

# Exploration of a climate mediated decline in a critically endangered southern hemisphere conifer over the last 40 years

Annabelle J. Rogers

Supervised by Dr. Edmund February and Dr. G. Tony Verboom

## Abstract

*Widdringtonia cedarbergensis* is a critically endangered conifer restricted entirely to the Cederberg Mountain range in the Western Cape of South Africa. This study aimed to assess whether contemporary climate change could be a driver in the recently documented ten-fold decline of *W. cedarbergensis* in the last 40 years. By building distribution models using Maxent bioclimatic modelling for pre- and post- 1970's point occurrence data, the distribution of the species pre- and post-1970's were compared and assessed for significant change. Models predicted a clear range contraction in *W. cedarbergensis* from pre- to post-1970. The present model predictions of suitability occur in a tight altitudinal band on the mid to upper slopes of the middle Cederberg (minimum of 1048m to a maximum of 1530m). However, the climatic predictions associate the present model distribution with relatively warmer and drier areas compared to that of the pre- 1970 model, suggesting a shift down slope rather than upslope. This is possibly due to the exaggeration of the upper limit of distribution for the pre-1970's model that predicts *W. cedarbergensis* to occur as high as 1850m. This is unlikely due to the high prevalence of frost at this elevation. Though any climatic signal was complicated due to historical data error, high confidence in the present model prediction adds a valuable contribution to a body of literature that documents the decline of *W. cedarbergensis* and has important implications for conservation management of the species.

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## Introduction

*Widdringtonia cedarbergensis* (Marsh) is a critically endangered conifer restricted entirely to the Cederberg Mountain range in the Western Cape of South Africa. The IUCN red list classified the Clanwilliam cedar as 'endangered' in 1998 before upgrading the species to 'critically endangered (CR)' with an A2 classification in 2013. The A2 classification is given to species that have declined rapidly (loss of  $\geq 80\%$  of numbers over the last 10 years) and the drivers of decline have not been addressed or may not be reversible (IUCN, 2013). The drivers of the decline of *W. cedarbergensis* remain much disputed. There exists three main hypotheses: commercial utilization, changes to fire regimes and late Quaternary climate change.

One of the most popular hypotheses is that extensive commercial utilization in the 18<sup>th</sup> and 19<sup>th</sup> centuries was severe enough to reduce the population below a threshold from which it could not recover (Hubbard 1937; Mustart and Bond 1994). Historical accounts suggest extensive use of cedar wood for much of the late 18<sup>th</sup> and early 19<sup>th</sup> centuries (Andrag 1977). However, the extent of this use is debated with commercial harvesting of wild individuals of *W. cedarbergensis* strictly controlled from the 1870s in response to concern over the rate of use (Luckhoff 1971). For commercial utilization to be responsible for the decline in species after exploitation ceased, there would have had to have been severe fragmentation of *W. cedarbergensis* to small inviable populations or a population bottleneck resulting in a loss of genetic diversity. Genetic studies have, however, found no evidence of a genetic bottleneck in *W. cedarbergensis* relative to its sister species *W. schwarzii*, a morphologically similar species endemic to the Baviaanskloof reserve in Eastern Cape of South Africa. The two species have similar morphologies and life histories and occupy regions of a similar size (Thomas & Bond 1997).

The second explanation for decline of *W. cedarbergensis* is a change in the fire regime. *Widdringtonia cedarbergensis* is fire sensitive, an unusual trait for a species existing exclusively in the fynbos where fire is a cyclically occurring ecosystem process (Bond et al 2005). The life history of the species makes it very sensitive to changes in the fire regime; adult stems are fire intolerant and though mildly serotinous (Manders, 1985), seedlings take up to fifteen years to set seed (Mustart and Bond 1994). A potential fire survival mechanism is thought to be aggregation into dense patches (Manders 1987; Mustart and Bond 1994)

but such dense natural stands are rarely seen today. Records from the Cederberg Wilderness Area for the past fifty years have indicated an increase in fire frequency in the area (Southey 2009). With such poor response to fire, this increase in frequency is believed by many to be a primary driver for the decline.

The final major hypothesis for the long term decline of *W. cedarbergensis* is climate change since the terminal Pleistocene. Meadows and Sudgen (1990) found an overall decline in fossilized *W. cedarbergensis* pollen from the terminal Pleistocene to the present that suggests the cedar decline has to be understood in the context of climate change over the past 14 000 years. Research using stable carbon and nitrogen isotope ratios of hyrax middens has suggested that the Cederberg has experienced marked climatic variance since the late Quaternary, with periods of significant drying (Meadows and Chase 2010; Chase et al 2011; Quick et al 2011). Meadows and Sudgen (1990) that may have driven species decline.

Commercial utilization, fire and climate change since the terminal Pleistocene all assume the state of today's populations is simply the result of a gradual long term decline. Despite this, there is some evidence to suggest that last 40 years in particular have experienced major decline. Monitoring plots in the area have shown a ten-fold reduction in population in the last 40 years (Fox 2003), whilst others show average annual mortality rates of nearly 2.5% (Bonara 2008). Anecdotal evidence suggests that the species decline has been further enhanced in the past 15 years; of 15 tress banded for a study in 1998, only one remains living to date (Edmund February, pers. Comm.). This suggests that the recent (in the last 40 years) decline is distinct from the species history of decline (Ed feb, *pers.comm*) and as such should be investigated separately as factors that may have driven a long term decline may not necessarily be behind the recent population crash.

Recent climate change in the Cederberg could be a driver of the current decline. The Cederberg is thought to be particularly sensitive to climatic change and modeling predictions suggest that the Cederberg will not be able to support fynbos vegetation in 50 years due to climate change (Midgley et al, 2003). Evidence from studies worldwide suggests that 30 years of contemporary climate change have been enough to impact current species distributions (Parmesan and Yohe 2003) with montane species being particularly prone to shifts in distribution (Lenoir et al 2008). The Cederberg has undergone notable

climatic change in the last 40 years; CO<sub>2</sub> concentrations have increased (February and Stock 1999) and records for Western Cape national parks show a widespread increase in temperature by up to 1.8 °C since 1960 (Ferreira et al 2013). Though no rainfall change has occurred over the past 100 years in the area (Hoffman et al 2008), several tree ring studies suggest that precipitation volume is not an important control on the growth of these trees (Dunwiddie & La Marche 1980; Zucchini & Hiemstra 1983; February & Stock 1999). This may be because the large and extensive rooting system of the tree allows it to access groundwater stores thereby decoupling its growth from rainfall (February & Stock 1998).

In addition to the support provided by the temporal co-occurrence of climate change and substantial decline in *W. cedarbergensis*, the current health of the trees also supports a hypothesis of climate mediated decline. Bonora's (2008) demographic study found that the proportion of trees with dense foliage cover has substantially decreased over the last 40 years. Decreased greenery can be indicative of warming in an area (Lapenis et al 2005) and is a physiological response to drought stress.

Using Maxent bioclimatic modelling, and assessments of population health, this study tests the hypothesis that contemporary climate change has powered the recently documented decline of *W. cedarbergensis*. By comparing models of *W. cedarbergensis* distribution using observational data from before and after 1970s, this study can assess whether the distribution of the species has changed through time. If the recently observed decline was related to the warming temperatures, one would expect the post-1970s model to show a range contraction to cooler areas at higher elevations as is well-documented for montane species of plants (Walther et al 2002; Parmesan & Yohe 2003; Lenoir et al 2008). If the decline was not related to climate, there should be no obvious altitudinal shift in suitability between pre- and post-1970 models. Though past-use may have removed much of the lower elevation trees before 1900, the lack of recent extraction should prevent a distinct altitudinal shift up the mountains in the past 40 years. We predict that bioclimatic modelling will show a contraction in the area of suitable habitat for *W. cedarbergensis* between the pre- and post- 1970's models to areas of higher elevation, as is typical with montane vegetation under climate warming scenarios.

## **Methods:**

### Study Area:

The Cederberg Mountain range forms the north-western backbone of the Cape Floristic Region (CFR). Located in the northern part of the Western Cape 200 km north-west of Cape Town, the Cederberg mountain area lies between -32°00' and -32°45'S and 18°50' and 19°25'E. As a winter rainfall area, the region receives lower average rainfall than other Cape mountain ranges, with an average rainfall of 700 mm per annum (Taylor, 1996). Significant rainfall gradients do occur within the area; rainfall increases with elevation, and from east to west (Taylor 1996). Gradients also exist in temperature, with the high elevations having mean annual temperatures of 10 – 11 °C in comparison to the lower elevations which are warmer (16–18 °C) (According to mapped bioclim data - Hijmans et al 2005).

The Cederberg Wilderness Area (henceforth CWA) consists of multiple conservancies and covers much of the Cederberg range (660 km<sup>2</sup>). Elevation ranges from 180 masl at Citrusdal asl to 2027 m asl at Sneeuberg (Higgins et al 2001). The vegetation is dominated by Cape Mountain fynbos at all elevations (Higgins et al, 2001). As with the rest of the CFR, fire in the Cederberg is an important ecosystem process. Records for the area suggest that the fire return interval is decreasing over time (Fox 2003; Bonora 2008; Southey 2009).

### Species Distribution Model:

The modelling of habitat suitability for *W. cedarbergensis* was done using maximum entropy (henceforth maxent). Maxent is a machine learning method that is notable for its ability to deal with small sample sizes and a lack of reliable absence data (Phillips et al 2006) making it ideal for rare species modelling (Engler et al, 2004). The model works on the principle of maximum entropy, estimating a probability distribution of occurrence by selecting that which is most uniform and subjecting that distribution to a set of constraints imposed by occurrence data (Phillips et al 2006). Maxent models have two essential inputs: occurrence data in the form of spatial coordinates and environmental variables for the area of occurrence. Unlike other SDM methods, Maxent does not require input of pseudo-absences by the user but instead uses probability distributions to automatically isolate random points from the given background area (Phillips et al 2006). Maxent, though relatively new, has proved to be robust and precise in comparison to older methods (Elith et al 2006).

Modelling was done using the freeware programme R (ver 2.15.2; R Core Team 2012), with the *dismo* (Hijmans et al 2013) and raster packages (Hijmans & van Etten 2013). The Maxent java add-in (version 3.3.3k) was accessed and run through R. For the purpose of bioclim modelling, I treated the area between 18°54'-19°30' E and -32°48'--32°0' S as the background for the model, an area of 66.72 km by 88.96 km. This area includes all recorded *W. cedarbergensis* occurrence points and formed the available background area for the species pseudo-absence points generated by the Maxent model.

Two distribution models were built using Maxent, the first based on all specimen collection localities dating from before 1970, and the second using collection localities dating from after 1970. Each model was built separately using the partition method whereby one third of the occurrence data points were randomly assigned to a testing data set whilst the remaining two thirds were the training data set. The training data set was used to build the models and make predictions on habitat suitability. The testing data set was reserved for testing the model using ROC curves and AUC values. Following model evaluation, both the pre- and post-1970 models were built using the full complement of data points relevant to each.

Once the final models had been generated and the final predictions computed, the overlay function in the raster library (Hijmans & van Etten, 2013) was used to calculate suitability differences between the two models. The resulting layer documented the magnitude and direction of change in suitability in each pixel present.

#### Occurrence Data

Occurrence data for *W. cedarbergensis* came from a variety of sources and were sorted into pre-1970 and post-1970 (henceforth present) data sets.

The pre-1970 data set consisted of 19 records, all from the PRECIS database (SANBI, 2013). The records ranged in age from 1895 to 1970. All records received for *W. cedarbergensis* were geo-referenced using ARC-GIS and a 1:50,000 topographical map of South Africa by analysts within SANBI.

The edited present data set consisted of 69 GPS localities from three sources. Fifteen records, ranging in age from 1972 to 1986, came from PRECIS, eight came from Fox's (2003)

study of Manders' (1986) permanent monitoring plots, and 46 came from a study by Higgins (2001).

Environmental Variables:

The environmental variables used were obtained from Worldclim, a 30 arc-second global climate data model (Hijmans et al, 2005). Worldclim provides climatic layers of 19 climatic variables (summary of bioclim variables in Appendix I) with a spatial resolution of 0.86 km<sup>2</sup> at the equator. The resolution of 1 km<sup>2</sup> is suited to historical occurrence data from the early to mid-20<sup>th</sup> century due to imprecision in translation of a written description to a GPS locality (Engler et al, 2004).

Principal components analysis (PCA) was performed on the 19 bioclim variables to eliminate co-linearity between the layers. The first four PCA layers were included in analysis as they represented a cumulative 99.2% of variance in climatic data with PCA1, 2, 3 and 4 explaining 79.4%, 11.7%, 5.9% and 2.1% of the variance respectively. The variables that strongly contributed to PC1 were those that described the conditions of the warmest season. The variables contributing to PC2 and PC3 are measures of temperature stability and winter conditions. PC4 is contributed to most by temperature seasonality (>0.75).

**Table1:** table showing the five variables with the highest contribution to each principal component layer and the direction of their influence. Variables emboldened contributed 0.75 or greater to the loadings of the layer.

| PC1                                      |      | PC2                                   |      | PC3                                   |      | PC4                                      |      |
|--|------|---------------------------------------|------|---------------------------------------|------|--|------|
| Variable                                 | Sign | Variable                              | Sign | Variable                              | Sign | Variable                                 | Sign |
| Precipitation of Warmest Quarter         | +    | Min Temperature of Coldest Month (°C) | +    | Temperature Seasonality               | +    | <b>Precipitation Seasonality</b>         | +    |
| Precipitation of Driest Quarter (mm)     | +    | Isothermality                         | +    | Precipitation of Wettest Quarter (mm) | +    | Mean Temperature of Coldest Quarter (°C) | -    |
| Mean Temperature of Warmest Quarter (°C) | -    | Precipitation of Wettest Month (mm)   | +    | Precipitation of Wettest Month (mm)   | +    | Mean Temperature of Wettest Quarter (°C) | -    |
| Mean Diurnal Range (°C)                  | -    | Precipitation of Coldest Quarter (mm) | +    | Precipitation of Coldest Quarter (mm) | +    | Min Temperature of Coldest Month (°C)    | -    |
| Max Temperature of Warmest Month (°C)    | -    | Temperature Seasonality               | -    | <b>Isothermality</b>                  | -    | Precipitation of Driest Month (mm)       | -    |

## Model Evaluation

The pre-1970's and present models were evaluated by calculating the area under the receiver operating characteristic (ROC) curves. ROC curves plot the sensitivity of the model (the fraction of all occurrence data presences that are predicted correctly) versus the specificity of the model (the fraction of all generated pseudo-absences that are predicted correctly). In a presence-only context AUC values can be interpreted as the probability that a presence site has a higher predicted suitability value than a pseudo-absence site when both are picked at random (Elith et al 2006, Phillips et al 2006). With presence-absence data the AUC values range from 0 to 1 with a score of 0.5 indicating the prediction is no better than random. AUC values of less than 0.7 show poor performance, between 0.7 and 0.9 show good performance and values  $> 0.9$  show very good model performance (Pearce & Ferrier 2000). However, with presence only data the maximum achievable AUC value is slightly less than 1 (Lobo et al 2008).

Each observed model was evaluated 100 times using the training data set and each time the evaluation ran, the presence data were randomly resorted into the testing and training groups. The final AUC values for each of the pre-1970's and the present model were calculated as the mean of all the AUC values calculated on 100 evaluation runs.

To evaluate whether the prediction obtained from the observed model was better than random, null models were generated. For each of the pre-1970's and present models, 100 null models were built, each using a different set of random occurrence points drawn from the same background area and the same predictor layers. The number of random occurrence points for the null models equalled that used in the true models (Reas and Steege 2007); 19 random points for the pre-1970's null models and 69 for the present null models. Each of the null models generated were evaluated 100 times, each time with different training:testing repartitionings. The average AUC for each null model calculated and all 100 average AUC values were plotted in a histogram for comparison to the observed models.

### Climatic associations of predicted suitability:

To assess whether the present model was associated with a different climatic envelope to that of the past model, the pixels containing higher suitability ( $>0.75$ ) values were extracted

from the pre-1970's and present prediction landscapes. These points were then overlaid onto each of the 19 bioclim variables and corresponding climatic values extracted for each variable. The climatic values for the pre-1970's and present models were plotted onto the same axes to permit an assessment of how the climatic associations of the species have changed through time. The pre-1970 and present climatic means for each bioclim variable were tested for significant difference using a two-sided independent t-test assuming unequal variance. Suitable pixels (>0.5) as predicted by the pre-1970's and present models were isolated and their elevation values extracted. The pre-1970 and present elevation ranges were plotted in a histogram to assess to degree to which an altitudinal shift is evident.

#### Population health:

To evaluate how well the suitability changes predicted by the models fit health of existing populations, average measures of tree health for each of four large populations in the Cederberg were correlated against amount of change predicted for the locality using simple linear correlation.

Population health data were gathered from four wild populations- Heuningvlei (Rocklands), Sneeuberg, Driehoek and Welbedacht. Based on methodology used by Higgins (2001), the health of randomly selected trees was assessed. For each tree selected, the height was estimated and GPS coordinates recorded. For dead trees, the presence of leaves, twigs and bark was recorded, and it was noted whether the tree had fallen or remained standing. For living trees, the percentage cover of live canopy was recorded by estimating the amount of green foliage present relative to bare branches. The number of cones on the tree was estimated using four categories where 0= no cones on the tree, 1= 1-8 cones, 2 = 9-64 cones, 3 = 65 –512 cones, and 4 = >512 cones. Presence of fire char and strip barking on the stem was also noted.

### **Results**

#### Mapped suitability predictions:

The mapped suitability predictions for the past model identified *W. cederbergensis*-suitable habitat (green colouration) as being widespread in the CWA. Areas of high suitability (>0.8) included Krakadouw (32.50 ° S, 19.05° E, Figure 1A) at the northern extreme of the CWA and

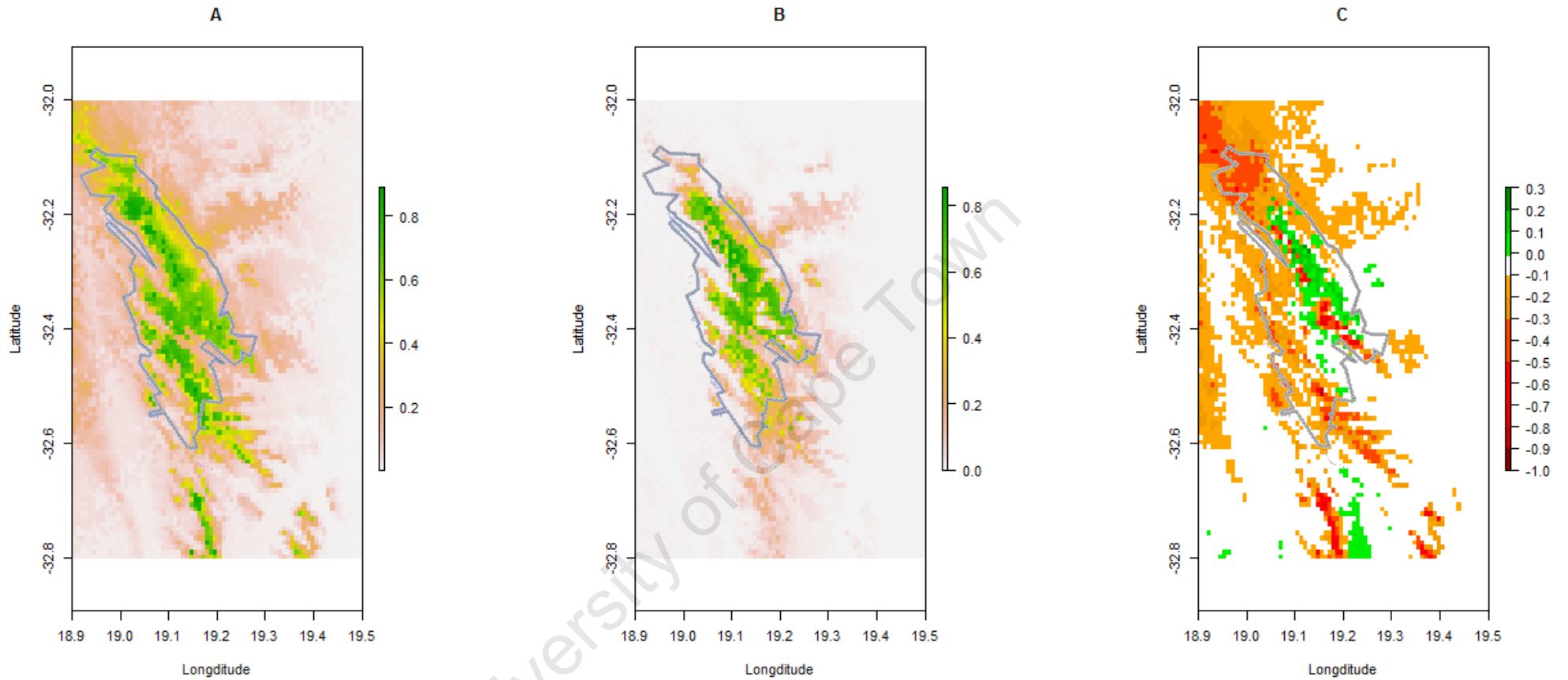
the higher elevation area around Sneeuberg (32.20 ° S, 19.15° E, Figure 1A) above Algeria Valley. Areas of high predicted suitability for *W. cedarbergensis* also existed outside the CWA, most prominently to the south around Middelneus and Grootberg (32.75° S, 19.17° E, Figure 1A). The low flats to the east and west of the CWA were predicted to have low suitability for *W. cedarbergensis*.

The present model showed a contraction of high suitability areas into mid elevation areas in the core of the CWA reserve. The area of highest suitability in the present model occurred in the central CWA around Skerpionesberg (32.32 ° S, 19.14 ° E, Figure 1B). Sneekop at 1931 m (32.39° S, 19.19° E, Figure 1B) and Sneeuberg at 2027 m (32.55° S, 19.20° E, Figure 1A), the highest elevation points in the CWA, both showed very low suitability values in the present model.

The mapped change in suitability showed very little area where there had been an increase in predicted suitability between the pre-1970 and present models (Figure 1C, areas in green). Although there was an apparent increase in suitability in the southern extreme of the map, this reflects a shift from 0 to 0.1, indicating that these areas were initially unsuitable and remain so in the present time. Areas that were initially suitable and increased in suitability in the present time occur only in the northern part of the CWA on the high mountain ridge formed between Tafelberg and Krakadouwspiek. Not all high elevation points improved in suitability – Sneekop (32.39° S, 19.19° E, Figure 1C) and Sneeuberg (32.55° S, 19.20° E, Figure 1C) were initially suitable but became unsuitable in the present model.

#### Model evaluation:

Both the past and present true models had average AUC values that were higher and fell outside the distribution of AUC values for the null models (Figure 2), indicating the true past and present models were a significantly better fit to the data than the random models. Each data point in the histogram represents a single null model in which the average AUC score was calculated 100 times, using 100 separate training:testing repartitionings. 100 null



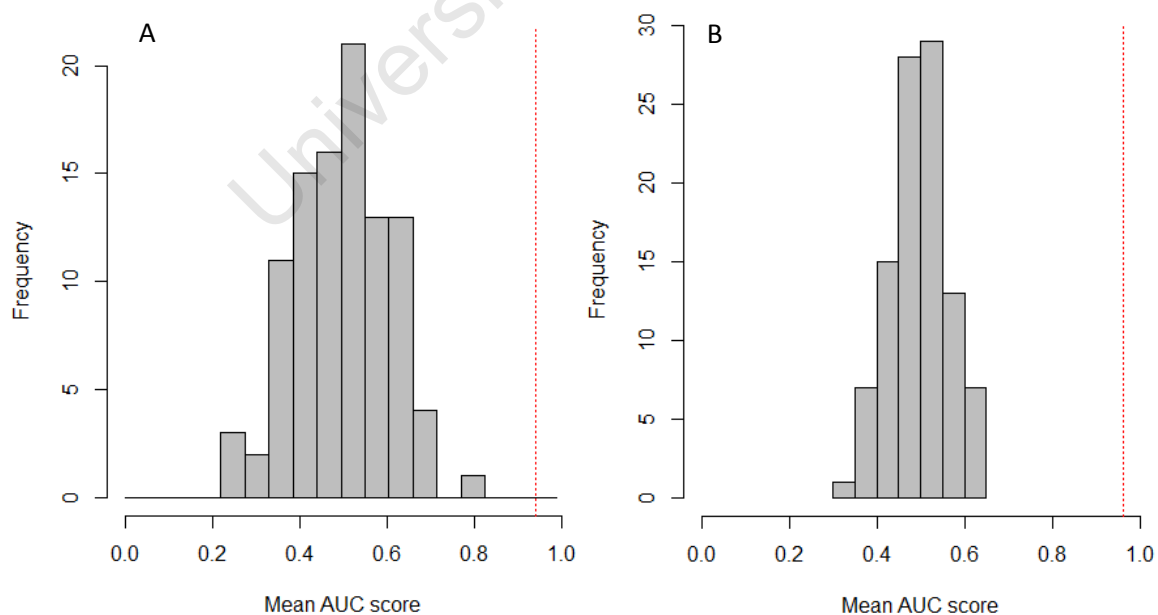
**Figure 1:** A- Maxent model prediction of habitat suitability in the Cederberg mountain range based on (A) pre-1970 and (B) post-1970 (Present model) occurrence records for *W. cedarbergensis*. Colour scales show green for high suitability and red for low suitability. (C) Overlay of pre-1970 and present model, showing a landscape of change in suitability between pre and post 1970 model predictions, using the function  $\{ \text{post-1970} - \text{pre-1970} \}$ . Colour scale indicates magnitude and direction of change in suitability, with green indicating an increase in suitability, white no change and red a decrease in suitability. The grey outline shows the Cederberg Wilderness area.

models were generated, each time with a new set of random data. The 100 null models generated to test the pre-1970 model formed a normal distribution centred on 0.495 (Figure 2A) (minimum score 0.2255; maximum score 0.807). The mean AUC score for the true pre-1970 model, calculated as the mean of 100 separate training:testing repartitionings for the given data, was 0.942 (minimum score 0.8930; maximum 0.9848). The present model null AUC values centred on 0.516 (minimum 0.3449; maximum 0.6396) in comparison to true present model with a mean of 0.962 (minimum score 0.9351; maximum score 0.9351).

Climatic variables and Elevation

The pre-190 model climate range of suitable areas was typically much wider than that found in the present model. The present model climate ranges represented a small subset of the pre-1970's range and was consistently associated with warmer, drier conditions.

The present model temperature ranges were centred on mean temperature values that are between 1 - 2 °C higher than those of the pre-1970 model for all temperature variables. The variables with the largest difference between pre-1970 and present model means were measures of the annual/diurnal ranges or temperature extremes in the warmest



**Figure 2:** Model significance analysis using frequency of AUC distribution for 100 random models evaluated 100 times each (bars in grey) against the mean AUC score calculated for the real models evaluated 100 times (red vertical line) for (A) the pre-1970 model and (B) the post-1970 model.

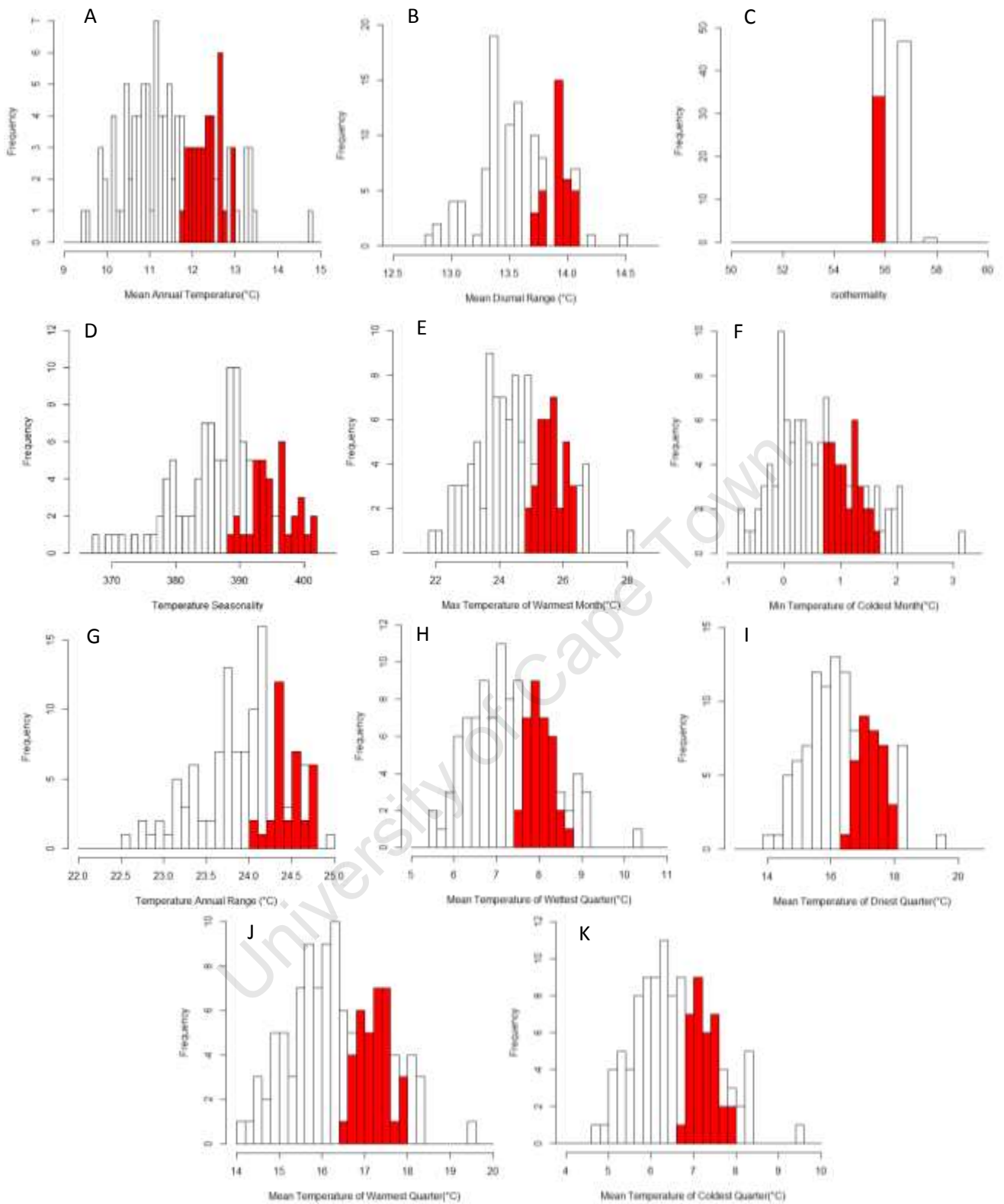
months: mean diurnal range (°C) (Figure 3B), temperature seasonality (Figure 3D), maximum temperature of warmest month (°C) (Figure 3E), mean temperature of driest quarter (°C) (Figure 3I), and mean temperature of warmest quarter (°C) (Figure 3J).

The present model was also associated with drier conditions in comparison to the pre-1970's model. Variables with the most significant difference between means related to annual precipitation (mm) (Figure 4A), and amount of winter precipitation received; precipitation of wettest month (mm) (Figure 4B), precipitation of wettest quarter (mm) (Figure 4E), and precipitation of the coldest quarter (mm) (Figure 4H).

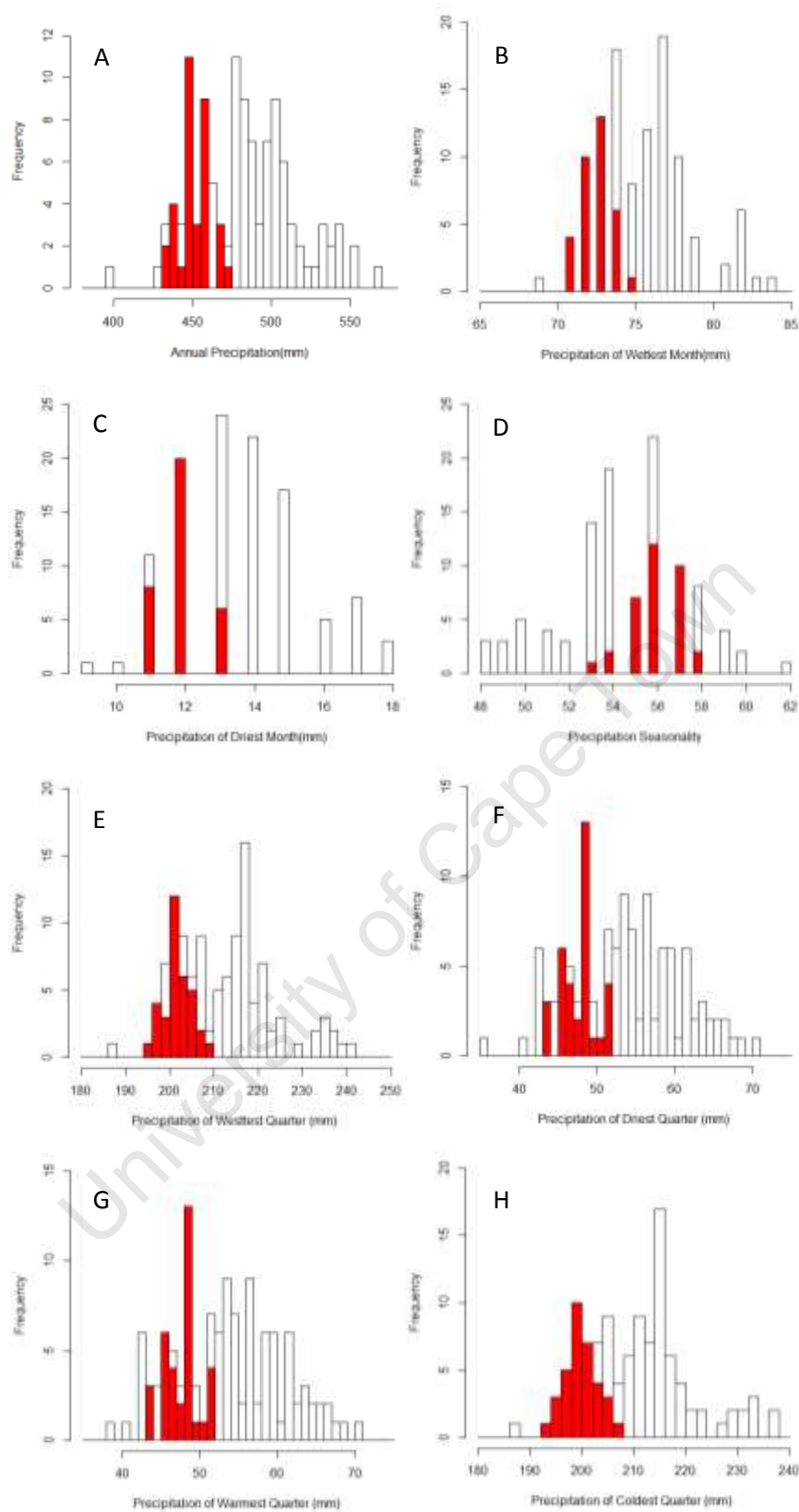
Altitudinal change in between the pre-1970 and the present model showed a contraction of pre-1970 model altitudinal range to a narrower altitudinal band in the present model (Figure 5). There was no significant difference in the means of the two distributions ( $t = 1.0346$ ,  $df = 827.941$ ,  $p\text{-value} = 0.3011$ ) and the highest frequency of suitable points in both the pre-1970 and present model was found to occur at about 1300 m.

#### Population health:

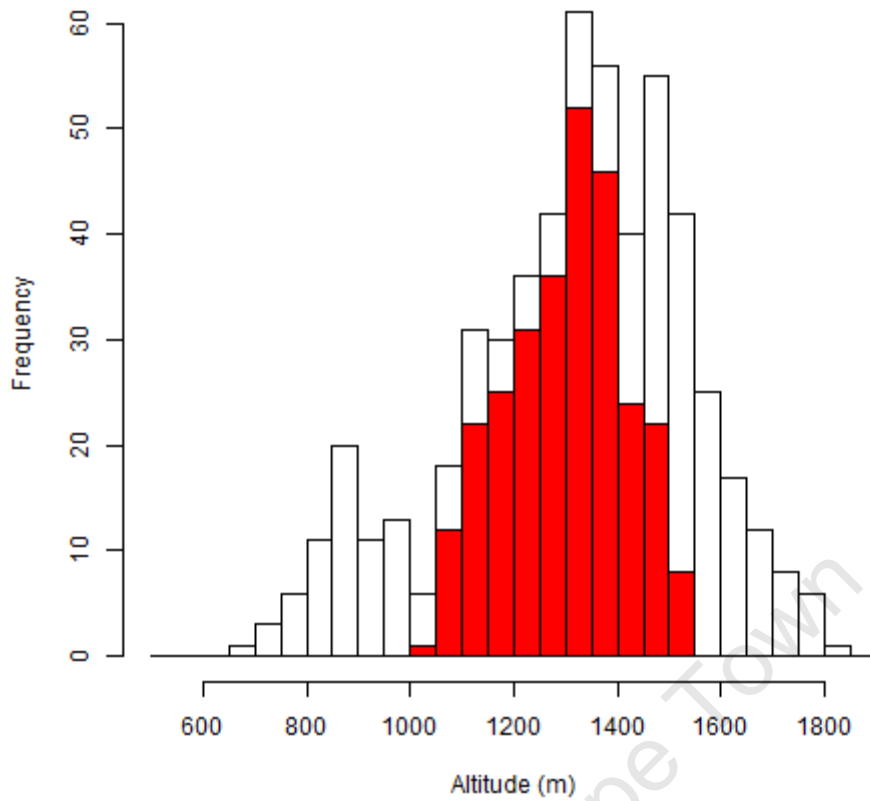
Testing the model with change values predicted for real populations and the associated health of those populations resulted in a strong correlation ( $R^2 = 0.9082$ ,  $df = 2$ ,  $p = 0.031$ ) for percentage canopy cover (Figure 6). Sneeuberg, the highest elevation point, was both the population with the most negative change and the lowest average canopy cover (Figure 6). All other measures, including proportion of living adults bearing cones and the ratio of dead to live trees, showed no significant trend or pattern with amount of change predicted for the location.



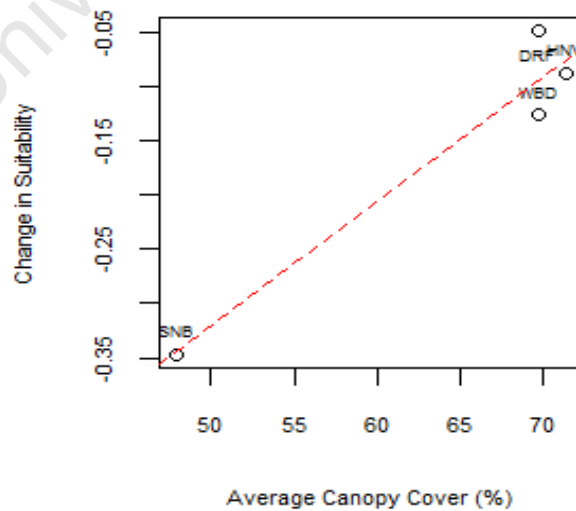
**Figure 3:** Plots of precipitation values for pixels in the pre-1970 model and in the present model that have a suitability prediction of greater than 0.75. The white bars show the distribution of precipitation values from pixels in the pre-1970 model, and the red bars show values from the present model. All plots shown have significantly different pre-1970 and present model ( $p > 0.0001$ ). The plots correspond to **(A)** Annual Mean Temperature ( $^{\circ}\text{C}$ ) ( $t = -7.562$ ,  $df = 132.0$ ,  $p < 0.0001$ ), **(B)** Mean Diurnal Range ( $^{\circ}\text{C}$ ) ( $t = -9.040$ ,  $df = 131.8$ ,  $p < 0.0001$ ), **(C)** Isothermality ( $t = 9.3845$ ,  $df = 99.0$ ,  $p < 0.0001$ ), **(D)** Temperature Seasonality ( $t = -9.869$ ,  $df = 107.5$ ,  $p < 0.0001$ ), **(E)** Maximum Temperature of Warmest Month ( $^{\circ}\text{C}$ ) ( $t = -8.267$ ,  $df = 132.0$ ,  $p < 0.0001$ ), **(F)** Minimum Temperature of Coldest Month ( $^{\circ}\text{C}$ ) ( $t = -6.049$ ,  $df = 131.9$ ,  $p < 0.0001$ ), **(G)** Mean Annual Range ( $^{\circ}\text{C}$ ) ( $t = -10.445$ ,  $df = 127.668$ ,  $p < 0.0001$ ), **(H)** Mean Temperature of Wettest Quarter ( $^{\circ}\text{C}$ ), **(I)** Mean Temperature of Driest Quarter ( $^{\circ}\text{C}$ ) ( $t = -7.986$ ,  $df = 132.0$ ,  $p < 0.0001$ ), **(J)** Mean Temperature of Warmest Quarter ( $^{\circ}\text{C}$ ) ( $t = -7.986$ ,  $df = 132.0$ ,  $p < 0.0001$ ) and, **(K)** Mean Temperature of Coldest Quarter ( $^{\circ}\text{C}$ ) ( $t = -7.081$ ,  $df = 132.0$ ,  $p < 0.0001$ )



**Figure 4:** Plots of precipitation values for pixels in the pre-1970 model and in the present model that have a suitability prediction of greater than 0.75. The white bars show the distribution of precipitation values from pixels in the pre-1970 model, and the red bars show values from the present model. All plots shown have significantly different pre-1970 and present model means ( $p > 0.0001$ ). The plots correspond to **(A)** Annual Precipitation (mm) ( $t=9.708$ ,  $df=132.0$ ,  $p<0.0001$ ), **(B)** Precipitation of Wettest Month (mm) ( $t=9.727$ ,  $df=132.0$ ,  $p<0.0001$ ), **(C)** Precipitation of Driest Month (mm) ( $t=8.3947$ ,  $df=131.9$ ,  $p<0.0001$ ), **(D)** Precipitation Seasonality (Coefficient of Variation) ( $t=-4.204$ ,  $df=129.111$ ,  $p=4.85e-05$ ), **(E)** Precipitation of Wettest Quarter (mm) ( $t=9.970$ ,  $df=131.0$ ,  $p<0.0001$ ), **(F)** Precipitation of Driest Quarter (mm) ( $t=8.406$ ,  $df=131.5$ ,  $p<0.0001$ ), **(G)** Precipitation of Warmest Quarter (mm) ( $t=8.551$ ,  $df=131.7$ ,  $p<0.0001$ ), **(H)** Precipitation of Coldest Quarter (mm) ( $t=10.207$ ,  $df=132.0$ ,  $p<0.0001$ ).



**Figure 5:** Histogram plot showing the elevation of each pixel in which the probability of presence of *W. cedarbergensis* was greater than that of absence (i.e. model prediction for pixel was greater than >0.5) for the pre-1970 model (white bars) and the present model (red bars).



**Figure 6:** Scatter plot showing the change in suitability of the location of four wild populations of *W. cedarbergensis* surveyed in the CWA plotted against the average canopy cover of living trees from a randomly sampled subset of the population where the red dashed line indicates a linear model fit with an  $R^2$  value of 0.8027.

## Discussion

Bioclimatic models based on herbarium specimen data reveal a significant contraction in the spatial and altitudinal distribution of *W. cedarbergensis* from the pre-1970 period to the post-1970 period. As the climate was kept constant in both models and the only two inputs into the modeling exercise were observational records and climate data, the change in predicted suitability is indicative of a real change in distribution of trees from pre- to post-1970. The current predicted range was found to be a geographic subset of the species former predicted range with a clear contraction to a narrow mid slope altitudinal band from a range that previously extended to both higher and lower elevations. Most significantly a clear altitudinal shift by almost 400 m upslope was evident at the lower limit of *W. cedarbergensis* distribution when compared to the pre- 1970 distribution. A contraction of this magnitude fits well with previous estimates of range; Higgins et al (2001) found the species to be most abundant in a narrow band between 1200-1400m whilst much earlier studies (Andrag 1977; Manders 1986) estimated an altitudinal range of 800m to 1 650 m. The contraction in suitability revealed by modelling is generally supported by population health data. Out of all four populations, Sneeuwberg hut was the least healthy (according to per cent canopy cover) and also experienced one of the largest decreases in suitability in the entire study. The other three populations, all of which occur in areas that have experienced slight decreases in suitability over time, had much healthier canopy cover averages. That the populations in poorest health occur in areas where suitability has dropped steeply between the pre-1970's and present lends strong support to the model. This approach does have limitations as the strong correlation between predicted change and health was largely reliant on the Sneeuwberg hut population. This population experienced a devastating fire in January 2013 that is partially responsible for such poor canopy cover in the population. Previously the Sneeuwberg hut population was considered to be the most healthy population in the Cederberg (Edmund February, personal communication).

Although range contraction of the type reported here is a common response to recent climate change, a comparison of the climatic environments represented by the pre- and post-1970 ranges does not identify either elevated temperature or rainfall reduction as drivers of range contraction in *W. cedarbergensis*. If the shift were climate caused, the present model range should occupy relatively colder and wetter areas of the Cederberg that

are found at higher elevations. The climatic range associated with the present model shows the opposite trend and occupies a range that is both warmer and drier – conditions that are associated with a move to lower elevations. Previous study on the species suggests that this is unlikely. Using pollen cores, Meadows and Sudgen (1990) assert that *W. cedarbergensis* was more abundant in the cooler and wetter climate of the late Quaternary. Additionally, warmer and drier areas will also carry higher risk of fire, an implausible move for a fire intolerant species.

The association of the present distribution with warmer drier areas could be a result of the upper distributional limit of the pre-1970's distribution of *W. cedarbergensis*. The range predicted by the pre-1970s model for the past distribution includes high elevation areas (up to 1800m) that have minimum temperatures of below 0°C. The available evidence suggests, however, that *W. cedarbergensis* is incapable of occurring at this elevation owing to the regular occurrence of winter frost (Dunwiddie & La Marche, 1980; Higgins et al 2001). The result of this exaggeration in upper limit is a decrease in the mean temperature associated with the pre-1970's range due to cooler temperatures at higher elevation as well as an increase in mean rainfall volumes due to increasing rainfall with elevation. As a result of this, the post-1970 shift in climate is exaggerated and seems to shift to drier warmer environs.

While the failure of the bioclim models to identify a role for elevated temperature and/or reduced rainfall as a driver of range contraction suggests that other factors are responsible, this result may partly be the result of errors in the data underlying the models, particularly the pre-1970 model. Error in historical records is a common problem when using old records to predict past range shifts (Engler et al 2004; Miller et al 2007; Graham et al 2008; Tingley & Beissinger 2009). Bioclimatic modeling has a strong reliance on observation data and any error in such locations could have large impacts on model predictions (Engler et al 2004). Three points exist in the pre-1970's data set that place trees at the summit or near the summit of Sneeuberg at 1900m. However, it is highly unlikely that these points represent actual observations due to the cold temperatures at the summit. In hindsight, it is more likely that the trees were from the Sneeuberg Hut population at 1300m. Despite this speculation, three independent records place trees near the summit and so they were left in the model.

In addition to the potential error in extreme elevation localities, most of the pre-1970 data points occur at high elevation (>1300 m). The general lack of lower elevation records does not agree with the literature that suggests the tree was fairly common at lower elevations in the past (Manders 1987). Additionally this study had a very small sample size with only 19 pre-1970 records available. Even though Maxent is notable in its ability to deal with both small samples sizes and location error (Elith et al 2006; Graham et al 2008), such a small number of records means that errors in location could have large impacts on the range prediction. The seeming lack of abundance of lower elevation points, the unsupported occurrence of extreme high elevation trees and the small sample size all suggest that the data for the pre-1970 model are not an adequate representation of the historical distribution of *W. cedarbergensis*. This in turn casts doubt on the reliability of the pre-1970 model in predicting the previous distribution of *W. cedarbergensis*.

The error in the models can be overcome in future modelling attempts by accessing more pre-1970's occurrence records for the species, perhaps from the Department of Agriculture, Forestry and Fisheries or from CapeNature's CWA division. Additionally, more rigorous data cleaning protocols are needed, with unlikely or uncertain points removed from consideration.

Even with ideal data, bioclim models are prone to exaggeration of species distribution. Climate models such as the one used in this study cannot show the realised species niche – the geographic area within the climate space actually occupied (Hutchinson 1957). The fundamental and realised niches differ due to the effects of biotic interaction (e.g. limited dispersal, competitive exclusion, and disturbance) (Hutchinson 1957). This is evident in the pre-1970s model that predicts a high degree of suitability in the mountains to the south of the CWA, around Middelneus and Grootberg, while the literature suggests that the distribution of *W. cedarbergensis* is restricted to the Cederberg Range (Andrag 1977, Higgins et al 2001). Even though the area around Middelneus is climatically suitable, biotic factors could limit the spread of the species to these areas such as the heavy, wingless seeds of *W. cedarbergensis* that lend the species a very low dispersal potential (Manders 1986).

Possible other factors contributing to observed changes in distribution could be fire. The median fire interval has decreased in the Cederberg since the 1970's (Southey, 2009). Though fire occurs at all elevations (Southey, 2009) and as such should not create a distinct

elevation contraction, if climate forces *W. cedarbergensis* into a smaller and smaller geographic area over time, fire can compound the decline by destroying populations growing in climatically suitable places.

Whatever the cause, evidence for a significant contraction in the spatial extent and elevation range occupied by *W. cedarbergensis* has important management implications, particularly in guiding replantation efforts. From 1987, Cape Nature began a programme of planting nursery-reared seedlings in the Cederberg (Mustart, 2008). The model results could be used to streamline replanting process for success. As all populations surveyed exist in areas that have experienced a drop in suitability over time, this research suggests that CapeNature should be establishing new populations in more favourable climatic areas rather than augmenting existing populations. This may be of limited use in the long term, however, as the entire area is predicted to warm drastically in the next 50 years (Midgley et al 2002; 2003). *Widdringtonia cedarbergensis* is a long lived species with a generation time of over 100 years and a long maturation period. As such, it does not have the life history traits to respond effectively to major climate change in the next 50 years. The species is doomed to extinction in the wild if temperatures increase as predicted.

## **Conclusion**

In the debate surrounding the decline in *W. cedarbergensis*, novel approaches to exploring an old problem are necessary. This study has provides strong evidence that *W. cedarbergensis* has undergone a range contraction since the 1970's, retreating to both a geographically and climatically restricted area in comparison to its former distribution. However, confidence in the representativeness of the pre-1970 model data in outlining the species true former distribution is low as a result of historical data inaccuracy and small sample sizes. The study was unable to identify a role for elevated temperature and/or reduced rainfall as a driver of the range contraction as data error obscured any climatic signature. However, the study still has important management implications, particularly with guiding re-plantation efforts. With more pre-1970's data records and more rigorous data cleaning, confidence in future modeling attempts will be improved. This first attempt at modeling range changes in *W. cedarbergensis* adds to a body of literature that documents the decline of *W. cedarbergensis* in time but not in space.

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University of Cape Town

## Appendix I

**Table 1:** Name and calculation of each of the 19 bioclim variables used in the PCA analysis for the four PCA layers used in the pre-1970 and present model.

| Label | Name                                     | Description   |
|-------|--|---|
| BIO1  | Annual Mean Temperature (°C)             |   |
| BIO2  | Mean Diurnal Range (°C)                  | (Mean of monthly (max temp - min temp))                               |
| BIO3  | Isothermality (%)                        | (Mean diurnal range /mean annual range) (* 100)                       |
| BIO4  | Temperature Seasonality (%)              | (standard deviation *100)   |
| BIO5  | Max Temperature of Warmest Month (°C)    |   |
| BIO6  | Min Temperature of Coldest Month (°C)    |   |
| BIO7  | Temperature Annual Range (°C)            | (Max temperature of warmest month - min temperature of coldest month) |
| BIO8  | Mean Temperature of Wettest Quarter (°C) |   |
| BIO9  | Mean Temperature of Driest Quarter (°C)  |   |
| BIO10 | Mean Temperature of Warmest Quarter (°C) |   |
| BIO11 | Mean Temperature of Coldest Quarter (°C) |   |
| BIO12 | Annual Precipitation (mm)                |   |
| BIO13 | Precipitation of Wettest Month (mm)      |   |
| BIO14 | Precipitation of Driest Month (mm)       |   |
| BIO15 | Precipitation Seasonality                | (Coefficient of Variation)  |
| BIO16 | Precipitation of Wettest Quarter (mm)    |   |
| BIO17 | Precipitation of Driest Quarter (mm)     |   |
| BIO18 | Precipitation of Warmest Quarter (mm)    |   |
| BIO19 | Precipitation of Coldest Quarter (mm)    |   |

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