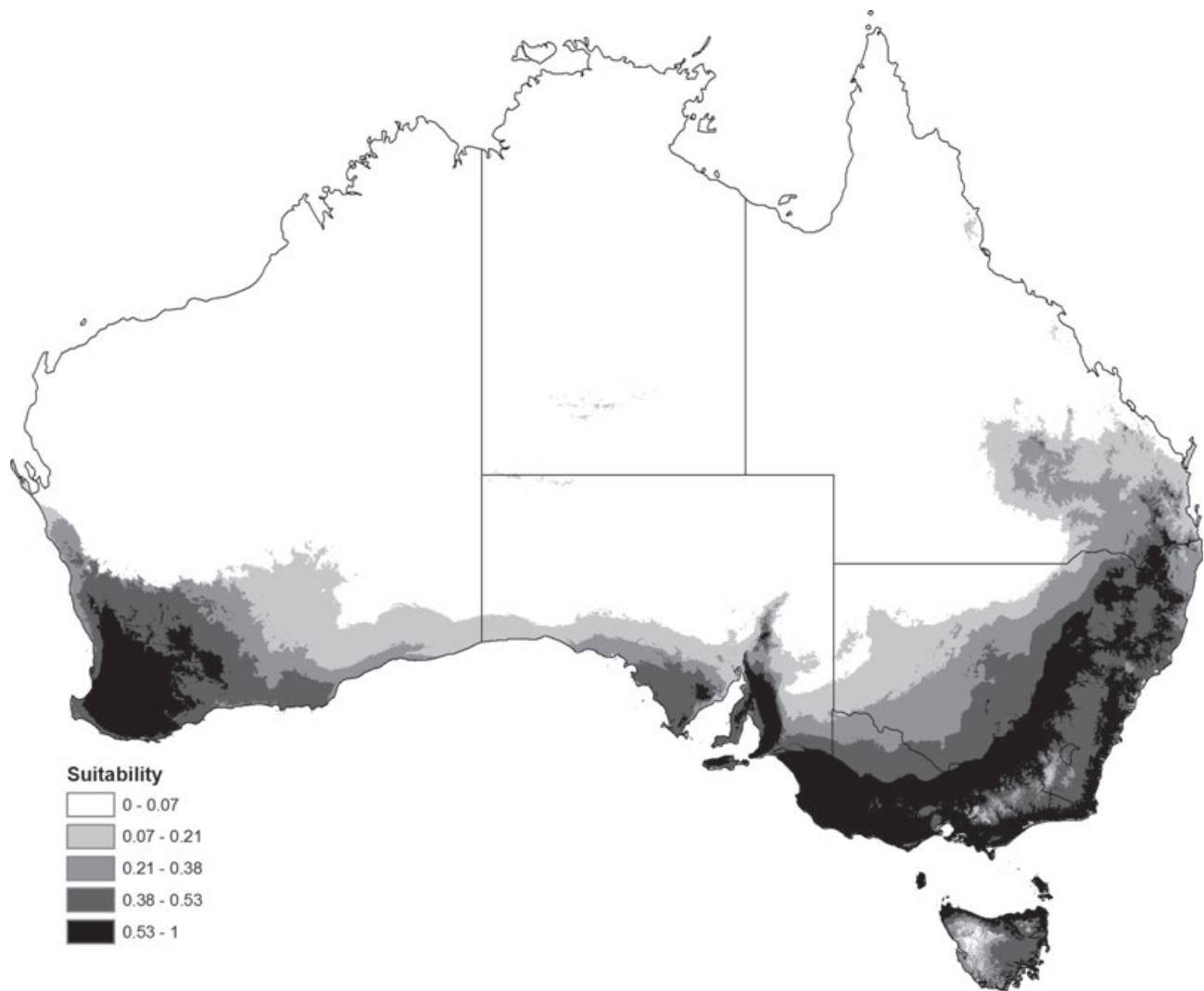
**Figure 2** MAXENT model output of habitat suitability for *Penthaleus major* in Australia. Shading represents suitability of area in terms of climate space. Model built on present climate (1950–2000 averaged) data and three predictor variables (Table 1). Area under the curve value for model = 0.900.

Suitability
- 0 – 0.07
- 0.07 – 0.21
- 0.21 – 0.38
- 0.38 – 0.53
- 0.53 – 1

## Discussion

In the present study, we provide the current and most accurate Australian distributions for the three cryptic *Penthaleus* species, including Western Australian distributions for the first time. Wallace and Mahon (1971) mapped the distribution of *Penthaleus* spp. in Western Australia, although this was before the identification of the three separate species. The distribution of *P. major* mapped in the present study broadly agrees with Wallace and Mahon (1971). However, these findings are in contrast to the situation in eastern Australia, where *P. major* has expanded its range (Robinson & Hoffmann, 2001; Umina *et al.*, 2004). Weeks and Hoffmann (1999) and Robinson and Hoffmann (2001) collected *P. major* further inland than this species had previously been found (c.f. Wallace & Mahon, 1971). This could be a reflection of changing climatic conditions or differing farming practices in eastern Australia, which has created additional suitable habitats for this species.

The present study identified *P. falcatus* and *P. tectus* in Western Australia for the first time. Given the widespread and overlapping distributions of *P. major* and *P. falcatus* in eastern Australia, Umina *et al.* (2004) speculated the latter would exist in Western Australia. Although *P. falcatus* was only collected at seven out of the 202 sites sampled in Western Australia, these sites were relatively widespread across the sampled area. This suggests the low numbers of *P. falcatus* collected in Western Australia may not be a result of unsuitable climatic conditions. Instead, *P. falcatus* may be restricted by some other factor, such as host plant availability. *Penthaleus falcatus* is less polyphagous than both *P. major* and *P. tectus*, being largely restricted to some broad-leaved weed species and brassica crops (Weeks & Hoffmann, 1999; Umina & Hoffmann, 2004). These plants were relatively rare across the sampled area (S. McColl, unpublished data), particularly compared with grasses and cereal crops, which are known hosts of *P. major* and *P. tectus*. The presence of *P. falcatus* in Western Australia is important
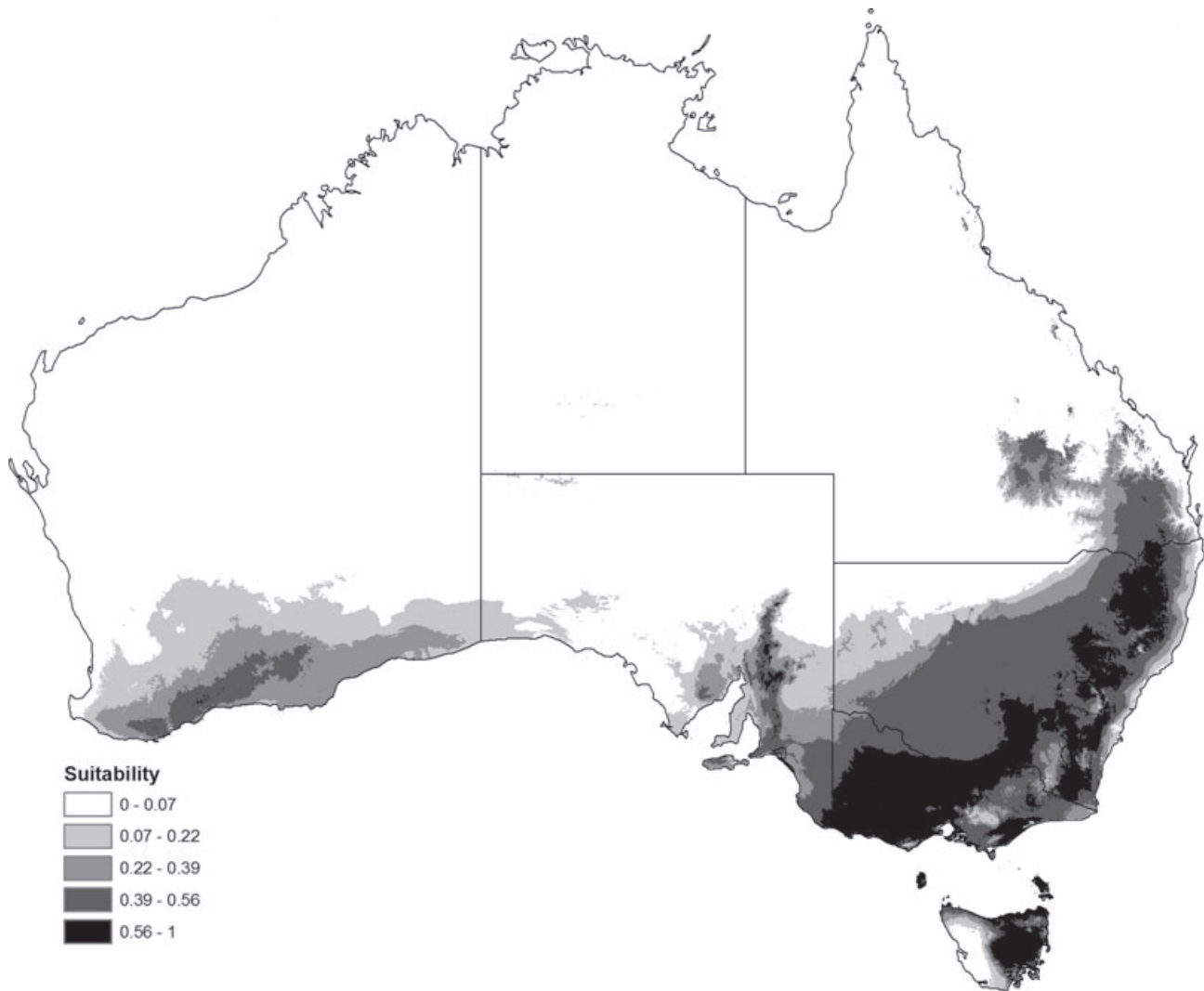
**Figure 3** MAXENT model output of habitat suitability for *Penthaleus falcatus* in Australia. Shading represents suitability of area in terms of climate space. Model built on present climate (1950–2000 averaged) data and three predictor variables (Table 1). Area under the curve value for model = 0.919.

considering the high inherent tolerance of this species to many currently registered pesticides (Umina & Hoffmann, 1999; Robinson & Hoffmann, 2001). In eastern Australia, this high tolerance has been correlated with control failures in the field, where *P. falcatus* have persisted after multiple pesticide applications at up to twice the recommended field rate (Umina & Hoffmann, 1999; Robinson & Hoffmann, 2001). Robinson and Hoffmann (2001) showed that control failures concerning the *Penthaleus* species were disproportionately skewed towards *P. falcatus*, despite this species being relatively rare.

*Penthaleus tectus* is now known from four disjunct regions in separate States in Australia. This species was found at seven sites within a restricted area northeast of Perth in Western Australia and recorded at one locality in South Australia. The MAXENT model highlights an area north of Adelaide that provides further suitable habitat in South Australia, which indicates future field surveys should target this area. The absence of *P. tectus* in Tasmania may reflect a lack of sampling,

although models for the current distribution failed to identify suitable climate space for this species and future projections also predict only a very restricted area of suitable habitat in Tasmania.

The MAXENT models describe separate geographical distributions (or climate space) for the three *Penthaleus* species and link these to different climatic variables, something that was not achieved in an earlier attempt using the semi-mechanistic modelling method, CLIMEX (Robinson & Hoffmann, 2001). Because of a lack of any experimentally determined variables for *Penthaleus* spp., CLIMEX models were unable to discriminate individual species biology and relate these to known distributions, in particular for *P. tectus*. The current and comprehensive distribution for *Penthaleus* spp. enabled us to use MAXENT to accurately determine predictor variables that are associated with known localities for each species, describe suitable climate space and predict how this may change in the future. This is particularly insightful for the morphologically
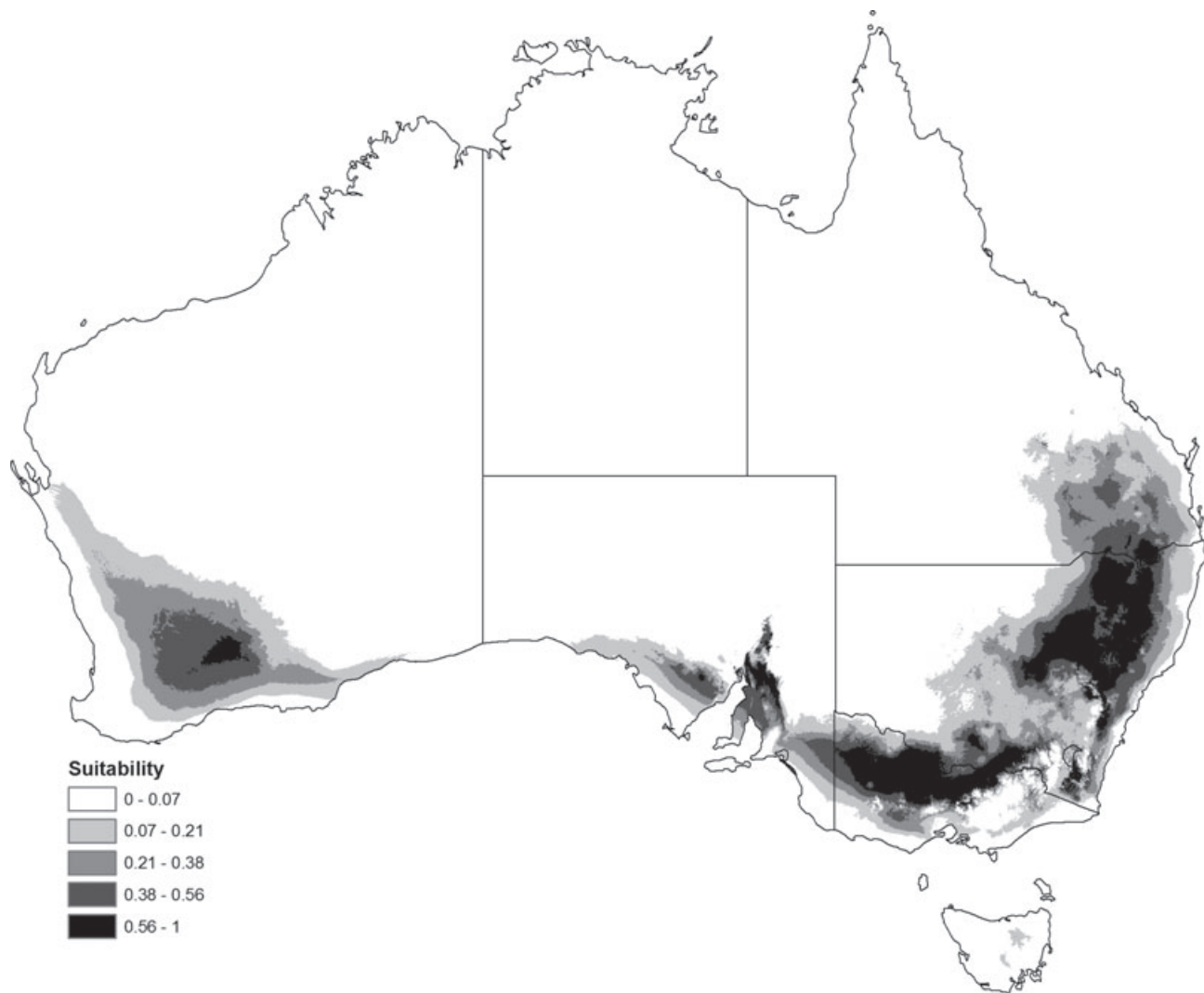
**Figure 4** MAXENT model output of habitat suitability for *Penthaleus tectus* in Australia. Shading represents suitability of area in terms of climate space. Model built on present climate (1950–2000 averaged) data and three predictor variables (Table 1). Area under the curve value for model = 0.957.

cryptic *Penthaleus* species, which, although often occurring sympatrically, show clear differences in climatic responses (Robinson & Hoffmann, 2001).

The prominence of 'Precipitation of Coldest Quarter' in models for both *P. major and P. tectus* and, to a lesser extent, *P. falcatus* is supported by the winter-active biology of the mites and strengthens the relevance of the correlative approach used here. It is interesting that *P. falcatus* was strongly influenced by 'Precipitation of the Driest Quarter' because, during this time, the species is in diapause. This may imply *P. falcatus* has a less-resistant diapause stage than the other species. Because the area where *P. falcatus* is presently found is expected to become drier over the summer period, a less-resistant diapause stage could help explain why climate space for this species decreases markedly in areas such as Western Australia and South Australia under these projections. In addition, the current distributions for *P. falcatus* and *P. tectus* in Western Australia are largely outside the habitat predicted

suitable in our models. This could be a result of differences in physiological responses between populations in eastern and Western Australia. Genetic clonal types of *P. major* have been shown to differ in their relative fitness on both spatial and temporal scales (Weeks & Hoffmann, 1998). Additionally, clones of both *P. major* and *P. falcatus* can differ in their response to pesticides, which may reflect selection on a local and geographic level (Umina & Hoffmann, 1999). Although the clonal types of each *Penthaleus* spp. present in eastern and Western Australia have not been directly compared, any differences that exist could affect the observed distribution of the species as a whole. This is particularly apparent for *P. falcatus* and *P. tectus* because these species appear to be quite rare in Western Australia.

Correlative models assume all distribution points of a species represent populations that are in equilibrium with climate (Heikkinen *et al.*, 2006). By sampling widely across environmental gradients where a species occurs, correlative models
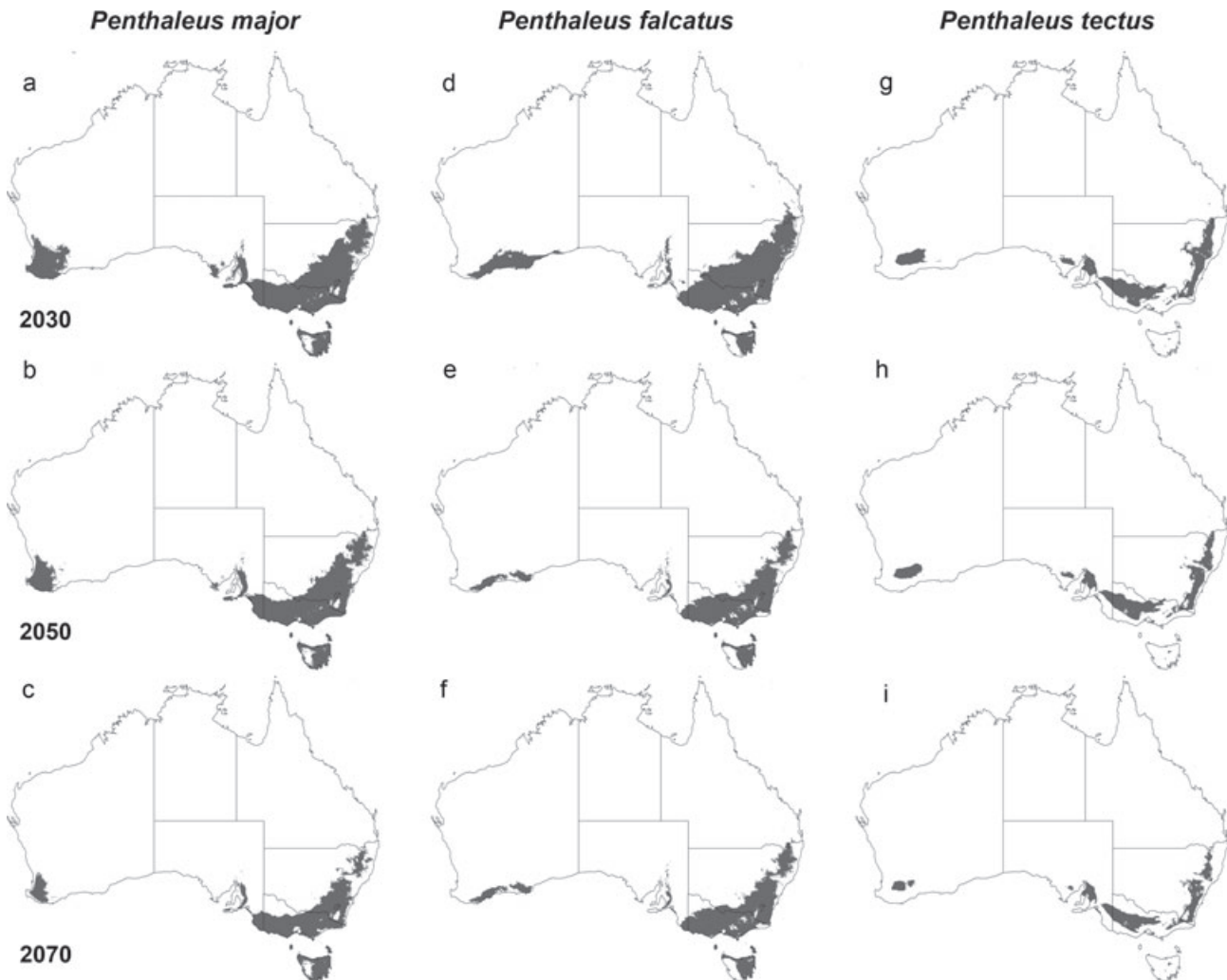
**Figure 5** Climate change projections for *Penthaleus* spp. in Australia for 2030, 2050 and 2070 under A1FI Special Reports on Emission Scenarios. Each projection uses the same set of variables as the present-day distribution models. (a–c) *Penthaleus major* projections; (d–f) *Penthaleus falcatus* projections; and (g–i) *Penthaleus tectus* projections. Shading represents suitable area in terms of climate space.

are able to capture at least some variation in the predictor variable response across populations (Phillips *et al*., 2006; Beaumont *et al*., 2009), simply by incorporating more combinations of environmental conditions (Thuiller *et al*., 2004; Heikkinen *et al*., 2006). Sampling widely will also incorporate genetic diversity at some level, although the potential evolutionary ability of populations to adapt to changing conditions would require experimental determination (Hoffmann & Sgrò, 2011). If *Penthaleus* spp. populations do adapt to future climate, our models still provide a prediction of the core future climate space, although the distribution may extend beyond this.

*Penthaleus* spp. are found throughout the circumpolar regions of the world (Umina *et al*., 2004), although these records are sparse and species may have been misidentified. Thus, our models cannot be validated with international datasets. Nevertheless, having models constructed in Australia for correctly identified *Penthaleus* spp. will provide useful validation datasets for future models of these species. Seasonal

fluctuations will allow *Penthaleus* spp. to expand (or retract) beyond the present ranges projected by these models, although sampling over a range of years, as in the present study, accounts for much of this variation. In addition to climate, the distributions of *Penthaleus* spp. are likely to depend on a range of variables, including environmental components (soil type), biotic interactions (competitive exclusion, host plant availability) and farming practices (irrigation and land use) (Hoffmann *et al*., 2008). Any effect of climate change on these variables is likely to affect *Penthaleus* spp. distributions. Although variables such as land use and vegetation information operate at a much finer scale than the climate predictors used in the present study, our models may be further enhanced by incorporating such information (Ficetola *et al*., 2007; Kharouba *et al*., 2009).

Our models show assemblages of *Penthaleus* spp. are expected to change substantially under future climate projections. Although the effects of climate change are not entirely predictable, these models give insight into the overall patterns

of future distributions of the three *Penthaleus* species. Our models predict localities where ideal conditions are likely to exist in the future for each species, reflecting a broad magnitude of climate impact rather than fine-scale simulation (Pearson & Dawson, 2003). Conditions such as microclimate and host-plant availability will provide some refuge for species under a changing climate. Assuming the availability of suitable host plants, outbreaks of *Penthlaeus* spp. would be expected to be more frequent within projected future climate space than outside it. The climate space available for *Penthaleus* spp. over the next 60 years is projected to retract across most regions of Australia. To further understand how climatic variables influence present and future distributions of *Penthaleus* spp., physiological parameters (such as moisture and temperature profiles) should be obtained for each species and used in mechanistic models (Kearney *et al.*, 2010).

*Penthaleus* spp. distributions are defined largely by climate (Wallace & Mahon, 1971; Robinson & Hoffmann, 2001) and our models reveal current and future climate space where the species are expected to persist as pests. By using correlative models, we were able to determine broad climatic processes that influence cryptic *Penthaleus* spp. distributions and how climate change projections may influence them. The results will provide an important basis for future planning of *Penthaleus* spp. management strategies. Future modelling to investigate pest status of earth mites under climate change should focus on specific mechanistic models aiming to incorporate species biological traits and adaptive potential. This will help identify the potential of each species to shift physiology in response to a changing climate. In terms of biotic interactions, it is also important to understand how climate may affect other pest earth mite species, such as *H. destructor*, which directly competes for resources with all three *Penthaleus* spp. (Weeks & Hoffmann, 2000; Umina & Hoffmann, 2005).

## Acknowledgements

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