University of Cape Town

Faculty of Science

Department of Biological Sciences

Thesis

Submitted in partial fulfilment of the requirements for the degree of

Honours (Biological Sciences)

Changes in abundance and distribution of *Protea caffra* in the central and northern Drakensberg as a consequence of climate and land use change

Daniel Mika-Nsimbi Poultney

Supervisors: Prof Timm Hoffman (Biological Sciences, Plant Conservation Unit, UCT), Prof Edmund February (Biological Sciences, UCT), Dr Anthony G Rebelo (South African National Biodiversity Institute), James Puttick (Biological Sciences, Plant Conservation Unit, UCT), Sam Jack (Biological Sciences, Plant Conservation Unit, UCT)

Biological Sciences

PLANT CONSERVATION UNIT

Abstract

The study investigated changes in populations of *Protea caffra* at five sites in the central and northern regions of the uKhlahlamba Drakensberg Park, a UNESCO world heritage site. Based on an archaeological study in 1994 that used charcoal remains to compare the size of *Protea* species populations in the Drakensberg to a much earlier era (between 1260 to 1880 BP), it was hypothesized that there would be a further decline in the number of individuals. A total of 76 historical photographs (dated from 1950–1995) were re-photographed in 2014 and the number of individual *P. caffra* plants in the two sets of photographs counted to assess the extent and rate of population change. The landform units were demarcated on each photograph according to their catenal position, aspect, elevation and the extent of rocky cover. Geological parameters for each landform unit were obtained from GoogleEarth, climatic data from the South African Atlas of Climatology and Agrohydrology and fire data from MODIS. In 76% of the landform units there was an increase in the number of individuals over time, in 17% a decrease and in 7% there was no change over time. Several hypotheses were generated from a conceptual model based on ecological insight into the study area to explain change in the abundance and distribution of *P. caffra*. Using an Akaike test, the input models were ranked according to how representative the explanatory variables were of the observed change. The model with *aspect* and *elevation* as explanatory variables was ranked the best predictor of change. A greater proportion of increase in the size of the population was found on lower slopes. With increasing atmospheric CO_2, *P. caffra* on the warmer lower slopes are likely to have increased photosynthetic rates and increased productivity. A greater proportion of landform units showing a decrease in *P. caffra* was shown at higher elevations. The reason could be higher fire intensity at higher elevations. The variation in change influenced by fire suggests it is an important regulator of P. caffra numbers. The fact that there is no relationship between fire frequency and landform units showing an increase in P. caffra implies that the majority increase in the species is more likely to be driven by climatic changes, i.e. increases in atmospheric CO_2 rather than a change in the fire regime. Increasing atmospheric CO_2 levels lead to enhanced growth rates, postburn recovery and resprouting of tree species in grasslands and savannas, which

could account for the majority increase in *P. caffra* populations in the grassland of the Drakensberg. This has important conservation management implications for the reserve, in that the current fire regimes do not appear to be having a negative impact on the abundance in *P. caffra*. Further, fire will continue to be an important management tool in maintaining the vegetation structure and grass-tree codominance in the reserve.

Acknowledgements

To all my supervisors, my sincere gratitude for your time and constructive input. To Professor Timm Hoffman, my primary supervisor, my gratitude will always be for your teaching me about research, and for your consistent intellectual guidance and support. It was Professor Edmund February's 1994 study that laid the groundwork for this investigation — thank you for recognising that in concluding this study there were at times too many voices and that I needed to follow my own way. To Dr Anthony Rebelo, thank you for bringing the potential relevance of study to the fore and for your detailed feedback. My sincere thanks to James Puttick for his feedback, technical assistance and invaluable statistical input, and to Sam Jack for his technical assistance and the excellent three-week fieldtrip we shared. A last word of thanks to Professor Ed Granger for the background information he provided to the study area and his continuous feedback throughout the study.

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Introduction

Dynamic ecological landscapes and their drivers

Ecosystems are dynamic and subject to change over time and space, and as part of long timescale climatic cycles (Pickett & Ostfield, 1995). Yet at the same time a defining feature of ecosystems is their resilience or capacity to withstand change without changing state (Gunderson, 2000). In this broad context of ecosystem equilibrium and flux, it is important to consider what structures ecological communities, so as to understand the drivers of change and their influence on particular ecosystems over time.

A central 21st century concern is with the human impact on ecosystems in the form of anthropogenic climate change and land use (Bomhard et al., 2005; Sala et al. 2000). The escalating effects of humans on the global environment, it is predicted, may result in global climate departing significantly from climatic cycles for millennia to come (Crutzen, 2002). While climate change is a global phenomenon, the effects on specific localities are different because of spatial and temporal variation (Higgins & Scheiter, 2012). Similarly, the impact of land management on ecosystems varies and depends on management regimes and geographic location. The influence of these two drivers on ecosystems is the focus of much research as they can potentially cause ecosystems to change state with consequences for subsequent land use and management (Sala et al., 2000; Scheiter & Higgins, 2009; Higgins & Scheiter, 2012; West et al., 2012).

Grassy ecosystem dynamics

Given the locality of the study area, it was important to consider what determines vegetation structure and change in grasslands. Grasslands are biomes that have more or less continuous grass cover and discontinuous tree cover. Such biomes can be described as *patch mosaic landscapes* with patches of grassland, scattered trees, or woodlands that vary in their proportions in different places and at different times (Gillson, 2004; Bond, 2008). There are two major grassland types, temperate and tropical grasslands, which differ in macroclimate, structure and composition of life forms and species (Mucina & Rutherford, 2006).

In environments with less than 650 mm rainfall per year, the primary constraint of woody cover is rainfall, where an increase in woody cover increases linearly with an increase in rainfall. In higher rainfall areas (>650 mm MAP), the primary constraint on woody cover is fire (Sankaran et al., 2005). High rainfall periods increase grass productivity, promote fires and suppress sapling escape in mesic savannas. In arid savannas and grasslands, high rainfall periods have the opposite effect, promoting tree increases because moisture usually limits establishment and sapling growth (Bond, 2008). Long intervals between fires promote sapling escape in mesic savannas. The model proposed by Sankaran et al. (2005) was for savannas which have more woody cover than grasslands, but grasslands could be expected to respond in a similar way.

Grass-tree competition is an important constraint on woody cover in grasslands. Grasses have traits that influence both direct (bottom-up) and indirect (top-down) interactions with woody plants (Bond, 2008). Grasses have dense fibrous root systems that tend to explore soil more intensively than tree roots (Partel & Wilson, 2002). However, trees are capable of sampling soils more extensively to find high-resource patches that are not occupied by grasses. Grasses have the competitive advantage over trees when they share the same below-ground space and grow at the same time as woody seedlings and saplings. The competition for dominance is further compounded by grasses drying out rapidly in the dry season and forming highly flammable fuels.

Given that fire is used as an ecosystem and land management tool, it is important to consider the consequences of fire for structuring grasslands and, in particular, the effect that fire has on *Protea caffra* trees. The probability of tree mortality is a function of fire frequency, fire intensity and tree height, and of resprouting ability (Bond, 2008). 'Gullivers' are saplings that are trapped in the flame zone and are unable to grow tall enough to escape the flames. Many resprouting species are tolerant of fire, resprouting from fire-protected roots and lignotubers, and perhaps for decades are unable to reach an adult, reproductive stage until they escape this flame zone. Escaping the flame zone is determined by the frequency and intensity of fires and the growth rate of trees.

The relative dominance of small trees (<5m tall) in savannas is responsive to fire regimes in grasslands and savannas (Higgins et al., 2007). Annual and biennial fires have shown to result in an increase in small tree dominance in savannas, whereas triennial fires have been shown to decrease small tree dominance. Fire season also has a significant effect on change in the dominance of small trees. The effect of growing season fires has been to reduce the dominance of small trees, whereas the effect of dormant season fires has been to increase small tree dominance. Higgins et al. (2007) found that the expected trend of a decrease in tree density with increasing fire frequency did not occur. The suggested reason for this was that savanna tree species are resilient due to the ability of most to resprout. Further, although stem mortality rates are high for small stems, it is low for larger stems (Higgins et al. 2007).

Climate change

The effects of global climate change on ecosystem states and vegetation shifts in ecological landscapes are of growing concern (Higgins & Scheiter, 2012; West et al., 2012; Sala et al., 2000). Fundamental drivers of vegetation change are increasing atmospheric levels of CO_2, a global increase in temperature and changes in rainfall patterns (Scheiter & Higgins, 2009). A prevalent trend of the impact of climate change on vegetation is bush encroachment. 'Bush encroachment', or the increase in woody plant cover in grasslands and savannas, has been observed in many parts of the world over the past century (Archer et al., 1995). The causes of these shifts have been debated, with some views focusing on global drivers, particularly the effects of increasing CO_2 on the tree/grass balance. Others are centered on changes in land use, especially increased grazing and the decreased use of fire (Bond, 2008).

Higgins & Scheiter (2012) used adaptive Dynamic Global Vegetation Models to project the likely future states of grasslands and savannas. Their DGVMs suggest that an increasing atmospheric CO_2 concentration will force transitions to vegetation states characterized by higher biomass and/or woody-plant dominance. Tropical grasslands, savannas and forest ecosystems are likely to shift to alternative states. In a southern African context, bush encroachment has been recognized since the late nineteenth century (O'Connor et al., 2014). There is compelling evidence for the effect of atmospheric CO_2 concentration on increased woody growth (Bond, 2008; Bond& Midgley, 2012; O'Connor et al., 2014).

There are two approaches to how increasing atmospheric CO_2 concentrations impact the structure of grassland communities in terms of the codominance of trees and grasses. One approach argues that reduced transpiration with increasing CO_2 would indirectly favour trees by allowing deeper percolation of moisture into soils, which would favour woody plant establishment because of their deeper roots (Polley et al., 1999). The second argument is that woody plants would be able to escape fire and herbivory more readily, owing to the direct effects of CO_2 fertilization on growth rates and postburn recovery (Bond et al., 2003), and to the enhanced resprouting ability of some trees (Hoffman et al., 2000).

Land management

Land use varies according to geomorphology and management. It is a broad term that includes land use for conservation, and also for purposes such as agriculture, industry and human settlements. Of interest in this study is ecosystem *management*, which is the type of land management typically implemented in protected areas for the purpose of conservation. Given the dynamic nature of ecosystems, there are several effective ways of implementing ecosystem management to protect land for conservation. These include maintaining ecological processes and their natural disturbance regimes, maintaining viable species populations to sustain these ecological processes, protecting the evolutionary potential of species in these ecosystems, and accommodating human use of land (Grumbine, 1994). Fire and the use of prescribed burning are now widely recognized as important in maintaining the ecosystem functioning of grasslands and savannas, and the codominance of trees and grasses in these biomes (Bond, 2008).

Historical context

A study by February (1994) undertaken at two sites in the Drakensberg formed an important backdrop to the current study. February investigated vegetation change in the area as a consequence of human impact, especially with regard to the movement of agriculturalists into the area by about 1600 AD. From an analysis of wood charcoal, the findings were that the common woody species most represented in the archaeological record was *Protea spp* (*P. caffra* and *P.*

roupelliae). The first site was in a protected area in the Drakensberg Reserve and the second on community land managed for grazing outside the protected area. Both reserve and community land showed far fewer proteas than what historical records indicated (charcoal specimens dated between 1260 and 1880 BP). The suggested reason for the decrease was the regular veld burnings which had increased with growing agricultural activity in surrounding land areas. The study concluded that there had been a steady decline in protea abundance in the Drakensberg, which was being replaced by open savanna grassland.

Adie et al. (2011) found that a regular fire interval of 2-3 years does not negatively affect the regeneration of *P. caffra*. However, bracken (*Pteridium aquilinum*) patches result in high intensity fires causing high mortality across all *P. caffra* size classes, ultimately resulting in the local extinction of populations. Bracken therefore has the potential to alter tree-grass interactions in these montane grasslands. The low fuel moisture levels and open structure of bracken promotes combustion, increasing above-ground temperatures and elevating flame heights. Fire during cool and moist conditions ignites less readily and spreads less easily over the terrain, with bracken often failing to ignite. These 'incomplete' fires effectively lengthen the interval between fires.

The land management strategy in the study area is to burn grassland generally every 2-3 years to maintain grass vigour, to limit the establishment of woody species and to reduce fuel accumulation (Adie et al., 2011; Bond, 1997; Everson, 1999).

The purpose of the study and the study species

Very little work has been done on quantifying how proteas have changed over the last half century, and therefore the relevance of the February (1994) and Adie et al. (2011) studies. The focus of the present study was on changes in the abundance of *P. caffra* in the central and northern Drakensberg, a protected area, and on patterns of distribution. It was anticipated that by understanding how *P. caffra* abundance has changed, and what may be reasons for such change, would be relevant to the future management of the Drakensberg Reserve, in terms of maintaining a balance in the grass-tree codominance of the ecosystem.

The study species

Protea caffra is commonly referred to as 'sugarbush' and is a familiar species inhabiting grassland vegetation, especially on escarpments and in the summer-rainfall regions of South Africa. It is a shrub or tree that can grow up to 8 m tall. (Protea Atlas Project) The study considered whether *P.caffra* (as a resprouting tree in grassland) will give some indication of the nature of vegetation change in the Drakensberg Reserve. The habitat of *P. caffra* is Cave (or Clarens formation) sandstone and occurs at elevations up to 2100 m (Protea Atlas Project). The species resprouts from an underground bole as a fire-adaptive strategy. Nonsprouting is the ancestral state in shrublands, with resprouting a prerequisite for successful speciation of *Proteaceae* in grasslands in the mid-Miocene (Lamont (2011; 2013)). Resprouting lineages retained this ability with ongoing speciation. This is an important functional trait in grassland as a fire-prone ecosystem where fire is vital to the maintenance of vegetation structure and composition (Mucina & Rutherford, 2006).

The aim of the study was to quantify how *P. caffra* abundance has changed in the Drakensberg over the latter half of the 20th century and to examine the pattern of change in relation to environmental variables in an attempt to understand the potential drivers of the observed change.

Methods

Study region

Changes in the abundance of *Protea caffra* were assessed at five sites in the central and northern regions of the uKhahlamba Drakensberg Park, a UNESCO world heritage site. These sites were Cathedral Peak, Monk's Cowl, Champagne Castle, Royal Natal and Giant's Castle.

The Drakensberg Reserve is a montane grassland and its climate is classified as temperate with summer rainfall. Mean annual rainfall varies from 640 mm to 1800 mm (Carbutt & Edwards, 2004; Tyson et al., 1976). The geology of the escarpment and plateau regions is dominated by basalt deposits, underlain by sandstones of the Clarens Formation, previously referred to as Cave Sandstone (Carbutt & Edwards, 2004). The sandstone typically occurs at elevations between 1600 m and 1800 m (Irwin et al. 1980).

Some of the current primary management concerns in the Drakensberg Reserve are fire disturbance regimes, biodiversity conservation, and water management for wildlife as well as for human use outside the reserve (Adie et al., 2011). Fire management has changed over the history of this protected area, which was initially managed by the Department of Forestry during the first half of the 20th century. In the late 1980s control of the State Forests and Wilderness Areas was passed to the Natal Parks Board. In 1993 all the 'protected areas' in the mountains were brought into a single entity called the Drakensberg Park (Mazel & Wright, 2007). Since the change of government in South Africa in 1994, the Ezemvelo KwaZulu-Natal (KZN) Wildlife has managed this protected area. With different land management agencies came different management strategies of the Reserve, and at times for different purposes (Granger, pers comm).

Figure 1 shows the study region. The white dots on the map are the geographic locations where the repeat photographs were taken.

Map of study region

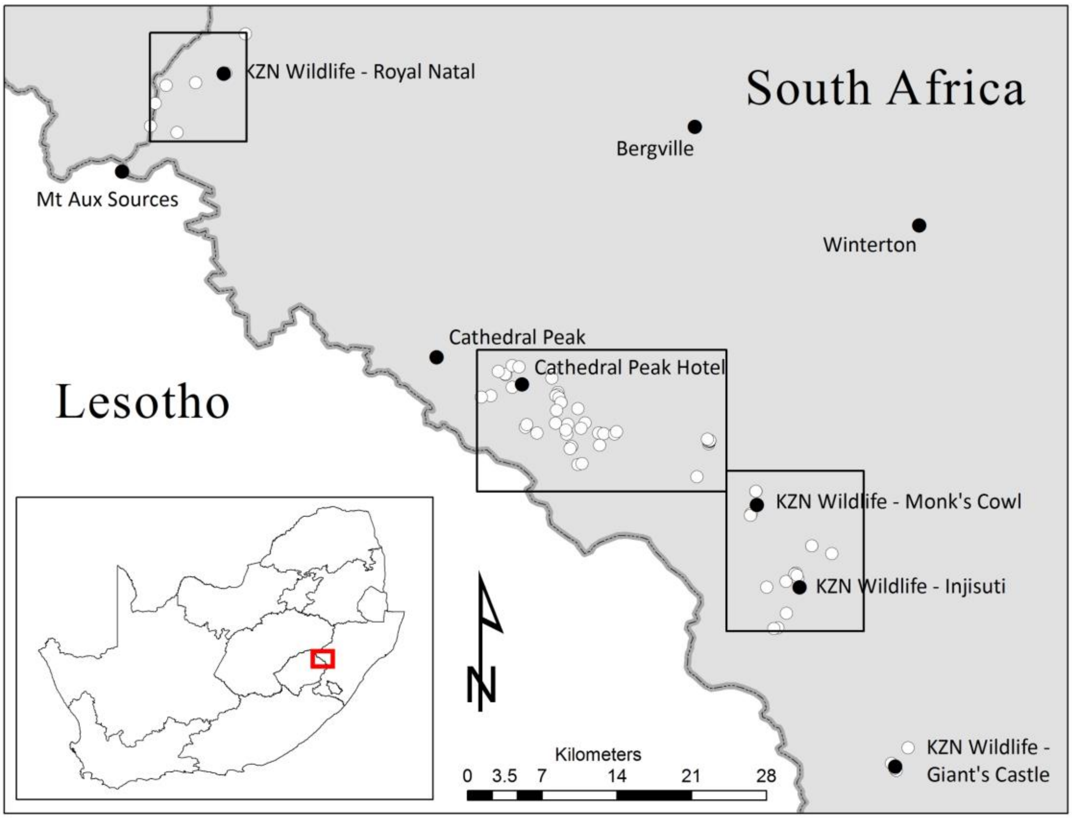


Figure 1. Map of study region. The grids frame study region sites and white dots represent the landform units.

Field work

A total of 76 photographs were repeated photographs from historical photographs obtained from the archives of the Plant Conservation Unit (PCU) at the University of Cape Town, with most photographs taken by two researchers who have worked in the Drakensberg Reserve over long periods, Ulrich Nanni and Ed Granger. The photographs ranged in date from 1950 to 1995, with the majority taken in the 1970s and 1980s (Figure 2). Photographs were chosen according to whether *Protea caffra* were present, or of documented landscapes in which proteas could now potentially be located (i.e. within the sandstone band), and whether the image was of sufficient quality to identify proteas and enable counts of individuals. The sites of the original photographs were located using the metadata description of the photographs and manually finding the best approximation of the location on Google Earth, using landscape features as reference points. Sites were located in the field using the coordinates obtained from Google Earth. The relative positions of landscape features in the photographs were then used to position a digital camera (Canon 5D Mark II) on a tripod at the location where the original photographer had been positioned. Photograph and site information, including GPS co-ordinates, aspect and a general description of vegetation change between the original and repeat photographs were recorded.

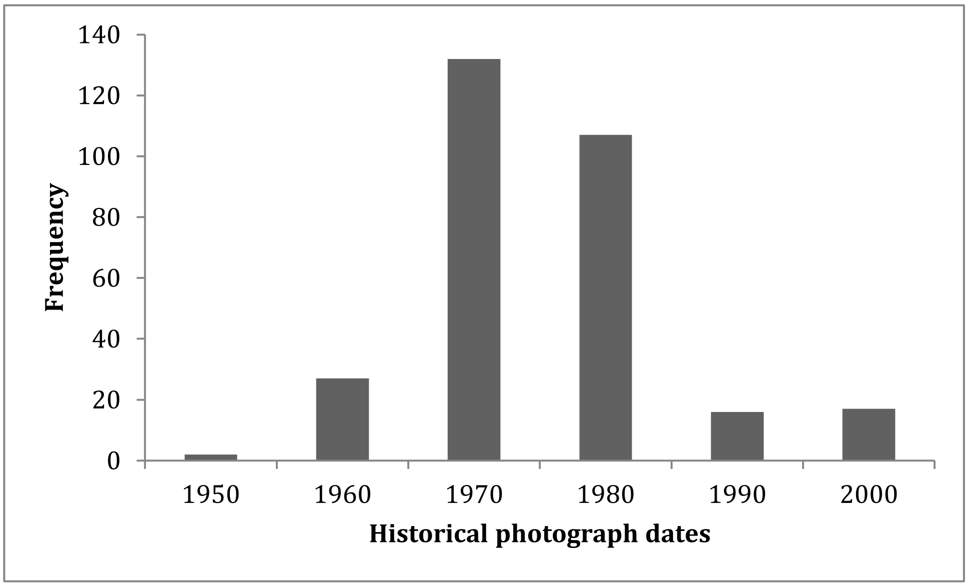


Figure 2. Frequency distribution of historical photograph dates

Photograph analysis

The photographs were matched using image editing software (Adobe Photoshop CS5). The historical and repeat photographs were rescaled by selecting two fixed points (e.g. mountain peaks or rocky outcrops) which were clear in both photographs and measuring the distance between the two points with the measuring tool function. The photographs were scaled to the same size so that this distance was the same between them. The repeat photograph was then overlaid on the historical photograph and the opacity adjusted so that it could be repositioned in such a way that it matched the original photograph.

Each of these matched photographs was divided into landform units (Figure 2), which were delineated according to aspect, slope angle, catenal position and degree of rockiness (1: low (0%–10%) rocky cover, 2: medium (10%–20%)

rocky cover, 3: high (>20%) rocky cover). The number of individuals was counted at each of the landform units in the historical and repeat photographs and recorded. The detectability of each of the landform units was categorized into three groups (1: good, 2: fair–good, 3: poor) according to clarity of the landform unit and the ability accurately to detect proteas. For the data analysis, category 3 landform units falling into the 'poor' category were discarded because of their low detectability.

Figure 3. Repeat photographs of a site at Mike's Pass, Cathedral Peak with demarcated landform units. Historical photograph (top) photographed by Ulrich Nanni (1961) and the repeat photograph by Sam Jack (2014).

Environmental and climatic data

The aspect and centre elevation of each landform unit was determined from Google Earth. Slope angle was calculated by using a trigonometric formula ($\tan\theta = {Top\ elevation - bottom\ elevation}/_{slope\ length}$) with these variables extracted from Google Earth. Top elevation is the highest elevation of the landform unit, and bottom elevation is the lowest point. Climate variables for each landform unit, including mean annual temperature (MAT), mean annual precipitation (MAP) and frost duration were extracted from the South African Atlas of Climatology and Agrohydrology (Schulze & Maharaj, 2007) using ArcGIS 10 (ESRI, 2011).

A measure of fire frequency within landform units was obtained using the MODIS MOD45B burnt area product (Roy et al., 2008). The MODIS product is a gridded dataset with a spatial resolution of 500 m and covers the period from 2000 to the present. The data were used to create a fire frequency map at 500 m resolution for the study area using ArcGIS to obtain a count of the number of fires occurring within each MODIS pixel between 2000–2013. These dates do not extend as far back as the photographs and the assumption was made that the fire frequencies for the different sites showed a similar trend before 2000.

The MODIS Collection 5 Active Fire product (MCD14ML) provides a measure of fire radiative power of fire burnings between 2000 and the present at a spatial resolution of 1 km and daily temporal resolution. Fire Radiative Power (FRP) data provide a measure of radiant heat output of detected fires and the data were used as a measure of fire intensity.

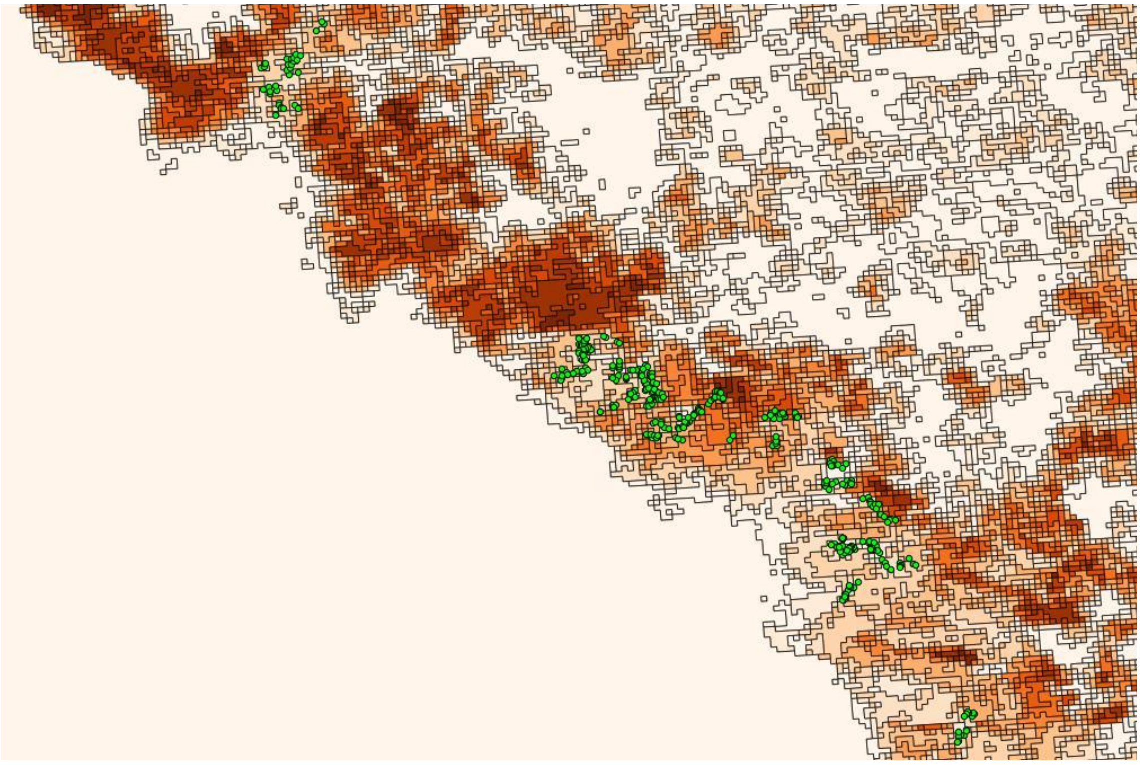


Figure 4. Fire frequency overlayed on the study area. Darker orange and red colours indicate higher frequencies and intensities, while the lighter colours indicate lower values.

Statistical Analyses

The change in *Protea caffra* counts was log transformed in order to approximate linear growth of populations rather than an exponential growth, as may be expected by the density dependence relationship of tree population growth. This change was divided by the number of years between photographs to obtain the rate of change in numbers. This was considered the most appropriate measure of change since the time frame between repeat photographs varied. The frequency distribution of the rate of change of *P. caffra* was plotted in order to assess the distribution of the data, as well as the most frequent categories of change at the sites.

As part of the data exploration phase, linear models were used to explore the relationship between change in *P. caffra* and environmental and climatic data. This was done using a correlations matrix to test whether any of the environmental variables provided the same information in explaining the change in abundance and distribution, in which case the more appropriate variable was selected. The 'appropriateness' was decided on the basis of what made more ecological sense. For example, elevation is likely to have an effect on temperature and may explain temperature variation, but temperature cannot account for a change in elevation.

The following steps aimed to better understand the pattern of change and what environmental drivers may be responsible for such change. A number of hypotheses were generated, using some ecological knowledge of the region to ascertain what environmental variables (or combinations thereof) may be responsible for the observed change in *P. caffra* abundance and distribution. These hypotheses were used as linear mixed effects models and the model that was most representative of the data was selected, using an Akaike test. Since the data were normally distributed, linear models could be used. Possible autocorrelation between landform units was corrected for by using linear mixed effects models and randomising the landform units.

The number of years between photographs was included as an explanatory variable in each model. This was to account for the fact that over smaller time frames, the change observed between the historical and repeat photographs is more likely to have been continuous and predictable, whereas over longer timeframes population sizes are more likely to have fluctuated and only the more recent changes in the population were observed.

The hypotheses were structured around three primary potential drivers of change. These were (1) an increase in temperature due to climate change in the study region, (2) variable fire regimes in the region, and (3) moisture availability at sites in the study region. These hypotheses were used as linear effects models and as input into an Akaike test. The Akaike test ranks the models with delta AIC (Δ_i) which provides a strength of evidence comparison and scaled ranking of candidate models. The larger the Δ_i value, the less plausible is the fitted model *i* as the best approximating model in the candidate set. It was important to consider which model ranked second best as well, as some measure of its standing with respect to the best model. The Akaike weights (ω_i) are a measure of the approximate probability that model *i* is in fact the best model in the set of models considered (Anderson et al., 2000). The relative likelihood of ω_i (the best fitting model) to ω_j (second best model) is calculated as ω_i/ω_j.

The best model obtained from the Akaike test was then summarized in order to assess how the selected combination of explanatory variables account for the observed trend in the predictor variable, being the change in *P. caffra*. Correlation plots were established to further investigate this relationship.

Ten landform units were selected that showed change both in the highest range of increase in *P. caffra*, and in the highest range of decrease. These photographs were qualitatively assessed to observe whether there were any discernible environmental factors that were prevalent in these landform units.

The data were further split into two categories: landform units that only showed an increase in *P. caffra*, and those that only showed a decrease. The effect of fire frequency on each of these categories was assessed using correlation curves. Since the MODIS data is rather coarse, and given that terrain has an important effect on fire, a further approach was taken to refine the fire frequency data. The fire frequency values for each landform unit were weighted relative to the amount of rocky cover present to establish fire frequency index values. Based on the assumption that rocky cover provides protection for vegetation, landform units with low rocky cover had more weight than those with high rocky cover. Higher fire frequencies were also weighted more, relative to lower fire frequencies. The highest fire frequency index values are therefore those that have a high fire frequency and low rocky cover.

The relationship between fire intensity and elevation was assessed using Fire Radiative Power (FRP) point data for landform units and correlating these against elevation. The statistical analyses were done in R Studio (R Core Team 2012) and Microsoft Excel 2010.

Results

Changes in protea abundance

The change in *P. caffra* counts was assessed in 302 landform units from 76 repeated photographs. Figure 5 provides a spatial overview of changes in protea abundance over the study area.

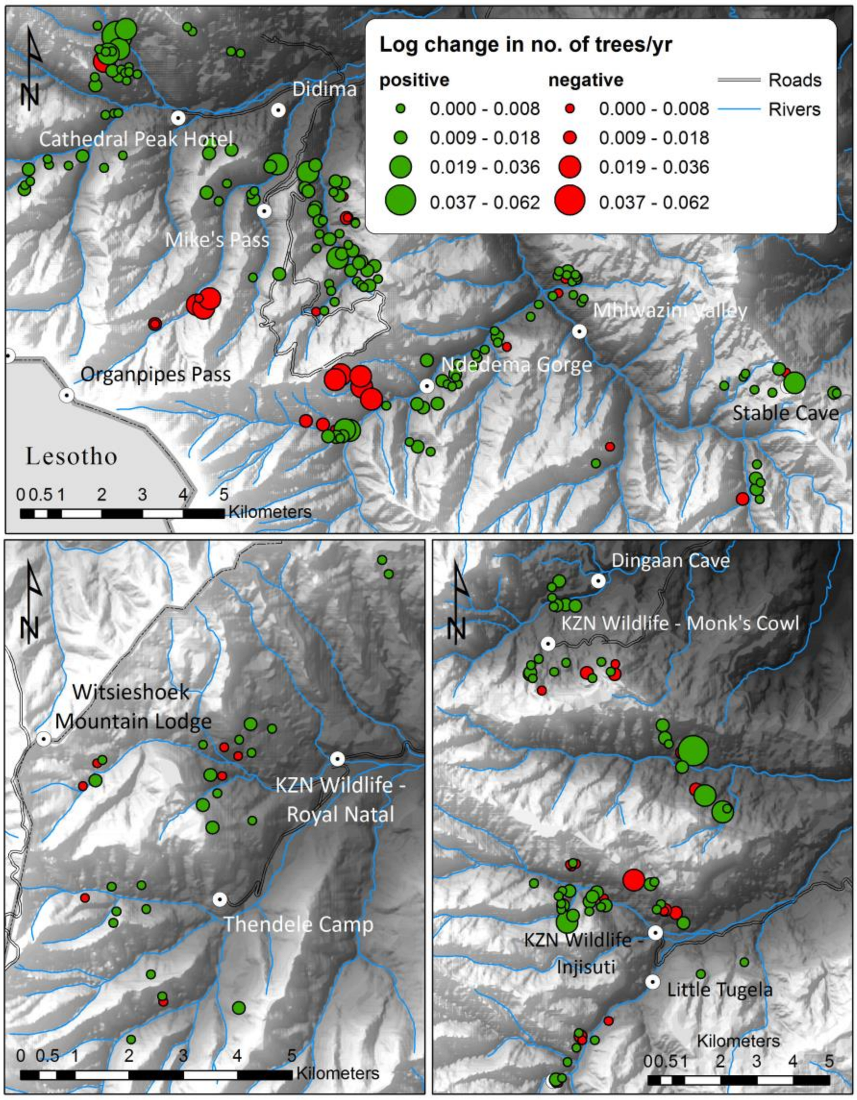


Figure 5: The change in counts per year of *P. caffra* at Cathedral Peak, Royal Natal, Monk's Cowl and Injasuti. Green circles show an increase in proteas and red circles show a decrease. The size of the circles is proportionate to the amount of change in numbers. The grids of figure 1 show where these sites are positioned in the study area.

The majority (76%) of landform units across the study area showed an increase in *P. caffra* numbers, assessed from a comparison between the historical and the repeat photographs. Some 17% of the landform units showed a decrease in *P. caffra* abundance and 7% remained unchanged. The most frequent category of change is an increase in *P.caffra* of between 0 and 100 individuals between the historical and repeat photographs (Figure 6).

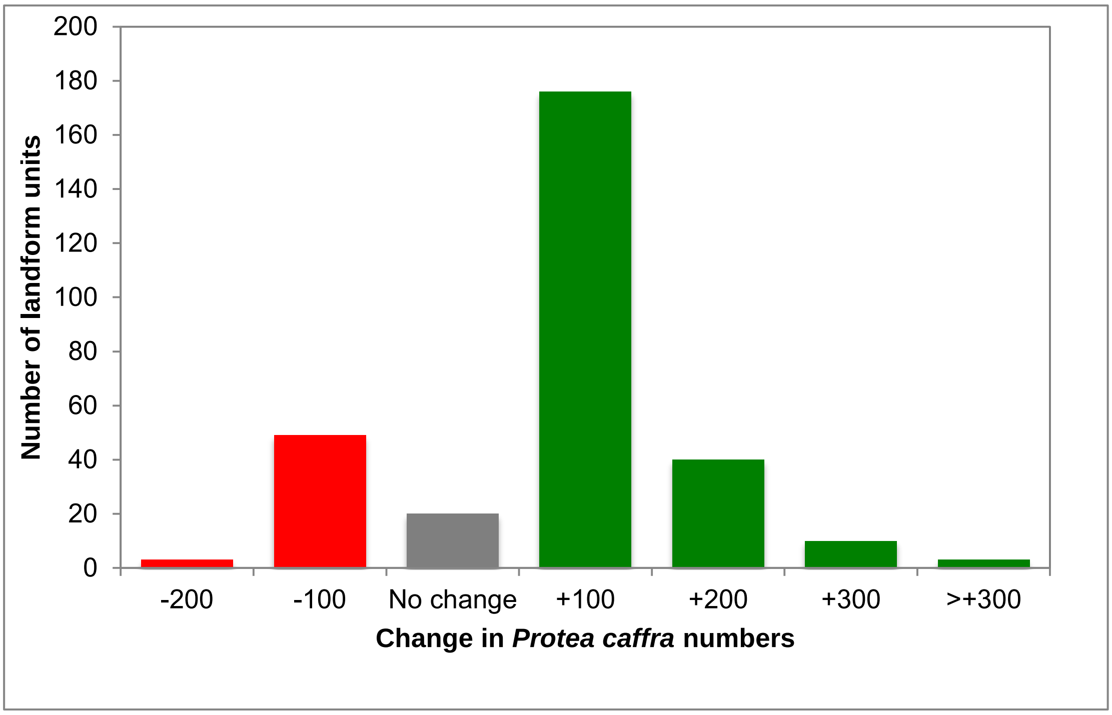


Figure 6. Frequency distribution of the log change in *P. caffra* counts per year

Explanatory variables

In assessing the drivers of *P. caffra* change, a correlation matrix was created (Appendix 1, Figure A) to assess whether any variables were co-correlated. The explanatory variables which correlated significantly with each other were elevation and mean annual temperature (Appendix 1, Figure B), and elevation and frost (Figure C). At higher elevations, there was a decrease in temperature and therefore also an increase in frost occurrence. Since temperature and frost are dependent on elevation, elevation was selected as the variable with the strongest explanatory power. Mean annual temperature (MAT) decreased significantly ($P<0.0001$) with an increase in elevation (Fig. B). However, there was a relatively large amount of variation in the data (R^2 value of 0.1899), possibly due to the influence of other environmental variables on temperature, for example aspect and slope angle. There was a significant increase in frost with an increase in elevation (Fig. C). However, there was a large amount of variation in this relationship (R^2 of 0.1242), possibly due to similar reasons, i.e. other environmental variables such as aspect and slope angle having an effect on frost.

Modelling potential drivers

The range of models used to explain the change in the density and distribution of *P. caffra* is shown in Table 1. The Akaike test ranked the models according to how well the explanatory variables explained the observed trend in protea change.

Table 1. Results of the Akaike test showing the relative delta AIC rankings and their relative AIC weight

Model number	Number parameters	Log likelihood	Delta AIC (Δ_i)	AIC weight (ω_i)	Explanatory variables used in models
6	7	697.9457	0	0.33528	Aspect+centre.elevation+Years
14	8	698.2542	1.382969	0.167919	Fire.frequency+Aspect+centre.elevation+Years
4	9	699.1276	1.636134	0.147954	centre.elevation*Aspect+Years
7	8	697.9457	1.99995	0.123346	Aspect+centre.elevation+slope.angle+Years
15	9	698.2954	3.300567	0.064372	Fire.frequency+Aspect+centre.elevation+Rockiness+Years
2	5	693.7394	4.412695	0.036915	centre.elevation+Years
1	6	694.6926	4.506235	0.035228	Aspect+Years
16	10	698.5146	4.86219	0.029485	Fire.frequency*Rockiness+Aspect+centre.elevation+Years
8	10	698.4346	5.022236	0.027217	Aspect*slope.angle+centre.elevation+Years
13	7	694.7719	6.347679	0.014029	Fire.frequency+Aspect+Years
17	5	692.5037	6.88403	0.010729	Fire.intensity+Years
5	9	695.1426	9.606151	0.002751	Aspect*slope.angle+Years
3	5	690.6387	10.61406	0.001662	slope.angle+Years
9	5	690.5457	10.80009	0.001514	Fire.frequency+Years
10	6	690.9087	12.07392	0.000801	as.factor(Rockiness)+Years
12	6	690.563	12.76533	0.000567	Fire.frequency+Rockiness+Years
11	7	690.6656	14.56015	0.000231	Fire.frequency*Rockiness+Years

Table 1 shows the best ranked model is model 6 (Δ_i=0). The explanatory variables that predict the change in *P. caffra* were aspect and elevation. The model had a 33.5% probability of being the best fitting model (ω_i=0.335). The second best ranked model was 14 (Δ_i=0.168). Model 6 had twice the predictive power of model 14 ($\frac{\mathrm{W}_{\text{model 6}}}{\mathrm{W}_{\text{model 14}}} = \frac{0.335}{0.168} = 1.994$).

The explanatory variables in model 6 were therefore considered further in their relationship to the predictor variable, *P. caffra* change.

Environmental variables explaining change

A summary of how aspect and elevation have influenced change is shown in Table 2.

Table 2. Summary of the effect of explanatory variables in model 6 on the observed outcome of *P. caffra* change

Variable	Rate of Change in *P. caffra* Value (logarithmic change per year)	p-value
Intercept	0.10477	<0.0001
North Aspect	-0.00660	0.0841
South Aspect	-0.01190	0.0041
Elevation	-0.00003	0.0115
Years	-0.00069	0.0006

Table 2 shows that there has been a slight decline in *P. caffra* on South facing slopes ($p<0.05$). North facing slopes also appear to have shown a decrease, however, this is not significant ($p>0.05$). There has been a large increase of protea numbers on East-West slopes ($p<0.0001$). There was a slight decrease in protea numbers with an increase in elevation ($p<0.05$).

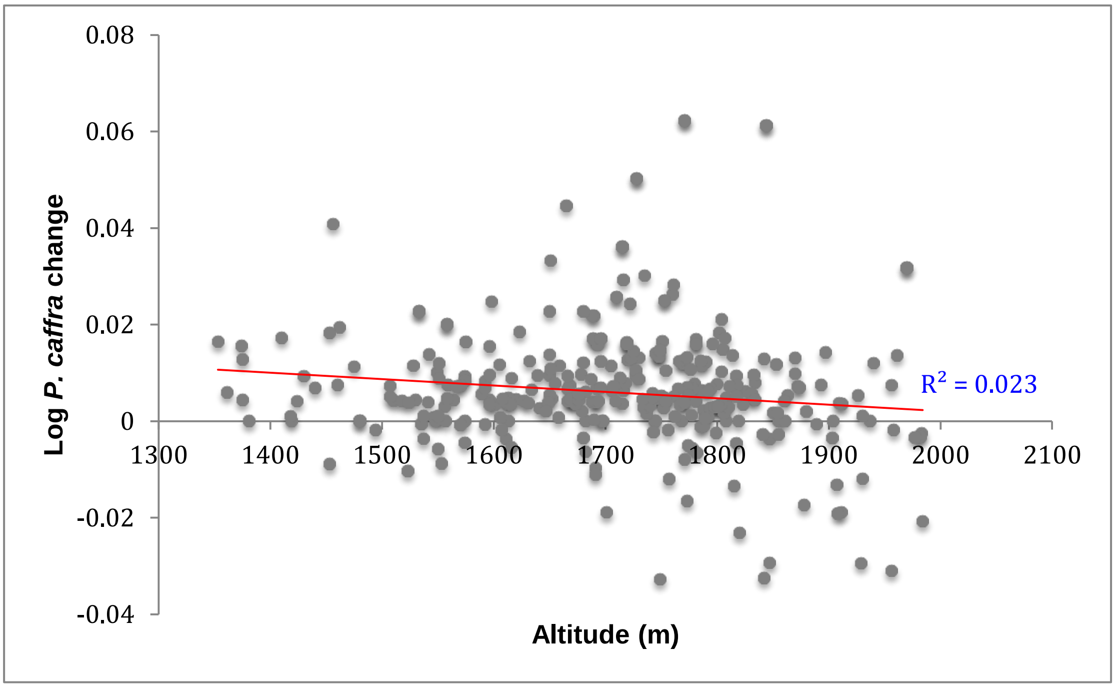
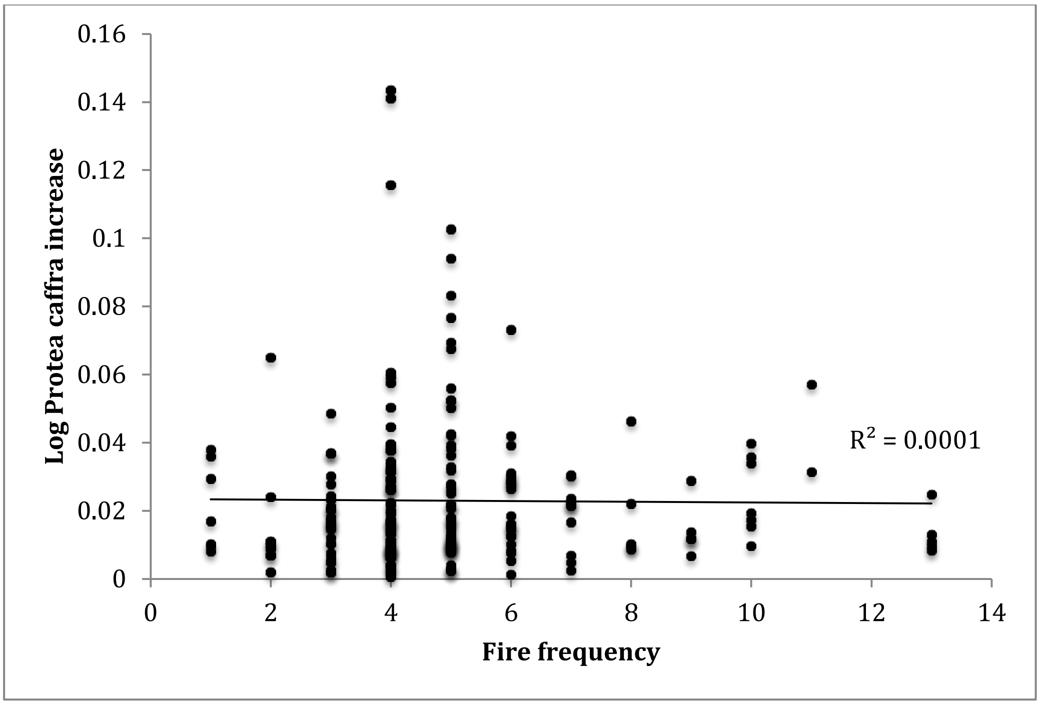


Figure 7. Relationship between the change in *P. caffra* and elevation.

There appears to be greater decrease in *P. caffra* at higher elevations. The correlation between change in proteas and altitude is a negative one ($p<0.05$). At lower elevations, more landform units show an increase. However, the sites which show the largest amount of increase are at higher elevations.

In this fire prone environment, it is important to further consider whether fire has any effect on *P. caffra* populations. Although the top ranked model does not have fire as an explanatory variable, the second best ranked model has fire frequency as an explanatory variable along with aspect and elevation.

The dataset was divided into sites which showed an increase in proteas, as well as sites that showed a decrease. These were examined separately to assess whether fire may be an important determining factor in influencing the type of change in *P. caffra* abundance.



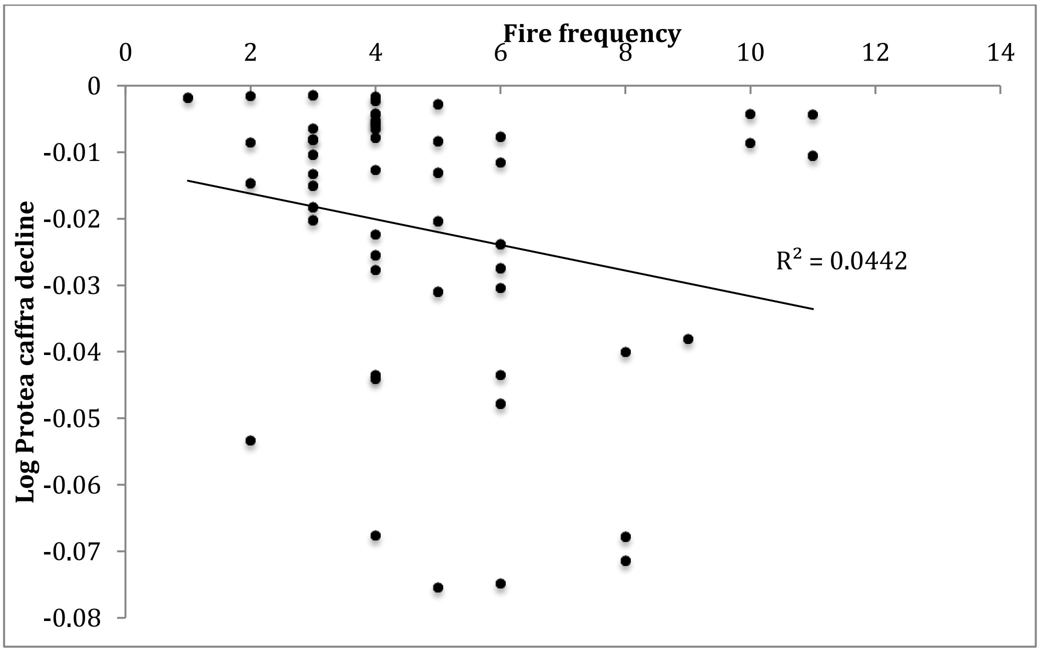
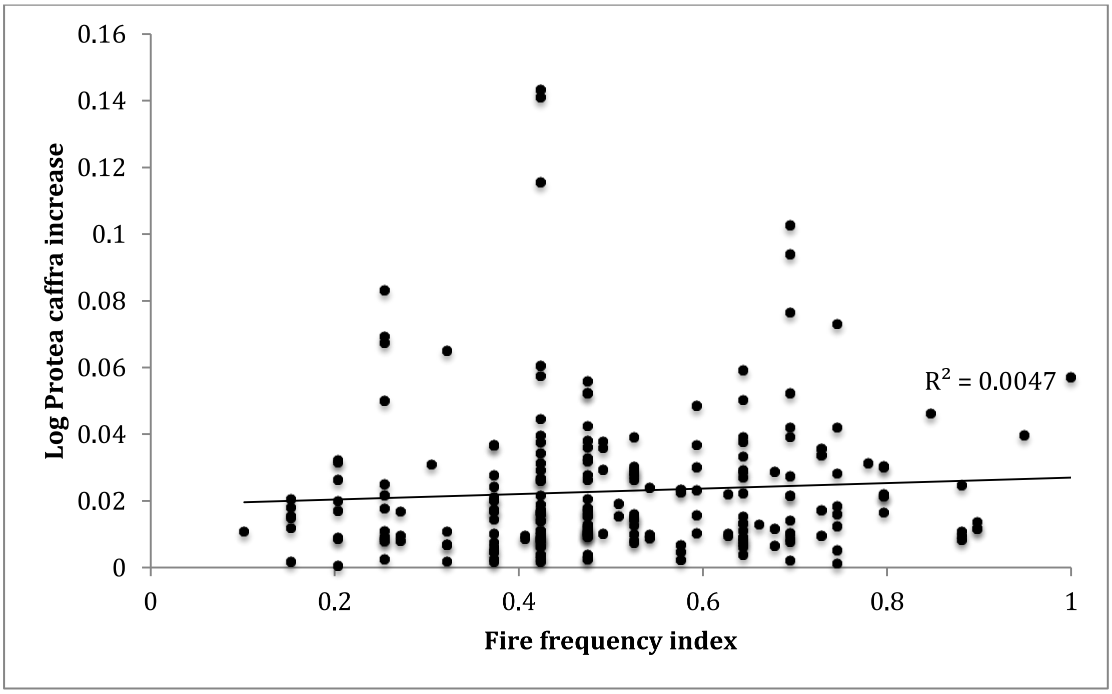


Figure 8. The relationship between change in fire frequency and 1. Landform units showing increase in *P. caffra* and 2. Landform units showing a decrease in *P. caffra*

There is no significant relationship between fire frequency and an increase in *P. caffra*. There does appear to be a negative correlation between *P. caffra* and fire frequency although the correlation coefficient is weak (R^2=0.0042).

Since the MODIS data is rather coarse, and as the grassland terrain has an important effect on fire, another approach was taken to refine the fire frequency data. The fire frequency values for each landform unit were weighted relative to the amount of rocky cover present. Based on the assumption that rocky cover provides protection for vegetation, landform units with low rock cover were given more weight than those with high rocky cover. Higher fire frequencies were also weighted more, relative to lower fire frequencies.



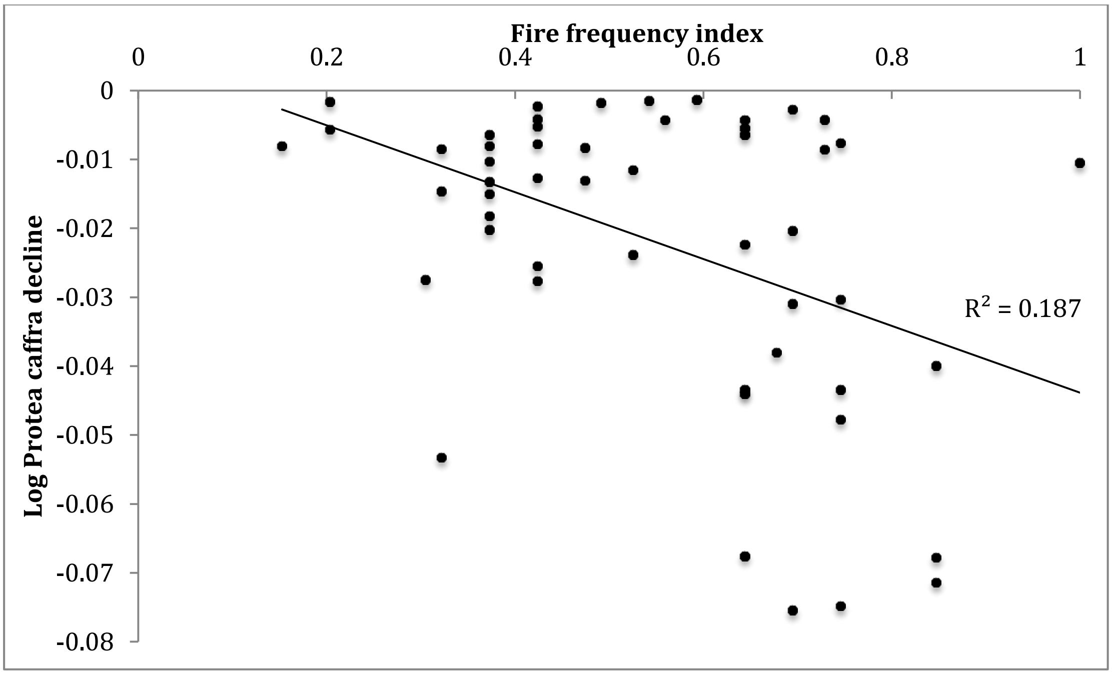


Figure 9. The weighted relationship between change in fire frequency and 1. Landform units showing increase in *P. caffra* and 2. Landform units showing a decrease in *P. caffra*

The strength of the correlation between the fire frequency index and the positive increase in *P. caffra* (Figure 10) remains weak (R^2=0.0038). However, the negative correlation between fire frequency index and the decrease in *P. caffra* has strengthened considerably. In order to explore this trend further, fire intensity was plotted against altitude (Figure 11).

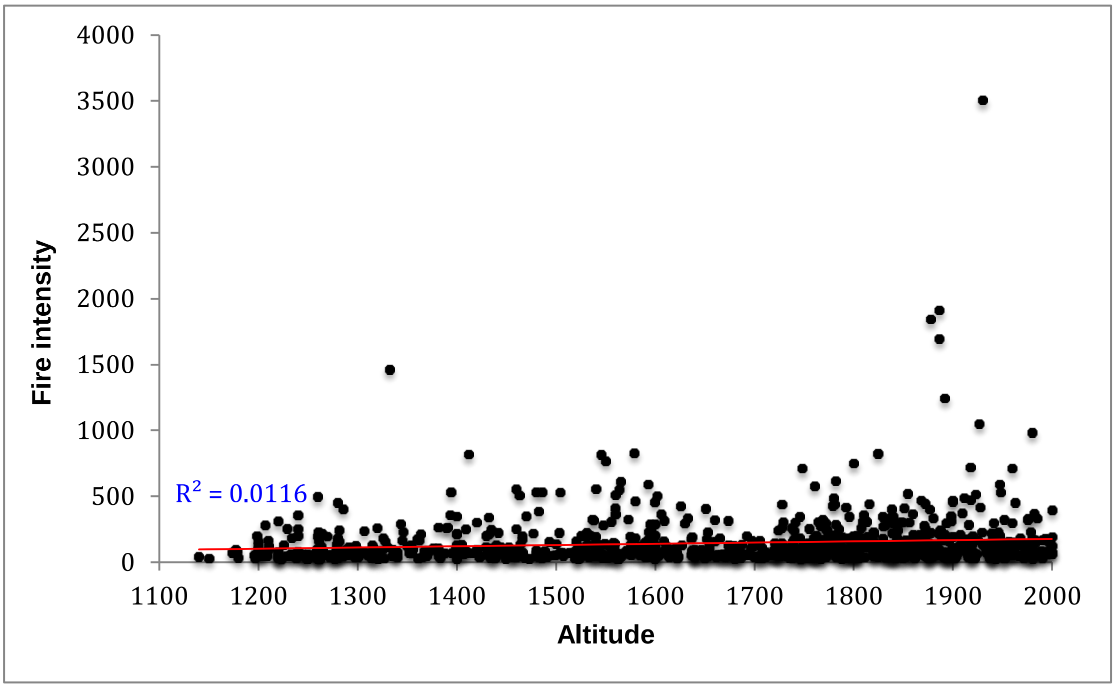


Figure 10. The relationship between altitude and fire intensity.

There is a cluster of sites which does show an increase in fire intensity at higher elevations, particularly around 1900m to 2000m.

Observational data

The qualitative assessment of a selection of photographs of landform units with the highest level of change of *P. caffra* (i.e. highest amount of increase and decrease) did not show a consistent trend in the landform units with the largest amount of increase in *P. caffra*. However, in the photographs showing a large amount of decrease of *P. caffra*, six of the ten landform units showed some level of cover of *Pteridium aquilinum.* The other four landform units were at a distance which made it difficult to discern the presence of *P. aquilinum*.

Discussion

Change in abundance of Protea caffra

Two central drivers in changing ecosystems are climate change and land use. The first objective of this study was to assess whether there has been a change in the abundance and distribution of *P. caffra* in the central and northern Drakensberg. The second was to assess how climate change and land management in this conservation area may be affecting *P. caffra* populations in the study area. Of further relevance was to consider what structures ecological communities and vegetation change within a grassland, and the environmental variables that could account for the patterns of change.

February's (1994) findings were that there had been a steady decline in protea savanna in the Drakensberg (his study included both *P. caffra* and *P. roupelliae*). In contrast, the main finding in this study was that there has been an increase in *P. caffra* numbers at the majority of landform units documented in the study area (Figure 6). The most frequent category of change was an increase in the count of *P.caffra* of between 0 and 100 individuals between the historical and repeat photographs. This trend is shown across sites with most landform units showing an increase in numbers (Figure 5).

Difference in findings

In line with the February (1994) finding, the hypothesis was that there would be a decline in *P. caffra*. There is, however, an important difference between the two studies. February's study sites were in protected and agricultural land and the concern was with the potential decline in protea numbers over a period of 300 years as agriculturalists moved into the Drakensberg foothills, compared to the estimated population sizes dating back to between 1260 and 1880 BP. He concluded that an important contributing factor which could explain the decline in protea savanna numbers could have been the increase in veld fires associated with farming and the burning of land for grazing. Fires that are too frequent prevent the establishment and growth to the reproductive maturity of trees (Bond, 2008), making this a plausible argument.

The current study's concern is with change in *P. caffra* as documented in photographs since 1950. Over this period, the whole study area has been in a protected reserve. The type of land use is specifically ecosystem and conservation management based, rather than managed for agricultural use. This primary difference could have led to the recovery of *P. caffra* populations in a regulated fire regime with long enough fire intervals to allow for recruitment and for juveniles to escape the fire zone, but that are frequent enough to prevent grass biomass from building up and resulting in fire intensity levels that would wipe out protea populations. The high incidence of small *P. caffra* in the region, as observed by Adie et al. (2011), would suggest that the current 2-3 year fire regime implemented in the Drakensberg Reserve does not negatively affect the regeneration of *P. caffra*. Additionally, the species is protected from human exploitation, the most obvious example being wood harvesting.

The cause of an increase in woody cover in grassy ecosystems is generally centered around the importance of change in land use (specifically the decreased use of fire) and climate change (increasing atmospheric CO_2 concentrations). Both of these suggested causes could be influencing the observed majority increase in *P. caffra* numbers. *P. caffra* may be responding better to fire disturbance than in the past, following the prediction of Bond et al. (2003) of an increase in tree cover with increased atmospheric CO_2 concentrations and consistency in fire regimes. As a resprouter, *P. caffra* could have enhanced resprouting ability with increasing atmospheric CO_2 levels (Hoffman, 2000), which would further allow the species to respond to the fire regime of the area.

Patterns of change and possible drivers

In modelling predictive drivers of change, the environmental variables that best explained the observed trends in *P. caffra* change were elevation and aspect (model 6, Table 1). The model output indicated a negative relationship between *P. caffra* change and elevation (Figure 7). The greatest fluctuation (both increase and decrease) occur at mid- to high elevations. A plausible reason for this variance is that the increase in *P. caffra* on lower slopes could be the result of higher temperatures and lower frost occurrence. With an increase in CO_2, plants have increased water, resource and light use efficiency and higher rates of photosynthesis (Drake et al., 1997). This could account for increased protea abundance across elevations. With these higher rates of photosynthesis, the higher temperatures associated with lower slopes (Appendix, Figure B) could be even more conducive to population expansion.

On higher slopes, there appears to be more *variable* change, i.e. many landform units show a large amount of increase as well as a large decrease in *P. caffra*. This is contrary to what may be expected with rising temperatures due to climate change, which would predict a shift of trees to higher elevations that are cooler (McCarty, 2001). An explanation for this trend could be that fire intensity is higher at higher elevations (Figure 11) which would account for the landform units that show a large decline in *P. caffra*. The reason for higher fire intensity could be that the higher elevations are on the periphery of the basalt substrate, which is more nutrient rich and a higher biomass of grasses could occur here. Fires passing through this high biomass of grass are therefore likely to have a higher intensity.

In addition, fires at the base of an elevation or a mountain slope (referred to as head-burns) will tend to race up-hill with tall flames, even in calm weather conditions. Consequently the fire-front passes rapidly across the ground and this may contribute to the survival of small plants. However, the tall flames, even though they move fast through the eco-community, can result in substantial damage to the leaves of taller plants (also to those that are greater than 4-5m). Proteas on higher slopes are therefore more likely to be exposed to the tall-flame fires. In contrast, 'back-burns', i.e. fires which are started at the top of a slope and burn slowly downhill, seldom produce tall flames. As a result, such fires would lead to the mortality of seedlings but not of reproductively mature adult trees (Granger, pers. comm).

Land management and fire

In addition to the effect of fire intensity on variation in the patterns of change of *P. caffra*, fire frequency is also likely to be an important driver in causing variation. The second best ranked model in the Akaike test (model 14, Table 1) has fire frequency as an additional explanatory variable to elevation and aspect in explaining the observed trend in *P. caffra* change.

There does not appear to be a relationship between the fire frequency index and landform units showing an increase in *P. caffra* (Figure 10) which indicates that fire does not seem to be a driver of change. However, fire does appear to have a pronounced influence on the variation of change. Along with variation in protea decline due to fire intensity, the relationship between the decline in *P. caffra* and fire frequency and rockiness (Figure 10) illustrates that areas with high fire frequency and little sheltered protection from rocky cover show higher decreases in *P. caffra* numbers. This suggests fire is an important regulator of *P. caffra* numbers. The fact that there is no relationship between fire frequency and landform units showing an increase in *P. caffra* implies that the majority increase in the species is more likely to be driven by climatic changes, i.e. increases in atmospheric CO_2 rather than a change in the fire regime.

Further, while *P. caffra* could survive the regular fire regimes of the Drakensberg Reserve, in areas where protea populations were surrounded by bracken (*Pteridium aquilinum*), fire intensity would be far higher and would lead to the local extinction of protea populations (Adie et al, 2011). Observational data of landform units in the study area showed that there is likely to be some association of landform units showing a decline in proteas with the presence of bracken. On the landform units that were close enough to distinguish bracken, there usually was some level of bracken cover at landform units showing a decline in proteas. High intensity fires associated with bracken could therefore be a further reason for the landform units showing a decline in *P. caffra*.

A limitation in these findings is that the fire data only extends as far back as 2000 and not to when the original photographs were taken. A change in fire trends over the latter half of the 20th century would therefore only partially be represented in this dataset.

Aspect

The results show that there has been a decrease in *P. caffra* on South slopes, a large increase on East and West slopes, while there has been no significant level of change on North slopes (Table 2). North-facing slopes are an optimal habitat for proteas because of high levels of sunlight and therefore warm and dry conditions (Irwin, 1980), compared to South slopes which receive less sunlight and are cool and moist. East-West slopes could be considered as in-between zones with regards to sunlight and temperature and were therefore clustered together as one category in the dataset.

The trend showing a significant increase in proteas on these East and West facing slopes is of interest. A plausible explanation for this is that, with increasing global temperatures, *P. caffra* populations which are most prevalent on the warmer and drier North facing slopes (Irwin et al., 1980), have been allowed to expand more onto the 'neutral' East-West facing slopes which would now be warmer and more conducive to *P. caffra* growth and survival.

South facing slopes are the cooler and moister slopes and are not typically the growing location of proteas. However, it is interesting to note that there has been a decrease in proteas on this slope. With increasing global temperatures, it could be expected that *P. caffra* populations might expand on these cooler slopes but this is not the case. The reason could be that there has been an increase in *Pteridium* cover on the South slopes, accounting for the higher mortality of the *P. caffra* populations. *Pteridium* has been found to be common on south-facing slopes at higher altitudes in certain regions (Grime & Loyd, 1972; Marrs & Watt, 2006).

Climate change and land management are shown to both be important factors influencing the vegetation structure of the Grassland in the Drakensberg Reserve. The primary finding of this study suggests that the current land management regime in the Drakensberg Reserve has not had a negative impact on *P. caffra*. In fact populations are increasing, most likely as a consequence of increasing atmospheric CO_2 levels. Certain fire frequencies and fire intensities are shown to cause a decrease *P. caffra* populations. Fire is therefore likely to become an increasingly important management tool in regulating the tree-grass codominance and vegetation structure of this conservation area and world heritage site.

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Appendix 1

Data exploration

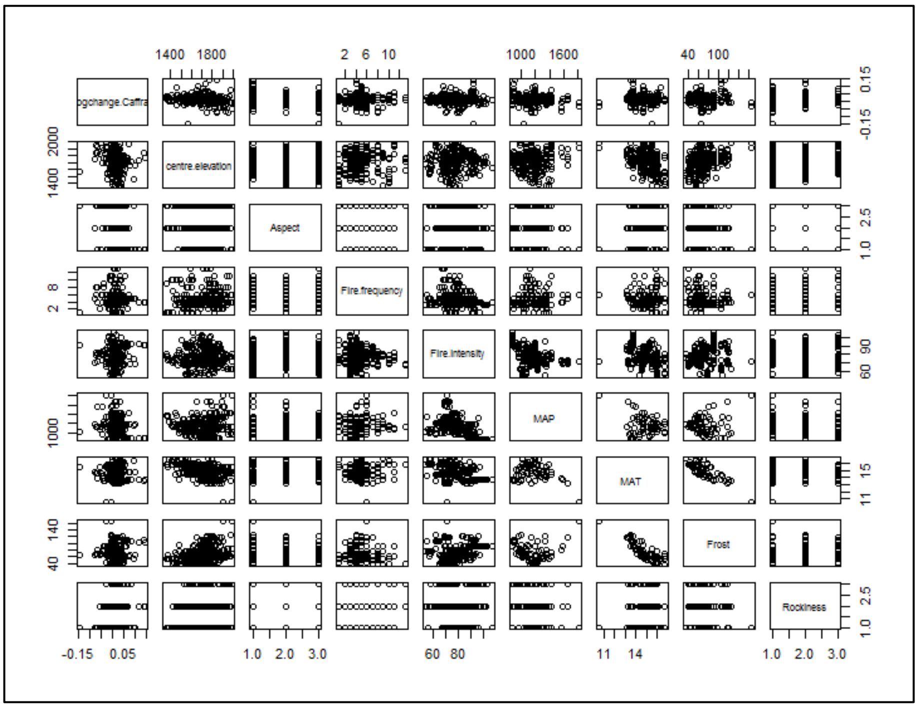

Figure A. Correlation matrix of the explanatory variables and response variable (change in proteas per year)

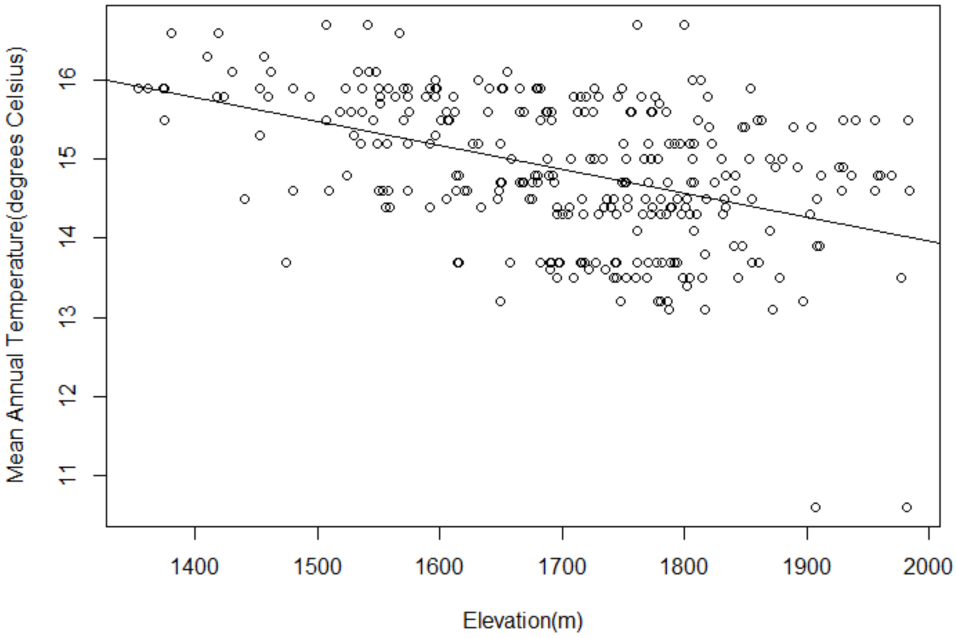

Figure B. The observed relationship between mean annual temperature (℃) and elevation across landform units.

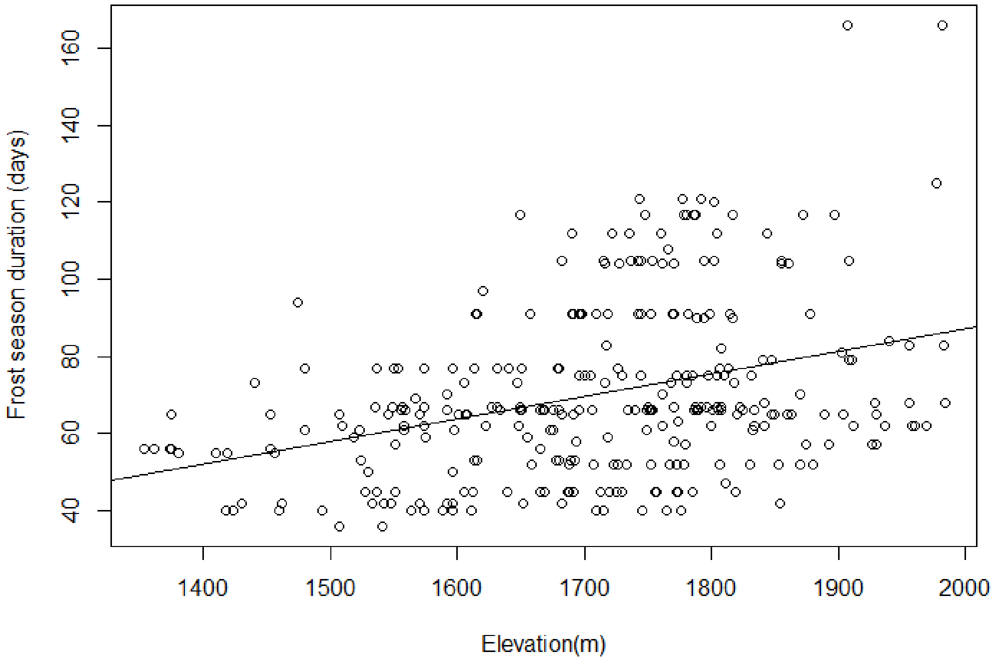

Figure C. The observed relationship between frost occurrence and elevation across landform units.

PLAGIARISM DECLARATION

1. I KNOW THAT PLAGIARISM IS WRONG. PLAGIARISM IS TO USE ANOTHER'S WORK AND PRETEND THAT IT IS ONE'S OWN.

2. I HAVE USED THE HARVARD CONVENTION FOR CITATION AND REFERENCING. EACH CONTRIBUTION TO,

AND QUOTATION IN, THIS THESIS FROM THE WORKS OF OTHER PEOPLE HAS BEEN

ATTRIBUTED, AND HAS BEEN CITED AND REFERENCED.

3. THIS THESIS IS MY OWN WORK.

4. I ACKNOWLEDGE THAT COPYING SOMEONE ELSE'S WORK, OR PART OF IT, IS WRONG, AND DECLARE THAT

THIS IS MY OWN WORK.

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