



University of Cape Town

Faculty of Science

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**Analysis of long-term changes in populations of the  
Clanwilliam Cedar (*Widdringtonia cedarbergensis*)  
using repeat photography**

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Edmund February (Biological Sciences, UCT)

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## **ACKNOWLEDGEMENTS**

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## **ABSTRACT**

Repeat photography photosets were used to analyse 20<sup>th</sup> century changes in populations of *Widdringtonia cedarbergensis* from four sites in the Cederberg Mountains, South Africa. Systematic evaluation of 115 photosets was combined with field observation and environmental data to determine the age class and degree of foliage cover, as well as fire frequency, rockiness of habitat, altitude, aspect of slope, annual mean temperature and annual precipitation for each tree viewed in photosets. Mortality and recruitment events were documented in each of the photosets. A total of 1315 trees were recorded in historical photographs (1931-1982), with 968 of these shown to have died in the repeat photographs (2007-2013), indicating 74% mortality. With only 45 (3.4%) recruits being recorded, the total current living population of *W. cedarbergensis* in the repeat photographs was 392. There was no significant difference found in mortality or recruitment across the sampled sites. From the historical to repeat photosets there was an 8% increase in the proportion of mature adults and a 13% increase in the proportion of *W. cedarbergensis* individuals with sparse foliage cover. A generalized linear model was used to determine the effects of environmental factors on *W. cedarbergensis* mortality in natural populations. An analysis of 823 natural trees indicated that trees experiencing a greater frequency of fire ( $p < 0.01$ ) and higher temperatures at lower altitudes ( $p < 0.01$ ) have significantly increased *W. cedarbergensis* mortality. Less rocky habitats ( $p < 0.01$ ) and northern and southern facing slopes ( $p < 0.01$ ) also significantly increased mortality of *W. cedarbergensis*. The model reported an R-squared value of 12%, indicating that although the results are highly significant, other factors not investigated in this study are likely to influence *W. cedarbergensis* mortality. Finer spatial resolution of the climatic factors investigated in this study would likely lead to an increase in the strength of the model. Furthermore, annual mean temperature has increased by an estimated 0.6°C over the last 40 years in the region, possibly contributing to mortality. This study's key finding is establishing the contribution of temperature to *W. cedarbergensis* mortality. Temperature's effect on *W. cedarbergensis* mortality should be interpreted within the context of both late Quaternary and anthropogenic climate change.

## INTRODUCTION

*Widdringtonia cedarbergensis* Marsh has been the subject of scientific research for over a century and is recognised as one of the most researched indigenous plant species in the fynbos biome (Richardson, 1993). Commonly known as the Clanwilliam cedar, it has a patchy distribution over approximately 250 km<sup>2</sup> and is endemic to the Cederberg mountain range of the Western Cape, South Africa (February et al, 2007). It typically grows at a range of altitudes, between 900 and 1500 m, on quartz-derived soils in the Cederberg Mountains, which are themselves named after the unique cedar trees. *W. cedarbergensis* is not in fact a true cedar as it is found in the Cupressaceae family. There are four species in the *Widdringtonia* genus, which are all endemic to southern Africa. *W. cedarbergensis* is listed as critically endangered on the IUCN red-list, with a recorded decline in area of occupancy and quality of habitat of more than 80% (Farjon et al, 2013). This decline has been well recorded over historical time (Hubbard, 1937; Smith, 1955; Lückhoff, 1971; Andrag, 1977; Meadows and Sugden, 1991) and concern has been expressed over its long term potential to survive (Manders, 1986).

### ***Cause of the decline***

There is much debate as to the real cause behind the decline of the Clanwilliam cedar (Mustart and Bond, 1994). The most popular views on the causes of the cedar population decline are: 1) 18<sup>th</sup> and 19<sup>th</sup> century over-exploitation of the tree as a timber source which has reduced and fragmented cedar populations (Hubbard, 1937; Lückhoff, 1971; Andrag, 1977). 2) Late Quaternary climate change which has led to alterations in the composition of cedars' co-occurring species and subsequent changes in the fire regimes (Meadows and Sugden, 1991). 3) Inappropriate or changed fire regimes, where frequent fires cause greater deaths of juveniles and intense wildfires cause greater adult death (Manders, 1987b). 4) The effects of recent anthropogenic climate change, leading to temperature increases and aridity in the north-western areas of the fynbos biome, thereby increasing cedar mortality.

A number of other factors influencing cedar survival have been suggested, such as livestock grazing which was permitted in the early- and mid-20<sup>th</sup> century and its potential negative effects on juveniles (Manders, 1986). Another well-discussed factor is the potential granivory and destruction of seedlings by rodents, rock hyraxes and baboons (Andrag, 1977; Manders, 1986). However, recent discoveries of rodent scatter-hoarding behaviour in the fynbos indicate that plants with nut-like seeds, such as *W. cedarbergensis*, may be dispersed and buried by scatter-hoarding rodents, which would aid in recruitment (Midgley et al, 2002b; Midgley and Anderson, 2005). Preliminary studies have also taken place to investigate the threat of diseases and pests on cedar trees, with no significant impact being found (Wingfield et al, 1988), although this study only investigated mature adults.

### ***Historical records***

In the 19<sup>th</sup> century cedar trees were the only readily available source of timber for any colonial settlers in the region (Lückhoff, 1971). Due to the excessive manner in which cedars were harvested in the early 19<sup>th</sup> century, which the British geographer Sir James Alexander described in 1838 as “without leave or license”, the felling of live cedars was banned in 1879 (Smith, 1955). In light of this exploitation, Hubbard (1937) suggested that the cedar’s range was likely to have previously been far greater than in 1937. However, others suggest that these anecdotal records may be exaggerated and argue that the decline of the cedar has taken place over thousands of years (Meadows and Sugden, 1991).

### ***Archaeological record***

Meadows and Sugden (1991) reason that factors other than over-harvesting of the cedar in the recent past have influenced its distribution, because it is currently altitudinally and geomorphologically restricted. They analysed fossil pollen deposits which suggested that the cedar did not exist in widespread, dense forest before present time. However, they found that the species has been in a steady decline from approximately 14.6 ka. This decline has been attributed to the climate

becoming warmer and drier in the late Quaternary leading to more severe fire regimes for the trees, including pre-colonial, human-altered fire regimes (Meadows and Sugden, 1991).

Cartwright (2013) recorded Clanwillam cedar charcoal remains in the Diepkloof Rock Shelter (DRS), located close to Elandsbaai on the Western Cape coast, approximately 60 km west of the Cederberg Mountains (Fig 1). These remains were dated to pre-Still Bay and Still Bay cultural periods which suggests that they are in excess of 71 ka (Cartwright, 2013), while no remains were present in the Howiesons Poort cultural period (~60 ka). The origin of these remains is contentious, however, with the author suggesting that the cedars former distribution may have been substantially greater under different climatic and soil moisture conditions. Alternatively, it has been well documented that the occupants of DRS travelled long distances between the coast, the Cederberg Mountains and the Karoo in South Africa's interior (Parkington, 2001), suggesting that they may simply have collected wood resources in the Cederberg Mountains and that the cedar's distribution hasn't significantly changed for approximately 60 ka.

### ***Fire sensitivity***

Clanwillam cedars are fire sensitive, but are surrounded by fynbos, which is a fire prone and adapted vegetation type. Some fynbos species have life histories that are dependent on fire for recruitment, such as the serotinous *Proteaceae*. Brown et al (1991) showed that fynbos in the Cederberg burns at an overall frequency of 11-15 years. However, Fox (2003) noted in her study area in the Cederberg that six fires occurred in a 26 year period (1977-2003), indicating that fire frequency may be increasing in some areas. The frequency of fire is particularly important for the regeneration of Clanwillam cedar populations. Individuals only produce their first cones after approximately 12 years, while full reproductive maturity is only reached after 40 years (Manders, 1986), a period that greatly exceeds both past and present fire intervals (Brown et al, 1991). Seemingly, most fynbos species would benefit from successive fires after 15 years less, but cedars will not. The Clanwillam cedar

can live for several centuries (February and Stock, 1999), which indicates that the species has an ability to persist in a fire-prone environment and suggests a potential change in factors affecting its mortality. The seasonality of fire has also been shown to have a significant impact on cedar mortality, with the natural fire season occurring between November and February and to a lesser extent March and April (Manders 1986; Brown et al, 1991).

Extant cedar trees have been noted to have an association with cliffs, rocky outcrops and very rocky slopes and rarely occur on sandy flats between rocky outcrops (Manders, 1986). This association with rocky areas has been attributed to protection from fire (Manders, 1986) and increased availability of water (February et al, 2007). Furthermore, the survival of planted seedlings is also associated with the high moisture contents found in rocky microhabitats (Manders and Botha, 1987; Mustart et al, 1995). This association may also be due to secondary dispersal by baboons or rodents (Higgins et al, 2001). Experimental work done by Manders (1987a) has shown that seed germination is suppressed by ground litter underneath Clanwilliam cedar trees and therefore most germination occurs post-fire once litter has been burnt-off.

### ***Climate change predictions***

Future predictions of climate change for the Cederberg area are for drier and warmer conditions (Midgley et al, 2002a, 2003). It has been suggested that, among other regions, the Cederberg Mountains would show the first indications of anthropogenic climate change and its effects on flora in the south western Cape (Midgley et al, 2002a). The Clanwilliam cedars are claimed not to be limited to any aspect, except in northern areas where they grow predominantly on eastern slopes (Andrag, 1977). February et al (2007) showed that although Clanwilliam cedars are not dependent on seasonal rains, they are dependent on reliable access to available water. Studies of future climate further suggest that if the current projections for this region are realised, then the Clanwilliam cedar will likely go extinct.

### ***Global and regional comparisons***

Global comparisons of conifer species indicate that temperature induced drought has been a major cause of mortality over the last 40 years. Allen (2010) reviewed more than 150 references that document 88 examples of forest mortality that were driven by climatic water or heat stress since 1970. Conifers represent more than a dozen of these reviewed cases. The review documents cases of mortality in numerous conifer genera caused by droughts, such as *Cedrus atlantica* from Algeria (Bentouati, 2008), *Juniperus procera* from Saudi Arabia (Fisher, 1997) and *Pinus edulis* from south western USA (Breshears et al, 2005; Mueller et al, 2005). With future predictions for drying and warming in the Cederberg and evidence of conifer mortality driven by climatic water or heat stress, it seems highly plausible that higher temperatures impact *W. cedarbergensis* mortality.

### ***Aims and predictions***

A primary aim of this study was to update the status of the Clanwilliam cedar tree and to better understand the continued reasons for its decline. This study documented long term changes in populations of the Clanwilliam cedar using the well-established technique of repeat photography (e.g. Hart and Laycock, 1996; Zier and Baker, 2006). Repeat photography was used spatially to analyse population health, recruitment and mortality rates and the relationship with environmental and climatic factors using a generalized linear model. It was hypothesised (1) that Clanwilliam cedar mortality would show no significant difference across its geographical range, but instead across its altitudinal range. It was further hypothesised (2) that the Clanwilliam cedar altitudinal restriction is likely due to climatic factors such as precipitation and temperature, while aspect, rockiness of habitat and fire frequency play significant roles in cedar mortality.

## **METHODS**

### ***Study Region***

The Cederberg Mountains have a Mediterranean-type climate with the majority of annual rainfall occurring in winter, while summers are hot and dry. Cederberg vegetation is comprised mainly of fynbos, which is a sclerophyllous and fire-prone vegetation type dominated by *Proteaceae*, *Ericaceae* and *Restionaceae* (Taylor, 1996; Mucina and Rutherford, 2006). The Cape Floristic Region, which includes of the fynbos biome, has exceptionally high plant diversity (11 420 plant species) with high levels of endemism (8 900 plant species) (Manning et al, 2012).

### ***Photographic Sites***

A total of 115 historical photographs, shot by various individuals between 1931 and 1982 and housed within the photograph-database at the Plant Conservation Unit, University Cape Town, were used in this study. The photograph sites covered the central and northern extent of the Cederberg Wilderness Area (CWA). In December 2007, sites situated in the areas of Crystal Pools, Skerpioensberg and Vogelsangvallei were revisited (hereafter called Skerpioenspoort; see Bonora, 2009). In September 2012, sites situated in the areas of Middelberg, Cathedral Rocks and Grootlandsvlakte were revisited (hereafter called Middelberg), while in April 2013, sites between Sleppad Hut, Welbedacht and de Rif (hereafter called Welbedacht) and Heuningvlei (stays as Heuningvlei) were revisited. Sites were relocated using a 1:50 000 map, a GPS and the historical photographs. A digital (Canon 5D Mark II) and a colour slide film camera (Canon EOS500) were used in the field with a tripod. Detailed photograph and site information, including GPS co-ordinates, altitude, aspect, a general ecological description and description of major changes in both the cedar populations but also in the surrounding vegetation at the sites was recorded. At each of the 115 sites, repeat photographs were taken and mortality and

recruitment rates were then calculated from the digitised original and repeat photographs.

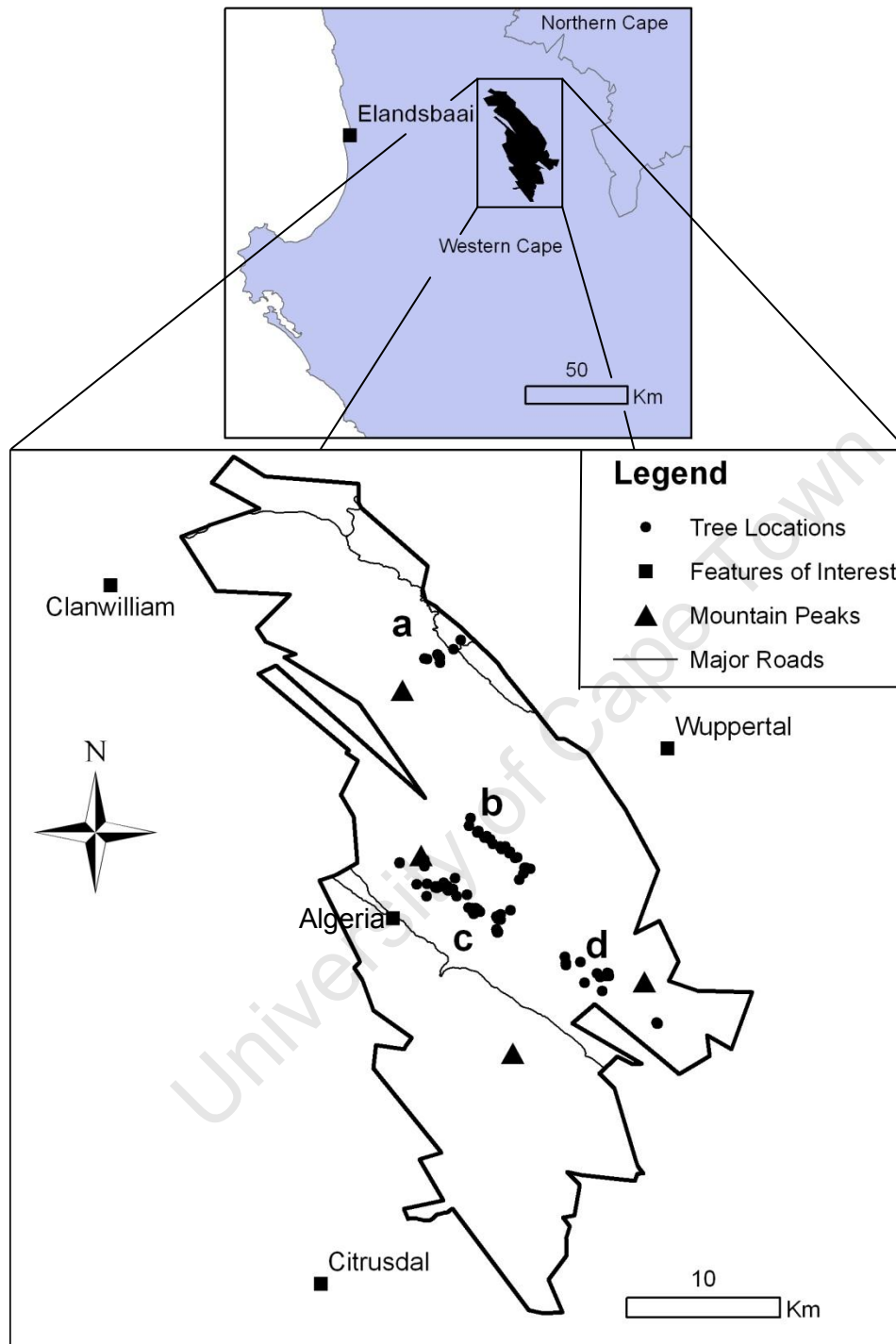


Figure 1. The locations of *W. cedarbergensis* trees at four different sites in the Cederberg Wilderness Area, Western Cape, South Africa: a) Heuningvlei, b) Skerpioenspoort, c) Middelberg and d) Welbedacht. Features of interest include the weather stations at Algeria Forest Station and Clanwilliam.

### ***Photograph Analysis***

Analysis of the repeat photographs was done using image editing software. The historical and repeat photographs are rescaled in the image editing software by selecting two fixed points (e.g. mountain peaks or rocky protrusions), which were clear in both photograph and measuring the distance between them using the measuring tool. This allowed for the historical and repeat photograph to be scaled to the same size. The repeat photograph was then overlaid on the historical photograph so that both photographs were present in one window on the screen. The opacity of the repeat photograph was then adjusted, allowing for repositioning and tilting of the repeat image until features of the two photographs were adequately aligned.

Once matched, the historical and repeat photographs could be analysed for changes in the populations of cedar trees at each location. In each photograph set, trees were labelled with a green (alive), red (dead), yellow (recruit since original photograph) or orange (already dead or senescent) number. At each site, trees were sequentially numbered per photograph set and the following data extracted: age class before and after and the density of foliage before and after. Age class categories were subjectively assigned as follows: juvenile (tree is shorter than 2m tall and stem erect with no branching of the primary trunk and limited or no reproductive capacity); mature adult (primary trunk branched and tree at full reproductive capacity); and lastly dead or senescent.

Foliage density classes were defined as: dense (>75% of the canopy fully covered and all branches in a healthy condition) and sparse (<75% of the canopy fully covered and few branches are dead or in a senescent state). Habitat type was classified at three different levels: open (<25% rockiness), rocky (25%<rockiness<75%) or well protected (>75% rockiness and placed on top of a rocky outcrop). A repeat photograph set from each separate fieldwork excursion is shown in Appendix 1.

### ***Population Dynamics***

Annual mortality and recruitment rates were calculated for the different sites. The sites represent relatively distinct populations of cedar trees across the range of its habitat. A distinction was made between man-made plantations (hereafter called plantations) and natural cedar populations. For each site the annual mortality (m) and recruitment (r) rates were calculated as:

$$m = (N_d/N_o) * 100/y$$

$$r = (N_n/N_t) * 100/y$$

where  $N_d$  = number of cedars not surviving from the historical photograph,  $N_o$  = number of cedars in the historical photograph,  $N_n$  = number of new cedars in the repeat photograph,  $N_t$  = number of cedars in the repeat photograph and  $y$  = the number of years between the two photographs. Population dynamics are therefore represented as the number of dead or recruited trees per hundred trees per year.

### ***Environmental and Climatic Data***

The fire history for each of the 115 sites was downloaded as an ArcView shapefile from the Biodiversity GIS (BGIS) portal, (<http://bgis.sanbi.org>). Fire histories were then compiled using ArcGIS software (ESRI, 2011) and fire frequencies extracted by placing fire “polygons” (representing the area of a fire event) on top of one another and counting the number of fire “polygons” that overlap where a tree or cluster of trees is found.

Estimated current annual mean temperature (°C) and annual precipitation (mm) values were extracted from the Worldclim interpolated climate surface (Hijmans et al, 2005) using the GPS coordinate of each tree. Observed climate data was obtained from the South African Weather Service for Clanwilliam (Fig 1) and the Agricultural Research Council for Algeria Forest Station (Fig 1). Clanwilliam (1870-2010) and Algeria Forest Station (1908-2008) were the only sites with long term precipitation record, while Clanwilliam (1963-2010) was chosen to show short term temperature records, as no long term records were available.

For each tree, altitude and aspect was determined using Google Earth's ground view function. These values were cross-referenced with altitude and aspect values recorded during study site visits using a GPS and a compass. Aspect was determined as north, south, east or west. North comprised of the angle from north-west to north-east (including north-west; not including north-east). North-east was included in the east category, south-east in the south category and south-west in the west category.

### ***Model Description***

The relationship between cedar tree mortality and altitude, aspect, habitat type, fire frequency, annual mean temperature (°C) and annual precipitation (mm) was determined using a generalized linear model for each individual tree in natural cedar populations. Tree mortality was used as the response variable and had two levels: alive or dead (0 or 1). The explanatory variables used were altitude, aspect, habitat type, fire frequency, annual mean temperature (°C) and annual precipitation (mm). The best fitting model was selected based on Akaike's Information Criterion (AIC) (Akaike, 1974). Both altitude (m) and annual precipitation (mm) were both removed as explanatory variables from the model. This increased the strength of the model, as it reduced the degrees of freedom, while losing little explanatory power due to co-correlation between: altitude, annual mean temperature (°C) and annual precipitation (mm). The statistical coding was written in R 3.0.1 (R Core Team, 2013).

## RESULTS

### *Population Dynamics*

A total of 1315 living trees were recorded in the historical photographs, of which 968 have since died (74%). With only 45 recruits being recorded over all of the sites, the total current living population of Clanwilliam cedars counted in the repeat photographs was 392. In the natural populations at Welbedacht, Skerpioenspoort and Middelberg, 598 of the 823 recorded trees have died (73%), leaving only 268 natural cedars at the sampled sites.

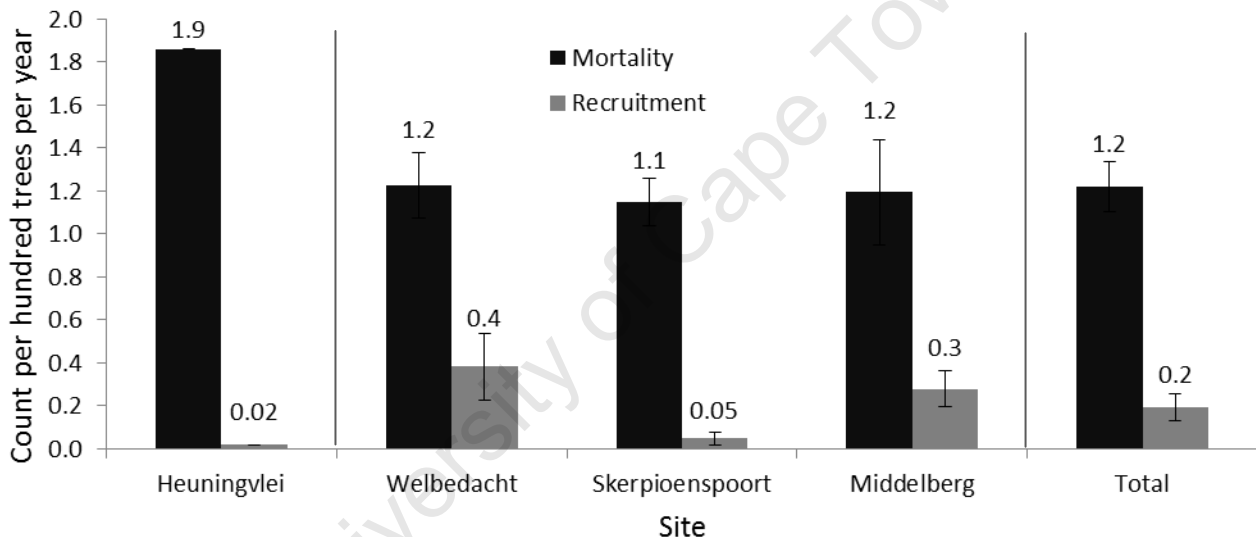


Figure 2. Annual mortality and recruitment rates (per 100 trees) and standard error bars of *Widdringtonia cedarbergensis* at each site analysed in the Cederberg Wilderness Area.

Heuningvlei, which only has plantations, has the highest annual mortality rate of 1.9% and the lowest annual recruitment rate of 0.02%. Welbedacht has an annual mortality rate of 1.2% and the highest annual recruitment rate of 0.4%. Skerpioenspoort has an annual mortality rate of 1.1% and a low annual recruitment rate of 0.05%. Middelberg's annual mortality rate is the highest amongst the natural populations at 1.2% with a recruitment rate of 0.3%. The overall annual mortality and recruitment rates for all sampled cedars in the Cederberg are 1.2% and 0.2%,

respectively. No significant difference was found between the sites at the 95% confidence level for annual mortality or recruitment, using separate one-way ANOVA analyses.

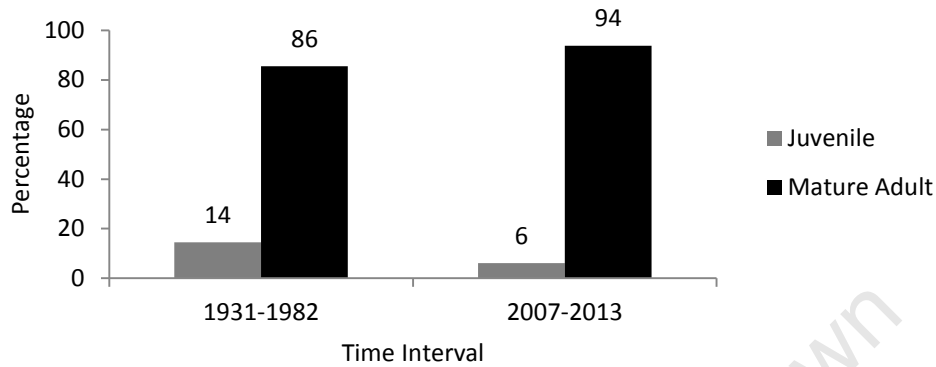


Figure 3. Age class structure of the *Widdringtonia cedarbergensis* population at each site analysed in the Cederberg Wilderness Area (n=1315 before, n=347 after) for historical photographs (1931-1982) and for repeat photographs (2007-2013).

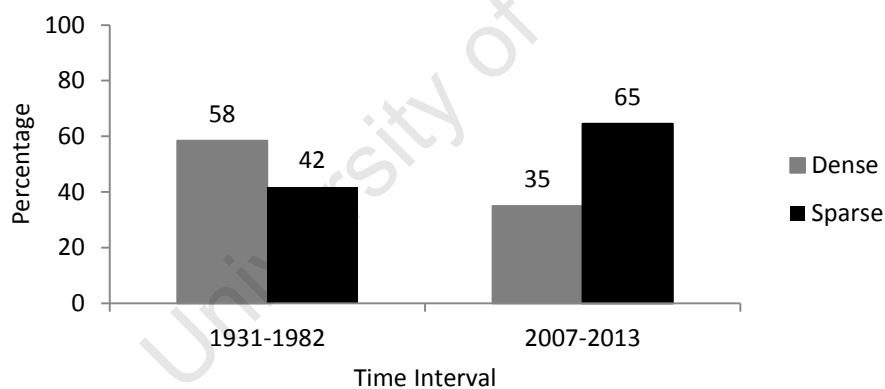


Figure 4. The density of foliage cover of the *Widdringtonia cedarbergensis* population at each site analysed in the Cederberg Wilderness Area (n=1315 before, n=347 after) for historical photographs (1931-1982) and for repeat photographs (2007-2013).

The historical photographs' age class structure had a greater proportion of juveniles (14%) than in the repeat photographs (6%) (Fig 3). Figure 4 shows that there are a greater proportion of trees with sparse foliage cover in the repeat photographs (65%) compared to the historical photographs (42%).

## Fire Frequency Maps

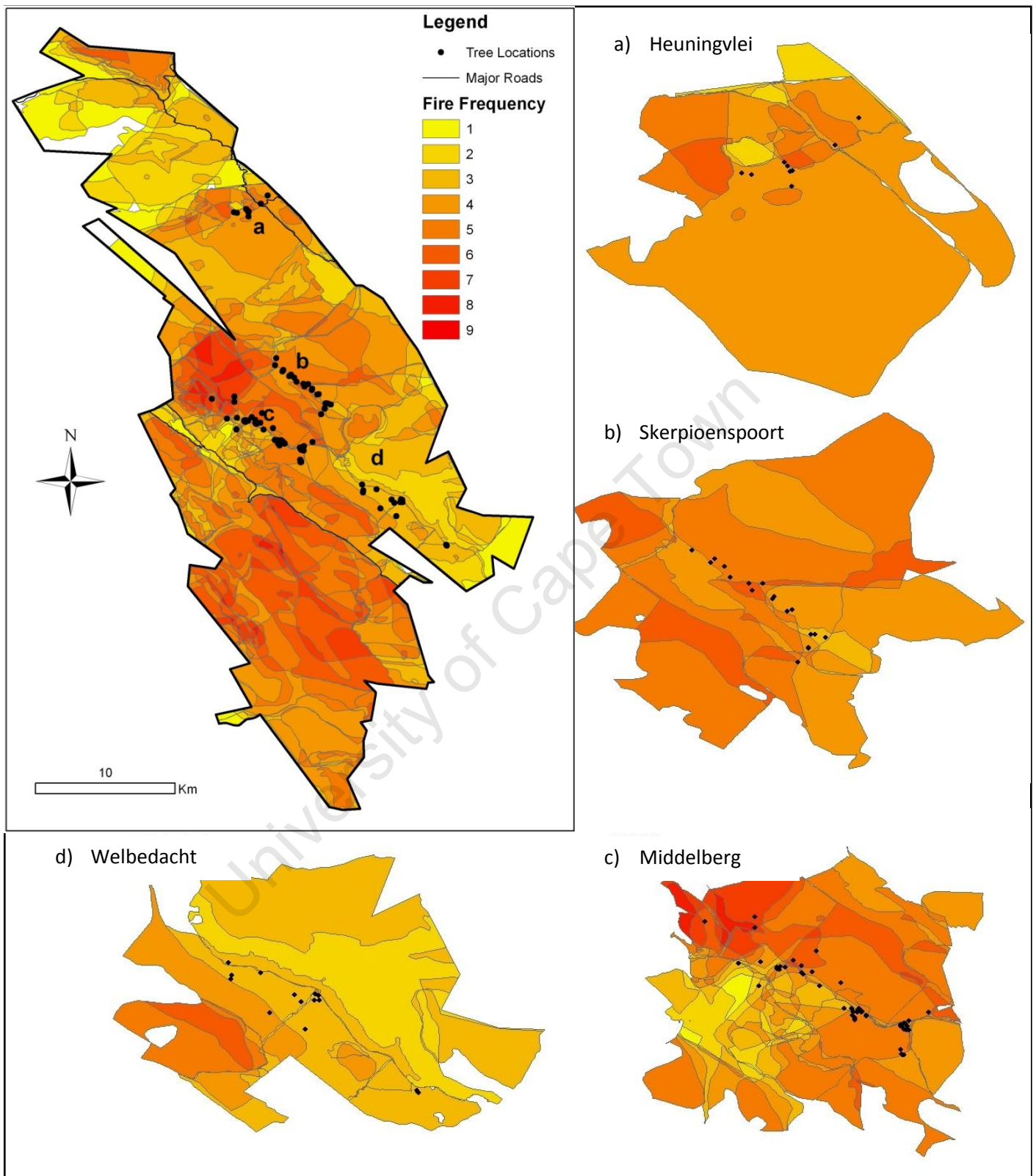


Figure 5. Fire frequency map of the Cederberg Wilderness Area with individual fire maps for all sites visited: a) Heuningvlei; b) Skerpioenspoort; c) Middelberg; and d) Welbedacht. The fire record is from 1944 to 2012.

The fire frequency that the cedar trees experienced at the Heuningvlei site (Fig 5a) ranged between four and five, with the median of four fires over the observed period of 68 years. The fire frequency for the cedar trees at the Skerpioenspoort site (Fig 5b) ranged from three to six fires with the median of five fires over the observed period. The fire frequency observed at the Middelberg site (Fig 5c) ranged from three to eight fires, with the most common frequency of fires being five over the observed period for the cedar trees. At the Welbedacht site (Fig 5d), the observed fire frequency that the cedar trees experienced ranged between three and four fires, with three fires being the most common frequency over the observed period. Over all the sites visited in the Cederberg Wilderness Area, the range of fire frequencies experienced by cedar trees was from three to eight fires, with five fires observed as the overall median (Fig 5).

Table 1. Estimated fire return intervals relative to the range of fire frequency occurring in the Cederberg Wilderness Area over the fire record (68 years) (Fire Interval = Fire Record Length/Fire Frequency).

Fire Frequency	Fire Return Interval (years)
1	68
2	34
3	22.7
4	17
5	13.6
6	11.3
7	9.7
8	8.5
9	7.6

Table 1 indicates that the estimated fire return interval at Heuningvlei is 17 years (median = four fires) over the 68 year fire record. The fire return interval at Skerpioenspoort and Middelberg is estimated to be 13.6 years (medians = five fires), while the estimated fire return interval at Welbedacht is the longest at 22.7 years (median = three fires) over the 68 year fire record (Table 1).

### Precipitation and Temperature Data

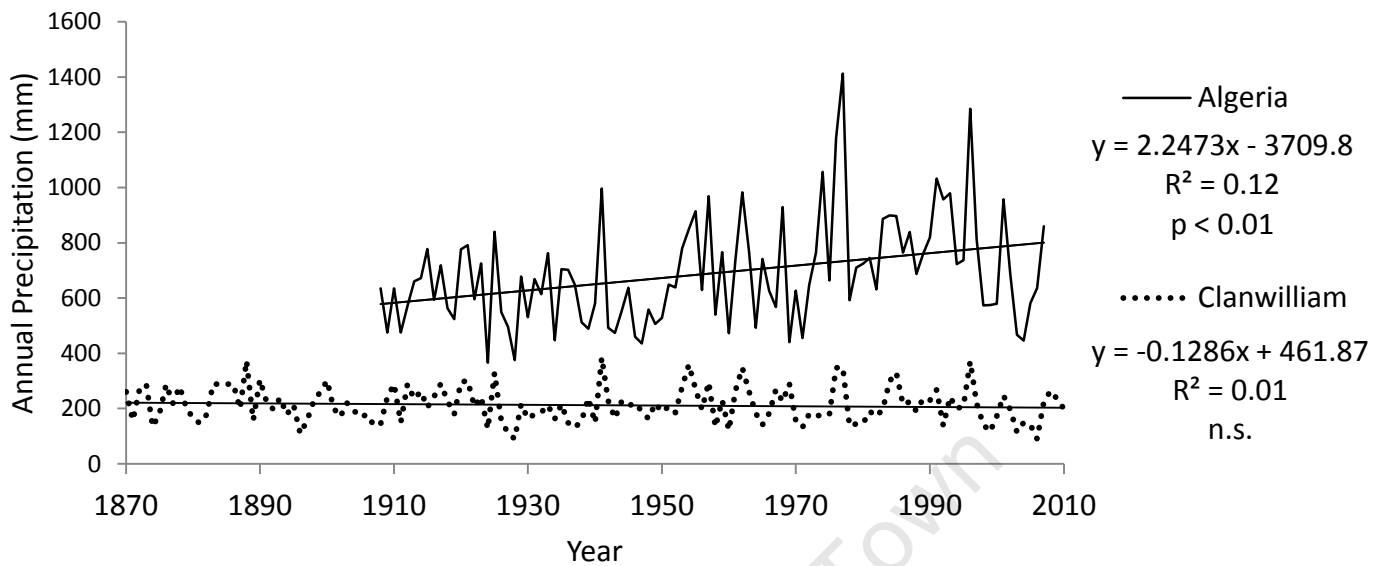


Figure 6. Annual precipitation (mm) at Algeria Forest Station (solid line) from 1908 to 2008 and Clanwilliam (dashed line) from 1870 to 2010 with trend-line equations,  $R^2$  values and significance levels, for each respectively.

There has been a significant ( $p < 0.01$ ) increase in annual precipitation at Algeria Forest Station over the last century (Fig 6). There is a large amount of variation in annual precipitation at Algeria Forest Station, as shown by the  $R^2$  value of 0.12 (Fig 6). The annual precipitation at Clanwilliam has shown no significant change ( $p > 0.05$ ) from 1870 to 2010, with a  $R^2$  value of 0.01 and very high variability (Fig 6). Algeria Forest Station has a larger range of annual precipitation values (366 to 1412 mm) and generally receives far more rain than Clanwilliam (90 to 385 mm) (Fig 6).

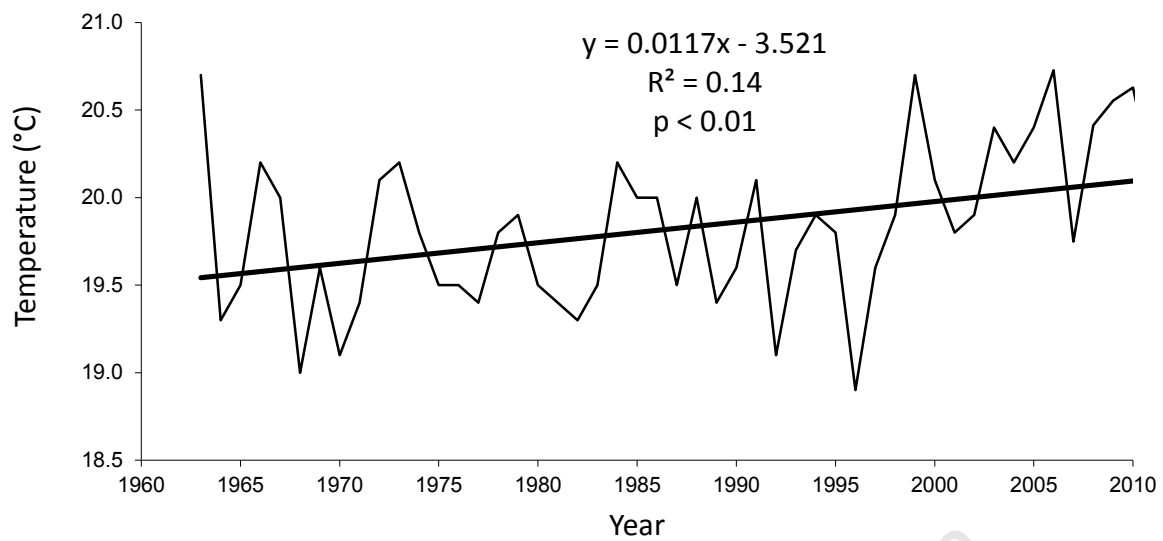


Figure 7. Annual mean temperature (°C) in Clanwilliam from 1963 to 2010 with a trend-line,  $R^2$  value and significance level.

There has been a significant ( $p < 0.01$ ) increase in annual mean temperature (°C) in Clanwilliam between 1963 and 2010 (Fig 7). There a large amount of variation in annual mean temperature in Clanwilliam, as shown by the  $R^2$  value of 0.14. An estimated increase of 0.6 °C has occurred from 1963 to 2010 (Fig 7).

**Observed *Widdringtonia cedarbergensis* mortality statistics**

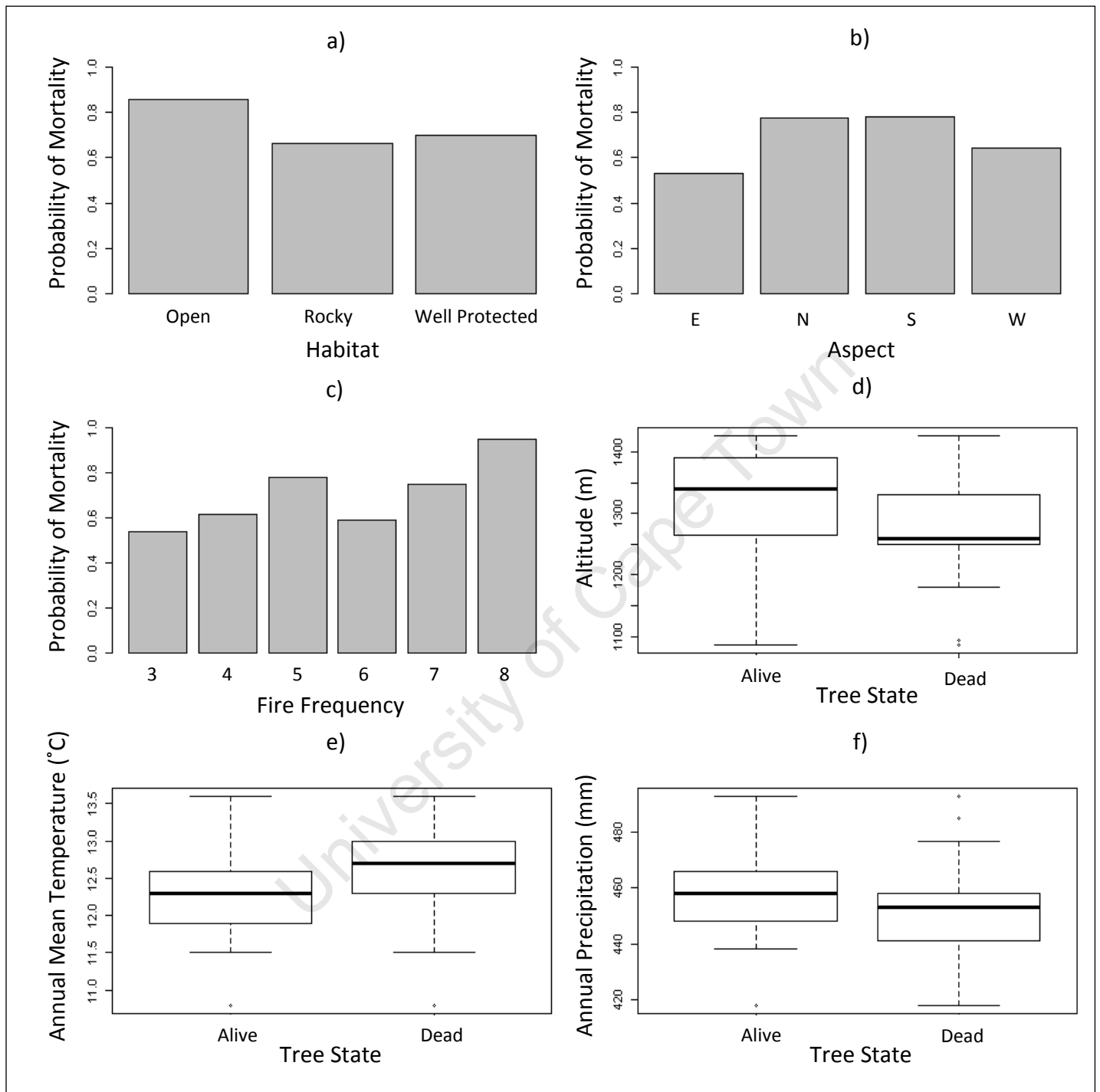


Figure 8a-f. Observational plots of mortality of *Widdringtonia cedarbergensis* mortality in natural populations at Skerpioenspoort, Middelberg and Welbedacht in the Cederberg Wilderness Area (n = 823). Figures 8a-c indicate the observed probability of cedar death in different habitats (a), at different aspects (b) and with different fire frequencies (c). Figures 8d-f indicate the observed mean, 1<sup>st</sup> and 3<sup>rd</sup>

quartiles and minimum and maximum values, as well as outliers where applicable for altitude (d), annual mean temperature (e) and annual precipitation (f) for trees that are either dead or alive.

The observed data indicate that there is a greater probability of mortality in open habitats followed by well protected and rocky habitats (Fig 8a), at North and South, then West and lastly East aspects (Fig 8b) and with a higher frequency of fires (with a small decline at 6 fires) (Fig 8c). Furthermore, the observed data indicate there are more dead trees at lower altitudes compared to higher altitudes with a range of 1086 to 1426 m (Fig 8d), with a higher annual mean temperature and range of 10.8 to 13.6 °C (Fig 8e), and with a lower annual precipitation and range of 418 to 493 mm (Fig 8f).

#### **Altitude and temperature correlation**

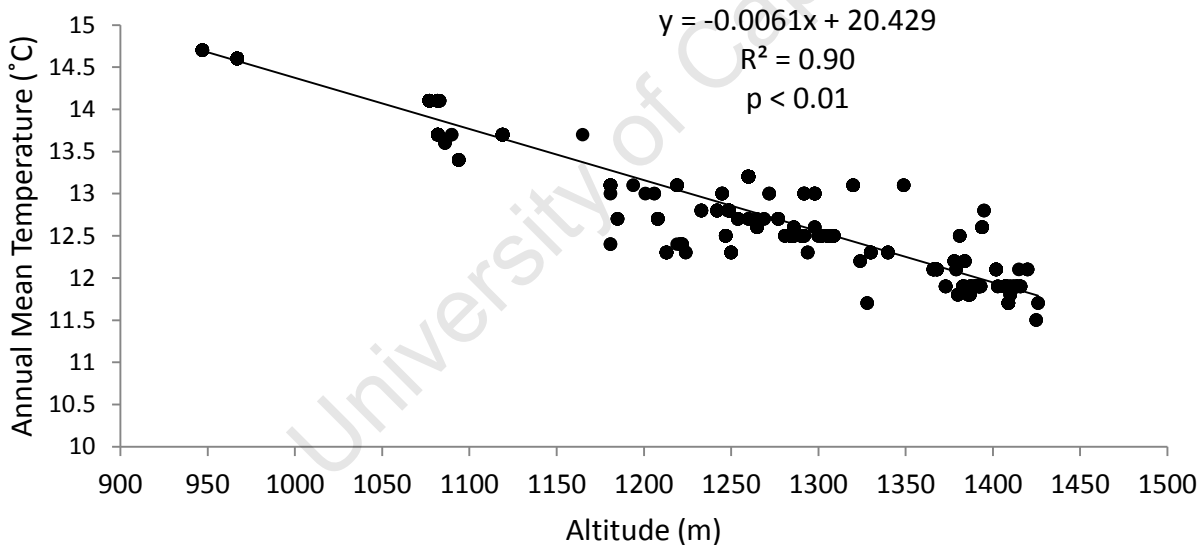


Figure 9. The observed relationship between altitude (m) and estimated annual mean temperature (°C) for all recorded *Widdringtonia cedarbergensis* trees (n = 823).

There is a strong ( $R^2 = 0.90$ ), significant ( $p < 0.01$ ), negative relationship between altitude and annual mean temperature for the observed *W. cedarbergensis* trees (Fig 9). This indicates that there is a temperature gradient, with temperatures decreasing with an increase in altitude (Fig 9).

### Generalized Linear Model

The model tested the relationship between mortality and habitat, fire frequency, aspect, annual mean temperature, altitude, annual precipitation and the interactions between habitat & fire frequency and aspect & annual mean temperature. Annual mean temperature and altitude are significantly correlated with one another (Fig 9) and therefore add unrealistic precision to the generalized linear model. Annual precipitation also strongly correlates with annual mean temperature and altitude. Due to these co-correlations annual precipitation and altitude were discarded from the model decreasing the degrees of freedom and increasing the amount of variation in mortality that the model could explain.

Table 2. ANOVA of the final fitted generalized linear model fit chosen using AIC and the respective p-values of the selected variables.

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	
NULL	NA	NA	865	1068.313039	NA	
Habitat	2	13.63373628	863	1054.679303	0.001095	**
Fire Frequency	1	28.84289742	862	1025.836405	7.85E-08	***
Aspect	3	21.45280823	859	1004.383597	8.48E-05	***
Annual Mean Temperature	1	47.0863793	858	957.2972179	6.79E-12	***
Habitat:Fire Frequency	2	4.996126819	856	952.301091	0.082244	.
Aspect:Annual Mean Temp.	3	6.830398283	853	945.4706928	0.077505	.

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 '' 1

Habitat, fire frequency, aspect and annual mean temperature all have a significant effect on cedar tree mortality ( $p < 0.01$ ) (Table 2). The interaction between habitat and fire frequency, as well as aspect and annual mean temperature are significant at the 90% confidence level (Table 2). The final fitted model reported an  $R^2$  value of 0.12. This indicates that the model can explain 12% of the variation found in *W. cedarbergensis* mortality.

### Generalized Linear Model Predictions on Cedar Tree Mortality

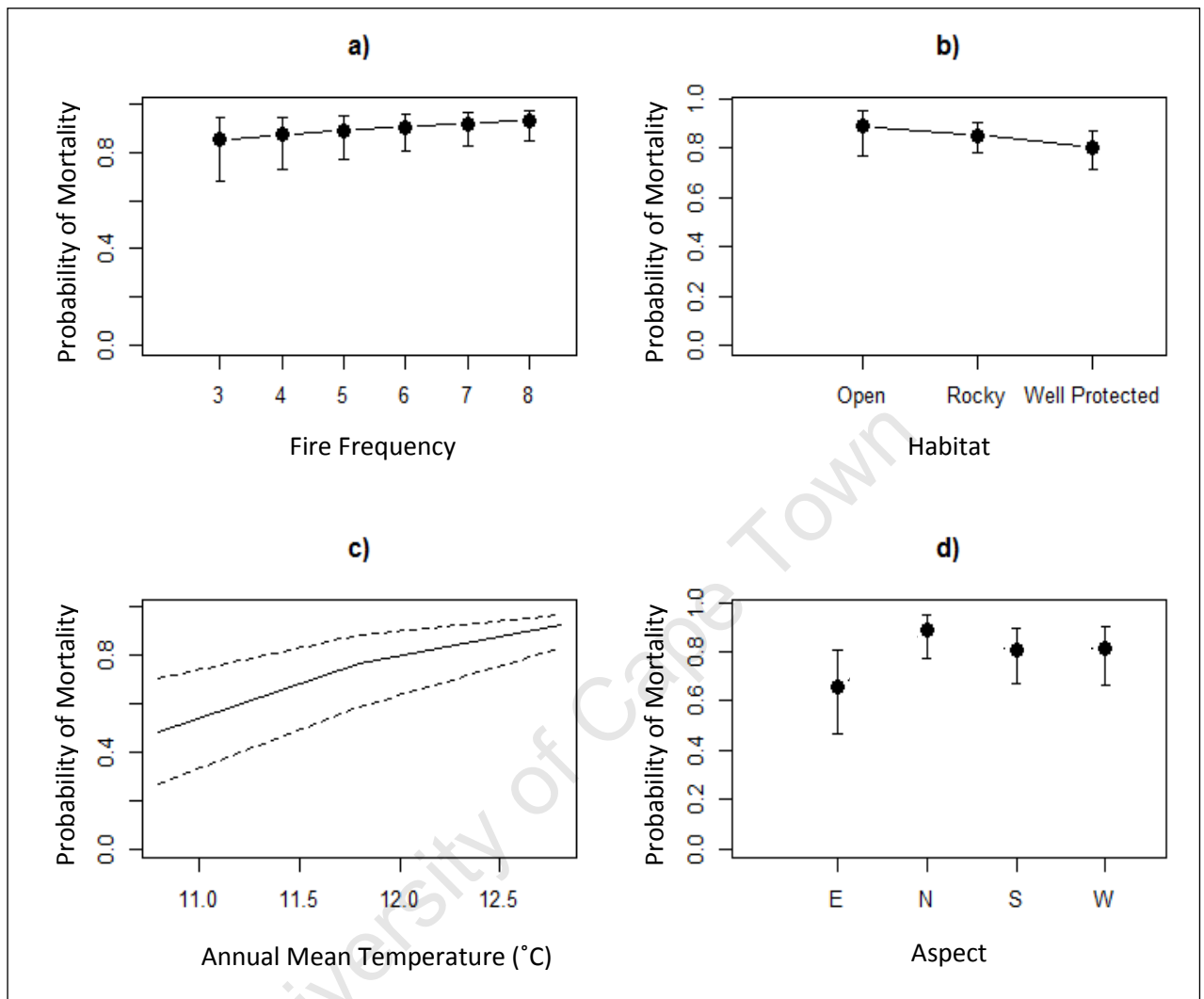


Figure 10a-d. The probability of mortality with 95% confidence intervals against predictions of single variable responses when all other model variables are set at medians, for cedar trees in natural populations: a) fire frequency, b) habitat, c) annual mean temperature and d) aspect.

From the generalized linear model, it is predicted that the probability of mortality for a cedar tree increases with: an increase in the frequency of fire (Fig 11a), a decrease in rockiness (Fig 11b) and an increase in annual mean temperature (Fig 11c). The predicted probability of mortality was greatest at north facing aspects, followed by south & west and lastly east (Fig 11d).

## **DISCUSSION**

### ***Population decline***

As many studies have shown before (Hubbard, 1937; Smith, 1955; Lückhoff, 1971; Andrag, 1977; Meadows and Sugden, 1991), this study further documents the cedar's decline. Specifically, this study documents the decline of the cedar in the mid- to end-20<sup>th</sup> century. In the historical photographs (1931-1982) a total of 1315 living cedar trees were counted in both natural and plantation populations. More than 74% of the trees recorded in the historical photographs were recorded as being dead in the repeat photographs (2007-2013). Out of the 392 living trees recorded in the repeat photographs only 11% (n=45) of these were recorded as juveniles.

No significant difference in annual mortality or recruitment was found between sites (Fig 2). Although the sites do not encompass the entire range of the cedar trees, it is evident that at three spatially separated sites with large natural populations, Welbedacht, Skerpioenspoort and Middelberg, there are high and consistent annual mortality rates. It is likely then, that the factors influencing cedar mortality act over its entire range and not on spatially isolated populations. Figure 2 further shows that annual recruitment rates are low, with the mean for all sites being just 0.2%. This is of particular concern for the species future survival, as natural annual recruitment levels are too low to compensate for the high annual mortality rates.

Further concern for the cedar's future survival is illustrated by the changes in age class structure (Fig 3) and the density of foliage cover (Fig 4) of all sampled cedar trees. These figures illustrate that the cedar population is not in a healthy state, as the repeat photographs have shown both a decrease in the proportion of juveniles (Fig 3) and a decrease in the general health of the trees (Fig 4) with a greater proportion showing a sparse cover of foliage. This decline in health is potentially the first sign of plant stress due to carbon starvation or hydraulic failure and may be the ultimate cause of death for certain trees (Adams et al, 2012; Anderegg et al, 2012)

### ***Fire frequencies***

Brown et al (1991) suggested that a typical fire frequency interval for fynbos in the Cederberg is between 11 and 15 years. The fire frequencies shown in Figure 5 show that in the 68 years of recorded fires in the Cederberg the median number of observed fires over the region is five. This means that fires recur at an average of 13.6 years, supporting Brown et al's (1991) findings. Importantly, all of the tree locations recorded in this study were shown to overlap with the area of a past fire. Furthermore, no tree was shown to experience less than 3 fires in the 68 year period. This translates to a fire return interval of 22.7 years as a minimum period to escape fire. As previously discussed, cedar trees only begin to reach sexual maturity after approximately 12 years and need to wait approximately 40 years to reach full reproductive maturity (Manders, 1986). Manders (1987b) argues that prior to any anthropogenic influence, the cedars may have existed in denser communities, resulting in suppression of the fire-prone fynbos understorey and a lesser likelihood of frequent or intense fires. Therefore, he suggests that anthropogenic changes have led to a critical loss of mature adults as a result of natural wildfires, with a subsequent small yield of seed and seedling recruitment.

### ***Climate records***

Annual precipitation records from Algeria Forest Station (Fig 6) indicate an increase over the last century at a site in the Cederberg Wilderness Area. The annual precipitation in Clanwilliam (Fig 6) has shown a great amount of variability over the last century ( $R^2 = 0.01$ ), but no significant change ( $p > 0.05$ ). Annual mean temperature records from Clanwilliam indicate that an estimated increase of 0.6 °C has taken place over the last 50 years (Fig 7) ( $p < 0.01$ ). The general increase in temperature (Fig 7) supports predictions that the Cederberg area is getting warmer (Midgley et al, 2002a, 2003). However, predictions of drier conditions (Midgley et al, 2002a, 2003) are yet to be realised by the long term precipitation records, with an increase or no change at all shown in the Cederberg region (Fig 6).

### ***Factors affecting *Widdringtonia cedarbergensis* mortality***

The generalized linear model allowed for the relative influence of environmental factors affecting mortality to be analysed in combination. The model reported an  $R^2$  value of 0.12, indicating the ability to explain approximately 12% of the variation in the data. Therefore, there are likely to be a number of other factors not investigated in this study that contribute to cedar mortality. The addition of other important factors influencing mortality, such as pests and disease, may improve the explanatory power of the model. Furthermore, a greater sample of trees across the range of the Cederberg (e.g. in the Sneeuberg area) and finer spatial resolution data for fire frequency, temperature and available water that more accurately reflect microhabitat conditions would further improve confidence in the model results.

There remains a difficulty in studying a long-lived species whose ecology is so closely linked to fire. The relationship between fire frequency and fire intensity is usually described as more frequent fires burn more of the fuel load more often, lessening the intensity of the fire or alternatively less frequent fires allow the fuel load to accumulate resulting in more intense fires. However, the method of repeat photography only allows one to ascertain whether a tree has died during a time frame and not whether a specific event (e.g. a fire from a certain year) or the intensity of a fire was responsible for a death. Therefore, the presentation of fire frequency in relation to mortality should be interpreted in this context, as trees may have died during any of the fire events that may have passed their location in the recorded period.

The observed data indicates that open habitats, with less rock cover had a larger percentage of deaths than either the well protected or rocky sites (Fig 8a). Interestingly, there was little difference between rocky and well protected sites. This association is likely due to protection from fire, higher moisture contents and possibly secondary dispersal (Manders, 1986; Midgley et al, 2002). For aspect, north and south facing slopes showed the highest mortality probabilities, followed by west and then east facing slopes (Fig 8b). This was not expected, as southern slopes are likely to be cooler than northern slopes and therefore show less mortality. It is

speculated that the cooler, south facing slopes show similar mortality as they may accumulate a greater fuel load allowing for more intense fire events. Fire frequency showed a general increase in the likelihood of mortality with an increasing number of fires, despite a drop in the probability of death for six fires (Fig 8c). The decrease in the likelihood of death from five to six fires may have an ecological reason, such as more frequent fires being less intense fires, although beyond a threshold the sheer number of fire events would become damaging. However, it is more likely that the fire frequency is being misrepresented by a small sample size, with only 90 trees recording a frequency of six fires. Therefore, it seems likely that a consistent increase in fire frequency will result in a greater chance of cedar mortality. It is also likely that the lack of recruitment observed (Fig 2) is due to the high frequency of fire.

The observed data indicates that dead trees mostly occur at lower altitudes, whereas living trees occur across most of the range (Fig 8d). This suggests that the trees are shifting their range due to a change in an abiotic factor, such as temperature. Figure 8e supports this suggestion, indicating that dead trees generally occur at higher annual mean temperatures, while trees that are alive occur at sites with lower annual mean temperatures. Dead trees also occur at sites with a lower annual precipitation which could indicate a combined temperature and rainfall effect on the survival of cedar trees (Fig 8f).

The factors investigated in this study that most influence cedar death are shown to be annual mean temperature, fire frequency, aspect of slope and the amount of rockiness surrounding the tree or habitat. There is also a smaller influence from the interaction between the amount of rockiness and the frequency of fires – this is to be expected, as a greater cover of rockiness has been shown to protect trees from the effects of fire (Manders, 1986). The interaction between aspect and annual mean temperature also shows to be slightly significant, however, this interaction is contentious with both south and north slopes showing the greatest observed mortality. This supports the findings of Andrag (1977), who found that cedars are not limited to any aspect in their distribution, except in the northern areas.

The model output indicates the relative impact of each variable on the probability of mortality at that fire frequency, habitat, temperature or aspect (Table 2, Fig 10a-d). These results indicate a similar trend to those found in the observed data (Fig 8a-c, e). An increase in fire frequency is shown to increase the probability of cedar mortality (Fig 10a). An increase in rocky protection increases the probability of cedar survival (Fig 10b), while an increase in temperature is predicted to have large increase in the probability of death (Fig 10c). Lastly it is predicted that eastern slopes have the lowest mortality, followed by southern and western slopes and lastly northern slopes which appear to have the greatest probability of cedar death (Fig 10d).

### ***Reasons for decline***

Considering all of the results of this study within the context of the published literature from the last century, much can be said for the historical and current decline of Clanwilliam cedar. It seems likely, from archaeological evidence presented by Meadows and Sugden (1991) and Cartwright (2013) that the Cedar tree has been in a steady, but not severe decline for approximately 14 500 thousand years or longer. This decline has been attributed to long term warming and drying of the climate in the late Quaternary, perhaps causing more severe fire regimes.

Fire regimes have long been influenced by a pre-colonial human presence, which would have potentially affected tree mortality going back several thousand years (Meadows and Sugden, 1991). Subsequent to this, during colonial expansion into South Africa's interior, Clanwilliam cedar trees were widely used because they were the only readily available source of timber in the region (Hubbard, 1937; Smith, 1955). This removal is suggested to have had a serious impact on the Cedars current status, but it is difficult to place much faith in these records as they do not have accurate estimates of cedar mortality. However, what is clear is that the cedar trees were exploited for some time and it would be difficult to dispute that this contributed to their decline.

In the 20<sup>th</sup> century, there has been less clarity as to why the cedar has continued its decline. This study shows that there are factors today which are still strongly influencing the mortality of cedar trees. Manders (1987b) argues that inappropriate or changed fire regimes, with an increase in the frequency of fire, have increased cedar mortality. This is confirmed by the findings of this research, with greater fire frequencies leading to a greater likelihood of death (Fig 10a). This is further supported by the prediction that rockier habitats offer protection from fire (Fig 10b). The impact of fire frequency should be understood within the context of the cedar's life history, as fire return interval is far shorter than the time required for a recruit to reach full maturity.

However, the key contribution of this study is to highlight the significant impact of temperature on the survival of cedar trees over the last century (Fig 10c). Given that temperatures over the last five decades have been increasing at weather stations in the vicinity of the Cederberg region (Fig 7), predictions for the Cederberg are for warming and drying (Midgley et al, 2002a, 2003) and temperature change should be viewed as a serious threat to cedar mortality. Precipitation records indicate that the Cederberg is not drying, but is rather receiving more rainfall now than a century ago (Fig 6). An increase in precipitation has the potential to increase fuel loads leading to more intense fires, but may also ameliorate the effects of a temperature increase.

The debate over causative links between anthropogenic greenhouse emissions and climate change is settled (Thomas et al, 2004; Walther et al, 2002; IPCC, 2007). However, it is difficult to attribute a causative link between cedar mortality and changes in global or regional temperatures. This study shows a correlative link between the deaths of cedars at lower altitudes (Fig 8d), more observed and predicted deaths at higher temperatures (Fig 8e and Fig 10c, respectively) and an increase in temperatures in the cedar's distributional region (Fig 7). The effects of temperature have been shown to increase tree mortality in global and regional studies (Allen, 2010), indicating that Clanwilliam cedar populations at lower altitudes, where temperatures are greater (Fig 9), may be at their physiological limit and therefore prone to greater mortality. To confirm these findings, controlled empirical temperature experiments should be conducted on cedar trees to discern

their actual physiological limits. This type of investigation would allow for a causative link to be drawn between increasing temperatures and Clanwilliam cedar mortalities.

This study has shown that the *W. cedarbergensis* decline has strongly continued in the 20<sup>th</sup> century with 74% of recorded trees dying during the last 75 years. Over-harvesting and changes to the fire regime were likely the main causes of *W. cedarbergensis* mortality in the 18<sup>th</sup> and 19<sup>th</sup> century. The main reasons for the 20<sup>th</sup> century mortality appear to be high fire frequency and high temperatures at lower altitudes. This supports the first hypothesis (1) that there is no significant difference in mortality rates across the geographical range of *W. cedarbergensis*. The second hypothesis (2) is supported by the findings that fire frequency and temperature, as well as rockiness of habitat and aspect significantly influence *W. cedarbergensis* mortality. The key finding of the effect of temperature on *W. cedarbergensis* mortality should be viewed within the context of climate change in the late Quaternary and more recent anthropogenic climate change. Conservation efforts should be focused on protecting high altitude populations of *W. cedarbergensis* and limiting the frequency of fires.

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