Title: The effects of weather variability on patterns of genetic diversity

Running title: Weather variability affects genetic diversity

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Abstract

Short-term, localised climatic variations can rapidly alter species' geographic ranges and population sizes, but little is known about how they affect genetic diversity. We investigated the relationship between weather and range-wide genetic diversity in a marsupial, *Bettongia gaimardi*, using dynamic species distribution models (SDMs). Genetic diversity was lower in parts of the range where the SDM predicted high variability in suitable weather conditions over the period 1950–2009. This is likely an effect of lower population sizes and extinction-recolonisation cycles in places with highly variable weather. Spatial variation in genetic diversity was better predicted by variability in weather than by long-term climate averages. Our results illustrate the importance of weather in driving population dynamics and species distributions on decadal time-scales and thereby affecting genetic diversity. Modelling the links between changing weather patterns, species distributions and genetic diversity will allow researchers to better forecast biological impacts of climate change.

Introduction

Genetic diversity plays a crucial role in allowing species to persist under, and adapt to, future climate change (Pauls *et al.* 2013). In turn, climatic conditions can have large effects on the magnitude and spatial distribution of genetic diversity within species, which often reflect fluctuations in the geographic ranges of species over long periods of time. For example, during the Quaternary ice ages many taxa experienced cycles of contraction to refugia (areas with stable and favourable environmental conditions), followed by expansion during warmer periods, resulting in genetic signatures of greater diversity in refugial areas, and lower diversity in areas of recolonisation (Hewitt 1996, 2000). Although these effects of long-term, historical climate on genetic diversity are well documented across many taxa, we know much less about the effects of short-term weather, defined here as climatic variables over periods of several months to several years, on genetic diversity. Developing better models of the relationship between weather and genetic variation will be critical for predicting species responses to rapidly changing weather regimes and mitigating genetic losses in the near future.

Climate change is having substantial effects on not just mean conditions but variability in weather, with increases in extreme climatic events and associated impacts observed globally (IPCC 2014), and changes in inter-annual variability of rainfall in Tasmania since 1975 (Grose *et al.* 2010). Weather variability, as well as changes to mean weather conditions, may have an important influence on genetic diversity. For example, Cobben *et al.* (2011) simulated the effect of three different scenarios of temperature increase on neutral genetic diversity in a species with moderate dispersal abilities. Although loss of genetic diversity occurred under all

66 scenarios of temperature increase, scenarios with higher weather variability had
67 greater losses of individuals and genetic diversity. In addition, high weather
68 variability appeared to prevent full occupation of habitat even at times of optimal
69 weather, leading to greater genetic drift and thus reduced genetic diversity (Cobben
70 *et al.* 2011). Weather fluctuations can affect genetic diversity very rapidly, depending
71 on the generation times and adaptive capacity of species. For instance, experimental
72 increases in the intra-annual variability of precipitation caused significant loss of
73 genetic diversity in a prairie grass species over a 10-year period (Avolio *et al.* 2013).
74 The predictability of weather variation may also have important consequences for
75 adaptation and evolutionary potential. Variation in offspring size differs between
76 sticklebacks undergoing a regime of predictable temperature variation and those
77 under a stochastic variation regime, suggesting different resource allocation
78 strategies are being triggered by different regimes (Shama 2017).

79 Species distribution models (SDMs, also called ecological niche models) can provide
80 a useful tool for predicting the relationship between weather and species occurrence
81 (Reside *et al.* 2010; Bateman *et al.* 2012b; Fancourt *et al.* 2015; Bateman *et al.*
82 2016), and hence may be useful for modelling genetic diversity in weather-sensitive
83 species. SDMs have typically used long-term (e.g., 30- or 50-year) means of climatic
84 variables as predictors of distribution, providing a static representation of geographic
85 distribution (Elith *et al.* 2006). However, short-term weather variables, such as
86 average temperature or precipitation values in the 1 – 3 years preceding a species
87 record (Bateman *et al.* 2012b; Fancourt *et al.* 2015), or seasonal measures (Bennie
88 *et al.* 2013; Hereford *et al.* 2017), can also be used to make SDMs. These dynamic,
89 weather-based SDMs can better account for temporal variation and extreme weather
90 events that affect the persistence and abundance of species over shorter time-scales

than long-term climatic models (Bateman *et al.* 2012b). By modelling the relationship between occurrence records of a species and temporally-matched weather variables, and then projecting the SDM over consecutive time periods, average weather suitability over time can be calculated across the species' range (Fancourt *et al.* 2015; Bateman *et al.* 2016). Temporal variance in suitability can also be calculated, allowing identification of areas where weather suitability has fluctuated over time, and, conversely, areas that have always been suitable. Weather-based SDMs have been shown to be useful for defining species distributions (Bateman *et al.* 2012b; Bateman *et al.* 2016), characterising and predicting short-term fluctuations in abundance over time (Fancourt *et al.* 2015), and predicting range shifts (Bennie *et al.* 2013; Hereford *et al.* 2017). As genetic diversity can be influenced by all of these processes, weather-based SDMs may provide insight into changes in genetic variation across space and time.

In this study, we create a weather-based SDM for a threatened, weather-sensitive marsupial, *Bettongia gaimardi* (the eastern bettong), and test the ability of both mean weather suitability and variation in weather suitability since 1950 to predict population genetic diversity across the species' range. To distinguish the effects of weather from the signature of longer-term climatic niche, we also test the relationship between genetic diversity and climate suitability, modelled using an SDM created from 30-year climatic means. We demonstrate a strong negative relationship between genetic diversity of local populations, and the degree of variability of weather experienced by those populations, along with a smaller influence of mean weather suitability. We also show that population genetic diversity in this species is much better predicted by the pattern of weather suitability than by long-term climate suitability.

Methods

Study species

Bettongia gaimardi is a small (around 1.8 kg) marsupial that currently occurs only on the 68,000 km^2 island of Tasmania, off the southern coast of continental Australia. The species became extinct in southeastern mainland Australia early in the 20^{th} century. *B. gaimardi* occurs in dry, open woodlands and forests in the eastern half of the island. Its primary food source is 'truffles' (i.e., the hypogeous sporocarps formed by ectomycorrhizal fungi) associated with the roots of many species of native flora, although other food sources such as fruit and leaves may also be eaten when truffle production is reduced (Johnson 1994b). As the availability of truffles is linked to weather patterns, particularly seasonal rainfall (Beaton *et al.* 1985), we expect the abundance and distribution of *B. gaimardi* to be sensitive to weather. In another closely-related, fungivorous species, *Bettongia tropica*, weather models have proven useful for identifying habitat suitability and range edges (Bateman *et al.* 2012a; Bateman *et al.* 2012b).

Genetic sample collection

Ear biopsies were collected from 188 live-trapped or road-killed *B. gaimardi* individuals at 17 sites across Tasmania in 2006-2007 and 2015-2017 (Figure 1). Collections were made under the approval of the University of Tasmania Animal Ethics Committee (permits A14586 and A14879) and the Department of Primary Industries, Parks, Water and Environment Animal Ethics Committee (permit 9/2006-08). Numbers of animals sampled at each site are given in Figure 1. We genotyped individuals using a reduced representation sequencing technique, DArTseq™ [Diversity Arrays Technology (DArT PLD), Canberra], and obtained 2,748 single

nucleotide polymorphism (SNP) markers after filtering. DArTseq™ is a proprietary complexity reduction technique using restriction enzymes targeting low copy regions of the genome, in combination with next-generation sequencing (Kilian *et al.* 2012; Cruz *et al.* 2013; Melville *et al.* 2017), and is increasingly being used to generate datasets for population genomic and phylogeographic studies (Grewe *et al.* 2015; Feutry *et al.* 2017; Melville *et al.* 2017; Martin *et al.* 2019). We also sequenced a ~350 bp section of the mitochondrial DNA control region for each individual. Laboratory protocols and SNP filtering methods are provided in Appendix S1 in the Supporting Information.

Characterising genetic diversity and structure

We calculated three different metrics of population genetic diversity. We used the package *diversity* (Keenan *et al.* 2013) in the R statistical environment (R Core Team 2017) to calculate allelic richness (AR) and expected heterozygosity (He), averaged across all SNP loci. AR was rarefied to take into account sample size (El Mousadik & Petit 1996), and He has been found to be robust to sample size when a large number of loci are used (Gorman & Renzi 1979). Allelic richness reflects the long-term evolutionary potential of a population, and is more sensitive to the loss of genetic variation in small populations than heterozygosity, and so the two measures are complementary (Allendorf *et al.* 2012). We also calculated haplotype diversity (*h*) from the mtDNA data, which is the equivalent of expected heterozygosity for haploid data, using Arlequin (Excoffier & Lischer 2010).

Populations experiencing high levels of gene flow will exhibit similar levels of genetic diversity, and would thus not provide effectively independent data points for investigation. For this reason, we quantified pairwise genetic differentiation (F_{ST})

between all populations based on SNP genotypes, using the package *strataG* (Archer *et al.* 2017), in R with 1000 permutations to calculate *p* values. We then controlled for false discovery rate in the *p* values using the Benjamini-Yekutieli correction (Benjamini & Yekutieli 2001). All populations were significantly differentiated from each other (F_{ST} ranged from 0.035 – 0.370, *p* values 0.045 – 0.009), suggesting that they could be treated as independent samples of genetic diversity.

Weather and climate models

Records of *B. gaimardi* across Tasmania were collated from published sources, and from mammal spotlighting surveys conducted in Tasmania by the Tasmanian Department of Primary Industries, Parks, Water and Environment (DPIPWE). Records spanned the years 1961 – 2009. We did not include duplicate samples from the same locality in the climate model, or samples from the same locality and time period in the weather model. This resulted in a total of 773 records that were included in the climate model, and 1043 in the weather model.

For the climate suitability model, climate variables based on long-term climate means (1961–1990) were derived from ANUCLIM 5.1 (Houlder *et al.* 2000), using monthly averages and an 80 m digital elevation model re-sampled from ~250 m (GEODATA 9 second DEM ver. 2; Geoscience Australia, www.ga.gov.au). The variables included in the climate model were mean annual temperature (°C), temperature seasonality, maximum temperature of warmest period (°C), minimum temperature of coldest period (°C), annual precipitation (mm), precipitation of wettest quarter (mm), precipitation of driest quarter (mm) and precipitation seasonality. We used MaxEnt 3.3.2 (Phillips *et al.* 2006) with default settings (with the exception of

188 using all features except threshold) to develop a climate-based model of *B. gaimardi*
189 distribution, using 10,000 background points selected at random from a 50 km buffer
190 around the occurrence points. MaxEnt was selected because it performs well
191 compared to other individual methods for presence-only species distribution
192 modelling (Elith *et al.* 2006) and avoids the added complexity of ensemble-based
193 approaches, which may substantially influence predictive performance(Hao *et al.*
194 2019). This method has been demonstrated to work well for creating weather- and
195 climate-based SDMs in a closely-related species (Bateman *et al.* 2012b), and within
196 the Tasmanian landscape (Fancourt *et al.* 2015).

197 The weather models were created following the methodology of Bateman *et al.*
198 (2012b). Records of daily temperature maxima, minima and means and precipitation
199 were accessed from the Australian Water Availability Project (AWAP) (Raupach *et*
200 *al.* 2009). Daily weather data were aggregated into 14 variables: the mean,
201 minimum, maximum and standard deviation (seasonality) of monthly temperatures
202 and the sum and coefficient of variation (seasonality) of precipitation for periods of
203 both 6 and 12 months prior to each occurrence record, and the sum of precipitation
204 for the wettest and driest quarters for the 12 months prior to the occurrence record.
205 Given a generation time of about 3 years in *B. gaimardi* (Burbidge *et al.* 2016), this
206 was chosen as an appropriate amount of time to allow for lags between weather
207 conditions and population response (Bateman *et al.* 2012b). We developed a model
208 using MaxEnt with 100,000 background points that were selected from across
209 Tasmania in proportion to the spatial and temporal biases in the occurrence data.
210 We then used MaxEnt to project weather suitability for *B. gaimardi*, based on this
211 model, at monthly intervals from 1950 – 2009, in each grid cell across Tasmania.

212 Based on all of the monthly model projections, we calculated the mean and standard
213 deviation of weather suitability in each cell in the period 1950 – 2009.

214 For both the weather and climate models, we used 10-fold cross validation and the
215 “Area Under the operating Curve” (AUC) criterion to test how transferable the
216 weather- and climate-based models were in time and space, and the training AUC to
217 test how well each model represented the current distribution of *B. gaimardi*.

218 *Testing ability of models to predict genetic diversity*

219 We calculated the centroid of each sampling site in ArcGIS 10.5 by fitting a minimum
220 convex polygon to the trapping location of individuals in that site. The areas of these
221 mean convex polygons ranged from 0.007 km^2 – 6.24 km^2. The centroid of each
222 polygon was then calculated using the feature to point tool. We then extracted mean
223 values of the climate and weather variables for the site within a 5 km-radius buffer
224 around the centroid from the rasters of climate suitability, mean weather suitability
225 and standard deviation of weather suitability in R.

226 We built linear models to examine the ability of weather and climate to explain
227 genetic diversity. We controlled for the effects of sampling year by including this as a
228 variable in all models, including the null, to account for differences in conditions
229 between years and the fact that the age and associated DNA degradation of a
230 sample can affect the genetic diversity detected (Schultz *et al.* 2018). We built
231 models with year plus each of the weather and climate variables individually, and
232 then built two combined models. The first combined model contained year and both
233 weather variables, and the second contained all variables. The absolute pairwise
234 correlations among the weather and climate variables were all less than 0.7, so we

were not concerned about multicollinearity when including these variables in the same models.

Because the effect of environmental variables on animal behaviour and genetic variation can vary with spatial scale (Anderson *et al.* 2010; McGarigal *et al.* 2016), we repeated the above regressions using mean climate and weather suitability values within larger (10 km-radius) and smaller (2 km-radius) buffers around the centroid of each site. There was no significant relationship between sample size and genetic diversity that could potentially bias our conclusions (He: Pearson's r = -0.03, p = 0.91; AR: Pearson's r = -0.04, p = 0.88; h: Pearson's r = -0.08, p = 0.77).

Results

Using 2,748 putatively neutral SNP makers, we found that expected heterozygosity (He) in 188 individuals across 17 sampled populations, averaged across all SNP loci, ranged from 0.18 – 0.30, and allelic richness (AR) ranged from 1.41 – 1.70. Thirteen mitochondrial DNA haplotypes were identified among the sampled individuals. The number of mitochondrial DNA haplotypes found at each population ranged from 1 – 3, and haplotype diversity (h) ranged from 0.00 to 0.73.

Both the weather-based and the climate-based SDMs provided meaningful predictions of *B. gaimardi* distribution (weather model: mean training AUC = 0.815, mean testing AUC ± s.d. = 0.795 ± 0.013; climate model: training AUC = 0.783, testing AUC = 0.701 ± 0.021). In the weather model, high probability of presence was associated with moderate annual precipitation (~ 500mm), minimum temperature of the coldest month between -2 and 4°C, high temperature seasonality and low precipitation in the driest quarter (~25 – 100mm), all measured in the 12 months preceding a record (Table S2.1). In the climate model, high probability of

presence was associated with low precipitation in the driest and wettest quarters, high maximum temperature of the warmest month (> 20°C), and low precipitation seasonality (Table S2.2).

Mean weather suitability was highest in the eastern half of Tasmania, where the climate is relatively dry and warm, corresponding with the known range of *B. gaimardi* (Figure 1a). Weather suitability was most variable on the northern and eastern coasts and in far south-eastern Tasmania (Figure 1b). There was an inverse relationship between mean weather suitability and weather variability at the genetic sampling sites (Pearson's $r = 0.69$, $p = 0.002$). Climate suitability was also highest in the eastern half of Tasmania (Figure S2.1), but there was no significant correlation between climate suitability and either mean weather suitability (Pearson's $r = 0.19$, $p = 0.45$) or weather variability at the sampling sites (Pearson's $r = -0.43$, $p = 0.08$).

Each of the three measures of genetic diversity was best predicted by models that included standard deviation of weather suitability and sampling year. Weather (s.d.) was significant in each of these models (Table 1). For He and AR, this model had high adjusted R^2 values (He = 0.463, AR = 0.527). For all genetic metrics, the model containing climate suitability and year ranked lowest, below the null model (year only). For He and AR, the models containing year and mean weather suitability, and year and both weather variables, were also within the top model set ($\Delta AIC = 2$). Adjusted R^2 values were substantially lower for haplotype diversity than for the other two measures (Table 1).

All three measures of genetic diversity decreased as the standard deviation of weather suitability increased (Table 1, Figure 2). In most models, greater mean weather suitability was associated with greater genetic diversity, although this

283 variable was not significant in any model (Table 1, Figure 2). There was a slight
284 negative relationship between climate suitability and genetic diversity across all
285 models, but climate was also not significant in any model (Table 1, Figure 2). The
286 null model containing just sampling year was significant for AR and He, but not for *h*.

287 When the regressions were repeated using weather and climate variables calculated
288 within larger and small buffers (10 km and 2 km radii) around each sampling site,
289 there was little difference in the results (Appendix S3). The top-ranked model (year
290 and standard deviation of weather) and the bottom-ranked model (year and climate)
291 were the same across all buffer sizes and genetic metrics. The coefficients and
292 significance of variables were very similar between the 5 km and 10 km scales.
293 However, when weather and climate values were calculated within the smaller 2 km
294 buffer, standard deviation of weather suitability was no longer significant for *h*, and
295 the null model ranked above the full model and the model containing just year and
296 mean weather suitability for *h* (Appendix S3).

297 Discussion

298 *Biological and conservation implications of links between weather and genetic*
299 *diversity*

300 The most likely mechanism by which weather could affect populations of *B. gaimardi*
301 is by controlling the availability of their main food source, 'truffles' (the fruiting bodies
302 of ectomycorrhizal fungi). Truffle abundance is strongly influenced by rainfall, soil
303 moisture and temperature (Johnson 1994a; Bateman *et al.* 2012a), and is positively
304 related to measures of fitness in *B. gaimardi*, such as body condition and growth rate
305 of pouch young (Johnson 1994b), as well as to their population density (Taylor
306 1993a). In the closely-related species *Bettongia tropica* the effects of weather

conditions on truffle densities may explain lower abundance of the species and reduced competitive advantage at its southern range edge (Bateman *et al.* 2012a).

In areas with more variation in weather suitability over time, we found that population genetic diversity in *B. gaimardi* was lower. In these areas, conditions may periodically become unsuitable for *B. gaimardi* due to insufficient truffle production, leading to periods of very low population density, and possibly local extinctions and recolonisations over time. Small population sizes can lead to loss of alleles due to genetic drift, and reductions in heterozygosity due to inbreeding (Allendorf *et al.* 2012). Additionally, if local extinction-recolonisation cycles occur due to weather variability, this is likely to lead to founder effects and bottlenecks causing changes in allele frequencies and the rapid loss of genetic diversity relative to source populations (Cobben *et al.* 2011; Allendorf *et al.* 2012). During recolonisation, the leading edges of expanding populations may also have reduced genetic diversity due to selective pressure on alleles that are linked to neutral diversity (selective sweeps; Smith & Haigh 1974) or the stochastic effects of genetic drift (allele surfing; Excoffier *et al.* 2009). In combination, these effects are likely to lead to much lower population genetic diversity in areas that have experienced substantial variation in their suitability due to weather fluctuations over time. Although mean weather suitability was not significant in any model, it also seemed to have some influence on genetic diversity in *B. gaimardi*, as it appeared in models that were within the top model set for all markers. In areas of lower mean weather suitability, we would expect generally lower availability of truffles. This would reduce ecological carrying capacity and lead to smaller population sizes, and hence lower genetic diversity, than in areas of high mean suitability.

It is important to note that high average weather suitability need not always be associated with increased genetic diversity. Depending on life-history traits, demography and other environmental factors, species and populations may respond in different ways, or with different magnitudes, to fluctuations in weather. The interaction between weather suitability and other environmental conditions, such as fire regimes (Banks *et al.* 2017), can have large effects on genetic diversity. In addition, density-dependent dispersal may lead to movement of individuals from more stable areas with higher-density populations into areas of lower suitability (Matthysen 2005), which could ultimately lead to greater genetic diversity in these areas if migrants arrive from genetically divergent sources. For conservation planning, it is thus critical to consider the effects of weather suitability in conjunction with anthropogenic and natural stressors and demographic factors that influence or threaten the species. In the case of *B. gaimardi*, the amount and quality of the species' habitat (open dry sclerophyll forest and woodland) has a substantial effect on the carrying capacity of an area (Gardiner *et al.* 2018). In particular, habitat loss in areas with high average weather suitability may reduce their carrying capacity and connectivity with other areas, causing losses of diversity.

For species where a positive relationship has been demonstrated between genetic diversity and weather suitability, areas that maintain high weather suitability with little fluctuation over time may act as refugia under climate change. Conservation strategies should thus give high priority to maintaining and protecting populations in these areas by protecting and restoring core habitat, and improving connectivity between these regions and more marginal sites.

Modelling the relationship between genetic variation and weather

This study demonstrated for the first time the potential for weather metrics derived from SDMs (particularly variation in suitability over time) to predict genetic diversity across a species' range. To date, the use of climate models as predictors of genetic diversity has largely focused on using SDMs based on contemporary and historical climate means (such as during the Last Glacial Maximum) to examine the effects of historical and current suitability and distributional shifts on genetic variation (Knowles & Alvarado-Serrano 2010; Gugger *et al.* 2013; He *et al.* 2013; Jezkova *et al.* 2015; Lanier *et al.* 2015; Paz *et al.* 2019). We have showed that dynamic, weather-based SDMs were much better predictors of both mitochondrial genetic diversity and genome-wide SNP diversity in *B. gaimardi* than were static models of contemporary climate. This is consistent with observations that models based on long-term climate means can also underestimate the distributional and demographic impacts of climate change on species, by failing to identify areas of marginal habitat with frequent periods of unfavourable weather (Reside *et al.* 2010; Bateman *et al.* 2012b).

Species distributions and population dynamics are affected by short-term weather patterns in a wide range of taxa, such as butterflies (Bennie *et al.* 2013), plants (Hereford *et al.* 2017), carnivorous marsupials (Fancourt *et al.* 2015), and migratory bird species (Bateman *et al.* 2016), and hence weather may also be a good predictor of genetic diversity in these groups. However, life history traits can moderate the effects of climatic and weather variables on local colonisation and extinction dynamics (White *et al.* 2018) and species distributions (Bateman *et al.* 2016). Thus, to determine the broader utility of weather-based SDMs for predicting genetic diversity, and to further investigate the relationship between genetic diversity and

short-term weather patterns, similar studies to ours should be conducted on a phylogenetically-diverse range of species with varying life history traits.

The observed relationship between genetic variation and weather suitability, as with other environmental variables, is likely to depend strongly on the spatial scales at which studies take place (Anderson *et al.* 2010). We tested the relationship between weather and genetic diversity at three different scales, and found that variation in weather suitability within all buffer sizes (2 km, 5 km or 10 km radius; ~ 13 km^2 ~ 79 km^2 and ~314 km^2) was a good predictor of genetic diversity. These scales are all substantially larger than both the average monthly home ranges of *B. gaimardi* (0.61 km^2) in agricultural regions of Tasmania (Taylor 1993b), and the minimum convex polygons fitted to the trapping locations of all individuals at each site (0.007 km^2 – 6.24 km^2). This suggests that weather suitability interacts with demographic and genetic processes occurring at the broader population or meta-population scale. Thus, it will be important for future studies to consider the appropriate spatial scale for the calculation of SDMs and the extraction of weather suitability values for a population, and it may be advisable to test multiple spatial scales.

Future applications: predicting genetic losses under climate change

Understanding and predicting the impacts of global climate change on genetic diversity will be critical for conserving species and biodiversity (Pfenninger *et al.* 2012; Pauls *et al.* 2013). Selective pressures induced by climate change may trigger micro-evolutionary responses, and the ability of species to survive will be influenced by their generation time and adaptive capacity relative to the rate and magnitude of change in climatic means and variability (Pauls *et al.* 2013). In this study, we identified very few putatively adaptive SNP loci through outlier analysis (Appendix

S1), and so, for clarity, we have only examined the relationship between weather and putatively neutral genetic diversity. However, a valuable extension of this work will be to examine the relationship between adaptive genetic diversity within populations and weather suitability and variability.

Species distribution modelling has been previously proposed as a tool to project losses of genetic diversity due to local extinctions and range shifts under climate change (Pfenninger *et al.* 2012). In contrast to the climate-based SDMs commonly employed, weather-based SDMs can take into account trends and variability over time-scales more relevant to organism lifespans and generation times (Bateman *et al.* 2012b), and thus provide potentially more accurate modelling of genetic diversity for weather-sensitive species. These models offer a promising new approach to predicting where losses of diversity may occur in response to changing weather conditions in the near future and identifying potential climate change refugia, facilitating longer-term conservation planning and assessments of species' genetic risk.

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Tables

Table 1. Weather and climate models for each of the three genetic diversity metrics. Models are ranked on AIC. * = significant values ($P < 0.05$). Degrees of freedom: [a]=14; [b]=13, [c]=12, [d]=15

Diversity metric	Model	Parameter estimate	S.E.	*t*	*P*	R^2 adj.	ΔAIC
Expected hetero-zygosity (SNP)	Year +	0.019	0.013	1.396 [a]	0.184	0.463	0.00
	Weather (s.d.)	-0.603	0.252	-2.391 [a]	0.031 *		
	Year +	0.033	0.012	2.716 [a]	0.017 *	0.407	1.70
	Weather (mean)	0.200	0.102	1.961 [a]	0.070		
	Year +	0.021	0.015	1.413 [b]	0.181	0.430	1.77
	Weather (mean) +	0.063	0.149	0.422 [b]	0.680		
	Weather (s.d.)	-0.483	0.386	-1.249 [b]	0.234		
	Year +	0.024	0.015	1.542 [c]	0.149	0.415	2.83
	Weather (mean) +	0.053	0.151	0.354 [c]	0.729		
	Weather (s.d.) +	-0.561	0.403	-1.393 [c]	0.189		
	Climate	-0.084	0.101	-0.826 [c]	0.425		
	Year	0.036	0.013	2.770 [d]	0.014 *	0.294	3.82
	Year +	0.037	0.015	2.497 [a]	0.026 *	0.246	5.78
	Climate	-0.021	0.110	-0.186 [a]	0.855		
Allelic Richness (SNP)	Year +	0.058	0.030	1.907 [a]	0.077	0.527	0.00
	Weather (s.d.)	-1.359	0.572	-2.374 [a]	0.032 *		
	Year +	0.089	0.027	3.290 [a]	0.005 *	0.482	1.54
	Weather (mean)	0.457	0.230	1.983 [a]	0.067		

	Year +	0.064	0.034	1.889 [b]	0.081		
	Weather (mean) +	0.155	0.337	0.461 [b]	0.652	0.499	1.73
	Weather (s.d.)	-1.060	0.875	-1.211 [b]	0.247		
	Year +	0.072	0.035	2.070 [c]	0.061		
	Weather (mean) +	0.130	0.337	0.385 [c]	0.707		
	Weather (s.d.) +	-1.277	0.899	-1.420 [c]	0.181	0.501	2.30
	Climate	-0.232	0.226	-1.026 [c]	0.325		
	Year	0.097	0.029	3.295 [d]	0.005 *	0.381	3.75
	Year +	0.102	0.033	3.036 [a]	0.009 *		
	Climate	-0.087	0.249	-0.350 [a]	0.731	0.343	5.60
Haplotype diversity (mtDNA)	Year +	-0.128	0.113	-1.136 [a]	0.275		
	Weather (s.d.)	-4.995	2.124	-2.352 [a]	0.034 *	0.182	0.00
	Year +	-0.095	0.126	-0.758 [c]	0.463		
	Weather (mean) +	-0.231	1.224	-0.189 [c]	0.853		
	Weather (s.d.) +	-6.243	3.265	-1.912 [c]	0.080	0.173	1.57
	Climate	-1.112	0.821	-1.355 [c]	0.200		
	Year +	-0.132	0.126	-1.045 [b]	0.315		
	Weather (mean) +	-0.109	1.259	-0.086 [b]	0.932	0.119	1.99
	Weather (s.d.)	-5.204	3.274	-1.590 [b]	0.136		
	Year +	-0.008	0.105	-0.080 [a]	0.938		
	Weather (mean)	1.371	0.892	1.537 [a]	0.147	0.023	3.01
	Year	0.014	0.108	0.131 [d]	0.897	-0.065	3.66
	Year +	0.045	0.123	0.366 [a]	0.720		
	Climate	-0.530	0.916	-0.579 [a]	0.572	-0.115	5.26

Figures

Figure 1:

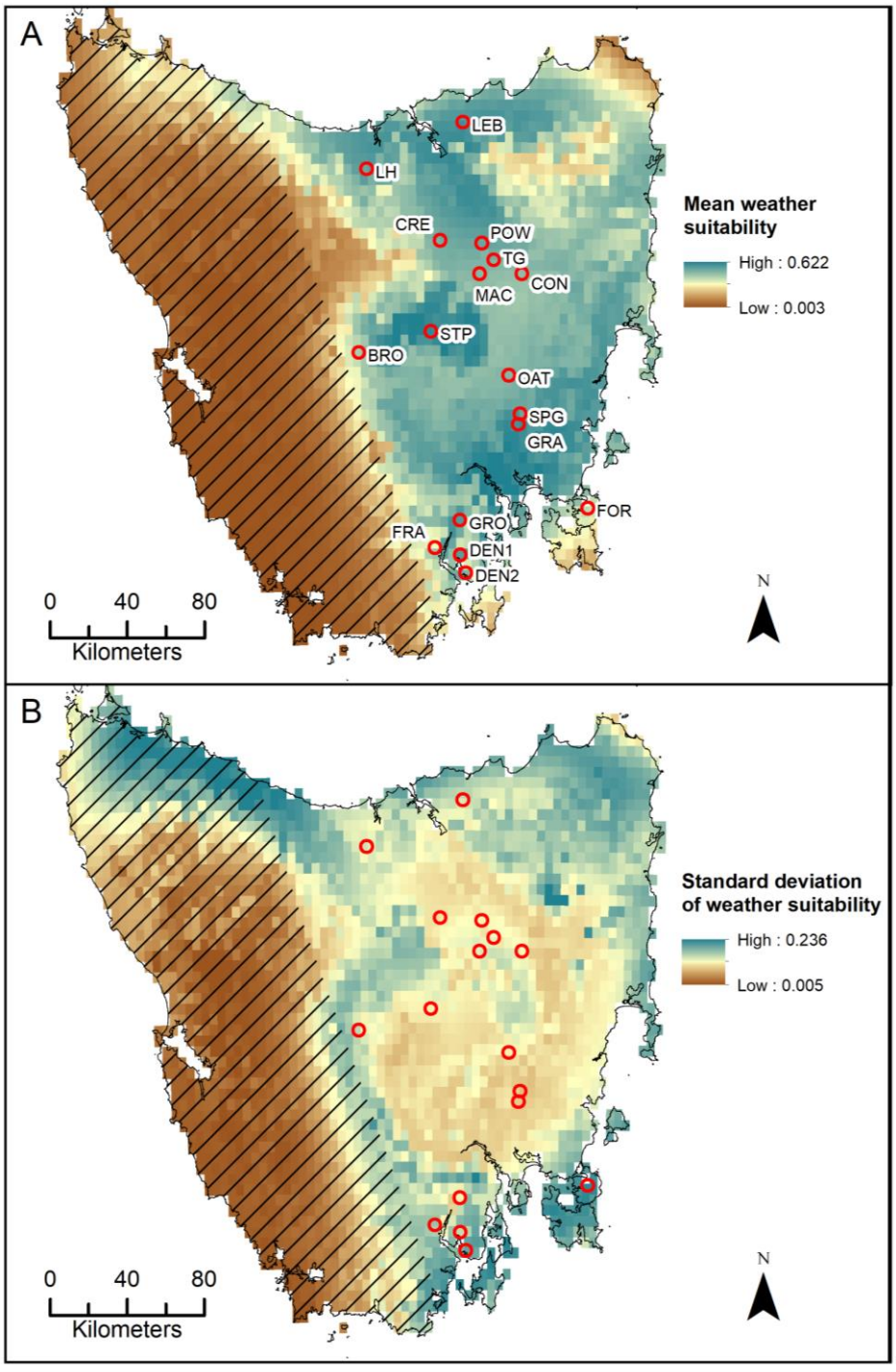
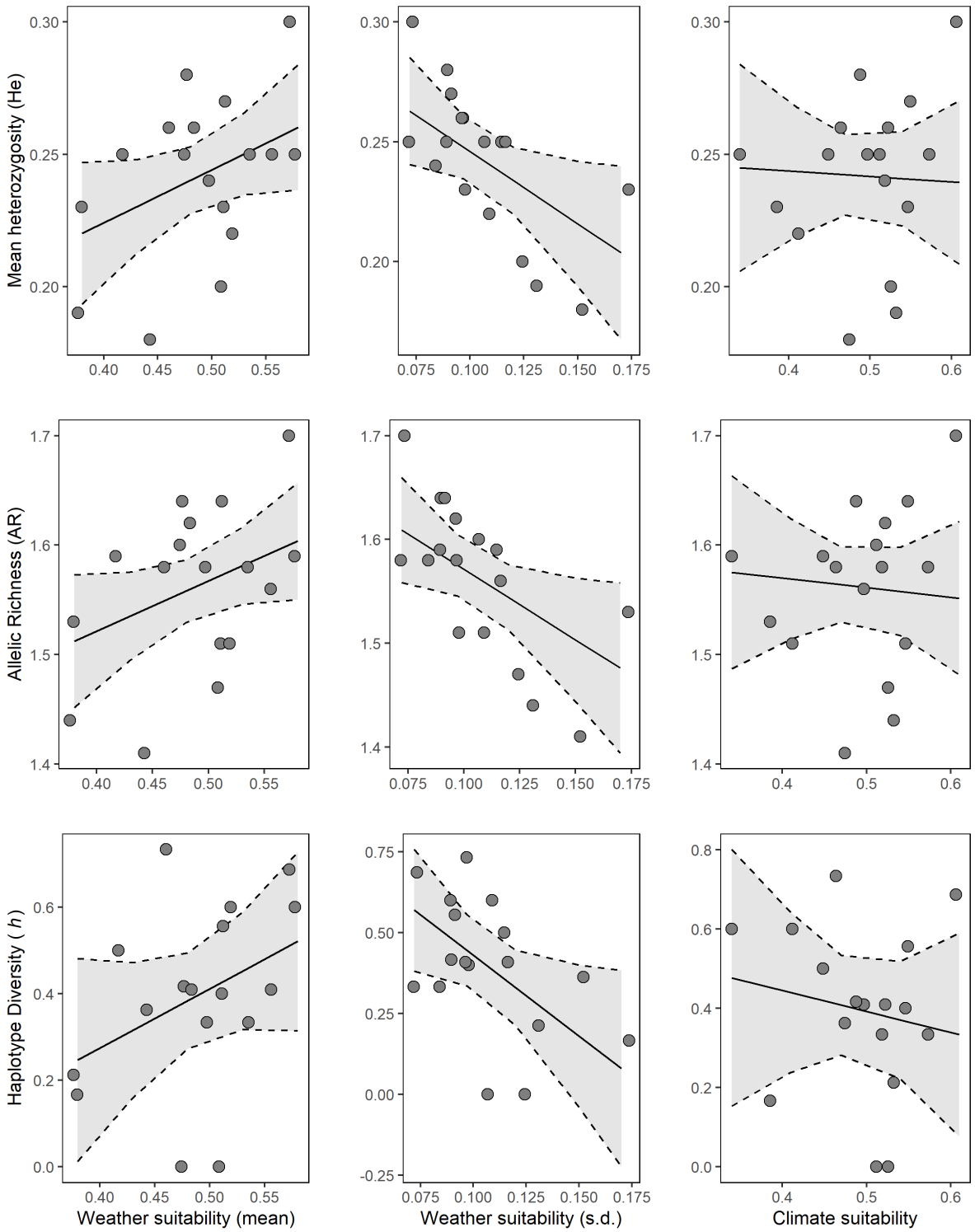


Figure 2:


Mean heterozygosity (He)
Allelic Richness (AR)
Haplotype Diversity (h)
Weather suitability (mean)
Weather suitability (s.d.)
Climate suitability

Legends:

Figure 1. Mean (A) and variability (B) of weather suitability for *Bettongia gaimardi*, based on monthly projections from 1950 – 2009. Cross hatching shows areas of the island that are outside the approximate known range of *B. gaimardi*. Locations of *Bettongia gaimardi* genetic sampling sites are indicated by red circles, and site names are shown in (A). Genetic sample sizes are: BRO = 4, CON = 6, CRE = 6, DEN1 = 7, DEN2 = 16, FOR = 12, FRA = 26, GRA = 26, GRO = 5, LEB = 19, LH = 5, MAC = 13, OAT = 9, POW = 9, SPG = 7, STP = 6, TG = 12.

Figure 2. Marginal effects of mean weather suitability, standard deviation of weather suitability (i.e., variability) and climate suitability for the three genetic diversity metrics, from the regressions containing that variable + year. Dashed lines show 95% confidence intervals. Grey points indicate actual values of sampled populations.