

Human Impact Enables an Ecological Niche Shift for Invasive Widow Spiders

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Abstract

Background: Predicting invasiveness requires understanding the propensity of a given species to thrive in areas with novel ecological challenges. The Australian redback spider, *Latrodectus hasselti*, a widow spider native to Australia and established in Japan, New Zealand, and Southeast Asia. We hypothesized that human impact is important for successful establishment of this anthropophilic species, and that climate factors may determine suitable habitat and thus predict invasive ranges.

Results: We used ecological niche models to predict the potential distributions of this invasive species and to infer variables most important for population persistence by relating species observations to climatic variables and measures of human impact. We found *L. hasselti* distributions are positively influenced by human impact, particularly in the native range. Native distributions were most strongly predicted by maximum temperature and invasive distributions by precipitation seasonality.

Conclusions: A strong climatic niche shift was detected in invasive populations compared to the natives. We infer that a preference for human-disturbed environments may underlie invasion and establishment in this species.

Background

Since Hutchinson's concept of the environmental niche was proposed [1], how environment conditions determine species distributions has been one of the classic questions in ecology and evolutionary biology [2–5]. While it can be relatively difficult to measure a species' fundamental environmental niche, the realized niches (ecological niches) can be estimated by empirical studies for most species [2, 6–10]. It has become increasingly important to describe and understand the extent to which species' realized environmental niche can change rapidly (i.e., niche shift) or remain stable (i.e., niche conservatism) in the context of ongoing global change [4]. Thus, comparing the differences and dynamics of species' environmental niches between different geographic areas or time periods, across a range of different taxa, is urgently needed to support a broader understanding of these phenomena, particularly for invasive species [2, 4, 7, 11].

Biological invasions provide good opportunities to explore the mechanisms important during colonization of new environments, and to investigate whether invasive species retain their niches when moving to new areas with environment conditions that differ from their native ranges [3, 12–14]. Previous reports on terrestrial plants, invertebrates, fish, amphibians, reptiles, and birds concluded that niche shifts are rare overall between native and invaded ranges [8, 13, 15–20]. However, the assumption of niche conservatism has been challenged by increasing evidence of shifts from several taxonomic groups in recent years (e.g., plants, insects, aquatic invertebrates, aquatic vertebrates, mammals) [15, 21–28]. The generality of conclusions about niche shift are unclear since studies of invasive species are heavily biased towards relatively few taxa (e.g., over 60% on insects and plants [11]). Understanding whether invasive species will typically be restricted in their new ranges by niche conservatism, or whether shifts

may allow broader distributions is important to conservation efforts. As one of the major drivers of global change, introduction and spread of invasive species can trigger biodiversity loss and ecosystem disruption in various ways [25, 29]. This may include agricultural and forestry losses through reduced yields and pathogen transmissions [30], and negative effects on human well-being due to invasive vectors of human diseases (such as the mosquito *Aedes aegypti* [31]). Therefore, exploring how niche changes may be part of invasion processes, and thus being able to predict distribution and spread, is critical for evaluating the impacts of invasive species [25, 32]. Such studies can be key to informing spatial prioritization and management policies against biological invasions [33].

There are a number of considerations necessary when seeking to determine whether biologically relevant ecological niche shifts have occurred. First, the most commonly used metrics measuring differences between realized environmental niches so far are changes of the niche centroid, such as the Euclidean distance between the mean positions of the native and exotic niche spaces [21], and the change of niche overlap, such as Schoener's *D* index [34–36]. However, an absence of a niche centroid shift does not necessarily indicate no real niche change [2]. A change of the niche envelope might occur without a shift in the centroid as a result of symmetric expansion, contraction, or displacement within environmental space. For example, a move to both warmer and colder or wetter and drier conditions may occur in such a way that the average temperature or precipitation niche positions keep stable [2, 17, 18, 21, 37, 38]. Thus, it is more appropriate to use more comprehensive measures of niche, such as Guisan et al. [2] unifying framework that decomposes niche change into three situations: unfilling (proportion of the native niche that does not overlap with the exotic niche), stability (proportion of the exotic niche overlapping with the native niche), and expansion (proportion of the exotic niche that does not overlap with the native niche). Second, demonstrating meaningful niche shifts may depend on choosing biologically relevant environmental variables for analysis [39, 40]. Third, mapping the availability of environmental conditions in geographic space could also be crucial for exploring niche differences between native and exotic ranges of an alien species [2]. Some environmental conditions that are common in the native range might be rare in the exotic range, and vice versa, because of the niche-biotope duality [41]. This may produce results that indicate niche shifts, but in reality this would arise from differences in the occurrence of conditions in different parts of the range, even if these do not impact the success of the species under study [5, 38]. Therefore, for a robust understanding of niche change of an invasive species, a standardized study should measure niche centroid dynamics and decompose the three niche-shift elements, simultaneously, while also considering the relative availability of multiple environment parameters with an understanding of how these are biologically relevant to the species under study. We used this approach to study the ecological niche of the invasive Australian redback spider (*Latrodectus hasselti*).

Generally, two approaches have been used in analyzing niche shifts of invasive species: comparisons of environmental attributes of native and exotic ranges based on direct observation of sites, and exotic ranges and detecting the overlaps of reciprocal predictions of native and exotic geographical distributions based on the outcomes of ecological niche models (ENMs; also named species distribution models, SDMs) [2, 4, 7, 34, 36, 42]. The first method uses univariate or multivariate tests or principle

component analysis (PCA), is an ordinal way to quantify niche difference, and has higher accuracy overall than the second method. However, this approach provides a less mathematical representation of the niche than the ENM method, and does not allow optimization of weighting among factors based on their importance in the species' ecology [2, 26, 42]. The ENM method predicts the invaded distribution with the model fitted in the native range, and vice versa, and then compares the situations of the two predictions [36, 42, 43]. It is a visualized way to detect niche difference and is particularly useful in assessing ENM transferability between native and exotic ranges [44]. Here, we take an integrated approach that utilizes the strengths and minimizes the weakness of each method by conducting ordinal analyses based on the results from ENMs to quantify ecological niche shifts [2, 34].

In addition to a focus on environmental factors, we also examine effects of human activities in our models. Human activities have obvious impacts on many ecological processes and distributions of animals and plants at different spatial and temporal scales, and this is particularly true for invasive species [25, 45–47], many of which are adapted to human-disturbed environments [47–50]. It has been suggested that alien species usually establish in disturbed areas at the early stages of the invasion process before range expansion [51]. Thus, anthropogenic impacts can affect the niche space of invasive species and should be identified as a promoter of invasion success under integrative scenarios [25, 45, 47]. There is some evidence that adding human footprint to climatic variables can improve predictions (e.g., in terrestrial plants [52]). Nevertheless, the role of human disturbance in mediating niche changes has received much less attention than other factors [18, 53].

In this study, we compared the ecological niche of invasive Australian redback spiders (*L. hasselti*, Thorell 1870, Araneae: Theridiidae) in its native and exotic ranges using an integrative approach that includes measures of human activities. The widow spiders (genus *Latrodectus*) include over 30 species found around the world [54] with medically important, neurotoxic venom [55], which makes invasive populations a particular concern [56]. Spiders in this genus are generalist predators that can survive for months without food, have a high reproductive output [57, 58], and may be easily introduced to new areas by human transport [59, 60], but nevertheless, to date only two species have been reported to be invasive (*L. hasselti* and *L. geometricus* [54]). *L. hasselti* is native to Australia, where it is common in urban habitats, and it has established populations in New Zealand (first recorded in 1981-1982 [61, 62]), Japan (first recorded in 1995 [63]), India [64], and Southeast Asia (the Philippines [65]), likely through international cargo shipments of steel, produce, or wood [66]. Here we examine the niche of native and exotic populations of *L. hasselti* using ENM and ordinal comparisons combined with considerations of environmental availability, and including analyses of niche centroid change, unfilling, stability, and expansion. In addition, we hypothesized that human impact supports the successful establishment of this anthropophilic species [66]. Thus, we also compare the influence of human disturbance on native and invasive populations.

Materials And Methods

Natural history

Past work suggests that variation in temperature and precipitation are important determinants of environmental suitability, range extent, survival, growth, and offspring development of *Latrodectus hasselti* [61, 66–69]. Although *L. hasselti* spiders can tolerate a wide range of temperatures, their growth may be slowed and egg sacs may cease development at low temperatures [70]. Matsuse et al. [68] reported that the greatest survival rate of the spiders was at 20°C; if under 5-10°C, they could survive for a month but did not grow or moult. Juvenile spiders can survive short exposure (20 minutes) to freezing temperatures, however, the developmental zero of the egg sacs (i.e., the temperature at which egg sac development ceases) is 15-18°C and the spiderlings do not emerge at 20°C [68, 69]. In addition to these effects of temperature, *L. hasselti* are adapted to xeric conditions, so may not be able to survive in areas with high precipitation or humidity [61]. *L. hasselti* forage less actively on rainy days, and flooding may destroy webs, both of which could negatively impact survival (our field observations), although protected microhabitats may provide protection against the rain for cobweb spiders [71], and such protection may be abundant in human-disturbed habitats [66].

Data collection and ecological niche modeling

The study area was across eastern and southern Asia and Oceania (45°N-60°S, 60°E-180°; Fig. 1). For these regions, a total of 2580 raw occurrences (GPS localities) of *L. hasselti* were collected from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>, [72]) database and published literature [66, 68, 73]. We compiled these location points into two subsets: native occurrences (Australia; 1967 localities) and invasive occurrences (other countries; 613 localities). Then, we used the CoordinateCleaner package to remove records collected in the museums and institutes [74]. To avoid georeferencing errors of the localities and over-fitting in the following distribution modeling, we checked all the location data in ArcGIS 10.0 (ESRI, Redland, USA) and removed duplicate occurrences at a spatial resolution of 1 km × 1 km so that each grid cell had only a single record [75–79]. Finally, 1099 and 86 occurrences were used for Australia and the other countries, respectively (Fig. 1a; Table S1 in Additional File 1).

Based on previous research [66] and our field observations, seven climatic parameters, which are the most ecologically relevant to survival, habitat use, and fitness of *L. hasselti*, were selected in constructing ecological niche models: annual mean temperature (AMT), mean diurnal temperature range (MDR), temperature seasonality (TS), maximum annual temperature (MaxT), minimum annual temperature (MinT), annual precipitation (AP), and precipitation seasonality (PS). Raster data of these variables were extracted from WorldClim V2 database [80, 81] and transformed into 1 km × 1 km equal-area grids in ArcGIS 10.0 with an UTM WGS 1984 projection. For human impact factor, we used the human footprint (HFP) data from Last of the Wild Data Version 2 [82] and Venter et al. [83] and transformed it into 1 km × 1 km rasters. Then, all the data were split into two subsets: native (Australia) and invasive (other countries).

Using a maximum entropy approach in the MaxEnt v3.3.3k [84–86], we predicted the potential distributions of *L. hasselti* in Australia (native distribution; AUS model) and other countries (invasive distribution; INV model), respectively, based on their respective subsets of occurrences and climatic

factors. MaxEnt has been shown to have good performance which consistently outperforms many other methods, especially under small sample size, noisy input data, and is robust to various levels of correlation among parameters [84, 87]. To explore the impacts of human activities on the spider distributions, a climatic model (using the seven climatic variables) and a full model (using the seven climatic variables and HFP) were processed simultaneously. As sampling bias in background points could decrease modeling effectiveness [84], we used a Kernel Density Estimator (KDE) surface to create 10,000 random background points in the Software for Automated Habitat Modeling (SAHM) [88–90]. To avoid reduction of model accuracy caused by an inappropriate model complexity or data organization, we selected model settings and conducted model choices by following Muscarella et al. [91] using the ENMeval 0.1.0 package in R 4.0.2 [92, 93]. That is, five feature class values (FC: linear, quadratic, product, threshold, hinge), eight regularization multiplier values (RM: 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4), five locality partition methods (jackknife, randomkfold, block, checkerboard1, checkerboard2) were calculated, and the mean values of the area under the receiver operating characteristics curve using the testing data across all data bins (mean AUC_{test}) and the mean values of the difference between the training and testing AUCs across all data bins (mean AUC_{diff}) were computed as the evaluation metrics for the goodness-of-fit and the degree of overfitting of the model. We used the Akaike Information Criteria corrected for a small sample size (AICc) to compare different parameter combinations and select models [93, 94]. As the models incorporating all environmental parameters (i.e., seven climatic variables for the climatic model, seven climatic variables and HFP for the full model) and with FC=linear, RM=1, and the randomkfold (k=10) partition method showed the best performances (see Results), in each model, 80% of the occurrence was randomly selected to generate a training set and the remaining 20% was an evaluation set. Other default settings of the software were adopted: maximum iterations (500), convergence threshold (10^{-5}) [84]. We selected logistic output format (habitat suitability value ranges from 0 to 1) and conducted jackknife procedures to evaluate relative contribution of each variable [84]. We ran ten cross-validation replications of the model and weighted them by their AUCs to obtain an ensemble distribution prediction and integrative impacts of variables [95, 96]. To convert continuous outputs into presence-absence maps, we extracted suitability values of the occurrences of *L. hasselti* within raw modeling results, and calculated the mean values as the thresholds (AUS climatic model: 0.702, AUS full model: 0.663; INV climatic model: 0.681, INV full model: 0.630) [97, 98]. That is, areas with predicted suitability above and below the threshold were respectively considered as “present” (suitable) and “absent” (unsuitable).

Quantifying niche differences

In climatic models, we extracted the data of each climate variable within the predicted distributional ranges of *L. hasselti* by pixel, and compared the means between AUS and INV using one-way ANOVAs. To explore centroid shift of its climatic niche, a principle component analysis (PCA) was processed in the “ade4” library in the R 4.0.2 software [99]. We compared the climatic spaces of the native and invaded distributional ranges of the spiders, and the magnitude and statistical significance of the niche shift between the two distributional clouds in the PCA graph were computed by a between-class analysis with a between-class inertia percentage [21]. Nine hundred and ninety-nine Monte-Carlo randomizations were

conducted to test this ratio [100]. We also calculated the Schoener's *D* and Hellinger's *I* in ENMTools to show the climatic niche overlap and similarity [43]. Then, we extracted the data of each climate variable for Australia and the other countries across the study area by pixel, and calculated three niche-shift elements (AUS vs. INV): unfilling, stability, and expansion [2]. We also mapped frequencies of the climate variables within the distributional ranges (occupied environment) and the total study area (available environment) for AUS and INV, respectively, to reveal the impacts of environmental availability to niche change. In addition, to show the influence of human activity on niche shift during invasion, we run a one-way ANOVA for HFP data in the distributional ranges between AUS and INV, and mapped the frequencies of HFP within the distributional ranges and the total study area for AUS and INV based on our full model.

Results

Our ecological niche models (FC=linear, RM=1, randomfold partition method: k=10; climatic model: seven climatic variables, full model: seven climatic variables+HFP) showed great performance for both of the native and invasive populations (Table 1). The areas of predicted suitable habitat for *L. hasselti* in Australia (native) were 4.46×10^6 km² and 3.15×10^6 km² based on the climatic and full models, respectively, and 1.40×10^6 km² and 0.93×10^6 km² for those in the other countries (invasive) (Fig. 1b, c). Our jackknife results revealed that the maximum temperature (MaxT) and temperature diurnal range (MDR) have high contributions to habitat quality for the native populations, while precipitation seasonality (PS) has a relatively greater impact for the invasive populations (Fig. 2). However, human impact had the greatest effects on habitat suitability in both areas, if human footprint (HFP) was included in the modeling processes (Fig. 2).

Table 1
Performances of the ecological niche models of native (AUS) and invasive (INV) populations of *Latrodectus hasselti*. AUC_{test} and AUC_{diff} are showed in mean±SE.

		AUC _{test}	AUC _{diff}	AICc	AICw
Climatic model	AUS model	0.809±0.022	0.027±0.005	2871.573	0.479
	INV model	0.958±0.040	0.022±0.003	706.659	0.563
Full model	AUS model	0.851±0.021	0.021±0.003	2668.910	0.488
	INV model	0.973±0.036	0.019±0.002	633.576	0.586

Ecological niche shift

Significant differences were detected on the means of each climatic factor between the native (AUS) and invasive (INV) habitats (all ANOVA $p < 0.001$; Fig. 3, 4). Two PCs were extracted in our principle component analysis, with a cumulative contribution of 75.8% (PC1: 43.5%, PC2: 32.3%; Fig. 5). According to the between-class analysis, a clear shift of climatic niche was found between these populations (AUS vs. INV: between-class inertia ratio=0.198, $p=0.001$; Fig. 5), and the Schoener's *D* and Hellinger's *I* indexes were

0.611 and 0.754, respectively. For the three niche shift elements, most of the climatic variables showed relatively high stability (values at or approaching the maximum score of 1.00). There were two climatic variables that warrant attention from this analysis: precipitation seasonality (PS, unfilling=0.138) and temperature seasonality (TS, expansion=0.672) (Table 2). Frequencies of each climatic variable within the suitable habitats and available habitats in Australia and the other countries were mapped in Fig. 6. For the impacts of human activity, we found a significant difference of HFP between AUS and INV populations (ANOVA $p < 0.001$, Fig. 4(h)). Intensity of human impact is generally lower in Australia comparing to the other countries, and INV population established in habitats with greater HFPs than those of AUS population (Fig. 6(h)).

Table 2
Three elements of niche shift for each climatic variable of *Latrodectus hasselti*.

	Niche unfilling	Niche stability	Niche expansion
Annual mean temperature (AMT)	0.003	0.990	0.010
Mean diurnal temperature range (MDR)	0.023	0.995	0.005
Temperature seasonality (TS)	0.000	0.328	0.672
Maximum annual temperature (MaxT)	0.000	0.956	0.044
Minimum annual temperature (MinT)	0.000	0.935	0.065
Annual precipitation (AP)	0.000	0.980	0.020
Precipitation seasonality (PS)	0.138	1.000	0.000

Discussion

We used an integrative approach that included biologically relevant climatic variables and a human impact metric to compare the niches of native and invasive distributions of the anthropophilic Australian redback spider (*L. hasselti*). Our model predicted that native *L. hasselti* generally distributes in the eastern, western, and southern coasts of Australia, confirming the conclusions of Vink et al. [66]. For the invasive populations, in addition to the areas where historical occurrence records were collected (e.g., Japan, New Zealand, eastern part of Papua New Guinea, western coast of India) [66, 101], suitable habitats for the redback spider are mainly located in the southern and eastern regions of China, northwestern regions of South Asia, southern regions of Indo-China Peninsula, eastern regions of Indonesia, and central Philippines (Fig. 1). These areas should be emphasized during the future field surveys as they have a high risk of invasion by *L. hasselti*.

In Australia, temperature variables are predicted to determine the distribution and habitat suitability for *L. hasselti* according to our jackknife results (Fig. 2(a)). That is, native redback spiders are most sensitive to the highest temperature (i.e., MaxT) and temperature variation (i.e., MDR). This may be because warm summers and stable summer temperatures (e.g., 15-25°C for 2-3 months) increase successful breeding

and offspring hatching, development, and growth [62, 66, 101]. However, precipitation becomes relatively more important when *L. hasselti* invades new areas (Fig. 2(b)), especially precipitation seasonality (i.e., PS), which is followed by the lowest temperature (i.e., MinT). Redback spiders are adapted to low relative humidity (i.e., arid habitats) in their native range, and their development and survival can be impacted by overwintering conditions (including temperature) [61, 66, 101]. Our data show that, as redbacks move outside of Australia, they have encountered generally colder and wetter environments and areas with more variable climates (Fig. 3, 4(e)-(g), 6(e)-(g)). Thus, despite the fact that human transport may regularly introduce *L. hasselti* spiders to new areas [60, 66, 73], our model suggests that the likelihood of establishment and spread will heavily depend on local humidity and temperature.

When human impact was included in the modeling, human footprint index (i.e., HFP) showed the highest contributions for both native and invasive populations (Fig. 2(c)(d)). Although human influence can lead to over one third of decreases in, and obvious fragmentation of, suitable habitat (see Results, Fig. 1(b)(c)), anthropic environments (e.g., urban areas, human modified habitats) may be beneficial to redbacks by providing shelter from unsuitable climates and extreme climatic events. Thus, human impact may allow redbacks to escape their natural climatic limitations, invade semi-natural ecosystems, and expand their distribution range [61, 66, 69, 73, 101]. The importance of human impact (high HFP, Fig. 2(c)(d)), is consistent with the suggestion of Vink et al. [66] that human-modified environments may support persistence by providing shelter from precipitation and high humidity, and that this is essential for success of arid-adapted redbacks. For example, selecting microhabitats around buildings and structures to build their webs may provide spiders protection from high and variable precipitation [71]. Moreover, since urban areas are known to be heat islands across seasons [102], high HFP could also buffer invasive redback populations against low winter temperatures, although there is currently little information available on this effect for spiders. A group of studies on the desert-adapted North American species *Latrodectus hesperus* indicate that populations thrive in urban heat island habitats (within its native range [103–105]). In the case of *L. hesperus*, however, urban spiders experience higher temperatures relative to natural habitats (rather than decreased minimum temperatures, as for redbacks in the invasive range), and this change is associated with reduced survival, poor nutritional condition, but also accelerated development and foraging activity, along with other behavioral changes which may allow persistence [105]. Similarly, recent studies comparing behavior of invasive and native populations of Australian redback spiders suggest that increased behavioural plasticity in web building, along with increased dispersal and sibling cannibalism, in invasive spiders could increase persistence in variable, disturbed habitats in the invasive range [106, 107].

Our study clearly revealed a climatic niche shift of Australian redback spiders during or subsequent to their invasion (between-class inertia ratio of first two PCs=0.198, $p=0.001$, Fig. 5; Schoener's $D=0.611$; Hellinger's $I=0.754$). *L. hasselti* spiders can persist in cooler and wetter environments after invading new areas compared to those in which they are found within Australia (native population) (Fig. 3, 4, 6). Research reported that redbacks and their spiderlings withstood and survived sub-zero winter temperatures in the field in New Zealand and Japan, which were previously assumed to be unsuitable for them because of the prevalence of low temperatures thought to be fatal [66, 67, 108]. Their occurrences

were also recorded in some temperate countries with relatively abundant rainfall where precipitation was formerly assumed to be too high for redbacks to persist [66]. However, studies to date do not provide concrete evidence suggesting changes in the fundamental niche of redback spiders. Detailed research, especially experimental studies and more empirical field studies, are required in the future. Our results do suggest that the shift of realized niche might be generally or, at least partly, related to the availability of appropriate environmental conditions, as the exotic range has overall lower temperatures, higher precipitation, and greater climatic fluctuations than the native range (Fig. 4, 6). In addition, according to our analysis of three elements of niche shift, we identified that the realized niche change of *L. hasselti* was mainly related to its expansion along axes of temperature variation (i.e., temperature seasonality, TS), contraction along precipitation variation (i.e., precipitation seasonality, PS), but there was generally niche conservatism along other climatic variable dimensions (Table 2).

Overall, our results show two strong influences of human impacts on redback spiders. First, human impacts clearly could cause loss and fragmentation of suitable habitat of *L. hasselti* in both its native and exotic ranges (Fig. 1). Second, compared to records from Australia, invasive spiders nevertheless inhabit environments with higher human activity intensities (Fig. 4(h)). Our data suggest there may be a greater anthropogenic influence overall in the invasive range compared to in Australia (e.g., high human population in East, South, and Southeast Asia; Fig. 6(h)). Previous studies in Japan and New Zealand reported that redbacks selected and preferred urban/sub-urban areas (e.g., ditch gratings, rainwater drains, fences, parking lots, cemeteries, buildings), semi-natural habitats (e.g., human-modified coastal sandy beaches and sand dune ecosystems), and artificial structures (e.g., seawalls, revetments, shore line protection structures) [66, 69, 73, 101]. These anthropogenic habitat modifications could provide *L. hasselti* with web-building sites and shelter from extreme (low) temperatures and water stresses (precipitation and humidity), which may outweigh costs from direct or indirect disturbance of human activities [66, 101]. We infer that the preference of *L. hasselti* for human-disturbed environments, and success in such habitats, may aid survival in new locations with less suitable climatic conditions, and thus underlie the ecological niche shift that enables successful invasion and establishment of this invasive species.

Declarations

Ethics approval and consent to participate

Not Applicable.

Consent for publication

Not Applicable.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

Z.L., M.A.M., and M.C.B.A. conceived and designed the study; Z.L., M.A.M., and M.C.B.A. collected and analyzed the data; all authors wrote the manuscript.

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Figures

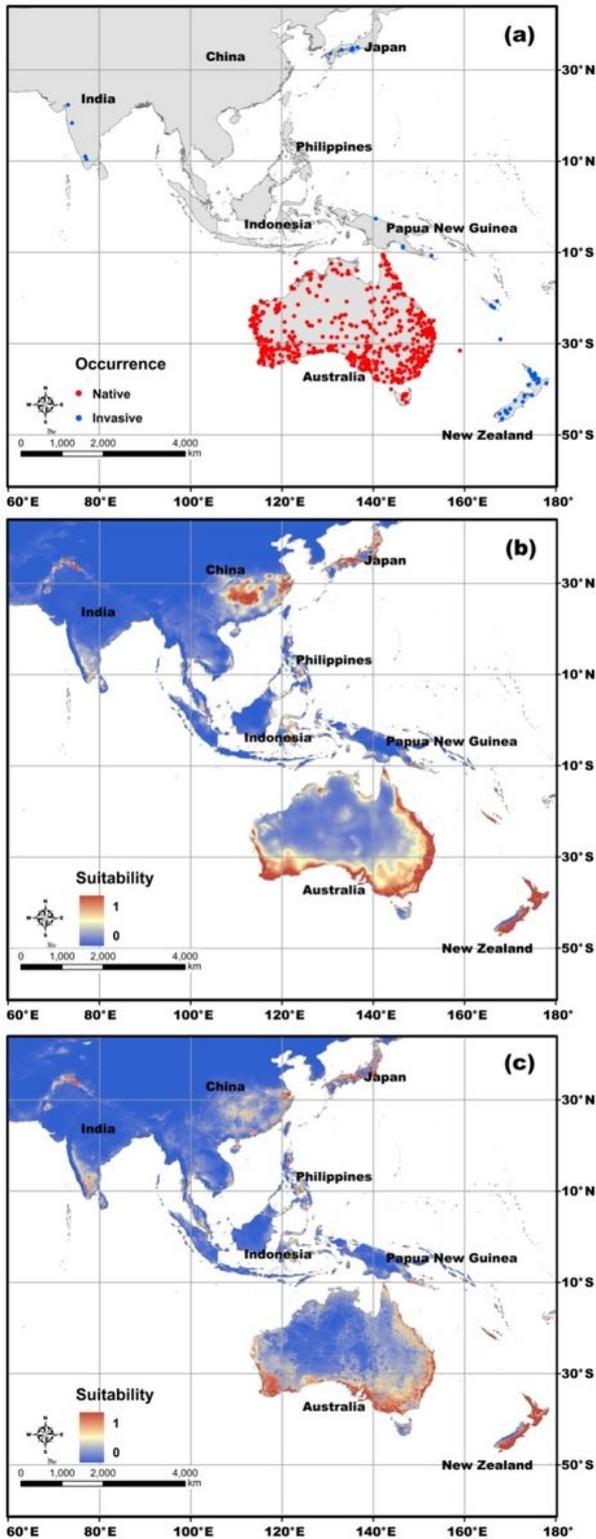


Figure 1

Study area, occurrence records, and habitat suitability of *Latrodectus hasselti*. (a) Map of the study area, with native occurrences (AUS) shown by red points and invasive occurrences (INV) by blue points. (b) Habitat suitability patterns based on climatic models. (c) Habitat suitability patterns based on full models. Habitat suitability patterns in Australia and countries other than Australia were processed from AUS and INV models, respectively.

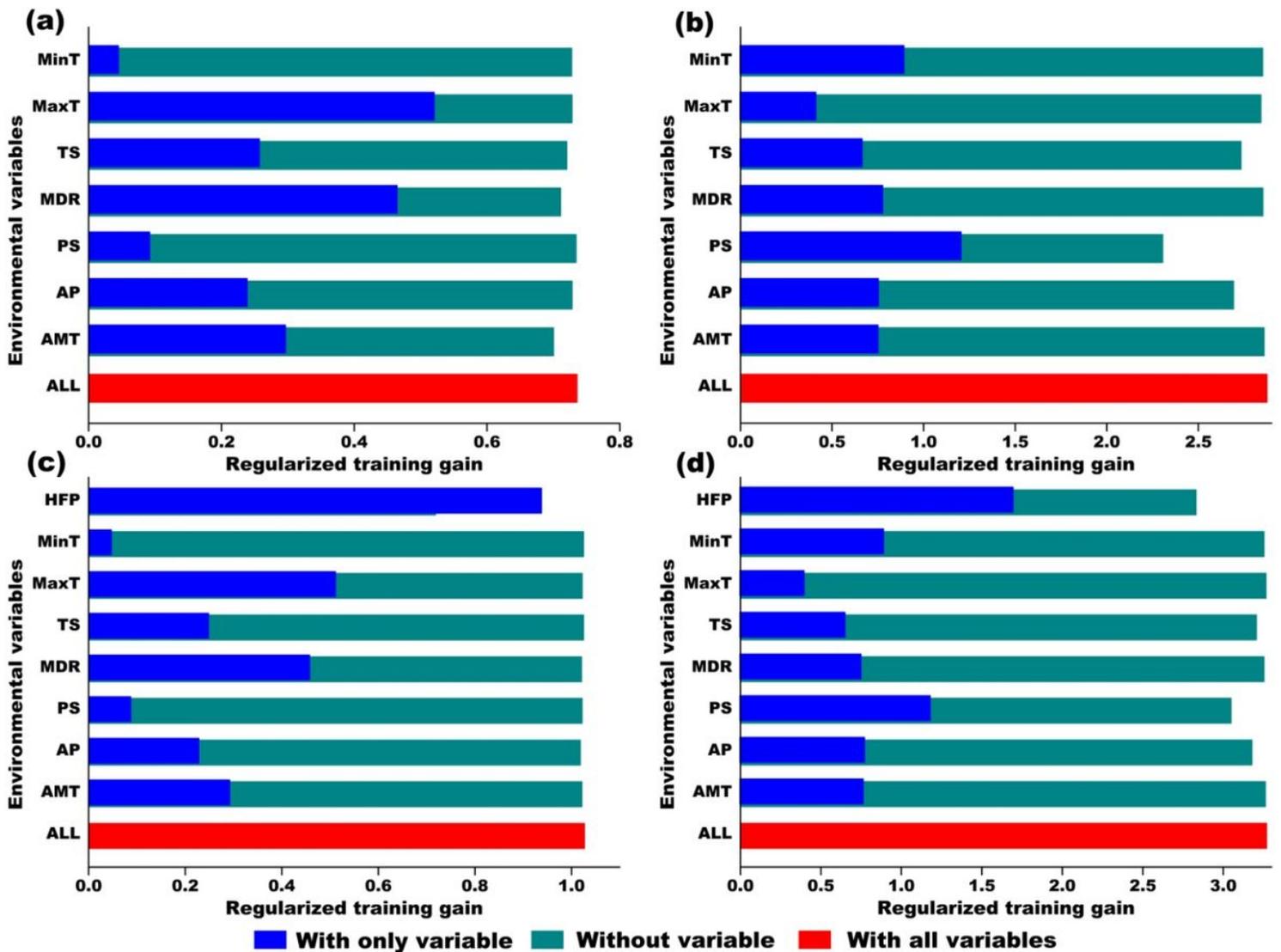


Figure 2

Results of jackknife analyses of the importance of environmental variables for *Latrodectus hasselti*. (a) AUS (Australian) climatic model, (b) INV (invasive) climatic model, (c) AUS full model, (d) INV full model. Climatic models include seven variables (see table 2 and figure 3). Full models include a measure of human impact index (Human Footprint, HFP) in addition to climatic factors.

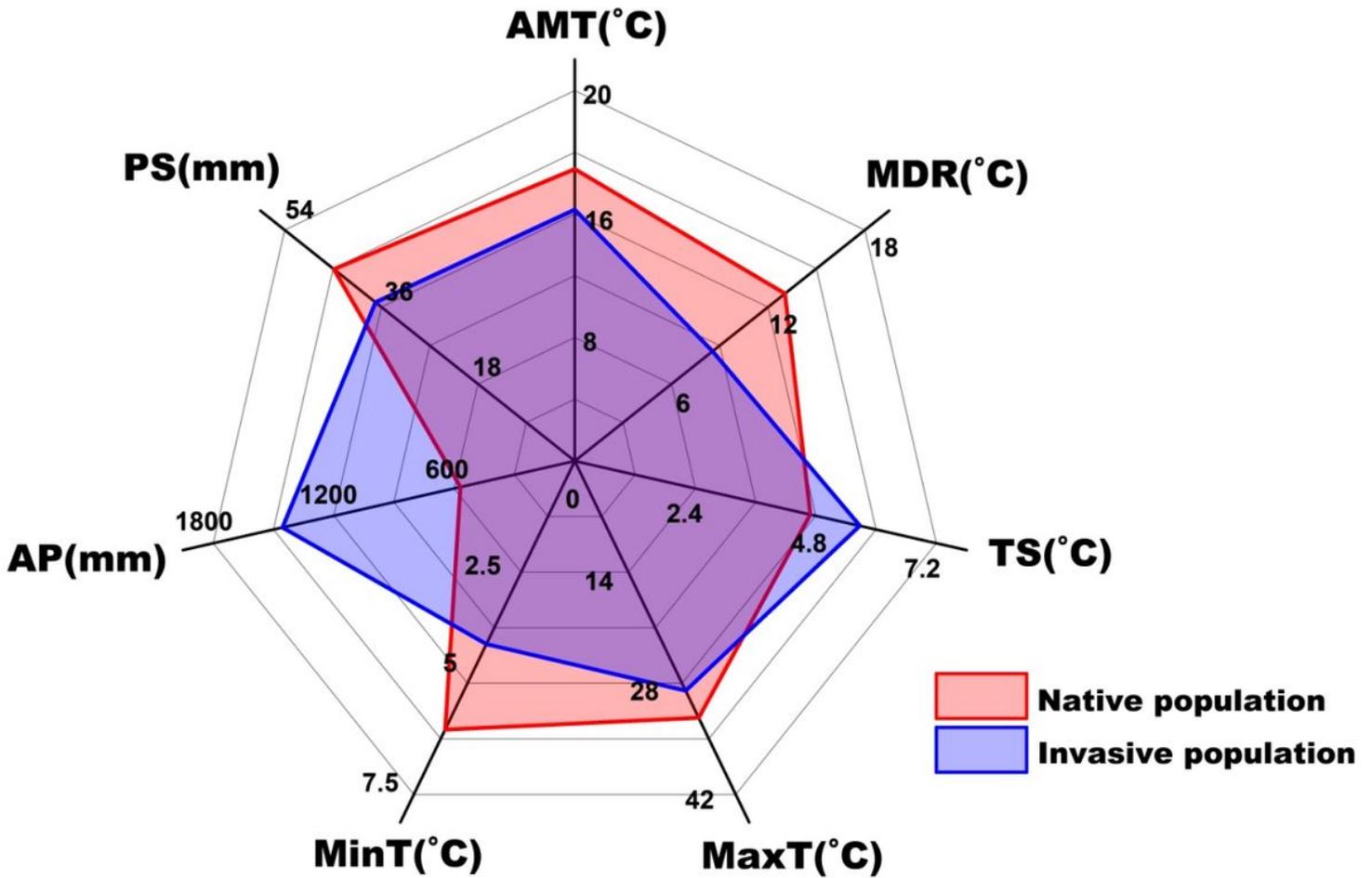


Figure 3

Means of seven climatic variables for native and invasive populations of *Latrodectus hasselti*.

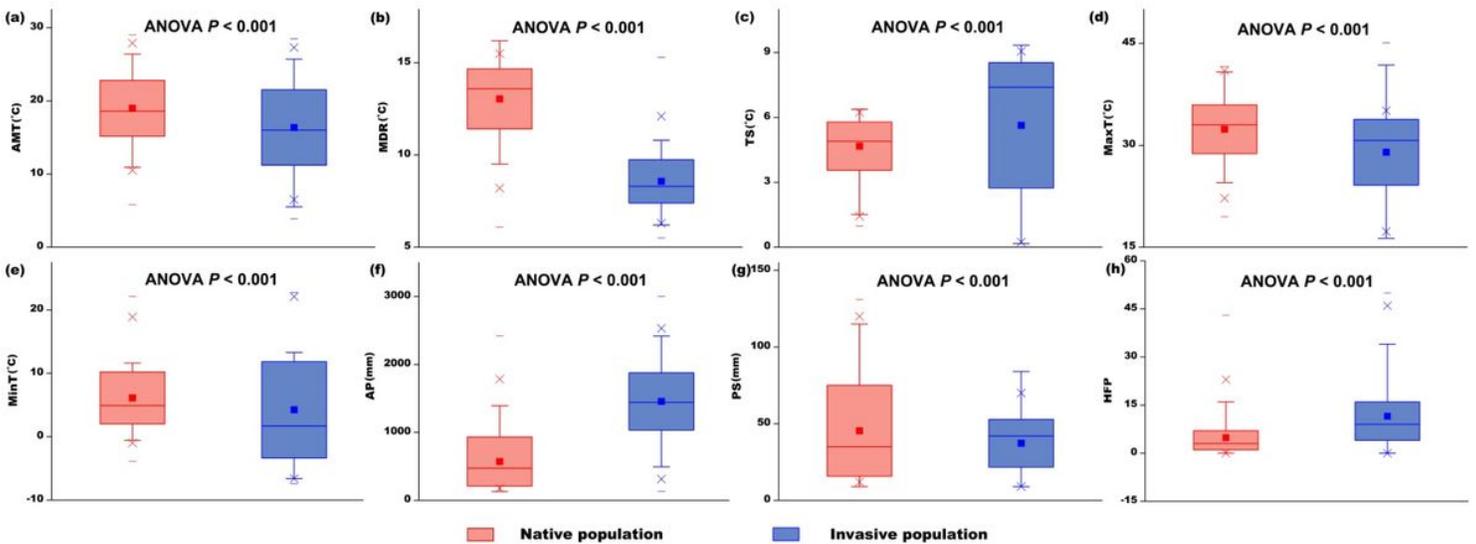


Figure 4

Native and invasive populations of *Latrodectus hasselti* differ significantly across eight environmental factors (based on one-way ANOVAs).

Figure 5

Principal components analysis for climatic factors shows invasive *Latrodectus hasselti* (blue) have a significant climatic niche shift comparing to natives (red). Open black arrow indicates the direction and magnitude of the shift.

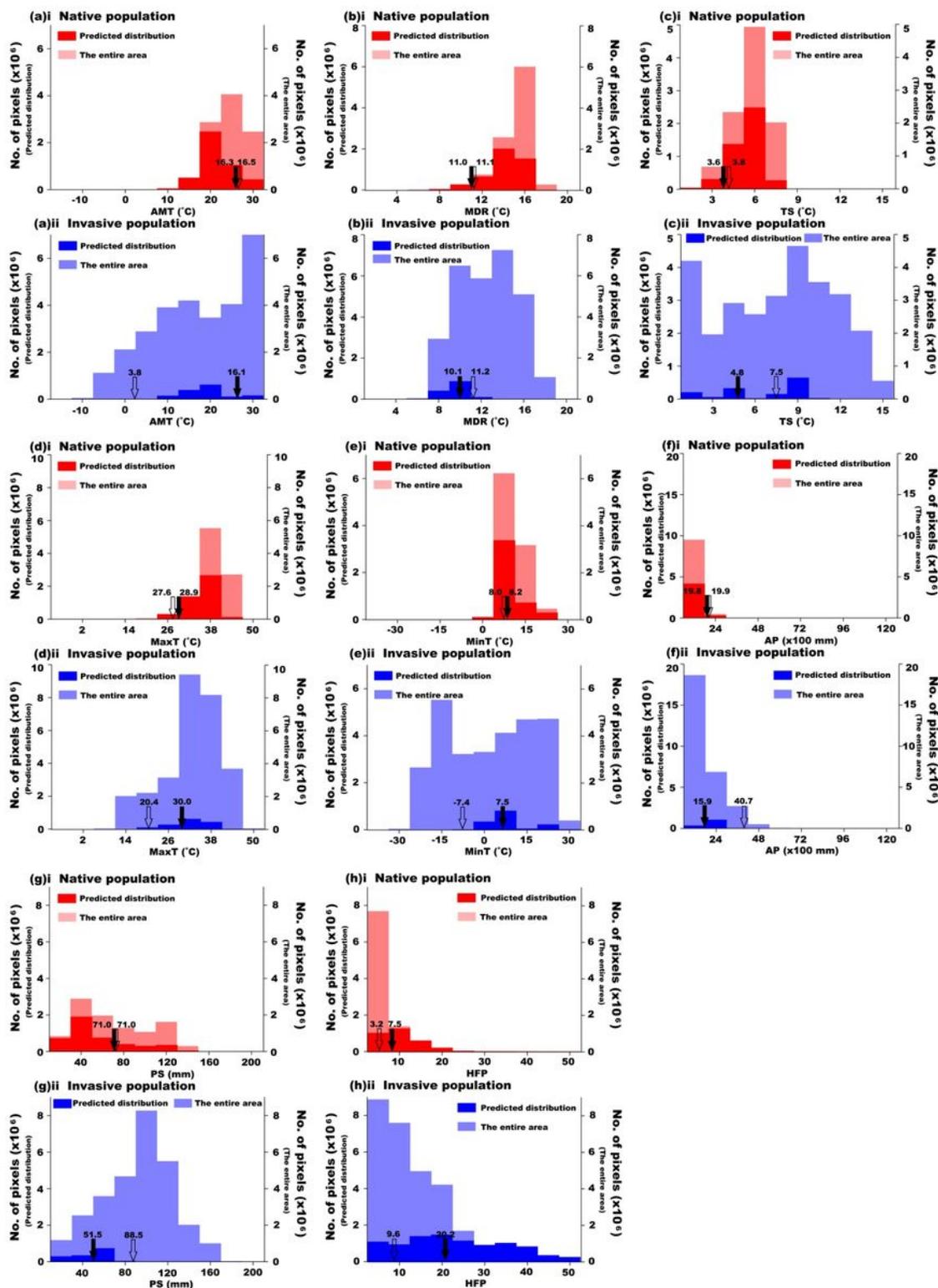


Figure 6

Frequencies of the eight environmental variables for the predicted distributions (dark colors; for native population, AUS: predicted distribution in Australia; for invasive population, INV: predicted distribution in our study area outside Australia) and the entire areas (light colors; AUS: Australia; INV: our study area outside Australia) of *Latrodectus hasselti* populations (AUS and INV): (a) AMT, (b) MDR, (c) TS, (d) MaxT, (e) MinT, (f) AP, (g) PS, (h) HFP. In each panel, the frequencies for AUS (red colors, i) and INV (blue colors,

ii) populations are shown separately. Solid arrows are means for predicted distributions, open arrows are means for the entire areas.

Supplementary Files

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