

A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags

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ABSTRACT

While poleward species migration in response to recent climatic warming is widely documented, few studies have examined entire range responses of broadly distributed sessile organisms, including changes on both the trailing (equatorward) and the leading (poleward) range edges. From a detailed population census throughout the entire geographical range of *Aloe dichotoma* Masson, a long-lived Namib Desert tree, together with data from repeat photographs, we present strong evidence that a developing range shift in this species is a 'fingerprint' of anthropogenic climate change. This is explained at a high level of statistical significance by population level impacts of observed regional warming and resulting water balance constraints. Generalized linear models suggest that greater mortalities and population declines in equatorward populations are virtually certainly the result, due to anthropogenic climate change, of the progressive exceedance of critical climate thresholds that are relatively closer to the species' tolerance limits in equatorward sites. Equatorward population declines are also broadly consistent with bioclimatically modelled projections under anticipated anthropogenic climate change but, as yet, there is no evidence of poleward range expansion into the area predicted to become suitable in future, despite good evidence for positive population growth trends in poleward populations. This study is among the first to show a marked lag between trailing edge population extinction and leading edge range expansion in a species experiencing anthropogenic climate change impacts, a pattern likely to apply to most sessile and poorly dispersed organisms. This provides support for conservative assumptions of species' migration rates when modelling climate change impacts for such species. *Aloe dichotoma's* response to climate change suggests that desert ecosystems may be more sensitive to climate change than previously suspected.

Keywords

Bioclimatic modelling, desertification, extinction, global warming fingerprints, migration, range shift.

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INTRODUCTION

Studies of the responses of terrestrial organisms to twentieth century warming have focused on range shifts of motile organisms (e.g. Hersteinsson & Macdonald, 1992; Parmesan *et al.*, 1999; Warren *et al.*, 2001; Parmesan & Yohe, 2003), stressing poleward range boundary extensions (Parmesan *et al.*, 1999). The studies of sessile organisms (Keeling *et al.*, 1996;

Menzel & Fabian, 1999; Abu-Asab *et al.*, 2001; Fitter & Fitter, 2002) have focused on non-lethal changes in the growth patterns. Both types of studies have focused most frequently on only a portion of a species' range.

There is concern that the adaptive responses of sessile organisms to rapid climate change may be constrained, thus causing population extinctions at the so-called 'trailing edge' of species' geographical ranges that are shifting in response to a

changing climate (Davis & Shaw, 2001). Such trailing edge extinctions should be first detected in terrestrial organisms that occupy extreme climatic environments such as deserts, where climate-related stresses exert direct control over population processes, especially at range margins (Jordan & Nobel, 1979). It is implicitly assumed by bioclimatic modelling approaches that trailing edge extinctions will be accompanied by simultaneous leading edge range expansions (Parmesan *et al.*, 1999), but lags in population expansions due to limiting rates of dispersal and establishment (Pitelka, 1997) undermined this assumption, especially for sessile species. Such lags have been observed, for example, in the difference in responsiveness of alpine plant range responses relative to mobile organisms such as butterflies (Walther *et al.*, 2002), and predicted for temperate zone American trees (Iverson *et al.*, 2004). Such constraints are likely to squeeze the ranges of non-motile organisms between a zone of active population die-back and of constrained expansion, thereby raising their risk of extinction, at least temporarily, even if climate change trends begin to stabilize.

Here we investigate impacts of regional climate change on population die-back in the long-lived, giant Namib Desert tree (*Aloe dichotoma* Masson), prompted by casual observations of widespread mortalities apparently induced by drought (i.e. water balance constraints). We test whether this pattern of population level mortality is in fact consistent with water balance changes, and furthermore, whether a spatial pattern consistent with the expected signal of anthropogenic climate change exists (i.e. higher mortality in equatorward, trailing edge sites, and lower mortality or stable/growing populations at poleward, leading edge sites). Such a pattern of die-back would provide credible evidence for the first time of the negative impacts of anthropogenic climate change on a sessile desert organism of the southern Hemisphere, especially if it could be linked with observed regional climatic changes, is consistent with modelled climate changes, and concurs with future projections of anthropogenic climate change impacts.

To accomplish this test, we conducted a detailed population census and related studies on this plant species throughout its entire geographical range in the Namib Desert and adjacent arid regions of southern Africa (a reach of roughly 11 degrees of latitude, between $\sim 32^\circ$ S and 21° S), in a region projected to experience significant warming and drying due to anthropogenic climate change (Hulme *et al.*, 2001). The stem-succulent growth form, succulent leaves, and shallow root systems of this species are common adaptations for rapid absorption and storage of water to allow survival through frequent droughts (Jacobsen, 1960; Barkhuizen, 1978). Individuals grow up to 10 m tall and usually occur in dense populations of up to 10,000 trees. A long life span [at least 200 years (Vogel, 1974) and possibly up to 350 years], and large geographical range ($\sim 200,000$ km²) make this a useful subject for a study of the impacts of long-term climate trends. In particular, because dead individuals decay relatively slowly *in situ*, often remaining standing for many years, it is possible to obtain a comparable measure of population mortality throughout the species' range.

METHODS

Characteristics of *Aloe* population mortality and mean individual condition

Where possible, we selected large, discrete populations and measured 100 live individuals in the densest part of each. We measured smaller populations where they provided a useful extension to the species' range and where no larger populations could be found. In such cases, the entire population was measured. Estimates for each live individual included degree of fungal pathogen infection of leaves and trunk (scores from 0 = no infection to 3 = severe infection); extent of apparent animal damage to the stem or trunk (scores from 0 = no damage to 3 = severe damage); the percentage of the total potential canopy that had been shed; and the percentage of the total potential canopy in which leaf abscission (shedding) had occurred. These statistics were averaged per population in the final analysis.

The number of dead trees within the area covered by a minimum polygon around the sampled live trees was used to derive the percentage of each population's mortality. In order to test this method for representivity of the whole population, we also used a 1000 \times 3 m linear transect spanning the population's altitudinal range and passing through its densest part to derive an estimate of population density. This provided a second estimate of relative mortality that was in agreement with the first estimate. Mortality from the transect analysis of mortality was positively correlated with that calculated from the survey method ($r = 0.86$, $n = 36$, $P < 0.001$, slope 0.86, intercept 5.15) with the intercept of this regression not significantly different from 0, and the slope not significantly different from 1.

Matched photographs

Photographs of *A. dichotoma* populations recorded 41–98 years previously were relocated and precisely matched using techniques broadly described by Rohde (1997). We counted all visible individuals in both of each pair of matched photographs (i.e. original and recent), and calculated the mean annual population change as a percentage from the equation:

$$N_{\text{recent}} = N_{\text{original}} \cdot r^t$$

or

$$r = (N_{\text{recent}}/N_{\text{original}})^{1/t}$$

where N_{recent} is the total number of individuals in the recent photograph, N_{original} the number in the original photograph, r is the compounded annual growth rate (which is multiplied by 100 to convert to percent), and t is the time difference in years between the photographs. Mean birth and death rates could also be calculated from the photographs but are not reported here.

We attempted to track the rate of decay of dead individuals between matched photographs, because a potential latitudinal bias in decay rates might skew measures of mortality (e.g. a potentially slower decay rate at drier sites towards the equator may allow more dead individuals to accumulate). Long-term

monitoring has now been established to measure decay rates of dead trees at different sites across the range, but at this stage we assume that decay rates are consistent throughout *A. dichotoma*'s range. The lack of geographical trends in fungal infection of both leaves and trunks supports this assumption, and it is even possible that decay rates are higher towards the equator with higher insolation levels and longer days leading to more rapid photo-degradation. None of the dead trees visible in the initial photographs was apparent after the 41–98 years interval between repeat photographs, indicating that we are reporting mortality trends in the past 40 years at most.

Climate records

To examine recorded past climatic trends within *A. dichotoma*'s range, we used data from the 15 stations in Namibia and north-western South Africa from which temperature records for at least 24 years were available (Table 1). In order to ensure that no periods of inconsistency or inaccuracy occurred in the records, we tested each time series for stationarity by visually assessing deviance from a straight line when cumulative temperature and rainfall values for neighbouring stations were plotted against each other (Gordon *et al.*, 1992). No stationarity effects were apparent. An index of water balance was calculated from this data set, as the difference between precipitation and potential evapotranspiration, the latter calculated using monthly means of mean daily temperature and total monthly precipitation (Thorntwaite, 1948). Annual trends (calculated from April to March in order to represent a growth year) were analysed using Robust MM Regression (Rosseeuw & Yohai, 1984).

In order to test the relationship between recorded changes in water balance and observed *A. dichotoma* population mortality,

water balance data from eight stations that were within 100 km of one or more study populations were used in a simple regression analysis. A single coastal station that qualified for this analysis was not considered due to the likely steep environmental gradient towards the interior from its coastal position.

We modelled adult mortality of *A. dichotoma* using generalized linear models with a binomial distribution and logistic link function (McCullagh & Nelder, 1989). In order to test if measures of the condition of adult individuals and adult mortality throughout the entire range of the species could be related to climate change over the latter half of the twentieth century (the maximum period over which dead individuals could be observed), we also developed a set of key climate parameters for 1960 and 2000, using the CRU CL 2.0 dataset (New *et al.*, 2000) to represent current climate (2000), and the GCM HadCM3 to derive modelled changes between 1960 and 2000 (incorporating both natural and anthropogenic sources of climate change). The CRU data were then adjusted using modelled changes to provide matching 1960 climate surfaces for each study site. These variables were used as explanatory variables in the generalized linear modelling, as was the mean altitude of the study site, and its latitude. Latitude data were converted to a biologically more meaningful measure of mean annual solar angle calculated by summing the zenith of the sun at midday for each day of the year, dividing by 365 and subtracting this value from 90°. The resulting index is the average angle of the sun above the horizon at noon – large values indicate high mean annual solar angle.

Bioclimatic modelling

To produce future scenarios of the possible impacts of climate change across *A. dichotoma*'s range, we used the generalized

Table 1 Stations in Namibia and South Africa within the range of *Aloe dichotoma* Masson at which temperature and rainfall records were available for 24 or more years. The table includes the mean decadal temperature change (°C) and the mean decadal water balance change (mm) for each station. Figures in bold were found to show statistically significant trends ($P < 0.01$) using robust regression.

Weather station	Latitude (degrees South)	Longitude (degrees East)	Start date	Time-series duration (years)	Decadal temperature change (degrees)	Decadal water balance change (mm)
Okaukuejo	19.183	15.917	1975	26	0.213	-3.66
Sitrusdal	19.933	16.383	1976	24	0.481	-11.25
Windhoek	22.567	17.100	1960	43	0.199	-4.34
Keetmanshoop	26.533	18.117	1970	31	0.269	-2.34
Luderitz	26.633	15.100	1960	39	0.062	-1.07
Upington	28.450	21.250	1952	51	0.308	-1.37
Alexander Bay	28.620	16.480	1952	50	0.141	-1.02
Henkries	28.970	18.100	1960	41	0.273	-2.39
Douglas	29.070	23.750	1976	24	-0.012	0.56
Pofadder	29.130	19.380	1941	59	0.170	0.43
Port Nolloth	29.230	16.870	1960	42	0.191	-0.74
Okiep	29.620	17.880	1959	27	0.163	-1.55
Prieska	29.670	22.750	1959	44	0.364	-0.48
Brandvlei	30.470	20.480	1960	32	0.075	-1.80
Calvinia	31.470	19.770	1959	44	-0.031	-0.86

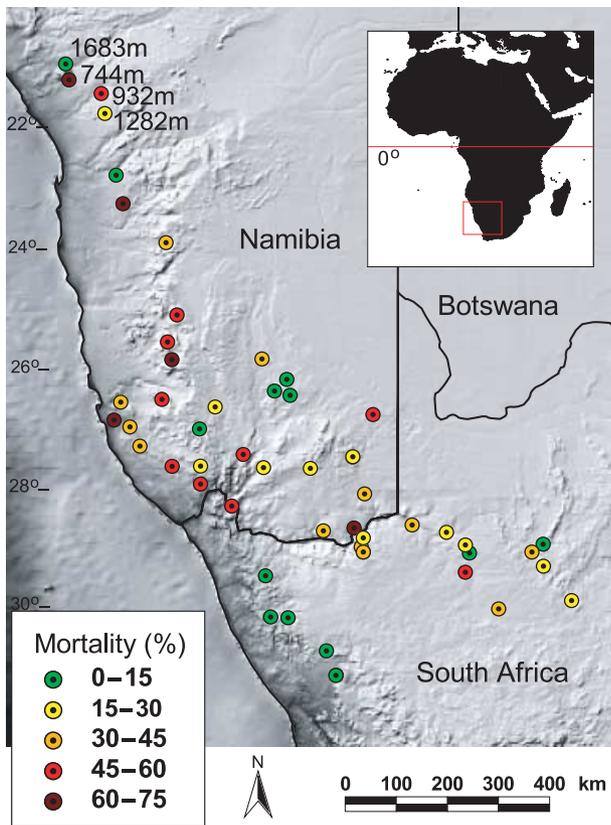


Figure 1 Map showing mortality of *Aloe dichotoma* Masson populations across the species' range. Green circles indicate populations with low mortality and red circles represent progressively higher mortality. Lighter and darker shades of background grey represent lower to higher altitudes respectively. For the four northernmost populations, altitudes have been specified on the map because two of the populations occur on inselbergs. Mortality appears patchy, but a general trend of lower mortality in southern populations is apparent, irrespective of altitude, and northern populations have increasingly greater mortality, except at high altitudes.

additive modelling (GAM) function in the bioclimatic niche modelling tool BIOMOD (McCarthy *et al.*, 2001; Thuiller, 2003). The CRU CL 2.0 data set (New *et al.*, 2000) was used to represent current (2000) climate, and future (2050) climate modelling was based on the moderate climate change projections produced by the HADCM3 General Circulation Model (Gordon *et al.*, 2000) using the B2 IPCC SRES scenario (Nakicenovic & Swart, 2000). The sampled distribution of *A. dichotoma* and matching climatic surfaces at a resolution of 10 min were then used to derive an optimal bioclimatic model of *A. dichotoma*'s current geographical range, and its response to future climate change modelled spatially.

RESULTS AND DISCUSSION

Population-level mortality for the 53 populations examined throughout the range of *A. dichotoma* ranged between 2% and 71% (mean = 32.1 ± 20.0%, Fig. 1), with a significant trend of

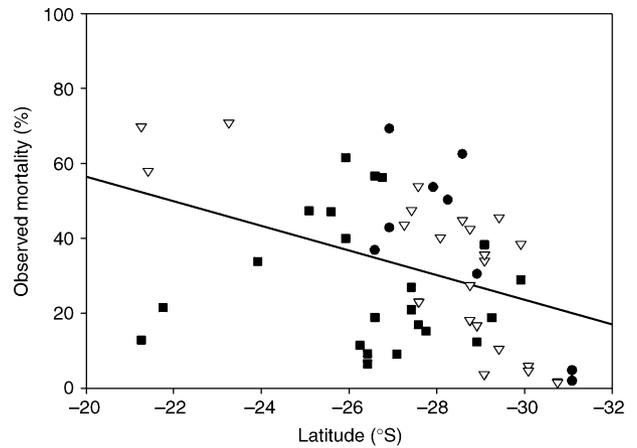


Figure 2 Graph showing the relationship between latitude (degrees South) and *Aloe dichotoma* Masson population mortality. Mortality follows a latitudinal cline of increase from the poleward to the equator-ward side of the species' range, as indicated by the solid regression line ($r = 0.393, n = 53, P = 0.004$). The mean altitudes at which these populations occur are indicated by ● (< 700 m), ▽ (700–1000 m) and ■ (> 1000 m). When regressed against altitude, the residuals of the above regression produced a significant trend ($r = 0.331, n = 53, P = 0.016$) showing that where mortality was lower than expected from the latitudinal trend, this can be explained by higher altitude of the population and conversely, that populations at low altitudes have higher than expected mortality. In combination, these results strongly suggest that *A. dichotoma* is undergoing the beginning of a systematic poleward and upwards range shift.

decreasing mortality from the equatorial to the poleward regions of the species' range ($r = 0.393, n = 53, P = 0.004$; Fig. 2). A regression of the residuals from this analysis against the altitude of each population also produced a significant trend ($r = 0.331, n = 53, P = 0.016$) – showing that low-altitude (warmer) populations show higher mortalities than do high-altitude (cooler) populations, particularly at the equatorial range edge. Overall, populations at poleward and high-altitude extremes tended to experience minimal mortality. Thus, population level mortality decreased along latitudinal and altitudinal clines in a pattern consistent with that expected under climate change, with the highest mortality generally in the 'trailing edge' (Davis & Shaw, 2001) of the species' geographical range.

We also sought to describe these data using more biologically meaningful explanatory variables. The simplest biologically meaningful model fitted using the generalized linear model included four explanatory variables and accounted for 27.2% of the deviance (Table 2). The explanatory variables were all abiotic. As mean annual solar angle increased latitudinally towards the equator, the probability of encountering live individuals in a given population decreased. The probability of encountering live individuals also increased with altitude. When both evapotranspiration in 1960 and the difference in evapotranspiration between 1960 and 2000 were included as explanatory variables, the model suggested that the probability of encountering live individuals decreased at sites that had experienced larger

Table 2 Results of the generalized linear model (binomial distribution, logit link function) relating the number of *Aloe dichotoma* Masson individuals which were alive in a given population to abiotic explanatory variables. This model explained 27.2% of the deviance. The *P*-values associated with all regression coefficients were less than 0.001 (i.e. $t_{45} > 3.52$).

Parameter	Regression coefficient	Standard deviation	<i>t</i> -value t_{45}
Constant	5.74	1.15	4.99
Mean annual solar angle (°)	-0.1374	0.0168602	-8.20
Altitude (m)	0.001052	0.000102	10.30
Evaporation 1960 (mm)	0.03186	0.00287	11.11
Evaporation difference (mm) (2000–1960)	-0.09144	0.00911	-10.03

Table 3 Results of the generalized linear model (binomial distribution, logit link function) relating the number of juvenile *Aloe dichotoma* Masson individuals which were alive to explanatory variables. The binomial totals were the number of individuals, both dead and alive, at the study sites. This model explained 14.7% of the deviance. The *P*-values associated with all regression coefficients were less than 0.001 (i.e. $t_{48} > 3.50$).

Parameter	Regression coefficient	Standard deviation	<i>t</i> -value t_{48}
Constant	3.2556	2.068	1.5863
Mean annual solar angle (°)	-0.132690	0.0294331	-4.51
Evaporation 1960 (mm)	0.0292947	0.0047768	6.146
Evaporation difference (mm) (2000–1960)	-0.0677	0.00142	-4.78

increases in evapotranspiration over the past four decades (Table 2).

The generalized linear model for juveniles included three explanatory variables (altitude was not found to be a significant explanatory variable) and accounted for 14.7% of the deviance (Table 3), about half that accounted for by the model for live adult plants. Nonetheless, the model for juveniles suggests the same general pattern as for live adult plants. We therefore conclude that the same broad factors that lead to mortality also inhibit germination, or diminish recruitment by causing juvenile mortality.

Repeat photographs also suggest a latitudinal cline in *A. dichotoma* mortality. The rates of change in population size varied between decreases of 4.73% per year and increases of 0.91% per year. These survival rates were negatively related to the index of mean annual solar angle ($r_7 = -0.70$, $P = 0.036$), and negatively related to latitude (Fig. 3), supporting the 'snapshot' observation of greater proportions of dead plants towards the equator shown in Fig. 2. The altitudinal range among the repeat photograph sites (300 m) was too small to test for altitude effects, especially given this small sample size.

Repeat photographs show that during the twentieth century, equatorward populations have experienced declines in population numbers of between 0.7% and 5% per annum, and poleward populations have increased their population size by between 0.25% and 0.91%. There is, further, a significant linear relationship between latitude and population growth rate ($r = 0.70$, $n = 9$, $P < 0.05$, Fig. 4), and while it is possible that this relationship represents a threshold response, the data presented here, especially for equatorward populations, are too few to test this hypothesis more fully.

What is the mechanism causing adult mortality in equatorward populations? In a large number of *A. dichotoma* individuals, we observed that terminal leaf rosettes slowly withered and eventually dropped to the ground, while the apical tips of supporting branches died under drought conditions (we term this 'shoot shedding'). These branches never re-developed leaves, presumably due to the loss of apical meristem. Our field observations and anecdotal evidence from local experts strongly suggest that shoot shedding is a typical response to water deficits in this species (Van Jaarsveld & Chown, 2001). We found a strong logarithmic relationship between the mean percentage of individuals' canopies lost to shoot shedding and population mortality ($r = 0.777$, $n = 24$, $P < 0.001$, Fig. 5), suggesting that high-mortality populations are experiencing long-term water stress.

Water stress in plants is the result of the interaction between precipitation and atmospheric vapour pressure deficit, itself a function of air temperature and relative humidity. Desert rainfall is variable and unsuited to trend analysis especially given the length of records available, but atmospheric warming is more reliably detected. Increasing air temperature is a key controller of plant water status, and would increase the rate of water loss from the succulent leaves of this CAM-photosynthetic species, especially during its night-time stomatal opening period, thereby hastening leaf and shoot desiccation. This stress is well captured by considering air temperature, the evaporative demand of the air, and water balance that combines these two measures.

Continental-scale analyses of temperature records for the twentieth century indicate that the Namib has undergone an increase in temperature as well as a reduction in precipitation (Hulme *et al.*, 2001). Local climatic records revealed significant

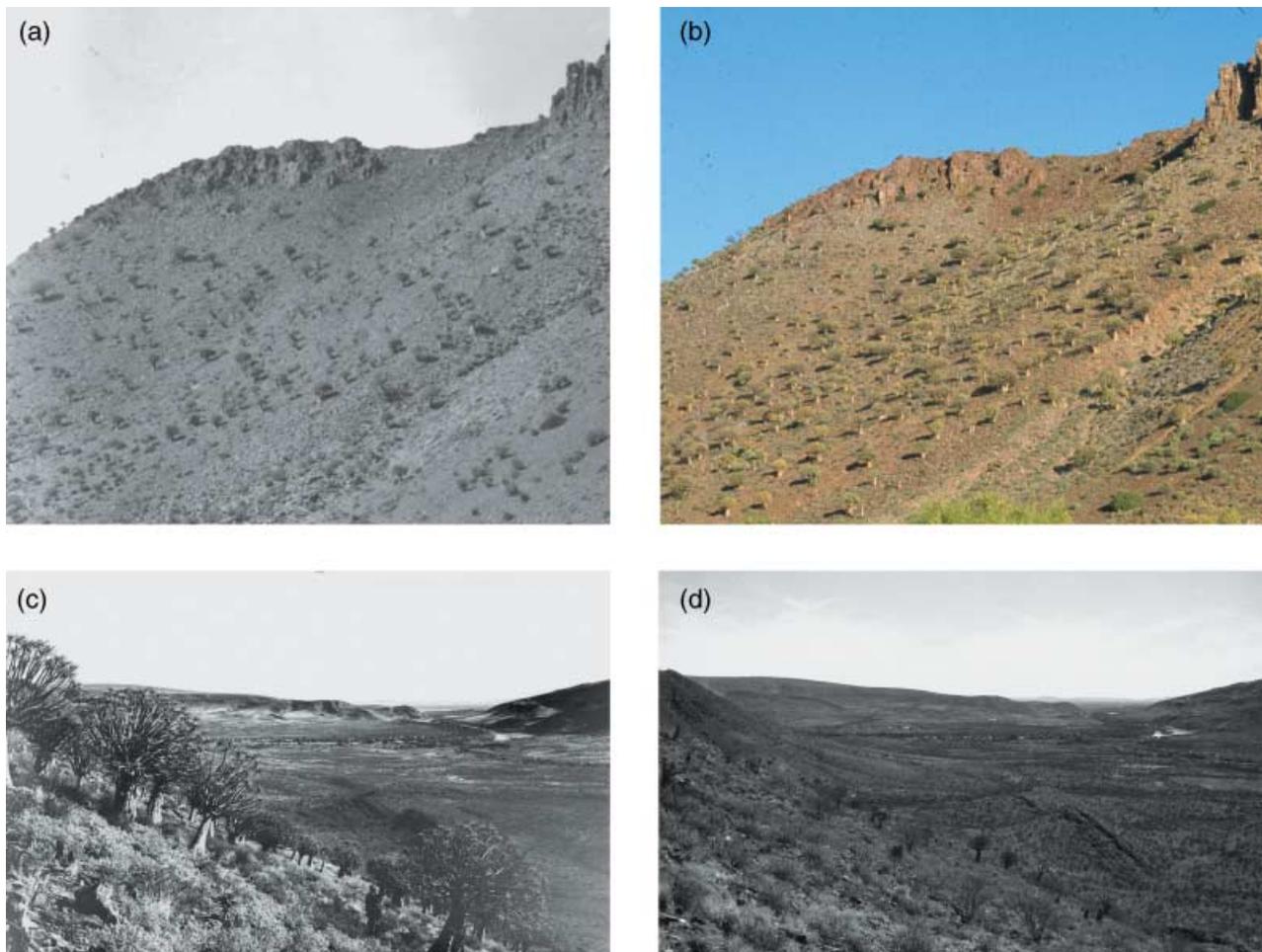


Figure 3 Repeat photographs of populations of *Aloe dichotoma* Masson taken in 1904 and 1918 and precisely matched in 2002. Photos (a) and (b) were taken at Hantamsberg, Calvinia (31°12.5′-South, 19°43.3′-East) in 1904 (Marloth) and 2002, respectively. From this and another pair of matched photographs taken at the site, a decadal population increase of 0.76% per year is inferred. Photographs (c) and (d) were taken in 1918 (Evans) and 2002 in the Westerberg, near Koegas (29°19.9′ S, 22°18.5′ E). A decadal population decrease of -0.85% per year is inferred from two matched photograph pairs taken at this site.

regional climate warming. We examined temperature and rainfall records from all available long-term weather stations in the regions in which *A. dichotoma* occurs (see Table 1). Fifty-three per cent of stations showed significant increases in temperature over the last 25–60 years while none showed a significant decline. There was no relationship between the duration of weather stations' time series and the magnitude of their mean temperature change. The mean decadal increase across all stations during this interval was 0.2 ± 0.1 °C. Water balance, a composite measure of temperature and rainfall reflecting the water available to plants, showed a significant decline at 33% of stations over the last 25–60 years. No stations showed a significant increase in water balance over this period. The relative severity of cumulative water stress in *A. dichotoma* is reflected by the percentage of months during the past decade in which water balance fell below -90 mm. Population mortality at study sites within 100 km of the long-term weather stations is positively correlated with this measure of cumulative water stress ($r = 0.491$, $n = 22$, $P = 0.021$; Fig. 6), strongly suggesting that a combination of water and heat

stress is responsible for the increased mortality in declining *A. dichotoma* populations.

Although the areas in which *A. dichotoma* occurs are too arid for agriculture, parts of its range are used for stock and game farming. The species is considered to be unpalatable, yet we observed a degree of herbivory by sheep, goats, donkeys, antelope, baboons, and porcupines, but no correlation between canopy herbivory and population mortality. We found mortality to be weakly related to degree of stem bark damage, presumably by herbivores ($r = 0.406$, $n = 35$, $P < 0.02$), but as it is unrelated to herbivore density (measured as the frequency of dung pellets in the area; $r = 0.11$, $n = 28$, $P > 0.56$), we conclude that some herbivory of *A. dichotoma* trunks (likely by porcupines) probably occurs only under conditions of extreme drought when more palatable food and water sources are unavailable. However, when we examined all other reasonable explanations for the observed mortality patterns in *A. dichotoma*, such as intraspecific competition, pathogen infection, pollution damage, and including exposure to human or animal persecution, we found that the

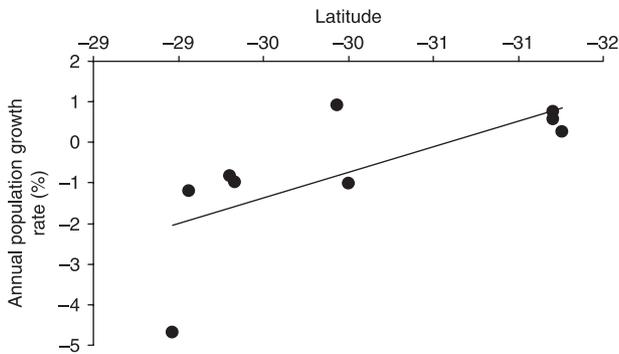


Figure 4 The relationship between latitude and mean annual population growth rate of *Aloe dichotoma* Masson populations as derived from repeat photographs taken between 41 and 98 years apart ($r = 0.70$, $n = 9$, $P < 0.05$).

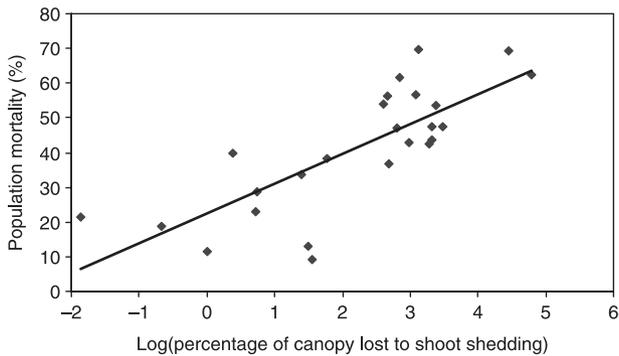


Figure 5 The relationship between *A. dichotoma* Masson population-level mean loss of canopy due to shoot shedding and population-level mortality ($r = 0.777$, $n = 24$, $P < 0.001$).

addition of any of these factors as explanatory variables to the generalized linear model of Table 2 resulted in only small changes to the regression coefficients for the abiotic variables, but did not modify the overall patterns described earlier.

Although the southern third and northern two-thirds of *A. dichotoma*'s range are separated by the political border between Namibia and South Africa, neither historical nor current land use and management methods differ markedly between the two countries. The areas in which *Aloe dichotoma* occurs are generally too sparsely vegetated for interspecific plant competition to limit recruitment success. The 'nurse rocks' and 'nurse shrubs' in which juveniles were frequently found germinating, probably due to the ameliorated microhabitats they create, are present at almost all localities, throughout the species' range and in the regions south of it.

Finally, niche-based spatial modelling techniques (Thuiller, 2004) show changes between the years 2000 and 2050 in the frequency of occurrence of *A. dichotoma* within each 10-min band of latitude that indicates a projected poleward shift in this species' geographical range that is consistent with the local extinction of equatorward populations currently showing high rates of mortality (Fig. 7). The mean altitude of 10' pixels in which climate change models project the species' presence

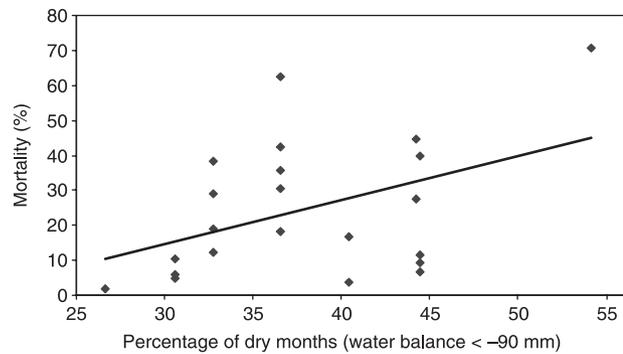


Figure 6 The relationship between the percentages of very dry months in the last 10 years (when water balance fell below -90 mm) and population-level mortality in *Aloe dichotoma* Masson at sites within 100 km of the weather stations at which mortalities were measured ($r = 0.49$, $n = 22$, $P < 0.02$).

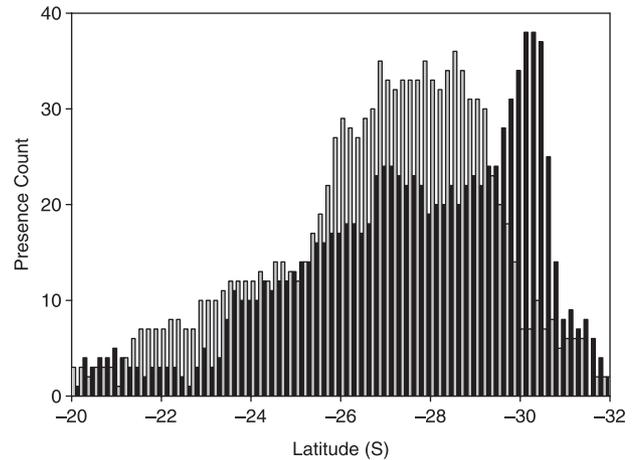


Figure 7 Comparisons between present and bioclimatically modelled future projections of the distribution range of *Aloe dichotoma* Masson. The figure shows the modelled frequency of *A. dichotoma* in each 10-min latitude band of its range for 2000 (grey bars) and 2050 (black bars). The projected mean latitude of the species' range shifts from -26.68 ± 2.81 degrees South in 2000 to -27.90 ± 2.5 degrees South in 2050. This equates to a mean altitudinal shift of 16 m per decade and a poleward range shift of 23 km per decade.

increases from 806 ± 354 m in 2000 to 885 ± 329 m in 2050 while the projected mean latitude shifts from $26.68 \pm 2.81^\circ$ S in 2000 to $27.90 \pm 2.5^\circ$ S. These modelled shifts equate to a mean altitudinal increase of 16 m per decade and a poleward range shift of 23 km per decade, considerably higher than the 6.1 ± 2.4 km per decade poleward range shifts recently collated for a broad variety of organisms including woody and herbaceous plants (Parmesan & Yohe, 2003). Given an estimated recruitment frequency of 15 years, *A. dichotoma* must disperse approximately 35 km southwards and 24 m upwards with each recruitment event in order to keep pace with its climatic niche.

No records exist of new populations of this conspicuous species establishing in areas projected to become suitable for the

species in the poleward parts of its range. This is despite having copious small, light wind-dispersed seeds and that it has been successfully planted, and recruits autonomously, well beyond its poleward range margin (I. Oliver, pers. comm.). While soil type and biotic interactions (e.g. competition) seem an obvious limiting factor for poleward migration for this species, soils of similar nature are clearly widespread further South of its southern range margin, and the issue of competition is not likely to be important in these open, low-density communities. More work is needed to determine if any of these factors, or simply the availability of establishment sites, may be limiting range expansion of this species.

The Succulent Karoo biodiversity hotspot lies almost entirely within the range of *A. dichotoma*, and represents the planet's richest arid biodiversity hotspot by far (Myers *et al.*, 2000). The hotspot contains over 5000 species, 40% of which are endemic (Cowling & Hilton-Taylor, 1999). Recent empirical work has shown the sensitivity of endemic Karoo succulent species to warming treatments in the field (Musil *et al.*, 2005).

Although it is extremely widespread and abundant, *A. dichotoma* qualifies as Endangered (criterion A3ce) according to the IUCN Red List Categories and Criteria for Red List Assessments (Standards and Petitions Working Group, 2005) based on population loss corresponding to modelled range loss (assuming a linear relationship) under a 'null migration' scenario. But in comparison with other species in its biome and even globally, succulence, gigantism, and a broad distribution range and bioclimatic niche probably make *A. dichotoma* relatively more robust to drought and climatic fluctuation. The species therefore provides a conservative indicator of the impacts of regional warming and drying in the Namib region. While insufficient data are available to model range shifts of all species, it seems likely that doing so would result in a substantial increase in the number of species qualifying as Threatened (defined as 'in immediate danger of extinction') according the IUCN Red Listing Categories and Criteria (Standards and Petitions Working Group, 2005). Thus, a large and rapid shift in conservation approach is clearly needed.

CONCLUSIONS

Our results suggest that *A. dichotoma*, a species with an extended juvenile period, is experiencing population declines at its equatorward limits (i.e. its 'trailing edge', *sensu* Davis & Shaw, 2001) in response to anthropogenic climate change trends. Generalized linear modelling shows that *A. dichotoma* populations in equatorward regions are relatively closer to critical climate limits, and that observed and modelled climate changes in the latter half of the twentieth century have likely caused these to be exceeded, resulting in elevated mortality and population declines. At the same time, we report the species' failure to expand polewards in relation to its shifting climatic envelope, despite good evidence suggesting positive population growth trends in established populations at poleward latitudes.

The geographical range of *A. dichotoma* is therefore apparently becoming progressively squeezed between an advancing equatorward zone of range contraction due to population declines, and a poleward zone of lagging range expansion. This study is

among the first to document such an imbalance between contraction and expansion trends by looking at population status throughout the entire geographical range of a species, but the pattern could well be repeated for sessile and poorly dispersed organisms globally.

Many projections of climate change impacts on biodiversity attempt to incorporate uncertainty due to migration constraints by contrasting 'full migration' and 'null migration' assumptions (e.g. Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller, 2004). The findings provided here provide support for conservative assumptions of migration rate in sessile organisms, with important implications for projections of species diversity under future climate change scenarios.

Global assessments suggest that deserts will show a relatively muted biodiversity response to climate change (Sala *et al.*, 2000). The results of this study argue against this conclusion and suggest that desert ecosystems are likely to become increasingly hostile to endemic biota, and thus more species-poor with intensifying global warming.

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