

Variation in intraspecific demography drives localised concordance but species-wide discordance in responses to Plio-Pleistocene climatic change

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Abstract

Understanding how species biology may facilitate resilience to climate change remains a critical factor in detecting and protecting species at risk of extinction. Many studies have focused on the role of particular ecological traits in driving species responses, but less so on demographic history and levels of standing genetic variation. We used environmental and genomic datasets to reconstruct the phylogeographic histories of two ecologically similar and largely co-distributed freshwater fishes to assess the degree of concordance in their responses to Plio-Pleistocene climatic changes. Although several co-occurring populations demonstrated concordant demographic histories, idiosyncratic population size changes were found at the range edges of the more spatially restricted species. Discordant responses between species were associated with low standing genetic variation in peripheral populations. This might have hindered adaptive potential, as documented in recent population declines and extinctions of the two species. Our results highlight both the role of spatial scale in the degree of concordance in species responses to climate change, and the importance of standing genetic variation in facilitating range shifts. Even when ecological traits are similar between species, long-term genetic diversity and historical population demography may lead to discordant responses to ongoing and future climate change.

1 **Introduction**

2 Understanding how or whether species may be able to adapt to current and future
3 climatic changes is critical for conservation management of threatened taxa [1].
4 However, predicting the susceptibility and extent of species loss due to climate
5 change remains a challenge. To this end, many studies have instead sought to
6 determine ecological traits that may confer resilience or susceptibility to climate
7 change across various taxa [2]. Ecological and physiological traits such as thermal
8 tolerance and dispersal capacity have been shown to be critical in driving adaptation
9 to climatic changes [3, 4]. Demographic and genetic traits such as population size,
10 stability and standing genetic variation (SGV) are however also important in
11 facilitating adaptation to new environmental stressors [5], and likely play a major role
12 in species responses to climate change [6-8].

13

14 From a genetic perspective, adaptation to novel climatic conditions more often relies
15 upon SGV than *de novo* mutations [9-11]. The degree to which SGV is maintained
16 within species or populations varies substantially across taxa and is influenced by a
17 combination of demographic, ecological and environmental factors. For example,
18 populations occurring at the edge of a species range often have lower connectivity
19 and genetic diversity than their more central counterparts [12], including reduced
20 diversity in climate-associated genes [13]. In marginal populations, persistence is
21 driven by the balance of the steepness of the selective environment and the
22 effectiveness of selection relative to genetic drift [14]. These components may
23 contrast with the core of the distribution, where larger carrying capacities and SGV
24 allow populations to persist closer to their selective optimum [15]. Thus, the
25 interaction and spatial variability of neutral (demographic) and adaptive (ecological)

26 traits are critically important in understanding how species ranges may shift under
27 climate change [16].

28

29 Understanding factors underlying species responses to historical climatic fluctuations
30 provides an empirical framework for determining how species may respond to
31 current and future environmental changes [17]. Extending phylogeographic analyses
32 from taxon-specific studies to assessments of how species assemblages have
33 responded to past climatic changes provides an approach to estimating the ubiquity
34 of species responses [18]. Similar species responses (concordance) across
35 disparate taxa often indicate that shared ecological traits underlie the response [19],
36 or demonstrate the ubiquity in impact of the environmental change in question [20].
37 Contrastingly, idiosyncratic responses (discordance) are often attributed to variation
38 in species-specific ecological traits [21]. However, intraspecific variation in
39 demography may lead to spatial variation in the degree of concordance, even across
40 ecologically similar species. For example, the interactive role of demography and
41 adaptive potential may lead to intraspecific variation at local scales, even if species-
42 wide patterns are concordant across taxa or vice versa [22, 23]. These patterns may
43 be reflected within species range shifts over time, where intraspecific variation in
44 demographic or ecological traits at range margins may drive interspecific
45 discordance in species responses to environmental change.

46

47 Biogeographic regions that experienced major environmental change in the past are
48 particularly useful for studying species responses to climate change. In this regard,
49 the southeast Australian temperate zone provides a model region to test how
50 species have responded to major environmental changes such as aridification and

51 eustatic changes. Mainland Australia has experienced significant environmental
52 changes since the late Miocene, which heralded the onset of major aridification [24].
53 Other than a brief humid period during the Pliocene [25], this aridification intensified
54 into the Pleistocene. While glacial periods in this region were not directly associated
55 with the formation of glaciers, major changes in precipitation and temperature shifted
56 ecosystems towards more arid conditions [26]. Concordantly, glacial maxima also
57 drove eustatic changes, expanding much of the continental shelf as sea levels
58 dropped [27]. The complex environmental history in southeast Australia, and its role
59 on the evolution of temperate species, has been demonstrated by a number of
60 phylogeographic studies (e.g. [28, 29]).

61

62 Freshwater-dependent species are important indicators of historical environmental
63 changes given their reliance on suitable habitat and often limited capacity for
64 dispersal [30]. Within temperate southeast Australia, the often co-distributed
65 southern (*Nannoperca australis*) and Yarra (*N. obscura*) pygmy perch provide an
66 ideal comparative study system. Both species possess highly similar morphology,
67 reproductive biology, salinity tolerance and habitat preferences, and also display
68 similar patterns of metapopulation structure [31-35]. Both species have low dispersal
69 capacity with little to nil contemporary connectivity among catchments [33, 35]. Both
70 species are relatively old (e.g. their lineages diverged around 13 million years ago
71 [36]) and show strong population structure, with two evolutionarily significant units
72 (ESUs) separating coastal and inland (Murray-Darling Basin) populations in *N.*
73 *australis* [28], and two clades each containing two ESUs in *N. obscura* [37]. Given
74 their isolated populations, it is expected that their long-term persistence along
75 landscapes depends on spatial variation of locally adaptive traits. This hypothesis is

76 consistent with studies of *N. australis* that show that patterns of adaptation in traits
77 related to reproductive fitness [38, 39], in levels of adaptive genetic diversity [34] and
78 in variance of gene expression [40] are strongly associated with hydroclimatic
79 gradients.

80

81 Despite their ecological similarities, the two species demonstrate marked differences
82 in conservation status, genetic diversity and total distribution range. While both
83 species are of conservation concern (*N. australis* as Near Threatened and *N.*
84 *obscura* as Endangered) within the IUCN Red List [41] and in state conservation
85 legislation, *N. obscura* is considered at higher risk due to their narrow range and
86 extremely low genetic diversity [35, 42]. These factors are implicated in the local
87 extirpation of *N. obscura* within the Murray-Darling Basin in the last five years,
88 following failed reintroductions after a large-scale drought impacted the region [41].
89 The relatively low genetic diversity of *N. obscura* is not thought to be the result of any
90 particularly severe past bottleneck [42], complicating determining factors underlying
91 this disparity. Additionally, it remains unclear whether the historical absence of *N.*
92 *obscura* in some regions where *N. australis* is found is the result of historical local
93 extinctions or a failure to initially colonise the habitat.

94

95 Here, we applied a comparative phylogeographic framework to explore the relative
96 roles of ecological and demographic traits on evolutionary history. We used genomic
97 datasets to estimate genetic diversity, phylogenetic relationships and demographic
98 history of these two freshwater fishes, in conjunction with species distribution
99 modelling. Then, we statistically evaluated regional concordance across co-occurring
100 populations to assess whether the species shared demographic responses to

101 Pleistocene glacial cycles. We predicted that evolutionary patterns, demographic
102 histories and distribution changes would be concordant across the two species if
103 ecological factors played a relatively strong role in determining species responses to
104 past climatic changes, with current differences owing to more recent factors.
105 Contrastingly, discordant histories would indicate that genetic diversity and
106 demography played a relatively larger role and underpinned their contemporary
107 differences in conservation status. Our framework also includes differentiation of
108 local-scale (population-level) and broad-scale (species-level) responses to assess
109 the role of intraspecific patterns in driving lineage responses.

110

111 **Methods**

112 **Sample collection and genomic library preparation**

113 The distribution of both species spans the southwest Victoria biogeographic province
114 and the lower reaches of the Murray-Darling Basin [31]. *Nannoperca australis* is
115 more widely distributed and is also found across eastern Victorian drainages,
116 northern Tasmania and the upper reaches of the southern Murray-Darling Basin [43].
117 The final sample contains all known genetically distinct populations (including
118 recently extirpated populations) across their full co-distributed range (electronic
119 supplementary material, Table S1). This equals to seven populations of *N. obscura*
120 and nine populations of *N. australis* occurring across all major drainages of the
121 region (Figure 1). An additional 10 and 15 *N. obscura* and *N. australis* (respectively)
122 from Lake Alexandrina within the lower Murray-Darling Basin were also included for
123 more targeted demographic reconstruction of these populations. For phylogenetic
124 analyses, five samples of a sister species (*Nannoperca vittata*) were included as
125 outgroup [36]. Specimens were collected using electrofishing, dip-, fyke- or seine-

126 netting. Either the caudal fin or the entire specimen was stored at -80°C at the South
127 Australian Museum, or in 99% ethanol at Flinders University.

128

129 DNA was extracted from muscle tissue or fin clips using a modified salting-out
130 method [44] or a Qiagen DNeasy kit (Qiagen Inc., Valencia, CA, USA). Genomic
131 DNA was checked for quality using a spectrophotometer (NanoDrop, Thermo
132 Scientific), integrity using 2% agarose gels, and quantity using a fluorometer (Qubit,
133 Life Technologies). The ddRAD (double digest restriction-site associated DNA)
134 genomic libraries were prepared in-house at the Molecular Ecology Lab of Flinders
135 University following [34]. The majority of the samples (56/98) were paired-end
136 sequenced on an Illumina HiSeq 2000 at Genome Quebec (Montreal, Canada). The
137 remaining samples were single-end sequenced on an Illumina HiSeq 2500 at the
138 South Australia Health and Medical Research Institute (SAHMRI).

139

140 **Sequence filtering, alignment and SNP calling**

141 Sequences were demultiplexed using the 'process_radtags' module of Stacks 1.29
142 [45], allowing up to 2 mismatches in barcodes. Barcodes were removed and
143 sequences trimmed to 80 bp to remove low-quality bases from the end of the reads.
144 Trimmed reads were aligned using PyRAD 3.0.6 [46], and further cleaned by
145 removing reads with >5 bp with a Phred score < 20. Loci were retained if they
146 occurred in at least ~80% of samples (22 in *N. obscura*; 30 in *N. australis*) within the
147 phylogenetic datasets.

148

149 For some population-specific analyses (e.g. some genetic diversity measures and
150 coalescent-based demographic histories), we subsampled our ddRADseq data with

151 loci re-aligned and SNPs called separately for each population (excluding those with
152 $n < 3$ due to low sample size) using PyRAD. This was done as most SNPs called at
153 the species level were monomorphic within individual populations and would have
154 significant effects on downstream analyses [47]. Only loci present in all individuals
155 were kept to prevent missing data from biasing the site-frequency spectrum (SFS),
156 used in all demographic analyses [48].

157

158 **Contemporary genetic diversity**

159 Summaries of population-level genetic diversity parameters (allelic richness and
160 gene diversity) were compared across populations within species, and between
161 species, using the R package *hierfstat* [49]. Given uneven sample sizes, rarefaction
162 was used ($n = 4$) to estimate mean values per locus per population. Due to the larger
163 sample sizes available for Lake Alexandrina populations, genetic diversity
164 parameters were also calculated using $n = 15$ rarefaction and loci aligned separately
165 within each Lake Alexandrina population. For these populations, we also calculated
166 effective population size (N_e) using NeEstimator [50] and a minor allele frequency
167 threshold of 0.02. Additionally, nucleotide diversity (π) within each population was
168 estimated using dnaSP 6.1 [51]. Differences in population means of genetic diversity
169 parameters between the two species were statistically evaluated using t-tests (two-
170 tailed t-test or Wilcox test).

171

172 **Phylogenetic and historical migration analyses**

173 Maximum likelihood (ML) phylogenies of each species were estimated using RAxML
174 8.2.11 [52] with the concatenated ddRAD alignments to estimate evolutionary
175 relationships. Phylogenies were estimated under the GTR-GAMMA model of

176 evolution and 1,000 RELL bootstraps for each species. Additionally, we estimated
177 gene trees for each RAD locus using IQ-TREE2 [53] to account for genome-wide
178 heterogeneity and incomplete lineage sorting. Gene and site concordance factors
179 [54] were estimated by comparing individual gene trees to the concatenated RAxML
180 tree.

181

182 As historical migration may impact the topology of a phylogenetic tree, we also used
183 TreeMix [55] to infer historical population connectivity. We iteratively increased the
184 number of migrations from 0 – n for each species (nine in *N. australis*; seven in *N.*
185 *obscura*) and evaluated the fit of each tree based on the standard error of the
186 covariance matrix. We further assessed the fit of the trees by calculating the
187 percentage of variance explained per model

188 (https://github.com/wlz0726/Population_Genomics_Scripts/tree/master/03.treemix).

189 The best supported number of migrations was determined by the asymptote of the
190 likelihood, where additional migrations did not substantially increase model
191 likelihood.

192

193 **Comparative demographic inference**

194 Long-term demographic histories for all populations were estimated using stairway
195 plots and the SFS. One-dimensional SFS were calculated for each independent
196 population alignment using an in-house script. Stairway plots were estimated
197 assuming a mutation rate of 10^{-8} mutations per site per generation, and a generation
198 time of one year for both species [42, 56]. Although both species reproduce annually,
199 most individuals do not live beyond one to two years in the wild [56]. We then
200 analysed co-distributed populations of *N. australis* and *N. obscura* under two

201 coalescent frameworks to statistically evaluate the degree of concordant
202 demographic history. The populations of Gnarkeet Creek (NauGCH and NobGCL),
203 Merri River (NauMRG and NobMRG) and Lake Alexandrina (NauALE and NobCHI)
204 were selected based on their contemporary co-occurrence and to represent the
205 geographic range of the overlap in species distributions (Figure 1).

206

207 We first used FastSimCoal2 [57] to simulate model-based demographic histories
208 over the last 30 Kyr. Simulations were conducted for each population under five
209 different single population demographic scenarios (electronic supplementary
210 material, Figure S1). Parameters were estimated using 40 optimisation cycles with
211 500,000 simulations per scenario, with the fit of the models estimated using Akaike
212 Information Criterion (AIC) and Akaike weights (electronic supplementary material,
213 Methods and Table S2). Confidence intervals for the parameters specified in the best
214 supported demographic model per population were estimated by simulating 100 SFS
215 and re-simulating point estimates using 500,000 iterations per SFS.

216

217 Additionally, we ran co-demographic model-based simulations using the aggregate
218 site frequency spectrum (aSFS) and hierarchical approximate Bayesian computation
219 in Multi-DICE [58] to determine if demographic histories were congruent across co-
220 distributed populations. A single model of exponential growth followed by exponential
221 decline was applied to all populations using broad uniform priors (electronic
222 supplementary material, Methods and Figure S2), based on results from
223 FastSimCoal2 (see Results). We first tested the proportion of co-contracting taxa (ξ),
224 and then fixed this hyperparameter to better explore the remaining parameters. A
225 “leave-one-out” approach using 50 pseudo-observed datasets was used to generate

226 a confusion matrix, with the most likely proportion of co-contracting taxa determined
227 using the top 1,500 simulations and Bayes Factors. Parameters were estimated
228 using 1.5 million coalescent simulations and posterior distributions estimated using
229 the top 100 simulations and the *abc* R package [59]. We further tested whether
230 demographic syndromes were broadly consistent across populations by comparing
231 the posterior distributions for N_e and bottleneck strength (ϵ).

232

233 **Contemporary and paleoclimatic environmental modelling**

234 Species distribution models (SDMs) were estimated using an ensemble modelling
235 approach within biomod2 [60]. We estimated SDMs for both species across eleven
236 time slices ranging from contemporary conditions to the Pliocene using the
237 PaleoClim database [61]. Occurrence records for both species were obtained from a
238 combination of sampled sites within this and past studies [28, 35, 36], as well as
239 from the Atlas of Living Australia (<http://www.ala.org.au/>). We filtered the occurrence
240 data to reduce the impact of spatial autocorrelation, resulting in final datasets of
241 1,021 and 163 observations for *N. australis* and *N. obscura*, respectively (electronic
242 supplementary material, Methods).

243

244 We selected eight non-correlated environmental variables for estimating species
245 distributions (electronic supplementary material, Table S3). These were annual
246 mean temperature (Bio1), mean diurnal range (Bio2), isothermality (Bio3),
247 temperature seasonality (Bio6), mean temperature of the wettest quarter (Bio8),
248 mean temperature of the driest quarter (Bio9), annual precipitation (Bio12) and
249 precipitation seasonality (Bio15). For the three oldest time periods, Bio2, Bio3 and
250 Bio6 were unavailable and thus not included within the projections. SDMs were

251 estimated using MaxEnt, random forest and generalised linear models, and an
252 ensemble model generated per time period using the weighted mean of all models.
253 All models were evaluated using both the relative operating characteristic and the
254 true skill statistic. We quantitatively assessed the relative stability of species
255 distributions over time by estimating the mean and standard deviation of suitability
256 over time for each species. Differences in distributional ranges between species
257 across time were estimated by converting SDMs to binary presence-absence maps
258 based on the minimum suitability of the top 90% of putative occurrences per model
259 (electronic supplementary materials, Methods).

260

261 **Results**

262 **Bioinformatics**

263 We obtained 21,051 ddRAD loci containing 53,334 filtered SNPs for *N. obscura* and
264 19,428 ddRAD loci containing 69,264 filtered SNPs for *N. australis*, with low missing
265 data in both alignments (electronic supplementary material, Figure S1). Genetic
266 diversity differed remarkably between the two species, with allelic richness, gene
267 diversity, nucleotide diversity and number of SNPs per population alignment being
268 significantly higher ($p \leq 0.01$) in *N. australis* (electronic supplementary material,
269 Table S1).

270

271 **Phylogenetic analysis**

272 Phylogenetic analysis of both datasets returned a highly supported phylogenetic tree
273 for each species. Site concordance factors broadly supported these patterns,
274 although gene concordance factors were low across both trees (electronic
275 supplementary material, Figures S4–S6) – this is not unexpected when gene trees

276 are estimated from short and relatively uninformative individual loci [54]. For
277 southern pygmy perch, the topology of this phylogenetic tree mirrored the
278 geographic range of the samples, with a clear division between the Murray-Darling
279 Basin ESU and the coastal ESU within the tree (Figure 2A). Within the coastal clade,
280 populations diverged in a longitudinal manner, with eastern populations as the most
281 recently diverged. In contrast, the phylogenetic tree for *N. obscura* did not
282 demonstrate the same precise patterns, with populations not diverging in an exactly
283 longitudinal manner. However, this was driven by a single outlier population
284 (NobMEC).

285

286 TreeMix inferred a greater number of migration events within *N. australis* (four) than
287 *N. obscura* (one event) (Figure 2B; electronic supplementary material, Figure S7).
288 Within *N. australis*, migrations were inferred both across populations of the coastal
289 lineage as well as into the Murray-Darling Basin. The strongest migrations were
290 between eastern coastal populations, and from the ancestor of the westernmost
291 coastal population into the ancestor of the Murray-Darling Basin lineages. For *N.*
292 *obscura*, the single migration inferred suggested historical gene flow from the
293 easternmost population to a more central population. Trees and migration edges for
294 both species were well supported by covariance matrices, with low pairwise
295 residuals (electronic supplementary material, Figure S8) and standard errors of < 1
296 for any given population for both species (electronic supplementary material, Figure
297 S9).

298

299

300 **Comparative demography**

301 Stairway plots demonstrated broadly similar demographic histories across the two
302 species, with most populations relatively stable or declining slightly over the last 1
303 Mya (Figure 3A). Populations within both species demonstrated variable
304 demographic histories, although populations of *N. australis* appeared generally more
305 stable over time. Both Lake Alexandrina populations (NobCHI and NauALE) showed
306 significant historical increases in N_e >200 Kya, and long-term stable population sizes
307 following this expansion.

308

309 Most populations chosen for comparative analysis demonstrated fluctuating
310 demographic histories (Figure 3B), with a period of pre-LGM (Last Glacial Maximum)
311 growth followed by a post-LGM decline (electronic supplementary material, Figure
312 S10). Only the eastern *N. obscura* population (NobGCL) contrasted this pattern, with
313 a model of low but constant population size more supported than other demographic
314 histories (Model 3). Strong post-glacial declines were present in Lake Alexandrina
315 populations of both species, with weaker declines in the more eastern population
316 pairs.

317

318 A confusion matrix suggested that the co-demographic model was more likely to
319 infer fully synchronous ($\xi = 1$) or fully asynchronous ($\xi = 0.167$) co-contractions over
320 intermediate proportions of taxa (electronic supplementary material, Figure S11).
321 Despite this, Bayes Factors supported a fully synchronous model over more
322 asynchronous models, and so ξ was fixed to 1 to better explore other parameters
323 (Figure 3C). Contemporary population sizes were inferred to be relatively small

324 across all populations with relatively weak post-glacial bottleneck strength (Figure
325 3D; electronic supplementary material, Table S5). These bottlenecks were similar in
326 magnitude across populations, as indicated by low values of the dispersion index
327 (Figure 3E). However, Multi-DICE did not recover the same timing of the bottleneck,
328 possibly due to relatively low resolution within the aSFS (Figure 3F). Overall, these
329 results support a widespread and concordant bottleneck across the six co-distributed
330 populations.

331

332 **Species distribution modelling**

333 Comparing the SDMs of the two species indicated much greater maximum
334 distribution and variation in distributional range in *N. australis* than in *N. obscura*.
335 *Nannoperca obscura* demonstrated long-term isolation to a relatively small region of
336 southwest Victoria, whilst *N. australis* demonstrated a significant range expansion
337 event throughout the early Pleistocene with a more recent contraction in the
338 Holocene (electronic supplementary material, Figure S12). Despite these
339 differences, both species maintained a shared climatic refugium in southwest
340 Victoria, highlighted by a region of high mean suitability in both species (Figure 4B).

341

342 Comparisons across the different methods indicated that RandomForest was more
343 conservative in estimating area (Figure 4A). While there was significant variation in
344 estimated area across the different methods, ensemble models approximately
345 captured the mean of all models. *Nannoperca australis* demonstrated significantly
346 larger distributions throughout the Pleistocene compared to the relatively stable
347 range of *N. obscura*, with the former spanning a range approximately twice as large
348 as the latter during the mid-Pleistocene (Figure 4A). These patterns were similarly

349 reflected within the standard deviations across timeslices per species, with *N.*
350 *australis* showing much higher variation over a larger area (Figure 4C).

351

352 **Discussion**

353 Our results demonstrate how spatial variation in demographic history may drive
354 species-wide discordant responses to past climatic changes, even when local-scale
355 impacts are concordant and species' ecological traits are similar. Specifically, we
356 show that within a shared climatic refugium for two co-distributed and ecologically
357 similar freshwater fishes, demographic histories were largely concordant. However,
358 towards the edges of this refugium demographic histories decreased in
359 concordance, suggesting that range edge populations of *N. obscura* were more
360 limited than *N. australis* in their capacity for expansion during more favourable
361 climatic conditions. Together, our findings determine the importance of intraspecific,
362 population-level dynamics in driving species-wide adaptation and resilience to
363 climate change.

364

365 The temperate zone of southeast Australia has undergone significant environmental
366 change since the Pliocene, owing to a combination of continent-wide aridification
367 [24], eustatic changes [28] and major hydrological rearrangements [62]. These
368 various aspects likely had significant impacts on the persistence and connectivity of
369 freshwater lineages across the region [43]. This was supported by the high level of
370 phylogenetic structure within *N. australis*, and the inferred migration pathways that
371 correspond well to those previously suggested through ancient hydrological conduits
372 [62]. Although phylogenetic patterns in *N. obscura* did not directly match the
373 longitudinal gradient of populations, earlier phylogenetic analyses using allozymes

374 and mitochondrial DNA showed a similar pattern [37]. This disjunction was attributed
375 to potential historical connections from Mount Emu Creek into more western
376 populations [35], although short branch lengths and low genetic diversity across the
377 species may also indicate incomplete lineage sorting as a factor [63]. For both
378 species, we denote two major clades: one of Murray-Darling Basin populations and
379 another of coastal populations in *N. australis*, as suggested elsewhere [43], and two
380 clades each containing two previously identified ESUs in *N. obscura* [37].

381

382 Within the species distribution models, a region of southwest Victoria was highlighted
383 as a climatic refugium for both species throughout the Plio-Pleistocene. This region
384 was consistently identified as suitable habitat for both species across all time slices.
385 Although glacial maxima were associated with cold and arid conditions across
386 Australia, coastal woodland habitats were likely buffered against intense aridification
387 by oceanic circulation and relatively higher humidity and rainfall [64]. Other
388 phylogeographical studies demonstrating limited impact of glacial maxima on
389 connectivity supports the identity of this climatic refugium [27, 64]. Co-occurring
390 populations within this shared refugium demonstrated highly congruent demographic
391 histories at both more ancient (>1 Myr) and more recent (since the LGM) temporal
392 scales. This concordance is expected when ecological traits, habitat preferences and
393 environmental stability are shared across the species in question [21]. Although
394 individual populations within each species demonstrated spatially variable
395 demographic histories, comparisons across the two species showed similar patterns
396 of N_e over time for most directly co-occurring populations.

397

398 Both pygmy perch species demonstrated temporally synchronous expansions during
399 the LGM with post-glacial contractions across central populations. Despite intense
400 inland aridification during glacial maxima, run-off in many southeast Australian rivers
401 were likely much greater during the LGM [65]. These increased river flows have
402 been attributed to seasonal snow melt of periglacial regions in the highlands and
403 reduced vegetation cover, creating large rivers with enhanced run-off [65, 66]. Colder
404 conditions and strong flows may have facilitated the observed concordant expansion
405 in populations at this time, with the steep decline in flows during the early Holocene
406 (14 – 7 Kya) potentially contributing to their more recent contraction [67]. However,
407 concordance was reduced for pairwise populations that occurred closer to the edge
408 of this shared refugium, suggesting the species had discordant responses at the
409 fringe of the range. Similarly, phylogenetic patterns at the species-wide level varied
410 between the two species, with clearer geographic sorting and historical migration
411 across *N. australis* lineages compared to *N. obscura*.

412

413 Spatial variation in demographic history, and by extension concordance across taxa,
414 may result from several different mechanisms [22, 68]. Particularly for narrowly
415 distributed species, edge-of-range effects on populations close to the ecological
416 tolerance threshold of the species may result in highly divergent patterns of
417 demographic history and genetic diversity compared to more central populations [12,
418 68]. By extension, the ecological range of species may be a strong factor driving
419 discordance when particular locations are at the periphery of the distribution of one
420 species, but not another. Given the broad similarity in ecological traits between the
421 two species and their co-occurring nature [69], it is unlikely that this discordance in
422 species-wide responses to past climatic changes is a result of different ecologies.

423 However, some variation in microhabitat preference seems to exist between species,
424 with *N. obscura* limited to larger, lowland channels and floodplains whereas *N.*
425 *australis* is also found in streams and dense swamps [69]. This suggests greater
426 habitat specialisation in *N. obscura*, which might drive lower SGV (or result from it)
427 and impede range expansions. Thus, we cannot completely rule out some role of
428 ecology and its interactions with genetic diversity in driving discordant responses.
429 The lower genetic diversity in *N. obscura* could not be directly attributed to notable
430 and widespread genetic bottlenecks, suggesting instead that the species suffered
431 from a consistent pattern of being genetically depauperate. Combined, these factors
432 suggest that long-term SGV may be a key factor driving the temporally and spatially
433 widespread discordance in response to Pleistocene climate changes.

434

435 Adaptive responses, particularly in scenarios of range expansion, are often driven by
436 soft sweeps of SGV [8]. While many studies focus on rapid adaptation from SGV in
437 terms of invasive species colonising new habitats [70], similar dynamics can be
438 expected to play a role in range expansions of native taxa [71]. In regard to range
439 shifts across the Pleistocene, higher SGV may have predisposed *N. australis* to
440 capitalise on the colder temperatures and stronger rivers of glacial periods and
441 subsequently expand. Similarly, historical connectivity across now-isolated river
442 drainages [28] likely facilitated interpopulation gene flow, which may have further
443 bolstered SGV and adaptive potential [68, 72]. This gene flow in *N. australis* may
444 have also facilitated range expansion if locally adaptive alleles were transferred into
445 edge populations [70]. Contrastingly, a lack of long-term SGV within *N. obscura* may
446 have prevented them from expanding under these conditions, leading to the species-
447 wide discordance. The spatial variation in the degree of concordance, with

448 discordance occurring at the edge of the *N. obscura* pre-glacial refugium, supports
449 this conclusion.

450

451 Discordant species-wide responses to past climatic change may play an important
452 role in contemporary genetic diversity and, by extension, current conservation
453 efforts. For example, low genetic diversity resulting from historical bottlenecks can
454 drive contemporary inbreeding depression [73]. Additionally, the parallels between
455 historical range expansion scenarios and current reintroductions to conserve species
456 demonstrates how historical processes may inform current practices [74]. For
457 example, reduced adaptive capacity in *N. obscura* may have contributed to their
458 local extirpation and to the failure of reintroductions of captive-born offspring at range
459 margins, as documented for the lower Murray-Darling Basin [41]. This contrasts to
460 the successful reintroduction of *N. australis* that simultaneously took place in that site
461 using the same captive-breeding design [41, 42].

462

463 Understanding how, and which, species may be able to adapt under contemporary
464 climate change remains a critical aspect of evolutionary biology [2]. Typically, this
465 framework has focused on understanding how ecological traits may underpin
466 individual species responses to climatic change [6]. However, demographic
467 parameters are also critical components for species susceptibility to contemporary
468 climate change [5]. Here, we demonstrate that intraspecific SGV may also be a
469 critical component of species responses to climatic changes, particularly in range-
470 edge populations. This corroborates studies indicating that adaptive potential is
471 largely driven by SGV prior to the origination of major selective pressure [9] and
472 suggests that considering broad ecology alone may not be enough to predict

473 species' ability to respond. Thus, understanding how the demographic history of
474 individual populations may predispose, or hinder, species adaptive potential is an
475 important component of conservation management of threatened species. For
476 species with low SGV, proactive measures such as assisted gene flow and
477 maintenance of effective population size may assist in their long-term conservation
478 [75].

479

480 Long-term standing genetic variation drove discordance in the response of closely
481 related and ecologically similar freshwater fishes to historical climate change, by
482 facilitating range expansion of one species but not the other. However, in the centre
483 of a shared habitat refugium, demographic histories were concordant, suggesting
484 that spatial variation in the degree of concordance is linked to the interaction of
485 standing genetic variation and distribution edge effects. Together, this demonstrates
486 the importance of the maintenance of standing genetic variation for adaptive
487 potential in response to climatic changes and the role of non-ecological traits in
488 driving patterns of concordance or discordance.

489

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496

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773

774 **Figure captions**

775 **Figure 1:** Contemporary distribution and sampling map for *N. australis* and *N.*
776 *obscura*. *Nannoperca australis* sampling sites are indicated in red, and *N. obscura*
777 sites in blue. The distribution of *N. australis* is indicated with light green shading and
778 dashed borders, with the distribution of *N. obscura* (also the region of co-occurrence)
779 in darker green. The solid black line indicates the boundary of major drainage
780 basins, and the dark blue line demonstrates the approximate shoreline during glacial
781 maxima. Bottom left inset depicts study region and major drainage basins in
782 Australia. Top right inset depicts the full extent of species distributions.

783

784 **Figure 2:** Phylogenetic histories and migration patterns in *N. australis* and *N.*
785 *obscura*. **A:** Maximum likelihood phylogenetic trees based on ddRAD loci.
786 Populations were reciprocally monophyletic and so were collapsed to the population
787 level for simplicity. Both trees were rooted using *N. vittata* as the outgroup, which
788 was dropped for visualisation. Node values show bootstrap support. Branch colours
789 indicate the drainage basin of origin for each population or clade. **B:** Best supported
790 ancestral migration patterns inferred using TreeMix based on SNP datasets. All
791 displayed migrations were statistically significant ($p < 0.05$). Arrows denote the
792 direction of inferred migrations, with the colour indicating their relative weights.

793

794 **Figure 3:** Demographic histories of *N. australis* and *N. obscura* populations. **A:**
795 Stairway plot reconstructions of demographic history. Inset stars indicate co-
796 occurring populations which were further explored within a codemographic
797 framework. Populations are arranged from westernmost to easternmost within each
798 species. **B:** Most likely individual demographic histories for co-occurring *N. australis*

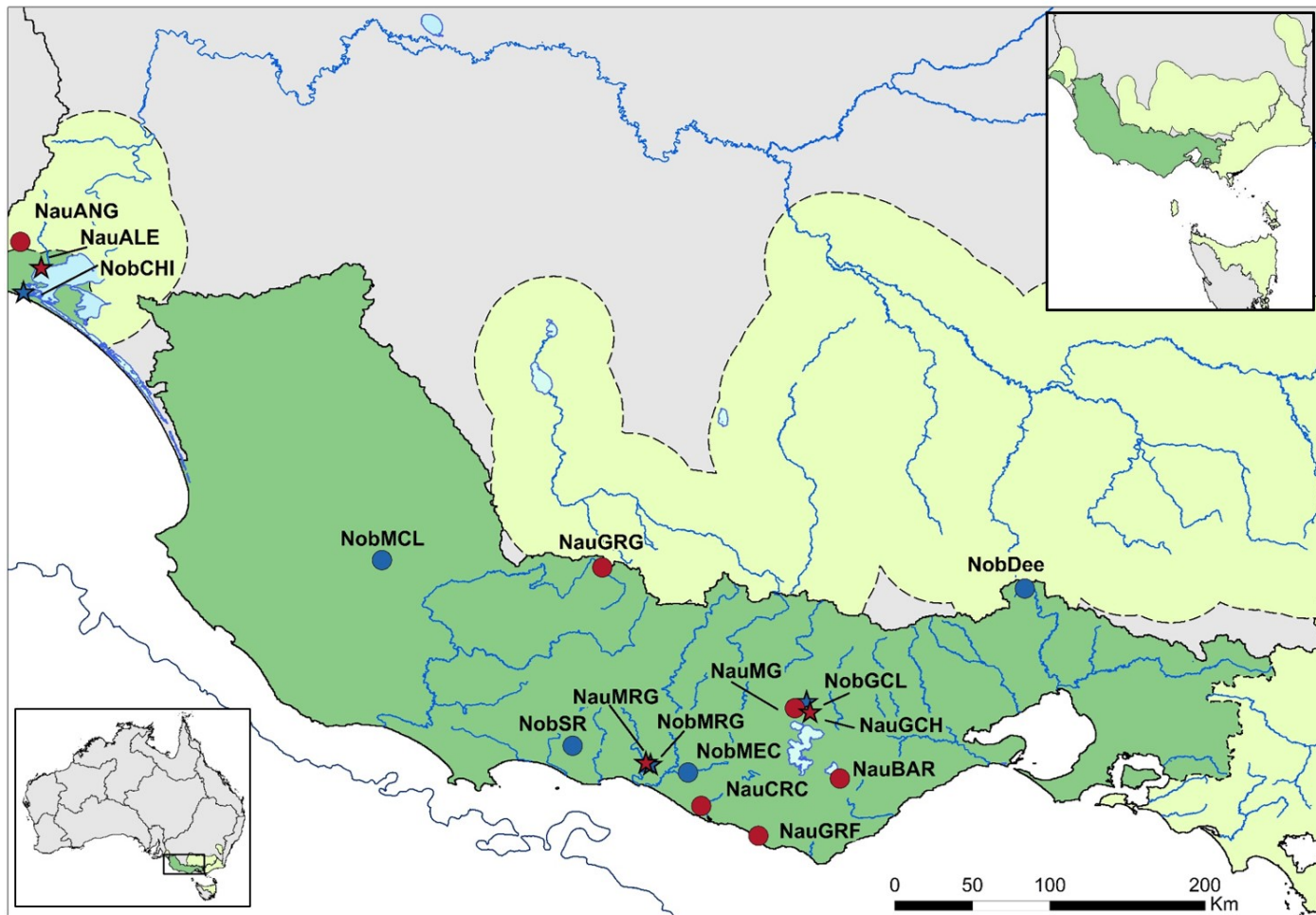
799 and *N. obscura* populations over the Pleistocene, simulated using FastSimCoal2.
800 Thick dark lines indicate mean N_e over time, calculated based on the means of
801 current N_e , rates of change and timing of switching rates (see Supplementary
802 Material). Shaded areas indicate 95% confidence intervals based on the 97.5% and
803 2.5% probability estimates for the same parameters. **C**: Bayes Factor matrix of the
804 proportion of populations showing synchronised bottlenecks (ξ) within a co-
805 demographic model using Multi-DICE. Each cell compares the model in the column
806 with the model in the row, with brighter colours indicating greater support for the
807 column. **D**: Posterior distribution of mean bottleneck strength (ϵ) across all six
808 populations. **E**: Posterior distribution of dispersion index of bottleneck strength
809 ($\text{Var}(\epsilon)/\text{Mean}(\epsilon)$) across all six populations. **F**: Posterior distribution of the timing of
810 the bottleneck event, in generations/years.

811

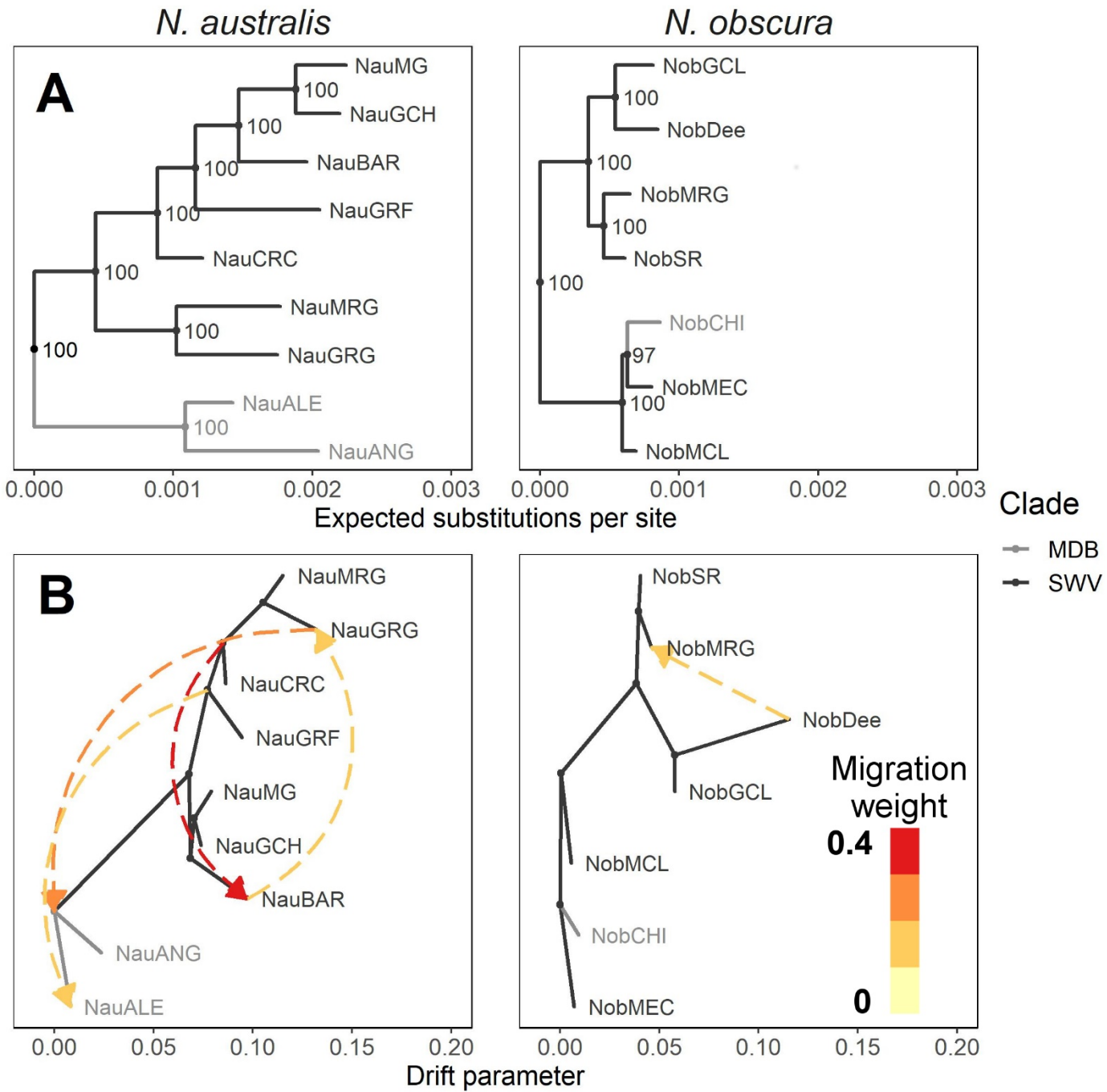
812 **Figure 4:** Comparisons of summaries of distributional changes over eleven time
813 periods spanning the Plio-Pleistocene. **A**: Distribution extent per species. Individual
814 models are indicated by points, with SDM method indicated by colour. The 95%
815 confidence interval across all individual models is shown by the pale blue ribbon.
816 The ensemble model is represented by a solid black line. **B**: Mean cell suitability
817 across all time periods. **C**: Variation (standard deviation) in cell suitability across all
818 time periods.

819 Figures

820 **Figure 1**



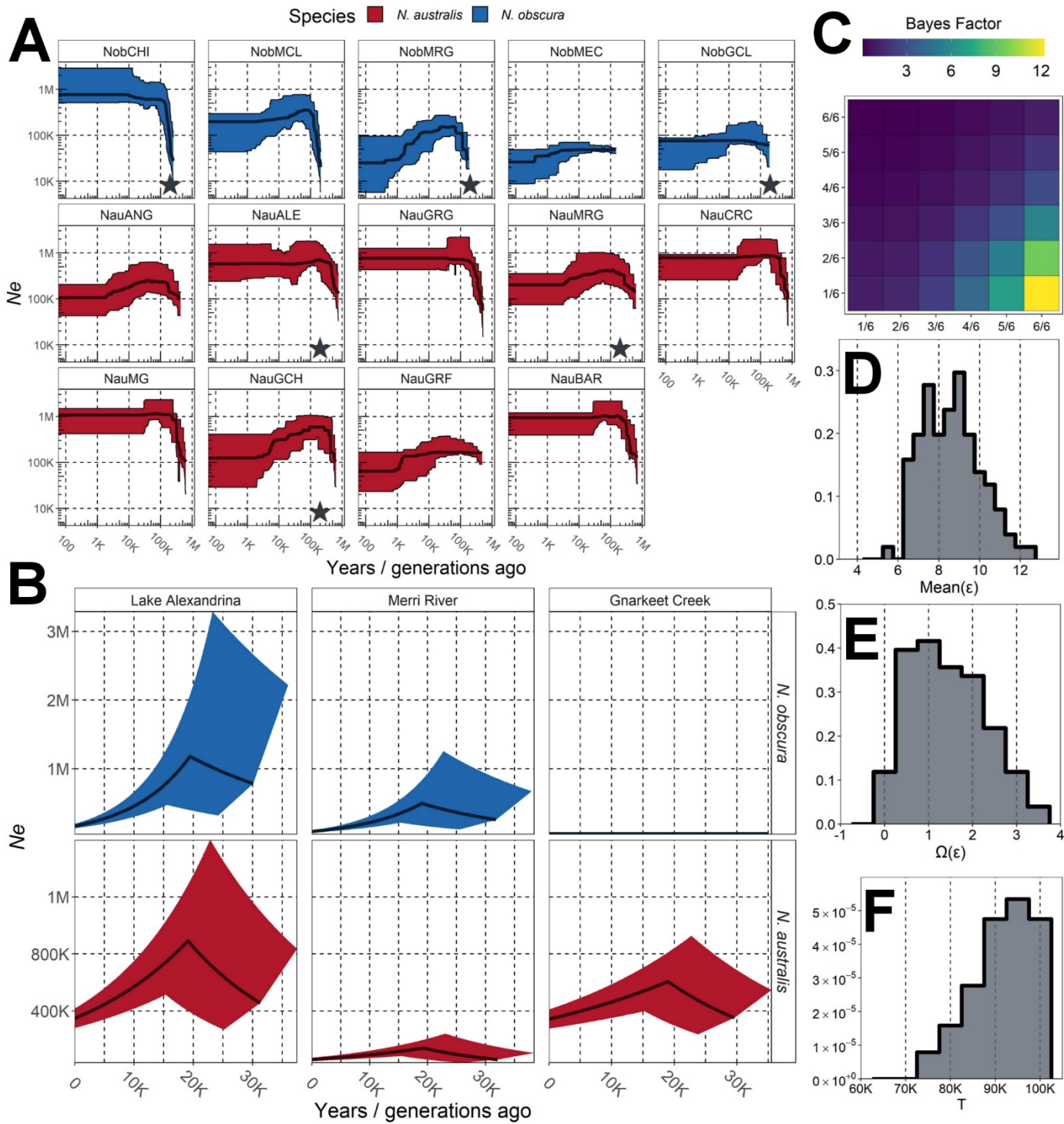
824 **Figure 2**



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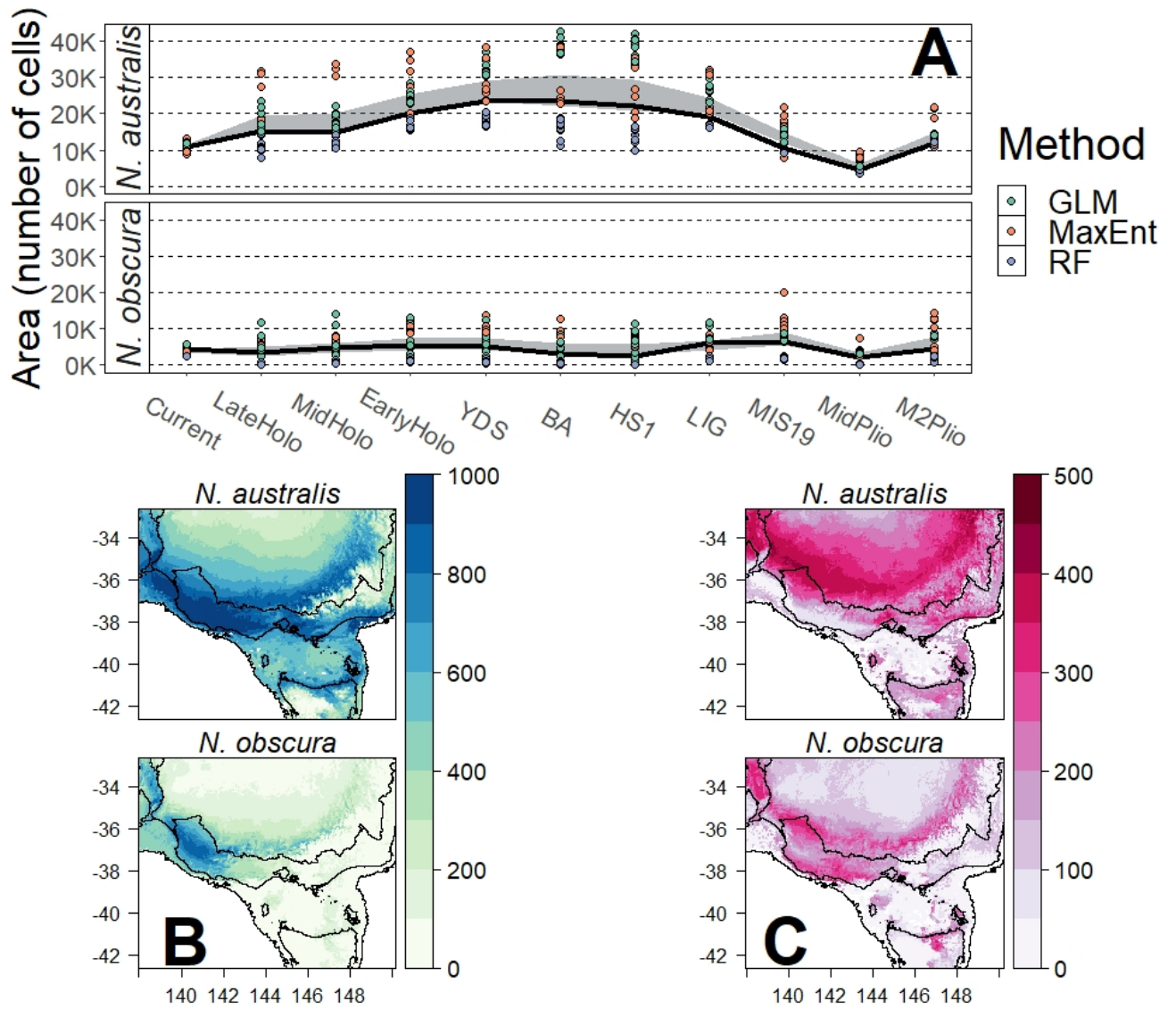
827 **Figure 3**



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829

830 **Figure 4**



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