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Climate change sentinel or false prophet? The case of Aloe dichotoma

Title: Climate change sentinel or false prophet? The case of *Aloe dichotoma.*

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Aim

Previous research suggests that equatorward populations of the iconic arborescent succulent *Aloe dichotoma* Masson are contracting in response to recent anthropogenic climate change (ACC) in southern Africa. However, previous studies didn't account for small-scale spatial heterogeneity, latitudinal climatic disjunctions, or when mortality occurred. We reassess *A. dichotoma's* suitability as an indicator species and comment on pitfalls in the selection of species with similar life-history characteristics.

Location

South-western Africa.

Methods

A 15 000 km distribution-wide roadside visual survey was conducted to capture demographic patterns and provide the means for extracting tightly-coupled climate profiles for the species. Rainfall and temperature gradients were assessed for latitudinal discontinuities indicating distinct equatorward-poleward climate zones. Repeat photographs and reference individuals were used to develop an index for dating the approximate time-since-death of dead trees at 14 latitudinally-spaced populations.

Results

The proportion of dead individuals was greatest within the southern third of the latitudinal distribution rather than at the equatorward range limit. The equatorward summer rainfall zone (SRZ) was significantly drier, rainfall more variable and temperatures hotter compared to the poleward winter rainfall zone (WRZ). This difference was associated with a generally greater proportion of dead individuals in the SRZ, and greater proportion of juveniles in the WRZ. Furthermore, juveniles appeared more sensitive to drought stress while adults were more resilient. Most mortality occurred several decades ago, was not more recent at the equatorward limit, and was drawn from the more drought resilient adult stage class.

Main conclusions

A. dichotoma mortality (and recruitment) patterns reflect prevailing differences in the SRZ and WRZ climate, while differing juvenile and adult drought stress tolerances and windthrow-mediated mortality reinforces this pattern. This, and strong indications of non-recent death suggest ACC is not responsible for observed mortality. An alternative hypothesis for current demographic patterns which incorporates palaeo-climatic evidence and *A. dichotoma* life-history characteristics is proposed. Long-term climate trends, recruitment-mortality dynamics, and potential climatic discontinuities should be considered before advancing species as indicators of ACC.

INTRODUCTION

Shifts in species ranges and physiology are now well documented responses to anthropogenic climate change (ACC) (Walther *et al.*, 2002; Parmesan, 2006; Fordham *et al.*, 2012). Several models predict shifts in species distributions in southern Africa (Midgley *et al.*, 2003; Midgley & Thuiller, 2011), but examples of observed changes have been slow to emerge. One exception is the iconic long-lived succulent desert tree, *Aloe dichotoma* Masson (recently renamed *Aloidendron dichotomum*), which has been heralded as the first ACC indicator plant species in southern Africa (Foden, 2002; Foden *et al.*, 2007; Foden & Stuart, 2009).

A. dichotoma's distribution covers an extensive area of ~200 000 km^2 and a latitudinal distance of over 1000 km in the arid western regions of the Northern Cape in South Africa and south-central Namibia. It is morphologically similar to two closely related sub-species, *A. pillansii* and *A. ramosissima*, which have more restricted distributions. *A. dichotoma* is slow growing, taking at least 20 to 40 years to reach reproductive maturity, recruits infrequently at an estimated interval of 15 years or more, and has a long lifespan of between 200 and 350 years (Foden, 2002; Foden *et al.*, 2007; Hoffman *et al.*, 2010). Growth form differences in height and branching frequency have been observed between individuals occurring at the equatorward versus poleward extremes, but what these growth form differences mean in terms of growth rate, reproductive potential and longevity have not been investigated (but see Drezner, 2014). Trees occur either as isolated individuals or more frequently in loose groupings which can form denser 'forests'. *A. dichotoma* is pollinated by certain bird species and bees, and releases wind-dispersed seeds with low dormancy from tall, erect inflorescences held in the canopy (Cousins & Witkowski, 2012).

In a study which sampled numerous discrete *A. dichotoma* populations across the latitudinal distribution, tree mortality was reportedly highest at the apparently hotter lagging (equatorward)

end of the distribution, and recruitment highest at the cooler leading (poleward) end (Foden *et al.*, 2007). Given strong evidence for regional warming associated with ACC (Kruger & Shongwe, 2004; Midgley *et al.*, 2005, Haensler *et al.*, 2010) this is arguably the pattern one might expect from a species impacted by climate change and led the authors to conclude that mortality was the result of recent equatorward warming which exceeded threshold water balance tolerances, resulting in mortality (Foden *et al.*, 2007; Midgley *et al.*, 2009). This desert-adapted species has since been widely cited as a climate change sentinel, while more general implications are that desert species and ecosystems may not be as resilient to ACC as previously thought (Foden & Stuart, 2009; Jackson & Sax 2009; Thomas, 2010; Dawson *et al.*, 2011).

Despite the evidence in favour of upholding *A. dichotoma* as an important southern African indicator species, the link between this warming and *A. dichotoma* mortality patterns is less certain (Hoffman *et al.*, 2010). In addition, while the direction of temperature trends is clear, historical rainfall trends in the region have not shown any consistent pattern of change (Hoerling *et al.*, 2006; New *et al.*, 2006). *A. dichotoma's* distribution stretches across two major climatic zones delineating separate biomes (Rutherford & Westfall, 1994). Equatorward populations are located within the Namibian summer rainfall zone (SRZ) characterized by a highly variable and hot summer convective rainfall regime (Tyson & Preston-Whyte, 2000). Conversely, poleward populations in the Northern Cape of South Africa are associated either with the slightly more mesic south-eastern end of the SRZ, or the winter rainfall zone (WRZ) in the west. Significantly, the WRZ climate is characterized by more consistent frontally-derived rainfall received in the cooler winter months (Tyson & Preston-Whyte, 2000). Previous studies spanning the winter-summer rainfall boundary have consistently found proportionally higher *A. dichotoma* mortality in SRZ populations, even at the poleward limit of the SRZ (Kaleme, 2003; Foden *et al.*, 2007). On the other hand, mortality throughout the WRZ is generally lower and recruitment greater. The prevailing northern summer

and southern winter climatic regimes might therefore act as important determinants of mortality and recruitment success.

Archival sources such as botanical field notes (Rutherford *et al.*, 2003) and historical photographs (Hoffman *et al.*, 2010) indicate that high mortality and low recruitment was already widespread across the species' range in the early to mid-20th century. *A. dichotoma's* stem and branches are comprised of a tough, fibrous tissue and consequently skeletons decay slowly under arid conditions. In rare instances large skeletons can even remain *in situ* for up to a century (Hoffman *et al.*, 2010). Observed mortality, especially with respect to large dead skeletons, may therefore be decades-old and not attributable to recent warming. Despite this, previous studies didn't assign a temporal signature to mortality, with the result that all recorded mortality was assumed to have occurred within roughly the preceding three decades (Foden *et al.*, 2007), arguably too short a time-frame in which ACC could convincingly be attributed as the cause (Parmesan *et al.*, 2011).

The above points highlight the need to revisit *A. dichotoma's* suitability as a southern African indicator species, but also more generally as an iconic desert succulent informing an international debate around the responses of long-lived desert-adapted species to changing climate. As such, our study addressed three fundamental issues which relate to the influence of ACC on *A. dichotoma* populations.

1) We designed a spatially continuous demographic sampling method across the species' latitudinal range to evaluate the validity of increasing equatorward mortality due to ACC.

2) We characterized differences between equatorward and poleward climatic regimes to understand what effect this might have had on *A. dichotoma* population dynamics.

3) We aimed to resolve the question of whether mortality was a recent response to ACC or part of a more gradual decline due to other factors, such as millennial-scale shifts in climate in

the region (Tyson *et al.*, 2000; Chase & Meadows, 2007) by categorizing skeleton ages since the time of death and determining the stage classes from which they were drawn.

We use our findings to draw attention to potential pitfalls in the selection of indicator species with similar life histories and distributional characteristics.

METHODS

A dual-scale sampling strategy, incorporating timing of mortality

Data collection comprised two separate approaches in order to a) capture basic demographic patterns spanning *A. dichotoma's* full geographical range, and b) sample certain populations in detail to better understand the timing of mortality (Fig. 1). Rapid distribution-wide sampling was achieved via an extensive roadside visual survey within the known distributional extent of the species. This entailed counting and assigning trees (both living and dead) to stage classes within successive 5 km transects (Nikon 8x42 binoculars), the beginning and end points of which were GPS marked (Garmin GPS60). Altitude at road level was noted and from this an estimate of the altitudinal range of *A. dichotoma* individuals in each transect was recorded. An estimate of the average lateral width of each transect, ranging between 200 m and 2 km (i.e. 100 m or 1 km either side of the road, respectively) was recorded in order to compute a density value per transect. If visibility was impaired due to glare or bad light, or excessively biased towards larger individuals due to obstruction by other vegetation, rockiness, etc., individuals and populations were excluded. Despite due care, the rapid visual survey approach likely under-represented very small juveniles, but this bias was considered to be latitudinally consistent. The roadside visual survey covered a distance of more than 15 000 km and recorded ~280 000 individuals.

[Figure 1]

Fourteen populations spaced at roughly equal intervals from equator to poleward latitudinal extremes were selected and where possible a minimum of 60 individuals (both living and dead) were sampled on each cardinal aspect, and capturing the full altitudinal range in each population. This amounted to a total of 2015 living and 1353 dead individuals. GPS position, basal

circumference at ground level and a stage class value for all sampled individuals was recorded. In addition, an estimated time-since-death value was recorded for each dead individual. This latter estimate was based on the rate of decay observed in several repeat photographs from different parts of the distribution (Hoffman *et al.*, 2010) and from repeated visits to reference individuals which had died since 2002. Structural criteria helped classify dead trees into one of six stages of decay (see Appendix S1). Additional tree-specific notes were made with regard to slope angle, dominant geology and signs of herbivore and pathogen damage, but preliminary data exploration didn't yield any consistent relationships between these factors and mortality (see also Foden, 2002) and they are therefore not discussed further.

Counted trees from both the roadside visual survey and 14 sampled populations were initially assigned to one of five stage class categories (juveniles, young adults, mature adults, senescents, and deads), using architectural criteria (see Appendix S2). In order to simplify analyses and interpretation, these categories were later collapsed from five to three stages, namely 'juveniles' and 'adults', representing low and high reproductive potentials respectively, and 'dead' individuals (see Appendix S2).

Density, proportional density and latitudinal gradients

Transect area and log-transformed (due to a five orders of magnitude difference in inter-transect absolute counts) count data were used to calculate density for transects where *A. dichotoma* was present. The proportional density of individual stage classes was calculated after removing transects containing less than 20 trees to prevent bias from transects with low counts. Proportional density was then averaged across half-degree latitudinal bands to assess latitudinal gradients.

A. dichotoma presence localities (i.e. ≥ 1 individual) along the roadside visual survey network of transects were used to extract climatic values from the well resolved (30 arc seconds or approx. 1 km) Worldclim interpolated climatic dataset (Hijmans *et al.*, 2005). These data, which included 15 rainfall and temperature variables, were averaged within corresponding half-degree latitudinal bands to construct coupled climate profiles for the species. An aridity index (AI) and measure of potential evapo-transpiration (PET) were also calculated according to Zomer *et al.* (2006) (see Appendix S3).

Mean temperature of the wettest quarter (TwetQ) was used to set the boundary between summer and winter rainfall zones as this represented a natural break point in the data. All transects with mean TwetQ greater than 15°C were classified as falling within the SRZ, and those equal to or less than 15°C, within the WRZ. This division was in near perfect spatial agreement with Schulze's (1997) map of precipitation seasonality in South Africa. Differences between the summer and winter rainfall zone climate were tested for statistical significance using *t*-tests assuming unequal variances.

Climate-stage class interactions

Proportional densities in the three stage classes are correlated and should thus be considered as a single multivariate response, rather than analysed as separate entities. Additionally, the proportions are constrained to sum to one, and thus analysing them directly using standard multivariate linear regression is inappropriate for reasons related to the so-called 'negative bias' problem (see e.g. Jackson, 1997). Aitchison's (1982) approach for dealing with proportions was adopted for analysing the relationship between proportional density and multiple climate variables. This approach focuses on the analysis of relative variation between components (i.e. between stage classes) rather than on absolute variation (which is constrained because of the

requirement that proportions/components must sum to one). It involves first transforming each

proportional density composition $[x_j, x_a, x_d]$ using the additive log-ratio transform into a new

vector, $\boldsymbol{y} = [\log(x_j/x_d), \log(x_a/x_d)]$. Here the choice of the dead category in the denominator is

arbitrary and does not affect the results because the coefficients that would have been obtained

under any other choice of baseline can be exactly recovered from the fitted model using log laws.

Any zero values in the denominator are replaced with a small positive constant (Martin-Fernandez

& Thio-Henestrosa, 2006). The transformed vector $\boldsymbol{y}$ can be thought of as containing 'co-ordinates'

defining two-dimensional vectors in unconstrained real space, which can be analysed using a

standard multivariate linear regression (MLR) model. A forward stepwise approach to model

selection was used, at each stage including the independent bioclimatic variable giving the largest

incremental reduction in error sums of squares, until no further variables were significant at the

10% level (R Core Team, 2013). Separate models were fitted for individuals falling in the summer

and winter rainfall zones.

RESULTS

Spatial distribution patterns of *A. dichotoma* in southern Africa

Both total *A. dichotoma* density and proportional density of individual stage classes displayed

considerable variability in space, often between adjacent 5 km transects (Figs. 2 & 3), highlighting

the utility of the continuous sampling approach in revealing areas of high and low recruitment and

mortality. A general pattern of increasing density was evident in a poleward direction (Fig. 2).

Density north of ~25°S was particularly low and populations more geographically isolated. This

was due to a longitudinal constriction in available mountainous habitat between the hyper-arid

Namib Desert to the west, and higher lying frost-prone areas to the east (Mendelsohn *et al.*, 2002).

Conversely, density and population size were generally greater south of the Gariep River, and

particularly within the WRZ. For example, the average density of live *A. dichotoma* individuals

within SRZ transects was 42.5 trees/km^2, while the density within WRZ transects was 191.1

trees/km^2. In addition, the proportion of transects that contained ≥1000 individuals was 20% in the

WRZ compared to ~7% in the SRZ.

[Figure 2]

With respect to specific stage classes, juvenile proportional density patterns indicated lowest

abundance between 23-26°S, increasing abruptly north of this to comprise 40% of total density

before declining again towards the northern range limit (Fig. 3). The southerly increase was more

gradual, eventually plateauing between 40-50% in the poleward WRZ. Adult individuals were

proportionally dominant within much of the Namibian SRZ, with densities frequently three times

that of juveniles and dead classes. Adult dominance decreased gradually south of ~25°S and from

~29°S adults were frequently co-dominant with juveniles. Dead proportional density was greatest

in areas bordering the Gariep River, and east and west of Karasberg in Namibia (i.e. between

approximately 28-29°S), while mortality was lowest within the Northern Cape WRZ in South Africa.

[Figure 3]

Associated climate and altitude patterns

A. dichotoma is distributed across complex altitudinal, rainfall and temperature gradients in both

the summer and winter rainfall zones (Fig. 4). Of the 15 bioclimatic variables analysed, 14 (as well

as altitude) indicated a statistically significant difference at the p < 0.001 level when comparing

summer and winter rainfall zones. For example, individuals in the SRZ were found, on average, over

230 m higher than those in the WRZ (t=12.0, df=290, p<0.001). Mean annual precipitation (MAP)

was significantly lower (by 44 mm) in the SRZ when compared to the WRZ (t=-14.8, df=312,

p<0.001), with the least rain falling at the equatorward extreme, at ~25°S, and within the Gariep

River valley, between 28-29°S (Fig. 4). Conversely, precipitation was both highest and least variable

at the south-eastern extreme of the SRZ and especially within the WRZ. Mean annual temperature

(MAT) was significantly greater in the SRZ compared to the WRZ (by 1.6°C; t=19.6, df=463,

p<0.001), peaking at the northern extreme of the range and within areas bordering the Gariep

River. Precipitation seasonality (i.e. coefficient of variation) indicated greater rainfall variability in

an equatorward direction (t=32.2, df=775, p<0.001), while a concomitant decrease in temperature

seasonality indicated warmer winters in the SRZ (t=11.4, df=599, p<0.001).

[Figure 4]

Mean precipitation (or temperature) of the wettest, driest, warmest and coldest quarters reflect

seasonal differences in temperature and the timing of rainfall (Fig. 4). In the SRZ, the amount of

precipitation falling in the wettest and warmest quarters (i.e. summer), compared to the driest and coldest (i.e. winter; note scale difference on y-axis), indicated that virtually the entire annual rainfall complement was received within the warmer summer months, and that almost no rain fell outside of this period. The deficit in winter rainfall was especially acute north of ~27°S, while summer rainfall was lowest within areas bordering the Gariep River. Similarly, in the SRZ the mean temperature of the wettest and warmest quarters (i.e. summer) indicated that temperature was greatest for latitudes surrounding the Gariep River valley, and to a lesser extent at the equatorward extreme.

In contrast to the SRZ, the WRZ received most of its rain in the colder winter months (Fig. 4). Moreover, with the exception of one latitudinal outlier, the minimum amount of dry season (i.e. summer) rainfall received by the WRZ equated to roughly the maximum amount of dry season (i.e. winter) rainfall received in the SRZ. This led to comparatively higher and more consistent average rainfall in the WRZ. While strongly delineating summer from winter rainfall seasons, average temperatures displayed little latitudinal variability in the WRZ in the colder, wetter months, while in the summer months temperatures tended to increase slightly towards the south.

The aridity index (AI) and potential evapo-transpiration (PET) reflect composite measures of climate, but were well correlated with MAP and MAT, respectively (Fig. 4). AI indicated high aridity in the northernmost part of *A. dichotoma*'s distribution and in the Gariep River area, while the south-eastern part of the SRZ and much of the WRZ were least arid. PET in the SRZ was lowest at ~25°S, increasing steadily north and south of this.

Multiple climate variable – stage class proportional density interactions

The final models after stepwise model selection are given by:

Summer rainfall zone:

$$\log(x_j/x_d) = \beta_0 + \beta_1(PwarmQ) + \beta_2(Pseason) + \beta_3(TwarmQ) + \epsilon_1$$

$$\log(x_a/x_d) = \beta_4 + \beta_5(PwarmQ) + \beta_6(Pseason) + \beta_7(TwarmQ) + \epsilon_2$$

Winter rainfall zone:

$$\log(x_j/x_d) = \beta_8 + \beta_9(PwarmQ) + \beta_{10}(TwetQ) + \beta_{11}(PET) + \epsilon_3$$

$$\log(x_a/x_d) = \beta_{12} + \beta_{13}(PwarmQ) + \beta_{14}(TwetQ) + \beta_{15}(PET) + \epsilon_4$$

Where PwarmQ = mean precipitation of the warmest quarter, Pseason = precipitation seasonality (co-efficient of variation), TwarmQ = mean temperature of the warmest quarter, TwetQ = mean temperature of the wettest quarter and PET = mean potential evapo-transpiration. The regression equation for the omitted ratio $\log(x_a/x_j)$ can easily be obtained by subtracting the two forms given above.

Ternary plots illustrate the observed proportional density of juveniles, adults and dead individuals relative to model predictions (Fig. 5). The MLR model did a reasonable job of capturing the shape, but not the extent of spread in proportional density values. This is especially true for the SRZ (Fig. 5a), where extreme spatial variability in stage classes is difficult to account for in terms of climate alone. Despite this, R^2 values suggest good explanatory power for the level of model complexity (Table 1).

[Figure 5]

Three bioclimatic variables emerged as important, although relatively weak determinants of stage class ratios in the respective rainfall zones (Table 1; Fig. 5). However, in most cases only two of the three variables were significantly related to the corresponding stage class ratio, and PET within the WRZ model had a non-significant relationship in all cases. The suite of bioclimatic variables accounting for the ratio of juvenile to dead individuals in the WRZ had the best explanatory power by some margin ($R^2 = 0.35$). The two weakest model R^2 values occurred in the SRZ involving the dead stage class ($R^2 = 0.13$ for adult/dead and $R^2 = 0.11$ for dead/juvenile), indicating a poor relationship between contemporary climate and the dead stage class category.

[Table 1]

Modelled 'climate lines' indicate how predicted stage class compositions change for a given change in each key climate variable (while holding other climate variables constant at their mean values) (Fig. 5). The general trends of these modelled relationships matched expectations. For example, within the SRZ, increased summer rainfall (PwarmQ) was predominantly associated with increases in the relative abundance of juvenile trees (Fig. 5a, green line). At the lower end of the observed range, an increase in summer rainfall resulted in a greater proportional density of juveniles, and a reduction in dead individuals. An increase in summer rainfall at the upper end of the range was associated with a consistently low density of dead trees (<10%), while juvenile numbers continued to increase and adults decline. Decreased rainfall variability (Pseason) was similarly associated with an increase in the relative abundance of juvenile trees at the expense of adults (Fig. 5a, blue line). An increase in summer temperatures (TwarmQ) was predominantly associated with an increase in the relative abundance of dead trees, while the proportion of adults declined sharply (Fig. 5a, purple line). Unexpectedly, the relative abundance of juvenile trees was also positively

related to summer temperatures over the observed range, although this ultimately declined as the proportional density of dead trees increased.

Within the WRZ, an increase in summer rainfall (PwarmQ) and winter temperatures (TwetQ) were positively related to the proportional density of juvenile trees (Fig. 5b, green and orange lines, respectively). At the lower end of these climate values (i.e. low PwarmQ and TwetQ), this increase in juvenile proportional density was coupled with a marked decrease in the proportional density of dead trees. At higher summer rainfall and winter temperature values the proportional density of dead trees remained very low (<10%) and continued increases in juvenile densities were offset by declining adult densities. Increases in PET had relatively little effect over the observed range of PET values (Fig. 5a, dark red line), but were associated with an increase in the proportional density of dead individuals and a decline in adults and juveniles in roughly equal proportions.

Mortality: Time-since-death and stage class of dead individuals

Pooled data from 14 sampled populations indicated that the bulk in estimated mortality timing occurred between ~21-60 years ago (64%) and that the highest frequency in observed mortality was old (i.e. estimated to have occurred more than 40 years ago) (see Appendix S4). Death within the last 10 years accounted for less than 10% of total mortality. There was no apparent latitudinal gradient in the timing of mortality, such as for example a trend toward relatively more recent mortality at the equatorward extreme or within the SRZ generally.

Basal circumference (BC) box and whisker plots indicated that dead individuals were derived almost exclusively from the larger adult, as opposed to the smaller juvenile, stage class category (see Appendix S5). For example, comparisons between median and 25th-75th percentile BCs for the adult and dead categories indicated a good deal of overlap and no significant difference, with the

exception of the Gannabos population. Here dead individuals were significantly *larger* than adults (p<0.001; Mann-Whitney U Test)). Conversely, juvenile BCs were significantly smaller than both adult and dead stage classes for all populations.

DISCUSSION

Evaluating the validity of increasing equatorward mortality due to ACC

The more spatially continuous sampling approach in the current study indicated complex climatic and demographic gradients and did not support the notion that *A. dichotoma* was clearly most stressed at the equatorward extreme. The complexity of demographic patterns is, no doubt, at least a partial reflection of local biotic (e.g. occasional herbivory and physical damage, pathogens, theft, etc.) and abiotic (geology, soil, slope, aspect, etc.) stressors. However, the more general patterns of juvenile, adult and dead proportional abundances are controlled by factors acting at a regional scale (Foden, 2002). Latitudinal climate profiles indicated that conditions were hot and dry at the equatorward limit, but that other more southerly latitudes were similarly unfavourable, and perhaps even more so. For example, while the proportion of dead individuals was high at the northern range limit, it was greatest within the Gariep River valley and surrounding Karasburg, which is located within the southern third of the distribution and at the southern end of the SRZ. In addition, the proportional density of the juvenile stage class, arguably the most vulnerable life history stage in large arborescent desert succulents (Steenbergh & Lowe, 1969; Pierson & Turner, 1998), increased north of 23°S after its lowest levels to the south of this latitude. It is important to note that these latitudinal mortality and recruitment patterns don't rule out ACC as a cause, but they caution against the assumption made in previous studies (e.g. Foden *et al.*, 2007) that environmental conditions necessarily follow a gradient from 'less favourable' at the equatorward end of the range to 'more favourable' at the poleward end.

Cooler temperatures experienced by populations at higher elevations might explain some of the complexity in the latitudinal response of stage classes, as is indicated by the generally higher altitude of populations in Namibia. But the influence of this factor was often weak or poorly

resolved in the data. Altitude and juvenile density, for example, were found to be poorly related in previous studies (e.g. Foden *et al.*, 2007), while this study found juveniles growing north of ~24°S to be *negatively* related to altitude. In addition, several low altitude northern populations, including some near the Swakop and Omaruru Rivers (the latter not previously recorded) were found to have a high proportion of recent recruits. So, while there is likely to be an ameliorative effect from altitude, it cannot be used as a general explanation for increased recruitment or reduced mortality at latitudes where climate is considered unfavourable.

Population dynamics across two fundamentally different climatic zones

Latitudinal climate profiles, tightly coupled to *A. dichotoma* presence localities derived from the roadside visual survey, highlighted substantial dissimilarities in the prevailing summer and winter rainfall zone climates. Significant differences in the amount and consistency of seasonal rainfall were especially evident, as were ambient temperatures under which seasonal rainfall occurred. These differences are due to separate meteorological systems influencing climate at the poleward and equatorward regions of the species' distribution. Circumpolar westerly winds deliver predictable frontal rains to the WRZ (Tyson & Preston-Whyte, 2000), while the variable position of the Intertropical Convergence Zone means that the SRZ experiences inherently more localized and temporally discrete convective thunderstorms (Sharon, 1981; Tyson & Preston-Whyte, 2000). This latitudinal climatic disjunction suggests that *A. dichotoma* individuals in the poleward WRZ exist under fundamentally different climatic conditions to those of the equatorward SRZ, with clear implications for historical and current recruitment and persistence strategies and mortality trends.

Indeed, we found the demographic structure of *A. dichotoma* populations to be quite different between rainfall zones. WRZ populations had a consistently higher proportion of juveniles, while the SRZ had a higher proportion of dead individuals. Several smaller studies have reported similar

patterns for *A. dichotoma*. For example, Kaleme (2003) found that populations re-photographed in the WRZ had consistently low mortality and high recruitment rates, whilst the converse was true for populations north of the winter-summer rainfall boundary. This difference was ascribed to the consistency of seasonal rainfall within the WRZ (Kaleme, 2003). Bolus *et al.* (2004) came to a similar conclusion (with the additional influence of coastal fog) in accounting for the persistence of populations of the closely related sub-species, *A. pillansii*. Many other examples exist of close species-climate associations from similar winter rainfall deserts (e.g. Drezner, 2006). Furthermore, a recently published study suggests that windthrow could be an additional significant contributor to skewed latitudinal mortality patterns in *A. dichotoma*, In the study, windthrow, a consequence of strong wind gusts and pulsed rainfall associated with convective SRZ storms, accounted for roughly a third of SRZ mortality and only 13% of WRZ mortality in 14 sampled populations (Jack *et al.*, 2014).

Sensitivity and resilience

The relationships between stage classes and climate suggested different drought tolerances (Jackson *et al.*, 2009). Juveniles, for example, were clearly proportionally abundant where there was a greater amount and consistency in dry season rainfall (especially within the WRZ). Water uptake and storage limitations and a higher desiccation rate (due to an unfavourable surface area to volume relationship) are known to affect the survival of juveniles in functionally-similar desert succulents such as *Carnegiea gigantea* (Turner *et al.*, 1966) and *Ferocactus acanthodes* (Jordan & Nobel, 1981), so a greater sensitivity to dry season moisture stress in juvenile *A. dichotoma* individuals was not surprising. In contrast, higher adult densities in areas of decreased dry season precipitation and increased precipitation variability indicated greater resilience to drought and a consequent ability to persist under conditions that would be deleterious to juveniles. Adult resilience is likely due to greater water storage capacity in the fibrous trunk, branches and leaves,

as well as extensive shallow rooting system. Moreover, adults' comparatively large size and greater reserves compared to juveniles is likely to confer additional resilience against pathogens (Augspurger & Kelly, 1984), opportunistic herbivory and structural damage.

Recruitment strategies

These contrasting sensitivities to climate influences, coupled with greater spatial and temporal variability in rainfall within the SRZ (Tyson & Preston-Whyte, 2000) could help explain the lack of recruitment, dominance of adults, and greater proportion of mortality within much of the central and northern part of the SRZ distribution. This general pattern would be reinforced by stochastic processes introduced as a result of very low natural population densities north of ~25°N (Midgley *et al.*, 1997; Courchamp *et al.*, 2008) Conversely, higher and more consistent rainfall in the WRZ, coupled with greater population densities, could account for why recruitment and establishment rates are so much higher at the poleward range limit. Crucially, neither of these interpretations need invoke ACC to explain the current demographic patterns evident in the respective rainfall zones. Both more frequent recruitment under consistently favourable climatic conditions (as exist in the WRZ) and infrequent pulsed recruitment, taking advantage of periodic spells in which climate is favourable (characteristic of the SRZ), can be viable strategies for long-term population persistence. This has been demonstrated by Duncan *et al.* (2006) for the closely related *A. pillansii*, and Wiegand *et al.* (2000) and Wiegand *et al.* (2004) for the long-lived and arid-adapted species, *Acacia raddiana.* Infrequent, pulsed recruitment events in SRZ *A. dichotoma* populations, as have been previously reported by Kaleme (2003), could be sufficient to sustain viable populations over adult life-spans of between 200 and 350 years (Foden *et al.*, 2007; Hoffman *et al.*, 2010). While more research on cohort recruitment and long-term population dynamics in *A. dichotoma* are required, it is clear that short term perspectives on long-lived and infrequently recruiting species,

as characterized by reports of negative replacement rates in several SRZ *A. dichotoma* populations (e.g. Midgley *et al.*, 2009; Hoffman *et al.*, 2010), need to be interpreted with caution.

Mortality: a recent response to ACC or longer-term climate shifts in the region?

Most arguments for or against *A. dichotoma's* promotion as a climate change indicator have, in the absence of published physiological or experimental work, relied on correlations between climate and demographic patterns. The time-since-death index developed in this study provides a novel way in which we can assess whether the species has been impacted by ACC. Time-since-death categories were calibrated by noting the rate of decay in skeletons visible in repeat photographs and by repeated visits to marked individuals where the year of death was known (Hoffman *et al.*, 2010). Not only was mortality consistently comprised of old dead skeletons (i.e. died more than 21-60 years ago) and lacking a proportional peak at the equatorward limit, it was also drawn virtually exclusively from the more drought resilient adult stage class. This is contrary to what one would expect if ACC was the cause, strongly suggesting that the majority of mortality reported in previous studies (e.g. Foden *et al.*, 2007; Midgley *et al.*, 2009) was likely not attributable to recent ACC. A possible alternative trigger for the bulk of this older mortality could be severe and prolonged regional drought that prevailed during the early 1930s and 40s (Anonymous, 1951), but additional research is required to establish this with greater certainty.

A complementary hypothesis

A complementary hypothesis explaining how current demographic patterns might have arisen over much longer timeframes, and which incorporates the influence of past climates, could prove helpful in deepening our understanding of *A. dichotoma* population dynamics and the species' ability to withstand ACC. Given poor dispersal ability and the inability to self-pollinate (Midgley *et al.*, 1997), the often geographically isolated and island-like contemporary distribution pattern (especially in

the SRZ) hints at a more continuous past distribution. This idea has been lent credence by preliminary genetic work (Midgley *et al.*, 2009) and a synthesis of multi-proxy palaeoenvironmental data for southern Africa (Chase & Meadows, 2007). The palaeoenvironmental review suggests that climate conditions similar to those found in the present day WRZ prevailed throughout much of the Namibian SRZ at the end of the last glacial maximum (LGM), ~17 ka (Chase & Meadows, 2007). Correspondingly, genetic diversity of SRZ populations indicates that they are most ancient, and are likely to have been present during the LGM (Midgley *et al.*, 2009). In addition, more recent, very high resolution records preserved in fossilized hyrax middens near the equatorward edge of the present day distribution, indicate that *A. dichotoma* populations at low latitudes experienced a phase of relatively humid conditions during the Holocene Altithermal (HA) between approximately 8700 – 3500 cal yr BP, followed by a period of marked aridity until very recently (Chase *et al.*, 2009). The expanded WRZ and the prolonged period of humid conditions during the HA are, therefore, likely to have facilitated an expansion in SRZ populations, followed by population contractions after the switch to arid conditions ~3500 cal yr BP.

If the above hypothesis is correct, it would imply that climatic conditions within the SRZ have been deleterious for millennia and this would have precluded or dramatically curtailed recruitment in the central and northern parts of the distribution. The resulting picture would closely match what is evident in the SRZ today: isolated and aging adult-dominated populations, often displaying inadequate replacement rates, but able to persist in certain locations due to a unique set of life history characteristics. These include drought resilience in the adult form, the ability to recruit during infrequent periods of good rainfall, and the ability of sensitive juveniles to take advantage of ameliorative micro-habitats, such as found under nurse-plants or in rock crevices (Foden *et al.*, 2007).

This explanation is admittedly speculative, but it highlights the need for a longer-term perspective in the case of *A. dichotoma*, and more generally in terms of species with long life histories. For such species, current distributional (and even demographic) patterns can be strongly influenced by historical contingencies, sometimes resulting in relict populations reflecting the 'ghosts of climates past' (after Connell, 1980), which may represent extinction debt currently being paid (Jackson & Sax, 2009).

Conclusion

The evidence in the current study suggests that there may be problems in the promotion of *A. dichotoma* as an indicator of ACC. We suggest that explanations for the species' current distribution and demographic patterns are complex, but can be more parsimoniously accounted for by the latitudinal climatic disjunction, long-term shifts in climate and unique life history characteristics which combine to influence the dynamics of recruitment, persistence and mortality through time. As with other long-lived, slow growing, infrequently recruiting and widespread arid-adapted species, responses to climatic drivers are likely to be slow, and stage class structure likely to lag behind contemporary climate.

More emphasis should be placed on long-term monitoring of *A. dichotoma* recruitment and survival across the latitudinal range (Midgley *et al.*, 2007), as well as genetic work to better establish how populations are related to one-another and consequently how they have shifted in the landscape. Along with an improvement in the resolution of palaeo-climatic proxies, this will allow a better understanding of what the drivers of past distribution shifts were. In addition, there is a need for empirical research into the sensitive regeneration niche and the capacity of juveniles to withstand changes in temperature and rainfall, including the physiological thresholds that lead to mortality (Dawson *et al.*, 2011). This knowledge is especially important in arid and hyper-arid systems,

where climate is likely to be the dominant driver of change (Noy-Meir, 1973). Given the

unprecedented rate of projected warming in southern Africa (Haensler *et al.*, 2010), these efforts

are urgently required.

ACKNOWLEDGEMENTS

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BIOSKETCH

This research forms part of the Plant Conservation Unit's focus on historical ecology in southern Africa. We investigate historical changes in the vegetation of the sub-continent as well as long-term changes in the dynamics of key climate change indicator species. [http://www.pcu.uct.ac.za/]

AUTHOR CONTRIBUTIONS

M.T.H., R.F.R. and S.L.J. conceived the ideas; S.L.J. and M.T.H. led the fieldwork; S.L.J. and I.D. analysed the data; and SLJ wrote the manuscript with input and comment from M.T.H., R.F.R. and I.D. All authors read and approved the final manuscript.

List of tables and table captions

Table 1. Coefficients for the combination of bioclimatic variables (±std error) which account for the greatest amount of variance in different stage class ratios in the summer rainfall zone (n=537) and winter rainfall zone (n=112). (* = $p<0.01$, ** = $p<0.001$).

	Juvenile/Adult	Adult/Dead	Dead/Juvenile
Summer rainfall zone			
R^2	0.19	0.13	0.11
Constant	-1.432 (0.82)	3.705 (0.66)	-2.273 (1.14)
PwarmQ	0.016 (<0.01)**	0.018 (<0.01)**	-0.034 (<0.01)**
Pseason	-0.035 (<0.01)*	-0.002 (<0.01)	0.037 (0.01)**
TwarmQ	0.086 (0.03)**	-0.133 (0.02)**	0.047 (0.04)
Winter rainfall zone			
R^2	0.20	0.15	0.35
Constant	-4.400 (2.06)	-5.683 (2.21)	10.083 (2.53)
PwarmQ	0.098 (0.03)*	0.132 (0.03)**	-0.230 (0.04)**
TwetQ	0.147 (0.22)	0.746 (0.24)*	-0.893 (0.27)*
PET	<0.001 (<0.01)	-0.003 (<0.01)	0.003 (<0.01)

List of figure captions

Figure 1. The putative historical distribution of *Aloe dichotoma* (Masson) based on GPS locations from herbarium records (PRECIS-National Herbarium Pretoria Computerised Information System) and two historical distribution maps. The northern grey shaded area is adapted from Mendelsohn *et al.*, (2002) and the southern grey shaded area is adapted from John Acocks field surveys *ca.* 1935-1977 (see Rutherford *et al.* 2003). Overlying this is the route undertaken during the roadside visual survey and the location of 14 sampled populations.

Figure 2. The total density (non-log-transformed) of *Aloe dichotoma* individuals per square kilometer along the roadside visual survey network of transects.

Figure 3. The proportional density of a) juvenile, b) adult and c) dead *Aloe dichotoma* individuals along the roadside visual survey network for all transects with ≥20 trees. Maps above illustrate spatial patterning of proportional density and graphs below represent proportional density averaged across half-degree latitudinal bands (±std deviation). Individuals within the SRZ (WRZ) are indicated by black diamonds (open squares).

Figure 4. Average values (±std deviation) within half-degree latitudinal bands for 15 bioclimatic variables in the summer (black diamonds) and winter (open squares) rainfall zones within the distribution range of *Aloe dichotoma*. Precipitation and temperature indices are in mm and °C, respectively. Differences between rainfall zones were significant (p<0.001) for all bioclimatic variables except precipitation of the wettest quarter.

Figure 5. Ternary plots of roadside visual survey observations within the summer (above) and winter (below) rainfall zones for all transects with ≥20 individuals. The right hand side of the triangle (bottom side, left hand side) shows juvenile (dead, adult) PDs to be read off horizontal axis lines (axis lines sloping diagonally up to the right, axis lines sloping diagonally down to the right). Observations are symbolized from white (equatorward extreme) to black (poleward extreme) within the respective rainfall zones based on five equally sized latitudinal bands. Model predicted values are given as red crosses within the ternary plots. Coloured climate variable lines describe how modelled stage class proportional density values change with respect to each other per unit increase (i.e. in the same direction as the arrow) or decrease in the specified climate variable. The upper area of the ternary plot roughly corresponds to roadside visual survey localities experiencing population 'growth', the bottom left to 'persistence' and bottom right to 'decline'.
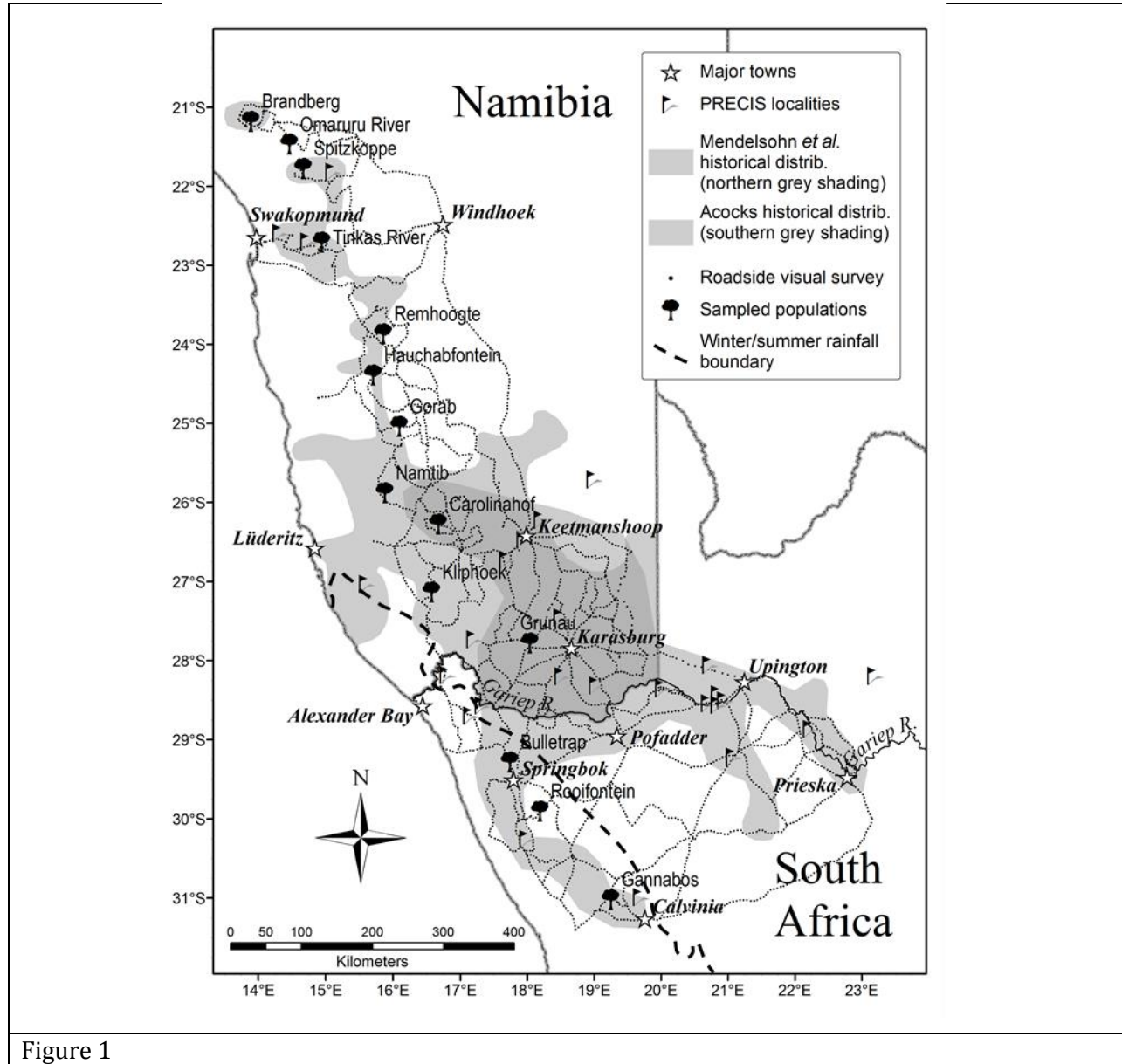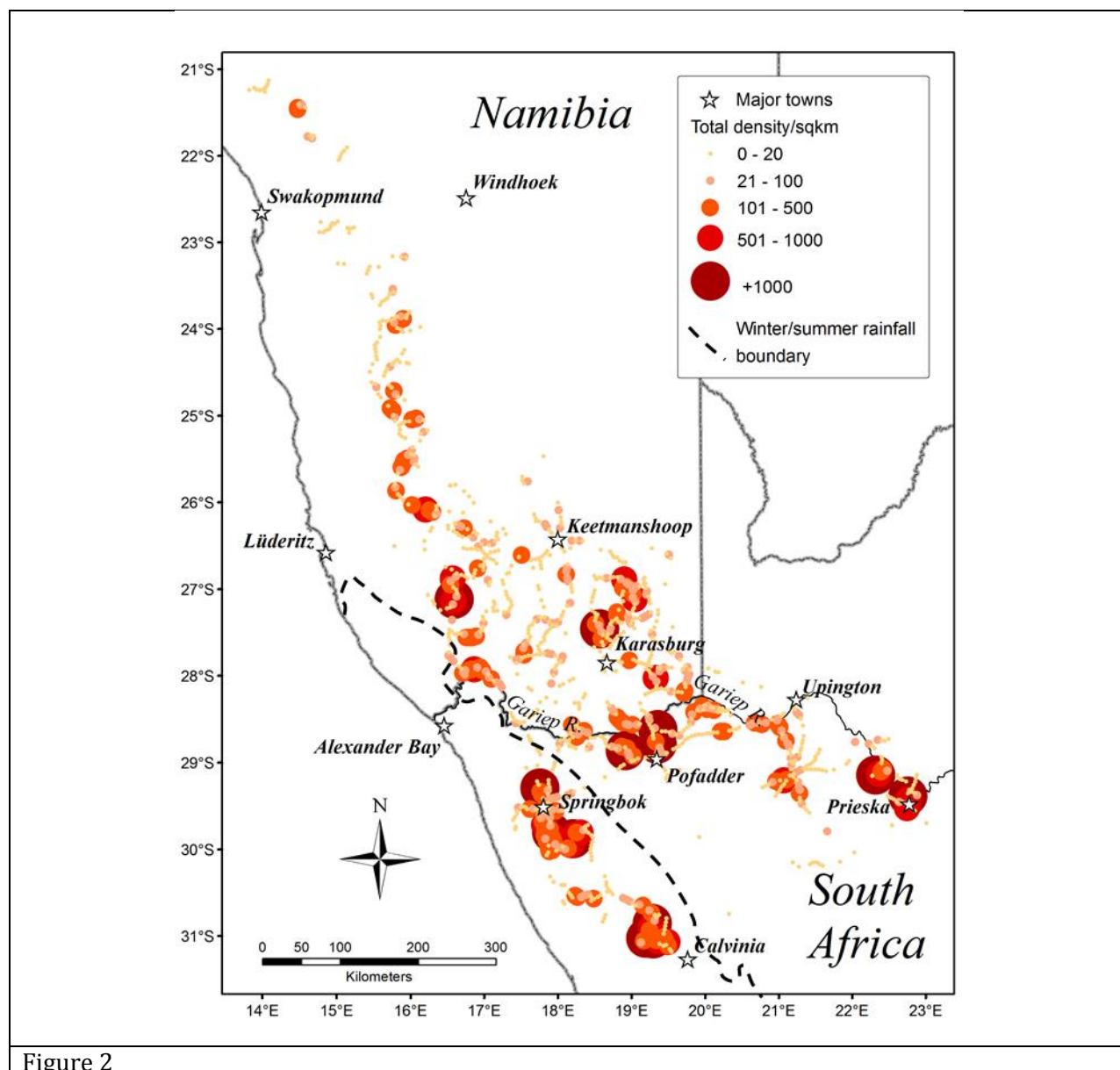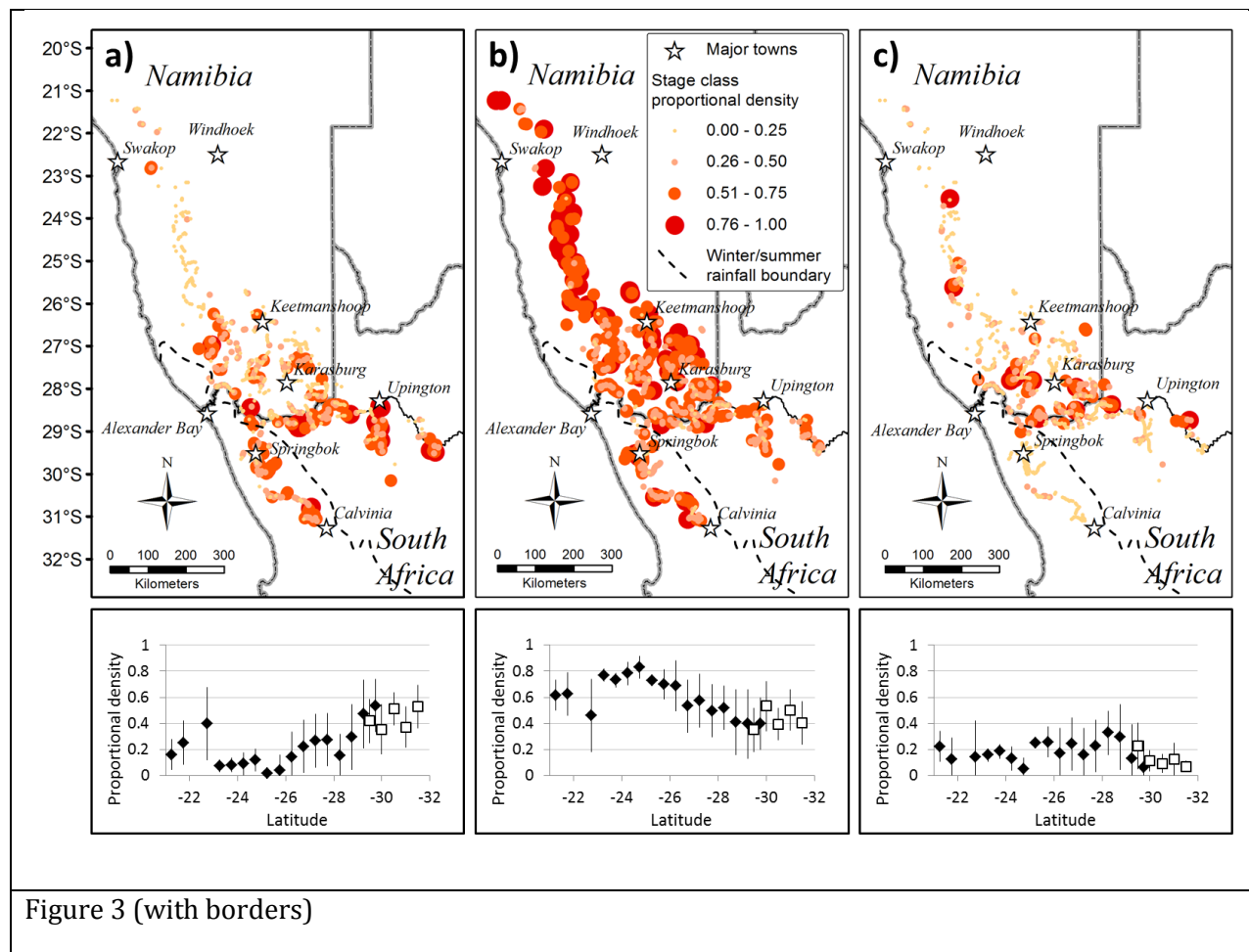
List of figures

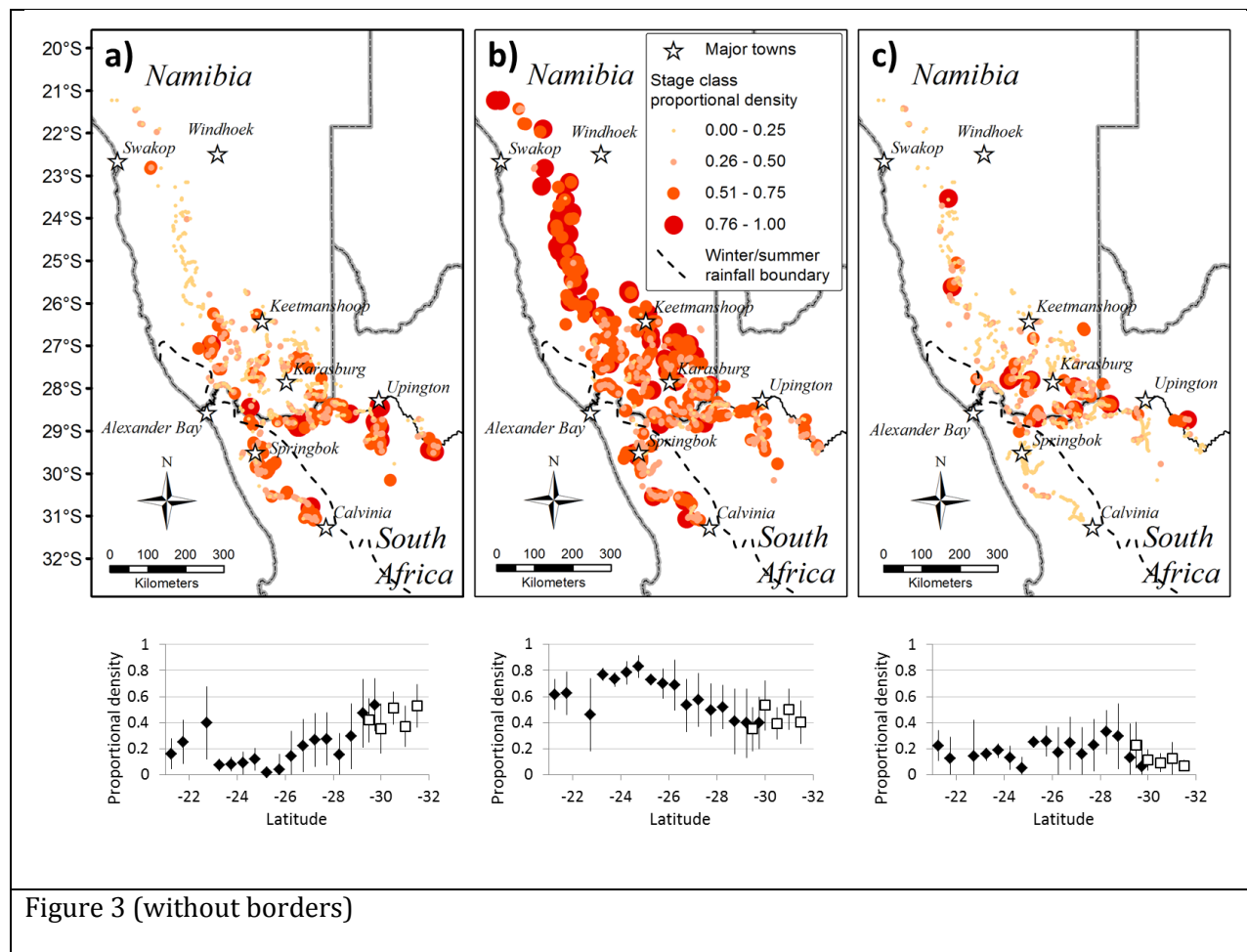Figure 1

Figure 2

Figure 3 (with borders)
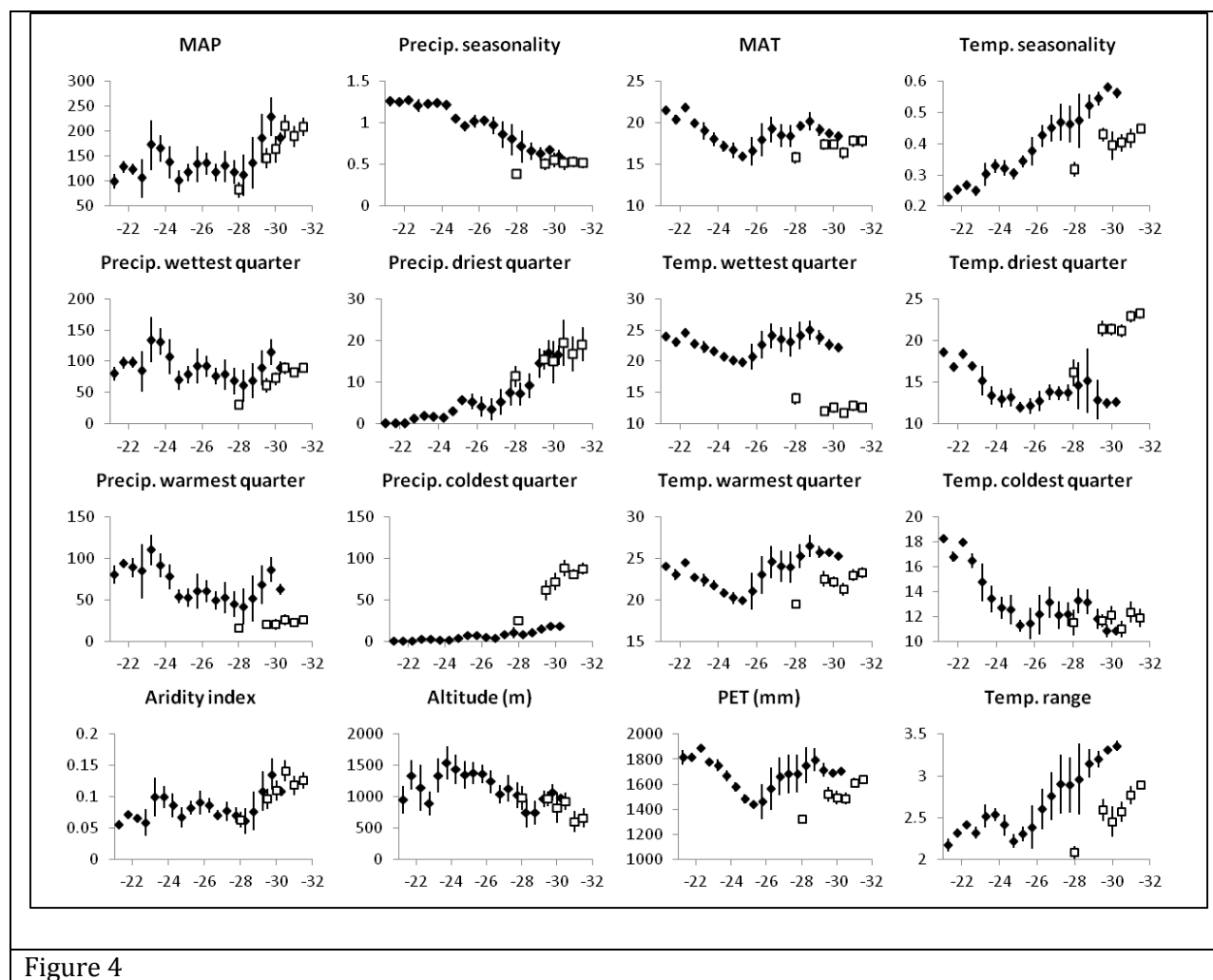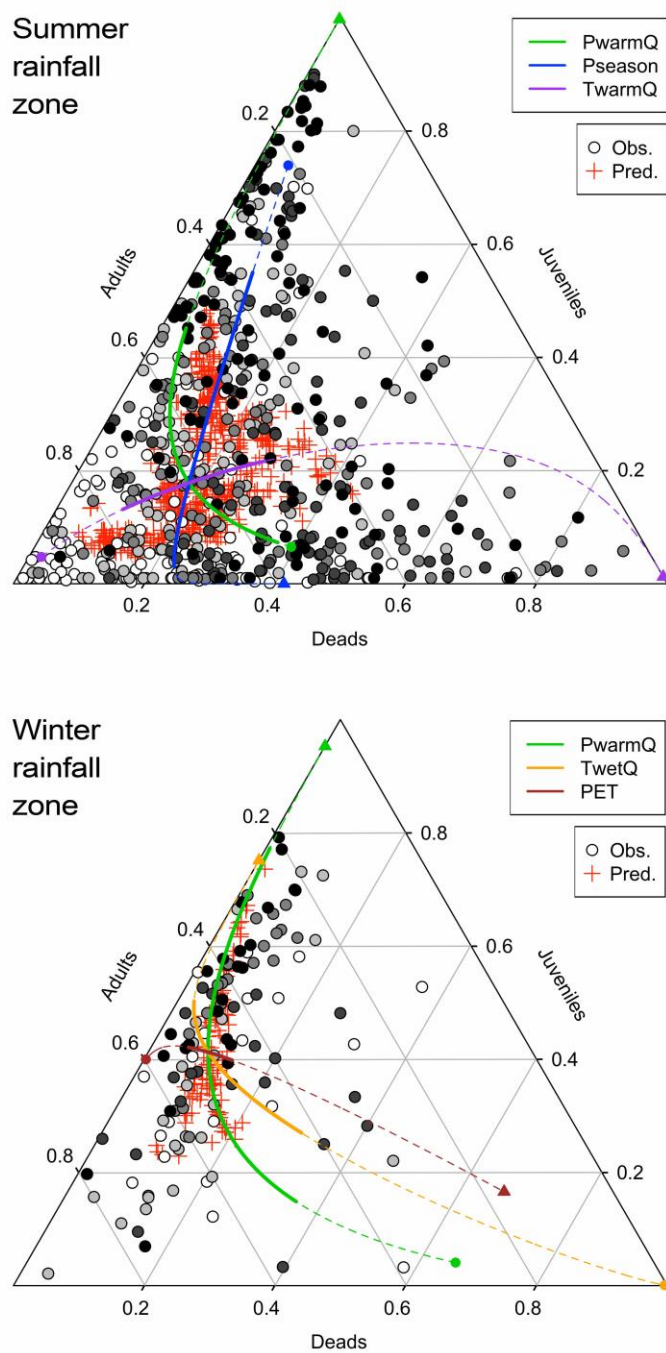
Figure 3 (without borders)

Figure 4

Figure 5

SUPPORTING INFORMATION

S1) Criteria used for estimating the time-since-death of *Aloe dichotoma* (Masson) skeletons (reproduced from Jack *et al.,* 2014).

Category	Time-since-death (yrs)	Leaves	% bark remaining	Branches	Stem decay	Growth rings	% plant remaining
1	1-5	Present	>95%	All; intact	None	Not visible	100%
2	6-10	Sometimes; dried out	50-75%	All; seldom intact	None	Not visible	90-95%
3	11-20	Absent	<40%	All; not intact	Slight	Not/barely visible	80-90%
4	21-40	Absent	<5%	>50% lower only	<25%	Becoming visible	~50%, usually trunk
5	41-60	Absent	Absent	<10% lowest only	25-50% or more	Clearly visible	~20-40%, trunk only
6	61+	Absent	Absent	Absent	>80%	Clearly visible	<5%, trunk only

S2) Stage class categories for *Aloe dichotoma* individuals based on architectural and reproductive characteristics (adapted from Jack *et al.*, 2014).

| Stage class	Original stage class	Plant height (m)	Canopy diameter (m)	Dichotomous branching nodes	Leaf rosettes	Reprod. mature
Juvenile	Juvenile	Generally <1.5	ca. 0.60	None	1	N
	Young adult	Variable, generally 2-3	1-1.5	1-3	mean=4.9	Y
Adult	Mature adult	Variable, generally 3-5.5	2-3.5	6-10	mean=63.4	Y
Dead	Senescent	Generally >4	2-4	8-12	mean=108	Y
	Dead	n/a	n/a	n/a	n/a	n/a

S3) Equations used to determine measures of aridity and potential evapo-transpiration.

Aridity Index (AI) = MAP / MAE,

where MAP = Mean Annual Precipitation and MAE = Mean Annual Potential Evapo-transpiration.

Potential Evapo-transpiration (PET) = 0.0023 * RA * (Tmean + 17.8) * TD0.5 (mm / day),

where Tmean = mean monthly temperature, TD = mean monthly temperature range, and RA = mean monthly extra-terrestrial radiation at the top of the atmosphere.
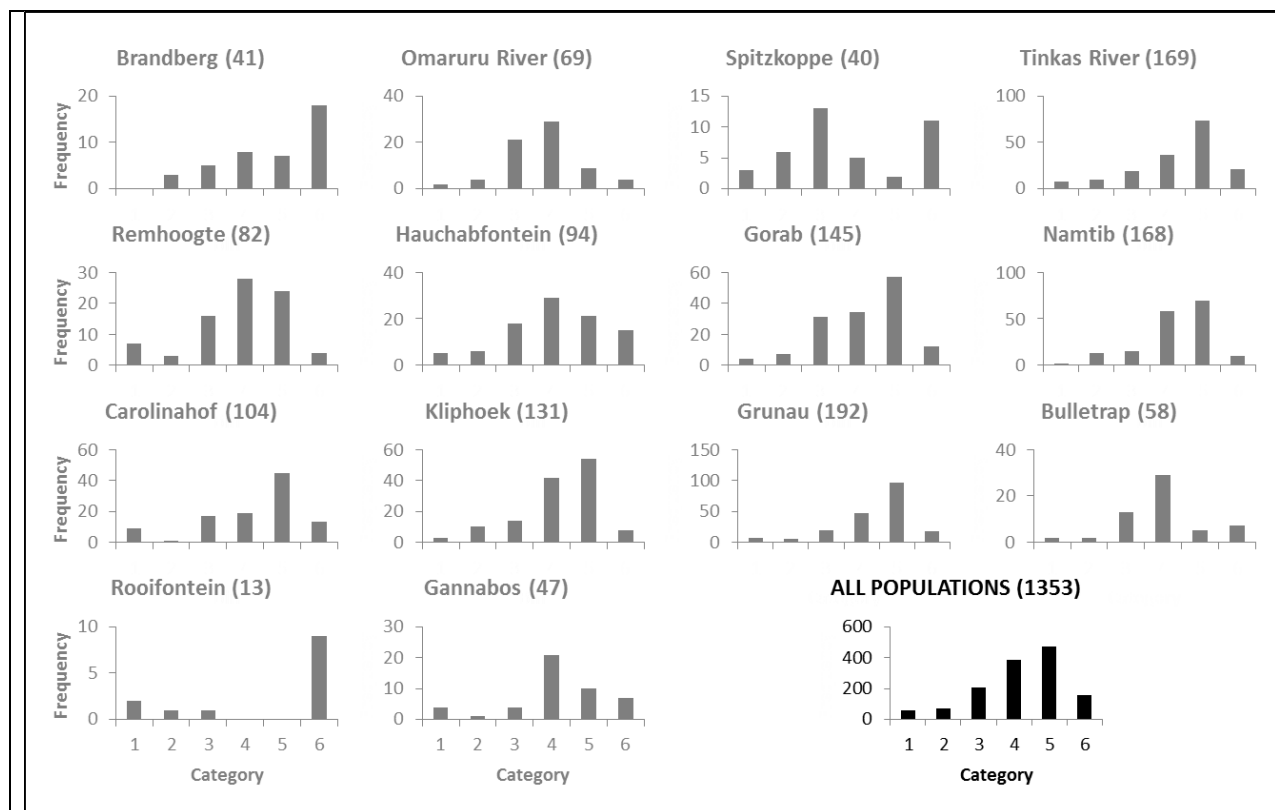
S4) Histograms of the estimated time-since-death for dead *Aloe dichotoma* individuals in 14 sampled populations. Category 1 = 1-5yrs; 2 = 6-10yrs; 3 = 11-20yrs; 4 = 21-40yrs; 5 = 41-60yrs; 6 = 60+yr (see Appendix S1). The sample number is in brackets next to the population name. Graphs are arranged in latitudinal order from equatorward to poleward extremes, read horizontally (see Fig. 1 for spatial location of sampled populations).
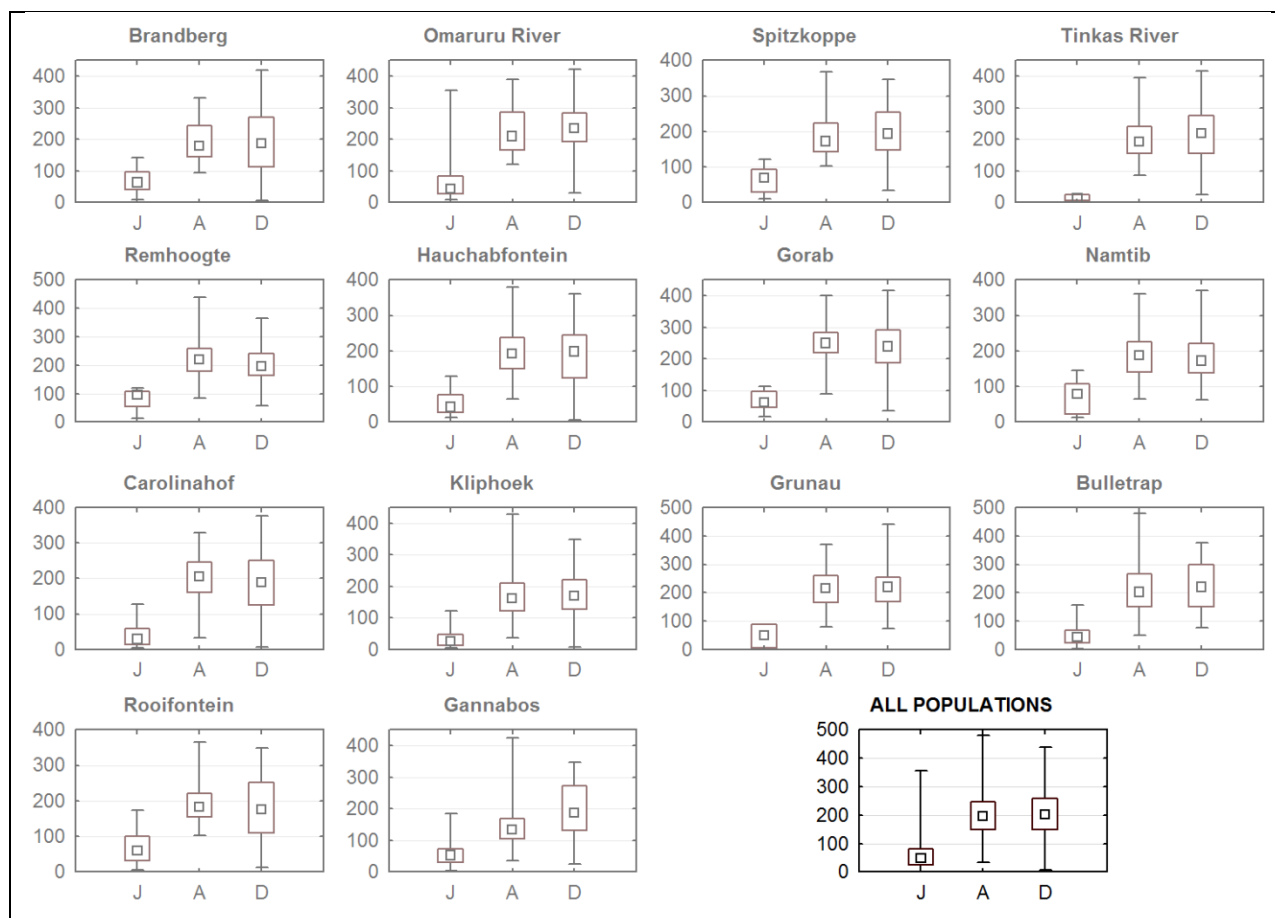
S5) Box and whisker plots indicating median (small box), 25th and 75th percentile (large box), and maximum and minimum values (whiskers) for the basal circumference (y-axis: cm) of each stage class (x-axis: J = juvenile; A = adult; and D = dead) at each population. Graphs arranged in latitudinal order, read horizontally.