

Remarkably different phylogeographic structure in two closely related lizard species in a zone of sympatry in south-eastern Australia

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comparative phylogeography; reptile; *Eulamprus*; glacial cycles; Great Dividing Range; invertebrates.

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Abstract

Phylogeographic structure is a product of a species' life history and dispersal patterns, geographic history, climatic history and chance. Comparative phylogeography, using carefully chosen model species, can highlight the relative contribution of each of these factors and identify common processes affecting communities. In this study we compare and contrast fine-scale phylogeographic patterns in two ground-dwelling species of water skink, *Eulamprus heatwolei* and *Eulamprus tympanum*, from the biogeographically well-characterized Tallaganda region in south-eastern Australia, and compare them against data from a number of invertebrate species from the same region. Using variation in mitochondrial sequence, we have uncovered dramatically different biogeographic histories for the two species, despite their marked behavioural and morphological similarity. *Eulamprus tympanum* shows an average corrected sequence divergence of 0.014 and patterns of geographic variation in haplotypes consistent with historical vegetational changes resulting from past glaciation cycles. In contrast, *E. heatwolei* shows an average divergence of only 0.0075, and geographic structure that reflects a recent and rapid colonization, perhaps following an ice age local extinction. These two contrasting patterns of variation have also been identified in invertebrate taxa as disparate as collembolans and spiders; these species show either deep structure, associated with local persistence, or little variation of structure, which we attribute to recent extinction and re-colonization. We argue that historical persistence versus extinction is a consequence of (often minor) differences in lifestyle and local habitat preference.

Introduction

Phylogeographic datasets allow the reconstruction of historical landscape processes that lead to biotic diversification (Avice *et al.*, 1987; Schneider, Cunningham & Moritz, 1998). Most phylogeographic studies are concerned with individual species, but to draw credible hypotheses regarding the climatic and geographical causes of genetic structure requires replication; without other co-distributed taxa to demonstrate concordance, structure resulting from stochastic lineage sorting or random catastrophic events cannot be ruled out. A comparative approach to phylogeography allows the development of testable hypotheses regarding biogeography and patterns of diversity, and therefore has greater power of inference than single-species studies (Avice, 2000; Arbogast & Kenagy, 2001; Nielson, Lohman & Sullivan, 2001; Riddle *et al.*, 2002).

Comparative phylogeography can aid the recognition of cryptic historical vicariance; if several co-distributed species have concordant phylogeographic breaks, it is more likely that these are a reflection of past environmental conditions

or a common barrier to gene flow, rather than parallel, neutral divergence (Irwin, 2002; Riddle *et al.*, 2002). Conversely, if co-distributed species show different patterns of genetic structure, insights into species-specific characteristics such as habitat specificity, dispersal ability and resistance to barriers can be gained (if the influence of random factors can be shown to be small). Consequently, the greater the diversity of taxa compared in phylogeographic studies, the greater the insights into the timing and extent of past and present environmental factors in moulding species and communities.

Until recently, phylogeographic studies have been biased towards vertebrate species structured over large spatial scales. The coarse resolution of these studies may lead to false inferences of long-distance dispersal (Templeton, 1998), overlook divergence caused by cryptic vicariant events (Moritz, 2002), and also make accurate placement of suspected biogeographic barriers difficult (Schaub & Moritz, 2001). Phylogeographic studies at fine spatial scales are less common despite the recent technological advances in our ability to detect underlying genetic diversity. Such

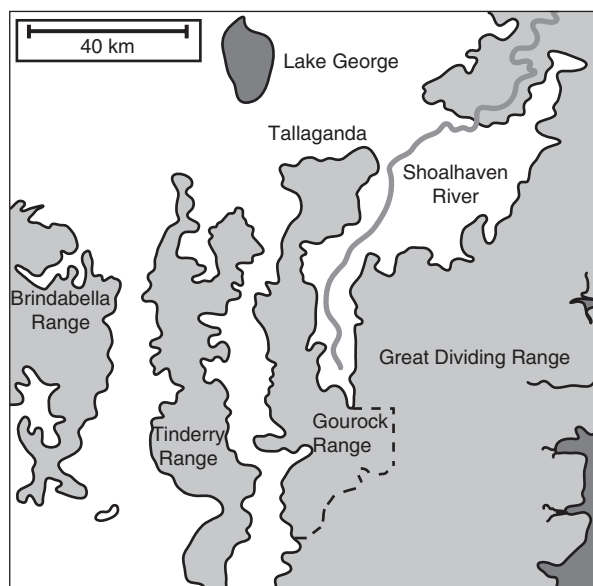


Figure 1 Schematic map showing the study area (Tallaganda on the Gourouk Range) and the surrounding region. Mountainous areas are shaded. White areas represent the low-altitude plains of the Southern Tablelands which surround the Gourouk Range.

studies give valuable insights into local migration, colonization and gene flow among populations and are particularly useful in revealing the effects of long-acting environmental change on taxa that experience their environment at fine spatial scales (Moritz *et al.*, 2001).

Tallaganda is a region in south-eastern New South Wales (NSW), Australia (Fig. 1), and is the focus of ongoing fine-scale phylogeographic and population genetic studies on a suite of saproxylic (rotting log dependent) and forest-floor-dwelling invertebrates (Garrick *et al.*, 2004; Beavis & Rowell, in press; Garrick, Sands & Sunnucks, in press; Woodman *et al.*, 2006). These studies have demonstrated considerable population sub-structuring and localized endemism, indicating evolutionary processes operating within restricted spatial scales. A phylogeographic study on a 'giant' saproxylic collembolan (Garrick *et al.*, 2004) allowed precise recognition of genetic contact zones, which were congruent with five previously recognized microbiogeographic regions at Tallaganda (see Materials and methods).

In this study, we generated phylogeographic datasets for two vertebrate taxa that display very different ecologies and dispersal abilities (and so presumably patterns of gene flow) to the invertebrates studied to date at Tallaganda. We chose two common forest-floor-dwelling lizard species from the *Eulamprus quoyii* species group: the southern water skink *Eulamprus heatwolei* and the highland water skink *Eulamprus tympanum*. These members of the herpetofauna are good model species for phylogeographic comparisons with invertebrate taxa because of their restriction to the same forest-floor habitat. By comparing phylogeographic patterns found in invertebrate taxa with the water skinks, we aimed to investigate how differing degrees of vagility and

habitat specificity to the forest-floor environment differentially shape the phylogeographic structure in these diverse taxa. Specifically, we tested the hypothesis that glacial/interglacial cycling during the Pleistocene differentially affected the genetic structure of taxa based on habitat specificity.

Materials and methods

Study site

This study was carried out in Tallaganda State Forest, Gourouk National Park and Badja State Forest (collectively referred to as 'Tallaganda'). Tallaganda (35°35'S–35°44'S and 149°28'E–149°30'E) forms a continuous 100 km (north–south) by 5–20 km (east–west) temperate forest within south-eastern NSW. It is located on the spine of the Gourouk Range, which connects to the main length of the Great Dividing Range (GDR) in its extreme south. Accordingly, Tallaganda is almost entirely surrounded by the low-lying areas of the Southern Tablelands (altitude *c.* 600 m), making it both topographically and ecologically isolated (Garrick *et al.*, 2004; Fig. 1). It is bounded to the north by the Lake George basin, to the east by the Shoalhaven River floodplain, and to the west by the Southern Tablelands and Tinderry Ranges. The escarpment of the Gourouk Range dominates the central area of the forest with altitudes between 1300 and 1500 m. The northern and southern regions are slightly lower and more undulating between 1000 and 1300 m.

This varied topography covers five microbiogeographic regions that follow major and/or minor catchment boundaries within Tallaganda (Fig. 2), and these catchments appear to shape phylogeographic structure in various low-vagility invertebrates (described in detail in Garrick *et al.*, 2004). Briefly, the Harold's Cross Region (HCR) lies in the far north of the Gourouk Range; the Eastern Slopes Region (ESR) dominates the high-altitude coastal slopes; the Anembo Region (AN) dominates the western slopes; and the Pike's Saddle Region (PSR) joins the southern extent of the Gourouk Range with the lower altitude Badja Region (BR), which in turn forms part of the tablelands that flank the mountainous GDR (Fig. 2).

Vegetation patterns at Tallaganda result from a mixture of landscape and local climatic processes. The eastern (coastal) slopes experience large amounts of orographic rain and are comprised mainly of wet sclerophyll forest. Valleys and gullies on this side of the range support a mesic understorey with stands of tree fern *Dicksonia antarctica* abundant in sheltered gullies, where moisture and nutrient levels are high (State Forests of New South Wales, 1995). The western slopes experience a rain-shadow effect and are primarily composed of more open dry sclerophyll forest.

Pleistocene environmental history in south-eastern Australia, and in particular the wider Tallaganda region, is very well understood. Lake George and the Shoalhaven River are notable sites for palaeoenvironmental study (Coventry & Walker, 1977; Hope, 1987; Nott & Price, 1991; Hesse, Magee

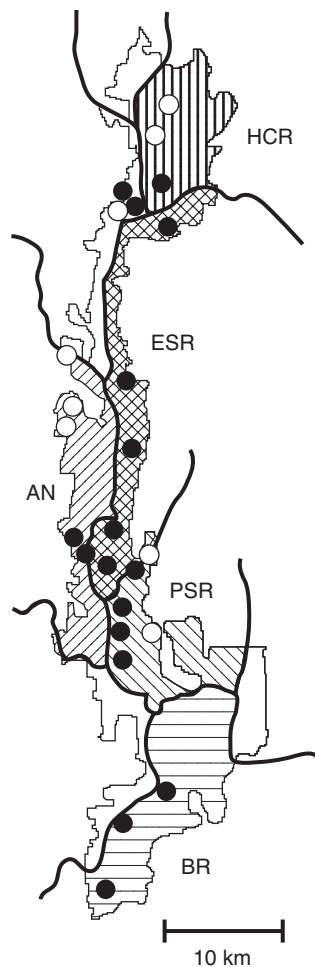


Figure 2 Hydrological divisions at Tallaganda on the Gourock Range illustrating the five microbiogeographic regions (shaded; adapted from Garrick *et al.*, 2004). HCR, Harold's Cross Region; ESR, Eastern Slopes Region; AN, Anembo Region; PSR, Pike's Saddle Region; BR, Badja Region where the site connects to the main length of the Great Dividing Range (see Fig. 1). Closed circles denote collection sites for *Eulamprus tympanum* and open circles denote collection sites for *Eulamprus heatwolei*. Each point may represent more than one individual.

& van der Kaars, 2004) and their proximity to Tallaganda gives excellent indications of the historical environmental conditions that characterize the region. Fossil pollen data from Lake George document altitudinal shifts in vegetation that followed the Pleistocene glacial/interglacial cycles (*c.* 1.2 million years before present). At glacial maxima, temperatures in south-eastern Australia are estimated to have been *c.* 9 °C cooler than today and precipitation was considerably reduced (Barrows, 2001; Hesse *et al.*, 2004). This caused depression of the upper tree line by 1200–1500 m (Singh & Geissler, 1985) to create a virtually treeless landscape with vegetation limited to a mosaic of alpine herb fields and grasslands (Nott & Price, 1991; Dodson & Ono, 1997; Hesse *et al.*, 2004). Active dune fields in the Shoalhaven River valley supplement evidence for treeless glacial landscapes, as con-

struction of such dunes would only have been possible with greatly reduced vegetation cover on the Gourock Range to the windward (west) side of the Shoalhaven valley (Hope, 1987; Nott & Price, 1991).

Current topography suggests that Tallaganda could have harboured multiple refugia during glacial cycles (G. Hope, pers. comm.). The ESR is deeply dissected by *c.* 15 east–west oriented creek lines (State Forests of New South Wales, 1995). During glacial periods, the valleys are likely to have remained protected from the severe winds and frosts on the mountaintops and plains, allowing small, forested refuges to survive through glacial extremes. Corridors of vegetation on creek lines may have linked these refugia, although it is also possible that some existed as isolated pockets. Range contractions from forest depression and the possibility of disconnected refugia at Tallaganda would have had inescapable impacts on the genetic structure of many taxa. These conditions undoubtedly played an important role in initiating phylogeographic differentiation among now extant lineages (Garrick *et al.*, 2004; Beavis & Rowell, in press).

The water skinks *E. heatwolei* and *E. tympanum*

The two species included in this study are terrestrial and diurnal skinks that are prominent members of the reptile fauna in mesic forests in eastern Australia (Greer, 1989; Wilson & Swan, 2003). They are closely related and morphologically very similar (O'Connor & Moritz, 2003). Both species are viviparous and active foragers that generally feed on arthropods (Greer, 1989), they display strong attachment to a few basking sites where most of their activity is focused (Greer, 1989; Bennett, 1997), and both prefer open sclerophyll forests with an abundance of large fallen logs for shelter and basking (Morrison, Keogh & Scott, 2002; Langkilde, O'Connor & Shine, 2003; Wilson & Swan, 2003; Stapley & Keogh, 2004, 2005). As the common names suggest, both are associated with streams and creeks or moist habitats and will readily take to the water if disturbed (Wilson & Swan, 2003).

Apart from these similarities, the two species may show a degree of habitat differentiation. In the south-east Australian ranges where their distributions overlap, it is thought that *E. tympanum* replaces *E. heatwolei* at higher altitudes (Spellerberg, 1972*a,b,c,d*; Greer, 1989; Hutchinson & Rawlinson, 1995). This may be indicative of a greater tolerance in *E. tympanum* for the drier sclerophyll forests commonly associated with high altitudes. If this is the case, then the two species may represent an altitudinal cline with *E. tympanum* above and *E. heatwolei* below, and the two existing in sympatry on the border of their altitude ranges. In Tallaganda, the two species are sympatric.

Taxonomic sampling and molecular methods

A total of 52 *E. tympanum* and 24 *E. heatwolei* were captured from 25 sites between October and December 2003 (Fig. 2). Animals were caught by noosing, and tissue

samples were taken from the tail tip. Samples were placed immediately in 100% EtOH and stored at -4°C . All animals were released at the site of capture following tissue collection. The mitochondrial ND4 gene and associated tRNAs were targeted for amplification with primers ND4 and tRNA-Leu with methods described in detail elsewhere (Scott & Keogh, 2000; Keogh *et al.*, 2003; Keogh, Scott & Hayes, 2005). The ND4 region was used because other work at comparable taxonomic levels in reptiles has indicated useful levels of variability in this gene (Scott & Keogh, 2000; Keogh *et al.*, 2003, 2005; O'Connor & Moritz, 2003; Reeder, 2003; Chapple & Keogh, 2004; Chapple, Keogh & Hutchinson, 2005). Sequences were edited with Sequencher 3.0 (Genes Codes Corporation) and provisionally aligned using the default parameters ClustalX (Thompson *et al.*, 1997). The final alignment was refined by eye.

Phylogenetic and population genetic analysis

Separate alignment files were constructed for each species. For each dataset ModelTest 3.06 (Posada & Crandall, 1998) was used to select the most appropriate model of molecular evolution for the data. The ModelTest estimates of empirical nucleotide frequencies, substitution rates, gamma distribution and proportion of invariant sites (I) were used for maximum likelihood (ML) analyses implemented in the computer program Phylogenetic Analysis Using Parsimony PAUP*. For each dataset two conservative analyses were run to evaluate support for any population structure that might be evident among haplotypes. First, the ModelTest estimates of empirical nucleotide frequencies, substitution rates, gamma distribution and proportion of invariant sites (I) were used to run 100 ML bootstrap pseudoreplicates. Second, unweighted parsimony analysis was used to produce a strict consensus tree of all equally most parsimonious haplotype trees. The results of these analyses were combined into a single figure for each species showing the strict consensus tree with ML bootstrap values mapped on to the same tree to demonstrate where the alternative analysis techniques agreed on topology.

Spatial autocorrelation

Spatial autocorrelation analysis was implemented in GenAlEx (Peakall & Smouse, 2006) to further test for local genetic structure at the microgeographic scale. The analysis assesses associations between physical distance and the genetic distance between samples and gives a visual representation of the spatial pattern of genetic structuring (Manel *et al.*, 2003). Although we used sequence divergence data for the spatial autocorrelation analysis, GenAlEx treats haplotypes as equally different states and gives no weight to the degree of difference among sequences. Therefore, this is essentially an F_{st} approach and not a Φ_{st} for which GenAlEx was originally designed. For both species, distance classes were created to cover the total 100 km length of the study site, and 999 random permutations were used to calculate 95% confidence intervals. A mean r of zero signifies no correlation,

and a positive r value suggests genetic correlation for that distance class. The point where the curve first crosses the x-axis gives a rough estimate of the extent of genetic patch size (non-random distribution of genotypes), although this must be interpreted in the context of distance class sizes and sample size.

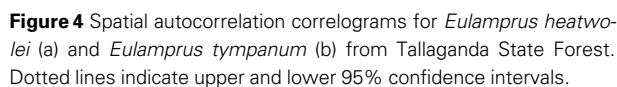
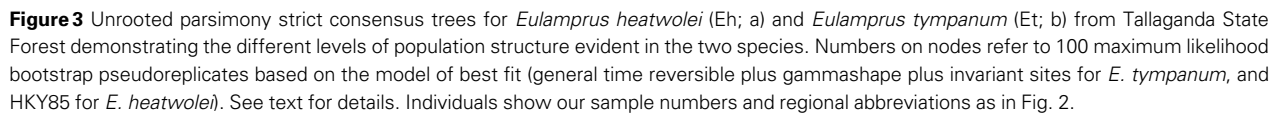
Results

Eulamprus heatwolei

The edited alignment for *E. heatwolei* from Tallaganda comprised 691 characters with 33 variable sites (4.8%). Of the latter, 19 (57.6%) were parsimony informative: two were first codon position, two were second codon position, 12 were third codon position and three were in the tRNAs. No premature stop codons were observed in coding sequence, which suggests that our sequences were functional mitochondrial genes. ModelTest supported the relatively simple HKY model of molecular evolution and gave a $-\ln L = 1139.5178$. The estimated parameters were as follows: nucleotide frequencies $A = 0.3494$, $C = 0.2602$, $G = 0.1318$, $T = 0.2586$; substitution rates were equal; proportion of invariant sites = 0; Ti/Tv ratio = 7.8708.

Fourteen unique haplotypes were identified among the 24 *E. heatwolei*. While there was sufficient genetic variation to detect population structuring across the geographic range, little was found. The unweighted parsimony analyses resulted in 27 most parsimonious trees. The strict consensus of these is essentially a 'star' phylogeny (Fig. 3a) that demonstrates a lack of population structure except for the presence of a discrete clade representing two animals with a unique haplotype (Eh26 and Eh29). The 100 ML bootstrap analysis in PAUP* using the above parameters also yielded a largely unresolved tree, with the two distinct haplotype groups clear and well supported (tree not shown). The mean corrected sequence divergence (HKY model) between unique haplotypes for *E. heatwolei* is 0.0075. Excluding the divergent haplotype, the mean corrected sequence divergence is much smaller: 0.0052. The divergent haplotype has a minimum of 14 base pair changes and a maximum of 24 in pairwise comparisons (data not shown). This is contrasted with a range of 0–9 base pair changes among the remaining haplotypes, with the divergent haplotype excluded.

A broader scale phylogenetic analysis of *E. heatwolei* (our unpubl. data) reveals a close relationship between the divergent haplotype in Tallaganda and *E. heatwolei* in the Brindabella Range. These two sites are c. 90 km apart and are separated by the Tinderry Range. Using this larger dataset, a Shimodaira–Hasegawa topology test implemented in PAUP* allowed us to soundly reject the hypothesis that the two haplotype groups are monophyletic ($P < 0.0001$). Whether the presence of the divergent haplotype at Tallaganda represents an ancient, widespread haplotype or a long-distance dispersal event is unclear. The spatial autocorrelation correlogram for *E. heatwolei* at



Thirty-seven unique haplotypes were identified among the 52 *E. tympanum* caught. The unweighted parsimony analyses resulted in 946 most parsimonious trees and the strict consensus of those trees was very similar to the ML analysis (Fig. 3b). Haplotypes displayed a high degree of phylogeographic structure. Thirty-four were restricted to one of the five microbiogeographic regions described in Garrick *et al.* (2004; Fig. 3b). The remaining three haplotypes were shared between adjacent regions, with one shared between HCR and ESR, another shared between ESR, PSR and AN, and another shared between PSR and AN. PSR

had the highest diversity with 15 unique haplotypes. This region was also the most intensively sampled.

The unrooted ML tree for *E. tympanum* strongly supports the existence of two distinct clades (bootstrap 89), one representing all animals from the northern regions of Tallaganda (HCR, ESR, AN and PSR; Fig. 3b). The 'northern' clade contains 31 of the 37 haplotypes present throughout Tallaganda. The branches within this northern clade are poorly supported (<50–62 bootstrap), and only two branches have bootstrap support above 70. Three of the nine individuals from BR are present in this northern clade (Et43, Et66 and Eh35tym) while the remaining six are each characterized by a unique haplotype and do not form a monophyletic group. The mean corrected sequence divergence (GTR model) between all unique haplotypes for *E. tympanum* is 0.0139. Within the northern clade, the mean corrected sequence divergence between unique haplotypes is 0.0139. Within the six remaining haplotypes unique to BR, the mean corrected sequence divergence is 0.0144. Considering this is between only six haplotypes, the southern BR accounts for much of the sequence diversity seen within Tallaganda for this species.

Spatial autocorrelation analysis also supports a significant degree of population structuring for *E. tympanum* within Tallaganda. In Fig. 4b, the correlation values are positive and significant up to 18 km with the x -intercept also occurring at this distance. There is a general decline in correlation with distance, whereby animals within 18 km of each other are more genetically alike than more distant animals. This local positive genetic structure rejects the null hypothesis of no spatial structure within *E. tympanum* at Tallaganda.

Discussion

Comparative phylogeography of *E. heatwolei* and *E. tympanum*

The phylogeographic patterns of *E. heatwolei* and *E. tympanum* in Tallaganda State Forest are very different. The consensus tree for *E. tympanum* displays considerable phylogeographic structure with a clade comprising animals from the northern regions of Tallaganda, to the exclusion of the majority of animals from the southern BR. The spatial autocorrelation analysis for *E. tympanum* also indicates significant levels of local population structuring. The consensus tree for *E. heatwolei*, however, does not display any spatial structure within Tallaganda, and this is further demonstrated in the spatial autocorrelation analysis.

These differences in structure were unexpected as the two species share apparently similar ecologies. Assuming the sampling to be representative of the genetic diversity in *E. heatwolei*, the difference between the species could be due to slightly different habitat preferences and the consequences of these amid past environmental change. This aspect of the biology of both species has been considered at length by Spellerberg (1972a,b,c,d). From our collections it is clear that *E. heatwolei* and *E. tympanum* exist sympatri-

cally at Tallaganda, indicating that Tallaganda lies at the interface of the two species' preferred habitat ranges. However, palaeoenvironmental data indicate that this would not have always been the case. The landscape changes associated with glacial and interglacial cycles during the Pleistocene dramatically altered the distribution of many species (Hesse *et al.*, 2004). Glacial cycles at Tallaganda would have seen the water skink populations follow depression of the tree line down into the refugia afforded in the deep valleys of the ESR. Although these areas would have been relatively well protected, the habitats they provided would have been much drier than pre-glacial conditions, probably reflecting those that previously existed on high-altitude slopes.

The preference of *E. heatwolei* for more mesic sites associated with lower altitudes would have severely limited its chance of long-term survival in glacial refugia (Spellerberg, 1972a,b,c,d). Contraction to suboptimal refugia, and the repeated isolation of populations during glacial periods, may have driven *E. heatwolei* to local extinction within Tallaganda (if it was present at that time). This is consistent with the absence of genetic spatial structure seen in this species today, and is characteristic of a recent colonization and population expansion in the region (Avice *et al.*, 1987). A tolerance for drier conditions associated with higher altitude in *E. tympanum* could have made this species less susceptible to Pleistocene extinction within Tallaganda. The strong phylogeographic structure we see in this species today is indicative of barriers to gene flow, where underlying divergence developed during periods of isolation in refugia has been conserved (Avice *et al.*, 1987).

Comparative phylogeography of *E. heatwolei* and *E. tympanum* with invertebrate taxa

The phylogeographic structure of an unnamed collembolan at Tallaganda demonstrated significant genetic differentiation among five regions, and abrupt genetic contact zones with little admixture across boundaries (Garrick *et al.*, 2004). This study has demonstrated strong phylogeographic patterns in *E. tympanum* but only a single phylogeographic break. This is congruent with the deepest split identified for the collembolan, on the catchment boundary between the ESR and the BR where Tallaganda connects to the GDR. Accordingly, *E. tympanum* in HCR, PSR, AN and ESR exist together on an isolated peninsula. This isolation appears to have separated the northern regions at Tallaganda from gene flow occurring in the greater length of the GDR and BR. It is common for isolated populations to be phylogenetically distinct, and there are many examples of this occurring on islands (e.g. *Chalcides* skinks, Brown & Pestano, 1998; tiger snakes, Keogh *et al.*, 2005), on the periphery of a species range (e.g. heath butterflies, Cassel & Tamaru, 2003; marbled murrelets, Congdon *et al.*, 2000) and in historically fragmented landscapes (e.g. prickly skinks, Cunningham & Moritz, 1998; Florida scrub skinks, Branch *et al.*, 2003; European perch, Nesbo *et al.*, 1999).

Vicariance through Pleistocene landscape change is likely to have reinforced the phylogeographic break caused by peripheral isolation. On the basis of current topology, we can infer that the low-altitude BR, which connects the regions of northern Tallaganda to the GDR, was probably treeless steppe during glacial periods (Garrick *et al.*, 2004). This environment would have severely hindered gene flow between the GDR and northern Tallaganda, allowing further divergence of already peripherally isolated populations. At interglacials when forests reconnected, gene flow would have resumed over the BR. Thus the congruent phylogeographic break observed in the collembolan and *E. tympanum* may also represent the contact point of population range expansions after glacial cycles. This single area of phylogeographic congruence demonstrates that despite contrasting taxonomy, ecology and dispersal abilities, the collembolan and *E. tympanum* have been similarly affected by past environmental changes.

The differing phylogeographic patterns between *E. heatwolei* and *E. tympanum* are very similar to those found in two funnel web spider genera currently being investigated at Tallaganda. Beavis & Rowell (in press) described phylogeographic structure in an unnamed species of forest-floor-dwelling funnel web, *Atrax* sp., and in an ecologically similar and unnamed saproxylic species, *Hadronyche* sp. (henceforth referred to as *Atrax* and *Hadronyche*, respectively). They found that the forest-floor dwelling *Atrax* displayed phylogeographic structure comparable to the collembolan and a high mean sequence divergence, while the saproxylic *Hadronyche* essentially had no structure and little mean sequence divergence (Beavis & Rowell, in press). The differences in genetic structure between the two superficially similar genera were characteristic of their differing degrees of habitat specificity, and mirror our data for the water skinks. The patterns displayed for *E. heatwolei* and *Hadronyche* are typical of type IV phylogeographic patterns recognized by Avise *et al.* (1987). The species both have high habitat specificity and experienced a recent range expansion into Tallaganda, possibly from refugia in the GDR, without any isolating barriers to gene flow (Avise *et al.*, 1987; Beavis & Rowell, in press). Phylogeographic structures in *E. tympanum* and *Atrax* are typical of type I patterns (Avise *et al.*, 1987). Both these species appear to have had a long history at Tallaganda and have experienced barriers to gene flow that has led to high sequence divergence and a significant degree of phylogeographic structure. That *E. tympanum* shows only two distinct regions while the structured invertebrates show five can be attributed to a greater potential for dispersal in skinks 'overwriting' the more superficial splits.

The results of this study have three major implications. Firstly, the different levels of phylogeographic structure between *E. tympanum* and *E. heatwolei* suggest that their slightly differing habitat preferences gave rise to very different responses to historical vicariant events. The effect of repeated range contractions on *E. heatwolei* also highlights the potential importance of refugia in the extinction process. Secondly, the phylogeographic congruence of *E. tympanum*

and the collembolan species demonstrates that the purported peripheral isolation of Tallaganda, and the landscape changes associated with glacial cycles have predictable genetic consequences that reach beyond taxonomy, ecology and dispersal ability. The similarities between the water skinks and the two funnel web genera suggest that habitat specificity appears to play a large role in determining genetic structure in extant lineages. Finally, the phylogeographic congruence demonstrated here between a vertebrate and an invertebrate may aid the development of future hypotheses regarding the genetic structure of other unsampled taxa at Tallaganda. By extending the results from the current study in this way, greater insights into regional species assemblages may be gained (Avise, 2000; Moritz, 2002).

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