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Variable responses of skinks to a common history of rainforest fluctuation: concordance between phylogeography and palaeo-distribution models

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Abstract

There is a growing appreciation of impacts of late-Quaternary climate fluctuations on spatial patterns of species and genetic diversity. A major challenge is to understand how and why species respond individualistically to a common history of climate-induced habitat fluctuation. Here, we combine modelling of palaeo-distributions and mitochondrial-DNA phylogeographies to compare spatial patterns of population persistence and isolation across three species of rainforest skinks (*Saproscincus* spp.) with varying climatic preferences. Using Akaike Information Criterion model-averaged projections, all three species are predicted to have maintained one or more small populations in the northern Wet Tropics, multiple or larger populations in the central region, and few if any in the south. For the high-elevation species, *Saproscincus czechurai*, the warm–wet climate of the mid Holocene was most restrictive, whereas for the generalist *S. basiliscus* and lower-elevation *S. tetradactyla*, the cool–dry last glacial maximum was most restrictive. As expected, *S. czechurai* was the most genetically structured species, although relative to modelled distributions, *S. basiliscus* had surprisingly deep phylogeographical structure among southern rainforest isolates, implying long-term isolation and persistence. For both *S. basiliscus* and *S. tetradactyla*, there was high genetic diversity and complex phylogeographical patterns in the central Wet Tropics, reflecting persistence of large, structured populations. A previously identified vicariant barrier separating northern and central regions is supported, and results from these species also emphasize a historical persistence of populations south of another biogeographical break, the Tully Gorge. Overall, the results support the contention that in a topographically heterogeneous landscape, species with broader climatic niches may maintain higher and more structured genetic diversity due to persistence through varying climates.

Keywords: palaeoclimate, palaeo-distribution, phylogeography, pleistocene refugia, tropical rainforest

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Introduction

It is becoming increasingly obvious from fossil, palaeoecological and phylogeographical evidence that the climate fluctuations of the Quaternary had dramatic effects on the distributions of organisms, which is reflected currently in spatial patterns of species and genetic diversity (Hewitt 2000; Jansson & Dynesius 2002). From these same sources, it is also evident that species varied in their spatial and temporal scale of response to common histories of habitat fluctuation, such that community composition is highly dynamic (see Graham *et al*. 1999; Jackson & Overpeck 2000; Ponel *et al*. 2003; Jackson 2004; Albino 2005; Barnosky & Shabel 2005). Beyond describing varying scales of response, a major challenge is to identify ecological traits that predict sensitivity to past climate-induced habitat change. Obvious candidates include dispersal ability, area requirements,

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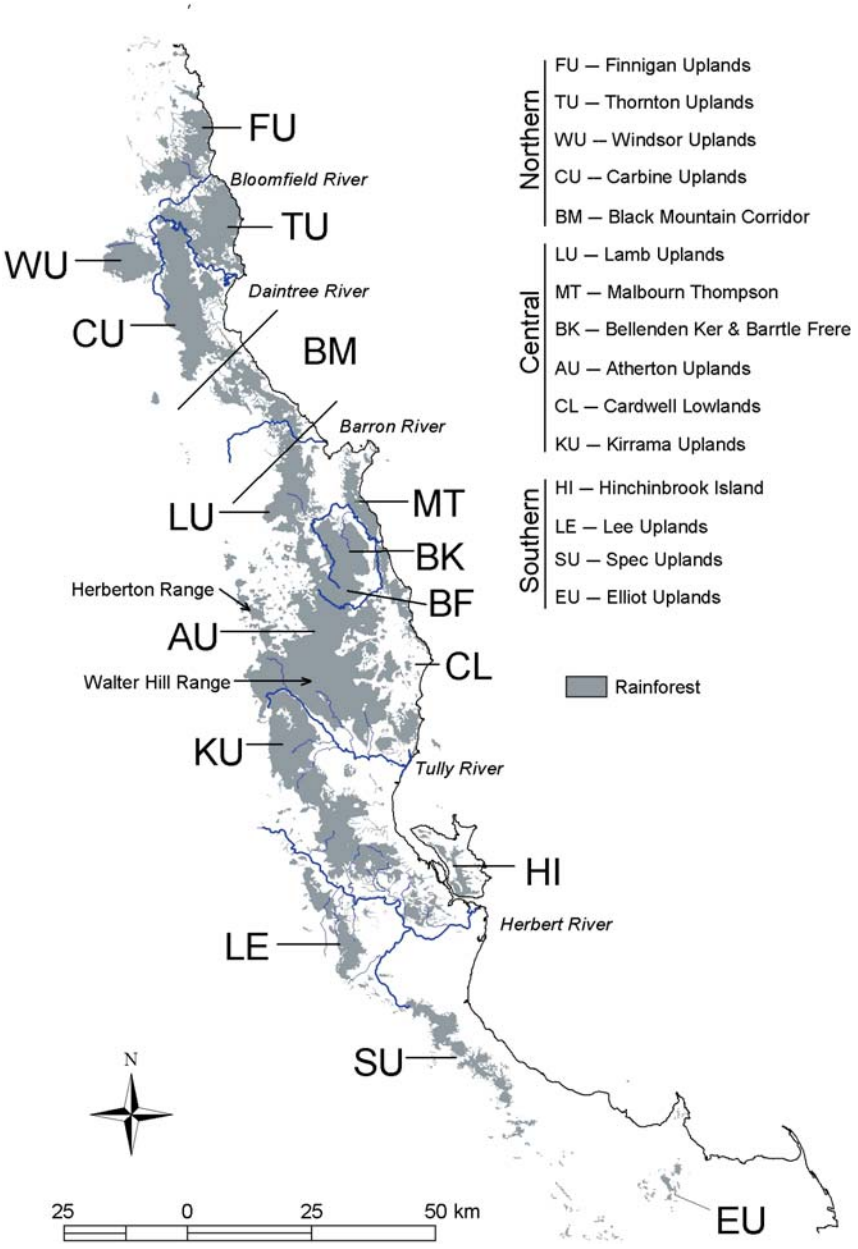

Fig. 1 Distribution of rainforest within the Wet Tropics study region with recognized bioregions designated following Williams & Pearson (1997).

habitat specialization and climate specialization. Recently, much has been made of the effects of physiological limitations and 'niche conservation' in promoting isolation and divergence in topographically complex environments, especially in the tropics (Janzen 1967; Wiens & Graham 2005; Ghalambor *et al*. 2006; Kozak & Weins 2007). In topographically complex areas, maximum diversity is expected for species with persistently subdivided populations. Given low dispersal and small area requirements, this is expected for species occupying intermediate climatic niches, such that the species' range is fragmented in most climates but still persistent within refugia in restrictive climates. Species specialized to lowland climates should experience less isolation, whereas montane taxa will be strongly isolated but also more prone to local extinction under warmer or drier climates.

Here, we use a comparative approach to evaluate the effect of climatic niche specialization on responses of rainforest lizards to climate-driven fluctuation of the Australian Wet Tropics (WT) rainforests (Fig. 1). For this intensively studied system, palaeo-ecological evidence demonstrates alternating episodes of contraction of angiosperm rainforest to mesic peaks and adjacent coastal lowlands during cold–dry glacial periods and expansion under more permissive interglacials (reviewed in Kershaw *et al*. 2005). Modelling of upland rainforest habitats under restrictive (cold–dry, warm–wet) and permissive (cold–wet, current) late Quaternary climates predicts persistence of multiple, small refugia in the topographically complex northern WT, very restricted refugia in the south and larger, more connected refugia in the central WT (Nix 1991; Graham *et al*. 2006; Hilbert *et al*. 2007; VanDerWal *et al*., in press). The broad features of this refugial model are supported by a combination of phylogeography and palaeo-modelling for an endemic species of snail (Hugall *et al*. 2002) and reflected in patterns of species (Williams & Pearson 1997; Graham *et al*. 2006) and in phylogenetic (Bouchard *et al*. 2005; Moritz *et al*. 2005) and phylogeographical (Moritz *et al*. 2000; Bell *et al*. 2007) diversity. However, there are also striking differences among species phylogeographies, reflecting different spatial and temporal scales of response to this history of climate-driven rainforest fluctuation (see Schneider *et al*. 1998; Hugall *et al*. 2002). This has generally been attributed to differences in aspects of species' ecologies, but typically the species compared differ in too many ways to identify a causal factor. However, previous studies of species with similar dispersal potential and body size have pointed to increased specialization (to rainforest in birds, Joseph *et al*. 1995; to cooler climates in dung beetles, Bell *et al*. 2007) as a contributing factor.

We focus on three species of rainforest litter skinks (*Saproscincus*) that differ in elevational ranges and thermal physiology but are otherwise ecologically similar. Together with a species (*Saproscincus hannahae*) from rainforests to the south, these three taxa form the monophyletic 'northern clade' of this mesic forest genus (Moussalli *et al*. 2005). The most widespread, *S. basiliscus*, occurs from the southern extreme of the study region (Elliot Uplands, EU) to the Thornton Uplands (TU) in the north (Fig. 1) and is most abundant up to 1000 m above sea level (a.s.l.). Although predominantly associated with rainforest habitat, *S. basiliscus* can also be found in other mesic vegetation types such as riparian gallery forest, wet sclerophyll and vine thickets. The northernmost rainforests of the WT (Finnegan Uplands, FU, and adjacent Thornton lowlands, TL; Fig. 1) are occupied by the sister species, *S. lewisi* (Couper & Keim 1998; Moussalli *et al*. 2005), which is also considered here when relevant. The second focal species, *S. tetradactyla*, has a slightly more restricted latitudinal range [Carbine Uplands (CU) to Spec Uplands (SU)] and occurs mostly below 500 m a.s.l. The third, *S. czechurai*, is a high elevation (primarily > 600 m a.s.l.) specialist and ranges from the KU in the south to TU in the north. Both *S. tetradactyla* and *S. czechurai* are rainforest-restricted, predominantly to mesophyll and notophyll rainforest types, respectively.

To infer historical responses to rainforest fluctuation we combine statistical modelling of palaeo-distributions with analysis of mitochondrial-DNA (mtDNA) phylogeography (Hugall *et al*. 2002), an approach that is becoming increasingly used in historical biogeography (Cruzan & Templeton 2000; Carstens & Richards 2007; Jakob *et al*. 2007; Knowles *et al*. 2007). We derive models based on logistic regressions with the Akaike Information Criterion (AIC) model averaging to predict palaeo-distributions under glacial and interglacial climatic extremes, using palaeoclimate reconstructions for the last glacial maximum (LGM) and the mid-Holocene (Kershaw & Nix 1988) as representative palaeoclimate scenarios. We investigate two Holocene palaeoclimate scenarios, namely a cool–wet period and a warm–wet period occurring before and after the mid-Holocene, respectively. Although a number of studies within the WT have clearly shown that intraspecific divergences predate the Pleistocene in a number of rainforest associated taxa (e.g. Joseph *et al*. 1995; McGuigan *et al*. 1998; Schneider & Moritz 1999), palaeoclimate reconstructions for the LGM and the mid-Holocene provide a sound working model with which to investigate the distributional consequences of extreme climatic shifts during the Quaternary. We assess predicted palaeo-distributions in light of the distribution of sequence diversity and major phylogeographical lineages for the mitochondrial, protein-coding *ND4* gene. At a finer scale, we examine measures of genetic diversity and signatures of population expansion to assess demographic patterns associated with more recent glacial cycles.

Methods

Laboratory procedures and population genetic analyses

Tissues were obtained from surveys conducted during 1999–2005 as part of a broader biodiversity assessment program. Populations to be sequenced were chosen to represent topographically defined subregions across the full range of each species (Williams *et al*. 1996: Fig. 1), ideally with multiple geographically separate sites within each subregion. DNA extraction, amplification and sequencing procedures are described in Moussalli *et al*. (2005). Both forward and reverse sequences were obtained for the *ND4* subregion (plus three 3′ flanking *tRNAs*: *tHIS*, *tSER*, *tLEU*) for a total of 212 individuals across all species (*Saproscincus basiliscus*, $n = 139$; *S. tetradactyla*, $n = 35$; *S. czechurai*, $n = 38$) with most sequences spanning approximately 890 bp. In the case of *S. czechurai*, we identified sequences for individuals sampled from Bellenden Ker as pseudo-genes, with a 10 bp deletion occurring in positions [279 : 289] (nucleotide positions follow those in Kumazawa & Nishida (1995) for *Eumeces egregious*, GenBank Accession No. NC000888). To address this, we constructed both forward and reverse primers that incorporated the region of base deletion. Only the second segment of the *ND4* subregion (approximately 600 bp), however, was successfully amplified for this population. We checked the *ND4* protein-coding region against translated amino acid sequences using MEGA version 4.0 (Tamura *et al*. 2007). No premature stop codons were apparent, consistent with the assumption that *ND4* sequences represent functional copies that encode a protein. Sequences are lodged with GenBank, Accession Nos FJ195092–FJ195325.

Population genetic analyses were based on the Tamura–Nei model of sequence evolution, with estimates of nucleotide diversity (π) and net sequence divergences (d_A) among populations calculated in MEGA (Tamura *et al*. 2007). Analysis of molecular variance (AMOVA, Excoffier *et al*. 1992) was used to examine the degree of phylogeographical structuring. Isolation by distance (IBD) was assessed using the Mantel test, correlating population pairwise genetic distance (Slatkin's linearized F_{ST}) with the log of geographical distance between centroids of sampling localities. To test for historical demographic expansion we used Fu's F_S neutrality statistic, which measures departure from expectations of selective neutrality and population equilibrium (Fu 1997). AMOVAs, tests for IBD and population expansion were conducted in Arlequin 3.11 (Excoffier *et al*. 2005) for each bioregion within the WT (Williams & Pearson 1997; Fig. 1) for which we had a sample size of five or more individuals. For these tests, statistical significance was evaluated relative to 1000 simulated samples. To test the robustness of major clades we applied Bayesian phylogenetic methods (MrBayes 3.12, Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003), using a slightly more parameter-rich model of sequence evolution (GTR) than that employed for the population genetic analyses. We chose the GTR model as it represents the closest approximation of the Tamura–Nei model in MrBayes. Two simultaneous runs were executed with convergence determined via an assessment of average standard deviation of split frequencies (< 0.01).

Modelling current distributions

We compiled occurrence points for all species of *Saproscincus* from museum records (Queensland Museum) and recent biodiversity survey records (S. E. Williams, unpublished results). All records were examined for geo-referencing or species identification errors (Couper & Keim 1998) prior to use. We modelled current species distributions using logistic regressions and pseudo-absence methodology (Ferrier & Watson 1997; Zaniewski *et al*. 2002), with the number of pseudo-absence records determined by the proportion of rainforest vs. non-rainforest vegetation types within the spatial extent of the WT (approximately 1 : 4.5). We considered two primary climate covariates, rainfall and temperature, but because the importance of each covariate potentially varies depending on the season, we investigated a total of eight climate indices, namely, mean temperature and total precipitation of the wettest (TWeQ, PWeQ), driest (TDQ, PDQ), warmest (TWaQ, PWaQ) and coldest quarters (TCQ, PCQ). All climate surfaces were based primarily on the WT 80 m Digital Elevation Model (WT DEM; Accad 1999) and derived using ANUCLIM (Houlder *et al*. 2000). Spatial extrapolation to the region south of the Paluma Ranges, namely the Elliot Uplands (see Fig. 1), was accommodated by combining the WT 80 m DEM with the GEODATA 9-sec (250 m) DEM (AUSLIG 2001).

To reduce redundancy and potential colinearity, we derived an all-subset candidate set of models such that only one temperature and one rainfall covariate was considered at any one time. Both linear or second-order polynomials were examined for all covariates, resulting in a final candidate set of 80 models (see Table S1, Supporting information). For each model within the candidate set, we calculated the AIC and the difference (denoted Δ) between the AIC of each model and the model having the highest AIC score. The Akaike Weight was then derived for all models following Burnham & Anderson (1998). Covariate weights were also derived by summing model weights across all models containing the covariate of interest, providing an index by which each covariate can be ranked in terms of information content. Based on the model weights, a 95% confidence set was derived by summing up ranked weights to 0.95. Model-averaged coefficient estimates and unconditional standard errors were based on this confidence set.

Given that the candidate set is derived as an all-subset of the covariates under investigation, a 'full model-averaging' approach was taken to calculate model parameters and associated errors (see Burnham & Anderson 1998: section 5.36). The 'full model' approach differs from the standard averaging approach in that averaged coefficients are derived for all covariates under investigation, not just those found in the best AIC model. Furthermore, coefficient averages are based on all models in the confidence set, not just those containing the covariate of interest. Accordingly, as the covariate Akaike weight decreases, the model averaged coefficient 'shrinks' towards zero. This approach is specifically advocated for all-subset modelling because many models are typically considered, and consequently there is a greater tendency for the best AIC model not to be strongly weighted. Under these conditions, model averaging conditional on the best AIC model is discouraged (Burnham & Anderson 1998).

To assess model performance, we used the area under the receiver operating characteristic curve (AUROC: Mertz 1978) as a summary measure of overall classification accuracy (i.e., capacity to discriminate between occupied and unoccupied records). The area under the curve can vary from 0.5 indicating no discrimination capacity to 1, indicating perfect discrimination capacity. Values between 0.7 and 0.9 generally indicate good discrimination. We derived AUROC and associated standard errors by calculating the average and standard deviation over 10 000 bootstrap replicates of the original data, sampled with replacement. All analyses were done using the statistical

Table 1 Monthly climate anomalies for the Wet Tropics, calculated such that they are in concordance with palaeo-climate reconstructions for the two summary precipitation indices, annual mean precipitation (AMP) and precipitation of the driest quarter (PDQ), documented in Kershaw & Nix (1988) for (a) the warm–wet Holocene period (5–3.6 kybp) (b) the cool–wet Holocene period (7.5–6 kybp), and (c) that documented in Nix (1991) for the last glacial maximum (~18 kybp). Annual mean temperature anomalies are indicated for each period and are applied uniformly across all months

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	AMP	PDQ
Current monthly percentages of AMP	17	20	19	11	6	4	3	3	2	2	4	8		
(a) Warm & Wet (5–3.6 kybp)														
Temperature = +2 °C for all months														
Precipitation anomalies (%)	+5	0	+5	10	+20	+25	+30	+40	+45	+40	+27	+15	+12	+42
(b) Cool & Wet (7.5–6 kybp)														
Temperature = –2 °C for all months														
Precipitation anomalies (%)	0	0	0	+10	+20	+40	+80	+115	+125	+115	+80	+20	+20	+118
(c) LGM (~18 kybp, Nix 1991)														
Temperature = –3.5 °C for all months														
Precipitation anomalies (%)	–52	–53	–52	–50	–48	–46	–42	–40	–39	–40	–44	–48	–50	–40

package SAS 9.1, specifically PROC LOGISTIC for performing logistic regression, and SAS/IML and SAS/MACRO languages for automating, covariate blocking, all-subset fitting, AIC full model averaging and the calculation of AUROC.

Modelling palaeo-distributions

To facilitate comparison with previous phylogeographical studies (McGuigan *et al*. 1998; Hugall *et al*. 2002, 2003; Bell *et al*. 2007), we used the palaeo-climate reconstructions by Kershaw & Nix (1988) for northeastern Australia. To derive quarterly palaeo-climate surfaces, we first calculated current monthly climate surfaces using the subprogram GROCLIM within the package ANUCLIM (Houlder *et al*. 2000). We then estimated monthly rainfall palaeo-climates such that resulting summary indices — annual mean precipitation (AMP) and precipitation of the driest quarter (PDQ) — were consistent with those of Kershaw & Nix (1988) (Table 1). Temperature palaeo-anomalies were held constant across all months. Based on the monthly palaeo-climate surfaces, we calculated quarterly climate surfaces in ArcView. We then derived predicted palaeo-distributions by extrapolating the AIC model averaged logistic regression based on the current distribution to quarterly palaeo-climate surfaces. To take into account the exposure of the continental shelf during the LGM (sea level approximately –120 m; Yokoyama *et al*. 2000), we combined the DEM described above with a digital 1-km bathymetric grid (Petkovic & Buchanan 2002). Note, however, that this is purely exploratory as predicted climate surfaces based on ANUCLIM's smoothing spline models are totally extrapolative. Lastly, we derived stability surfaces, which represent regions of persistent suitable habitat over the glacial cycle, by multiplying the predicted relative likelihood surfaces of all four climate periods.

For one species, *S. czechurai*, preliminary models indicated a strong negative association with temperature. *S. czechurai* is common at high elevations (above 1000 m) in several regions of the WT: Atherton Uplands (AU), Lamb Uplands (LU), Carbine Uplands (CU) and Windsor Uplands (WU), including the summits of Mt Bellenden Ker and Mt Bartle Frere (BK). These summits represent the coldest environments in the current landscape with average minimum temperatures during the warmest and coldest quarters of approximately 18 °C and 11 °C, respectively; the latter approaching the experimentally determined minimum temperature at which the righting response is possible (*c*. 10 °C; G. Langham, unpublished data). At least for quarterly average minima, this lower temperature threshold is not exhibited in the current environmental space of the WT but is likely to have existed during the cooler climatic periods. Accordingly, we also explored an alternative model in which we imposed a lower temperature limit. This was achieved by generating additional pseudo-absence records, derived from the LGM palaeo-climate surfaces, for regions above 1000 m (representing the coldest regions during the coldest period).

Results

Phylogeography and population demographics

Levels of overall sequence diversity and divergence varied considerably among the three focal species of *Saproscincus* from the WT (Fig. 2). Phylogeographical structuring was pronounced in *Saproscincus basiliscus,* which comprises two highly divergent lineages (Fig. 2a) separated by a net Tamura–Nei sequence divergence of 13.0%, a level similar to that between *S. basiliscus* and its sister species *S. lewisi* (13.3%). Using the more parameter-rich model of sequence

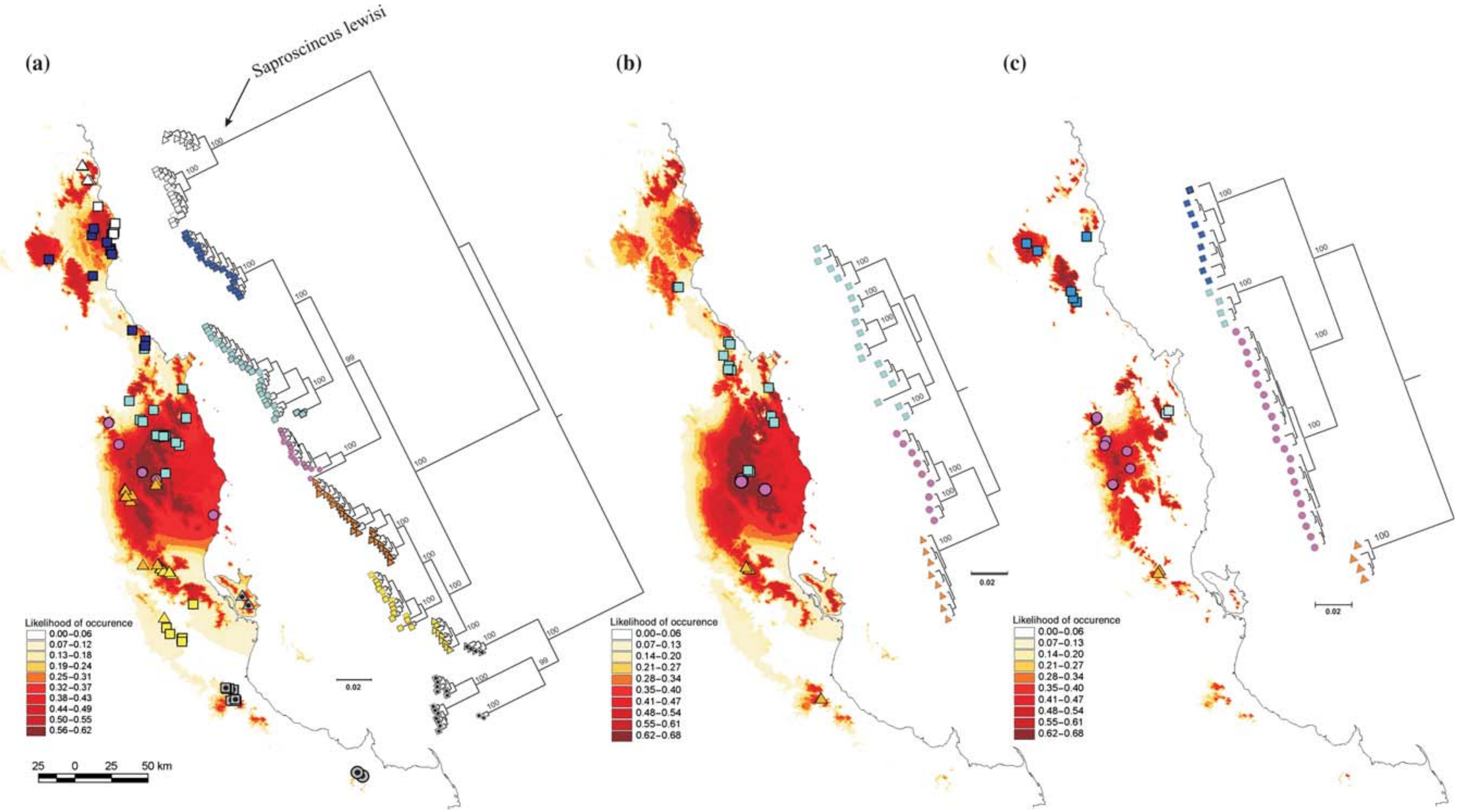

Fig. 2 Bayesian consensus trees based on the GTR model of sequence evolution with major geographical lineages overlaid onto AIC model averaged spatial predictions of the likelihood of occurrence for (a) *Saproscincus basiliscus* (b) *S. tetradactyla* and (c) *S. czechurai.* Note that the highly divergent northern-most lineage in (a) represents the sister species *S. lewisi.* Nodes having > 90% posterior probability are indicated.

evolution (GTR) from the Bayesian phylogenetic analysis, the pairwise divergence between the major clades of *S. basiliscus* is 24% and that between *S. basiliscus* and *S. lewisi* is 22%. Overall, *S. basiliscus* has strongly structured diversity ($\pi = 0.072$, $\Phi_{ST} = 0.87$), high net divergence among subregions (mean $d_A = 9.5\%$) and significant IBD (rY1 = 0.57, $P < 0.01$). The northern lineage of this species, which spans most of the species' range [TU to the Lee Uplands (LE), Fig. 1], has high, geographically structured diversity ($\pi = 0.043$; $\Phi_{ST} = 0.79$), including one clade with an internal split ($d_A = 4.5\%$) across the Black Mountain Corridor (BMC) and complex geographical structuring across the Atherton Uplands (AU) and Kirrima Uplands (KU). Overall, genetic structuring within the northern clade conforms to a model of IBD (rY1 = 0.43, $P < 0.01$). The southern lineage comprises populations from Hinchinbrook Island (HI), Spec Uplands (SU) and Elliot Uplands (EU) and is also diverse and strongly structured ($\pi = 0.049$, $\Phi_{ST} = 0.83$), with net sequence divergences of 8–9% between the three geographical isolates. A signature of population expansion based on Fu's F_S neutrality statistic was marginally significant for two northern bioregions, the TU ($n = 9$, $F_S = -1.28$, $P = 0.06$) and the BMC ($n = 5$, $F_S = -1.19$, $P = 0.09$), and the Herberton Range in the central WT (HR, $n = 13$, $F_S = -1.4$, $P = 0.03$). Other bioregions with sufficient data for analysis (KU and LE) did not depart from neutral expectations. The narrowly distributed sister species of *S. basiliscus*, *S. lewisi*, has two moderately divergent clades ($\Phi_{ST} = 0.83$; $d_A = 2.2\%$) located in the Finnegan Uplands (FU) and Thornton Lowlands (TL), respectively, and separated by the warmer and drier Bloomfield River lowlands.

The mtDNA phylogeography for the high-elevation specialist *S. czechurai* (Fig. 2c) is also highly structured, comprising four major clades, one centred on the northern subregions (TU, CU, WU), another on Mt Bellenden Ker (BK), the third on the high elevation areas of the Atherton Uplands extending out to the Herberton Range (AU–HR) and the fourth in the Kirrima Uplands (KU). Overall, the species has high diversity ($\pi = 0.044$, overall $\Phi_{ST} = 0.96$), and, like *S. basiliscus*, has high sequence divergence among major phylogeographical lineages (mean $d_A = 7.3\%$) and an overall pattern of IBD (rY1 = 0.44, $P = 0.027$). For *S. czechurai*, the KU samples represent the most divergent clade (mean $d_A = 11\%$), a deeper split than between the two clades on either side of the BMC (mean $d_A = 8.4\%$ between northern subregions and BK). Sufficient data for the neutrality test was available only for CU and AU, with the former marginally departing from neutrality (CU, $n = 6$, $F_S = -1.18$, $P = 0.07$; AU, $n = 21$, $F_S = -0.93$, $P = 0.31$).

For the lower-elevation species, *S. tetradactyla*, despite overall diversity being high ($\pi = 0.04$) and only a weak indication of IBD (rY1 = 0.3, $P = 0.1$), it had shallow geographical structuring (overall $\Phi_{ST} = 0.74$, but mean $d_A = 3.7\%$) relative to the other two species. The deepest split in the phylogeography was between the southernmost populations (KU and SU) and the rest, with a net divergence of 4.3%. North of the Tully River (CU to AU), geographical structuring was limited and did not conform to an IBD model (rY1 = 0.03, $P = 0.6$). Relatively low net divergences were observed within this region with 1.8% separating northern and central lowland populations [CU to LU vs. the Cairns to Cardwell Lowlands (CC)] and 2.4% between the central and southern CC lowlands. The KU and SU populations combined showed a significant signature of population expansion ($n = 8$, $F_S = -1.39$, $P < 0.05$). No other population for which sufficient samples were available (LU and southern CC) exhibited departure from neutrality (results not shown).

To enable direct comparison across species and with modelling results, we also summarized the partitioning of mtDNA sequence variation within and across three broad biogeographical areas of the WT (Table 2) — northern (FU to BMC), central (LU to KU) and southern (HI to EU) (see Fig. 1). While exhibiting moderate phylogeographical structure, northern isolates of *S. basiliscus* and *S. czechurai* harbour less diversity relative to the central WT, with the former species exhibiting a significant signature of population expansion (TU, CU and WU, see Table 2). In terms of the southern WT, high and strongly structured genetic diversity was observed for *S. basiliscus*; whereas for *S. tetradactyla*, the SU population was associated with a population expansion and re-colonization event from the KU (Table 2, also palaeo-distribution predictions below). No populations of *S. czechurai* have been recorded in the southern WT. In contrast to results for each species as a whole, there were no signatures of IBD within the three broad biogeographical regions.

Statistical models of current distributions

Models of current distributions were developed for all three focal species (there were too few records for *S. lewisi*). Distribution models for all three species had high discrimination, ranging from 85% to 95% (AUROC, Table 3). A low to moderate level of model-selection uncertainty exists, however, with up to 19 of 80 candidate models falling within the 95% confidence set (Table 3). This reinforces the need for model averaging. The most informative temperature covariates (having the highest AIC weights) for all three species were those representing the summer period (either the wettest or warmest quarters, Table 3), with *S. czechurai* clearly having a greater preference for relatively cooler conditions, while the converse was the case for *S. tetradactyla* (Fig. 3). Although the estimated temperature profile for *S. basiliscus* was comparable to that of *S. tetradactyla*, it was less defined (relatively lower amplitude, Fig. 3) and indicated a wider tolerance range for this species. In terms of precipitation, covariates representing the winter months

Table 2 Genetic diversity statistics and modelled refugia in major biogeographical regions of the Wet Tropics (WT): northern WT (FU to BMC), central WT (LU to KU) and southern WT (HI to EU). Stability indicates bioregions identified in the stability surface as having persisted across all modelled climates (Figs 4 and 5). Question-marks indicate areas identified with low probability; Φ ($_{\mathrm{ST}}$) and mean d_A are based on bioregional subdivision of the dataset consistent with that given in Fig. 1. Correlation coefficients are given for isolation-by-distance and Fu's F_S statistic for the neutrality test. Statistical significance is indicated as follows: *$0.1 > P > 0.05$; **$0.05 > P > 0.01$; and ***$P < 0.001$. Na, not applicable

			Broad biogeographical regions		
Species	Parameter	Total	Northern	Central	Southern
Saproscincus basiliscus	Stability		FU†, TU, CU?	AU, KU, MT	HI
	theta(π)	0.072	0.003	0.042	0.049
	Φ ($_{\mathrm{ST}}$)	0.87	0.61	0.75	0.83
	Mean d_A	0.095	0.002	0.043	0.078
	IBD	0.57***	0.71*	0.33	0.72
	F_S		–5.15**	– 1.45	3.75
S. tetradactyla	Stability		TU/TL	CC/AU	None
	theta(π)	0.040	Na	0.040	Insufficient data
	Φ ($_{\mathrm{ST}}$)	0.74	Na	0.59	Insufficient data
	Mean d_A	0.037	Na	0.025	Insufficient data
	IBD	0.30*	Na	0.15	Insufficient data
	F_S		Na	– 0.56	–1.39**§
S. czechurai‡	Stability		TU, CU?	AU, BK, KU	Na
	theta(π)	0.044	0.008	0.029	Na
	Φ ($_{\mathrm{ST}}$)	0.96	0.45	0.96	Na
	Mean d_A	0.073	0.009	0.085	Na
	IBD	0.44**	–0.21	0.81	Na
	F_S		–1.82	1.46	Na
S. lewisi	Stability†		FU†, TU	Na	Na
	theta(π)	0.015	0.015	Na	Na
	Φ ($_{\mathrm{ST}}$)	0.83	0.83	Na	Na
	Mean d_A	0.022	0.022	Na	Na
	F_S		–0.45	Na	Na

†Stability areas for *S. lewisi* are inferred from *S. basiliscus* model.
‡Stability estimates are for temperature constrained model (see Materials and methods).
§Expansion analyses based on CR and SU populations combined.

(either the driest or coldest quarter) were the most informative (Table 3), with an overall preference across all species for relatively high rainfall (Fig. 3). However, *S. czechurai* tolerates slightly lower precipitation levels, possibly due to compensation via lower trans-evaporation and/or cloud-stripping at higher altitudes (see McJannet *et al*. 2007).

Spatial predictions for the three species suggest little difference between *S. basiliscus* and *S. tetradactyla* under the current climate regime, but greater restriction to higher altitudes for *S. czechurai* (Fig. 2). This is evident in both the standard and temperature constrained model for *S. czechurai* (see also Fig. 5); however, restriction and fragmentation of suitable habitat is less severe in the latter model. Aside from the variability among the three species in climate profiles, predicted distributions were concordant in that: (i) the northern section of the BMC represents unsuitable habitat; (ii) suitable habitats in the northern WT were fragmented into four distinct regions [Finnigan (FU), Carbine (CU), and Windsor Uplands (WU) and the Thornton Uplands and Lowlands (TU/TL)]; (iii) the southern isolates, Hinchinbrook Island (HI), Spec Uplands (SU) and Elliot Uplands (EU), potentially represent suitable habitat, albeit small in extent; and (iv) the largest predicted area of suitable habitat was across the central WT (LU to KU, and for *S. basiliscus* and *S. tetradactyla*, the adjacent lowlands, CC), which appeared to be largely continuous for *S. basiliscus* and *S. tetradactyla*, but more fragmented for *S. czechurai*.

Predictions of potential palaeo-distributions

The predicted potential distributions were more distinct for past climates (Figs 4 and 5). For *S. basiliscus,* isolation among northern (CU, WU and TU) and southern regions (HI, SU and EU) was predicted in the warm–wet (mid Holocene) as well as the current climate; indeed, other than retraction from the lowlands, there was very little difference between the models for the two periods (Fig. 4a). Most

Table 3 Model-averaged coefficients (*ma*Coeff.; both linear and quadratic terms), unconditional standard errors (*u*SE) and Akaike weights (*w*) per covariate for each study species. Area under the receiver operating characteristic curve (AUROC) is given next to species' name. Quarterly temperature indices are as follows: TweQ, temperature of the wettest; TdQ, temperature of the driest; TwaQ, temperature of the warmest; TcQ, temperature of the coldest quarter. Quarterly precipitation indices follow the same logic. NC, number of candidate models falling with the 95% confidence set out of a candidate set of 80 models. Empty cells indicate that none of the models within the 95% confidence set contained that particular covariate

	TweQ		TdQ		TwaQ		TcQ		PweQ		PdQ		PwaQ		PcQ		NC
Saproscincus basiliscus AUROC = 0.85 ± 0.02																	
*ma*Coeff	0.160	–0.000358	–0.003	0.000004	0.077	–0.000169	0.001	–0.000015			28.33	–2.44			1.53	–0.13	11
uSE	0.130	0.000254	0.004	0.000008	0.076	0.000154	0.010	0.000022			6.46	0.61			1.47	0.12	
w	0.460	0.416840	0.099	0.024000	0.242	0.203510	0.200	0.062980			0.94	0.94			0.06	0.06	
S. tetradactyla AUROC = 0.86 ± 0.02																	
*ma*Coeff	0.390	–0.000822	–2.6E-04		0.288	–0.000603	0.007	–0.000021	1.21	–0.06	17.82	–1.52	0.04	0.00	8.27	–0.69	19
uSE	0.230	0.000485	3.0E-04		0.212	0.000432	0.009	0.000024	1.33	0.07	8.99	0.80	0.04	0.00	6.31	0.53	
w	0.530	0.520640	0.021		0.394	0.378600	0.048	0.030350	0.09	0.04	0.61	0.61	0.01	0.00	0.29	0.29	
S. czechurai AUROC = 0.95 ± 0.01																	
*ma*Coeff	–0.080	0.000087			–0.163	0.000197			20.87	–1.44	6.88	–0.62	2.02	–0.14	22.29	–1.92	11
uSE	0.070	0.000122			0.136	0.000234			17.17	1.18	5.95	0.54	2.04	0.14	10.47	0.91	
w	0.380	0.131870			0.622	0.233600			0.21	0.21	0.17	0.17	0.02	0.02	0.60	0.60	
S. czechurai (minimum temperature constrained) AUROC = 0.95 ± 0.01																	
*ma*Coeff	0.260	–0.000660			0.442	–0.001089			20.87	–0.47	6.23	–0.62	2.69	–0.18	14.49	–1.18	12
uSE	0.170	0.000422			0.197	0.000480			17.17	0.46	5.36	0.45	2.83	0.19	8.35	0.68	
w	0.390	0.392490			0.608	0.607510			0.21	0.12	0.27	0.23	0.04	0.04	0.55	0.53	

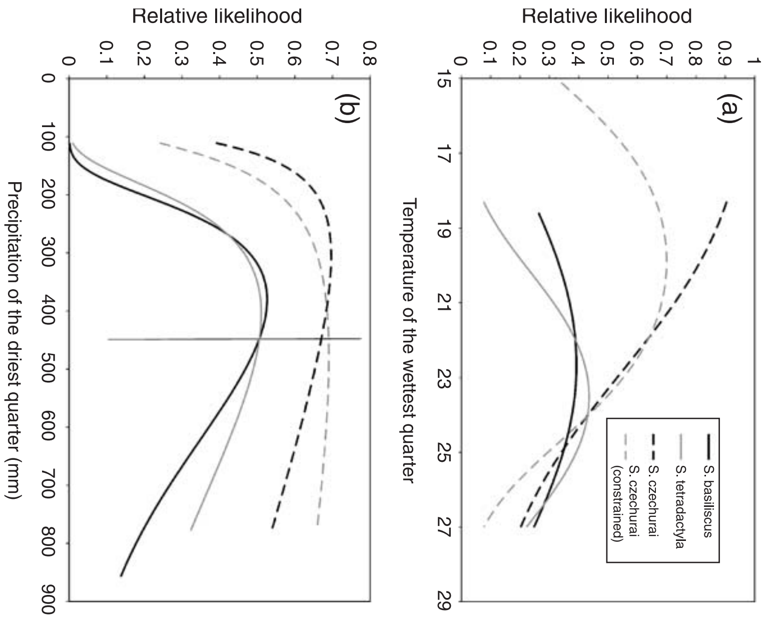

Fig. 3 Partial relative likelihood profiles for (a) temperature of the wettest quarter and (b) precipitation of the driest quarter for each species, plotted as the likelihood of occurrence across the range of each covariate when all other covariates are held constant at the mean of the presence records. Regions receiving greater than 450 mm precipitation during the driest quarter are restricted to the mountain peaks of Bartle Frere and Bellenden Ker.

pronounced, however, was the severity of contraction of these isolates during the LGM, with suitable habitat north of the BMC primarily retreating to the TU/TL and FU subregions, while for the southern isolates, persistence was predicted for HI, but not the other subregions (SU, EU). For the central WT, despite major shifts in predicted distributions between the most restrictive climates (towards the lowland and eastern AU in the LGM and towards higher regions in warm-wet conditions), a large area of suitable habitat was predicted to have persisted (Fig. 4a). The exceptions are the Lamb Uplands and Kirrima Uplands (LU, KU), which were predicted to have undergone major contraction and fragmentation during the LGM. Conversely to the LGM, the most dramatic of the palaeo-predictions was the great expansion associated with the cool, wet interglacial, with almost complete connectivity of all major biogeographical regions, except for EU (Fig. 4a).

Combining model predictions provides a stability surface, areas predicted to have retained suitable habitat across all climatic conditions (Fig. 4a, left). This suggests a large refugial area across the eastern AU with increasing

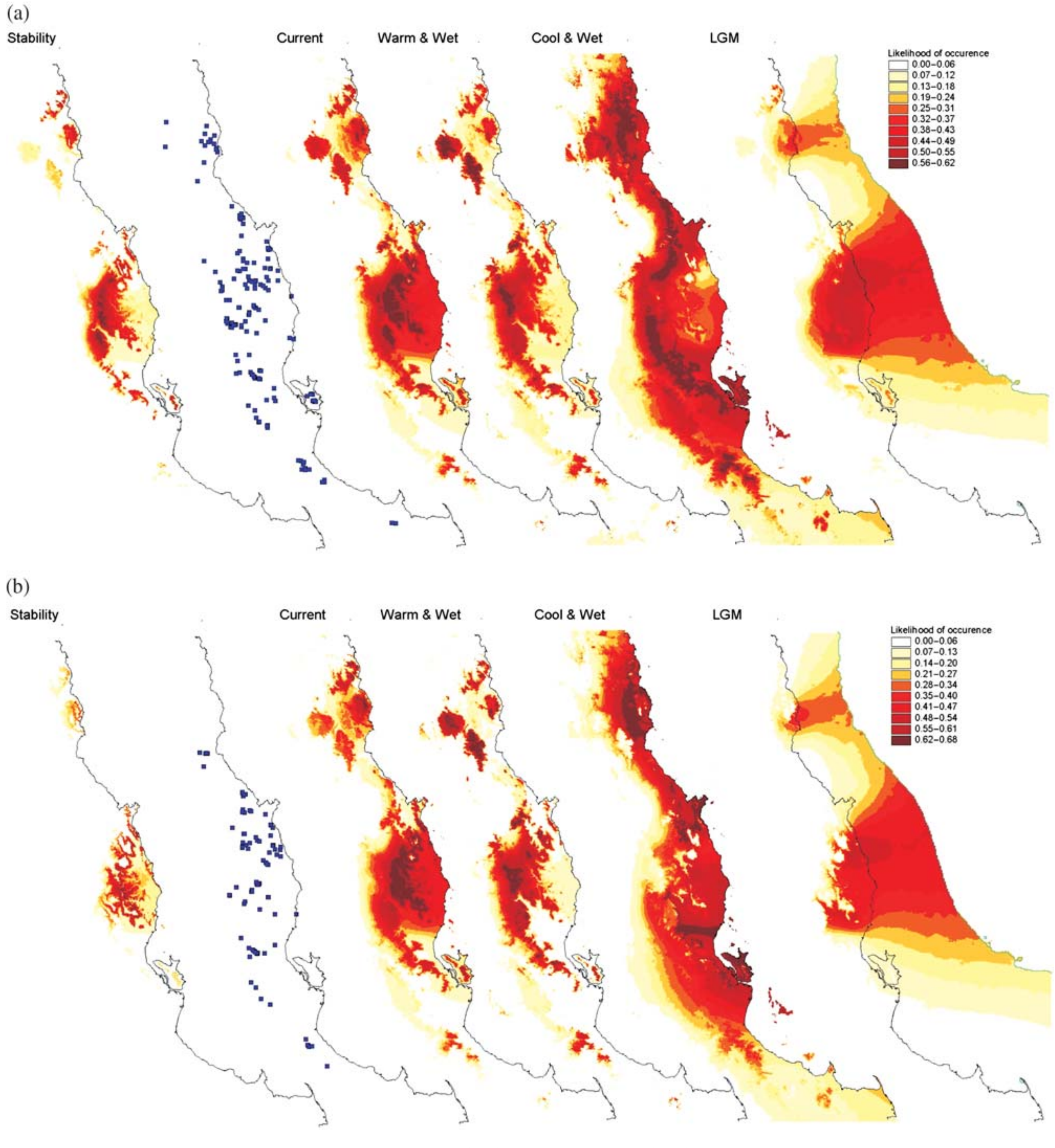

Fig. 4 Predicted likelihood of occurrence for (a) *Saproscincus basiliscus* and (b) *S. tetradactyla* under different palaeo-climate scenarios. From left to right: stability surface; record localities used in current distribution modelling; predicted distribution under current climate; warm–wet Holocene; cool–wet Holocene; and the last glacial maximum (LGM). For the LGM, predictions are extrapolated to regions up to 120 m below current sea levels.

fragmentation through KU to the south and LU to the north, two isolated refugia in the north (FU and TU) and one in the south (HI). For the southern isolates, SU and EU, we conducted sensitivity analysis whereby models were extrapolated under incrementally less stringent temperature and rainfall anomalies (data not presented). It was only under a much relaxed precipitation anomaly (80% vs. 50% of current conditions) that suitable habitat was predicted to have persisted through the LGM within the SU. Even under these conditions, however, EU remained unsuitable.

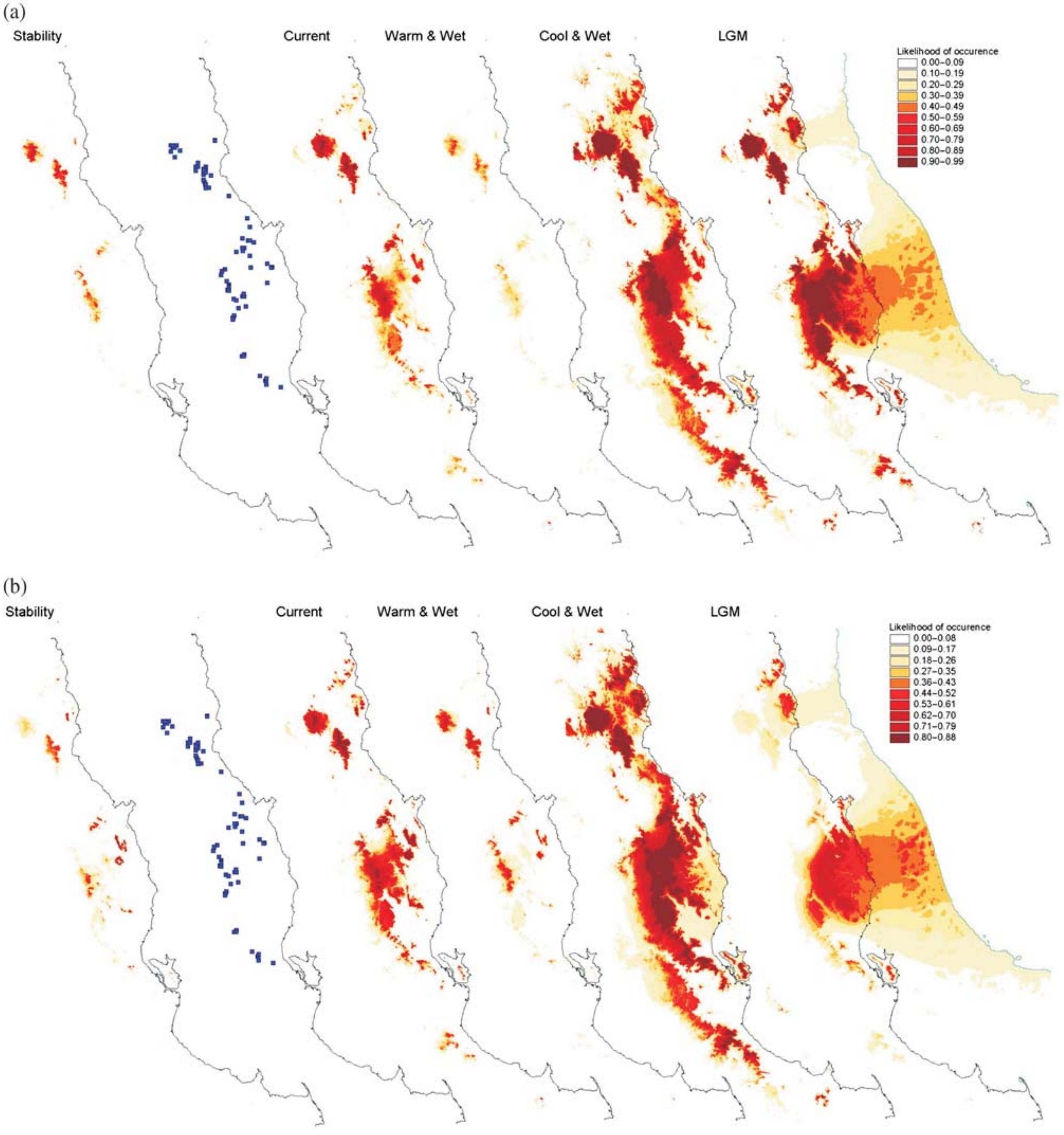

Fig. 5 Predicted likelihood of occurrence for (a) *Saproscincus czechurai* (standard model) and (b) *S. czechurai* (minimum-temperature-constrained model) under varying palaeo-climate scenarios. From left to right: stability surface; record localities used in current distribution modelling; predicted distribution under current climate; warm–wet Holocene; cool–wet Holocene; and the last glacial maximum (LGM). For the LGM, predictions are extrapolated to regions below 120 m of current sea levels.

Predicted distributions for the warm–wet and current climate for *S. tetradactyla* were very similar to those for *S. basiliscus*, but those for the cool–dry and cool–wet climate were more strongly centred on lowland areas (TL in the north and CC centrally). This reflects the preference of this species for lower elevation rainforests. The net result is a stability surface with fewer predicted refugia and restriction of the major AU refugium to the flanking lowlands. The montane species, *S. czechurai*, differed markedly from the other two in that the greatest predicted reduction in potential habitat was during the warm–wet period rather than the cold–dry glacial period (regardless of whether the standard or temperature constrained model is used). Using the model with a lower temperature threshold imposed, there was stronger predicted persistence under warm–wet conditions and a more conservative prediction for the cold–dry LGM. Both models predict multiple refugia in the northern WT, with one (standard model) or multiple fragmented refugia (temperature-constrained model) predicted in the AU–KU region.

Comparison of phylogeographical patterns and modelled refugia

For *S. basiliscus*, molecular evidence for the northern WT (Table 2) was consistent with contraction of populations to a single refugium with subsequent expansion. Distribution models predicted two refugia, in the FU and TU/TL, respectively (Fig. 4a, left). The former is currently occupied by *S. lewisi* only (sister species to *S. basiliscus*), while both *S. basiliscus* and *S. lewisi* are found in the latter. Based on observed divergence levels, *S. lewisi* is likely to have persisted in both the FU and TL. The combined molecular and distribution model evidence suggests expansion of *S. basiliscus* from TU to both CU and WU and across the BMC to the south. For the central WT, the stability surface suggests a large, relatively continuous refugium centred on the AU. Some fragmentation was evident, however, namely in the LU, MT and KU. Molecular evidence indicated retention of high, structured diversity, consistent with the distribution models. In particular, the high nucleotide diversity within KU ($\pi = 0.016$), in conjunction with the stability surface predictions, suggests retention of populations across a fragmented refugial landscape. For the southern WT, there was some conflict between modelled refugia and the molecular data. The only predicted refugium was on HI, which is consistent with a unique phylogeographical lineage on the island. However, moderate genetic diversity was found in the LE population ($\pi = 0.007$), despite suitable habitat only being predicted under the cold–wet scenario. Most likely, this currently isolated population was re-colonized by multiple genetic lineages from the KU region during the early Holocene. The most obvious conflicts between the molecular and distribution data were for SU and EU. The molecular evidence indicates that each of these persisted in isolation, with high diversity in the case of SU ($\pi = 0.018$), but neither area was predicted as a refuge in the models.

For *S. tetradactyla*, smaller lowland refugia were predicted with strong separation between the northern and central WT and no persistent areas in the south. Consistent with the models, molecular evidence (Fig. 2, Table 2) did suggest less phylogeographical structure in the central region relative to either *S. basiliscus* or *S. czechurai* (Table 2) and strong population expansion across KU to SU. Lastly, for *S. czechurai*, strong fragmentation was evident from the mtDNA phylogeography and is consistent with the presence of multiple, isolated refugia predicted in the models, particularly the temperature-constrained model. Both models predict multiple refugia in the north (CU and, less consistently, TU and WU), with potential for dispersal among these regions under cool–wet conditions being stronger in the temperature-constrained model. Although samples sizes were small for TU and WU ($n = 1$ and 2, respectively), shared and/or closely related haplotypes (Fig. 2) suggest recent connectivity between the three areas; however, there is no evidence for population expansion (Table 2). For the central WT, the temperature-constrained model (Fig. 5b) predicts multiple small and isolated refugia in AU, BK and KU, which was supported by the presence of strongly differentiated mtDNA clades in each area (Fig. 2, Table 2).

Discussion

Comparative phylogeography

The present study builds on previous phylogeographical work for this system by adding new taxa and focusing on a group of related taxa that are ecologically similar, except for having different elevational and climatic ranges. Broad-scale phylogeographical concordance within the WT has been documented across a wide variety of vertebrate and invertebrate taxa (Joseph *et al*. 1995; Schneider *et al*. 1998; Schneider & Moritz 1999; Moritz 2000; Hugall *et al*. 2002; Moritz *et al*. 2005). The most consistent phylogeographical division is across the BMC, and the prominence of this biogeographical barrier is further supported by LGM palaeo-distribution predictions of mesothermal rainforest (Nix 1991), the terrestrial snail *Gnarosophia bellendenkerensis* (Hugall *et al*. 2002) and dung beetles of the genus *Temnoplectron* (Bell *et al*. 2007). Results presented here add to this body of evidence for vicariance-driven intraspecific diversification, with *Saproscincus basiliscus* and *S. czechurai* showing phylogenetic discontinuities across the BMC, and predicted LGM palaeo-distributions clearly indicating major contraction and isolation of suitable habitat either side of this biogeographical break. Divergence across the BMC was notably greater in *S. czechurai* compared to the other two species (8.4% in S. czechurai, *c*. 4.5% in *S. basiliscus* and 1.7% in *S. tetradactyla*), suggesting that the BMC represents a greater geographical barrier to this high-elevation specialist compared to its more generalist and lowland congeners. Both molecular data and distribution models strongly suggest that contraction under restrictive climates was severe for populations north of the BMC (see also Schneider & Moritz 1999), with both *S. basiliscus* and *S. czechurai* exhibiting low nucleotide diversity in this region and the LGM distribution greatly reduced to the Thornton and Finnigan Uplands. The extent of contraction appears to have been most severe for *S. basiliscus,* given the strong signature of subsequent population expansion. Although *S. lewisi* seems to have persisted in both the Finnigan and Thornton Uplands, there is little evidence for multiple refugia north of the BMC in any of the three focal species, in contrast to several other taxa (snails, Hugall *et al*. 2002; beetles, Bell *et al*. 2007).

In contrast to the north, moderate to deep phylogeographical structure is evident south of the BMC, in the central WT, for all three species. In other species, such phylogenetic diversity and geographical structuring within the central region has been interpreted as the persistence of multiple refugia (Schneider & Moritz 1998; Hugall *et al*. 2002). For both *S. basiliscus* and *S. tetradactyla*, but particularly *S. basiliscus,* however, there is little support from either the current or palaeo-distribution predictions for major fragmentation within the central WT. Rather, the central region is characterized by contraction of suitable habitat either from the west during the LGM or from the eastern lowlands during the warm interglacial. The high genetic diversity in these species within the central WT suggests either that large relatively stable populations have persisted throughout most of the glacial cycles of the Quaternary and the divergent clades represent retention of ancient polymorphism, or that there have been multiple isolated refugia. The latter possibility would suggest that current distribution models are too generalized, and that additional factors limit the species distributions.

Within the central WT, there is a prominent phylogeographical break across the Tully River catchment, although fewer taxa have shown phylogenetic discontinuity across this region compared to the BMC. In an earlier comparative study of herpetofauna in the WT (Schneider *et al*. 1998), only one of six species examined had a highly divergent clade within the Kirrima Uplands (KU), namely the waterfall frog *Litoria nannotis*, with mean sequence divergence of approximately 10% (based on Kimura 2 parameter model for the mitochondrial *Cytochrome-b* gene). More recently, genetic structure within two additional species, the snail *Gnarosophia bellendenkerensis* (Hugall *et al*. 2002) and the dung beetle *Temnoplectron aeneopiceum* (Bell *et al*. 2007), have reinforced the importance of the KU as a significant phylogeographical unit. In our study, all three species of *Saproscincus* have divergent clades within the KU, with *S. czechurai* exhibiting greater net divergence across the Tully River than across the BMC. However, palaeo-distribution models predict suitable habitat along the KU during the LGM only for *S. basiliscus*. Predicted suitable habitat across the KU tends to be highly fragmented during the LGM and smaller in extent than the Thornton refugium north of the BMC. This may explain why few species appear to have maintained populations within the KU throughout the climate fluctuations of the Quaternary. In contrast to the LGM predictions, substantial connectivity between the Kirrima and Atherton Uplands is predicted throughout the Holocene for *S. basiliscus* and *S. tetradactyla* (see also Hugall *et al*. 2002; Bell *et al*. 2007). For *S. czechurai*, however, this connectivity is only evident in the cool–wet interglacial. Such connectivity is supported by the fact that for many species, the KU is simply a phylogenetic continuation of the Atherton Uplands (see Schneider *et al*. 1998; Schneider & Moritz 1999). This connectivity is clearly evident in the current study, with the geographically intermediate Walter Hill Ranges representing a region of admixture/contact between the divergent mitochondrial lineages for both *S. basiliscus* and *S. tetradactyla.*

One of the most striking findings of this study is the long-term isolation and persistence of southern populations of *S. basiliscus* in the Spec Uplands, Hinchinbrook Island and, most interestingly, the Elliot Upland. Sequence divergence between the southern and northern lineages is substantial and possibly dates as far back as the late Miocene (Moussalli *et al*. 2005). Furthermore, divergence within the southern lineages clearly predates the Pleistocene (mean $d_A = 8\%$). To date, relatively few species are believed to have maintained long-term populations within the Spec Uplands. Rather, the general pattern is one of extinction followed by re-colonization from the north, a phylogeographical pattern exemplified by *S. tetradactyla* (see also Joseph *et al*. 1995; Schneider *et al*. 1998; Schneider & Moritz 1999). The only other species having long-term persistence in the Spec Uplands are the rainbow skink *Carlia rubrigularis* (Dolman & Moritz 2006) and the waterfall frog, *Litoria nannotis* (Schneider *et al*. 1998), although multiple colonizations from the northern, genetically diverse, Kirrima Range clade could not be ruled out for the latter species. The persistence of *S. basiliscus* in the Elliot Uplands is even more surprising, given that of the 83 species of upland WT endemic vertebrates (Williams 2006), only four species of birds have been recorded this far south: namely the tooth-billed catbird *Ailuroedus dentirotis,* the bridled honeyeater *Lichenostomus frenatu*, the grey-headed robin *Poecilodryas albispecularis and* Victoria's riflebird *Ptiloris victoriae.* In all four cases, however, recent dispersal cannot be ruled out. At an interspecific level, the sister relationship between the microhylid frogs, *Cophixalus neglectus* (Bartle Frere and Bellenden Ker) and *C. mcdonaldi* (Elliot Uplands), at comparable sequence divergence to that between northern and southern lineages of *S. basiliscus* (see Hoskin 2004), and the presence of several locally endemic faunal species (Moritz *et al*. 2001; Hoskin *et al*. 2003), attests to the persistence of rainforest at the Elliot Uplands during peak glacial periods. Given the high level of sequence divergence between the southern and northern lineages of *S. basiliscus*, comparable to that between *S. basiliscus* and its parapatrically distributed sister species *S. lewisi*, the southern lineage may, in fact, represent a separate species. One possible reason for the failure of the palaeo-distribution model to predict southern refugia other than on Hinchinbrook Island it is that the southern populations of *S. basiliscus* could have physiological limits different from those of the northern lineage.

Agreement and discord between distributional dynamics and molecular data

There is increasing interest in combining molecular data with fossil data or spatial models of past distributions to gain insights into historical processes shaping current species distributions and genetic diversity (Haney & Taylor 2003; Bell *et al*. 2007; Carstens & Richards 2007; Swenson 2008). The present study illustrates the utility of the approach, particularly in identifying how both interglacial and glacial periods can potentially underpin pronounced phylogeographical structure and in identifying the location and extent of refugia associated with distinct phylogeographical units (see also Hugall *et al*. 2002). While both sources of information provide independent insight into the evolutionary landscape of a region, both have assumptions and limitations. In terms of the molecular data, inference from a single locus must be treated with caution when inferring vicariance-induced diversification, because strong phylogeographical structure can also result from either extinction of intermediate haplotypes or stochastic lineage sorting in conjunction with low dispersal (Neigel & Avise 1993; Avise 2000; Irwin 2002). The comparative approach presented here, however, of combining multiple species and two independent sources of historical data, provides a stronger basis for inference than from a single species and locus (Bermingham & Moritz 1998).

There is as much, if not more, uncertainty associated with palaeo-distribution predictions. In addition to uncertainty in choice and significance of the chosen climate covariates (i.e. model selection uncertainty), the suitability of varying modelling procedures (Elith *et al*. 2006; Pearson *et al*. 2006), and the validity of the assumption that distributional limits reflect physiological limits and are constant over time (Davis *et al*. 1998; Swenson 2008), there is also the uncertainty associated with the palae-oclimate reconstructions themselves (see Jordan 1997; Hesse *et al*. 2004). Even assuming that the palae-oclimate estimates are accurate, there is the added assumption that temperature and precipitation changes were uniform across the study region. Recent insights from 'General Circulation Model' simulations, although still at a relatively coarse scale, clearly indicate that this may not necessarily be the case (Pinot *et al*. 1999; Broccoli 2000; Diffenbaugh & Sloan 2004; Drost *et al*. 2007). Lastly, palaeo-distribution predictions, particularly for extreme periods such as the glacial maxima, are largely extrapolative, given that analogues of past climatic conditions are typically absent in the current environment (D'Costa *et al*. 1989; Kershaw & Bulman 1996; D'Costa & Kershaw 1997).

Limitations in modelling palaeo-distributions were clearly evident in terms of predicted refugia for the southern lineage of *S. basiliscus* and in terms of the minimum temperature profile of *S. czechurai*. In the former case, with the exception of Hinchinbrook Island, no suitable habitat was predicted in the southern WT during glacial maxima, in stark contradiction to the molecular data. As suggested above, one possible explanation is that the genetically divergent southern lineage is also physiologically distinct. Alternatively, physiological limits as estimated in the current bioclimatic model are not constant through time; but rather, populations are able to evolve and compensate *in situ* to climatic shifts. Equally plausible, however, is that climatic shifts may not have been uniform across the WT and/or our climate surface derivation greatly underestimates precipitation due to lack of consideration, for example, of cloud-stripping at high altitudes (see McJannet *et al*. 2007). In the case of *S. czechurai*, lower temperature limits that may potentially exist during the glacial maximum have no present day analogue. While artificially imposing a lower temperature limit improved model performance, the imposed lower limits were subjective. One potential approach to dealing with such limitations would be to use physiological data to obtain more realistic climatic profiles based on energy balance models. Under this approach, physiological limits associated with metabolic rate and reproduction could be related to (calibrated with) broad-scale climate covariates, which in turn can provide a basis for predicting species (or population) distributions (Kearney & Porter 2004). Such models would reduce the uncertainty regarding physiological limits that arises from associative modelling in general, as observed for *S. czechurai*, possibly providing greater confidence in extrapolating spatial distributions under extreme palaeo-climate scenarios (see Strasburg *et al*. 2007; Kearney *et al*., in press). More importantly, comparing correlative with biophysical models provides a framework for identifying differences between a species' fundamental and realized niche (Kearney 2006). Such a comparison could prove insightful, not only within a phylogeographical context, but also in the reconstruction of palaeo-climates themselves, which are predominantly based on correlative models.

Niche breadth and response to climate fluctuation

The intermediate climatic niche hypothesis outlined in the Introduction predicts that dispersal-restricted species with intermediate niche breadth (relative to total environmental space) should show greatest genetic diversity because they have higher persistence through climate fluctuations but are still subject to geographical structuring under most conditions. By contrast, more specialized species could suffer greater local extinction under extreme conditions (warm-adapted species under cold conditions; cold-adapted under warm conditions). Understanding these limits from analyses of responses to past climate changes is central to predicting responses to future climate warming (Davis *et al*. 1998; Thuiller 2003, 2004). Comparison of the three focal species in this study is generally consistent with these predictions. While both *S. czechurai* and *S. basiliscus* exhibit fragmentation and isolation, the molecular data support greater fragmentation, contraction and isolation for the high elevation specialist, *S. czechurai,* and greater persistence for the intermediate niche species, *S. basiliscus*. As expected, the warm-adapted species, *S. tetradactyla,* shows greater contraction and restriction to the lowlands under cooler climates and less phylogeographical structure relative to the other two species. All three species are morphologically and ecologically similar but differ in their elevational ranges and associated climatic preferences, suggesting that the observed differences in response to past climate change reflects differences in their climatic niche rather than other ecological traits.

With the exception of southern *S. basiliscus*, we observed generally good concordance between the molecular data and the palaeo-distribution models, indicating conservatism of bioclimatic niches over multiple glacial cycles for all three species. Current climatic preferences of all three species extrapolated to past climates accord well with geographical patterns of genetic diversity, suggesting that the species have maintained their respective climatic preferences at least throughout the late Pleistocene. Such climatic niche conservatism coupled with extreme glacial fluctuations has underpinned the deep phylogeographical structure observed for *S. czechurai* and *S. basiliscus* across the central and northern WT. Thus, while strong differentiation across a temperature gradient is evident between species, most importantly between the closely related taxa *S. czechurai* and *S. tetradactyla* (Moussalli *et al*. 2005) — a pattern also observed in other tropical systems (Graham *et al*. 2004) — it is clear that conservatism of the bioclimatic niche (Wiens & Graham 2005) has contributed to genetic diversification within this tropical system.

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Supporting Information

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

Table S1 All-subset candidate set of models for which logistic regressions were calculated. Quarterly indices are as follows: Quarterly temperature indices are as follows: TweQ, temperature of the wettest; TdQ, temperature of the driest; TwaQ, temperature of the warmest; TcQ, temperature of the coldest quarter. Quarterly precipitation indices follow the same logic. The suffix 'QUAD' indicates a quadratic terms for the respective indices