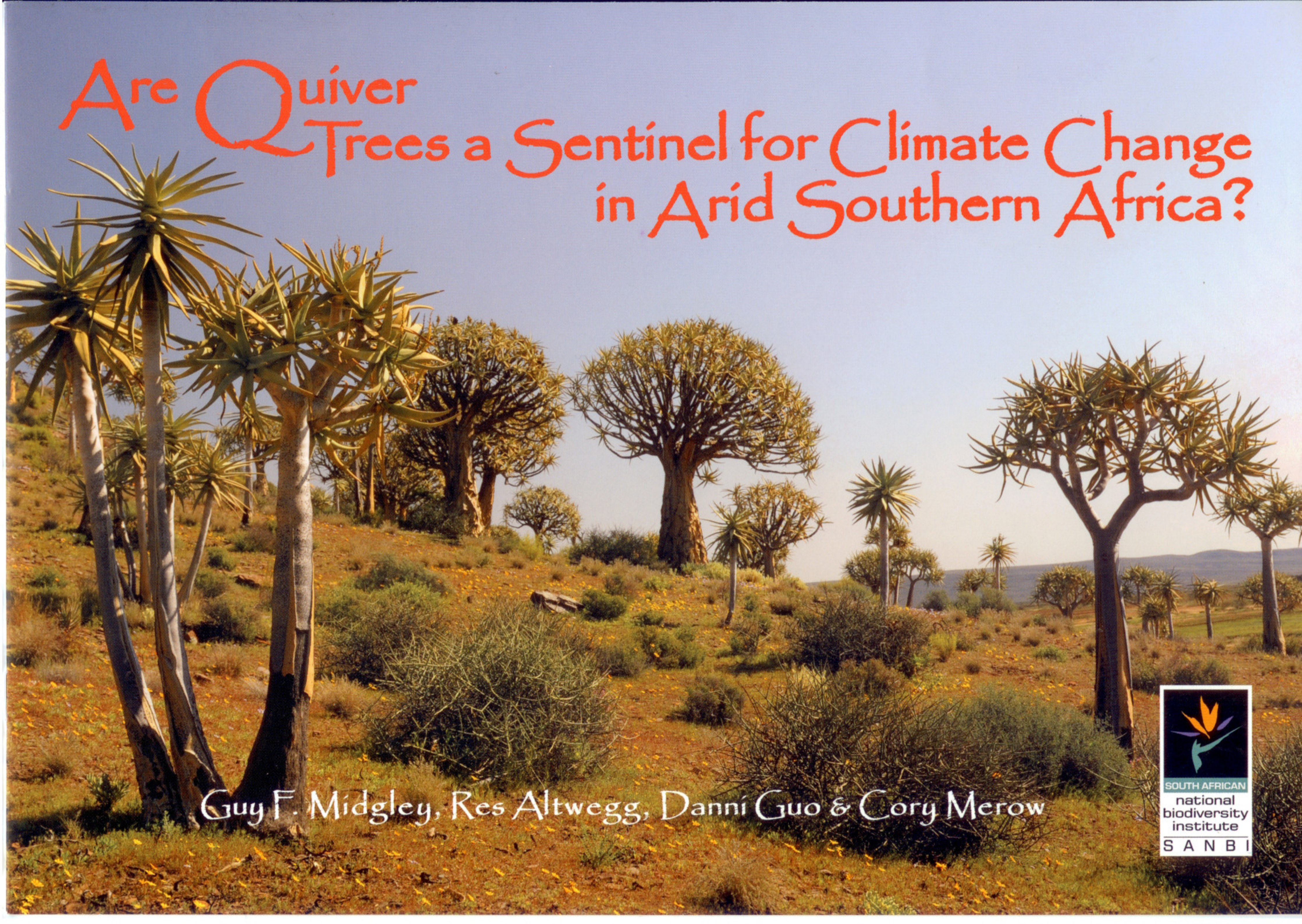
Are Quiver Trees a Sentinel for Climate Change in Arid Southern Africa?



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Overview

The effects of climate change are increasingly visible around the world. At any one time, wild plants are impacted by climate, land use, and a host of other drivers, while perhaps still reacting to changes in conditions they experienced in the past. This makes it very difficult to tease out the effects of recent observed climate change on wild populations. Not surprisingly, signs of climate change have first been found near the poles and on mountain tops where extreme temperature conditions limit plant growth. By the same argument, climate change should have large effects on desert plants that often operate at their physiological limit. However, life in deserts still remains relatively poorly studied, and the potential impact of climate change on these incredible systems is unclear. This booklet summarises a study on the quiver tree (*Aloe dichotoma,* known as kokerboom) in arid Namibia and South Africa. We provide a preliminary report of patterns of response that are broadly consistent with recent climate change, but that will require further work to demonstrate with a high level of confidence. Our findings show that quiver trees are doing relatively poorly in the hottest and driest part of their range but they are doing relatively well near their cooler southern range edge. While a lot still needs to be unraveled about the ecology and physiology of quiver trees, this species provides a good opportunity for us to test our understanding of how climate change affects desert plants. Our insights from current patterns of population change, and from genetic studies that give us a glimpse of the deeper past, we believe this species serves as a critical sentinel for changes that are affecting this fragile ecosystem as a whole.

Background

The quiver tree is a majestic feature of the succulent Karoo and the Desert Biomes of the south western region of Africa. This extraordinary desert tree with its large succulent leaves and beautifully sculpted stem occupies a geographic range stretching from Niewoudtville, South Africa in the south to the Brandberg, Namibia, in the north. It is found in the characteristic isolated populations of desert aloes, from near the west coast, to as far inland as central Bushmanland in the east.

The quiver tree's home is the richest desert system in the world in terms of biodiversity, but also one which has been subject to intense changes in land use over the past century or so, has seen major political shifts, and is subject to extreme weather events and a harsh climate. These landscapes and their biodiversity have inspired many people over the centuries, as is in evidence in the rock art of the original inhabitants, and in countless modern paintings and photographs of this breathtaking area.

Now the specter of climate change hangs over the region, as it does in many parts of the world. Climate change, caused by people's activities such as the burning of fossil fuel and deforestation, is resulting from an increase in greenhouse gases in the world's atmosphere (see Box 1). Anthropogenic (human-caused) greenhouse gases, notably carbon dioxide (CO_2), which is present in trace amounts in our nitrogen and oxygen rich atmosphere, are critical in controlling how much of the sun's energy is trapped and retained in the atmosphere after it has been re-radiated from the earths surface. It has been known for more than a century, but reconfirmed by modern science, that doubling the earth's CO_2 concentration will raise the mean global temperature by roughly 3°C.

A change in air temperature has been observed globally, which is a clear signal of the greenhouse gas increase that we have caused already (a >30% increase in CO_2 since European industrialization), and other changes are underway. These include an increasing heat content of the ocean, melting of land-bound ice in glaciers, the reduction in thickness and seasonal extent of the arctic ice cap, and a multitude of responses in wild species. These include shifts in the geographic ranges of species towards the poles (tracking cooler temperatures), upwards in altitude (i.e. up mountain slopes), the disruption of the timing of migratory species' arrival and departure, and very negative impacts such as coral bleaching.

When combined with the other multitudinous stresses to which wild species are exposed, it has been concluded by the Intergovernmental Panel on Climate Change (IPCC) that ecosystems will be unable to adapt naturally to the combined effects of these stresses and those due to climate change. Climate change alone is projected to threaten between 20 and 30% of global biodiversity if global mean temperature rises between 2–3°C above pre-industrial levels.

In 2007, the latest IPCC report summarized the results of thousands of studies showing observed responses by a wide variety of wild species – but the vast majority of these are in the northern hemisphere and at high, cool latitudes, where low temperature is an important limit to biological activity. But there was amazingly little information available to this global review of trends in the southern hemisphere, and at latitudes where high temperatures, rainfall and rainfall variability limit biology. And there was almost no information for desert ecosystems.

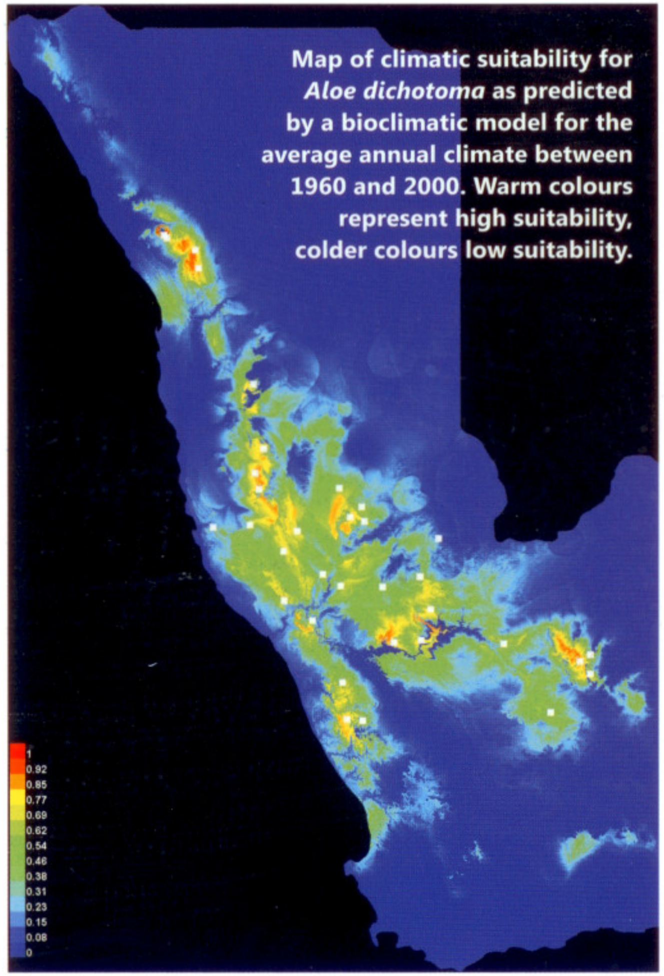
A growing awareness of this lack of information in 2002 prompted our group at SANBI to explore a way to begin plugging this gap, and specifically to test if any species of the arid west might be showing responses to warming or even drying trends. We centered on this region because most of the projections of climate change show that this is where adverse impacts might be expected first in the southern Africa. We had been working in the region for some time, and had observed healthy populations of quiver trees in the southern reaches of its range – such as near Niewoudtville. Yet we began hearing stories of populations showing signs of decline further north. Not even knowing the full extent of the species' range, we decided to use this iconic species as a test case. This booklet describes our journey of studying the quiver tree and our attempts to decipher its recent history. It is the story of a few dedicated field biologists, an emerging pattern, and a huge ongoing learning curve in the doing and communicating of science, and in disentangling the wide range of stresses on wild species.

Scoping the problem

The region we tackled is problematic in many ways for the question being considered. It straddles two countries, South Africa and Namibia, creating issues with many logistical aspects. It is amongst the most poorly covered by climate monitoring stations in South Africa, and coverage in Namibia is even sparser. Knowledge of historical trends is also thin, although some early botanists had taken good quality photographs that could reveal changes over several decades. To test such an important and difficult question in the absence of historical trends, we needed therefore to find a species with a lifespan of sufficient duration to reveal long term shifts. Furthermore, the species needed to have a population structure that was measurable within a fairly short time-span to allow many sites to be sampled. A high degree of visibility in the landscape was also important, to help the rapid identification of measurable populations, and to identify individuals in the landscape with a high degree of accuracy.

The quiver tree fits the bill on all counts, with an initially unexpected added advantage – once dead, individuals may remain standing for many years and possibly even decades, allowing one to quantify the relative health of populations by establishing the proportions that have died. This would allow us to develop far more sophisticated approaches that use estimates of population growth rates across life stages. This is called a demographic approach.

A rough idea of a species' climatic requirements can be obtained through so-called bioclimatic models. These statistical tools relate a species' presence to climate at the sites where they occur. They can then be used to map other potentially suitable areas either at present time, or predicted for the future under climate change. The quiver tree's distribution turns out



Map of climatic suitability for *Aloe dichotoma* as predicted by a bioclimatic model for the average annual climate between 1960 and 2000. Warm colours represent high suitability, colder colours low suitability.

Box 1. The challenge of climate change

Trace gases such as carbon dioxide (CO_2) are important for the temperature of the earth's atmosphere, and for our lives and the lives of all species on the planet. This is because greenhouse gases like CO_2 absorb radiation emitted from the earth's surface after it is warmed by the sun. The temperature of the atmosphere affects living things directly, of course, but is also important for patterns of weather around the world. Since people began reducing the forest cover of the earth and burning fossil fuels (coal, gas and oil), the CO_2 content of the earth's atmosphere has increased by more than 30%. Forests (and other vegetation types) are important in absorbing and storing carbon on land, and their ongoing destruction now contributes about 20% of the annual CO_2 emitted. Fossil fuels contain carbon that was stored hundreds of thousands of years ago by ancient vegetation from an atmosphere far richer in CO_2 than ours today. These ancient plants were buried over thousands of years, and their carbon was locked away and transformed underground, until we discovered the value of this energy rich resource over the past few centuries. From a basic physical understanding of greenhouse gases, and reconstruction of changes in temperature and CO_2 over thousands, millions and hundreds of millions of years, we now know that doubling CO_2 in the atmosphere will lead to a roughly 3°C increase in global mean temperature, and likely changes in climate patterns. These are likely to include increases in rainfall in some areas, reductions in others, and generally higher temperatures around the world. For the region in which quiver trees are growing, less rainfall and higher temperatures are expected over the next few decades.

to be strongly related to rainfall. Of course, this approach does not reveal any mechanisms for why the species occurs where it does. To gain a deeper understanding, we therefore examine demography: age distribution, survival, and reproduction.

The arid western region of southern Africa has become warmer and drier over the past 30 years. This is especially true for the Richtersveld area, while in Namibia the trend has somewhat been interrupted by a series of good rainfall years recently. If the distribution of quiver trees is limited by climate, we would therefore expect that the low-altitude northern populations, as well as the populations near the Richtersveld would struggle to survive and reproduce. Populations in the south, for example near Niewoudtville, should do well since the climate there appears to be increasingly suitable for quiver trees.

Taking the first snapshots

Over the course of two long field trips in 2001 and 2002, Wendy Foden and various assistants, including Graeme Ellis, collected population structure data on populations across the full range of the quiver tree. Early reports from Wendy on her longest trip into Namibia were discouraging, as she found a very variable pattern of mortality as she trekked across the landscape, and we became resigned to the likelihood that the explanations for mortality were more complex than climate change alone. Nonetheless, Wendy pushed on to sample the most remote populations, including a marathon climb up the Brandberg in Namibia in searing heat in midsummer to sample an extremely healthy population at the northernmost tip of the quiver tree's range. On her return, she began to analyse her large data set.

The initial findings, published in the journal *Diversity and Distributions* in 2007 (13, pp. 645–653), describes the initial patterns obtained using analyses of the proportions of mortality and new individuals (recruits) across latitude gradients. The findings were relatively straightforward – there was a simple but not clear-cut linear relationship between mortality of adult plants and latitude such that northern populations had higher mortality than southern populations. Despite the apparent variation around this basic relationship we felt that the significance of the regression indicated that the pattern in the data was indeed real. This seemed to support the hypothesis – we had expected more mortality in the warmer parts of the range if a gradual shift in climate was causing critical thresholds for survival to be exceeded under the most extreme conditions within the range.

This justified a deeper search of the data. Wendy began by seeing if she could come up with an explanation for the variability that was consistent with the climate change explanation. This step was justifiable by the principle of "Occham's Razor" which states that the most likely explanation for a pattern is that which is simplest, or in other words, that explanation which needs the fewest additional explanatory variables.

The power of this approach is that it tries to explain mortality patterns across the entire range of the quiver tree. It does not invoke a separate mechanism for each population. However, it does not deny the importance of local process. Local processes certainly contributed to mortality observed in each population, but it is unlikely that they could have fortuitously caused a consistent pattern at the larger landscape scale.

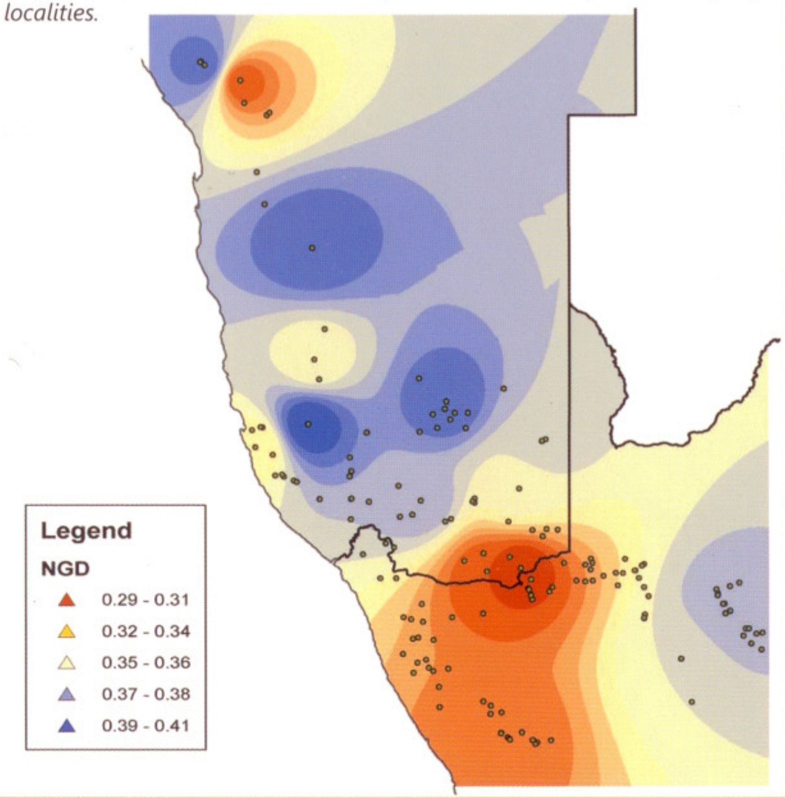
The first step was to test if altitude helped explain the pattern. Because we expect high altitude sites to be cooler and moister than those at low altitudes, Wendy tested if the variation in mortality not explained by latitude could have been related to the particular altitude of each population. The result was, yes, higher altitude sites had healthier populations. The behaviour of dying plants suggested that a decline in water balance, induced either by reducing water supply, higher temperatures, or both might be implicated. Dying trees showed drought stress by shedding their leaves – a clear stress response. But to be even more sure, Wendy tested if a variety of other stresses might be affecting this pattern – including distance to the nearest road, presence of grazing or browsing animals, fungal infections were all explored. Damage to bark by porcupine gnawing was the only other stress that correlated with mortality at the landscape level suggesting that in drier sites, porcupines afflicted quiver trees especially hard.

Finally, with the help of statistician Professor Les Underhill of the University of Cape Town, Wendy and the team applied a multiple regression that tested the importance of altitude, latitude AND the likely change in climate between the 1960s and 2000 to confirm the hypothesis. The results were clear – it seems likely that the observed pattern is a result of recent climate change.

Developing the picture – the evolutionary history of key aloe populations

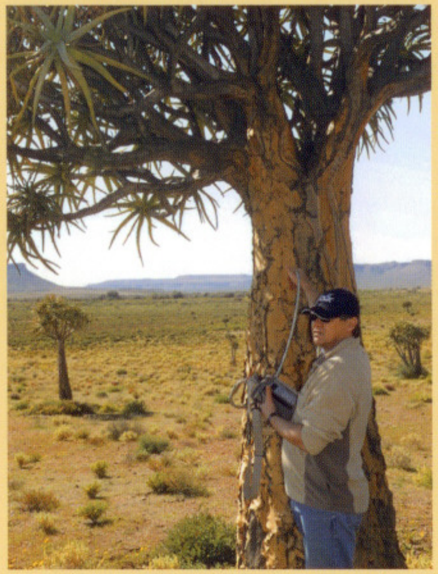
As part of her study, Wendy Foden collected leaves of selected aloe populations to be used in genetic studies. This was done for two reasons – firstly simply to be sure that the species we were collecting was *Aloe dichotoma* (due to uncertainty in some populations resulting from possible hybridization with this species and closely related desert aloes), and secondly to develop an idea of the likely evolutionary history of key populations, and the relative length of time they had been in place.

The distribution of genetic variation in Aloe dichotoma. *Data based on Nel's gene diversity (NGD) calculated from amplified fragment length polymorphisms (ALFPs) and DNA sequence data. Dots represent sampling localities.*



Box 2. Stem photosynthesis in quiver trees

Desert plants use all sorts of tricks to maximize their carbon uptake. The quiver tree is no exception. The species firstly uses a well known trick that allows it to open the pores (stomata) on its leaves during the night to fix carbon when the air is cooler and more moist than during the daytime. This carbon is stored in the form of acids in the vacuoles of its leaf cells until the following morning, when CO_2 is released internally to the leaf and fixed using the sun's energy. This is known as Crassulacean Acid Metabolism (CAM) pathway, after the first plants discovered to be using this metabolic pathway. But the quiver tree uses another trick – its golden brown and flaky stem bark hides a secret that we discovered in late 2008 – the species is able to photosynthesize through its bark, and fix carbon directly via its surface stem tissue! This is obviously important in supplying carbon to the stem tissues of this plant, and may partly explain why the species eventually dies from old age – its bark becomes too opaque and occluded by dirt to let enough light through.



Dr Jacqui Bishop, now at the University of Cape Town, conducted a series of tests and analyses that reveal a fascinating spatial pattern (see Figure). This shows that most populations in the central and northern parts of the range generally have had a longer history than those in the south (except a small population in the north). The population with the highest level of genetic diversity is found in the middle of the range latitudinally, though the Brandberg population in the far north is also among the most diverse. This signals that these populations are the most ancient, and likely to have persisted longest through periods of climate change such as the mid-Holocene warming of around 6000 years ago, and even the cold glacial times more distant in time than 15 000 years ago. It is also very clear that the southernmost populations in South Africa are amongst the least diverse and are likely to be have been established more recently.

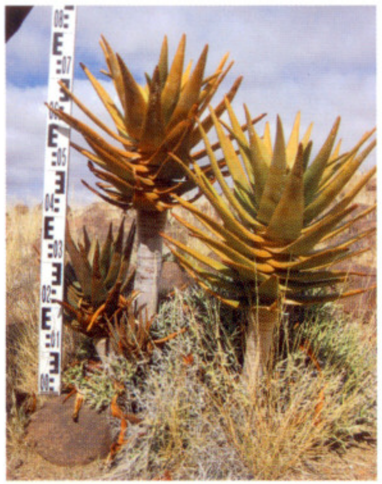
This conclusion is confirmed by previous work which found that the western and northern Cape was likely colder and wetter during the glacial times of more than 15 000 years ago, and that these aloe populations were probably established in these regions since the world warmed after the last ice age.

Refining the work

A second snapshot

The 2002 survey yielded a snapshot of the status of these populations. Such a snapshot can show patterns clearly, but for a thorough assessment of the vulnerability of quiver trees to climate change, we need to understand the processes that have led to the observed pattern. For example, the proportion of dead individuals was clearly visible, but it was not always clear how long ago individual trees had died. A single snapshot also gives no information on how quickly (or slowly) trees can grow. Understanding these basic demographic processes requires observation over time.

In 2008 a field team therefore set out to resample the populations for which demographic data were collected in 2002. Graeme Ellis and Megan Yates visited 41 quiver tree populations across the whole range of the species. Most of these populations had also been visited in 2002, and Graeme and Megan applied the same field methods as were used during the first field trip. In particular, they also made a special effort to find again trees for which individual GPS coordinates had been taken in 2002. While two snapshots in time still do not provide all the information we ideally would like to have, we are now in a much better position to judge the state of these populations. We now have a solid basis from which to start a long-term monitoring program, which we hope will allow us to refine our understanding continually.



The new data

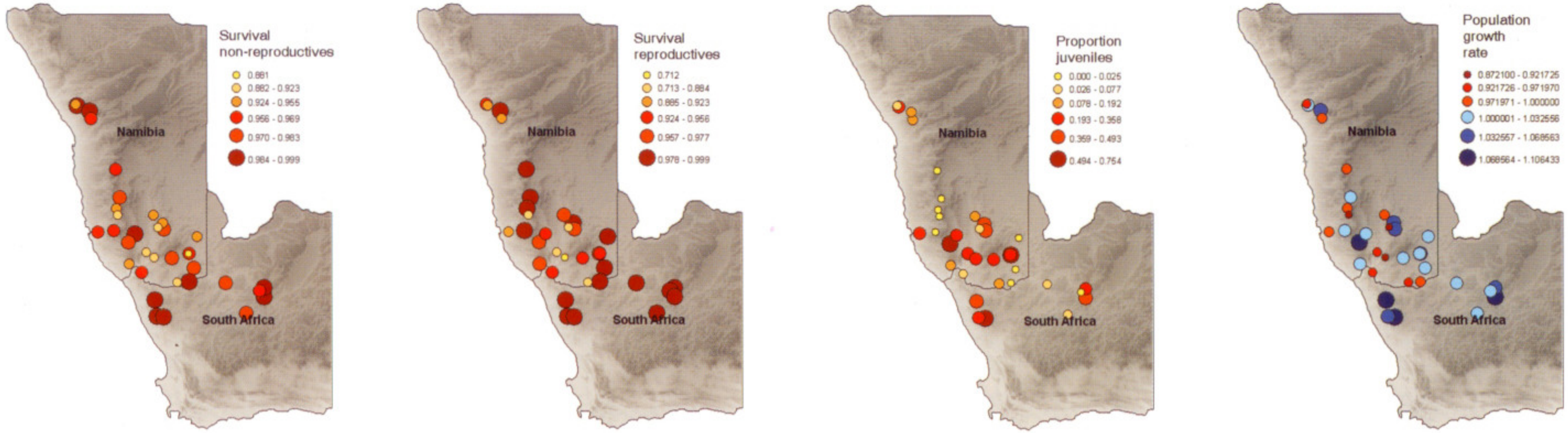
The second field trip yielded new data on mortality that happened between the two field trips. We also have a measure of reproduction: the number of seedling trees per adult in the sample. Together, these two demographic quantities allow us to judge whether the populations are able to sustain themselves. We used a simple technique, so-called matrix population models, to predict the population growth rate given the observed demographic rates. We had to assume that the observations are representative of what is happening on a longer time scale, i.e. also that conditions are not changing. Of course, conditions are changing. The parts of South Africa and Namibia in which quiver trees occur has become warmer and drier over the past 30 years. However, Namibia experienced a series of uncharacteristically good rainfall seasons in the time between our two field samples. If quiver trees rely on sufficient rainfall for recruitment, and this is being impacted by extremely high temperatures, our assessment is clearly too optimistic. We are therefore cautious for now, but expect that further observations will allow us to refine the predictions as we are gaining a deeper understanding of the population ecology of this species, and its reaction to environmental variation.

The results show that populations to the south are doing well. They had very low mortality and relatively good reproduction, which is predicted to support slowly growing populations. Populations that could not sustain themselves under the observed demographic rates are towards the north of the range, and along the Orange River where temperatures are extremely high. In broad terms, the pattern observed in 2002 is thus confirmed by our new data.

Lessons learned

Despite a rather clear emerging picture, there are many aspects of quiver tree population dynamics that remain poorly understood. For example, due to their long lifespan the trees only occasionally need to produce successful seeds. In theory, the populations could persist through boom-and-bust cycles. If so, we should clearly see groups of equal-aged trees. Our current data suggest that this has occasionally happened in some populations, but it is not a general pattern across the species' range. Furthermore, we found a level of mortality in some populations that would not be sustainable with rare recruitment events.

One surprising discovery was that one population of quiver trees can re-root after they have fallen over. This sometimes happens to trees in windstorms, as they are very shallow rooted. This happened to around ten individuals at the base of Brandberg mountain in Namibia some time before 2002.



***Demographic analysis of the data collected in 2008**: the proportion of trees (separated into pre-reproductive and reproductive age classes) surviving since 2002; the number of juveniles per reproductive tree as a measure of reproduction; and the projected population growth rate showing whether a population could sustain itself (>1) with the observed demographic rates or whether it would decline (<1).*

The fallen trunks had died but the canopy branches, where they touched the ground, have continued growing and were alive in 2008. This seems to be an evolutionary innovation, as it is not found in any other population, and should be conserved at all costs if this population is threatened.

But the main lesson we learned was the potential value of a focused and directed campaign to track the maturation and ageing process in these trees. These data would allow us to build far more reliable models of the population viability under climate change, and guide conservation efforts more effectively. One purpose of this booklet is to raise interest in this effort, and to engage those who are lucky enough to have easy access to populations in helping us achieve this aim.

Conclusions

It looks as though climate change **IS** having an impact on quiver trees. The large-scale patterns of quiver tree population health is certainly in agreement with the expected effect of climate change. However, quiver tree population dynamics remain poorly understood despite these efforts, and we must work to fill in the details. Other questions could then be addressed. How does climate change interact with local factors? What is the relative importance of short-term events (extreme droughts or particularly favourable years) and the slower long-term trends in climate? How quickly can quiver trees establish new populations? To answer these and more questions, we want to continue monitoring these populations, hopefully with the help of a dedicated an excited band of collaborators!

A toppled tree with re-rooted branches

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