1 **Title** Phylogeographic parallelism: concordance of patterns in closely related species
2 illuminates underlying mechanisms in the historically glaciated Tasmanian landscape

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16 **Running header** Phylogeography of the Tasmanian metallic snow skink

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18

19 Abstract

20 Phylogeography provides a means to understand mechanisms that shaped the distribution and
 21 abundance of species, including the role of past climate change. While concordant
 22 phylogeographic relationships across diverse taxa suggest shared underlying mechanisms
 23 (“phylogeographic parallelism”), it is also possible that similar patterns are the product of
 24 different mechanisms (“phylogeographic convergence”), reflecting variation among taxa in
 25 factors such as environmental tolerances, life histories, and vagility. Hence, phylogeographic
 26 concordance among closely related and ecologically similar species can yield a more
 27 confident understanding of the past mechanisms which shaped their distribution and
 28 abundance. This study documented mitochondrial and nuclear phylogeographic patterns in the
 29 ectotherm skink, *Niveoscincus metallicus*, which occupies historically glaciated regions of
 30 Tasmania, and contrasted these with the closely related and broadly sympatric *N. ocellatus*.
 31 Major phylogeographic breaks were similar in location between the two species, and
 32 indicative of isolation caused by retreat from high elevation areas during glaciations, but with
 33 long-term persistence at multiple low elevation sites. Hence, Pleistocene glacial refugia were
 34 altitudinal rather than latitudinal, a pattern mirrored in other temperate Southern Hemisphere
 35 taxa. This study also examined phylogeographic patterns across the intermittently inundated
 36 Bassian Isthmus between mainland Australia and the island of Tasmania, and revealed that
 37 structuring is similarly maintained when populations were physically isolated during
 38 interglacial rather than glacial stages.
 39

40 Introduction

41 Phylogeography provides a means to understand factors that shaped the distribution and
 42 abundance of species, including their responses to past climates (Hewitt, 2004). Past
 43 population dynamics are recorded in the genes of species, and robust quantitative frameworks
 44 are developing for the incorporation of such information into projections of species range and
 45 abundance (Fordham *et al.*, 2014), which is relevant for biodiversity conservation (Blois *et al.*,
 46 2010). However, the value of phylogeography depends on the extent to which its results can
 47 be predicted across other regions and taxa (e.g., Bermingham & Avise, 1986; Avise, 1992;
 48 Carstens *et al.*, 2005; DeChaine & Martin, 2006). In this context, patterns from mid- to high-
 49 latitude regions of Western Europe and North America became paradigmatic within
 50 phylogeography (Taberlet *et al.*, 1998; Hewitt, 2000, 2004); elevated and endemic genetic
 51 variation at low latitude regions and lower genetic variation and phylogeographic structure
 52 across higher latitudes was interpreted as signatures of recolonization of previously glaciated
 53 areas from low latitude refugia. However, investigations in less extensively glaciated or
 54 unglaciated regions of the world often failed to recover patterns consistent with widespread
 55 extirpation and subsequent postglacial recolonisation from sparse refugia (e.g., Lessa *et al.*,
 56 2003; Byrne, 2008; Byrne *et al.*, 2008; Byrne *et al.*, 2011; Qiu *et al.*, 2011; Sersic *et al.*, 2011;
 57 Breitman *et al.*, 2012; Lorenzen *et al.*, 2012; Turchetto-Zolet *et al.*, 2013). Other studies have
 58 also indicated long-term persistence with relatively subtle range movements through time in
 59 areas heavily affected by Pleistocene glaciations (Rull, 2009; Tzedakis *et al.*, 2013; de
 60 Lafontaine *et al.*, 2014). Therefore, phylogeographic patterns, and the inferences drawn from
 61 them, could be influenced by idiosyncrasies related to region or species (but these are also of
 62 value; see Papadopoulou & Knowles, 2016).

63 While concordant phylogeographic patterns are considered indicative of shared underlying
 64 histories, diverse phylogeographic responses to the same environmental change are expected
 65 among species owing to variation in environmental tolerances, life histories, and vagility
 66 (Jackson & Overpeck, 2000; Soltis *et al.*, 2006; Stewart *et al.*, 2010; Papadopoulou &
 67 Knowles, 2016). Therefore, even when shared patterns are observed among species, these
 68 may represent “phylogeographic convergence”—reflecting coincidence of patterns from
 69 different mechanisms—rather than “phylogeographic parallelism”, or the operation of the
 70 same mechanism. It is now widely advocated that studies attempting to attribute differences in
 71 phylogeographic patterns to differences in species attributes benefit from comparisons of
 72 closely related species, because these will differ in fewer other potentially confounding

73 variables (Williams, 1994; Turner & Trexler, 1998; Dawson *et al.*, 2002; Whiteley *et al.*,
74 2004; Hickerson & Cunningham, 2005; Burrige *et al.*, 2008). The corollary of this is that
75 shared patterns among closely related taxa are less likely to reflect phylogeographic
76 convergence, and more likely to represent robust replicates for the inference of underlying
77 mechanisms (Dawson, 2012; Dawson *et al.*, 2014).

78 Reptiles have been highlighted as excellent model species in phylogeographic studies
79 (Camargo *et al.*, 2010). As ectotherms, they depend on heat from the environment to sustain
80 metabolism and reproduction, and are therefore sensitive to changes in climate (Sinervo *et al.*,
81 2010). Reptiles also tend to have limited dispersal abilities (Metts *et al.*, 2000), which means
82 that the genetic signatures of historical distributional changes are likely to persist for longer
83 than in more vagile species such as large mammals and birds (Araújo *et al.*, 2008). Therefore,
84 we expect that comparative phylogeographic studies of closely related reptiles will be more
85 likely to observe shared patterns reflecting the same underlying mechanism, or where patterns
86 differ, they can be more confidently ascribed to differences among these species with respect
87 to morphology, physiology, life history, or behaviour. While many phylogeographic studies
88 have exploited reptiles to increase our understanding of faunal responses to environmental
89 change (Dubey & Shine, 2010; Breitman *et al.*, 2012; Vera-Escalona *et al.*, 2012; Nelson-
90 Tunley *et al.*, 2016), few have analysed closely related species (e.g., Hare *et al.*, 2008).

91 There have been substantial efforts to overcome the early dearth of phylogeographic studies
92 on Southern Hemisphere taxa (Beheregaray, 2008), and some generalisations have been made
93 regarding biotic responses to Pleistocene climate fluctuations in this region, and contrasting
94 with patterns in the Northern Hemisphere (Byrne, 2008; Byrne *et al.*, 2008; Wallis & Trewick,
95 2009; Byrne *et al.*, 2011; Sérsic *et al.*, 2011; Wallis *et al.*, 2016). Tasmania—the only
96 Australian location that was directly influenced by Pleistocene glaciations (Colhoun &
97 Barrows, 2011)—experienced Last Glacial Maximum (LGM) temperature depressions up to
98 6.5°C (Colhoun, 1985; Fletcher & Thomas, 2010), with tree-lines close to the modern day sea
99 level (Gibson *et al.*, 1987). While Tasmania has been the subject of several phylogeographic
100 studies (Chapple *et al.*, 2005; Macqueen *et al.*, 2009; Worth *et al.*, 2009; Zhang *et al.*, 2014)
101 (McKinnon *et al.*, 2004; Nevill *et al.*, 2010; Worth *et al.*, 2011), it remains unclear whether its
102 fauna responded to Pleistocene glaciations by widespread contraction into geographically
103 discrete refugia, or instead persisted in multiple regions. Cliff *et al.* (2015) have conducted the
104 most comprehensive range-wide phylogeographic study of a Tasmanian vertebrate, the
105 spotted snow skink *Niveoscincus ocellatus*, and revealed regional persistence but also

106 contrasting patterns throughout the species' range: there was evidence of population
 107 persistence and limited gene flow within the historically and presently milder northeast, while
 108 the southeast and glacially-effected central regions were characterised by patterns consistent
 109 with greater post-glacial gene flow and demographic expansion.

110 We conducted a phylogeographic study in the metallic snow skink *Niveoscincus metallicus*, to
 111 contrast against the previous results for the congeneric *N. ocellatus* (Cliff *et al.*, 2015). Both
 112 species are widespread across Tasmania and occupy a broad elevational range, from sea level
 113 to ~1000-1200 m (Figure 1), roughly equivalent to the regional subalpine tree line (Melville
 114 & Swain, 1999), and therefore have similar thermal niches (Melville & Swain, 2003;
 115 Caldwell *et al.*, 2017). *Niveoscincus metallicus* is also distributed across the islands of Bass
 116 Strait and into southeast mainland Australia (Figure 1). While *N. metallicus* is typically found
 117 in close proximity to deep litter or other shelter, such as fallen logs or rocks, *N. ocellatus* is
 118 obligate saxicolous (Melville & Swain, 1997). The analysis of *N. metallicus* enables us to test
 119 phylogeographic convergence with *N. ocellatus*, and if present, provide stronger inference of
 120 the mechanism underlying their phylogeographic history. We also assess the phylogeographic
 121 relationships of Tasmanian, mainland Australian, and Bass Strait *N. metallicus* populations
 122 with respect to their persistence and isolation across the periodically emergent Bassian
 123 Isthmus, a question relating to Pleistocene sea level change (Lambeck & Chappell, 2001) that
 124 has been addressed for a range of taxa (Chapple *et al.*, 2005; Keogh *et al.*, 2005; Symula *et al.*,
 125 2008; Dubey & Shine, 2010; Chapple *et al.*, 2011b; Haines *et al.*, 2014; Ng *et al.*, 2014).

126

127 **Materials and Methods**

128 Tissue was obtained from a total of 779 *N. metallicus* from 56 locations across the species'
 129 geographic and elevational range (Figure 1, Supplementary Table 1), with the exception of
 130 King Island and southwest Tasmania. Sites were selected to ensure coverage of the same area
 131 investigated by Cliff *et al.* (2015) for *N. ocellatus*. Field collections were supplemented by
 132 institutional collections (Supplementary Table 2). Between 1–23 individuals were sampled
 133 per site (Supplementary Table 1). We employed *N. ocellatus* and *N. pretiosus* as outgroups.
 134 We sequenced several *N. pretiosus*, but also noted that other d assigned to this species
 135 (GenBank accession numbers HQ454789, DQ675234) fell deep within the *N. metallicus* tree,
 136 and we included these in our study as *N. metallicus*.

137 Genomic DNA extraction and PCR amplification of partial mitochondrial ND2 (c. 543 bp)
138 and ND4 (c. 864 bp), and partial nuclear β -globin (intron 2, c. 782 bp) were conducted
139 following Cliff *et al.* (2015). These regions exhibited useful levels of intraspecific genetic
140 diversity in previous studies of squamates (Bell *et al.*, 2010; Chapple *et al.*, 2011b).
141 Sequencing of both mtDNA strands was conducted in instances where sequence quality was
142 low. All β -globin sequences were obtained from both strands. DNA sequences were edited
143 and aligned in Geneious version 6.1.8 (Biomatters).

144 Ambiguous double peaks were observed in some ND2 sequence chromatograms, probably
145 representing a nuclear pseudogene (Bensasson *et al.*, 2001). The protein coding regions of
146 both mitochondrial genes were translated to ensure that sequences did not contain premature
147 stop codons, that would indicate a divergent non-coding pseudogene. ND2 sequences from
148 300 individuals were obtained, and ND4 sequences were obtained from 340 individuals,
149 representing 57 localities (Supplementary Table 1). Sequences from individuals where both
150 ND2 and ND4 amplified successfully were concatenated, giving a total of 1406 bp for 284
151 individuals from 52 sites. A total of 72 individuals with sequence data for only one
152 mitochondrial marker were omitted from the concatenated dataset, due to concerns about the
153 effect of large amounts of missing data on phylogenetic inference (Lemmon *et al.*, 2009).
154 Two sampling sites (Mount Bischoff and Cataract Gorge) were entirely omitted from the
155 concatenated dataset because of substantial double peaks in ND2 sequences.

156 β -globin sequences were obtained from 84 individuals (168 alleles), representing 35 localities
157 (Supplementary Table 1). Several individuals were excluded from this dataset based on
158 heterozygous length mutations, resulting in long sections of superimposed chromatogram
159 traces. PHASE 2.1.1 (Stephens *et al.*, 2001) was used to infer allelic states for individuals that
160 were homozygous for sequence length but heterozygous at more than one nucleotide. PHASE
161 input files were prepared and post-processed in SEQPHASE (Flot, 2010).

162 Bayesian phylogenetic reconstruction was conducted in MrBayes 3.2.2 (Ronquist *et al.*, 2012)
163 on unique haplotypes identified from concatenated sequences. Individuals sharing the same
164 sequence were assigned to haplotypes using TCSv1.21 (Clement *et al.*, 2000), ensuring that
165 individuals with missing or ambiguous data at the same nucleotide position, but with
166 otherwise identical sequences, were assigned to the same haplotype. mtDNA sequences were
167 partitioned by gene region and analysed under substitution models suggested by jModelTest
168 2.1.7 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012) using the Bayesian Information
169 Criterion. When the most supported substitution model was not available in MrBayes, the

170 next most complex model available was implemented. For ND4, TrN+I+ Γ was selected by
 171 jModelTest and GTR+I+ Γ was implemented in MrBayes, and for ND2, TrN+ Γ was selected
 172 and GTR+ Γ was implemented. Two parallel runs were completed in MrBayes, each of 5.5 x
 173 10⁶ generations, with four Markov Chain Monte Carlo (MCMC) chains with a heating
 174 parameter of 0.1 and sampling every 500 generations. The initial 25% of samples were
 175 discarded as burnin. Log files were checked using Tracer 1.6 (Rambaut & Drummond, 2013)
 176 to ensure that effective sample sizes were greater than 200 and that stationarity and
 177 convergence were achieved during model runs. The consensus tree was viewed and edited in
 178 FigTree v1.4.2 (Rambaut, 2014). Node support was assessed by posterior probabilities, with
 179 values greater than or equal to 0.95 considered to support the branching pattern.

180 Estimates of molecular diversity (haplotype diversity and nucleotide diversity) were
 181 calculated in Arlequin 3.5 (Excoffier & Lischer, 2010). The number of polymorphic and
 182 parsimony informative nucleotide sites and mean uncorrected genetic distances (p-distances)
 183 between sequences assigned to each mitochondrial clade were calculated in MEGA6.0
 184 (Tamura *et al.*, 2013). Population structure was quantified and assessed for mitochondrial and
 185 nuclear data using two approaches: Analysis of Molecular Variance (AMOVA; Excoffier *et al.*,
 186 1992) and Spatial Analysis of Molecular Variance (SAMOVA; Dupanloup *et al.*, 2002).
 187 AMOVA was performed in Arlequin. Sequence variation was hierarchically partitioned based
 188 on the membership of individuals to (i) major regional mitochondrial clades (Φ_{CT} ; clades
 189 defined from Bayesian phylogenetic analysis), (ii) geographic sites within clades (Φ_{SC}), and
 190 (iii) geographic sites across the entire study range (Φ_{ST}). The significance of estimated
 191 fixation indices was tested using 1000 permutations of the data. SAMOVA was performed
 192 using K = 2 to 7 groups in the SAMOVA package.

193 Divergence dating analyses were completed in BEAST 2.2.1 (Bouckaert *et al.*, 2014).
 194 Sequences were partitioned by gene region and substitution models suggested by jModelTest
 195 were implemented. To test for significant variation in mutation rates among different branches,
 196 a relaxed lognormal molecular clock model was implemented with a coalescent constant
 197 population size prior, run for 50 x 10⁶ generations and sampled every 5000 generations. Given
 198 that the rate variation parameter was close to zero, indicating that rates did not vary
 199 significantly between branches, a strict molecular clock was employed for estimating
 200 divergence times (Drummond & Suchard, 2010) with a normally distributed clock prior of
 201 mean 1.52% (standard deviation 0.5%) sequence divergence per million years (which equates
 202 to a lineage rate of 0.0076 substitutions per site per million years with a standard deviation of

0.0025). This rate was derived from several previous estimates of mitochondrial divergence in squamates based on fossil calibrations (Chapple *et al.*, 2011b). Results were visualised in Tracer to ensure that effective sample sizes were greater than 200 and that model runs had converged. The first 25% of samples were discarded as burnin and TreeAnnotator (Bouckaert *et al.*, 2014) was used to produce a maximum clade credibility tree with mean node heights. Uncertainty in node ages was assessed by examining the 95% high posterior density of values. Due to shallow levels of divergence and the potential for reticulate evolution in nuclear sequences (Huson & Bryant, 2006), allele networks rather than phylogenetic trees were reconstructed for β -globin using the TCS statistical parsimony algorithm (Clement *et al.*, 2000), implemented in PopART (<http://popart.otago.ac.nz/index.shtml>; Leigh & Bryant, 2015). Congruence of relationships among alleles and each individual's assignment to a mitochondrial clade were assessed visually. Alignments of phased sequences revealed several insertions or deletions (indels), which were present in a homozygous condition within a particular individual. Indels were coded as binary characters using SeqPhase (Muller, 2006). Network analyses with and without indel characters did not differ in topology and further analyses omitted indel information.

219

220 **Results**

221 *Mitochondrial variation*

222 Mitochondrial sequences were highly variable; from a total of 1406 base pairs, 439 sites were
223 polymorphic and 304 sites were parsimony informative. A total of 215 unique haplotypes
224 were identified from 284 individuals with sequence data for both ND2 and ND4. Overall
225 haplotype diversity was high ($H = 0.99$, Table 1), with few haplotypes represented by more
226 than one individual or more than one locality.

227 Bayesian phylogenetic analysis of mitochondrial haplotypes recovered four major clades: a
228 northwestern, a northeastern (including mainland Australia and the Bass Strait islands), a
229 southeastern and a southern clade (Figure 2). These clades were geographically distinct,
230 highly divergent and received strong posterior support (Figure 2). The level of
231 phylogeographic structure varied within the major clades, with the northeast clade the most
232 geographically structured (Figure 2). Northeast Tasmania was monophyletic, as were
233 mainland Australia and each of the Bass Strait islands (with the exception of Flinders Island
234 and the adjacent Mt Chappell Island), with strong posterior support (Figure 2). The order of

divergence between these clades was well resolved with the exception of Clarke Island (Figure 2). The mainland Australian clade was nested among the Bass Strait island clades. There was relatively little phylogeographic structure among populations from the northeast of Tasmania. The southeast clade encompassed the largest land area, and several lineages were geographically clustered although not monophyletic (e.g. the northern Midlands, the east coast, Mt Wellington and surrounds, the eastern Central Plateau and the western Central Plateau; Figure 2). The northwest clade was the most divergent; however, this was the least internally structured geographically (Figure 2). The southern clade had limited evidence of spatial structuring (Figure 2). Geographic overlap between southeast and northwest clades occurred at Lake St Clair, while overlap between southeast and northeast clades occurred in northeast Tasmania at Hillwood and Ben Lomond, each representing high elevation sites (Figure 3). Uncorrected genetic distances between major clades were considerable, with approximately 7% sequence divergence separating the northwest clade, while the remaining clades were separated from one another by 4–5% sequence divergence.

The divergence dating tree recovered the same clades as the non ultrametric tree (Supplementary Figure 1). The divergence of the northwest clade was placed at 10.0 Ma (95% HPD: 4.5–18.4 Ma). The southern clade diverged around 5.8 Ma (2.5–10.6 Ma), and the split between the northeast and southeast clades occurred around 4.4 Ma (1.9–8.1 Ma). Within the major clades, deep internal branches diverged approximately 2.8–1.5 Ma. Within the northeast clade, the divergence between Tasmania and the group comprising the Bass Strait islands and mainland Australia was dated to around 2.8 Ma (1.2–5.2 Ma), while mainland Australian populations diverged 1–2 Ma.

The greatest gain in mitochondrial Φ_{CT} occurred at $K = 4$ groups in SAMOVA, and the assignment of sampling sites to groups was equivalent to the four major mitochondrial clades resolved by phylogenetic analyses. High and significant levels of population structure were detected among all comparisons tested using AMOVA: among all sampling sites, among sites within regional clades, and among regional clades, with the highest proportion of variation (63%) attributable to regional clades (Table 2). Each regional clade was also significantly more structured than would be expected by chance alone, with the exception of the Northwestern clade, in which considerably more variation was contained within populations rather than among populations (Table 2). The Northeastern clade was the most highly structured clade, followed by the Southeastern and Southern clades (Table 2). AMOVA was also conducted on groups of populations within the Northeastern clade (Table 2); the island

268 populations were highly structured, mainland Australian populations were somewhat less
269 structured and north-eastern Tasmanian populations were significantly but comparatively
270 weakly structured (Table 2).

271 *Nuclear variation*

272 Nuclear (β -globin) sequences were much less variable than mitochondrial sequences, with 87
273 polymorphic and 44 parsimony informative nucleotide sites from a total of 782 bp. In addition,
274 there were three single nucleotide indels, and longer indels of 12, 13, 14 and 16 bp. A total of
275 83 unique β -globin haplotypes were recovered from 168 alleles (84 individuals) from 34
276 locations across the species range (Table 1). Several haplotypes represented multiple
277 individuals from several sampling locations, and network analysis revealed little
278 phylogeographic structure (Supplementary Figure 2). During SAMOVA the greatest increase
279 in Φ_{CT} was detected at $K = 2$, with the mainland Australian sites plus Rodondo Island (north
280 Bass Strait) and Waddamana (south Central Plateau) grouped together, and all remaining sites
281 allocated to the other group. Significant levels of population structure were detected by
282 AMOVA based on the mitochondrially-defined groups: among regional groups, among
283 populations within groups, and among populations (Table 2). The relative amount of
284 structuring of each major regional group was mostly consistent with mtDNA. The northeast
285 clade had the highest level of population genetic structure, followed by the southeast clade. In
286 contrast to the mitochondrial results, the northwest clade was significantly structured and was
287 more highly structured than the southern clade (Table 2).

288

289 **Discussion**

290 We revealed significant structuring of genetic variation across the range of *N. metallicus*,
291 including distinct mtDNA clades corresponding to Tasmania's northwest, northeast (including
292 Bass Strait islands and mainland Australia), southeast, and south. The phylogenetic network
293 recovered from nuclear sequence data failed to resolve the same groups, but revealed
294 significant regional partitioning of variation consistent with the mtDNA pattern. The dated
295 mtDNA phylogeny indicates that the *N. metallicus* regional groups were established prior to
296 the Pleistocene, and hence persisted through multiple glacial-interglacial cycles. The broad
297 mitochondrial phylogeographic patterns and corresponding divergence timescales are
298 strikingly similar to those found in *N. ocellatus* (Figure 3; Cliff *et al.*, 2015). These species
299 are closely related, have similar distributions and thermal niches (Caldwell *et al.*, 2017), and

300 differ mainly in their dominant habitat, with *N. ocellatus* being obligate saxicolous (Wapstra
301 *et al.*, 1999), while *N. metallicus* is typically found in close proximity to deep litter or other
302 shelter such as fallen logs or rocks (Rawlinson, 1974; Melville & Swain, 1999). Therefore,
303 the concordant mtDNA patterns in these species are more likely to reflect a shared underlying
304 mechanism (phylogeographic parallelism) than chance coincidence (phylogeographic
305 convergence).

306 Isolation into multiple Pleistocene refugia is the most parsimonious explanation for the
307 presence of regional phylogeographic structuring within Tasmanian *Niveoscincus*. This
308 hypothesis is supported by the presence of contact zones between divergent lineages at high
309 elevation areas that experienced glacial and periglacial activity during the LGM (Colhoun *et al.*, 1996; Taberlet *et al.*, 1998; Barrows *et al.*, 2002; Hewitt, 2011). Similarly, divergence
310 between haplotypes in the high elevation eastern Central Plateau was shallow, suggesting
311 recent colonisation and expansion into this region. During Pleistocene glaciations the
312 distribution of *N. metallicus* was probably limited by cold conditions and the absence of
313 suitable habitat across large areas of its current range, isolating populations into regional
314 refugia. The effect of temperature on reproduction in widespread lowland and restricted alpine
315 *Niveoscincus* species in Tasmania is well studied (Jones & Swain, 1996; Swain & Jones,
316 2000b; Swain & Jones, 2000a; Atkins *et al.*, 2007; Wapstra *et al.*, 2009; Cadby *et al.*, 2010;
317 Pen *et al.*, 2010; Uller *et al.*, 2011), and a mechanistic link between thermally limited
318 reproduction and distribution has been established (Olsson & Shine, 1998, 1999; Wapstra *et al.*, 1999). The distribution of generalist lowland *Niveoscincus* (*N. ocellatus* and *N. metallicus*)
320 is currently limited by cold conditions in high elevation (~1100-1200 m) areas (Wapstra *et al.*,
321 1999), and cold, alpine environments were more extensive during Pleistocene glaciations
322 (Kirkpatrick & Fowler, 1998; Colhoun & Barrows, 2011; Colhoun & Shimeld, 2012). LGM
323 temperature depressions were up to 6.5°C (Colhoun, 1985; Fletcher & Thomas, 2010) and
324 tree-lines were close to the modern day sea level in places (Gibson *et al.*, 1987).

326 The absence or contraction of vegetation communities during Pleistocene climate cycles may
327 have also affected the distribution of *N. metallicus*. This species does not occur in closed wet
328 forest and is absent above the subalpine tree-line (Melville & Swain, 1999). During
329 Pleistocene glaciations, the dominant woodland and open forest habitat of *N. metallicus* was
330 displaced by semiarid grassland and extensive areas of subalpine vegetation in Tasmania and
331 southern Australia (Kirkpatrick & Fowler, 1998; Kershaw *et al.*, 2007; Colhoun & Shimeld,
332 2012). However, vegetation changes were unlikely to influence the distribution of rock habitat

for *N. ocellatus*, and given concordant phylogeographic patterns with *N. metallicus*, it would appear that climate was the main driver of past distributions in both species.

The divergences between major *N. metallicus* clades appear to predate the LGM, and have been maintained across multiple favourable interglacial periods when population connections may have been established. Glacial periods may have reinforced or resurrected isolation of these lineages following interglacial periods. For instance, our present day (interglacial) sampling revealed peripheral overlap of the major *N. metallicus* clades, and this has also been observed for *N. ocellatus* following fine-scale sampling along a transect across clade boundaries (Burridge, unpublished). Similarly, the major phylogeographic breaks do not reflect contemporary landscape features that would restrict dispersal in either of these species, which are patchily but more-or-less continuously distributed with the exception of areas above 1100 m elevation. However, the most likely areas for lineage exchange correspond to central and high-elevation areas of Tasmania that would have been most affected by Pleistocene glaciation. Lineages exchanged at their spatial peripheries during previous interglacials may have failed to be retained in subsequent low elevation glacial refugia, hence reinforcing prior phylogeographic structuring. High-density blocking may have also reduced the invasion of lineages from adjacent clades during interglacials (Hewitt, 2011; Waters, 2011; Waters *et al.*, 2013). Intra-specific competition can also maintain phylogeographic structuring. For example, victory in aggressive encounters between adult male *N. microlepidotus* is strongly correlated with territorial residency, with 72% of conflicts resulting in the losing male leaving the contested territory (Olsson & Shine, 2000). However, competition among females is required with respect to mtDNA structuring.

In northwest Tasmania there is strong evidence for the long-term isolation of lineages across a diverse range of taxa, with candidate isolating mechanisms already identified. Distinct lineages are observed for *N. ocellatus* (Cliff *et al.*, 2015), Tasmanian pademelon (Macqueen *et al.*, 2009), Tasmanian devil (Jones *et al.*, 2004; Brüniche-Olsen *et al.*, 2014), Eastern quoll (Cardoso *et al.*, 2014), Tasmanian tree frog (Zhang *et al.*, 2014), White's skink (Chapple *et al.*, 2005) and the canopy tree species *Eucalyptus obliqua* (Bloomfield *et al.*, 2011). The isolation of these lineages may have been facilitated or reinforced by glaciers in the Mersey and Forth River valleys that extended to within 20 km of the present-day coastline (Colhoun *et al.*, 1996). During glacial periods, the low lying central north of Tasmania was probably also arid and treeless (Kirkpatrick & Fowler, 1998), further inhibiting movement in a range of taxa, although pollen records are lacking for this region (Colhoun & Shimeld, 2012). In contrast,

366 Kirkpatrick and Fowler (1998) suggested that northwest Tasmania was a refugium for
 367 sclerophyll woodland at the LGM, which is corroborated by pollen evidence (Colhoun &
 368 Shimeld, 2012), and would promote distinct northwest lineages of those taxa listed above.

369 Genetic isolation between the remaining major clades may also reflect utilisation of distinct
 370 refugia during Pleistocene glaciations. In particular, accumulating evidence suggests that
 371 northeast Tasmania was an important glacial refugium for a number of species. The region
 372 supports genetically distinct populations within the rainforest tree species *Nothofagus*
 373 *cunninghamii* (Worth *et al.*, 2009; Sheedy *et al.*, 2015) and *Atherosperma moschatum* (Worth
 374 *et al.*, 2011), and several eucalypt species (McKinnon *et al.*, 2004; Nevill *et al.*, 2010; Gauli
 375 *et al.*, 2014; Nevill *et al.*, 2014). Genetic evidence and vegetation modelling indicate that the
 376 eastern foothills of the Ben Lomond Plateau supported eucalypt woodland at the LGM
 377 (Kirkpatrick & Fowler, 1998; Gauli *et al.*, 2014). However, immediately to the south, LGM
 378 pollen records indicate extensive areas of semi-arid grassland extending inland from the
 379 central east coast (Colhoun & Shimeld, 2012; Mackenzie & Moss, 2014). The Midlands
 380 region was probably also more arid and treeless during glaciations (Sigleo & Colhoun, 1981;
 381 Kirkpatrick & Fowler, 1998; Colhoun & Shimeld, 2012), and may have been unsuitable for
 382 persistence of *N. metallicus*, but a stronger understanding of its physiological responses and
 383 tolerance of *N. metallicus* to aridity is required to infer potential responses to aridity-driven
 384 environmental changes (Caldwell *et al.*, 2015). Refugia would have also existed to maintain
 385 the Southeast and South clades. The presence of non-alpine adapted *Niveoscincus* on Pedra
 386 Branca, an islet on the continental shelf to the south of Tasmania, indicates persistence during
 387 the time of glacial low sea stands (Rounsevell *et al.*, 1985).

388 Despite concordance in the broad regional phylogeographic patterns in *N. metallicus* and *N.*
 389 *ocellatus*, a striking difference occurred within northeast Tasmania. In contrast to *N. ocellatus*,
 390 there was a lack of lowland site monophyly for mtDNA sequence variation within the
 391 Northeastern clade for *N. metallicus*. This may reflect differences in habitat requirements in
 392 areas continuously occupied during the Pleistocene. As *N. metallicus* is more a habitat
 393 generalist, it would therefore experience greater effective population sizes and gene flow, and
 394 consequently less phylogeographic structuring. Similar explanations have been offered for
 395 differences in gene flow and population structure in other co-distributed reptile species
 396 (Haines *et al.*, 2014; Podnar *et al.*, 2014)

397 In Tasmanian *N. metallicus*, phylogeographic structuring has been maintained when
 398 populations were potentially connected during interglacials. Populations from the Bass Strait

islands and mainland Australia were also individually divergent and monophyletic, but these regions were isolated during interglacials and terrestrially connected during glacial periods (marine transgressions). For example, during the last glacial period, this land bridge was exposed from about 42 ka to 14 ka (Lambeck & Chappell, 2001). Similar to the explanation for phylogeographic structuring in Tasmania, mixing between Bass Strait island and mainland Australian lineages may have been inhibited during low sea stands by high density blocking or intraspecific competition, and signatures of any mixing may have been lost during (interglacial) isolation caused by elevated sea levels. Alternatively, the Bassian Isthmus may have represented a formidable barrier to dispersal for this species. Aridity during late Pleistocene glacial cycles (Kershaw *et al.*, 2003; McLaren & Wallace, 2010; McLaren *et al.*, 2012) may have prevented the establishment of suitable habitat, restricting dispersal across the isthmus. Although evidence is limited, most of the Bassian Isthmus was probably semi-arid and dominated by grasslands at the LGM (D'Costa *et al.*, 1993; Kirkpatrick & Fowler, 1998). Either or both of these factors must have been significant for *Niveoscincus*, because phylogeographic studies of other reptiles across Bass Strait did not recover Tasmanian and Bass Strait populations as monophyletic, either with respect to one another (Fairbairn *et al.*, 1998; Dubey & Shine, 2010; Ng *et al.*, 2014), or relative to mainland Australian populations (Chapple *et al.*, 2005; Keogh *et al.*, 2005; Chapple *et al.*, 2011b). A faster rate of lineage sorting is unlikely to explain the greater phylogeographic structuring in these two *Niveoscincus* across Bass Strait, because their effective population sizes are unlikely to be substantially smaller than any of these other reptiles.

The presence of broad phylogeographic structuring within *N. ocellatus* and *N. metallicus* that predates the LGM is consistent with multiple studies conducted on amphibians and squamates distributed in southeast Australia (Byrne, 2008; Symula *et al.*, 2008; Dubey & Shine, 2010; Byrne *et al.*, 2011; Chapple *et al.*, 2011a; Chapple *et al.*, 2011b; Haines *et al.*, 2014; Ng *et al.*, 2014), and the temperate Southern Hemisphere more broadly (Wallis & Trewick, 2009; Sersic *et al.*, 2011; Breitman *et al.*, 2012; Vera-Escalona *et al.*, 2012; Turchetto-Zolet *et al.*, 2013). High haplotype and nucleotide diversity within all regional clades also suggests that *N. metallicus* populations persisted in multiple locations within each region, rather than being constricted to a single refugia from which they subsequently expanded. Hence, the emerging Southern Hemisphere pattern is one of persistence and diversification in multiple glacial refugia broadly across the current species range (Byrne, 2008; Byrne *et al.*, 2011; Haines *et al.*, 2014).

432 Southern Hemisphere patterns contrast with those reflecting widespread extirpation and low
 433 latitude refugia, as observed for several Northern Hemisphere taxa (Taberlet *et al.*, 1998; but
 434 see Stewart & Lister, 2001; Hewitt, 2004; Stewart *et al.*, 2010; Hewitt, 2011). However,
 435 recent work in southern regions of Europe and North America has also revealed increasingly
 436 complex phylogeographic patterns indicative of long-term persistence in multiple refugia
 437 (Canestrelli *et al.*, 2007; Gómez & Lunt, 2007; Nieto Feliner, 2011; Canestrelli *et al.*, 2012;
 438 Podnar *et al.*, 2014; Bellati *et al.*, 2015). It appears that the paradigm of high latitude
 439 extirpation and long-range postglacial re-colonisation from a small number of low latitude
 440 refugia does not apply universally, and that complex, localised and species-specific responses
 441 to Pleistocene climatic oscillations are the general expectation in unglaciated and
 442 comparatively lightly glaciated temperate regions (Soltis *et al.*, 2006; Byrne, 2008; Wallis &
 443 Trewick, 2009; Byrne *et al.*, 2011; Turchetto-Zolet *et al.*, 2013). However, here we also show
 444 that major phylogeographic breaks can be shared by similar species, suggesting the operation
 445 of a common mechanism.

446

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459

460 **References**

461 Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. &
 462 Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and
 463 amphibians. *Ecography*, **31**, 8-15.

- 464 Atkins, N., Swain, R.O.Y., Wapstra, E. & Jones, S.M. (2007) Late stage deferral of
465 parturition in the viviparous lizard *Niveoscincus ocellatus* (Gray 1845): implications
466 for offspring quality and survival. *Biological Journal of the Linnean Society*, **90**, 735-
467 746.
- 468 Avise, J.C. (1992) Molecular population structure and the biogeographic history of a regional
469 fauna - a case-history with lessons for conservation biology. *Oikos*, **63**, 62-76.
- 470 Barrows, T.T., Stone, J.O., Fifield, L.K. & Cresswell, R.G. (2002) The timing of the Last
471 Glacial Maximum in Australia. *Quaternary Science Reviews*, **21**, 159-173.
- 472 Beheregaray, L.B. (2008) Twenty years of phylogeography: the state of the field and the
473 challenges for the Southern Hemisphere. *Molecular Ecology*, **17**, 3754-3774.
- 474 Bell, R.C., Parra, J.L., Tonione, M., Hoskin, C.J., Mackenzie, J.B., Williams, S.E. & Moritz,
475 C. (2010) Patterns of persistence and isolation indicate resilience to climate change in
476 montane rainforest lizards. *Molecular Ecology*, **19**, 2531-2544.
- 477 Bellati, A., Carranza, S., Garcia-Porta, J., Fasola, M. & Sindaco, R. (2015) Cryptic diversity
478 within the *Anatololacerta* species complex (Squamata: Lacertidae) in the Anatolian
479 Peninsula: Evidence from a multi-locus approach. *Molecular Phylogenetics and*
480 *Evolution*, **82**, 219-233.
- 481 Bensasson, D., Zhang, D.-X., Hartl, D.L. & Hewitt, G.M. (2001) Mitochondrial pseudogenes:
482 evolution's misplaced witnesses. *Trends in Ecology & Evolution*, **16**, 314-321.
- 483 Bermingham, E. & Avise, J.C. (1986) Molecular zoogeography of freshwater fishes in the
484 southeastern United States. *Genetics*, **113**, 939-965.
- 485 Blois, J.L., McGuire, J.L. & Hadly, E.A. (2010) Small mammal diversity loss in response to
486 late-Pleistocene climatic change. *Nature*, **465**, 771-775.
- 487 Bloomfield, J.A., Nevill, P., Potts, B.M., Vaillancourt, R.E. & Steane, D.A. (2011) Molecular
488 genetic variation in a widespread forest tree species *Eucalyptus obliqua* (Myrtaceae)
489 on the island of Tasmania. *Australian Journal of Botany*, **59**, 226-237.
- 490 Bouckaert, R., Heled, J., Kuhnert, D., Vaughan, T., Wu, C.H., Xie, D., Suchard, M.A.,
491 Rambaut, A. & Drummond, A.J. (2014) BEAST2: A Software Platform for Bayesian
492 Evolutionary Analysis. *PLoS Computational Biology*, **10**
- 493 Breitman, M.F., Avila, L.J., Sites, J.W. & Morando, M. (2012) How lizards survived
494 blizzards: phylogeography of the *Liolaemus lineomaculatus* group (Liolaemidae)
495 reveals multiple breaks and refugia in southern Patagonia and their concordance with
496 other codistributed taxa. *Molecular Ecology*, **21**, 6068-6085.
- 497 Brüniche-Olsen, A., Jones, M.E., Austin, J.J., Burridge, C.P. & Holland, B.R. (2014)
498 *Extensive population decline in the Tasmanian devil predates European settlement*
499 *and devil facial tumour disease*.
- 500 Burridge, C.P., Craw, D., Jack, D.C., King, T.M. & Waters, J.M. (2008) Does fish ecology
501 predict dispersal across a river drainage divide? *Evolution*, **62**, 1484-1499.
- 502 Byrne, M. (2008) Evidence for multiple refugia at different time scales during Pleistocene
503 climatic oscillations in southern Australia inferred from phylogeography. *Quaternary*
504 *Science Reviews*, **27**, 2576-2585.
- 505 Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S.,
506 Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N. &
507 Wyrwoll, K.H. (2008) Birth of a biome: insights into the assembly and maintenance of
508 the Australian arid zone biota. *Molecular Ecology*, **17**, 4398-4417.
- 509 Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill,
510 D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N.,
511 Sniderman, J.M.K., Sunnucks, P. & Weston, P.H. (2011) Decline of a biome:
512 evolution, contraction, fragmentation, extinction and invasion of the Australian mesic
513 zone biota. *Journal of Biogeography*, **38**, 1635-1656.

- 514 Cadby, C.D., While, G.M., Hobday, A.J., Uller, T. & Wapstra, E. (2010) Multi-scale
515 approach to understanding climate effects on offspring size at birth and date of birth in
516 a reptile. *Integrative Zoology*, **5**, 164-175.
- 517 Caldwell, A.J., While, G.M. & Wapstra, E. (2017) Plasticity of thermoregulatory behaviour in
518 response to the thermal environment by widespread and alpine reptile species. *Animal*
519 *Behaviour*, **132**, 217-227.
- 520 Caldwell, A.J., While, G.M., Beeton, N.J. & Wapstra, E. (2015) Potential for thermal
521 tolerance to mediate climate change effects on three members of a cool temperate
522 lizard genus, *Niveoscincus*. *Journal of Thermal Biology*, **52**, 14-23.
- 523 Camargo, A., Sinervo, B. & Sites Jr, J.W. (2010) Lizards as model organisms for linking
524 phylogeographic and speciation studies. *Molecular Ecology*, **19**, 3250-3270.
- 525 Canestrelli, D., Cimmaruta, R. & Nascetti, G. (2007) Phylogeography and historical
526 demography of the Italian treefrog, *Hyla intermedia*, reveals multiple refugia,
527 population expansions and secondary contacts within peninsular Italy. *Molecular*
528 *Ecology*, **16**, 4808-4821.
- 529 Canestrelli, D., Salvi, D., Maura, M., Bologna, M.A. & Nascetti, G. (2012) One Species,
530 Three Pleistocene Evolutionary Histories: Phylogeography the Italian Crested Newt,
531 *Triturus carnifex*. *PLoS one*, **7**
- 532 Cardoso, M.J., Mooney, N., Eldridge, M.D.B., Firestone, K.B. & Sherwin, W.B. (2014)
533 Genetic monitoring reveals significant population structure in eastern quolls:
534 implications for the conservation of a threatened carnivorous marsupial. *Australian*
535 *Mammalogy*, **36**, 169-177.
- 536 Carstens, B.C., Brunsfeld, S.J., Demboski, J.R., Good, J.M. & Sullivan, J. (2005)
537 Investigating the evolutionary history of the Pacific Northwest mesic forest
538 ecosystem: hypothesis testing within a comparative phylogeographic framework.
539 *Evolution*, **59**, 1639-1652.
- 540 Chapple, D.G., Keogh, J.S. & Hutchinson, M.N. (2005) Substantial genetic substructuring in
541 southeastern and alpine Australia revealed by molecular phylogeography of the
542 *Egernia whitii* (Lacertilia : Scincidae) species group. *Molecular Ecology*, **14**, 1279-
543 1292.
- 544 Chapple, D.G., Chapple, S.N.J. & Thompson, M.B. (2011a) Biogeographic barriers in south-
545 eastern Australia drive phylogeographic divergence in the garden skink, *Lampropholis*
546 *guichenoti*. *Journal of Biogeography*, **38**, 1761-1775.
- 547 Chapple, D.G., Hoskin, C.J., Chapple, S.N.J. & Thompson, M.B. (2011b) Phylogeographic
548 divergence in the widespread delicate skink (*Lampropholis delicata*) corresponds to
549 dry habitat barriers in eastern Australia. *BMC Evolutionary Biology*, **11**, 191-208.
- 550 Clement, M., Posada, D. & Crandall, K.A. (2000) TCS: a computer program to estimate gene
551 genealogies. *Molecular Ecology*, **9**, 1657-1659.
- 552 Cliff, H., Burrige, C.P. & Wapstra, E. (2015) Persistence and dispersal in a Southern
553 Hemisphere glaciated landscape: the phylogeography of the spotted snow skink
554 (*Niveoscincus ocellatus*) in Tasmania. *BMC Evolutionary Biology*, **in press**
- 555 Colhoun, E. & Barrows, T. (2011) The Glaciation of Australia. *Quaternary Glaciations -*
556 *Extent and Chronology : A closer look* (ed. by J. Ehlers, P.L. Gibbard and P.D.
557 Hughes), pp. 1037-1045. Elsevier, Amsterdam, Netherlands.
- 558 Colhoun, E. & Shimeld, P. (2012) Late-Quaternary vegetation history of Tasmania from
559 pollen records. *Peopled Landscapes: archaeological and biogeographical approaches*
560 *to landscapes* (ed. by S. Haberle and B. David). ANU Press, Canberra.
- 561 Colhoun, E.A. (1985) Pre-Last Glacial Maximum vegetation history at Henty Bridge,
562 Western Tasmania. *New Phytologist*, **100**, 681-690.
- 563 Colhoun, E.A., Hannan, D. & Kiernan, K. (1996) Late Wisconsin glaciation of Tasmania.
564 *Papers and Proceedings of the Royal Society of Tasmania* (ed by, pp. 33-45

- 565 D'Costa, D.M., Grindrod, J. & Ogden, R. (1993) Preliminary environmental reconstructions
566 from late Quaternary pollen and mollusc assemblages at Egg Lagoon, King Island,
567 Bass Strait. *Australian Journal of Ecology*, **18**, 351-366.
- 568 Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new
569 heuristics and parallel computing. *Nature Methods*, **9**, 772-772.
- 570 Dawson, M.N. (2012) Parallel phylogeographic structure in ecologically similar sympatric
571 sister taxa. *Molecular Ecology*, **21**, 987-1004.
- 572 Dawson, M.N., Hays, C.G., Grosberg, R.K. & Raimondi, P.T. (2014) Dispersal potential and
573 population genetic structure in the marine intertidal of the eastern North Pacific.
574 *Ecological Monographs*, **84**, 435-456.
- 575 Dawson, M.N., Louie, K.D., Barlow, M., Jacobs, D.K. & Swift, C.C. (2002) Comparative
576 phylogeography of sympatric sister species, *Clevelandia ios* and *Eucyclogobius*
577 *newberryi* (Teleostei, Gobiidae), across the California Transition Zone. *Molecular*
578 *Ecology*, **11**, 1065-1075.
- 579 de Lafontaine, G., Amasifuen Guerra, C.A., Ducousso, A. & Petit, R.J. (2014) Cryptic no
580 more: soil macrofossils uncover Pleistocene forest microrefugia within a periglacial
581 desert. *New Phytologist*, **204**, 715-729.
- 582 DeChaine, E.G. & Martin, A.P. (2006) Using coalescent simulations to test the impact of
583 quaternary climate cycles on divergence in an alpine plant-insect association.
584 *Evolution*, **60**, 1004-1013.
- 585 Drummond, A.J. & Suchard, M.A. (2010) Bayesian random local clocks, or one rate to rule
586 them all. *Bmc Biology*, **8**
- 587 Dubey, S. & Shine, R. (2010) Evolutionary Diversification of the Lizard Genus *Bassiana*
588 (*Scincidae*) across Southern Australia. *PLoS one*, **5**
- 589 Dupanloup, I., Schneider, S. & Excoffier, L. (2002) A simulated annealing approach to define
590 the genetic structure of populations. *Molecular Ecology*, **11**, 2571-2581.
- 591 Excoffier, L. & Lischer, H.E.L. (2010) Arlequin suite ver 3.5: a new series of programs to
592 perform population genetics analyses under Linux and Windows. *Molecular Ecology*
593 *Resources*, **10**, 564-567.
- 594 Excoffier, L., Smouse, P.E. & Quattro, J.M. (1992) Analysis of Molecular Variance Inferred
595 from Metric Distances among DNA Haplotypes - Application to Human
596 Mitochondrial-DNA Restriction Data. *Genetics*, **131**, 479-491.
- 597 Fairbairn, J., Shine, R., Moritz, C. & Frommer, M. (1998) Phylogenetic Relationships
598 between Oviparous and Viviparous Populations of an Australian Lizard (*Lerista*
599 *bougainvillii*, *Scincidae*). *Molecular Phylogenetics and Evolution*, **10**, 95-103.
- 600 Fletcher, M.-S. & Thomas, I. (2010) A quantitative Late Quaternary temperature
601 reconstruction from western Tasmania, Australia. *Quaternary Science Reviews*, **29**,
602 2351-2361.
- 603 Flot, J.F. (2010) SEQPHASE: a web tool for interconverting phase input/output files and fasta
604 sequence alignments. *Molecular Ecology Resources*, **10**, 162-166.
- 605 Fordham, D.A., Brook, B.W., Moritz, C. & Nogués-Bravo, D. (2014) Better forecasts of
606 range dynamics using genetic data. *Trends in Ecology & Evolution*, **29**, 436-443.
- 607 Gauli, A., Steane, D.A., Vaillancourt, R.E. & Potts, B.M. (2014) Molecular genetic diversity
608 and population structure in *Eucalyptus pauciflora* subsp. *pauciflora* (Myrtaceae) on the
609 island of Tasmania. *Australian Journal of Botany*, **62**, 175-188.
- 610 Gibson, N., Kiernan, K. & Macphail, M. (1987) A fossil bolster plant from the King River,
611 Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, **121**, 35-42.
- 612 Gómez, A. & Lunt, D. (2007) Refugia within Refugia: Patterns of Phylogeographic
613 Concordance in the Iberian Peninsula. *Phylogeography of Southern European Refugia*
614 (ed. by S. Weiss and N. Ferrand), pp. 155-188. Springer Netherlands.

- 615 Guindon, S. & Gascuel, O. (2003) A simple, fast, and accurate algorithm to estimate large
616 phylogenies by maximum likelihood. *Systematic Biology*, **52**, 696-704.
- 617 Haines, M.L., Moussalli, A., Stuart-Fox, D., Clemann, N. & Melville, J. (2014) Phylogenetic
618 evidence of historic mitochondrial introgression and cryptic diversity in, the genus
619 *Pseudemoia* (Squamata: Scincidae). *Molecular Phylogenetics and Evolution*, **81**, 86-
620 95.
- 621 Hare, K.M., Daugherty, C.H. & Chapple, D.G. (2008) Comparative phylogeography of three
622 skink species (*Oligosoma moco*, *O. smithi*, *O. suteri*; Reptilia: Scincidae) in
623 northeastern New Zealand. *Molecular Phylogenetics and Evolution*, **46**, 303-315.
- 624 Hewitt, G.M. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907-913.
- 625 Hewitt, G.M. (2004) Genetic consequences of climatic oscillations in the Quaternary.
626 *Philosophical Transactions of the Royal Society of London Series B-Biological*
627 *Sciences*, **359**, 183-195.
- 628 Hewitt, G.M. (2011) Quaternary phylogeography: the roots of hybrid zones. *Genetica*, **139**,
629 617-638.
- 630 Hickerson, M.J. & Cunningham, C.W. (2005) Contrasting Quaternary histories in an
631 ecologically divergent sister pair of low-dispersing intertidal fish (*Xiphister*) revealed
632 by multilocus DNA analysis. *Evolution*, **59**, 344-360.
- 633 Huson, D.H. & Bryant, D. (2006) Application of phylogenetic networks in evolutionary
634 studies. *Molecular Biology and Evolution*, **23**, 254-267.
- 635 Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to
636 environmental changes of the late Quaternary. *Paleobiology*, **26**, 194-220.
- 637 Jones, M.E., Paetkau, D., Geffen, E.L.I. & Moritz, C. (2004) Genetic diversity and population
638 structure of Tasmanian devils, the largest marsupial carnivore. *Molecular Ecology*, **13**,
639 2197-2209.
- 640 Jones, S.M. & Swain, R. (1996) Annual reproductive cycle and annual cycles of reproductive
641 hormones in plasma of female *Niveoscincus metallicus* (Scincidae) from Tasmania.
642 *Journal of Herpetology*, **30**, 140-146.
- 643 Keogh, J.S., Scott, I.A.W. & Hayes, C. (2005) Rapid and repeated origin of insular gigantism
644 and dwarfism in Australian tiger snakes. *Evolution*, **59**, 226-233.
- 645 Kershaw, A.P., McKenzie, G.M., Porch, N., Roberts, R.G., Brown, J., Heijnis, H., Orr, M.L.,
646 Jacobsen, G. & Newallt, P.R. (2007) A high-resolution record of vegetation and
647 climate through the last glacial cycle from Caledonia Fen, southeastern highlands of
648 Australia. *Journal of Quaternary Science*, **22**, 481-500.
- 649 Kershaw, P., Moss, P. & Van Der Kaars, S. (2003) Causes and consequences of long-term
650 climatic variability on the Australian continent. *Freshwater Biology*, **48**, 1274-1283.
- 651 Kirkpatrick, J.B. & Fowler, M. (1998) Locating likely glacial forest refugia in Tasmania using
652 palynological and ecological information to test alternative climatic models.
653 *Biological Conservation*, **85**, 171-182.
- 654 Lambeck, K. & Chappell, J. (2001) Sea Level Change Through the Last Glacial Cycle.
655 *Science*, **292**, 679-686.
- 656 Leigh, J.W. & Bryant, D. (2015) PopART: Full-feature software for haplotype network
657 construction. *Methods in Ecology and Evolution*, **6**, 1110-1116.
- 658 Lemmon, A.R., Brown, J.M., Stanger-Hall, K. & Lemmon, E.M. (2009) The Effect of
659 Ambiguous Data on Phylogenetic Estimates Obtained by Maximum Likelihood and
660 Bayesian Inference. *Systematic Biology*, **58**, 130-145.
- 661 Lessa, E.P., Cook, J.A. & Patton, J.L. (2003) Genetic footprints of demographic expansion in
662 North America, but not Amazonia, during the Late Quaternary. *Proceedings of the*
663 *National Academy of Sciences of the United States of America*, **100**, 10331-10334.
- 664 Lorenzen, E.D., Heller, R. & Siegmund, H.R. (2012) Comparative phylogeography of
665 African savannah ungulates. *Molecular Ecology*, **21**, 3656-3670.

- 666 Mackenzie, L. & Moss, P. (2014) A late Quaternary record of vegetation and climate change
667 from Hazards Lagoon, eastern Tasmania. *Quaternary International*,
668 Macqueen, P., Goldizen, A.W. & Seddon, J.M. (2009) Response of a southern temperate
669 marsupial, the Tasmanian pademelon (*Thylogale billardierii*), to historical and
670 contemporary forest fragmentation. *Molecular Ecology*, **18**, 3291-3306.
671 McKinnon, G.E., Jordan, G.J., Vaillancourt, R.E., Steane, D.A. & Potts, B.M. (2004) Glacial
672 refugia and reticulate evolution: the case of the Tasmanian eucalypts. *Philosophical
673 Transactions of the Royal Society of London. Series B: Biological Sciences*, **359**, 275-
674 284.
675 McLaren, S. & Wallace, M.W. (2010) Plio-Pleistocene climate change and the onset of aridity
676 in southeastern Australia. *Global and Planetary Change*, **71**, 55-72.
677 McLaren, S., Wallace, M.W. & Reynolds, T. (2012) The Late Pleistocene evolution of palaeo
678 megalake Bungunna, southeastern Australia: A sedimentary record of fluctuating lake
679 dynamics, climate change and the formation of the modern Murray River.
680 *Palaeogeography Palaeoclimatology Palaeoecology*, **317**, 114-127.
681 Melville, J. & Swain, R. (1997) Spatial separation in two sympatric skinks, *Niveoscincus*
682 *microlepidotus* and *N. metallicus*, from Tasmania. *Herpetologica*, **53**, 126-132.
683 Melville, J. & Swain, R. (1999) Habitat associations and natural history of the Tasmanian
684 "snow skinks" (*Niveoscincus* spp.) *Papers and Proceedings of the Royal Society
685 of Tasmania*, **133**, 57-64.
686 Melville, J. & Swain, R. (2003) Evolutionary correlations between escape behaviour and
687 performance ability in eight species of snow skinks (*Niveoscincus*: Lygosominae)
688 from Tasmania. *Journal of Zoology*, **261**, 79-89.
689 Metts, B.S., Winne, C.T., Scott, D.E., Gibbons, J.W., Greene, J.L., Buhlmann, K.A., Poppy,
690 S., Mills, T., Tuberville, T.D., Ryan, T.J. & Leiden, Y. (2000) The Global Decline of
691 Reptiles, Déjà Vu Amphibians: Reptile species are declining on a global scale. Six
692 significant threats to reptile populations are habitat loss and degradation, introduced
693 invasive species, environmental pollution, disease, unsustainable use, and global
694 climate change. *BioScience*, **50**, 653-666.
695 Muller, K. (2006) Incorporating information from length-mutational events into phylogenetic
696 analysis. *Molecular Phylogenetics and Evolution*, **38**, 667-676.
697 Nelson-Tunley, M., Morgan-Richards, M. & Trewick, S.A. (2016) Genetic diversity and gene
698 flow in a rare New Zealand skink despite fragmented habitat in a volcanic landscape.
699 *Biological Journal of the Linnean Society*, **119**, 37-51.
700 Nevill, P., Després, T., Bayly, M., Bossinger, G. & Ades, P. (2014) Shared phylogeographic
701 patterns and widespread chloroplast haplotype sharing in Eucalyptus species with
702 different ecological tolerances. *Tree Genetics & Genomes*, **10**, 1079-1092.
703 Nevill, P.G., Bossinger, G. & Ades, P.K. (2010) Phylogeography of the world's tallest
704 angiosperm, *Eucalyptus regnans*: evidence for multiple isolated Quaternary refugia.
705 *Journal of Biogeography*, **37**, 179-192.
706 Ng, J., Clemann, N., Chapple, S.J. & Melville, J. (2014) Phylogeographic evidence links the
707 threatened 'Grampians' Mountain Dragon (*Rankinia diemensis* Grampians) with
708 Tasmanian populations: conservation implications in south-eastern Australia.
709 *Conservation Genetics*, **15**, 363-373.
710 Nieto Feliner, G. (2011) Southern European glacial refugia: A tale of tales. *Taxon*, **60**, 365-
711 372.
712 Olsson, M. & Shine, R. (1998) Timing of parturition as a maternal care tactic in an Alpine
713 lizard species. *Evolution*, **52**, 1861-1864.
714 Olsson, M. & Shine, R. (1999) Plasticity in frequency of reproduction in an alpine lizard,
715 *Niveoscincus microlepidotus*. *Copeia*, 794-796.

- 716 Olsson, M. & Shine, R. (2000) Ownership influences the outcome of male-male contests in
717 the scincid lizard, *Niveoscincus microlepidotus*. *Behavioral Ecology*, **11**, 587-590.
- 718 Papadopoulou, A. & Knowles, L.L. (2016) Toward a paradigm shift in comparative
719 phylogeography driven by trait-based hypotheses. *Proc Natl Acad Sci U S A*, **113**,
720 8018-24.
- 721 Pen, I., Uller, T., Feldmeyer, B., Harts, A., While, G.M. & Wapstra, E. (2010) Climate-driven
722 population divergence in sex-determining systems. *Nature*, **468**, 436-438.
- 723 Podnar, M., Bruvo Mađarić, B. & Mayer, W. (2014) Non-concordant phylogeographical
724 patterns of three widely codistributed endemic Western Balkans lacertid lizards
725 (Reptilia, Lacertidae) shaped by specific habitat requirements and different responses
726 to Pleistocene climatic oscillations. *Journal of Zoological Systematics and*
727 *Evolutionary Research*, **52**, 119-129.
- 728 Qiu, Y.X., Fu, C.X. & Comes, H.P. (2011) Plant molecular phylogeography in China and
729 adjacent regions: Tracing the genetic imprints of Quaternary climate and
730 environmental change in the world's most diverse temperate flora. *Molecular*
731 *Phylogenetics and Evolution*, **59**, 225-244.
- 732 Rambaut, A. (2014) *FigTree v1.4.2*.
- 733 Rambaut, A. & Drummond, A.J. (2013) *Tracer v1.6*.
- 734 Rawlinson, P.A. (1974) Biogeography and ecology of the reptiles of Tasmania and the Bass
735 Strait area. *Biogeography and Ecology of Tasmania* (ed. by W. Williams), pp. 291-
736 338. W. Junk, The Hague, Netherlands.
- 737 Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B.,
738 Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian
739 Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic*
740 *Biology*, **61**, 539-542.
- 741 Rounsevell, D., Brothers, N. & Holdsworth, N. (1985) The status and ecology of the Pedra
742 Branca skink, *Pseudemoia palfreymani*. *Biology of Australian frogs and reptiles* (ed.
743 by G. Grigg, R. Shine and H. Hehmann), pp. 477-480. Surrey Beatty & Sons, Sydney.
- 744 Rull, V. (2009) Microrefugia. *Journal of Biogeography*, **36**, 481-484.
- 745 Sersic, A.N., Cosacov, A., Cocucci, A.A., Johnson, L.A., Pozner, R., Avila, L.J., Sites, J.W.
746 & Morando, M. (2011) Emerging phylogeographical patterns of plants and terrestrial
747 vertebrates from Patagonia. *Biological Journal of the Linnean Society*, **103**, 475-494.
- 748 Sérsic, A.N., Cosacov, A., Cocucci, A.A., Johnson, L.A., Pozner, R., Avila, L.J., Sites, J.W.
749 & Morando, M. (2011) Emerging phylogeographical patterns of plants and terrestrial
750 vertebrates from Patagonia. *Biological Journal of the Linnean Society*, **103**, 475-494.
- 751 Sheedy, E.M., van de Wouw, A.P., Howlett, B.J. & May, T.W. (2015) Population genetic
752 structure of the ectomycorrhizal fungus *Laccaria* sp A resembles that of its host tree
753 *Nothofagus cunninghamii*. *Fungal Ecology*, **13**, 23-32.
- 754 Sigleo, W. & Colhoun, E.A. (1981) A short pollen diagram from Crown Lagoon in the
755 Midlands of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*,
756 **115**, 181-188.
- 757 Sinervo, B., Méndez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa
758 Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-
759 Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., De la Riva, I.J., Sepulveda,
760 P.V., Rocha, C.F.D., Ibargüengoytia, N., Puntriano, C.A., Massot, M., Lepetz, V.,
761 Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J. & Sites, J.W.
762 (2010) Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches.
763 *Science*, **328**, 894-899.
- 764 Soltis, D.E., Morris, A.B., McLachlan, J.S., Manos, P.S. & Soltis, P.S. (2006) Comparative
765 phylogeography of unglaciated eastern North America. *Molecular Ecology*, **15**, 4261-
766 4293.

- 767 Stephens, M., Smith, N.J. & Donnelly, P. (2001) A new statistical method for haplotype
768 reconstruction from population data. *American Journal of Human Genetics*, **68**, 978-
769 989.
- 770 Stewart, J.R. & Lister, A.M. (2001) Cryptic northern refugia and the origins of the modern
771 biota. *Trends in Ecology & Evolution*, **16**, 608-613.
- 772 Stewart, J.R., Lister, A.M., Barnes, I. & Dalen, L. (2010) Refugia revisited: individualistic
773 responses of species in space and time. *Proceedings of the Royal Society B-Biological
774 Sciences*, **277**, 661-671.
- 775 Swain, R. & Jones, S.M. (2000a) Maternal effects associated with gestation conditions in a
776 viviparous lizard, *Niveoscincus metallicus*. *Herpetological Monographs*, **14**, 432-440.
- 777 Swain, R. & Jones, S.M. (2000b) Facultative placentotrophy: half-way house or strategic
778 solution? *Comp Biochem Physiol A Mol Integr Physiol*, **127**, 441-51.
- 779 Symula, R., Keogh, J.S. & Cannatella, D.C. (2008) Ancient phylogeographic divergence in
780 southeastern Australia among populations of the widespread common froglet, *Crinia
781 signifera*. *Molecular Phylogenetics and Evolution*, **47**, 569-580.
- 782 Taberlet, P., Fumagalli, L., Wust-Saucy, A.G. & Cosson, J.F. (1998) Comparative
783 phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, **7**,
784 453-464.
- 785 Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular
786 Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution*, **30**,
787 2725-2729.
- 788 Turchetto-Zolet, A.C., Pinheiro, F., Salgueiro, F. & Palma-Silva, C. (2013)
789 Phylogeographical patterns shed light on evolutionary process in South America.
790 *Molecular Ecology*, **22**, 1193-1213.
- 791 Turner, T.F. & Trexler, J.C. (1998) Ecological and historical associations of gene flow in
792 darters (Teleostei : Percidae). *Evolution*, **52**, 1781-1801.
- 793 Tzedakis, P.C., Emerson, B.C. & Hewitt, G.M. (2013) Cryptic or mystic? Glacial tree refugia
794 in northern Europe. *Trends in Ecology & Evolution*, **28**, 696-704.
- 795 Uller, T., While, G.M., Cadby, C.D., Harts, A., O'Connor, K., Pen, I. & Wapstra, E. (2011)
796 Altitudinal divergence in maternal thermoregulatory behaviour may be driven by
797 differences in selection on offspring survival in a viviparous lizard. *Evolution*, **65**,
798 2313-2324.
- 799 Vera-Escalona, I., D'Elía, G., Gouin, N., Fontanella, F.M., Muñoz-Mendoza, C., Sites, J.W.,
800 Jr. & Victoriano, P.F. (2012) Lizards on Ice: Evidence for Multiple Refugia in
801 *Liolaemus pictus* (Liolaemidae) during the Last Glacial Maximum in the Southern
802 Andean Beech Forests. *PLoS one*, **7**, e48358.
- 803 Wallis, G.P. & Trewick, S.A. (2009) New Zealand phylogeography: Evolution on a small
804 continent. *Molecular Ecology*, **18**, 3548-3580.
- 805 Wallis, G.P., Waters, J.M., Upton, P. & Craw, D. (2016) Transverse Alpine Speciation Driven
806 by Glaciation. *Trends in Ecology & Evolution*, **31**, 916-926.
- 807 Wapstra, E., Swain, R., Jones, S.M. & O'Reilly, J. (1999) Geographic and annual variation in
808 reproductive cycles in the Tasmanian spotted snow skink, *Niveoscincus ocellatus*
809 (Squamata : Scincidae). *Australian Journal of Zoology*, **47**, 539-550.
- 810 Wapstra, E., Uller, T., Sinn, D.L., Olsson, M., Mazurek, K., Joss, J. & Shine, R. (2009)
811 Climate effects on offspring sex ratio in a viviparous lizard. *Journal of Animal
812 Ecology*, **78**, 84-90.
- 813 Waters, J.M. (2011) Competitive exclusion: phylogeography's 'elephant in the room'?
814 *Molecular Ecology*, **20**, 4388-4394.
- 815 Waters, J.M., Fraser, C.I. & Hewitt, G.M. (2013) Founder takes all: density-dependent
816 processes structure biodiversity. *Trends in Ecology & Evolution*, **28**, 78-85.

817 Whiteley, A.R., Spruell, P. & Allendorf, F.W. (2004) Ecological and life history
818 characteristics predict population genetic divergence of two salmonids in the same
819 landscape. *Molecular Ecology*, **13**, 3675-3688.

820 Williams, C.F. (1994) Genetic consequences of seed dispersal in 3 sympatric forest herbs .2.
821 microspatial genetic structure within populations. *Evolution*, **48**, 1959-1972.

822 Worth, J.R.P., Jordan, G.J., McKinnon, G.E. & Vaillancourt, R.E. (2009) The major
823 Australian cool temperate rainforest tree *Nothofagus cunninghamii* withstood
824 Pleistocene glacial aridity within multiple regions: evidence from the chloroplast. *New*
825 *Phytologist*, **182**, 519-532.

826 Worth, J.R.P., Marthick, J.R., Jordan, G.J. & Vaillancourt, R.E. (2011) Low but structured
827 chloroplast diversity in *Atherosperma moschatum* (Atherospermataceae) suggests
828 bottlenecks in response to the Pleistocene glacials. *Annals of botany*, **108**, 1247-1256.

829 Zhang, Z.Y., Cashins, S., Philips, A. & Burridge, C.P. (2014) Significant population genetic
830 structuring but a lack of phylogeographic structuring in the endemic Tasmanian tree
831 frog (*Litoria burrowsae*). *Australian Journal of Zoology*, **62**, 238-245.

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Figure 1. Recorded distribution of *Niveoscincus metallicus* (small hollow circles) and locations of sampling sites (dark grey circles). Base map: 250 m Digital Elevation Model (GeoScience Australia).

839 **Figure 2.** Bayesian inference tree of *Niveoscincus metallicus* reconstructed from 1406 bp of
840 ND2 and ND4 mitochondrial DNA sequence. Major regional clades and major subdivisions
841 within clades are indicated by vertical grey bars. Posterior probabilities >0.95 are indicated by
842 black dots. Posterior probability values are included above key nodes. Branch lengths are
843 scaled proportional to the scale bar. Branches to outgroups were truncated (indicated by
844 dashed lines across branches). Analysis was conducted on unique haplotypes, and the
845 numbers in parentheses after site names indicate the number of individuals belonging to that
846 haplotype at that site. If only one individual per site was recorded, numbers in parentheses
847 were omitted.
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851 **Figure 3.** *Niveoscincus metallicus* sampling locations coloured by four major regional
852 mitochondrial clades. Sites representing two clades are shown by circles with two colours.

853 The geographic distribution of mitochondrially-defined clades in *N. ocellatus* is indicated by
854 dashed lines. Base map: 250 m DEM (GeoScience Australia).
855

856 **Table 1.** Genetic diversity quantified by haplotype diversity (H) and nucleotide diversity (π) among groups and
857 all samples based on 1406 base pairs of ND2 and ND4 mitochondrial sequence for *Niveoscincus metallicus*.
858 Individuals were allocated to groups defined by regional mitochondrial clades. Sequences from admixed sites
859 representing two mitochondrial clades were included in the analysis.

Clade / subclade	H	π
SE	0.9974 ± 0.0016	0.01608 ± 0.00789
NE	0.9938 ± 0.0030	0.02038 ± 0.00997
- mainland Australia	0.9692 ± 0.0196	0.00046 ± 0.00024
- Bass Strait	0.9715 ± 0.0196	0.02014 ± 0.01013
- NE Tasmania	0.9905 ± 0.0114	0.00903 ± 0.00463
NW	0.9942 ± 0.0193	0.01229 ± 0.00645
S	0.9841 ± 0.0107	0.01147 ± 0.00582
Total	0.9985 ± 0.0005	0.03985 ± 0.01911

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863 **Table 2.** Analysis of molecular variance (AMOVA) comparing mitochondrial and nuclear genetic structure
 864 within sampling sites and among and between groups defined by major mitochondrial clades in *Niveoscincus*
 865 *metallicus*. Analyses were conducted with and without admixed sites (sites representing more than one
 866 mitochondrial lineage: Ben Lomond, Hillwood and Lake St Clair).

Source of variation	mtDNA			nDNA		
	Fixation index	% total	P-value	Fixation index	% total	P-value
All samples						
– <i>with admixed sites</i>						
Among regional groups	0.63 (Φ_{CT})	63.41	<0.0001	0.15 (Φ_{CT})	14.62	0.0230
Among sites within regional groups	0.62 (Φ_{SC})	23.04	<0.0001	0.65 (Φ_{SC})	55.47	<0.0001
Among sites	0.86 (Φ_{ST})	13.55	<0.0001	0.70 (Φ_{ST})	29.91	<0.0001
– <i>without admixed sites</i>						
Among regional groups	0.61 (Φ_{CT})	64.44	<0.0001			
Among sites within regional groups	0.62 (Φ_{SC})	22.04	<0.0001			
Among sites	0.86 (Φ_{ST})	13.52	<0.0001			
Southeast clade						
– <i>with admixed sites</i>						
Among populations	0.64 (Φ_{ST})	63.96	<0.0001	0.64 (Φ_{ST})	63.75	<0.0001
– <i>without admixed sites</i>						
Among populations	0.62 (Φ_{ST})	61.68	<0.0001			
Northwest clade						
– <i>with admixed sites</i>						
Among populations	0.15 (Φ_{ST})	14.55	0.0639	0.43 (Φ_{ST})	42.63	<0.0001
– <i>without admixed sites</i>						
Among populations	0.14 (Φ_{ST})	14.04	0.0599			
Southern clade						
Among populations	0.47 (Φ_{ST})	47.94	<0.0001	0.21 (Φ_{ST})	21.06	0.0028
Northeast clade						
– <i>with admixed sites</i>						
Among populations	0.79 (Φ_{ST})	79.03	<0.0001	0.89 (Φ_{ST})	89.44	<0.0001
– <i>without admixed sites</i>						
Among populations	0.79 (Φ_{ST})	79.17	<0.0001			

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870 **Table 3.** Uncorrected mean genetic distances ($\pm$ standard error from 500 bootstrap replicates) between regional
871 clades detected from phylogenetic analysis of 1406 base pairs of ND2 and ND4 mitochondrial sequence for
872 *Niveoscincus metallicus*.

	NE	SE	NW	S
NE				
SE	0.041 $\pm$ 0.004			
NW	0.074 $\pm$ 0.006	0.076 $\pm$ 0.006		
S	0.043 $\pm$ 0.004	0.049 $\pm$ 0.004	0.073 $\pm$ 0.006	

873