



# Historical refugia have shaped biogeographical patterns of species richness and phylogenetic diversity in mite harvestmen (Arachnida, Opiliones, Cyphophthalmi) endemic to the Australian Wet Tropics

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## ABSTRACT

**Aim** We tested the hypothesis that areas that acted as historical refugia during restrictive climate regimes currently harbour higher levels of biodiversity than areas that lacked refugia.

**Location** The rain forests of Australia's Wet Tropics, the largest remaining fragments of the humid forest habitats that once covered the Australian continent.

**Methods** We generated a model of climatic suitability for arachnids in the genus *Austropurcellia*, a group of small, dispersal-limited mite harvestmen that are found throughout the Wet Tropics. We then projected this model onto palaeoclimate data layers from time slices going back to the Last Glacial Maximum and summed suitability over time to arrive at a measure of stability. We compared the power of metrics of present and past climatic suitability and stability to predict diversity (species richness and phylogenetic diversity) across subregions of the Wet Tropics.

**Results** We found statistically significant correlations between measures of diversity (species richness and phylogenetic diversity) and present climatic suitability, LGM climatic suitability and our stability metric across subregions of the Wet Tropics. Although stability lost predictive power when analyses were corrected for spatial autocorrelation, and present-day mean climatic suitability lost predictive power when corrected for spatial autocorrelation under one of our geographical binning schemes, mean climatic suitability during the Last Glacial Maximum had a positive and significant relationship to both number of species and phylogenetic diversity in all analyses.

**Main Conclusions** Our results support a model of biodiversity preservation within historical refugia, resulting in higher present-day diversity in refugial areas than in non-refugial areas. Although previous studies of the Wet Tropics biota have demonstrated a relationship between habitat stability and diversity, ours is the first such study to consider phylogenetic diversity in addition to number of species.

## Keywords

*Austropurcellia*, climate, extinction, Pettalidae, phylogeny, stability

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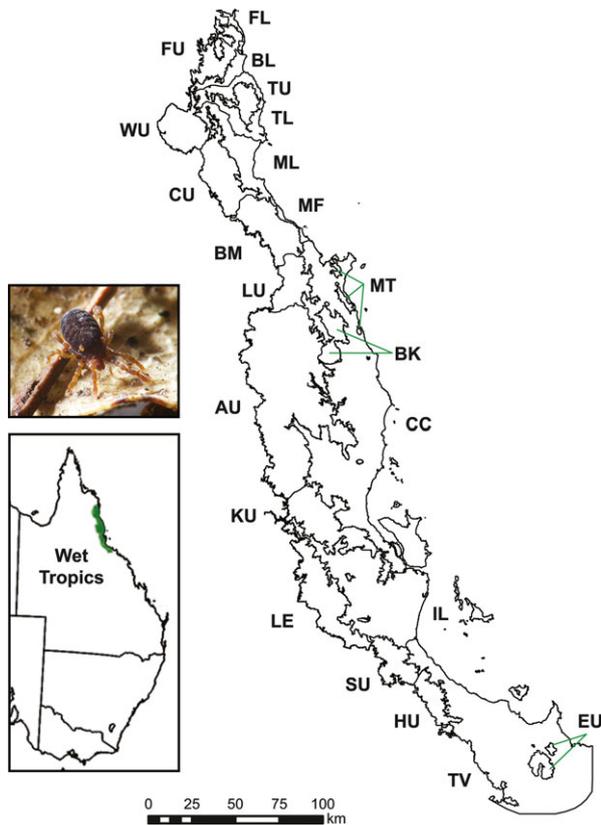
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## INTRODUCTION

What is the biogeographical legacy of historical refugia? Nearly half a century ago, Haffer (1969) proposed the

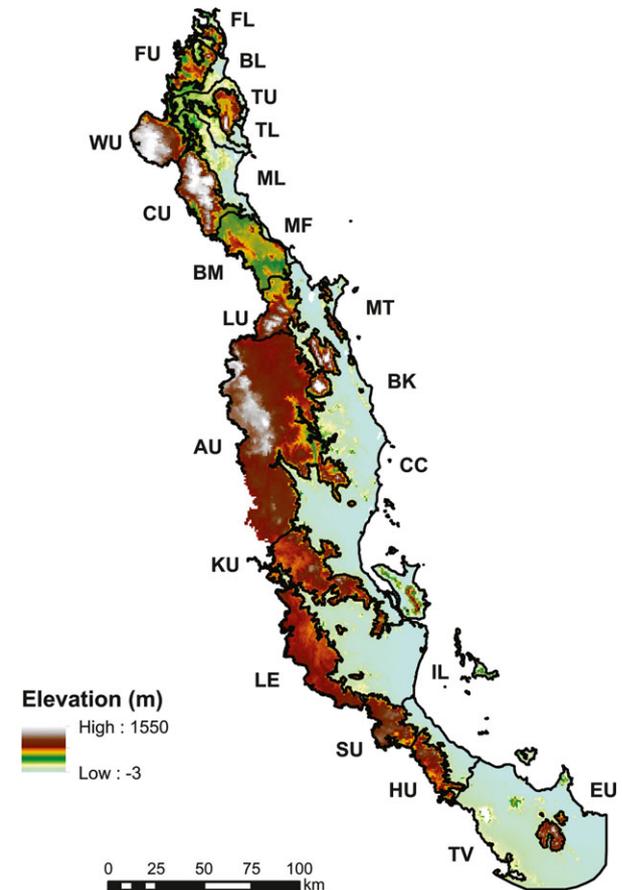
hypothesis that tropical forest diversity could be related to speciation via isolation within refugia during the Pleistocene, when periods of drier environmental conditions resulted in fragmentation and contraction of forest habitats. Molecular

phylogenetic methods have subsequently permitted tests of this hypothesis in rain forest faunas from various parts of the world, with the conclusion that in most cases species-level divergences pre-date the Pleistocene glacial cycles (Hewitt, 2000; Moritz *et al.*, 2000; Rull, 2008). More recently, authors have focused on the role of Pleistocene forest refugia in preserving lineages, effectively acting as biodiversity museums (*sensu* Stebbins (1974)). For example, Carnaval *et al.* (Carnaval & Moritz, 2008; Carnaval *et al.*, 2009) demonstrated that long-term habitat stability predicts species endemism and genetic diversity in the Brazilian Atlantic biodiversity hotspot. As hypotheses to explain the diversity of rain forest faunas have evolved, the Australian Wet Tropics (Fig. 1) have emerged as a model system for understanding the role of historical processes in establishing current biogeographical patterns (e.g. Schneider & Moritz, 1999; Graham *et al.*, 2006, 2010; Moussalli *et al.*, 2009; Bell *et al.*, 2012).



**Figure 1** Map of the Wet Tropics showing subregions following Williams & Pearson (1997). Inset figures represent the life habitus of *Austropurcellia* (shared by Gonzalo Giribet) and a map of eastern Australia with shaded area indicating location of the Wet Tropics. Subregion abbreviations: FL, Finnigan Lowlands; FU, Finnigan Uplands; BL, Bloomfield Lowlands; TU, Thornton Uplands; TL, Thornton Lowlands; WU, Windsor Uplands; ML, Mossman Lowlands; CU, Carbine Uplands; MF, Macalister Foothills; BM, Black Mountain; MT, Malbon-Thompson; LU, Lamb Uplands; BK, Bellenden Ker/Bartle Frere Uplands; AU, Atherton Uplands; CC, Cairns-Cardwell Lowlands; KU, Kirrama Uplands; LE, Lee Uplands; IL, Ingham Lowlands; SU, Spec Uplands; HU, Halifax Uplands; EU, Elliot Uplands; TV, Townsville Lowlands.

The Wet Tropics rain forests are distributed along a north–south span of coastal ranges approximately 500 km in length (Fig. 1), with the presence of forest habitats throughout the area largely controlled by rainfall (Moritz *et al.*, 2009). Various authors have tested hypotheses about the role of habitat contraction, fragmentation and expansion in shaping the spatial distribution of diversity of the area (e.g. Hugall *et al.*, 2002; Dolman & Moritz, 2006; Moussalli *et al.*, 2009; Bell *et al.*, 2012). Palynological data and palaeoclimate modelling both indicate that these forests underwent significant contractions and expansions throughout the Pleistocene; temperature and rainfall were greatly reduced at the Last Glacial Maximum (LGM, 18 ka), which was followed by an Early Holocene cool-wet phase (Pleistocene–Holocene Transition, PHT, 8–7.5 ka) and a warm-wet phase (Holocene Climatic Optimum, HCO, 5–3.5 ka), prior to the establishment of the current climate (Kershaw & Nix, 1988; Hugall *et al.*, 2002; Moritz *et al.*, 2009; VanDerWal *et al.*, 2009). Researchers have demonstrated that rain forest refugia have persisted throughout these climatic changes in some areas of the Wet Tropics, particularly in areas of high elevation (Fig. 2), whereas in other areas rain forest has been less stable (Graham *et al.*, 2006, 2010; Hilbert *et al.*, 2007). Therefore, this system is ideal for testing the hypothesis that areas in which refugia of suitable habitat persisted during restrictive climatic



**Figure 2** Elevation across the Wet Tropics.

regimes currently harbour higher levels of biodiversity than areas from which suitable habitat disappeared.

Williams & Pearson (1997) proposed the hypothesis that differential local extinction during periods of rain forest contraction has shaped levels of endemism in vertebrates of the Wet Tropics. Graham *et al.* (2006) used palaeoclimate modelling to examine the relationship between the diversity of the region's vertebrate fauna and stability of rain forest habitat, represented by a sum of habitat suitability across the LGM, PHT, HCO and present conditions. They found a positive correlation across subregions of the Wet Tropics, and demonstrated that while this metric of stability was a significant predictor of diversity across birds, mammals, reptiles, aquatic-breeding frogs and terrestrial-breeding microhylid frogs, its explanatory power was strongest for the dispersal-limited microhylid frogs. Dispersal-limited short-range endemic taxa are expected to be more vulnerable to local extinction than vagile groups, and less likely to recolonize areas from which they are extirpated (MacArthur & Wilson, 1967). Therefore, the spatial distribution of present-day diversity in such groups should be strongly influenced by the location of historical refugia. In the current study, we focus on the role of refugia in shaping the diversity of an extraordinarily dispersal-limited group of animals, the mite harvestmen.

Mite harvestmen are a suborder of tiny arachnids with extremely limited dispersal abilities; each species is known from a range typically only 20–50 km in its largest dimension. Australia is home to two genera of mite harvestmen from the Gondwanan family Pettalidae Shear, 1980, one endemic to Western Australia and the other endemic to Queensland. Each of these genera is strongly supported as monophyletic in all analyses of molecular data, although they are likely not sister taxa (Boyer & Giribet, 2007, 2009; Giribet *et al.*, 2012; Boyer *et al.*, 2015). The Queensland genus *Austropurcellia* Juberthie 1988 is an ancient lineage, estimated to have originated during the Cretaceous (Giribet *et al.*, 2012). As such, we expect that most cladogenetic events within *Austropurcellia* pre-date the Pleistocene glacial cycles, and unpublished work in the lab of SLB supports this expectation. Because this group is dispersal-limited, we expect that the distribution of diversity of these animals across a region will have been strongly shaped by differential local extinction. That is, areas that encompass the locations of historical refugia should harbour higher diversity than areas that lacked refugia during restrictive climatic regimes.

The majority of *Austropurcellia* species are found in the Wet Tropics, especially in upland areas (Fig. 2), with a handful of additional species from outside of the Wet Tropics known from humid forests in Central and Southeast Queensland (Boyer *et al.*, 2015). This group has received very little attention from taxonomists until recent years, with over half of the named species described in 2012 and later (Boyer & Reuter, 2012; Popkin-Hall & Boyer, 2014; Boyer *et al.*, 2015). Despite a lack of taxonomic work, hundreds of museum collections of these animals exist, thanks in large part to ambitious entomological surveys of the Wet Tropics carried out

by the Queensland Museum in the 1980s–1990s (Yeates *et al.*, 2002; Yeates & Monteith, 2008). Work in the lab of one of the authors (SLB) has resulted in distribution maps for the 15 described species as well as seven currently undescribed mite harvestman species from the Wet Tropics, comprising the first detailed biogeographical survey of these animals.

We used our distribution data to generate a model of climatic suitability for *Austropurcellia*, and projected this model onto palaeoclimate data layers from the LGM, PHT, HCO and the present, resulting in maps quantifying geographical patterns of climatic suitability for *Austropurcellia* over time. Using species distribution data and new molecular phylogenetic data, we then explored the relationship of current and historical patterns of climatic suitability to species richness and phylogenetic diversity across different subregions of the Wet Tropics.

## MATERIALS AND METHODS

### Sampling

The specimens for this study were obtained through fieldwork by SLB, CMB and collaborators as well as loans from the collections at the Field Museum of Natural History, the Western Australia Museum, the California Academy of Sciences, the Museum of Comparative Zoology at Harvard University, the Musée D'Histoire Naturelle Genève, the Australian National Insect Collection, and, most importantly, the Queensland Museum (QM). The specimens had been collected by means of Berlese funnels or directly sifted from leaf litter. We examined a total of 231 collections of *Austropurcellia* from the Wet Tropics, and also considered information on type localities available in species descriptions. A complete table of specimens and localities is available upon request from SLB.

We are confident that we now know the vast majority (i.e. c. 95%) of the *Austropurcellia* species in the Wet Tropics (Boyer *et al.*, 2015; Popkin-Hall & Boyer, 2014; Boyer & Reuter, 2012, and one manuscript currently submitted). Consultation with Queensland entomologist Geoff Monteith, who led QM leaf-litter arthropod surveys for multiple decades and continues to serve as the focal contact for entomologists visiting Northern Queensland, has bolstered our confidence that our current survey does not exclude significant areas that might include unknown diversity, and that it accurately represents the relative diversity of subregions. The only subregion that we consider currently under-sampled to the point that it likely harbours multiple unknown species is the Finnigan Uplands. Very few biologists have collected in this area, as there are no marked trails or access points. We have recently described two new *Austropurcellia* from this subregion (manuscript submitted), and the models generated in the current study indicate that this subregion is highly climatically suitable for the animals. We note that we used multiple strategies in our analyses of diversity that should

help to address the issue of uneven sampling across subregions. First, we performed all of our analyses under two different geographical binning schemes, one in which each subregion is considered individually and one in which we combined adjacent subregions that share species (such as the Finnigan and Thornton Uplands) into larger geographical bins. Second, we performed a subset of our analyses excluding areas of zero richness. Although the models generated in the current study and extensive ground-truthing by SLB, CMB and collaborators both corroborate the low diversity of these areas, we recognize that establishment of absence is difficult if not impossible to achieve, especially for cryptic organisms.

### Specimen identification

Specimens were sorted under an Olympus SZX10 light microscope (Olympus Corporation, Tokyo, Japan). In many cases, examination with scanning electron microscopy was necessary for species identification. In these instances, one male was dissected so that its appendages were mounted on one stub and its body was mounted in ventral view on another. Details of key anatomical characters and SEM methodology followed Boyer *et al.* (2015). Collections of female and juvenile mite harvestmen are not identifiable to species as only males bear species-specific morphological characters. Therefore, locality data from collections of females and/or juveniles only were included for the purposes of building models of climatic suitability, and not used for analyses of biodiversity unless they had been identified using molecular data in previous studies (Boyer *et al.*, 2015) or unpublished work in progress.

### Ecological niche modelling and calculation of relative stability

We compiled latitude and longitude information for every known georeferenced *Austropurcellia* collection from the Wet Tropics. Of the 231 collections examined, 103 represented unique georeferenced localities. To generate ecological niche models, coordinates for presence data and spatial data layers were imported into MAXENT 3.3.3e (Phillips *et al.*, 2006). Seventy-five per cent of coordinate points were used as training data for generating the model, while the remaining 25% were used as test points to assess the accuracy of the model. Data layers for present-day conditions included the standard 19 bioclimatic ('BIOCLIM') data layers. The area under the curve (AUC) for training data was 0.951 and 0.949 for test data, indicating that our model accurately predicts *Austropurcellia*'s distribution. The resulting model was projected on palaeoclimate data layers for Northern Queensland at 250-m resolution. The palaeoclimate layers included at each time point were annual mean temperature, annual mean precipitation, precipitation of the driest quarter, precipitation of the wettest quarter, temperature of the warmest quarter and temperature of the coldest quarter. Following Graham *et al.*

(2006), time points used in this study represent the LGM (18 ka), the PHT (7.5 ka), the HCO (5 ka) and the present. The past time points represent cool-dry, warm-wet and cool-wet periods relative to the present climate, and therefore, represent a diverse set of climatic departures from current conditions.

ASCII files of model output from every time point were imported into ARCGIS 9.3 (ESRI, Redland, CA, USA) and converted to raster layers. For any given point on the map, suitability for each time point ranged from 0 (entirely unsuitable) to 1 (entirely suitable). The suitability values for the four time points were summed, resulting in a metric of mean suitability over time or 'stability' (*sensu* Graham *et al.*, 2006) that ranged from 0 to 4.

### Geographical binning of data

We divided the Wet Tropics into the subregions of Williams & Pearson (1997) which represent a modification of the areas identified by Winter (1984) based on mammal distributions (Fig. 1). In 2002, Yeates *et al.* (2002) used a parsimony analysis of endemism to group some of these subregions into broader areas of endemism. This work was based on distributions of flightless insects, and therefore we expect these groupings be particularly relevant for defining biologically meaningful geographical units for dispersal-limited leaf-litter arachnids.

We performed two analyses of our dataset. In the first, we binned our data by the subregions of Williams & Pearson (1997), which we subsequently refer to as the 'standard subregions.' In the second, we combined sets of 2–3 subregions that (1) are geographically adjacent to each other, (2) cluster together in the parsimony analysis of endemism of Yeates *et al.* (2002) and (3) share at least one species of *Austropurcellia*. Using these criteria, we combined the following sets of subregions: Finnigan Uplands and Thornton Uplands; Windsor Uplands and Carbine Uplands; Atherton Uplands, Bellenker Mt/Bartle Frere, and Lamb Uplands; and Spec Uplands and Halifax Uplands (Fig. 1). We refer to the geographical binning scheme that combines those subregions into single units as using 'combined subregions.'

Under each geographical binning scheme, we calculated mean climatic suitability of each geographical bin during the present-day, LGM, PHT and HCO, as well as mean stability.

### Calculation of diversity metrics

In ARCGIS 9.3 (ESRI), we imported the distribution data for every collection identifiable to species. For each geographical bin (subregion or combined set of subregions), we calculated the number of species and phylogenetic diversity. Phylogenetic diversity for each geographical bin was calculated using an ultrametric tree, following methods described below.

We constructed a phylogeny for *Austropurcellia* using previously published mitochondrial DNA sequence data for 13 species and new data for three species, representing in total

16 of the 22 known Wet Tropics species (15 described and seven undescribed, unpublished data of SLB), as well as two species from southern Queensland. Previously published sequences were drawn from the datasets published by Boyer *et al.* (2015); new sequence data are available on GenBank, accession numbers KU195677–KU195685. We used data from two mitochondrial loci, COI (789 bp) and 12S (407 bp); methods for DNA extraction and PCR followed Boyer *et al.* (2015). Models for sequence evolution were chosen in jMODELTEST (Posada, 2008). The model for each COI codon position was GTR + I + G, and the model for 12S was TPM1f + G. For analyses in BEAST 1.7 (Drummond *et al.*, 2012), we used unlinked substitution rates and base frequencies for each data partition, estimated base frequencies, and four gamma categories. We used a lognormal relaxed clock with linked clock models and trees. Speciation was modelled as birth–death with incomplete sampling. The analysis was run for 100 million generations, with the first 10 million discarded as burn-in. The consensus tree was rooted with a split between a clade that includes two species from Southeast Queensland and *A. clousei* (the southernmost Wet Tropics species for which DNA sequence data are available) and a clade that includes the remaining Wet Tropics species, based on previous phylogenetic analysis of the genus (Boyer *et al.*, 2015).

Six species currently lack molecular data, and therefore were not included in the phylogeny. In these cases, we estimated the phylogenetic distance that would be contributed by the species in question. We did so by assigning placement of lineages within our phylogeny, based on shared morphological characters and geographical location of species' ranges. For example, there is no DNA sequence data for *Austropurcellia woodwardi* from the Atherton subregion (Fig. 1), but it is morphologically similar to *A. despectata* and both species are from the central Wet Tropics. Previous research has demonstrated that *Austropurcellia* species from the central Wet Tropics form a well-supported monophyletic clade (Boyer *et al.*, 2015), and that all of the species in the clade share key morphological characters. Therefore, we assigned *A. woodwardi* a placement within the central Wet Tropics clade that reflects both its geographical location and its morphological affinities. Using similar reasoning, we assigned placement within our phylogeny to undescribed species from Roaring Meg Creek, Mount Finnigan, the Black Mountain Range and Mount Elliot.

### Regression analyses

We compared the power of present-day mean climatic suitability, LGM mean habitat suitability and mean stability (summed mean suitability) to predict spatial variation in *Austropurcellia* diversity. We performed linear regressions in JMP 12.1 (SAS Institute, Inc., Cary, NY, USA) on both number of species and phylogenetic diversity using each of those predictors under both of our geographical binning schemes (standard subregions or combined subregions). In the case of

significant correlations between diversity and more than one of our predictive variables, we performed a backward multiple regression to identify which variable was the best predictor of diversity. In order to correct for spatial autocorrelation, we found the geographical mid-point of each geographical bin and used SAM: Spatial Analysis in Macroecology 4.0 (Rangel *et al.*, 2010) to calculate corrected p-values for each regression based on the geographically effective degrees of freedom.

Because we incorporated specimens collected by a variety of different researchers with different goals and following different protocols, we do not consider absence data or collecting effort in the current study. In the vast majority of cases (including our own collecting work), researchers' sampling effort was not standardized to a volume of leaf litter or number of person-hours per locality, rendering it unsuitable for assessing abundance or establishing absence. Therefore, in the case of significant correlations between diversity and predictive variables, we performed an additional regression analysis excluding areas of zero richness.

## RESULTS

### Species ranges and phylogenetic relationships

Half of all Wet Tropics *Austropurcellia* species (11 of 22) have ranges restricted to a single subregion. An additional seven are restricted to two subregions, three species have ranges that include three subregions, and *A. vicina* is the most widespread species, found in five subregions (Fig. 3).

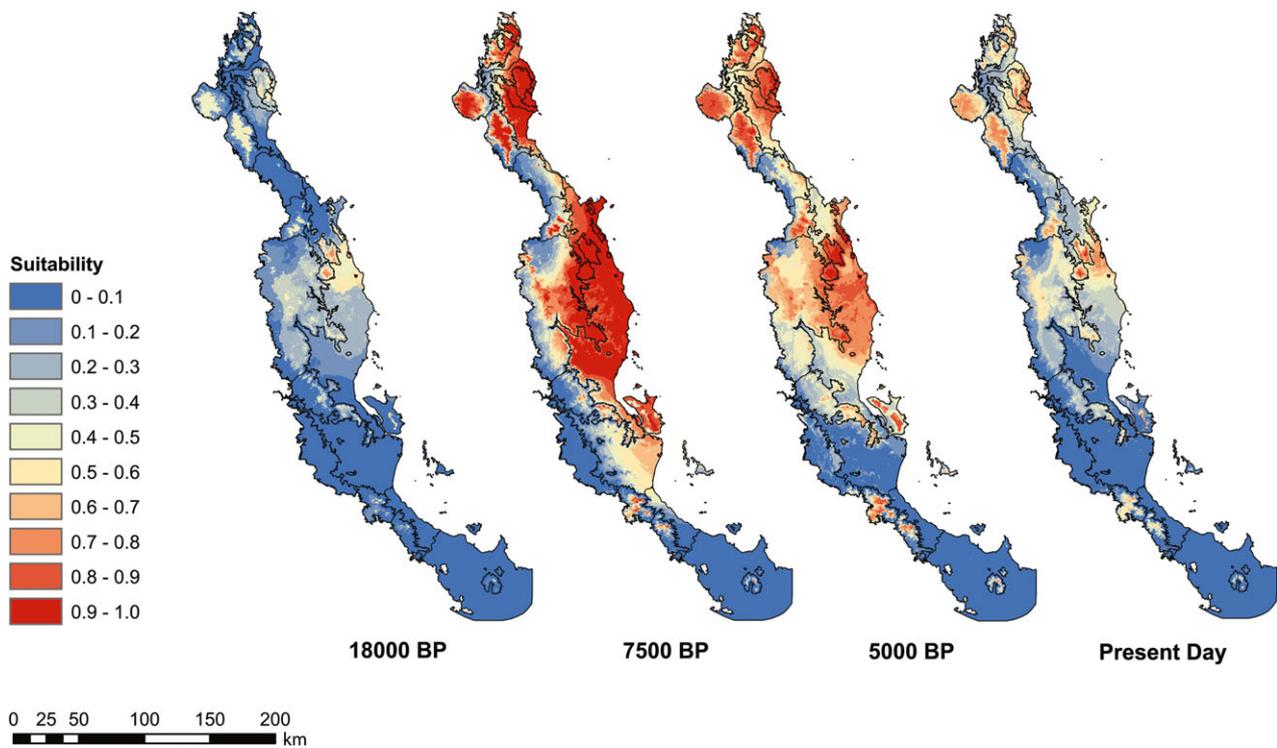
Relationships among species reflect previous findings (Boyer *et al.*, 2015), and placement of the three taxa previously lacking molecular data affirm the propensity for geographically proximate species to be closely related (Fig. 3). *Austropurcellia forsteri* is closely related to *A. arcticosa* and *A. giribeti*, with all three occurring in the Thornton Lowlands and adjacent upland areas. *A. n. sp.* Baldy Mountain is closely related to other species from the Atherton Uplands. *A. n. sp.* Lamb Range is sister to *A. culminis*, a clade which is in turn sister to *A. vicina*, whose species range includes the Lamb Uplands.

### Modelling of suitable climatic conditions

Modelling of suitable climatic conditions for *Austropurcellia* indicated very large contributions from two variables related to precipitation. The relative contribution to the model of precipitation of the driest quarter was estimated at 35.5%, and relative contribution of annual mean precipitation was estimated at 34.4%.

Projections of our model of climatic suitability onto different time slices revealed a history of expansion and contraction of areas of climatic suitability, with the greatest extent and connectivity of climatically suitable areas during the wet, cool period (7.5 ka) and greatest contraction and fragmentation of climatically suitable areas during the LGM (18 ka)





**Figure 4** Predicted distribution of climatic suitability during cool-dry (LGM, 18 ka), cool-wet (7.5 ka), warm-wet (5 ka), and present-day climates.

caused these relationships to lose significance. We found positive and significant relationships between mean suitability of subregions during the LGM and both number of species and phylogenetic diversity. While this result was robust to correction for spatial autocorrelation (Table 1), it was not robust to exclusion of subregions lacking *Austropurcellia*.

#### Diversity analyses with combined subregions

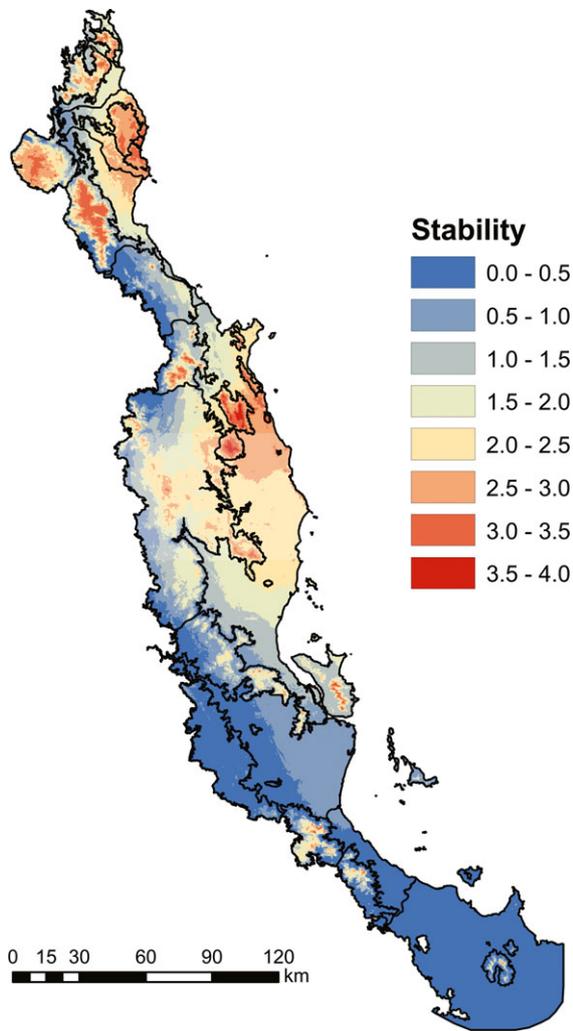
Our second analysis combined some of the 'standard' Wet Tropics subregions of Williams & Pearson (1997) and Winter (1984) into larger geographical bins based on areas of flightless insect endemism (Yeates *et al.*, 2002). We tested for a relationship between number of species per geographical bin and area of geographical bin, and found no relationship when we included all bins ( $R^2 = 0.073$ ,  $P = 0.3$ ) or when we included only bins in which *Austropurcellia* is present ( $R^2 = 0.201$ ,  $P = 0.1$ ). Similarly, there was no relationship between phylogenetic diversity per geographical bin and area ( $R^2 = 0.023$ ,  $P = 0.6$  for all geographical bins;  $R^2 = 0.127$ ,  $P = 0.3$  for only geographical bins containing *Austropurcellia*). Therefore, we did not correct for area in subsequent analyses.

We found a positive and significant relationship between our diversity metrics and mean stability; however, this relationship was not significant at the  $P < 0.05$  level when analyses were corrected for spatial autocorrelation. We found positive and significant relationships between diversity and

mean suitability of geographical bins during both the present and the LGM, and both of these results were robust to correction for spatial autocorrelation. The relationship between phylogenetic diversity and mean present suitability was significant when geographical bins lacking *Austropurcellia* were excluded ( $R^2 = 0.426$ ,  $P = 0.02$ ), while the relationship between number of species and mean present suitability lost significance when areas lacking *Austropurcellia* were excluded ( $R^2 = 0.315$ ,  $P = 0.06$ ). However, the relationship between both measures of diversity and mean climatic suitability during the LGM was robust to the exclusion of areas lacking *Austropurcellia* ( $R^2 = 0.428$ ,  $P = 0.02$  for number of species;  $R^2 = 0.432$ ,  $P = 0.02$  for phylogenetic diversity). Finally, a stepwise regression confirmed that mean suitability during the LGM is the best predictor of both number of species and phylogenetic diversity.

#### DISCUSSION

Modelling of suitable climatic conditions for *Austropurcellia* reveals an archipelago of 'islands' of suitability within the Wet Tropics, with variables related to precipitation contributing nearly 70% of the information in the model. When we projected this model of climatic suitability for *Austropurcellia* onto palaeoclimate data layers, we found that the size and connectivity of these islands has changed under different climatic regimes. During the warm-wet Holocene Climatic Optimum (5 ka) and the cool-wet Pleistocene–Holocene



**Figure 5** Relative stability, represented by the sum of climatic suitability summed over time periods from the LGM through the present (Fig. 4).

transition (7.5 ka) areas of climatic suitability for *Austropurcellia* were more extensive and more connected than they are today. During the cool-dry Last Glacial Maximum (LGM, 18 ka), areas of climatic suitability were contracted and fragmented relative to their present-day extent (Fig. 4). Several previous studies have also found evidence for multiple forest refugia scattered throughout the Wet Tropics during the

LGM based on such diverse sources as pollen data (Kershaw, 1994; Schneider & Moritz, 1999), palaeoclimate modelling (Nix, 1991; VanDerWal *et al.*, 2009) and phylogeographical patterns (Schneider *et al.*, 1998; Schneider & Moritz, 1999; Hugall *et al.*, 2002).

Summation of suitability across four climatically divergent time slices demonstrates that upland areas have had higher mean climatic suitability over time than lowland areas (Figs 2, 4 and 5). VanDerWal *et al.* (2009) predicted that within the Wet Tropics species richness should be lower in lowland rain forest and higher in upland taxa owing to the severe contractions of the lowland rain forest during the LGM, and our results are in line with that prediction.

Our analyses indicate that climatic suitability during the LGM is the best predictor of present-day diversity, outperforming present-day climatic suitability and our stability metric. This result holds whether data are binned geographically using the standard Wet Tropics subregions or when some of those subregions were combined into larger geographical units. However, the most dramatic gain in predictive power of LGM mean climatic suitability relative to present-day mean climatic suitability is seen when some subregions are combined (Table 1). While the standard Wet Tropics subregions were established based on the distribution of mammals across the region, our combination of selected adjacent subregions into larger geographical bins is based both on distribution of *Austropurcellia* species (subregions were combined only when they share a species), and on the areas of endemism found by Yeates *et al.* (2002) in their study of flightless insect diversity across the Wet Tropics. We expect the areas of endemism discovered in small-bodied, dispersal-limited terrestrial arthropods to provide a particularly biologically relevant geographical context in which to analyse data for mite harvestmen, and our results support this expectation. Additionally, we find that consideration of phylogenetic diversity rather than a simple count of the number of species provides a tighter correlation with our predictive variables in all cases (Table 1). Phylogenetic diversity incorporates an explicit consideration of history, effectively reducing the diversity “score” for areas that contain a large number of closely related species, and raising it for areas that contain a small number of distantly related species. This effect can be seen in the two areas that have the highest mean climatic suitability during the LGM, one of which

**Table 1** Results of regression analyses under two geographical binning schemes. Bold indicates results that were robust to correction for spatial autocorrelation (significance values given in columns labelled *Corr. p*). Underlining indicates results that were robust to the exclusion of areas of zero diversity.

	Standard subregions						Combined subregions					
	Number of species			Phylogenetic diversity			Number of species			Phylogenetic diversity		
	<i>R</i> <sup>2</sup>	<i>p</i>	<i>Corr. p</i>	<i>R</i> <sup>2</sup>	<i>P</i>	<i>Corr. p</i>	<i>R</i> <sup>2</sup>	<i>p</i>	<i>Corr. p</i>	<i>R</i> <sup>2</sup>	<i>p</i>	<i>Corr. p</i>
Present-day suitability	0.301	0.008	0.06	0.440	<0.001	0.06	<b>0.383</b>	<b>0.008</b>	<b>0.02</b>	<b>0.488</b>	<b>0.002</b>	<b>0.02</b>
LGM suitability	<b>0.324</b>	<b>0.006</b>	<b>0.02</b>	<b>0.356</b>	<b>0.003</b>	<b>0.02</b>	<b>0.559</b>	<b>&lt;0.001</b>	<b>0.01</b>	<b>0.588</b>	<b>&lt;0.001</b>	<b>0.002</b>
Stability	0.321	0.006	0.05	0.399	0.002	0.06	0.265	0.04	0.08	0.376	0.009	0.06

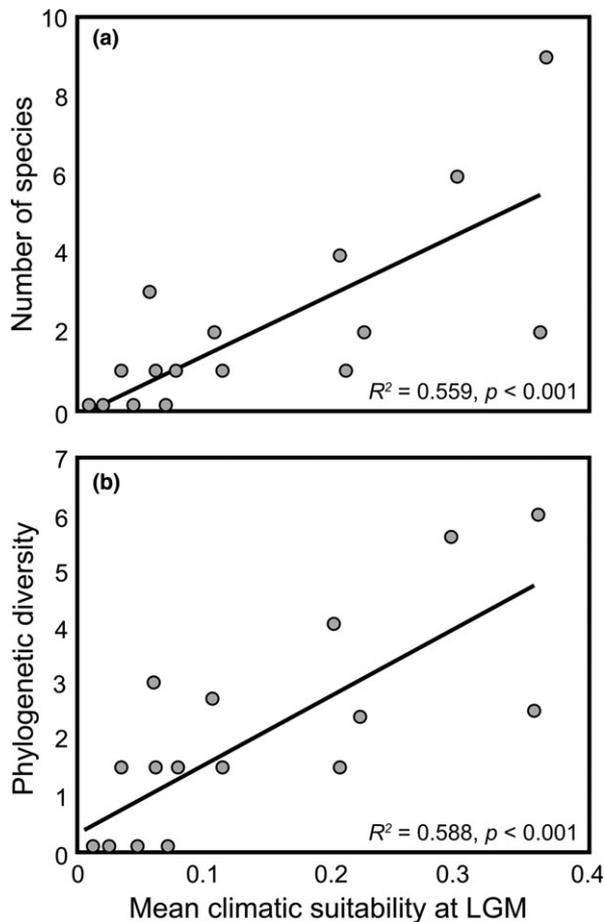
(AU+BK+LU) harbours a high number of closely related species, while the other (MT) harbours two species that are not each other's closest relatives. These two areas had very similar mean climatic suitability during the LGM, and the differences between their diversity 'scores' becomes smaller when phylogenetic diversity is taken into account than it is when species are merely counted (Figs 4 and 6).

Following Graham *et al.* (2006), we considered the sum of climatic suitability across four different time slices to represent a metric of 'stability' of climatic suitability over time. This metric predicted diversity, but the result was not robust to correction for spatial autocorrelation or exclusion of areas that are totally uninhabited by *Austropurcellia*. In addition, we note that the  $R^2$  values associated with the correlation between stability and diversity are lower in most of our analyses than the  $R^2$  values associated with present-day mean climatic suitability and LGM mean climatic suitability. This could be due to the inclusion in the stability metric of time slices when areas inhabitable by *Austropurcellia* were much more widespread than they are today due to increased rain-

fall. That is, today's distribution of climatically suitable areas could be considered refugial relative to the distribution of suitable areas during the high-rainfall HCO and PHT. Therefore, we would expect a metric influenced by those climatically 'favourable' or 'permissive' time periods to provide weaker predictions of current diversity than a measure of LGM suitability alone. We acknowledge the caveat that although the term 'stability' has been used in the current study and others (e.g. Graham *et al.*, 2006; Carnaval *et al.*, 2009) to describe a sum of suitability scores across time slices, it does not represent a measure of variance. That is, an area that has been very suitable during a number of periods and very unsuitable during an equal number of time periods could receive the same 'stability' score as an area that has been moderately suitable during all time periods. As such, the use of the term 'stability' to describe this metric is potentially misleading.

Our results extend the paradigm established by Graham *et al.* (2006), which demonstrated that within the Australian Wet Tropics, the historical distribution of rain forest habitat is a more powerful predictor of diversity for dispersal-limited organisms such as microhylid frogs than it is for vagile organisms such as birds. Mite harvestmen are extremely dispersal-limited animals, with most species known from only a handful of localities within a 50-km radius (e.g. Boyer & Giribet, 2009; Boyer & Reuter, 2012). In this group, widespread species are the exception rather than the rule, and in cases where researchers have performed population genetic analyses of such widespread 'species,' cryptic species have been either revealed (Clouse & Wheeler, 2014) or suggested (Boyer *et al.* 2007; Fernandez & Giribet, 2014). Therefore, we expect that these animals should be particularly vulnerable to extinction when suitable habitats contract. Although Graham *et al.* (2006) explored the relationship between habitat history and diversity, our study is the first to incorporate a phylogenetic component into calculation of levels of diversity across the Wet Tropics and thereby explicitly incorporate an historical element into that calculation. Our results support the findings of Edward (2011), who suggested based on a qualitative assessment that both the highest number of species and the highest phylogenetic diversity of Wet Tropics goblin spiders coincide geographically with the areas of stable rain forest habitat identified by Graham *et al.* (2006).

Despite the Wet Tropics' status as a biodiversity hotspot and the considerable attention paid to the region by evolutionary biologists, much of the invertebrate fauna remains woefully understudied. Work on flightless insects has demonstrated that rates of subregional endemism are much higher in these groups than in vertebrates (Yeates *et al.*, 2002), highlighting the outstanding opportunities that arthropods offer to students of biodiversity working in the region. There are a few notable biogeographical studies of invertebrates from the area; for example, work on dung beetles has demonstrated a break between species that coincides geographically with a major genetic break found in many Wet Tropics vertebrates, occurring at the Black Mountain



**Figure 6** Diversity of geographical bins (subregions or combined subregions) in relation to mean climatic suitability during the Last Glacial Maximum (LGM) (Fig. 4). (a) Number of species versus mean climatic suitability during the LGM. (b) Phylogenetic diversity of species versus mean climatic suitability during the LGM.

Corridor (Bell *et al.*, 2004, 2007). Additionally, a pioneering study by Hugall *et al.* (2002) related genetic divergences within the terrestrial gastropod *Gnarosiphia bellendenkerensis* to many small refugia predicted to have existed during the LGM – and perhaps during earlier periods of climatic oscillation throughout the Quaternary.

Dispersal-limited arachnids have excellent potential for studies of biogeographical history. For example, such short-range endemics (*sensu* Harvey, 2002) have been used to test the Gondwanan vicariance hypothesis (Boyer & Giribet, 2007), the New Zealand Oligocene drowning hypothesis (Boyer & Giribet, 2009), the museum model of biodiversity preservation in African tropical forests (Murienne *et al.*, 2013) and the role of aridification in diversification of forest-restricted animals across Queensland (Rix & Harvey, 2012a). Arachnologists have recently published authoritative accounts of the diversity of Wet Tropics goblin spiders (Edward & Harvey, 2014) and assassin spiders (Rix & Harvey, 2012b), laying groundwork that could support comparative studies of animals that are co-distributed with and ecologically similar to *Austropurcellia*. We hope that our study will encourage such future work on the evolutionary history of the arachnid fauna of the Wet Tropics.

Prior to 2012, there were only five species of mite harvestmen described from Queensland. Work by SLB, CMB and collaborators has resulted in an additional ten described and seven undescribed species known from the Wet Tropics, plus three from further south in Queensland. The current study would not have been possible without years of collecting effort and taxonomic work on these animals, highlighting the important role of biodiversity discovery in furthering our understanding of the evolutionary dynamics driving biogeographical patterns.

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## BIOSKETCH

**Sarah Boyer** is broadly interested in the systematics and biogeography of terrestrial and freshwater invertebrates. Discovering, describing and understanding the biodiversity of Southern Hemisphere harvestmen is the main focus of her research programme.

Author contributions: T.M.M. and A.M.L. performed geographical analyses; C.M.B. performed fieldwork, generated preliminary data, and performed exploratory analyses; K.H.K. helped to develop the conceptual framework for the project. S.L.B. conceived the ideas, supervised and performed fieldwork and lab work, conducted analyses and wrote the manuscript.

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