

Thermoregulatory traits combine with range shifts to alter the future of montane ant assemblages

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1 **ABSTRACT**

2 Predicting and understanding the biological response to future climate change is a pressing
3 challenge for humanity. In the 21st century, many species will move into higher latitudes and
4 higher elevations as the climate warms. In addition, the relative abundances of species within
5 local assemblages is likely to change. Both effects have implications for how ecosystems
6 function. Few biodiversity forecasts, however, take account of both shifting ranges and
7 changing abundances. We provide a novel analysis predicting the potential changes to
8 assemblage level relative abundances in the 21st century. We use an established relationship
9 linking ant abundance and their colour and size traits to temperature and UV-B to predict
10 future abundance changes. We also predict future temperature driven range shifts and use
11 these to alter the available species pool for our trait-mediated abundance predictions. We do
12 this across three continents under a low greenhouse gas emissions scenario (RCP2.6) and a
13 business-as-usual scenario (RCP8.5). Under RCP2.6, predicted changes to ant assemblages
14 by 2100 are moderate. On average, species richness will increase by 26%, while species
15 composition and relative abundance structure will be 26% and 30% different, respectively,
16 compared with modern assemblages. Under RCP8.5, however, highland assemblages face
17 almost a tripling of species richness and compositional and relative abundance changes of
18 66% and 77%. Critically, we predict that future assemblages could be reorganised in terms of
19 which species are common and which are rare: future highland assemblages will not simply
20 comprise upslope shifts of modern lowland assemblages. These forecasts reveal the potential
21 for radical change to montane ant assemblages by the end of the 21st century if temperature
22 increases continue. Our results highlight the importance of incorporating trait-environment
23 relationships into future biodiversity predictions. Looking forward, the major challenge is to
24 understand how ecosystem processes will respond to compositional and relative abundance
25 changes.

26 INTRODUCTION

27 Climate change has significant implications for human prosperity and the biodiversity on
28 which it depends (IPCC, 2014; Pecl *et al.*, 2017). As a result, generating predictions of the
29 state of biodiversity following climate change is now a major goal for ecologists and
30 environmental scientists (Urban, 2015). The most frequently reported and predicted changes
31 are large-scale species range shifts. As the climate warms, species move to remain within
32 their environmental niche. This leads to dramatic shifts of species away from the equator and
33 the lowlands, and into high latitude and high elevation areas as global temperature regimes
34 change (Parmesan & Yohe, 2003; Parmesan, 2006; Chen *et al.*, 2011; Poloczanska *et al.*,
35 2013; Warren & Chick, 2013). These range shifts can result in increased extinction risk for
36 individual species (Erasmus *et al.*, 2002; Visser & Both, 2005; Urban, 2015; Pecl *et al.*,
37 2017) and could have large consequences for ecosystem functioning and stability as
38 assemblages of species are reorganised (Walther, 2010).

39 Changes to species distributions, however, are only one manifestation of a suite of ecological
40 changes that are expected to result from 21st century climate change. These include
41 alterations to demography, and to the absolute and relative abundances of individuals within
42 their geographic ranges (Johnston *et al.*, 2013; Crase *et al.*, 2015; Gaüzère *et al.*, 2015;
43 Tayleur *et al.*, 2016; Bowler *et al.*, 2017). Understanding and predicting this small-scale
44 assemblage level response to climate change has been repeatedly highlighted as a key, but
45 often neglected, component of our ecological forecasting toolbox (Suding *et al.*, 2008;
46 Walther, 2010; Urban *et al.*, 2016). This matters because an assemblage where a single
47 species makes up 90% of the individuals, for example, and an assemblage where all species
48 are represented equally will look and function very differently (Walther, 2010). Indeed,
49 several studies of ecosystem functioning have shown how changes in the relative abundances
50 or occurrences of one or more taxa can lead to large changes in the rates and modes of

51 function delivery (Slade *et al.*, 2007; Manning *et al.*, 2016; Griffiths *et al.*, 2018; Ashton *et*
52 *al.*, 2019).

53 Despite the importance of both niche-based range shifts (i.e. species occurrence) and
54 assemblage-level abundance changes in determining the future state of biodiversity following
55 climate change, these two factors are rarely investigated in combination (but see Dullinger *et*
56 *al.*, 2012). Many studies use species distribution modelling techniques to project future
57 species ranges (Guisan & Thuiller, 2005; Colwell *et al.*, 2008; Urban *et al.*, 2016), and a
58 growing literature is making use of species traits to predict how relative abundance changes
59 may alter assemblages (Shipley *et al.*, 2006; Frenette-Dussault *et al.*, 2013; D'Amen *et al.*,
60 2015). Either large-scale range shifts or abundance-based assemblage changes could lead to
61 species becoming extinct or newly dominant, but there is little explicit understanding of how
62 they may interact with each other.

63 Previously, we found that darker coloured and larger bodied ant species dominate cold
64 environments, such as high elevations and latitudes, while lighter coloured and smaller
65 species tend to dominate in hotter environments (Bishop *et al.*, 2016; Gibb *et al.*, 2018).
66 Darker colours typically enable organisms to heat up faster than if they had light colouration,
67 while larger bodies lose heat more slowly than small bodies (Willmer & Unwin, 1981;
68 Stevenson, 1985; Spicer *et al.*, 2017). This colour trend was reversed in hot environments
69 with high UV-B levels - an effect that we hypothesized was influenced by the role of melanin
70 in defending against harmful UV-B irradiation. The biophysical links between ambient
71 temperature, UV-B, colour and body size that we suspect drive these patterns, however, are
72 unlikely to be specific to ant assemblages. They operate at a range of scales and in a variety
73 of taxa including dragonflies (Zeuss *et al.*, 2014; Pinkert *et al.*, 2017), butterflies (Ellers &
74 Boggs, 2004), beetles (Schweiger & Beierkuhnlein, 2015), birds (Delhey, 2017), plants
75 (Koski & Ashman, 2015) and microorganisms (Cordero *et al.*, 2018).

76 This trait-environment relationship is important because temperature will increase (IPCC,
77 2014), while the direction of change in UV-B irradiance will depend on geographic location
78 and emission levels (Bais *et al.*, 2015; Lamy *et al.*, 2018) in the 21st century. Critically, these
79 environmental changes will act through species traits to favour some species over others.
80 Therefore, relative abundances at the local level will change in accordance with the body size
81 and colouration of species. Several studies predict smaller body sizes (Sheridan & Bickford,
82 2011; Gibb *et al.*, 2018; Tseng *et al.*, 2018) and lighter (Zeuss *et al.*, 2014; Delhey, 2017) or
83 darker (Roulin, 2014) colours for animals as the 21st century progresses.

84 Here, we combine predictions of potential trait-mediated abundance changes with anticipated
85 range shifts to simulate how montane ant communities will respond to climate change. Ants
86 are recognised as a major functional component of terrestrial ecosystems (Evans *et al.*, 2011;
87 Zelikova *et al.*, 2011; Ewers *et al.*, 2015; Parr *et al.*, 2016; Griffiths *et al.*, 2018).

88 Understanding how their diversity and assemblage structure is likely to change will be key to
89 anticipating how entire ecosystems will be altered in the future. Furthermore, the continental
90 scale of our dataset, and the observation of the trait-environment relationships in other taxa,
91 makes for an important first step in understanding the potential impact of this relationship on
92 future species abundances.

93 We forecast potential range shifts for our study species by using a simple climate-envelope
94 model (Colwell *et al.*, 2008) based on projections of future climate and adiabatic lapse rates
95 (the rate at which temperature declines with elevation). We forecast abundance changes by
96 first predicting future assemblage averages of colour and body size and then using a
97 maximum-entropy based model (Shipley *et al.*, 2006) to estimate the most likely distribution
98 of species relative abundances. We simulate future changes under a reduced greenhouse gas
99 emissions scenario (RCP2.6) and an unmitigated baseline scenario (RCP8.5) to provide an
100 upper and lower estimate of possible biodiversity futures.

101 Specifically, we assess the potential for species richness and composition of montane ant
102 assemblages to change throughout the 21st century if we base our predictions on trait-based
103 abundance changes, range shifts or a combination of both. We also ask whether the
104 combination of these two processes predicts the formation of non-analogous assemblages,
105 i.e., assemblages for which there is no contemporary equivalent, in terms of species
106 composition or relative abundance structure (Le Roux & McGeoch, 2008; Keith *et al.*, 2009).

107

108 **METHODS**

109 **Observed data**

110 We sampled epigaeic ant assemblages during the austral summer using pitfall traps on 14
111 elevational transects (108 separate elevational sites) across Africa, Australia and South
112 America. Transects ranged from 0 to 3000 m a.s.l. (Bishop *et al.*, 2016). In Africa and
113 Australia replicate pitfall trapping grids followed the same protocol. In South America, the
114 spatial arrangement, number of traps and size of the traps differed slightly. All traps were
115 placed during the austral summer and were open for 5 days and nights in Africa, and 7 days
116 and nights in the Australia and South America. Further details on trapping materials are
117 found in Appendix S1 and Bishop *et al.* (2016). For each transect, assemblages were pooled
118 at the elevational band level (bands were separated from each other by 100 to 300 vertical
119 metres) for this analysis. For each species, we recorded body size, as measured by Weber's
120 length. Weber's length is defined as the length between the anterodorsal margin of the
121 pronotum and the posterodorsal margin of the propodeum and is a commonly used measure
122 of body size in ants (Brown, 1953). We recorded Weber's length to the nearest 0.01 mm. We
123 recorded colour as a categorical variable using a predetermined set of colours by a limited
124 number of observers. We converted these colours to HSV (hue, saturation and value) values

125 and retained the v (value, or lightness) as a measure of how light or dark in colour a species
126 is. This measure of lightness is bounded by 0 and 1. Values of 0 are dark while values of 1
127 are light. Both traits were recorded from six specimens per species per elevational transect,
128 where possible. Further details can be found in Bishop *et al.* (2016) and in Appendix S1.

129 We calculated assemblage weighted means (AWM) of body size and colour lightness for the
130 ant assemblages using the formula:

$$131 \quad AWM = \sum_{i=1}^S p_i x_i$$

132 Where S is the number of species in an assemblage, p_i is the proportional abundance of each
133 species and x_i is the trait value (lightness or body size) of each species. The difference
134 between this analysis and that in Bishop *et al.* (2016) is that here, replicate assemblages
135 within the same elevational band on the same elevational transect are pooled together to form
136 a single assemblage.

137 We assessed the relationship between each assemblage-weighted trait (colour lightness and
138 body size) and temperature and UV-B irradiance using linear mixed models (LMMs). Current
139 temperature and UV-B data were taken from the climatic surfaces WorldClim 2 (Fick &
140 Hijmans, 2017) and glUV (Beckmann *et al.*, 2014), respectively. We extracted mean
141 temperature and UV-B irradiation for January to March (the austral summer months, when
142 we sampled ants) for each elevational transect and took an average within each elevational
143 band. As temperature and UV-B are correlated, we used the residuals of the relationship as
144 the UV-B variable. We used second order polynomial terms to detect curvature and an
145 interaction between temperature and residual UV-B was included. Assemblage weighted
146 lightness was logit-transformed prior to modelling with a Gaussian distribution. To account
147 for the geographical configuration of our study sites we used a nested random effects

148 structure of transect within mountain range within continent. We centred and scaled all
149 explanatory variables. We used bias corrected Akaike information criterion (AICc) values to
150 compare all possible models. Each of the 108 data points used in these models represents an
151 assemblage of ants from a single elevational band.

152 We tested our dataset for structural bias in the AWMs by randomly shuffling the traits of
153 each species within a given regional pool and refitting the mixed effects models 2000 times
154 (Hawkins *et al.*, 2017). We used the same explanatory variables as selected by the best fitting
155 original models and extracted a marginal R^2 (R^2_m = due to fixed effects only) for both colour
156 and body size for each randomisation. We compared our original R^2_{ms} to the randomly
157 generated R^2_{ms} . For colour and body size, our original R^2_{ms} were in the 1st and 0.99th
158 percentile, respectively (Appendix S2). This means that randomly assigning species names to
159 trait values could not recreate our observed patterns – implying that there is no problem of
160 structural bias in this dataset influencing the trait-environment relationship (Hawkins *et al.*,
161 2017).

162

163 **Future data**

164 We use two different climate change scenarios to make future projections of montane ant
165 biodiversity. We use Representative Concentration Pathway (RCP) 2.6 and RCP8.5. RCP2.6
166 predicts a mean increase in temperature, relative to preindustrial levels of 1°C (range of 0.3-
167 1.7°C) by 2100 while RCP8.5 predicts an increase of 3.7°C (range of 2.6-4.8°C IPCC,
168 2014). If greenhouse gas emissions are in line with the Paris Agreement of 2015, then
169 RCP2.6 is a likely future climate scenario. If not, and emissions continue on their current
170 trajectory, the planet faces the future that RCP8.5 describes (Sanford *et al.*, 2014). We
171 extracted estimates for regional temperature change from the IPCC (2014) for all of our study
172 sites for RCP2.6 and RCP8.5. UV-B irradiance will also change in the 21st century. We use

173 predicted estimates of UV-B change under RCP2.6 and RCP8.5 for all of our study sites from
174 Lamy *et al.* (2018). As both the IPCC (2014) temperature data and Lamy *et al.* (2018) UV-B
175 irradiance data are given in relative or percentage change, we calculate absolute values for
176 the 21st century based on our observed data from the WorldClim 2 and gIUV surfaces.

177 We generated predictions of future assemblage weighted colour lightness and body size for
178 all sites by combing the observed LMMs of colour and body size with the time series of
179 future temperature and UV-B changes. We used the “predict.lme” function in R (Bates *et al.*,
180 2014) to predict future AWM colour lightness and body size under future temperature and
181 UV-B conditions. As a result, predictions of future AWM lightness and body size were
182 driven by changing temperatures and changing UV-B irradiation levels. Predictions of future
183 AWMs were made for each year from 2011-2100.

184

185 **Trait simulation**

186 In the trait simulation, we forecast the state of future ant assemblages based only on changes
187 to relative abundance predicted by the trait-environment relationship. We did not simulate
188 dispersal: species were not permitted to move out of the sites in which we originally observed
189 them. We use a Community Assembly by Trait-based Selection (CATS) model (Shipley *et*
190 *al.*, 2006; Shipley, 2010; Sonnier *et al.*, 2010). The CATS model predicts the relative
191 abundances of different species given a defined species pool, the traits of those species and
192 the expected average trait value (assemblage weighted mean, AWMs) (Shipley *et al.*, 2006;
193 Laughlin & Laughlin, 2013).

194 The CATS model uses a series of constraint equations to produce a set of possible vectors of
195 species relative abundances (Shipley, 2010; Laughlin & Laughlin, 2013). First, the model
196 constrains abundances to sum to 1:

197
$$\sum_{i=1}^S p_i = 1$$

198 Where p_i is the predicted abundance of species i and S is the number of species in the pool.

199 This constraint equation is always the same.

200 Second, the model constrains the set of possible relative abundance vectors depending on the

201 predicted AWM:

202
$$\sum_{i=1}^S t_i p_i = \bar{T}$$

203 Where p_i is the predicted abundance of species i , t_i is the trait value of species i , S is the

204 number of species in the pool and \bar{T} is the AWM. This constraint equation differs across

205 different sites (and in our case, through time) as the supplied AWM (\bar{T}) changes. This

206 equation refines the set of possible relative abundance vectors to those that produce the same

207 AWM as that supplied.

208 The final prediction is made using only one vector from the set. The final vector is that which

209 maximizes the relative entropy function:

210
$$H(p, q) = - \sum_{i=1}^S p_i \ln(p_i/q_i)$$

211 Where \ln is the natural log, p_i is the predicted abundance of species i , q_i is the prior

212 probability of species i and S is the number of species in the pool. The solution with the

213 highest entropy is that which minimises the difference between the predicted abundances (p_i)

214 and the prior information (q_i). Under a maximally uninformative prior, where all species have

215 the same probability of selection, the model will choose the most even distribution of species

216 abundances. Under all other cases, the function will choose the vector which deviates the

217 least from the prior information. Further information on the mathematical formulation of the
218 CATS model and its comparison to other trait-based predictive frameworks can be found in
219 Shipley (2010), Shipley *et al.* (2006) and Laughlin and Laughlin (2013). We use this CATS
220 approach to predict relative abundances of mountain-top ants into the 21st century (further
221 information in Appendix S3).

222 Before running the simulation, we tested how well CATS could predict the observed relative
223 abundances of ants in all of our assemblages when provided with prior information on which
224 species were present in each elevational band. We calculated R^2 to measure how well the
225 predicted relative abundances matched the observed. The CATS model was implemented
226 using the “maxent” function in the “FD” package of R (Laliberté & Shipley, 2011).

227 We ran the CATS model for each elevational band, from each elevational transect, from the
228 observed data year (arbitrarily assigned as 2010) to 2100. In each year, we supplied our
229 predictions of future AWM colour lightness and body size. We assigned species not present
230 in a given elevational band a prior of 0 and those that were present an even probability of
231 selection. This prior means that species richness cannot increase under this simulation. The
232 output from this procedure was a vector of relative abundances for each year of the
233 simulation, for each elevational band, within each mountain transect and for each RCP
234 scenario.

235 If a species' predicted relative abundance was less than 0.0001 (one in ten thousand), it was
236 classed as extinct and was removed from the available species pool. Consequently,
237 assemblages in this simulation could lose species but they could not gain them. This
238 threshold of relative abundance was based on the smallest relative abundance recorded from
239 our field observations. Different thresholds around this value make little difference to our
240 results (Appendix S4).

241

242 Range Shift Simulation

243 In the range shift simulation, we forecast the future state of ant assemblages using a simple
244 climate-envelope model. As a result, this simulation predicted future species occurrence only,
245 not relative abundance. There are limited data available on the geographic ranges of the
246 species in our study beyond this dataset itself. As a result, we are unable to incorporate the
247 entire geographical ranges of these species into comprehensive species distribution models.
248 We use the simple method developed by Colwell *et al.* (2008) to assess potential elevational
249 range shifts using only temperature for transect data. Consequently, we interpret our forecasts
250 as potential changes in elevational range.

251 We first calculated the elevational distributions for all species in the dataset. We set the
252 distribution of each species to encompass the highest and lowest elevations from which we
253 sampled it. We assume ranges are inclusive and recorded a species as being present at all
254 elevations between the highest and lowest recorded occurrences. We set range limits to
255 extend halfway to the next neighbouring elevational band above and below (Colwell *et al.*,
256 2008). Second, we calculated empirical adiabatic lapse rates, the rate at which temperature
257 declines with elevation, for each mountain. We estimated the slope of the relationship
258 between temperature and elevation for each mountain using simple linear regression and used
259 this as the adiabatic lapse rate. We simultaneously used WorldClim 2 and data logger
260 estimates of temperature. For the Australian transects and the Mariepskop transect in South
261 Africa we only used WorldClim 2 estimates. Table S5 shows the estimated lapse rates for
262 each transect.

263 We used the data on species elevational distributions, adiabatic lapse rates and predicted
264 future temperature changes to predict the shifting ranges of the ant species on each transect
265 and, by extension, the shifting assemblage compositions, into the 21st century. Ranges were

266 shifted upslope relative to the observed baseline depending on the predicted temperature
267 increase or decrease for a given year. The rate of this vertical movement was set by the
268 adiabatic lapse rate of each transect. This procedure is identical to that used by Colwell *et al.*
269 (2008). All species on the same transect move upslope at the same rate. Across the entire
270 dataset, the average upslope shift by 2100 was 145 m for RCP2.6 and 1050 m for RCP8.5.
271 When a species range overlapped with a sampling site at a given time point, it was classed as
272 present.

273

274 **Combined Simulation**

275 The final simulation combines the trait and range shift simulations. The combined simulation
276 runs in almost the same way as the trait simulation. We predict relative abundance changes
277 based on predicted changes in AWM lightness and body size using CATS. Behind this
278 process, however, is a changing species pool. Whereas the trait simulation was static and did
279 not allow new species to enter a given elevational band, the combined simulation moves
280 species upslope (and downslope) through time according to their predicted range changes. As
281 a result, the available species pool that the CATS model is able to select from changes as the
282 simulation runs. We ran this simulation under RCP2.6 and RCP8.5.

283

284 **Interpretation**

285 It is not possible to predict accurately patterns of change all the way to 2100 for some
286 lowland assemblages under the range shift and combined simulations because we do not have
287 data on the species that may enter these areas from even lower elevations or lower latitudes.
288 This could cause an artificial lowland biotic attrition in these locations (Colwell *et al.*, 2008).
289 For each year we use the predicted temperature change and the adiabatic lapse rate of each

290 mountain to calculate where the “lower predictive limit” is. We only include data from
291 assemblages that are above this limit in a given year (Appendix S6). This means that we
292 exclude the very lowest assemblages on each mountain, and that there are fewer predictions
293 available in 2100 compared with earlier years. This effect is less severe in RCP2.6 than
294 RCP8.5 due to the smaller temperature change.

295 For each simulation and climate change scenario, we extract five different metrics from each
296 year in the 21st century and plot these through time. These metrics are: (1) percentage change
297 in species richness, (2) percentage of the original fauna lost, (3) Sørensen’s total
298 compositional dissimilarity, (4) Simpson’s turnover-based dissimilarity and (5) the
299 abundance weighted Bray-Curtis dissimilarity. All measures are relative to the start of the
300 simulation. For example, we calculate dissimilarities as the dissimilarity between a given year
301 and the year 2010 (our observed data), while the species richness metrics are all proportional
302 to the richness values recorded in 2010. We calculate the average and 95% CI across sites for
303 each of these metrics through time separately for RCP2.6 and RCP8.5. For the range shift and
304 combined simulations, the year 2010 is based on our current predictions, rather than current
305 observations. Our current predictions have slightly elevated species richness ($11 \pm 0.03\%$,
306 mean \pm SE) due to the interpolation of species ranges. We compared current predictions to
307 future predictions to avoid artificially inflating the degree of change estimated due to our
308 range interpolation procedure alone.

309 To detect the formation of non-analogous assemblages in the combined simulation we find
310 the closest modern (year 2010) assemblage, from any elevation, in terms of species
311 composition for each future (year 2100) assemblage. We use Sørensen’s dissimilarity metric
312 to do this. We then calculate the abundance-based dissimilarity between the future
313 assemblages and their closest modern analogue using Bray-Curtis similarity. Large
314 Sørensen’s dissimilarities would indicate that future assemblages have no modern analogue,

315 as this is an occurrence-based metric. Alternatively, a low Sørensen's dissimilarity but a high
316 Bray-Curtis dissimilarity would indicate that future assemblages have similar species
317 compositions to modern assemblages, but different distributions of relative abundance.
318 Between these pairs of future assemblages and their modern analogues, we also calculate a
319 mean and maximum rank shift, expressed as a percentage of the largest possible shift. To do
320 this we calculate the rank abundance of each species in each of the future-modern analogue
321 pairs. We then calculate the absolute change in ranks between each species and divide either
322 the maximum change or the mean change by the number of species. This is an extension of
323 the mean rank shift metric of Collins *et al.* (2008).

324

325 **RESULTS**

326 As expected, we recovered the same trait-environment relationship as in Bishop *et al.* (2016)
327 after pooling at the elevational band level within a transect - ant assemblages were, on
328 average, darker in colour and larger in worker body size in cold environments (Fig. S7). The
329 CATS model performed well and predicted 75% of the variation in observed relative
330 abundances. This level of accuracy is comparable with previous studies, for example,
331 Frenette-Dussault *et al.* (2013) reported an accuracy of 40% when using two traits and ~70%
332 when using six traits. We use only two traits here.

333

334 *Occurrence metrics*

335 Predicted species richness changes varied strongly by simulation type and climate change
336 scenario (Fig. 1). Across all three simulations, assemblages showed larger changes to overall
337 richness and lost more of their original fauna in RCP8.5 compared with RCP2.6. In the trait

338 simulation, species richness declined by 10% in RCP2.6 and by 15% in RCP8.5, averaged
339 across all assemblages by 2100 (Fig. 1a, d). In the range shift simulation, species richness
340 increased by 29% in RCP2.6 and by 193% in RCP8.5, averaged across all assemblages by
341 2100 (Fig. 1b, e). In addition, 14% of the original fauna was lost in RCP2.6 and 43% in
342 RCP8.5. In the combined simulation, the change in species richness was not as much as in the
343 niche simulation (RCP2.6 = 26%, RCP8.5 = 186%, Fig. 1c) but a larger fraction of the
344 original fauna was lost (RCP2.6 = 20%, RCP8.5 = 47%, Fig. 1f).

345 Predicted compositional changes also varied strongly by simulation type and climate change
346 scenario (Fig. 2). Again, predicted changes were much greater under RCP8.5 compared with
347 RCP2.6. In the trait simulation, compositional dissimilarity (as measured by Sørensen's
348 dissimilarity) by 2100 was 0.07 in RCP2.6 and 0.11 in RCP8.5, on average (Fig. 2a). This
349 was entirely due to nested patterns of compositional change as the trait simulation only
350 allows for extinction, not colonisation (as measured by Simpson's dissimilarity, Fig. 2d). In
351 the range shift simulation, compositional dissimilarity by 2100 was 0.22 under RCP2.6 and
352 0.64 under RCP8.5 (Fig 2b). In RCP2.6 this overall compositional dissimilarity was almost
353 evenly made up of turnover and nestedness (average turnover by 2100 for RCP2.6 = 0.1, Fig.
354 2e). For RCP8.5, turnover was a larger component of overall compositional dissimilarity
355 (average turnover by 2100 for RCP8.5 = 0.41, Fig. 2e). In the combined simulation, a similar
356 pattern to the niche simulation was seen for both total compositional dissimilarity (RCP2.6 =
357 0.27, RCP8.5 = 0.65, Fig. 2c) and turnover dissimilarity (RCP2.6 = 0.12, RCP8.5 = 0.38, Fig.
358 2f).

359

360 *Abundance metrics*

361 Predicted abundance weighted dissimilarity is greater for RCP8.5 than for RCP2.6 and shows
362 differences between the trait and combined simulations (Fig. 3). In the trait simulation,
363 abundance dissimilarity is 0.15 by 2100 under RCP2.6 and 0.37 under RCP8.5 (Fig. 3a). In
364 the combined simulation, abundance dissimilarity is 0.33 by 2100 under RCP2.6 and 0.78
365 under RCP8.5 (Fig. 3b).

366

367 *Modern-future analogues*

368 While future assemblages tended to have a close modern analogue in terms of species
369 occurrence, this was not true when considering assemblage structure and relative abundances.
370 The average occurrence-weighted Sørensen's dissimilarity between predicted assemblages in
371 2100 and their closest modern analogue was 0.08 for RCP2.6 and 0.11 for RCP8.5 (Fig. 4a).
372 The average abundance-weighted Bray-Curtis dissimilarity between these same pairs of
373 future and modern assemblages was 0.36 under RCP2.6 and 0.51 for RCP8.5 (Fig. 4a). In
374 RCP2.6, average mean rank shift was 19% and average maximum rank shifts were 42%. For
375 RCP8.5, the average mean rank shift was 30% and the average maximum was 70%. A
376 maximum rank shift of 100% is the highest possible, whereby the most common species
377 becomes the rarest species, or vice versa.

378 **DISCUSSION**

379 We have forecast the future of mountain ant diversity using a novel combination of trait-
380 mediated abundance predictions and temperature driven range shifts. We find that ant
381 assemblages are likely to change drastically in terms of species richness, composition and
382 abundance structure by 2100. In addition, we predict that while future assemblages will have
383 modern analogues in terms of species occurrence, they will have an entirely different
384 abundance distribution. These changes are likely to have a significant impact on the way
385 these mountain systems function as ants mediate ecosystem processes and interact with many
386 other members of the food web (Gómez & Oliveras, 2003; Zelikova *et al.*, 2011; Parr *et al.*,
387 2016). Our findings differ strongly, however, between alternative scenarios of climate
388 change. Our predictions of species richness changes are much more optimistic under RCP2.6,
389 which is a likely climate future only if the greenhouse gas emissions targets set at the Paris
390 Climate Agreement of 2015 are met (Sanford *et al.*, 2014).

391 Biodiversity forecasts are expanding beyond shifting distributions (Pearson & Dawson, 2003)
392 to predict assemblage level information, phylogenetic and functional diversity (Del Toro *et*
393 *al.*, 2015; Graham *et al.*, 2017), and to incorporate a variety of biotic effects such as species
394 interactions (Araújo & Luoto, 2007) and dispersal abilities (Dullinger *et al.*, 2012). Here, we
395 provide a novel analysis predicting assemblage level relative abundances and potential range
396 shifts from an established trait-environment relationship. The general form of the trait-
397 environment relationship we use here appears to be a feature of many ectotherm assemblages
398 and populations (Zeuss *et al.*, 2014; Pinkert *et al.*, 2017). The data we use are also relatively
399 more straightforward to collect compared with species interaction coefficients or dispersal
400 abilities, and simpler to assess for completeness compared with data for interaction networks
401 (Vizentin-Bugoni *et al.*, 2016). Directional changes to species relative abundances may also

402 be easier to detect through time compared to species occurrences, because changes in species'
403 rank abundances are more sensitive to change than occurrences, highlighting the usefulness
404 of long-term monitoring schemes. As a consequence, the approach is a useful additional one
405 for assessing assemblage level changes, which have been highlighted as a key requirement
406 for the ecological forecasting toolbox (Suding *et al.*, 2008; Walther, 2010; Urban *et al.*,
407 2016).

408 Central to our forecasts are the different kinds of assemblage level change that each
409 simulation emphasises. Both the trait and range shift simulations are unrealistic in isolation,
410 but provide a minimum estimate of each effect in the absence of the other. The combined
411 simulation predicts a unique set of future assemblages that neither the trait nor the range shift
412 simulation could predict on their own. Under the combined simulation, we predict that future
413 assemblages will support a similar set of species to modern ones from further downslope
414 (similar observations have been made for plants and moths, Vittoz *et al.*, 2008; Chen *et al.*,
415 2009), but that their abundance structure will be reorganised (Fig. 4). This means that
416 assemblages will not simply move upslope unchanged as the climate warms – they will also
417 face a reorganisation in terms of which species are common and which are rare.

418 Notably, most work on the formation of non-analogous assemblages focuses on novel species
419 co-occurrences (Keith *et al.*, 2009; Graham *et al.*, 2017). Our forecasts, however, show that
420 changes to abundance may be an underappreciated aspect of non-analogous assemblage
421 formation and highlight the importance of considering both species occurrence and relative
422 abundance (Walther, 2010; Simpson *et al.*, 2011). The way in which these changes play out
423 in reality, however, will depend on the form of the dispersal kernels across the species in the
424 assemblages involved (Urban *et al.*, 2012; Alexander *et al.*, 2017) and the reorganisation of
425 biotic interactions. At this stage, however, there are no independent data (Early & Keith,

426 2019) to assess inter- and intraspecific interactions among ants at these scales and inferring
427 this information is fraught with difficulty (Stuble *et al.*, 2017)

428 All the changes we predict are likely to have a significant impact on ecosystem functioning
429 and energy flow in mountain environments, especially given the numerical and functional
430 dominance of ants in many terrestrial ecosystems (Griffiths *et al.*, 2018). We predict that
431 future high elevation assemblages will likely contain more species than they do now. Given
432 the positive relationship between ant diversity and the rate of ecosystem functioning (Fayle *et*
433 *al.*, 2011; Griffiths *et al.*, 2018) it may be that, as more species move upslope, ant mediated
434 functions such as scavenging, waste removal and seed dispersal will increase. This picture is
435 complicated, however, by our prediction of large changes to the relative abundances of
436 species based on their traits. By 2100, the assemblage weighted mean body size in our dataset
437 will be 11.5% smaller under RCP8.5, on average, which suggests that the species responsible
438 for performing ecosystem functions will also be smaller – the consequences of this for
439 functioning are hard to predict. While we are certain that the role of ants in mountain
440 ecosystems will change substantially in the future, we can only speculate on the ways in
441 which this will happen.

442 Although our forecast for the future under RCP8.5 predicts large changes to ant biodiversity
443 in mountain regions, our predictions under RCP2.6 are much more optimistic. Under this
444 scenario of climate change, we expect species ranges to move upslope by 145 m and,
445 correspondingly, our estimates of species loss, species gain and compositional and abundance
446 change are much reduced in comparison to RCP8.5. What seems to be shared between the
447 two scenarios, however, is the formation of abundance-based non-analogue assemblages. In
448 RCP2.6, the degree of rank abundance reorganisation is smaller in comparison to RCP8.5,
449 but remains substantial (Fig. 4). In sum, we support the view that reducing greenhouse gas

450 emissions and limiting temperature rises to below 2°C by 2100 is necessary for positive
451 outcomes for global conservation and ecosystem integrity (Warren *et al.*, 2018).

452 Our simulations of range shifts assume a “full dispersal scenario” (Colwell *et al.*, 2008;
453 Fitzpatrick *et al.*, 2011). Species ranges move upslope as the climate warms and there are no
454 lags or limits in dispersal capacity. This is probably a reasonable assumption to make for
455 ants. The geographic distances between different elevations in our dataset are relatively
456 small, ants are renowned dispersers (e.g. Wilson, 1961) and winged reproductive individuals
457 may be aided by updrafts in montane environments. On the other hand, it has been argued
458 that the social and modular nature of ant colonies confers a high degree of persistence in the
459 face of environmental perturbations and extremes (Andersen, 2008). This kind of non-
460 equilibrium process may limit the available space for newly arrived dispersers to establish.
461 This establishment limitation is especially true when considering competitive interactions
462 between dominant and subdominant ant species, the outcome of which can also be influenced
463 by temperature (Parr, 2008; Roeder *et al.*, 2018). These effects would disrupt the “full
464 dispersal scenario” that we have assumed. Determining in more detail which factors limit or
465 promote species distributions, dispersal ability and establishment capacities will greatly
466 increase our ability to predict and understand future change (Fitzpatrick *et al.*, 2011;
467 Alexander *et al.*, 2017).

468 In addition to processes such as competition and establishment limitation disrupting our
469 simulation assumptions, vegetation-mediated changes to microclimate and soil properties
470 may have a large influence on ant assemblages in the 21st century (Ríos-Casanova *et al.*,
471 2006; Munyai & Foord, 2012). The real world is more complicated than we can currently
472 simulate and, because of this, we interpret our results as reflecting the maximum potential of
473 range shifts and thermoregulatory traits to influence assemblage-level change.

474 In particular, our range shift simulation is relatively simple. Due to the lack of information
475 available on full species ranges, dispersal abilities and biotic interactions, we were restricted
476 in the modelling tools available that could predict elevational range shifts. Consequently, we
477 used the method developed by Colwell *et al.* (2008) to minimise the assumptions we made
478 about the biology and ecology of the ant species involved. The caveats are that our data may
479 be underestimating true species ranges; that microclimatic variation removes the necessity for
480 species to migrate upslope; and that the influence of biotic interactions between newly
481 dominant or co-occurring species are ignored. Collecting the necessary data to account for
482 these effects is an ongoing challenge (Early & Keith, 2019), particular for invertebrates.

483 In summary, we predict large changes to mountain ant assemblages due to temperature driven
484 range shifts and trait-mediated abundance change. Many more species will be present in high
485 elevation sites in the future, as has been found for plants (Steinbauer *et al.*, 2018), and their
486 composition and abundance structure will change substantially. These changes will be much
487 larger under RCP8.5 than RCP2.6, but both scenarios predict a future where highland
488 assemblages are compositionally analogous to lowland ones but with a reorganised
489 abundance structure. Going forward, it will be critical to understand how changes in relative
490 abundance will contribute to cascading effects on the wider food web and ecosystem
491 functioning.

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502

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725 **TABLES**

726 No tables.

727 **FIGURE CAPTIONS**

728 **Figure 1.** Plots showing predicted changes in species richness (expressed as a percentage
729 change, a-c) and the original fauna (expressed as a percentage of the original fauna lost, d-f)
730 for trait, range shift and combined simulations. Blue lines refer to predictions made for
731 RCP2.6, red lines are for RCP8.5. Lines are loess smoothed averages taken from across all
732 assemblages and mountain transects. Coloured polygons represent 95% confidence intervals.

733

734 **Figure 2.** Plots showing predicted changes in total compositional dissimilarity (Sørensen's
735 dissimilarity, a-c) and turnover dissimilarity (Simpson's dissimilarity, d-f) for trait, range
736 shift and combined simulations. Blue lines refer to predictions made for RCP2.6, red lines
737 are for RCP8.5. Lines are loess smoothed averages taken from across all assemblages and
738 mountain transects. Coloured polygons represent 95% confidence intervals.

739

740 **Figure 3.** Plots showing predicted changes in abundance weighted dissimilarity (Bray-
741 Curtis) for trait and combined simulations. Blue lines refer to predictions made for RCP2.6,
742 red lines are for RCP8.5. Lines are loess smoothed averages taken from across all
743 assemblages and mountain transects. Coloured polygons represent 95% confidence intervals.
744 No plot is presented for the niche simulation because it uses only occurrence data.

745

746 **Figure 4.** Plots showing the relationship between future assemblages in the combined
747 simulation and their closest modern analogues. In (a), dissimilarity between future
748 assemblages and their closest modern analogues is given. Modern analogues are those with

749 *the smallest occurrence-weighted dissimilarity (“Occ.”, Sørensen’s dissimilarity).*
750 *Abundance-weighted dissimilarity (“Abund.”, Bray-Curtis) between the future and closest*
751 *modern analogues is also given. Panels (b) and (c) show the average and maximum change*
752 *in rank abundance between future and modern pairs, expressed as a percentage of the largest*
753 *possible shift in rank. Blue boxes are for RCP2.6, red boxes are for RCP8.5.*