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1 **Title**

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

4

5 **Running title** Phylogeography of the Tasmanian metallic snow skink

6

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29

30 **Conflicts of interest**

31 The authors declare they have no conflicting interests.

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32 **Abstract**

33 **Aim**

34 Knowledge of species responses to past environmental change provides a basis to predict and
35 mitigate the outcomes of future environmental change. While paradigm studies of
36 comparative phylogeography have surveyed dissimilar taxa as a means to identify generalities
37 of species responses to past environmental change, the fact that such taxa are dissimilar also
38 raises the chances that any shared patterns reflect coincident responses from different
39 processes (“phylogeographic convergence”). Here we advocate for and demonstrate the utility
40 of examining closely-related, co-distributed species in comparative phylogeographic studies
41 aimed at inferring the environmental processes driving distributional change. Closely-related
42 species with similar environmental requirements represent valid phylogeographic replicates,
43 meaning that shared historical distributional responses can more confidently be attributed to
44 the operation of the same process (“phylogeographic parallelism”).

45 **Location**

46 Tasmania, temperate southeast Australia

47 **Taxa**

48 We compared phylogeographic patterns observed in two closely related, co-distributed skink
49 species (*Carinascincus*) sharing similar ecological and physiological tolerances.

50 **Methods**

51 Using mitochondrial and nuclear DNA, we reconstructed relationships between populations
52 across the known range of *C. metallicus* and compared it with that of *C. ocellatus*. We also
53 compared dated phylogenies inferred using Bayesian approaches, and analyses of population
54 structure and diversity.

55 **Results**

56 We found remarkably similar geographic patterns of genetic diversity in these two species
57 that suggest they responded similarly to Plio-Pleistocene climate cycling. We infer that glacial
58 cold and aridity forced these species into similar lowland refugial regions throughout
59 Tasmania and the Bass Strait Islands.

60 **Main conclusions**

61 Examining phylogeographic patterns in closely-related, co-distributed species allows for
62 confident inference of mechanisms driving historical distributional changes. This is an
63 important step towards generating robust predictions of species responses to future
64 environmental change.

65

66 **Keywords**

67 Australia, Bassian Isthmus, comparative phylogeography, phylogeographic parallelism, Plio-
68 Pleistocene, Niveoscincus, Tasmania.

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69 **Introduction**

70 Phylogeography provides a means to understand factors that shaped the distribution and
71 abundance of species, including their responses to past climates (Hewitt, 2004). Past
72 population dynamics are recorded in the genes of species, and robust quantitative frameworks
73 are developing for the incorporation of such information into projections of species range and
74 abundance (Fordham et al., 2014), which is relevant for biodiversity conservation. However,
75 the value of phylogeography depends on the extent to which its results can be generalised
76 across regions and taxa (e.g., Bermingham & Avise, 1986; Carstens et al., 2005; DeChaine &
77 Martin, 2006). In this context, patterns from mid- to high-latitudes of Western Europe and
78 North America became paradigmatic within phylogeography (Taberlet et al., 1998; Hewitt,
79 2004); high and endemic genetic variation at low latitudes and lower genetic variation and
80 phylogeographic structure across higher latitudes were interpreted as signatures of
81 recolonization of previously glaciated areas from low latitude refugia. However,
82 investigations of less extensively glaciated or unglaciated regions of the world often failed to
83 recover patterns consistent with widespread extirpation and subsequent postglacial
84 recolonisation from sparse refugia (Byrne, 2008; Byrne et al., 2011; Sérsic et al., 2011;
85 Breitman et al., 2012; Lorenzen et al., 2012; Turchetto-Zolet et al., 2013). Other studies have
86 also indicated long-term persistence with relatively subtle range movements through time in
87 areas heavily affected by Pleistocene glaciations (Rull, 2009; Tzedakis et al., 2013).
88 Therefore, phylogeographic patterns, and the inferences drawn from them, could be
89 influenced by idiosyncrasies related to region or species (but these are also of value; see
90 Papadopoulou & Knowles, 2016).

91 Given that diverse phylogeographic responses to the same environmental change are expected
92 among species owing to variation in environmental tolerances, life histories, and vagility
93 (Bhagwat & Willis, 2008; Papadopoulou & Knowles, 2016), the potential also exists that
94 shared phylogeographic patterns among such species may represent coincident products of
95 different processes, rather than the operation of the same process. In the same way that studies
96 attempting to ascribe differences in phylogeographic patterns to differences in species
97 attributes benefit from comparisons of closely related species—because these will differ in
98 fewer other potentially confounding variables (Dawson et al., 2002; Whiteley et al., 2004;
99 Hickerson & Cunningham, 2005; Burrridge et al., 2008)—shared phylogeographic patterns
100 among closely related and ecologically-similar taxa will be less likely to reflect the operation
101 of different underlying processes (Dawson, 2012). Given that phylogeographic patterns
102 represent an attribute or character-state of a species, we can describe the origins of identical
103 phylogeographic patterns among species in the same manner as the character-states for any
104 other trait (e.g., limb morphology). Therefore, we can distinguish the possession of identical
105 phylogeographic patterns as either “phylogeographic convergence” (the product of different
106 processes), or “phylogeographic parallelism” (the product of the same process).

107 Reptiles have been highlighted as excellent model species in phylogeographic studies
108 attempting to understand the impact of environmental change on species distributions
109 (Camargo et al., 2010). As ectotherms, they depend on heat from the environment to sustain
110 metabolism and reproduction, and are therefore sensitive to climatic changes (Sinervo et al.,
111 2010). Reptiles also tend to have limited dispersal abilities, which means that genetic
112 signatures of historical distributional changes are likely to persist for longer than in more
113 vagile species such as large mammals and birds (Araújo et al., 2008). Therefore, we expect
114 comparative phylogeographic studies of closely related reptiles are more likely to reveal
115 shared patterns reflecting the same underlying process, or where patterns differ, they can be
116 more confidently ascribed to morphological, physiological, life history, or behavioural
117 differences between these species. While many phylogeographic studies have examined
118 reptiles to increase our understanding of faunal responses to environmental change (Dubey &
119 Shine, 2010; Breitman et al., 2012; Vera-Escalona et al., 2012), few have analysed closely
120 related species (e.g., Hare et al., 2008).

121 Tasmania is the only Australian location substantially influenced by Pleistocene glaciations
122 (Barrows et al., 2002), experiencing temperature depressions of 3.7–6.5°C during the Last
123 Glacial Maximum (LGM, 25–15,000 years ago) (Colhoun, 1985; Fletcher & Thomas, 2010),
124 with tree-lines located near modern day sea level (Gibson et al., 1987). Rainfall was perhaps
125 effectively halved, and arid and semi-arid landforms were widespread in areas which are now
126 mesic (McIntosh et al., 2012; Augustinus et al., 2017). Cliff et al. (2015) conducted perhaps
127 the most comprehensive range-wide phylogeographic study of faunal responses to Pleistocene
128 glaciations in Tasmania, examining the spotted snow skink *Carinascincus ocellatus*, revealing
129 contrasting patterns throughout the species' range: there was evidence of population
130 persistence and limited gene flow within the historically and presently milder northeast, while
131 the southeast and glacially-affected central regions were characterised by patterns consistent
132 with greater post-glacial gene flow and demographic expansion.

133 Here we investigated the phylogeography of the metallic snow skink *Carinascincus*
134 *metallicus*, and compared it with previous results for *C. ocellatus* (Cliff et al., 2015). Both
135 species are small, viviparous, and widespread across Tasmania, with similar thermal niches
136 (Melville & Swain, 2003; Caldwell et al., 2017), and occupying a broad elevational range,
137 from sea level to ~1000–1300 m, roughly coincident with the regional subalpine tree-line
138 (Melville & Swain, 1999). *Carinascincus ocellatus* occurs on Flinders and surrounding
139 islands, while *C. metallicus* occurs across the Bass Strait islands and into southeast mainland
140 Australia (Figure 1). While *C. metallicus* is typically found in close proximity to deep litter or
141 other shelter, such as fallen logs or rocks, *C. ocellatus* is obligate saxicolous (Melville &
142 Swain, 1997). The analysis of *C. metallicus* allows us to test for phylogeographic
143 concordance with *C. ocellatus*, and if present, provide stronger inference into the processes
144 underlying their phylogeographic histories (phylogeographic parallelism). We also assess the

145 phylogeographic relationships between Tasmanian, Bass Strait and mainland Australian *C.*
146 *metallicus* populations with respect to their movement and persistence across the periodically
147 emergent Bassian Isthmus, a question relating to Pleistocene sea level change (Lambeck &
148 Chappell, 2001).

149

150 **Materials and Methods**

151 Tissue was obtained from a total of 781 *C. metallicus* representing 1–23 individuals from 57
152 locations across the species' geographic and elevational range (Figure 1, Supplementary
153 Table 1, 2), with the exception of King Island and far southwest Tasmania. Sampling covered
154 the area investigated by Cliff et al. (2015) for *C. ocellatus*. We used samples of *C. ocellatus*
155 and *C. pretiosus* as outgroups. We sequenced several *C. pretiosus*, and noted that other
156 sequences assigned to this species (GenBank accession numbers HQ454789, DQ675234) fell
157 deep within the *C. metallicus* tree, and we included these in our study as *C. metallicus*.

158 DNA extraction, PCR amplification, and sequencing of partial mitochondrial ND2 (c. 543 bp)
159 and ND4 (c. 864 bp), and partial nuclear β -globin (intron 2, c. 782 bp) followed Cliff et al.
160 (2015). Ambiguous double peaks were observed in some ND2 sequence chromatograms,
161 probably representing a nuclear pseudogene (Bensasson et al., 2001). The protein coding
162 regions of both mitochondrial genes were translated to ensure that sequences did not contain
163 premature stop codons that would indicate a divergent non-coding pseudogene. ND2
164 sequences from 296 individuals were obtained, and ND4 sequences were obtained from 336
165 individuals, representing 53 localities (Supplementary Table 1). Sequences from individuals
166 where both ND2 and ND4 amplified successfully were concatenated, giving a total of 1406 bp
167 for 281 individuals from 51 sites. A total of 70 individuals with sequence data for only one
168 mitochondrial marker were omitted from the concatenated dataset, due to concerns about the
169 effect of large amounts of missing data on phylogenetic inference (Lemmon et al., 2009).
170 Three sampling sites (Mt Bischoff, Cataract Gorge and Mt Oakleigh) were entirely omitted
171 from the concatenated dataset because of substantial double peaks in ND2 sequences.

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

178 Bayesian phylogenetic reconstruction was conducted in MrBayes 3.2.2 (Ronquist et al., 2012)
179 on unique haplotypes identified from concatenated sequences. Individuals from Mt Bischoff
180 and Cataract Gorge were retained within the ND4 dataset, and a separate phylogenetic

181 analysis was conducted on this dataset, allowing these individuals to be allocated to regional
182 clades (Supplementary Figure 3, 4); Mt Oakleigh ND4 sequences were spurious, and
183 therefore this site was not included in any analysis. Individuals sharing the same sequence
184 were assigned to haplotypes using TCSv1.21 (Clement et al., 2000), ensuring that individuals
185 with missing or ambiguous data at the same nucleotide position, but with otherwise identical
186 sequences, were assigned to the same haplotype. mtDNA sequences were partitioned by gene
187 region and analysed under substitution models suggested by jModelTest 2.1.7 (Darriba et al.,
188 2012) using the Bayesian Information Criterion. When the most supported substitution model
189 was not available in MrBayes, the next most complex model available was implemented as
190 this approach encapsulates the specified model as a possible case within the more complex
191 model. For ND4, TrN+I+ Γ was selected by jModelTest and GTR+I+ Γ was implemented in
192 MrBayes, and for ND2, TrN+ Γ was selected and GTR+ Γ was implemented. Two parallel runs
193 were completed in MrBayes, each of 5.5×10^6 generations, with four Markov Chain Monte
194 Carlo (MCMC) chains with a heating parameter of 0.1 and sampling every 500 generations.
195 The initial 25% of samples were discarded as burnin. Log files were checked to ensure that
196 effective sample sizes were greater than 200 and that stationarity and convergence were
197 achieved.

198 Estimates of molecular diversity (haplotype diversity and nucleotide diversity) were
199 calculated in Arlequin 3.5 (Excoffier & Lischer, 2010). The number of polymorphic and
200 parsimony informative nucleotide sites and mean uncorrected genetic distances (p-distances)
201 between sequences assigned to each mitochondrial clade were calculated in MEGA6.0
202 (Tamura et al., 2013). Population structure was quantified and assessed for mitochondrial and
203 nuclear data using Analysis of Molecular Variance (AMOVA; Excoffier et al., 1992) and
204 Spatial Analysis of Molecular Variance (SAMOVA; Dupanloup et al., 2002). AMOVA was
205 performed in Arlequin. Sequence variation was hierarchically partitioned based on (i) the
206 membership of individuals to major regional mitochondrial clades (Φ_{CT} ; clades defined from
207 Bayesian phylogenetic analysis), (ii) geographic sites within clades (Φ_{SC}), and (iii) geographic
208 sites across the entire study range (Φ_{ST}). The significance of estimated fixation indices was
209 tested using 1000 permutations of the data. SAMOVA was performed using $K = 2$ to 7 groups
210 in the SAMOVA package.

211 Divergence dating analyses were completed in BEAST 2.2.1 (Bouckaert et al., 2014).
212 Sequences were partitioned by gene region and substitution models suggested by jModelTest
213 were implemented. To test for significant variation in mutation rates among different
214 branches, a relaxed lognormal molecular clock model was implemented with a coalescent
215 constant population size prior, run for 50×10^6 generations and sampled every 5000
216 generations. Given that the rate variation parameter was close to zero, indicating that rates did
217 not vary significantly between branches, a strict molecular clock was employed for estimating
218 divergence times (Drummond & Suchard, 2010) with a normally distributed clock prior of

219 mean 1.52% (standard deviation 0.5%) sequence divergence per million years (which equates
220 to a lineage rate of 0.0076 substitutions per site per million years with a standard deviation of
221 0.0025). This rate was derived from several previous estimates of mitochondrial divergence in
222 squamates based on fossil calibrations (Chapple et al., 2011).

223 Due to shallow divergence and the potential for reticulate evolution in nuclear sequences,
224 allele networks rather than phylogenetic trees were reconstructed for β -globin using the TCS
225 statistical parsimony algorithm implemented in PopART
226 (<http://popart.otago.ac.nz/index.shtml>; Leigh & Bryant, 2015). Congruence of relationships
227 among alleles and each individual's assignment to a mitochondrial clade were assessed
228 visually. Alignments of phased sequences revealed several insertions or deletions (indels),
229 which were present in a homozygous condition within a particular individual. Indels were
230 coded as binary characters using SeqPhase (Muller, 2006). Network analyses with and
231 without indel characters did not differ in topology and further analyses omitted indel
232 information.

233

234 **Results**

235 Mitochondrial variation

236 From a total of 1406 base pairs, 439 sites were polymorphic and 304 sites were parsimony
237 informative. A total of 211 unique haplotypes were identified from 281 individuals with
238 sequence data for both ND2 and ND4. Overall haplotype diversity was high ($H = 0.99$, Table
239 1), with few haplotypes represented by more than one individual or more than one locality.

240 Bayesian phylogenetic analysis recovered four major clades: a northwest, a northeast
241 (including mainland Australia and the Bass Strait islands), a southeast and a southern clade
242 (Figure 2). These clades were geographically distinct, highly divergent (uncorrected genetic
243 distances $>4\%$; Table 2) and received strong posterior support (Figure 2). The level of
244 phylogeographic structure varied within the major clades, with the northeast clade the most
245 geographically structured (Figure 2). Northeast Tasmania was monophyletic, as were
246 mainland Australia and each of the Bass Strait islands (with the exception of Flinders Island
247 and the adjacent Mt Chappell Island), with strong posterior support (Figure 2). The order of
248 divergence between these clades was well resolved with the exception of Clarke Island
249 (Figure 2). The mainland Australian clade was nested among the Bass Strait island clades.
250 There was relatively little phylogeographic structure among populations from the northeast of
251 Tasmania. The southeast clade encompassed the largest geographic area, and several lineages
252 were spatially clustered although not monophyletic (e.g. the northern Midlands, the east coast,
253 Mt Wellington and surrounds, the eastern Central Plateau and the western Central Plateau;
254 Figure 2). The northwest clade was the most divergent; however, this was the least internally
255 structured geographically (Figure 2). The southern clade had limited evidence of spatial

256 structuring (Figure 2). Geographic overlap was observed between southeast and northwest
257 clades, and southeast and northeast clades (Figure 3).

258 The divergence dating tree recovered the same clades as the non ultrametric tree
259 (Supplementary Figure 1). The divergence of the northwest clade was placed at 10.4 Ma (95%
260 HPD: 4.5–19.6). The southern clade diverged around 5.9 Ma (2.7–11.1), and the split between
261 the northeast and southeast clades occurred around 4.6 Ma (2.0–8.6). Within the major clades,
262 deep internal branches diverged approximately 1.5–2.8 Ma. Within the northeast clade, the
263 divergence between Tasmania and the group comprising the Bass Strait islands and mainland
264 Australia was dated to around 2.9 Ma (1.2–5.4), while mainland Australian populations
265 diverged 1–2 Ma.

266 The greatest gain in mitochondrial Φ_{CT} occurred at $K = 4$ groups in SAMOVA, and the
267 assignment of sampling sites to groups was equivalent to the four major mitochondrial clades
268 resolved by phylogenetic analyses. High and significant levels of population structure were
269 detected among all comparisons tested using AMOVA: among all sampling sites, among sites
270 within regional clades, and among regional clades, with the highest proportion of variation
271 (63%) attributable to regional clades (Table 3). Each regional clade was also significantly
272 more structured than would be expected by chance alone, with the exception of the northwest
273 clade, in which considerably more variation was contained within sites rather than among
274 sites (Table 3). The northeast clade was the most highly structured clade, followed by the
275 southeast and southern clades (Table 3). AMOVA was also conducted on groups of sites
276 within the northeast clade (Table 3); the island sites were highly structured; mainland
277 Australian sites were somewhat less structured and northeast Tasmanian sites were
278 significantly but comparatively weakly structured (Table 3).

279 Nuclear variation

280 β -globin sequences were less variable than mitochondrial sequences, with 87 polymorphic
281 and 44 parsimony informative nucleotides from a total of 782 bp. There were three single
282 nucleotide indels, and longer indels of 12, 13, 14 and 16 bp. A total of 83 unique β -globin
283 haplotypes were recovered from 168 alleles (84 individuals) from 34 locations across the
284 species range (Table 1). Several haplotypes represented multiple individuals from several
285 sampling locations, and network analysis revealed little phylogeographic structure
286 (Supplementary Figure 2). During SAMOVA the greatest increase in Φ_{CT} was detected at $K =$
287 2, with the mainland Australian sites plus Rodondo Island (north Bass Strait) and Waddamana
288 (south Central Plateau) grouped together. Significant levels of population structure were
289 detected by AMOVA based on the mitochondrially-defined groups: among regional groups,
290 among sites within groups, and among sites (Table 2). The relative amount of structuring of
291 each major regional group was mostly consistent with mtDNA. The northeast clade had the
292 highest level of population genetic structure, followed by the southeast clade. However, the

293 northwest clade was significantly structured and was more highly structured than the southern
294 clade (Table 2).

295

296 **Discussion**

297 The potential that shared biogeographic patterns result convergently—from different
298 processes—has been previously demonstrated (Hawkins et al., 2012). The same possibility
299 also exists for shared phylogeographic patterns (Riddle & Hafner, 2006). Here we advocate
300 that shared phylogeographic patterns are more likely to reflect shared processes
301 (‘phylogeographic parallelism’) when based on closely-related, ecologically-similar species
302 (see also Dawson, 2012). In contrast, shared patterns among more distantly-related taxa that
303 likely differ in a range of attributes are at greater risk of ‘phylogeographic convergence’, and
304 these possibilities can be tested against both spatial and temporal criteria using approaches
305 such as approximate Bayesian computation (Hickerson et al., 2007; Cornuet et al., 2014).
306 While it is more common for comparative phylogeographic studies of closely-related species
307 to focus on the major differences between those species and any potentially consequent
308 differences in phylogeographic structuring (e.g., Dawson et al., 2002), the assumption that
309 studies of ecologically-similar closely-related taxa would yield similar phylogeographic
310 patterns clearly also needs to be tested. Where similar phylogeographic patterns are observed
311 among closely-related ecologically-similar species (e.g., Dawson, 2012), there can be
312 increased confidence in the explanations invoked for these patterns, and also for differences in
313 patterns relative to ecologically-distinct taxa. In contrast, observations of discordant
314 phylogeographic patterns for closely-related, ecologically-similar taxa call into question the
315 explanations for these patterns. For example, following observations of discordant
316 phylogeographic patterns between high latitude sister-species of intertidal gastropod,
317 differences in cold susceptibility during Pleistocene glaciations reflecting habitat differences
318 (intertidal versus subtidal) were implicated as greater predictors of phylogeographic
319 structuring in both species than their dispersal ability (Marko, 2004).

320 From our study, the broad mitochondrial phylogeographic patterns for *C. metallicus* are
321 remarkably similar to those found in *C. ocellatus* (Cliff et al., 2015), as depicted in Figure 3.
322 Therefore, the concordant mtDNA patterns in these species probably reflect shared underlying
323 processes (phylogeographic parallelism) given their close relationship and ecological
324 similarity, and our similar survey effort (individuals, populations, and DNA). Significant
325 structuring of genetic variation in both species was represented by divergent mtDNA clades in
326 Tasmania’s northwest, northeast (including Bass Strait islands), and southeast, with *C.*
327 *metallicus* also possessing a divergent clade in the south (Figure 3). Although the nuclear data
328 recovered from *C. metallicus* did not reveal monophyletic groups corresponding to broad non-
329 overlapping geographic areas, significant regional partitioning of population genetic variation
330 analogous to the mtDNA pattern was observed, consistent with expectations regarding

331 relative rates of lineage sorting in these markers (Funk & Omland, 2003); this was also the
332 case for *C. ocellatus* (Cliff et al., 2015). The dated mtDNA phylogeny indicates that *C.*
333 *metallicus* regional groups were established prior to the Pleistocene, and hence persisted
334 through multiple glacial-interglacial cycles, as was also inferred for *C. ocellatus* (Cliff et al.,
335 2015).

336 Isolation into multiple regional glacial refugia is the most parsimonious explanation for the
337 shared phylogeographic structuring within both *Carinascincus* species. During glacial
338 periods, the distribution of *C. metallicus* was probably limited by cold conditions. This
339 hypothesis is supported by the presence of contact zones between divergent *C. metallicus*
340 lineages in high elevation areas (Figure 3) that experienced glacial and periglacial activity
341 during the LGM (Colhoun et al., 1996; Colhoun, 2002). Similarly, divergence between
342 haplotypes within clades in the high elevation eastern Central Plateau was shallow, suggesting
343 recent colonisation and expansion into this region.

344 The effect of temperature on reproduction in widespread lowland and restricted alpine
345 *Carinascincus* species in Tasmania is well-studied (Jones & Swain, 1996; Swain & Jones,
346 2000; Pen et al., 2010; Uller et al., 2011), and a mechanistic link between thermally-limited
347 annual reproduction and altitudinal/climatic distribution limits has been established (Olsson &
348 Shine, 1998, 1999; Wapstra et al., 1999). *Carinascincus metallicus* and *C. ocellatus* do not
349 occur above the regional tree line (rising from ~900 m in southwest to ~1300 m in northeast
350 Tasmania, Kirkpatrick, 1982) because these areas are too cold to support annual reproduction
351 (Olsson & Shine, 1998; Wapstra et al., 1999). Above this elevation, they are replaced by
352 alpine-restricted *Carinascincus* with biennial reproduction (Olsson & Shine, 1998; Wapstra et
353 al., 1999). Tasmania was approximately 5.5°C colder during the LGM (Colhoun, 1985;
354 Kirkpatrick & Fowler, 1998; Fletcher & Thomas, 2010) and cold, alpine environments were
355 extensive during Pleistocene glacials (McIntosh et al., 2012). Assuming a lapse rate of 0.65°C
356 / 100 m (Colhoun, 2000), the elevational limit of *C. metallicus* and *C. ocellatus* would have
357 fallen by roughly 850 m, coinciding with estimates for the regional tree line which was
358 located near contemporary sea level in southwest Tasmania (Gibson et al., 1987) and to
359 around 450 m in northeast Tasmania (Colhoun, 2002). The approximate location of the LGM
360 tree line is indicated on Figure 1. Pollen and genetic evidence indicate woodland and open
361 forest habitat of *C. metallicus* may have persisted in sheltered valleys close to the present-day
362 sea level in northwest, northeast and southeast Tasmania (Colhoun, 1977; Kirkpatrick &
363 Fowler, 1998; Worth et al., 2009; Gauli et al., 2014). However, vegetation changes were
364 unlikely to influence the distribution of rocky habitats for *C. ocellatus*, and given concordant
365 phylogeographic patterns with *C. metallicus*, climatic factors appear to be the main driver of
366 past distributions in both species.

367 Divergences between major *C. metallicus* clades appear to pre-date the last glacial and
368 perhaps even the Pleistocene, and have therefore been maintained across multiple favourable

369 interglacial periods when population connections may have established. Glacial periods may
370 have reinforced or reinstated isolation of these lineages following interglacial periods. For
371 instance, our present day (interglacial) sampling revealed peripheral overlap of major *C.*
372 *metallicus* clades. This has also been observed for *C. ocellatus* following fine-scale sampling
373 along a transect across clade boundaries (Burridge, unpublished). Similarly, the major
374 Tasmanian phylogeographic breaks do not reflect contemporary landscape features that
375 restrict dispersal in either species, which are patchily but more-or-less continuously
376 distributed except in areas above ~1100 m in elevation. High-density blocking and
377 competitive exclusion may have reduced the mixing of lineages among adjacent clades during
378 interglacials (Hewitt, 2011; Waters et al., 2013). Low migration rates, high site fidelity and
379 small dispersal distances have also been observed in *Carinascincus* populations (Olsson &
380 Shine, 2003; Cunningham et al., 2017). These explanations may also apply to the
381 development of genetic divergence among the Tasmanian, Bass Strait, and mainland
382 Australian populations of *C. metallicus* that transcend multiple glacial periods, during which
383 these locations were connected terrestrially (Lambeck & Chappell, 2001). While increasing
384 aridity during late Pleistocene glacial cycles (McLaren & Wallace, 2010) may have also
385 restricting dispersal across the Bassian Plain, phylogeographic studies of other reptiles
386 suggest such movement was possible (Fairbairn et al., 1998; Chapple et al., 2005; Keogh et
387 al., 2005; Dubey & Shine, 2010; Chapple et al., 2011; Ng et al., 2014).

388 The genetic distinction of *Carinascincus* in northwest Tasmania is consistent with evidence
389 for local persistence of sclerophyll woodland during Pleistocene glaciation (Kirkpatrick &
390 Fowler, 1998; Colhoun & Shimeld, 2012), while glaciers in the Mersey and Forth River
391 valleys extended to within 20 km of the present-day coastline (Colhoun et al., 1996). During
392 glacial periods, the low-lying central north of Tasmania and the low relief Bassian Plain to the
393 north were probably arid, windswept treeless steppe (Kirkpatrick & Fowler, 1998), inhibiting
394 movement in a range of taxa, although pollen records are lacking for this region (Colhoun &
395 Shimeld, 2012). Distinct northwest Tasmanian lineages are also observed for *C. ocellatus*
396 (Cliff et al., 2015) and a range of other taxa (e.g., Chapple et al., 2005; Macqueen et al., 2009;
397 Bloomfield et al., 2011; Brüniche-Olsen et al., 2014; Zhang et al., 2014). Genetic isolation
398 between the remaining *Carinascincus* major clades may also reflect utilisation of disjunct
399 regional refugia during Pleistocene glaciations. Persistence of favourable climates and
400 habitats for *C. metallicus* in southeast and far southern Tasmania is supported by the presence
401 of *Carinascincus* on continental shelf islands south of Tasmania (Rounsevell et al., 1985),
402 plus genetic and pollen data that indicate present-day coastal southeast Tasmania was a
403 significant glacial refugium for woodland tree species (Colhoun, 1977; McKinnon et al.,
404 2004).

405 Despite similarities in the broad regional phylogeographic patterns in *C. metallicus* and *C.*
406 *ocellatus*, a notable difference occurred within northeast Tasmania. This region supports the

407 highest levels of genetic structuring for both species, suggesting their populations persisted
408 and diverged across multiple glacial cycles within localised lowland refugia throughout the
409 northeast, and genetic evidence suggests similar persistence in a range of other temperate taxa
410 (McKinnon et al., 2004; Worth et al., 2009; Worth et al., 2011; Gauli et al., 2014; Nevill et
411 al., 2014). However, in contrast to *C. ocellatus*, mitochondrial sequences in *C. metallicus*
412 were not monophyletic at each site in lowland northeast Tasmania. This difference may
413 reflect more specific habitat requirements and therefore lower effective population sizes,
414 connectivity and gene flow in *C. ocellatus*. Similar explanations have been offered for
415 differences in population structure in other co-distributed reptile species (Haines et al., 2014;
416 Podnar et al., 2014).

417 The value of phylogeography depends on the extent to which its results can be generalised
418 across regions and lineages (Dawson, 2012). While studies of multiple species are essential to
419 test for generalities, future phylogeographic studies should consider the value of collecting
420 data from closely related species, to either infer the importance of differences in species
421 attributes for differences in phylogeographic patterns (Dawson et al., 2002; Whiteley et al.,
422 2004; Hickerson & Cunningham, 2005; Burridge et al., 2008), or as in the case of our study,
423 to obtain confidence that shared phylogeographic patterns are indeed the product of shared
424 process (phylogeographic parallelism), rather than independent processes that have produced
425 similar genetic patterns (phylogeographic convergence).

426

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427 **Data availability**

428 Genetic sequence has been deposited with GenBank (Accession numbers #####–
429 #####).

430

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- 714

715 **Biosketch**

716 K.M.K. completed this research as part of a BSc(Honours) degree and is broadly interested in
717 biogeography and conservation of terrestrial organisms. E.W. is a behavioural ecologist who
718 studies reptiles, with an ongoing interest in species responses to climate change. C.P.B. is a
719 molecular ecologist with interests in historical biogeography, gene flow, and phylogenetics.

720 Author contributions: E.W. and C.P.B. conceived the ideas, K.M.K. and E.W. conducted
721 fieldwork, K.M.K, C.P.B. and B.S. completed laboratory work and data analyses, and K.M.K.
722 and C.P.B. led the writing.

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725 **Tables and Figures**

726

727 **Table 1.** Genetic diversity quantified by haplotype diversity (H) and nucleotide diversity (π)
 728 among groups and all samples based on 1406 base pairs of ND2 and ND4 mitochondrial
 729 sequence for *Carinascincus metallicus* sampled across their range in Tasmania and southeast
 730 Australia. Individuals were allocated to groups defined by regional mitochondrial clades.
 731 Sequences from admixed sites representing two mitochondrial clades were included in the
 732 analysis.

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

733

734 **Table 2.** Uncorrected mean genetic distances (\pm standard error from 500 bootstrap replicates)
 735 between regional clades detected from phylogenetic analysis of 1406 base pairs of ND2 and
 736 ND4 mitochondrial sequence for *Carinascincus metallicus* sampled across their range in
 737 Tasmania and southeast Australia.

	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	

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740 **Table 3.** Analysis of molecular variance (AMOVA) comparing mitochondrial and nuclear
 741 genetic structure within sampling sites and among and between groups defined by major
 742 mitochondrial clades in *Carinascincus metallicus* sampled across their range in Tasmania and
 743 southeast Australia. Analyses were conducted with and without admixed sites (sites
 744 representing more than one mitochondrial lineage: Ben Lomond, Hillwood and Lake St
 745 Clair).

Source of variation	mtDNA			nDNA		
	Fixation index	% total	P-value	Fixation index	% total	P-value
All samples						
– with admixed sites						
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
– without admixed sites						
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						
– with admixed sites						
Among populations	0.64 (Φ_{ST})	63.96	<0.0001	0.64 (Φ_{ST})	63.75	<0.0001
– without admixed sites						
Among populations	0.62 (Φ_{ST})	61.68	<0.0001			
Northwest clade						
– with admixed sites						
Among populations	0.15 (Φ_{ST})	14.55	0.0639	0.43 (Φ_{ST})	42.63	<0.0001
– without admixed sites						
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						
– with admixed sites						
Among populations	0.79 (Φ_{ST})	79.03	<0.0001	0.89 (Φ_{ST})	89.44	<0.0001
– without admixed sites						
Among populations	0.79 (Φ_{ST})	79.17	<0.0001			

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748 **Figure 1.** Geographic context of *Carinascincus metallicus* phylogeography in Tasmania and
749 southeast Australia. Distribution records for *C. metallicus* are indicated by small black circles
750 (derived from our observations and those from the “Tasmanian Natural Values Atlas” and the
751 “Atlas of Living Australia”) and tissue collection locations are indicated by grey circles.
752 *Carinascincus metallicus* are not found above the present-day tree line. The approximate Last
753 Glacial Maximum (LGM) tree line was digitised from Kirkpatrick (1997). Tasmania and the
754 Australian mainland were connected by land throughout most of the last glacial. Sea levels
755 during the LGM were approximately 120 m lower than today and rose to approximately -60
756 m by 14,000 years ago, breaking the land connection (Lambeck & Chappell, 2001). Datasets:
757 Surface Hydrology Polygons and Lines (Crossman & Li, 2015a, b), Digital Elevation Model
758 (Hutchinson et al., 2008), Australian Bathymetry and Topography Grid June 2009
759 (Whiteway, 2009).

760 **Figure 2.** Bayesian inference tree of *Carinascincus metallicus* reconstructed from 1406 bp of
761 ND2 and ND4 mitochondrial DNA sequence. Major regional clades and major subdivisions
762 within clades are indicated by vertical grey bars. Posterior probabilities >0.95 are indicated by
763 black dots. Posterior probability values are included above key nodes. Branch lengths are
764 scaled proportional to the scale bar. Branches to outgroups were truncated (indicated by
765 dashed lines across branches). Analysis was conducted on unique haplotypes, and the
766 numbers in parentheses after site names indicate the number of individuals belonging to that
767 haplotype at that site. If only one individual per haplotype per site was recorded, numbers in
768 parentheses were omitted.

769 **Figure 3.** Comparison of phylogeographic patterns found in *Carinascincus metallicus* and *C.*
770 *ocellatus*. Sample sites are indicated by circles, with colours representing allocation to
771 corresponding clades.

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