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Namib desert trees feel the heat of climate change

**Population declines and dispersal lags squeeze the geographic range of
a Namib tree Aloe in a changing climate**

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27

28

29 **Summary (A)**

30

31 While poleward species migration in response to recent climatic warming is widely
32 documented, few studies have examined entire range responses of broadly
33 distributed sessile organisms, including both trailing (equatorward) and leading
34 (poleward) range edges.

35

36 From a detailed population census of *Aloe dichotoma* Masson, a long-lived Namib
37 Desert tree-aloë, we present six pieces of evidence of a developing range shift in this
38 species, most parsimoniously explained by population level impacts of observed
39 regional warming and resulting water balance constraints. Equatorward population
40 declines are broadly consistent with bioclimatically-modelled projections under
41 anticipated anthropogenic climate change, but are not accompanied by modelled
42 poleward range extension.

43

44 This study is the first to show a marked lag between trailing edge population
45 extinction and slow leading edge range expansion in a species experiencing
46 anthropogenic climate change impacts, a pattern likely to apply to most sessile and
47 poorly dispersed organisms. This provides support for making conservative
48 assumptions of migration rate when modelling climate change impacts for such
49 species. *Aloe dichotoma*'s response to climate change suggests that desert
50 ecosystems may be more sensitive to climate change than previously suspected.

51

52 **Keywords (A)**

53 Bioclimatic modelling; desertification; extinction; global warming fingerprints;
54 migration; range shift

55

56

57 **Introduction (A)**

58

59 Studies of the responses of terrestrial organisms to latter 20th century warming have
60 focussed on range shifts of motile organisms [e.g.1-4], stressing poleward range
61 boundary extensions [1], or non-lethal changes in the growth patterns of sessile
62 organisms [5-8]. Both types of studies have focused most frequently on only a portion
63 of a species' range. However, there is concern that the adaptive responses of sessile
64 organisms to rapid climate change may be constrained, causing population
65 extinctions at the so-called "trailing edge" of species' geographic ranges that are
66 shifting in response to a changing climate [9]. Trailing edge extinctions should be
67 first detected in terrestrial organisms that occupy extreme climatic environments such
68 as deserts, where climate-related stresses exert direct control over population
69 processes, especially at range margins [10]. It is implicitly assumed by bioclimatic
70 modelling approaches that trailing edge extinctions will be accompanied by
71 simultaneous leading edge range expansions [1], but lags due to limiting rates of
72 dispersal, establishment and population expansions [11] are a significant threat to
73 this assumption, especially for sessile species. Such constraints are likely to
74 squeeze the ranges of non-motile organisms between a zone of population die-back
75 and of constrained expansion, thereby raising their risk of extinction, at least
76 temporarily, even if climate change trends begin to stabilize.

77

78 Here we demonstrate impacts of regional climate change on population die-back in
79 the Namib desert tree (*Aloe dichotoma*), almost certainly through induced water

80 balance constraints, in a spatial pattern consistent with the expected signal of
81 anthropogenic climate change (i.e. higher mortality in equatorial trailing edge sites).
82 The pattern of die-back provides credible evidence of the negative impacts of
83 anthropogenic climate change on sessile organisms, especially as it is linked with
84 observed regional climatic changes and is consistent with model projections of
85 anthropogenic climate change impacts. However, we find no evidence yet of
86 poleward range expansion, and only weak evidence of population expansion in
87 poleward populations, demonstrating a lag between trailing edge die-back and
88 leading edge expansion that may pose a serious threat to the long-term persistence
89 of this and other sessile or poorly-dispersed species.

90

91 We conducted a detailed population census and related studies on this long-lived
92 giant succulent plant throughout its entire geographic range in the Namib Desert and
93 adjacent arid regions of Southern Africa, a region projected to experience significant
94 warming and drying due to anthropogenic climate change [12]. The sizeable stem-
95 succulent growth form, succulent leaves and shallow root systems of this species are
96 common adaptations for rapid absorption and storage of water to allow survival of
97 frequent droughts [13,14]. Individuals grow up to 10m tall and usually occur in dense
98 populations of up to 10 000 trees. A long life span (approximately 200 years [15],
99 and expansive range (21°-31° South, ~200 000 km²) make this a useful species for
100 studying significant long-term climate trends. In particular, because dead trees
101 decay slowly in the arid Namib climate (as revealed by repeat photography), we were
102 able to obtain a consistent relative measure of population mortality throughout the
103 species' range.

104

105

106 **Results (A)**

107

108 We examined 53 populations throughout the entire geographic range of the species
109 and found that population-level mortality ranged between 2% and 71% (mean=32.1 ±
110 20.0%, see Fig. 1), with a significant trend of decreasing mortality from the equatorial
111 to the poleward regions of the species' range ($r=0.393$, $n=53$, $p<0.004$; see Fig. 2). A
112 regression of the residuals from this analysis against the altitude of each population
113 also produced a significant trend ($r=0.331$, $n=53$, $p<0.016$) – showing that low-altitude
114 (warmer) equatorial populations are approaching localised extinction, while high
115 altitude (cooler) populations have experienced lower mortality. Populations at
116 poleward and high altitude extremes tended to experience only minimal mortality.
117 Thus population level mortality decreased along latitudinal and altitudinal clines in a
118 pattern consistent with that expected under climate change, with the highest mortality
119 generally in the “trailing edge” [9] of the species' geographic range.

120

121 Repeat photographs also suggest a latitudinal cline in *Aloe dichotoma* mortality. We
122 examined a series of 22 photographs of nine *Aloe dichotoma* populations taken
123 between 1904 and 1918 and precisely matched these with repeat photographs in
124 2002. The six northernmost populations have experienced declines in population
125 numbers of between 1.5% and 8% per decade but the three southernmost
126 populations have increased in numbers by between 4% and 17% per decade (Fig. 3).
127 The altitudinal range between the sites (300m) is too small to infer an altitudinal cline
128 but we found a clear relationship between latitude and mortality rate (the fraction of
129 deaths in percent of observed individuals per century) ($r= -0.906$, $n=9$, $p<0.001$).

130

131 What might be causing adult mortality in these populations? In a large number of
132 *Aloe dichotoma* individuals, we observed that terminal leaf rosettes slowly withered
133 and eventually dropped to the ground, while the apical tips of supporting branches
134 died under drought conditions (we term this “shoot shedding”). These branches
135 never re-developed leaves, presumably due to the loss of apical meristem. Our field

136 observations and anecdotal evidence from local experts strongly suggests that shoot
137 shedding is a typical response to water deficits in this species [16]. We found a
138 strong logarithmic relationship between the mean percentage of individuals' canopies
139 lost to shoot shedding and population mortality ($r=0.777$, $n=24$, $p=0.00$), suggesting
140 that high-mortality populations are experiencing long term water stress.

141

142 Water stress in plants is the result of the interaction between precipitation and
143 atmospheric vapour pressure deficit, itself a function of air temperature and relative
144 humidity. Desert rainfall is variable and unsuited to trend analysis especially given
145 the length of records available, but atmospheric warming is more reliably detected.
146 Increasing air temperature is a key controller of plant water status, and would
147 increase the rate of water loss from the succulent leaves of this CAM-photosynthetic
148 species, especially during its night-time stomatal opening period, thereby hastening
149 leaf and shoot desiccation.

150

151 Continental scale analyses of temperature records for the last century indicate that
152 the Namib has undergone an increase in temperature as well as a reduction in
153 precipitation [12]. Local climatic records revealed significant regional climate
154 warming. We examined temperature and rainfall records from all available long-term
155 weather stations in the regions in which *Aloe dichotoma* occurs. Fifty three percent
156 of stations showed significant increases in temperature over the last 25-60 years
157 while none showed a significant decline. The mean decadal increase across all
158 stations during this interval was $0.2 \pm 0.1^\circ\text{C}$. Water balance, a composite measure of
159 temperature and rainfall reflecting the water available to plants, showed a significant
160 decline at 33% of stations over the last 25-60 years. No stations showed a
161 significant increase in water balance over this period. The relative severity of
162 cumulative water stress in *Aloe dichotoma* is reflected by the percentage of months
163 during the past decade in which water balance fell below -90 mm. Furthermore,

164 population mortality at study sites within 100km of the long-term weather stations is
165 positively correlated with cumulative water stress ($r=0.491$, $n=22$, $p<0.021$), strongly
166 suggesting that a combination of water and heat stress is responsible for the
167 increased mortality in declining *Aloe dichotoma* populations.

168

169 Where atmospheric warming is the chief cause of localised extinction we would
170 expect lower mortality in cooler microhabitats. To test this hypothesis, we selected
171 populations occurring on extensive steep slopes, and assigned all live and dead
172 trees to one of three roughly equal-sized altitude categories, namely lower, middle
173 and upper slopes. Combining results from all sites, we found significantly higher
174 mortality than expected on lower, warmer slopes ($\chi^2 = 21.49$, $d.f. = 2$, $p<0.00002$).
175 This result is consistent with a climate change explanation of mortality, and confirms
176 that, even at a local scale, individuals in cooler climatic refuges (i.e. higher altitude)
177 have a lower probability of mortality.

178

179 We examined all other reasonable explanations for the observed mortality patterns in
180 *Aloe dichotoma*, such as intra-specific competition, pathogen infection, pollution
181 damage or exposure to human or animal persecution. We found no relationship
182 between mortality and tree density or the degree of pathogen infection of trunks or
183 leaves. Although the areas in which *Aloe dichotoma* occurs are too arid for
184 agriculture, parts of its range are used for stock and game farming. The species is
185 considered to be unpalatable, yet we observed a degree of herbivory by sheep,
186 goats, donkeys, antelope, baboons and porcupine, but no correlation between
187 canopy herbivory and population mortality. We found mortality to be weakly related to
188 degree of stem bark damage, presumably by herbivores ($r=0.406$, $n= 35$, $p<0.02$),
189 but as it is unrelated to herbivore density (measured as the frequency of dung pellets
190 in the area; $r=0.11$, $n=28$, $p>0.56$) we conclude that some herbivory of *Aloe*
191 *dichotoma* trunks (likely by porcupines) probably occurs only under conditions of

192 extreme drought when more palatable food and water sources are unavailable,
193 resulting in a weak auto-correlation between stem bark damage and population
194 mortality.

195

196 Finally, niche-based spatial modelling techniques [17], utilising the sampled
197 distribution and climatic surfaces at a resolution of 10 minutes were used to derive
198 *Aloe dichotoma*'s current and future modelled ranges, assuming widely-used
199 projections of anthropogenic climate change [18]. The modelled frequency of
200 occurrence of *Aloe dichotoma* within each 10 minutes of latitude for the years 2000
201 and 2050 (see Fig. 4A) indicates a projected poleward shift in this species'
202 geographic range. The trend of progressive projected range decline with decreasing
203 latitude is similar to the latitudinal trend in measured mortality of sampled populations
204 (Fig. 4B), strongly suggesting that anthropogenic warming underlies the negative
205 trends in population persistence in this species in the equatorial regions of its
206 geographic range.

207

208 The mean altitude of 10' pixels in which climate change models project the species'
209 presence increases from 806 ± 354 m in 2000 to 885 ± 329 m in 2050 while the
210 projected mean latitude shifts from 26.68 ± 2.81 degrees South in 2000 to $27.90 \pm$
211 2.5 degrees South in 2050. These modelled shifts equate to a mean altitudinal
212 increase of 16m per decade and a poleward range shift of 23 km per decade,
213 considerably higher than the 6.1 ± 2.4 km per decade poleward range shifts recently
214 collated [2].

215

216 No records exist of new populations of this highly prized species establishing in areas
217 projected to become suitable for the species in the poleward parts of its range, even
218 though it has been successfully planted and recruits autonomously in more poleward
219 locations [19]. Within-population recruitment (i.e. the percentage of individuals in the

220 population <1m in height) was generally low, but ranged from 0.0 % to 40.4%
221 (mean=10.1 ± 9.9%), showing a weak negative relationship with latitude ($r=-0.26$,
222 $n=53$, $P>0.064$).

223

224

225 **Discussion (A)**

226 These results suggest that *Aloe dichotoma*, a species with an extended juvenile
227 period, may be experiencing the earliest stages of poleward expansion, but that low
228 rates of juvenile recruitment, individual plant growth and dispersal limit migration in
229 relation to its shifting climatic envelope. The geographic range of *Aloe dichotoma* is
230 becoming squeezed between an equatorward zone of rapid range contraction due to
231 population extinctions, and a poleward zone of lagging range expansion. This study
232 is the first to document a lag in leading edge range expansion, but the pattern is likely
233 to be repeated for sessile and poorly dispersed organisms globally.

234

235 Many projections of climate change impacts on biodiversity attempt to incorporate
236 uncertainty due to migration constraints by contrasting “full migration” and “null
237 migration” assumptions [e.g.17,20,21]. These findings provide strong support for
238 conservative assumptions of migration rate in sessile organisms, and have large
239 implications for projections of global species’ diversity loss.

240

241 The Succulent Karoo, the planet’s only arid biodiversity hotspot [22], contains over 5
242 000 species, 40% of which are endemic [23]. This hotspot lies almost entirely within
243 the range of *Aloe dichotoma*. Although it is extremely widespread and abundant, *Aloe*
244 *dichotoma* qualifies as Vulnerable (criterion A3c,e) according to the IUCN Red List
245 Assessment criteria, based on population loss corresponding to modelled range loss
246 under a “null migration” scenario. Succulence, gigantism and a broad distribution
247 range probably make *Aloe dichotoma* particularly robust to drought and climatic

248 fluctuation, and the species provides a conservative indicator of climatic warming in
249 the Namib region. While insufficient data are available to model range shifts of all
250 species, it seems likely that doing so would result in a drastic increase in the number
251 of species qualifying as Threatened (defined as “in immediate danger of extinction”)
252 according the IUCN Red Listing criteria. A large and rapid shift in conservation
253 approach is clearly needed.

254

255 Desert ecosystems are frequently perceived as more tolerant of global warming and
256 a recent global assessment suggests that they will show a relatively muted
257 biodiversity response to climate change [24]. The results of this study argue strongly
258 against this conclusion and suggest that desert ecosystems are likely to become
259 increasingly hostile and species-poor with intensifying global warming.

260

261

262 **Materials and Methods (A)**

263

264 Aloe population characteristics (B)

265 We selected large, discreet populations and measured 100 live individuals in the
266 densest part of each. We measured smaller populations where they made an
267 important contribution to describing the species’ range and no larger ones could be
268 found. In these cases we measured the entire population. Estimates for each
269 individual included degree of fungal pathogen infection of leaves and trunk (scores);
270 extent of animal damage to the stem or trunk (score); the percentage of the total
271 potential canopy removed and the percentage of the total potential canopy in which
272 leaf abscission occurred.

273

274 The number of dead trees within the area covered by the 100 sampled live trees was
275 used to derive the percentage of each population’s mortality. We used a 1,000 x 3

276 metre transect through the population to derive an estimate of population density.
277 This also provided a second estimate of relative mortality and this was generally in
278 agreement with the first estimate.

279

280 Photographs (B)

281 Mortality within the photographed populations was calculated as $M = [D/(D+S)] [n/$
282 $100\text{yrs}] [100 \text{ \%}]$; where: M = mortality rate expressed as the fraction of deaths in
283 percent of observed individuals per century; D = number of dead individuals; S =
284 number of surviving individuals; and n = number of years between photographs.

285

286 Climate records (B)

287 We used data from all stations in Namibia and north-western South Africa from which
288 temperature records of 24 or more years are available (15 stations). We tested for
289 stationarity by visually assessing deviance from a straight line when cumulative
290 temperature and rainfall values for neighbouring stations were plotted against each
291 other [25]. Water Balance was calculated as the difference between precipitation and
292 potential evapotranspiration [26] based on monthly means of mean daily temperature
293 and total monthly precipitation. Annual trends (calculated from April to March in order
294 to represent a growth year) were analysed using Robust MM Regression [27].

295

296 Eleven stations had water balance data for more than 12 of the last 15 years. Eight of
297 these stations were within 100km of one or more study populations and these were
298 used for comparison with *Aloe dichotoma* population mortality (22 populations). A
299 single coastal station was removed from the analysis as the steep environmental
300 gradient away from the coast makes it unrepresentative of conditions at inland
301 populations.

302

303 Bioclimatic modelling (B)

304 The CRU CL 2.0 dataset [28] was used to represent current climate. Future (2050)
305 climate modeling was based on the moderate prediction of climate change produced
306 by the HADCM3 General Circulation Model [29] using the B2 IPCC SRES scenario
307 [30]. BIOMOD [18,31], a biodiversity modeling tool was used to produce scenarios of
308 the possible impacts of climate change on *Aloe dichotoma's* range.

309

310

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312

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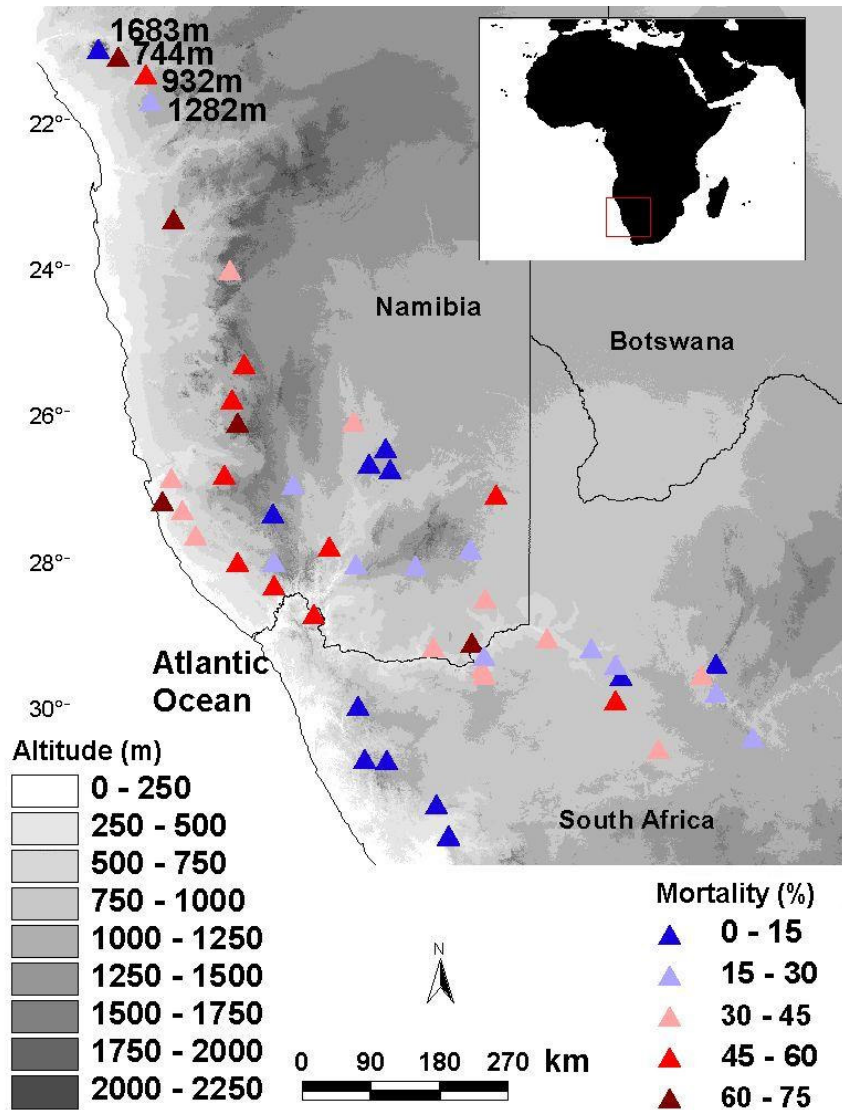
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385
386

387 **Acknowledgements (A)**

388

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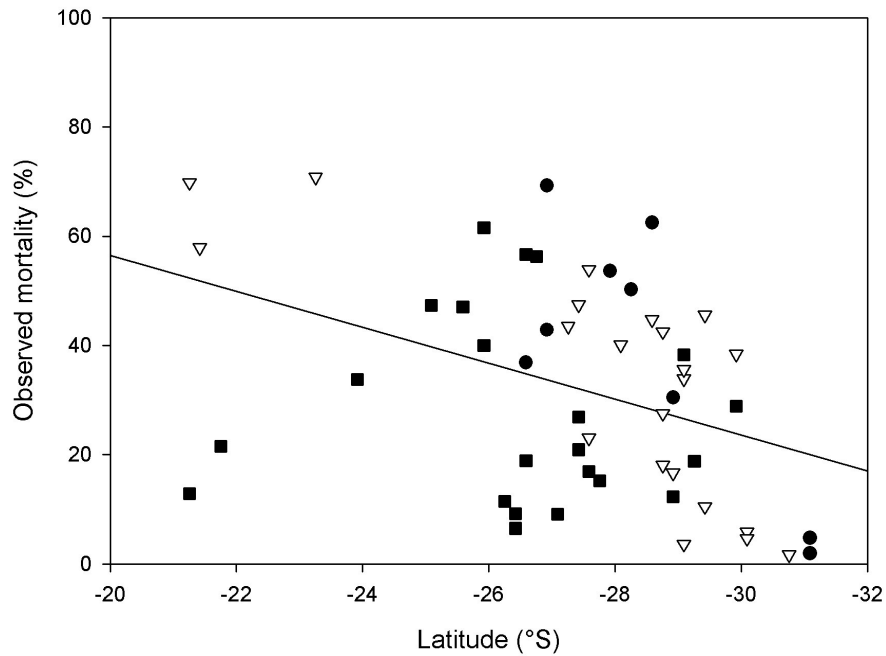


397

398 Fig. 1

399 Map showing mortality of *Aloe dichotoma* Masson populations across the species'
 400 range. Blue triangles indicate populations with low mortality and red triangles
 401 represent progressively higher mortality. Lighter and darker shades of background
 402 grey represent lower to higher altitudes (in metres) respectively. For the four
 403 northernmost populations, altitudes have been specified on the map because two of
 404 the populations occur on inselbergs. Mortality appears patchy, but a general trend of
 405 lower mortality in southern populations is apparent, irrespective of altitude, and
 406 northern populations have increasingly greater mortality, except at high altitudes.

407



407

408 Fig. 2

409 Graph showing the relationship between latitude (degrees South) and *Aloe*
 410 *dichotoma* Masson population mortality. Mortality follows a latitudinal cline of
 411 increase from the poleward to the equator-ward side of the species' range, as
 412 indicated by the solid regression line ($r=0.393$, $n=53$, $P<0.004$). The mean altitudes
 413 at which these populations occur are indicated by • (<700m), ▽ (700-1000m) and ■
 414 (>1000m). When regressed against altitude, the residuals of the above regression
 415 produced a significant trend ($r=0.331$, $n=53$, $P<0.016$) showing that where mortality
 416 was lower than expected from the latitudinal trend, this can be explained by higher
 417 altitude of the population and conversely, that populations at low altitudes have
 418 higher than expected mortality. In combination, these results strongly suggest that
 419 *Aloe dichotoma* is undergoing the beginning of a systematic poleward and upwards
 420 range shift.



A



B



C



D

421

422

Fig. 3

423

424

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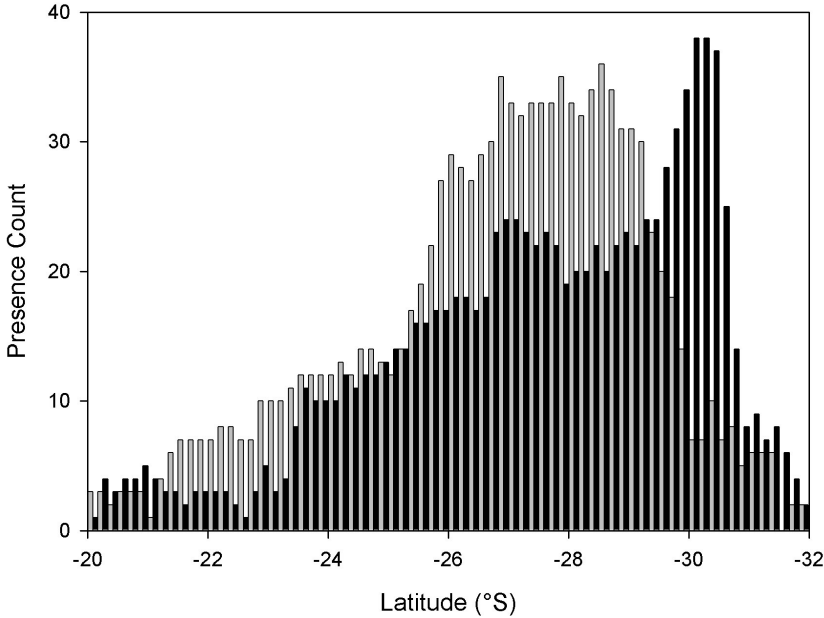
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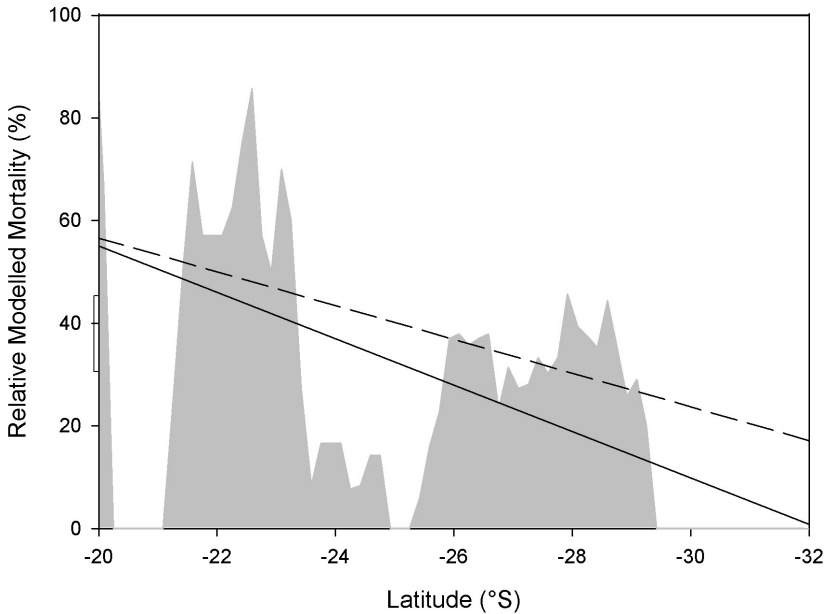
428

Repeat photographs of populations of *Aloe dichotoma* Masson taken in 1904 and 1918 and precisely matched in 2002. A and B were taken at Hantamsberg, Calvinia (31°12.5' South, 19° 43.3' East) in 1904 (Marloth) and 2002 respectively. From this and another pair of matched photographs taken at the site, a decadal population increase of 109% is inferred. C and D show photographs taken in 1918 (Evans) and 2002 in the Westerberg, near Koegas (29°19.9' South, 22°18.5' East). A decadal

429 population decrease of 47% is inferred from 2 matched photograph pairs taken at this
430 site.



431 A



432 B

433

434 Fig. 4

435 Graphs showing comparisons between present and bioclimatically modelled future
436 projections of *Aloe dichotoma*'s Masson distribution range and mortality. A. shows

437 the modelled frequency of *Aloe dichotoma* in each 10 minute latitude band of its
438 range for 2000 (grey bars) and 2050 (black bars). The projected mean latitude of the
439 species' range shifts from -26.68 ± 2.81 degrees South in 2000 to -27.90 ± 2.5
440 degrees South in 2050. This equates a mean altitudinal shift of 16m per decade and
441 a poleward range shift of 23 km per decade. Graph B shows the projected relative
442 mortality of *Aloe dichotoma* by 2050 (shaded grey), based on the relative number of
443 existing populations occurring inside versus outside the 2050 bioclimatic envelope
444 (see methods). The dashed line represents the modelled trend of mortality; while the
445 similarly sloped solid line represents the mortality trends measured during the
446 population census.