ECOGRAPHY

Research

Are forest-shrubland mosaics of the Cape Floristic Region an example of alternate stable states?

Michael D. Cramer, Simon C. Power, Anastas Belev, Lindsey Gillson, William J. Bond, Michael T. Hoffman and Lars O. Hedin

M. D. Cramer (http://orcid.org/0000-0003-0989-3266) (michael.cramer@uct.ac.za), S. C. Power, L. Gillson, W. J. Bond and M. T. Hoffman, Dept of Biological Sciences, Univ. of Cape Town, Cape Town, South Africa. – A. Belev and L. O. Hedin, Dept of Ecology and Evolutionary Biology, Princeton Univ., Princeton, NJ, USA.

Ecography
42: 1–13, 2018
doi: 10.1111/ecog.03860

Subject Editor: Thorsten Wiegand
Editor-in-Chief: Miguel Araújo
Accepted 3 September 2018

The idea of alternate stable states (ASS) has been used to explain the juxtaposition of distinct vegetation types within the same climate regime. ASS may explain the co-existence of relatively inflammable closed-canopy Afrotemperate forest patches ('Forest') within fire-prone open-canopy Fynbos in the Cape Floristic Region (CFR) on sandstone-derived soils. We evaluated the hypothesis that although fire and local topography and hydrology likely determined the paleogeographic boundaries of Forest, present-day boundaries are additionally imposed by emergent edaphic properties and disturbance histories. We studied vegetation and edaphic properties of Forest-Transition-Fynbos vegetation at two sites within the CFR on sandstone-derived soils and tracked historical change using aerial photography. Whereas Forest and Fynbos have changed little in extent or density since 1945, transition vegetation increased into areas formerly occupied by Fynbos. Forest soils were ubiquitously more nutrient-rich than Fynbos soils, with transition soils being intermediate. These edaphic differences are not due to geological differences, but instead appear to have emerged as a consequence of different nutrient cycling within the different ecosystems. Soil nutrients are now so different that a switch from Fynbos to Forest is unlikely, in the short term (i.e. decades). Floristically and nutritionally, transitional vegetation is more similar to Fynbos than Forest and may be less resilient to changes in exogenous drivers (e.g. fire). Our findings are consistent with the idea that geologically Forest and Fynbos are largely fire-derived long-term ASS, with the stability of each state reinforced by marked soil nutrient differences. In contrast, the intermediate transitional vegetation that might switch states is unlikely to be stable.

Keywords: Ecosystem resilience, edaphic properties, niche construction

Introduction

In theory, alternative stable states can develop despite sharing the same environment due to internal feedbacks (Lewontin 1969). In practice, however, there is considerable debate as to whether natural ecosystems display alternative states that remain stable over ecologically-relevant timescales, and whether shifts between states are caused by

NORDIC SOCIETY OIKOS

www.ecography.org

changes in exogenous disturbance agents (e.g. fire; Wilson and Agnew 1992) or by changes in endogenous ecosystem interactions (e.g. loss of predators, Beisner et al. 2003; increase in elephants, Pellegrini et al. 2017). The coexistence of contrasting vegetation types within the same climate envelope has commonly been interpreted as a case of such alternative stable states (ASS; Warman and Moles 2009, Staver et al. 2011, Hirota et al. 2011, Dantas et al. 2013, Pausas 2015). An alternative view is that physical factors other than climate (Veenendaal et al. 2015), such as edaphic limitations, local hydrology and land-use history (Sankaran et al. 2008, Staver et al. 2011) account for vegetation patterns. Since stabilising feedbacks alter soil and other environmental properties (Jobbágy and Jackson 2000, 2004), it has been difficult to differentiate between soils determining vegetation and the emergence of ASS, where different vegetation creates different soil properties. Soil chemistry is, however, more likely to change in response to different vegetation than soil physical properties (e.g. soil texture), providing a potential method for unscrambling the different processes.

Changes in the prevalence of fire have been suggested to account for the switch between fire-prone open-canopy and relatively poorly flammable closed-canopy vegetation in many contexts (Manders 1990, Manders and Richardson 1992, Manders et al. 1992, Staver et al. 2011, Wood and Bowman 2012, Coetsee et al. 2015, Paritsis et al. 2015). Since the boundaries between vegetation types may change over time, this suggests that the internal stabilising feedbacks of each stable state can be over-ridden. These boundaries may 'emerge' over long time periods (decades to centuries) driven by differences in fire frequencies (Jackson 1968). Alternately the boundaries may be the stable product of differential fire susceptibility 'imposed' by site characteristics (Mount 1979). This partial dichotomy between emergent and imposed vegetation patterning is highly relevent to the Forest-Fynbos boundary in the Cape Floristic Region (CFR) of South Africa that is characterised by high taxonomic (Power et al. 2017) and structural turnover (Forsyth and van Wilgen 2008). Patches of Afrotemperate Forest occur in a matrix of lower stature, fire-prone, open-canopy, sclerophyllous shrubby Fynbos. Forest-Fynbos boundaries can be sharp (< 10 m), although the vegetation may also grade through a transitional vegetation that is a mixture of both (ca < 100 m, McKenzie et al. 1977). Fire frequency and intensity are thought to be critical to determining Forest-Fynbos boundaries (Phillips 1931, McKenzie et al. 1977, Manders and Richardson 1992), which often occur along drainage lines, wind-shadows, slope-breaks and rock screes, all of which represent an imposed limit to fire frequency and/or intensity (van Wilgen et al. 1990, Geldenhuys 1994). Forest and Fynbos species, however, differ in flammability, with shrubby Fynbos being more fire-prone than tall Forests (van Wilgen et al. 1990, Kraaij et al. 2013). These differences in flammability suggest a degree of emergent spatial patterning of vegetation, with fire adaptation in Fynbos preventing the expansion of fire-sensitive Forest species (van Daalen 1981, Manders 1990). The spatial transitions between these vegetation types have consequently been considered to represent the coexistence of ASS (Coetsee et al. 2015), that are subject to anthropogenic modification of fire regimes (Poulsen and Hoffman 2015).

These vegetation boundaries can be associated with strong dissimilarities in soil nutrients (Masson and Moll 1987, Manders 1990, Cramer 2010, Cowling and Potts 2015). For example, Forest soils have higher C, N, Ca and K than Fynbos soils, even when occupying the same geology, implying that Forests increase the fertility of soils while frequent fires in Fynbos promote mineralization and loss of nutrients (Coetsee et al. 2015), potentially contributing to the resilience of the vegetation. If soils do have a role in dictating the structure and flammability of the vegetation, then the perturbation of vegetation by an altered fire regime would have to be sustained for long enough to override the inherent resilience of the ecosystem, including the soil properties, in order for the ecosystem to switch to an ASS. In the debate as to whether ASS exist between Forest and Fynbos, we therefore need to consider time and the degree to which the sites are fire-prone as a contibuting factors.

We hypothesised that Forest-Fynbos boundaries exhibit a degree of resilience to perturbation that is contingent on the contemporary edaphic circumstances. Consequently, switches between alternate stable states ought to be less likely where edaphic properties preclude one or the other of the alternate states. We predict that a consequence of edaphic discontinuities between Forest and Fynbos is that 1) despite occurring on soils derived from the same geology, Forests are constrained to more fertile soils and do not readily invade soils where Fynbos exists in a stable state, demonstrating that these are stable alternate states. 2) In contrast, the transitional vegetation with intermediate susceptibility to fire, occurring on soils that are also intermediate between Forest and Fynbos, is most likely to be sensitive to changes in disturbance. This transitional vegetation may tend towards canopy closure in the absence of disturbance and to a more open-canopy with disturbance, exhibiting the ability to switch to alternate states depending on disturbance regimes, but these switches are unlikely to be stable.

To evaluate these predictions, we explored the vegetation, topography, edaphic properties, and fire history of Forest-Transition-Fynbos in the CFR at two sites. We used species cover data and normalised difference vegetation indices (NDVI) to determine whether these vegetations are floristically and structurally distinct and therefore potentially could exist as alternate states (objective 1). Historical aerial photographs were used to test the prediction that Forest and Fynbos are constrained to particular zones, whereas Transition vegetation is more prone to range shifts (objective 2). To test the hypothesis that soil differences emerge from stable alternate states, soil textures and immobile soil elements were analysed to determine whether the soils were derived from a common geological parent material (objective 3). We tested for biotic alteration of edaphic properties by analysing plant-essential elements (objective 4). Since possible switches between alternate states could be linked to fire disturbance, we assessed soil charcoal as a proxy for the incidence of fire (objective 5). Finally, we determined whether vegetation states could be predicted from soil variables alone (objective 6).

Materials and methods

Study sites

The study was conducted at two sites (Fig. 1) situated in the Table Mountain National Park, Blinkwater ravine (33.960003°S, 18.394640°E) and Orange Kloof (33.994899°S, 18.394476°E). At Blinkwater the vegetation around the seasonal stream is Southern Afrotemperate

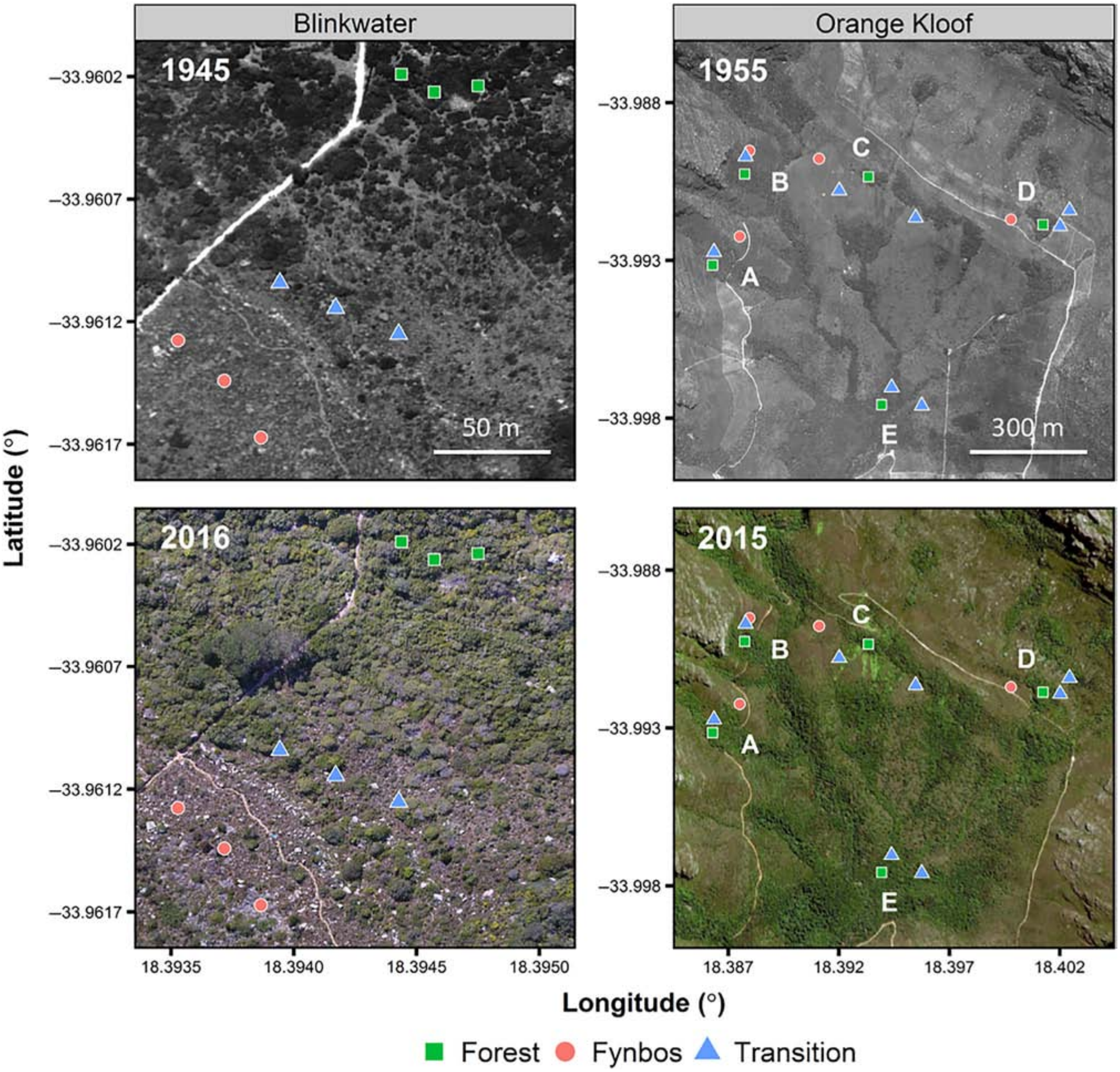

Figure 1. Historical aerial photographs of the Blinkwater and Orange Kloof sites compared to contemporary images. Within each site the sampling locations are marked for each of the vegetation types (Fynbos, Transition, Forest). Sampling at Orange Kloof was in a larger geographic area and occurred in five different sites. Site E lacked Fynbos vegetation and was on granite-derived soils (as opposed to sandstone-derived soils elsewhere) and was thus excluded from statistical analyses although the data was retained for presentation. At Blinkwater a walking path running southeast lies along a rock scree that defines the boundary between Transition and Fynbos vegetation. The large tree along the northwest path ('Pipe track') at Blinkwater is an alien *Pinus* sp.

Forest ('Forest', Mucina and Rutherford 2006) with trees up to 8 m in height. Adjacent to the ravine the Peninsula Sandstone Fynbos is dominated by ericoid and proteoid shrubs (< 2.5 m in height), in addition to graminoids (Mucina and Rutherford 2006). A transitional vegetation type ('Transition') dominated by shrub and tree species (< 4 m in height) occurs between Forest and Fynbos. The boundary between Transition and Fynbos on the southern side is coincident with a line of boulders running downslope (Fig. 1). Soils at the study site are skeletal overlying shallow Table Mountain Sandstone rock, although granitic outcrops and relatively isolated boulders also occur downslope. In each of the vegetation types we selected three, 10 × 5 m plots and from each three soil samples were collected.

Orange Kloof is a 285 ha valley that has been actively managed (i.e. prevention of harvesting and fires) for over 50 yr with no fire occurring since 1972 (McKenzie et al. 1977). The vegetation on west facing slopes at higher elevations is Peninsula Sandstone Fynbos while the lower valley and large sections of the east facing slopes are dominated by Southern Afrotemperate Forests, interspersed with Peninsula Granite Fynbos (Mucina and Rutherford 2006). The lower area is made up of Basement Granite frequently overlaid by Table Mountain Shale and Table Mountain Sandstone (McKenzie et al. 1977). The area designated Peninsula Granite Fynbos is today largely dominated by what we designated as Transition vegetation, but was termed 'scrub' by (McKenzie et al. 1977). At four sites, three 10 × 5 m plots covering each of the vegetation types (Fynbos, Transition and Forest) were selected and three surface soil samples collected near each. Where granitic soils are dominant, one comparison site was established, but from which Fynbos was missing (Fig. 1, site E). The plots with the three vegetation types were selected in close proximity, ensuring consistency in topography and geology (largely sandstone). In order to characterise the topography, the slope, elevation and aspect were extracted from the 10 m resolution digital elevation model of the city of Cape Town (<https://web1.capetown.gov.za>).

Vegetation assessment (objectives 1 and 2)

Within each plot the identity and percentage abundance of all plant species were recorded and NDVI measured (objective 1). NDVI at 10 m resolution was obtained through Google Earth Engine (https://developers.google.com/earth-engine) from the Sentinel-2 MultiSpectral Instrument for the period Jun 2005 – Jun 2016. A cloud mask was applied and NDVI over the time series calculated using the upper quartile of NDVI values to avoid interference by cloud cover. NDVI was calculated using $\text{NDVI} = \rho\text{NIR} - \rho\text{Red} / \rho\text{NIR} + \rho\text{Red}$ (Tucker 1979) in which ρ_{NIR} was the 842 nm band and ρ_{Red} the 665 nm band.

Repeat aerial photographs covering Blinkwater (1945–2015) and Orange Kloof (1955–2016) sites were used to quantify change in woody cover over time (objective 2). Prior to analysis, images were georeferenced using the coordinates of continuously identifiable control points (e.g. rocks, roads) obtained from Google Earth. Misalignments between images and control coordinates were corrected using thin plate spline transformation and cubic spline resampling, implemented in QGIS (Quantum GIS Development Team, <http://qgis.osgeo.org>). To quantify the extent of woody cover for each year, a 25 × 25 m grid with 5 m^2 cells was centred over each plot. Vegetation of each cell was then manually classified as either 'open-canopy' or 'closed-canopy' based on the presence of woody vegetation occupying ≥ 50% of the cell following the approach of Wood and Bowman (2012).

Soil and rock sampling and preparation (objectives 3, 4 and 5)

Surface leaf litter was removed and soils collected using a 0.07 m diameter auger to a depth of 0.3 m. Soils were air dried for 1 week, weighed, and then passed through a 1 mm sieve. Sieved samples were split by repeatedly quartering the soil (Gerlach et al. 2002) for physical and chemical analyses. Additional samples were collected for charcoal analysis at depths of 0–10 cm, 10–20 cm and 20–30 cm and air-dried for 48 h prior to analysis. Chemical characteristics of the soils were assessed using measures of extractable elements to assess plant available nutrients and characteristics of the intact soil total elemental composition from which organic material had been removed through dry-ashing (see below). Samples of granite and sandstone rocks occurring in or near Fynbos, Transition and Forest plots at Blinkwater were removed from boulders to provide a reference of geological parent material (objective 3). The rock surface was manually cleaned and washed to remove lichens and other deposits before being crushed.

Soil particle size analysis (objective 3)

Soils samples were heated to 450°C for 12 h to remove organic matter (dry-ashed) prior to particle size distributions being measured using a Malvern Master-Sizer 2000. Each sample was subjected to 300 s ultrasonic dispersal to ensure complete disaggregation of particles. The proportion of the soil particles in each size class was recorded and plotted. These size classes were then summed into categories representing clay, silt, very fine sand, fine sand, medium sand, coarse sand and very coarse sand, according to the Wentworth grain size chart (Williams et al. 2006).

Soil and rock total elemental analysis (objective 3)

Sieved and dry-ashed soil, and crushed rock samples were milled in a mortar and pestle to a fine powder. The samples were assessed in a Spectro Xepos X-Ray Fluorescence (XRF) analyzer (Spectro, Amatek materials analysis division, Kleve, Germany) in a helium atmosphere using a silicon drift detector. The instrument was calibrated by using a certified standard GBW07312 (National Research Center for CRMs, Beijing, China), for which elemental concentrations were obtained from NOAA technical memorandum NOS ORCA

68 (1992). Based on this data a weathering ratio was calculated as ([Ca] + [Mg] + [K])/[Zr] following the example of Chittleborough (1991), but substituting K for Na.

Available soil nutrient analysis (objective 4)

Mass spectrometer analysis for soil C, N, $\delta^{13}C$ and $\delta^{15}N$ was conducted in the Dept of Archeometry (Univ. of Cape Town). Approximately 40 mg of sieved soil was weighed into tin capsules (Elemental Microanalysis Ltd, Devon, UK) and combusted in a Thermo Flash EA 1112 series elemental analyzer from where the gasses were fed into a Delta Plus XP isotope ratio mass spectrometer (Thermo Electron Corporation, Milan, Italy). Two in-house standards and one IAEA standard were used to calibrate the results.

The Inst. for Plant Production (Dept Agriculture: Western Cape, South Africa) measured pH, electrical conductivity, K, Mn, Na, Cu, Zn, Ca, Mg and two measures of plant available P: P-Citric (extracted in 1% (w/v) citric acid) and P-Olsen (Olsen et al. 1954) following protocols of soil science society of South Africa (1990) on sieved soils. Soil pH was determined by shaking 2 g soil in 20 ml 1 M KCl at 180 rpm (Hermle Z420, Gosheim, Germany) for 60 min, centrifuging at 10 000 g for 10 min and measuring the supernatant pH. Exchangeable cations were extracted with NH_4-acetate and EDTA at pH 4.65, and their concentrations determined using a Thermo ICP iCAP 6000 series spectrometer (Thermofisher Scientific, Surrey, UK).

Charcoal analysis (objective 5)

Samples of 100 g of air-dried soil were stirred into 10% (w/v) KOH and left overnight before sieving through 1.4 mm mesh and washing with water. The sieved material was suspended in water in a petri dish and the charcoal fragments extracted by hand under a dissecting microscope. The fragments were counted and weighed after drying at 70°C for 48 h.

Statistical analysis

Chao estimates of extrapolated species richness from species accumulation curves (Chao 1987, Chiu et al. 2014) were determined using the specpool function of the 'vegan' library (Oksanen et al. 2016) in R (R Development Core Team). To compare turnover in species richness between vegetation types, Sørensen's dissimilarity coefficient was calculated using the function shared from the 'rich' library (Rossi 2011) in R. Analysis of similarity (ANOSIM) in the library 'vegan' library provided a test of whether there were significant differences between Forest, Fynbos and Transition vegetation types.

A one-way ANOVA followed by a post-hoc Tukey HSD test using the 'agricolae' library (de Mendiburu 2016) in R, was used to check for significant ($p < 0.05$) differences in topography, soil nutrients, rates of change in woody cover and NDVI between Forest, Transition and Fynbos across both study sites. To examine the separation or overlap of the three vegetation types (Forest, Transition, Fynbos) with respect to soil nutrition (objective 6), a linear discriminant function analysis (LDA) was conducted using the 'lda' function in the 'MASS' library (Venables and Ripley 2002) in R. We selected soil variables (pH, Ca, Mg, Olsen P, Na, K, Cu, Zn, Mn, total N, organic matter, clay and $\delta^{15}N$) that represent important plant and ecosystem characteristics. We also used texture classes in an analogous LDA, but this failed to separate the vegetation types (data not shown).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f3h1342> (Cramer et al. 2018).

Results

Current vegetation characteristics (objective 1)

Forest and Fynbos vegetation types are floristically distinct, as is evident from the fact that there were no shared species between them at Blinkwater and only 1% at Orange Kloof (Supplementary material Appendix 1 Table A1). We identified Transition vegetation as being a combination of elements of both Fynbos and Forest and located sample sites in areas in which change in vegetation has occurred over the last 6 decades (Fig. 1). At both Blinkwater and Orange Kloof, Transition vegetation shared elements of both Fynbos and Forest, but according to Sørensen's dissimilarity coefficients (Supplementary material Appendix 1 Table A1) was floristically more similar to Fynbos.

Although vegetation types at Blinkwater were relatively homogeneous between sites, there was significant turnover in species between the three vegetation types (Supplementary material Appendix 1 Fig. A1a). Forest and Transition at Orange Kloof had similar Sørensen's coefficients to those at Blinkwater, however, Fynbos exhibited greater variance between sites at Orange Kloof than at Blinkwater (Supplementary material Appendix 1 Table A1). The larger number of species and greater variance of Fynbos at Orange Kloof is probably the consequence of a broader geographic sampling. At both Blinkwater and Orange Kloof, the species pools of each vegetation type diminished in the following sequence Transition > Fynbos > Forest, consistent with Transition vegetation containing species from both Fynbos and Forest. Overall, the NDVI values at Blinkwater were lower than at Orange Kloof ($p = 0.017$, Supplementary material Appendix 1 Fig. A2). Moreover, NDVI was significantly higher in Forest than in Fynbos, with Transition being intermediate at both sites. Forest and Fynbos are thus floristically and structurally distinct at both sites and could therefore be considered distinct alternate states. Despite these vegetation differences, there were no significant differences in slope ($p = 0.509$), elevation ($p = 0.113$) or aspect ($p = 0.921$) between vegetation types across the study sites.

Vegetation change (objective 2)

Woody cover was high for Forest at both Orange Kloof and Blinkwater (Fig. 2a) and increased over the duration of the observations at Blinkwater (1945–2015) by 0.25% per annum, but remained completely unchanged at all Orange Kloof sites (1955–2016, Fig. 2b). Although woody cover of Fynbos and Transition is distinct at Blinkwater today, this was not the case in the preceding decades over which woody cover of both Fynbos and Transition increased (Fig. 1–2). At Orange Kloof, Fynbos woody cover has been lower than that of Transition from the 1960's onwards, with only small annual increases in Fynbos (0.08% per annum) while Transition increased at a faster rate (0.55% per annum, Fig. 2b), which is similar to the rate of change reported by Luger and Moll (1993) of 0.41% per annum (applying a linear regression to their data) for Orange Kloof. Forests and Fynbos are thus constrained to particular zones exhibiting little change in distribution, whereas Transition vegetation is more prone to range shifts.

Soil texture (objective 3)

Overall, soil texture was remarkably similar between vegetation types on sandstone-derived soils (Fig. 3). The only significant ($p < 0.05$) differences at Blinkwater involved very coarse sand, which was lower in the Fynbos than in either Transition or Forest soils (Supplementary material Appendix 1

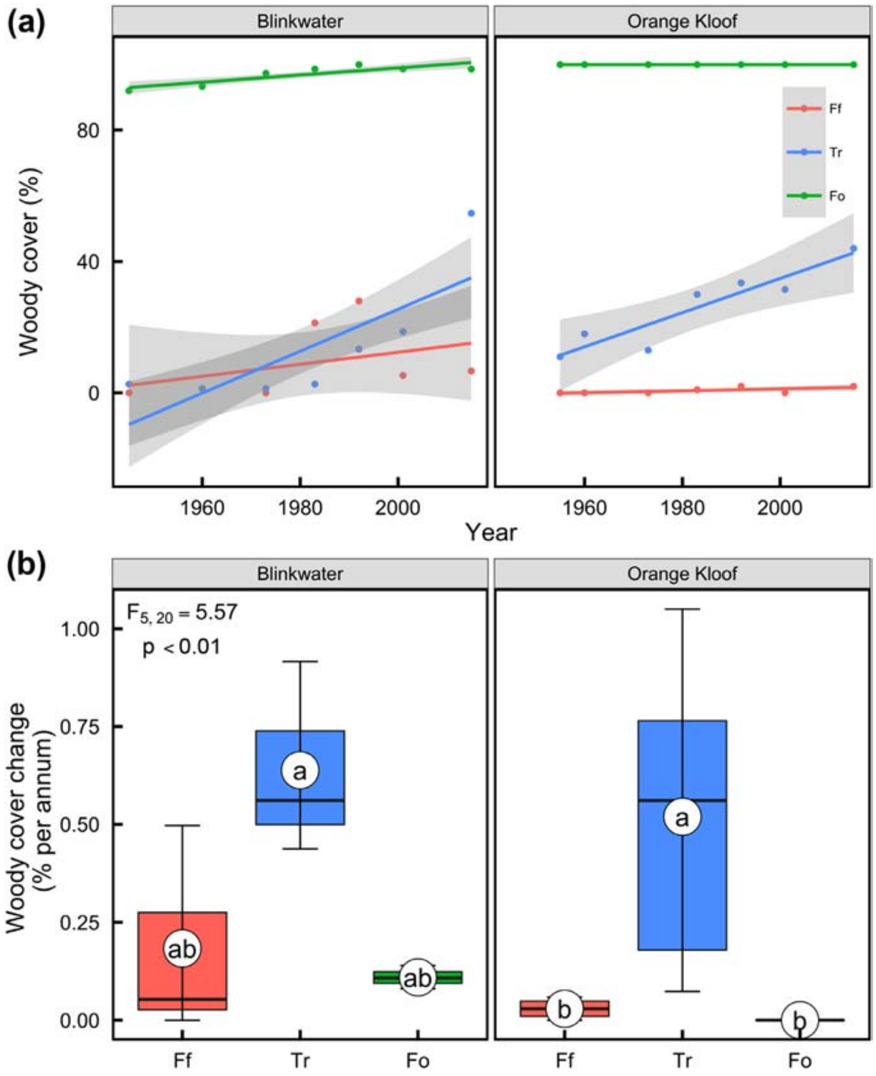

Figure 2. Differences in the change in woody cover with time between vegetation type (Fynbos = Ff, Transition = Tr, Forest = Fo) at both study sites. Lines represent linear fits and the grey bands are the 95% confidence intervals. Linear fits (a) for each individual plot were used to calculate the (b) rates of wood change for both sites and all vegetation types. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range and outliers above/below are shown as points. Circles represent the mean with letters indicating the significant interaction between vegetation types and sites from a one-way ANOVA, for which the F-value and p-value is given.

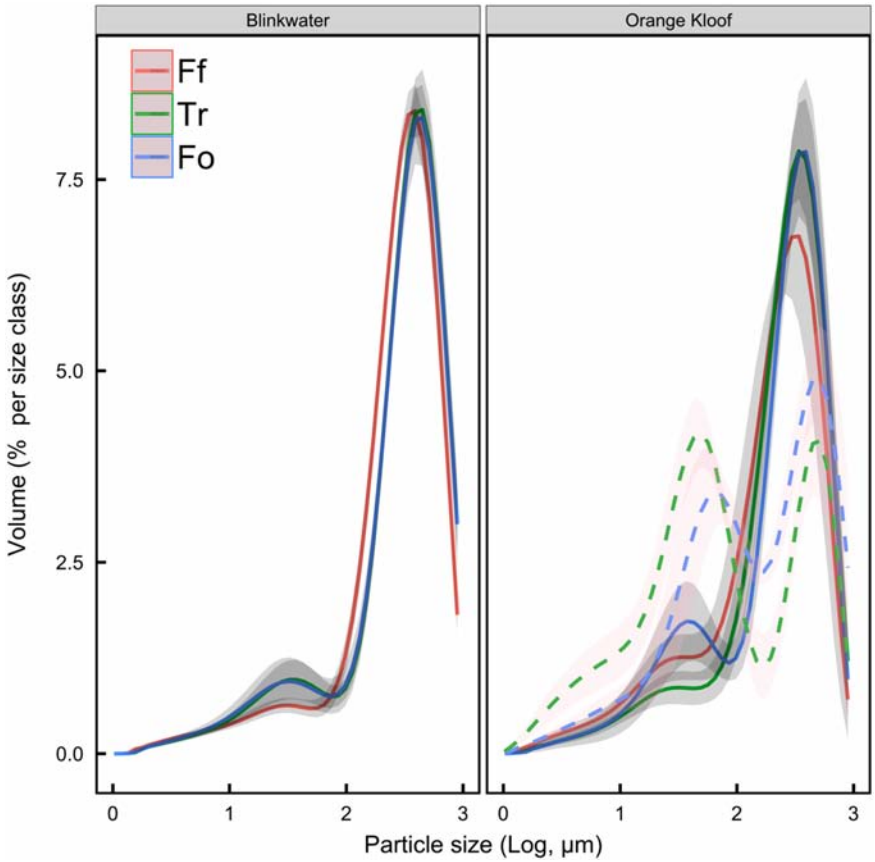

Figure 3. Comparison of the proportion of the soil volume (%) comprising different particle sizes (log scale) between vegetation type (Fynbos = Ff, Transition = Tr, Forest = Fo) at both study sites. Grey ribbons represent the 95% confidence bands. The broken lines with pink ribbons are for the Orange Kloof granitic site (Fig. 1) that was excluded from inclusion in statistical analyses.

Table A2). The texture of soils at Orange Kloof was similar to Blinkwater, but with more very fine sand at Orange Kloof in Transition, less coarse sand in Fynbos and less very coarse sand in all vegetation types. The lack of strong differences in texture indicates that the soils are derived from a common geological parent material. We reported site E at Orange Kloof (Fig. 1) separately from the others because this site had no Fynbos vegetation in the vicinity. Occurring on granite-derived soils, the site was also distinct in texture, having a greater concentration of finer material and correspondingly less coarse particles (Fig. 3).

Soil chemical properties (objectives 3 and 4)

Many plant available nutrient concentrations were considerably higher in granite than in sandstone rocks (Supplementary material Appendix 1 Table A3). As a consequence, we restricted sampling to sandstone-derived soils, apart from site E at Orange Kloof (Fig. 1). Fynbos soils had significantly lower total concentrations of C, P, Ca and Sr than Forest at both sites (Supplementary material Appendix 1 Fig. A3). Only at Orange Kloof were K, Fe and Al higher in Fynbos than in Forest. Generally, Transition soils were intermediate between Fynbos and Forest, except for Orange Kloof, where concentrations of C, P, Ca and Sr in Transition soils were more similar to the Fynbos than Forest soils. Of the properties affecting nutrient availability, pH, total N, P-citric, K, Ca, Mg, and organic matter were all higher in Forest than Fynbos soils at both sites (Fig. 4). Although Transition soils were intermediate between Fynbos and Forest at Blinkwater, Transition soils from Orange Kloof were generally statistically indistinguishable from those of Fynbos (Fig. 4).

To show the relative availability of P-citric and extractable K we expressed them as a proportion of their totals (Supplementary material Appendix 1 Fig. A4). For P a greater proportion of the P was available in Forest soils than in Fynbos. A similar pattern occurred for K at the Orange Kloof. N:P ratios were indistinguishable across vegetation types. Differences between ratios of P and K to Zr and the weathering ratio (Supplementary material Appendix 1 Fig. A4) generally showed higher values in Forest than in Fynbos, indicating greater loss of P and K and greater weathering of Fynbos than of Forest soils. The fact that Zr does not differ between Forest and Fynbos, together with the texture data indicates, that the soils are derived from a common geological parent material. Despite this, the plant available nutrients differed strongly.

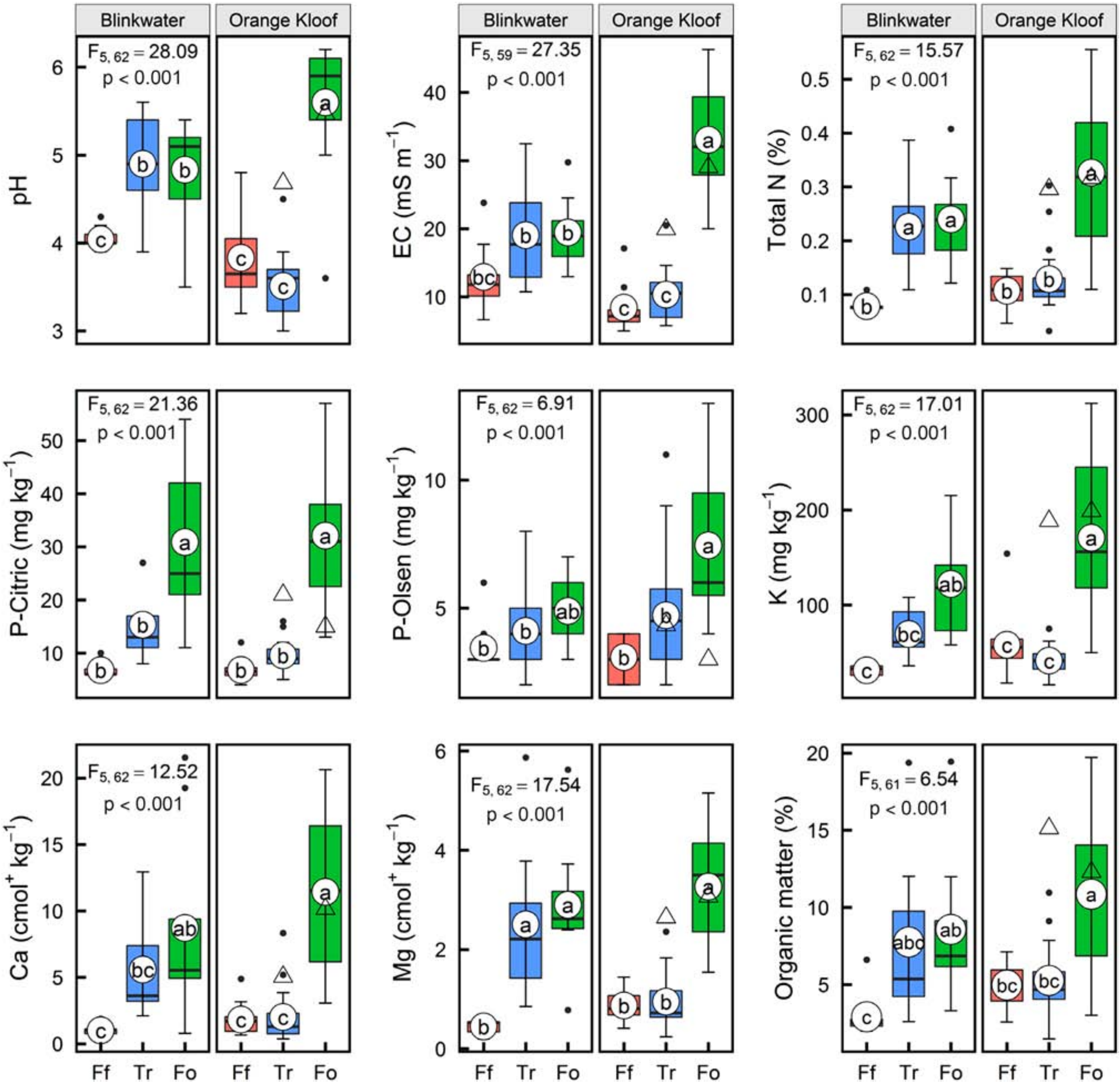

Figure 4. Variation in soil chemical characteristics determined using standard soil analysis protocols to assess plant–available nutrients between vegetation types (Fynbos = Ff, Transition = Tr, Forest = Fo) at both study sites. The measured characteristics include electrical conductivity (EC) and organic matter determined from weight loss on ignition. The boxes and horizontal lines represent the first and third quartiles and the medians, respectively. The whiskers represent 1.5 × the interquartile range and outliers above/below are shown as points. Circles represent the mean with letters indicating the significant interaction between vegetation types and sites from a one-way ANOVA, for which the F-value and p-value is given.

Charcoal (objective 5)

The weights and counts of charcoal in the soils were relatively high in all vegetation types at both sites (Fig. 5). The lack of significant differences between vegetation types probably reflects the high variability of the data due to quantification of charcoal being done by individually picking out fragments. Despite the variability, Orange Kloof had significantly greater concentrations of charcoal in Fynbos and Forest than did Blinkwater. This indicates that fires have occurred ubiquitously through these two areas, and that despite occasional fires in Forest prior to the era of aerial photographs, this has remained Forest (Fig. 1).

Prediction of vegetation based on soil data (objective 6)

Linear discriminant analysis (LDA) was able to clearly differentiate between the three vegetation types at Blinkwater,

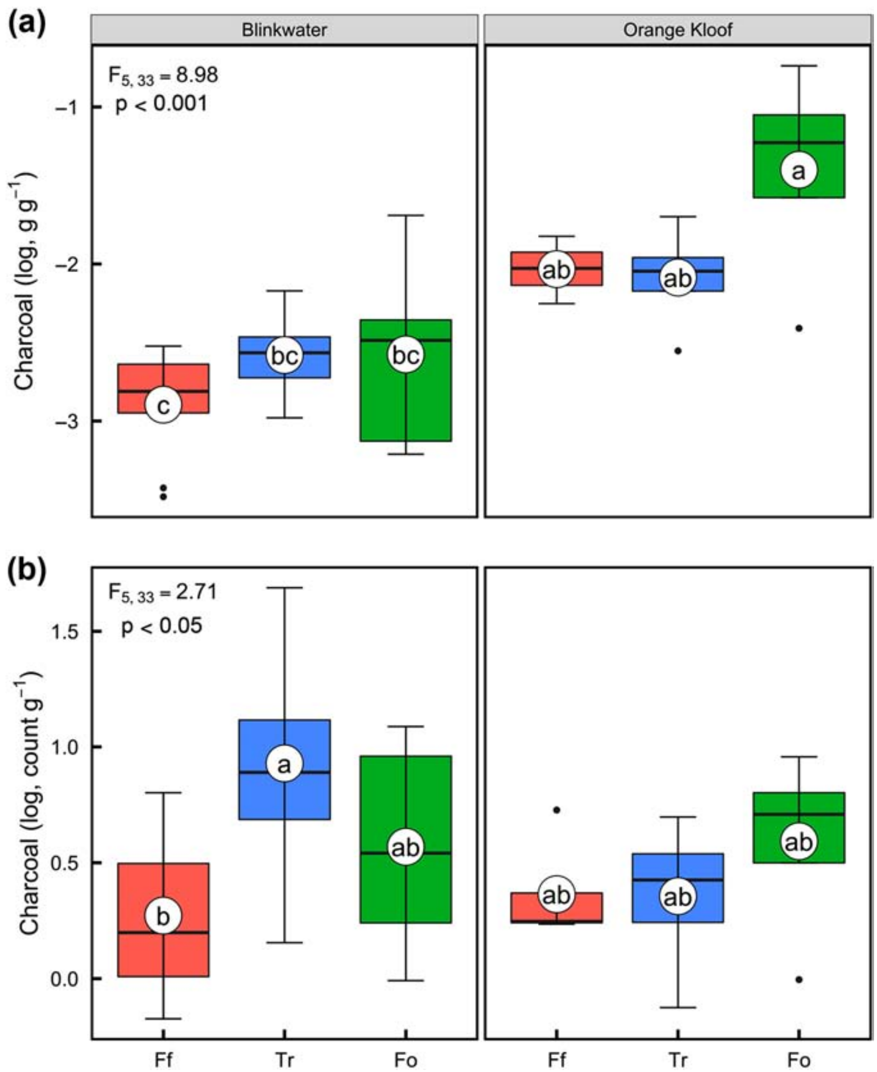

Figure 5. Variation in the weight and number of fragments of charcoal (logged) extracted per weight of soil between vegetation types (Fynbos = Ff, Transition = Tr, Forest = Fo) at both study sites. Other details as in Fig. 2.

based entirely on soil data (Fig. 6). At Orange Kloof, Fynbos and Transition showed considerable overlap, but Forest was still clearly differentiated. LDA, however, failed to separate these vegetation types when based on soil textural data (data not shown). This demonstrates that the vegetation is associated with distinct edaphic chemical properties, but not textural properties.

Discussion

We found no evidence for switches between floristically and structurally distinct Forest and Fynbos as ASS over the decades for which aerial photographs are available. The almost complete turnover in species between Forest and Fynbos illustrates that the structural differences in vegetation are not simply a matter of Fynbos 'etiolation' into Forest (Torello-Raventos et al. 2013, Veenendaal et al. 2015). The existence of Transition vegetation is consistent with the common occurrence of forest-savanna transition zones globally (Veenendaal et al. 2015), although there are examples at our study sites and elsewhere in the region where the Transition vegetation is either very small (i.e. < 10 m wide) or non-existent. The increased woody cover in Transition vegetation over time could be interpreted as providing support for the capacity of this Transition zone to exist as ASS (Coetsee et al. 2015). The fact that canopy closure is incomplete and that soil and vegetation properties are intermediate suggests, however, that this Transition vegetation may rather be an unstable seral stage (Phillips 1931).

The existence of charcoal in all vegetation types indicates exposure to fire. While fire return intervals in Fynbos are variable (7–55 yr, but mostly 10–20 yr) but relatively regular, fires do also occasionally transgress into Forest under high fire danger conditions (Kraaij et al. 2014). Furthermore, clearing and burning of forest vegetation is known to have taken

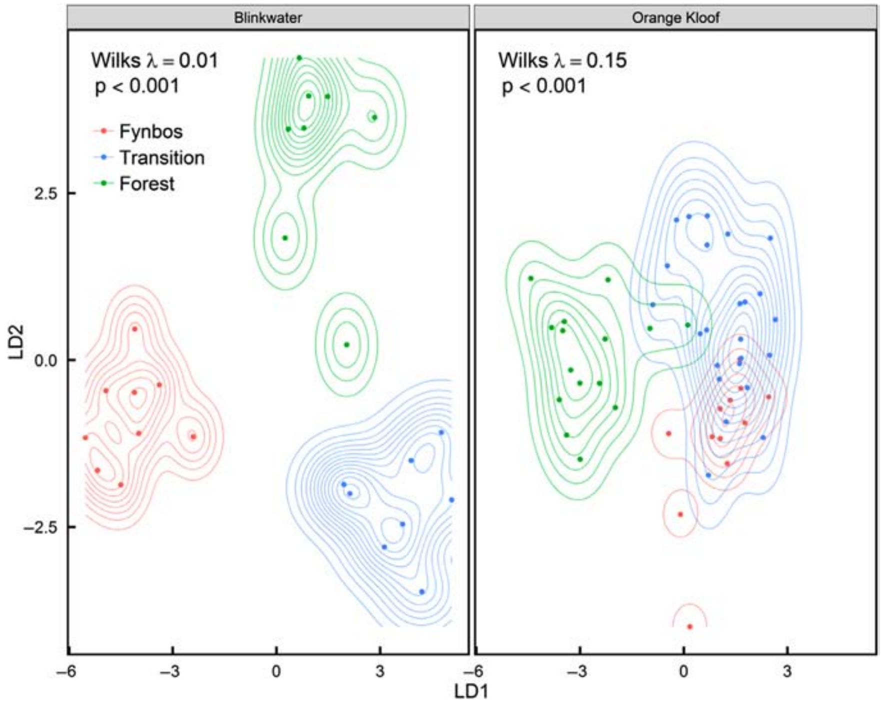

Figure 6. Linear discriminant analysis of the vegetation types at both sites using soil variables. For Blinkwater and Orange Kloof LD1 explained 86 and 69%, respectively, of the between-vegetation type explained variance. Results of MANOVA using Wilk's λ are shown. Soil properties determined using standard soil analysis protocols that were not collinear ($R < 0.7$) and were included in the LDA were pH, Ca, Mg, Olsen P, Na, K, Cu, Zn, Mn, total N, organic matter, clay and $\delta^{15}N$.

place in the 19th century (Poulsen and Hoffman 2015). The fact that fires have occurred in the Forests prior to the period covered by aerial photographs indicates that Forest is at least partially resilient to fire (i.e. vegetation recovers), since fire did not elicit a state change, consistent with the hypothesis that Fynbos and Forest are stable states. The fire-, land use-histories (Luger and Moll 1993, Poulsen and Hoffman 2015) and the edaphic circumstances suggest that the changes in Transition vegetation are at least partially the consequence of reestablishment of vegetation, rather than 'de novo' canopy closure.

For Forest and Fynbos to switch states, the climate and edaphic properties should be capable of supporting either vegetation type. The close juxtaposition of Forest and Fynbos plots in our study means that the climate is similar. The plots were also located in similar topographic positions (i.e. no significant difference in elevation, slope or aspect) although there may have been differences in local hydrology at some sites. Forest soils may be deeper than the Fynbos soils, but the sandstone derived soils at Orange Kloof are all generally relatively shallow (< 0.5 m deep; Campbell and Moll 1977, McKenzie et al. 1977, Masson and Moll 1987). Since there was also very little difference in soil texture between the Forest and Fynbos plots, this is consistent with Forest and Fynbos ecosystems representing long-term ASS on the same sandstone-derived geology. Concentrations of the relatively immobile element Zr (Shahid et al. 2013) also did not differ significantly between Forest and Fynbos, although the relatively lower K:Zr and P:Zr ratios likely indicates greater losses of K and P from Fynbos than from Forest soils. Moreover, the higher weathering ratio of Forest than Fynbos soils indicates that mobile elements have been leached (Cramer and Hoffman 2015) from Fynbos soils or lost through repeated pyro-mineralisation (Stock and Lewis 1986). The nutritional strategies of Fynbos that allow them to access scarce and sparingly available nutrients (reviewed by Cramer et al. 2014) may also exacerbate nutrient losses through leaching and fire. Thus, differences in pedogenic feedbacks between open- and closed-canopy vegetation (Wood and Bowman 2012, Staal and Flores 2015, Kitzberger et al. 2016) likely account for the strong nutritional differences between Forest and Fynbos soils, despite the shared geology. Taken together, this supports the hypothesis that edaphic differences are the product of divergent pedogenic pathways between Forest and Fynbos on the same geological substrate.

The Forest-Fynbos nutritional differences were particularly pronounced for pH, total N, total P, K, Ca and Mg. Since the sandstone-geology is shared, these nutritional differences have emerged as a consequence of divergent nutrient cycling in Forest and Fynbos (Hobbie 2015). In the case of Forest, a lack of frequent fires and the accumulation of organic carbon are likely to drive nutrient accumulation, whereas the lower stature open-canopy and fire-prone Fynbos results in nutrient depleted soils. Although the role of fire in dissipating soil nutrients has been questioned (Lloyd and Veenendaal 2016), there is considerable support for fire depleting nutrients in diverse ecosystems (Neary et al. 1999, Wan et al. 2001, Resende et al. 2011, Pellegrini et al. 2014, 2018) including in the CFR where nutrients mineralized by fire are prone to leaching if not taken up (Stock and Lewis 1986). These emergent differences in edaphic characteristics between Forest and Fynbos imply that fire does not merely 'sharpen' pre-existing edaphic discontinuities (Wilson and Agnew 1992), but creates them. These edaphic discontinuities represent a degree of resilience to change that, together with other emergent biotic factors (Kitzberger et al. 2016), supports the idea that these are ASS. We speculate that such large nutrient differences on geologically identical substrates only emerge over time scales of multiple decades to centuries. Therefore, from an edaphic perspective, intact Forest and Fynbos vegetation types are particularly stable alternative biome states, and this is likely accentuated by the fact that Fynbos occurs on some of the most nutrient depauperate soils globally (reviewed by Cramer et al. 2014).

Despite many consistent Forest-Fynbos differences in NDVI and edaphic properties, there is also a degree of variability in those between Orange Kloof and Blinkwater. These differences are probably related to differences in rainfall, proximity to the coast, aspect and land use histories. Despite these site-specific differences there were also extremely consistent differences in some soil nutrients between the sites. There has been considerable focus on scarce soil P as an indicator of Fynbos vegetation (reviewed by Cramer et al. 2014) and that was indeed consistently different between Forest and Fynbos soils at the two sites. However, there were also consistent differences in pH, EC, N, K, Ca and Mg. The turnover between Forest and Fynbos vegetation cannot therefore be associated with any one of these edaphic characteristics in isolation. Thus, soil differences do, at least in some cases, provide a mechanism for explaining bimodalities in tree cover (c.f. Staver et al. 2011).

Transition vegetation has been considered an example of expanding Forest (McKenzie et al. 1977). In our analysis, the Transition vegetation shared more floristic similarities with Fynbos than with Forest, is still far from the closed canopy and occurs on soils that are nutritionally intermediate, although more similar to Fynbos, particularly at Orange Kloof. This may indicate that the Transition vegetation is recovering from disturbance and is transitional in both space and time. We thus suggest that this Transition vegetation zone is a relatively unstable intermediate zone with respect to fire, water and nutrients, in which regime shifts could occur and may therefore exist as a relatively open- or closed-canopy forms. For example, protection from fire may result from the rocky scree southwest of the Transition vegetation at Blinkwater which likely reduces the fire incidence driven by prevailing south-westerly winds. Over prolonged time periods, less frequent exposure to fire than Fynbos coupled with smaller nutrient feedbacks (e.g. due to leaf litter and soil volume explored) than in Forest may explain the intermediate nutrient status of these Transition zones. Although this Transitional vegetation may also reflect recent climate or land management activities, as suggested for forest-savanna transitions (Veenendaal et al. 2015), we suggest that this Transition vegetation, and possibly also some forest-savanna transitional vegetation types, likely remain unstable due to intermediate fire- and edaphic-properties. In the absence of disturbance, however, will Transition vegetation continue to increase in density towards a Forest, or will it persist as Transitional vegetation between Forest and Fynbos? There is little information on the rate at which vegetation can alter soil chemical properties in the Fynbos sufficient to allow Forest closure. Palynological records from a site in the CFR, where the contemporary vegetation consists of a mosaic of Forest, Fynbos and Strandveld, suggest that a shift from Fynbos to Forest takes at least 750 yr (Quick et al. 2018). In Orange Kloof, colonising Forest trees (e.g. *Cassine peragua*, *Olea capensis*) can be observed both on the ground (pers. obs.) and from aerial photographs in Fynbos, but soil modification beneath their canopies has not been compared to uninvaded Fynbos, so there is no clear answer to this question as yet.

Conclusion

Considering the disparate nutritional characteristics of Forest and Fynbos, we suggest these biomes are generally unlikely to switch to an alternate state, unless perturbations persist for periods of multiple decades to centuries and are capable of altering soil properties. In this system, large differences in soil chemistry are commonly caused by the vegetation, and are not intrinsic (i.e. geological). Rates of vegetation change in this nutrient depauperate vegetation are, however, far slower than recorded for tropical grassy ecosystems which can switch to closed forest where fires are suppressed for 30 to 40 yr (Bond et al. 2005, Durigan and Ratter 2016). We conclude that fire patterns are both the cause and, at least partially, the consequence of differences in Forest-Fynbos vegetation structure (c.f. Veenendaal et al. 2015). Transitional areas between Forest and Fynbos with intermediate vegetation and edaphic characteristics, because of either different geologies or resulting from partial protection from fire, may more rapidly switch states, but are unlikely to be stable.

Acknowledgements – We thank the Edward Chirwa and Kervin Prayag for field and technical assistance.
Permit – We are grateful to South African National Parks for permission (CRC/2015/005--2012) to conduct research in the reserve.

References

Beisner, B. E. et al. 2003. Alternative stable states in ecology. – Front. Ecol. Environ. 1: 376–382.
Bond, W. J. et al. 2005. The global distribution of ecosystems in a world without fire. – New Phytol. 165: 525–537.
Campbell, B. M. and Moll, E. J. 1977. The forest communities of Table Mountain, South Africa. – Vegetatio 34: 105–115.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. – Biometrics 43: 783–791.
Chittleborough, D. J. 1991. Indices of weathering for soils and palaeosols formed on silicate rocks. – Aust. J. Earth Sci. 38: 115–120.
Chiu, C. H. et al. 2014. An improved nonparametric lower bound of species richness via a modified Good-Turing frequency formula. – Biometrics 70: 671–682.
Coetsee, C. et al. 2015. Forest and fynbos are alternative states on the same nutrient poor geological substrate. – S. Afr. J. Bot. 101: 57–65.
Cowling, R. M. and Potts, A. J. 2015. Climatic, edaphic and fire regime determinants of biome boundaries in the eastern Cape Floristic Region. – S. Afr. J. Bot. 101: 73–81.
Cramer, M. D. 2010. Phosphate as a limiting resource: introduction. – Plant Soil 334: 1–10.
Cramer, M. D. and Hoffman, M. T. 2015. The consequences of precipitation seasonality for mediterranean-ecosystem vegetation of South Africa. – PLoS One 10: e0144512.
Cramer, M. D. et al. 2014. Plant ecophysiological diversity. – In: Allsopp, N. et al. (eds), Fynbos: ecology, evolution and conservation of a megadiverse region. Oxford Univ. Press, pp. 248–272.
Cramer, M. D. et al. 2018. Data from: Are forest-shrubland mosaics of the Cape Floristic Region an example of alternate stable states? – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.f3h1342>.
Dantas, V. D. L. et al. 2013. Fire drives functional thresholds on the savanna – forest transition. – Ecology 94: 2454–2463.
de Mendiburu, F. 2016. agricolae: statistical procedures for agricultural research. – R package ver. 1.2-4, <https://CRAN.R-project.org/package=agricolae>.
Durigan, G. and Ratter, J. A. 2016. The need for a consistent fire policy for Cerrado conservation. – J. Appl. Ecol. 53: 11–15.
Forsyth, G. G. and van Wilgen, B. W. 2008. The recent fire history of the Table Mountain national park and implications for fire management. – Koedoe 50: 3–9.
Geldenhuys, C. J. 1994. Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa. – J. Biogeogr. 21: 49–62.
Gerlach, R. W. et al. 2002. Gy sampling theory in environmental studies. 1. Assessing soil splitting protocols. – J. Chemom. 16: 321–328.
Hirota, M. et al. 2011. Global resilience of tropical forest and savanna to critical transitions. – Science 334: 232–235.
Hobbie, S. E. 2015. Plant species effects on nutrient cycling: revisiting litter feedbacks. – Trends Ecol. Evol. 30: 357–363.
Jackson, W. D. 1968. Fire, air, water and earth – an elemental ecology of Tasmania. – Proc. Ecol. Soc. Aust. 3: 9–16
Jobbágy, E. G. and Jackson, R. B. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. – Ecol. Appl. 10: 423–436.
Jobbágy, E. G. and Jackson, R. B. 2004. The uplift of soil nutrients by plants: biogeochemical consequences across scales. – Ecology 85: 2380–2389.
Kraaij, T. et al. 2013. Lightning and fire weather in eastern coastal fynbos shrublands: seasonality and long-term trends. – Int. J. Wildl. Fire 22: 288–295.
Kraaij, T. et al. 2014. Drivers, ecology, and management of fire in fynbos. – In: Allsopp, N. et al. (eds), Fynbos: ecology, evolution and conservation of a megadiverse region. Oxford Univ. Press, pp. 47–72.
Kitzberger, T. et al. 2016. Fire–vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. – N. Z. J. Bot. 54: 247–272.
Lewontin, R. C. 1969. The meaning of stability. – Brookhaven Symp. Biol. 22: 13–23.
Lloyd, J. and Veenendaal, E. M. 2016. Are fire mediated feedbacks burning out of control? – Biogeosciences Discuss. doi:10.5194/bg-2015-660.
Luger, A. D. and Moll, E. J. 1993. Fire protection and afromontane forest expansion in cape fynbos. – Biol. Conserv. 64: 51–56.
Manders, P. T. 1990. Fire and other variables as determinants of forest/fynbos boundaries in the Cape Province. – J. Veg. Sci. 1: 483–490.
Manders, P. T. and Richardson, D. M. 1992. Colonization of Cape fynbos communities by forest species. – For. Ecol. Manage. 48: 277–293.
Manders, P. T. et al. 1992. Is fynbos a stage in succession to forest? Analysis of the perceived ecological distinction between two communities. – In: van Wilgen, B. W. et al. (eds), Fire in South African mountain fynbos. Springer, pp. 81–107.
Masson, P. H. and Moll, E. J. 1987. The factors affecting forest colonisation of fynbos in the absence of recurrent fire at Orange Kloof, Cape province, South Africa. – S. Afr. For. J. 143: 5–10.
McKenzie, B. et al. 1977. A phytosociological study of orange Kloof, Table Mountain, South Africa. – Vegetatio 34: 41–53.
Mount, A. B. 1979. Natural regeneration processes in Tasmanian forests. – Search 10: 180–186.
Mucina, L. and Rutherford. M. 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. Pretoria: South African National Biodiversity Inst., 807p.
Neary, D. G. et al. 1999. Fire effects on belowground sustainability: a review and synthesis. – For. Ecol. Manage. 122: 51–71.
Oksanen, J. et al. 2016. Vegan: community ecology package. – R package ver. 2.3-5, <http://CRAN.R-project.org/package=vegan>.
Olsen, S. R. et al. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circ. 939.
Paritsis, J. et al. 2015. Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia. – J. Veg. Sci. 26: 89–101.
Pausas, J. G. 2015. Alternative fire-driven vegetation states. – J. Veg. Sci. 26: 4–6.
Pellegrini, A. F. A. et al. 2014. Fire alters ecosystem carbon and nutrients but not plant nutrient stoichiometry or composition in tropical savanna. – Ecology 96: 1275–1285.
Pellegrini, A. F. A. et al. 2017. Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. – Ecol. Lett. 20: 307–316.
Pellegrini, A. F. A. et al. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. – Nature 553: 194–198.
Phillips, J. F. V. 1931. Forest-succession and ecology in the Knysna region. – Botanical survey of South Africa, Mem. no. 14, Government Printer, Pretoria.
Poulsen, Z. C. and Hoffman, M. T. 2015. Changes in the distribution of indigenous forest in Table Mountain National Park during the 20th century. – S. Afr. J. Bot. 101: 49–56.
Power, S. C. et al. 2017. Environmental correlates of biome-level floristic turnover in South Africa. – J. Biogeogr. 44: 1745–1757.
Quick, L. J. et al. 2018. A high-resolution record of Holocene climate and vegetation dynamics from the southern Cape coast

of South Africa: pollen and microcharcoal evidence from Eilandvlei. – J. Quat. Sci. 33: 487–500.
Resende, J. C. F. et al. 2011. Phosphorus cycling in a small watershed in the Brazilian Cerrado: impacts of frequent burning. – Biogeochemistry 105: 105–118.
Rossi, J.-P. 2011. rich: an R package to analyse species richness. – Diversity 3: 112–120.
Sankaran, M. et al. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. – Global Ecol. Biogeogr. 17: 236–245.
Shahid, M. et al. 2013. Behavior and impact of zirconium in the soil–plant system: plant uptake and phytotoxicity. – In: de Voogt, P. (ed.), Reviews of environmental contamination and toxicology. Springer, pp. 107–127.
Staal, A. and Flores, B. M. 2015. Sharp ecotones spark sharp ideas: comment on 'Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents – How different are co-occurring savanna and forest formations?' by Veenendaal et al. (2015). – Biogeosciences 12: 5563–5566.
Staver, A. C. et al. 2011. The global extent and determinants of savanna and forest as alternative biome states. – Science 334: 230–232.
Stock, W. D. and Lewis, O. A. M. 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African Coastal Fynbos Ecosystem. – J. Ecol. 74: 317–328.
Torello-Raventos, M. et al. 2013. On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. – Plant Ecol. Divers. 6: 101–137.
Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. – Remote Sens. Environ. 8: 127–150.
van Daalen, J. C. 1981. The dynamics of the indigenous forest-fynbos ecotone in the southern Cape. – S. Afr. For. J. 119: 14–23.
van Wilgen, A. B. W. et al. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. – J. Ecol. 78: 210–222.
Veenendaal, E. M. et al. 2015. Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents – How different are co-occurring savanna and forest formations? – Biogeosciences 12: 2927–2951.
Venables, W. N. and Ripley, B. D. 2002. Modern Applied Statistics with S. 4th ed. – Springer, NY.
Wan, S. et al. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems. – Ecol. Appl. 11: 1349–1365.
Warman, L. and Moles, A. T. 2009. Alternative stable states in Australia's wet tropics: a theoretical framework for the field data and a field-case for the theory. – Landscape Ecol. 24: 1–13.
Williams, S. J et al. 2006. Surficial sediment character of the Louisiana offshore Continental Shelf region: a GIS Compilation. – U.S. Geological Survey Open-File Report 2006-1195, online at <http://pubs.usgs.gov/of/2006/1195/index.htm>.
Wilson, J. B. and Agnew, A. D. Q. 1992. Positive-feedback switches in plant-communities. – Adv. Ecol. Res. 23: 263–336.
Wood, S. W. and Bowman, D. M. J. S. 2012. Alternative stable states and the role of fire-vegetation-soil feedbacks in the temperate wilderness of southwest Tasmania. – Landscape Ecol. 27: 13–28.

Supplementary material (Appendix ECOG-03860 at <www.ecography.org/appendix/ecog-03860>). Appendix 1.