



Forest and fynbos are alternative states on the same nutrient poor geological substrate



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ABSTRACT

We ask two questions concerning the creation and maintenance of boundaries between forest and fynbos biomes in the southern Cape, South Africa: 1) is the presence of forest vegetation constrained to nutrient-rich soils? and 2) do plant traits (specific leaf area, leaf area, leaf dry matter content, leaf nutrients) reflect underlying soil nutrient status? At seven paired sites where forest and fynbos occur adjacent to each other with identical geology and position in the landscape, we tested whether forest soils had a different nutrient status to that of fynbos soils. At three of these sites we measured a suite of plant traits and tested whether these traits were correlated with soil characteristics. The paired site comparisons found that forest soils had a higher nutrient status and higher soil C:N ratios than the fynbos soils. Nonetheless, when compared across sites many forest soils had a nutrient status that was equivalent or lower than some fynbos soils. In addition, the forest soils at our study sites are still relatively nutrient-poor when compared to those of other temperate ecosystems. Although fynbos vegetation had traits that confer higher nutrient use efficiency than forest, both forest and fynbos species seem to have traits that confer conservative resource strategies (e.g., low leaf N and high leaf dry matter content). We suggest that both fynbos and afrotemperate forest are dominated by communities that are adapted to nutrient-poor conditions, and that the increase in nutrient status observed in forest soils is driven by niche construction.

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1. Introduction

What controls the distribution of plant species has been extensively debated for over a century (Clements, 1916; Gleason, 1926; Wilson and Agnew, 1992; Hubbell, 2001; Keddy, 2007). The uncertainties concerning the role of climate and edaphic factors versus that of disturbance in vegetation distribution (Bond et al., 2003; Beckage et al., 2009; Accatino et al., 2010; Higgins et al., 2010) are primarily responsible for keeping this debate alive. Nutrient-poor soils often lack extensive forest cover and where forest occurs, it is often patchily distributed (Lopes and Cox, 1977; Specht and Moll, 1983; Manders, 1990; de Souza et al., 2007). Conversely, fertile soils are often associated with forests (Lloyd et al., 2008; Goodland and Pollard, 1973; Cole, 1986; Ruggiero et al., 2002; Quesada et al., 2009; Pasquini and Santiago, 2012; Vourlitis et al., 2013; Viani et al., 2014). Forests, however, can alter soils and are found on nutrient-poor soils (Jordan and Herrera, 1981 and sources therein). An example of forests found on nutrient-poor soils is the extensive Holm oak forests (*Quercus ilex*) occupying the Mediterranean during the Neolithic (Delano Smith, 1972). These forests occurred on nutrient-poor limestone soils but extensive harvesting has left them

covered with *garigue* (shrub-like) vegetation (Delano Smith, 1972). Jordan and Herrera (1981) propose that oligotrophic forests are able to match biomass productivity of forests on nutrient-rich soils by employing nutrient-conserving mechanisms. Nutrient-conserving mechanisms include: tight nutrient cycling in a thick root mat often associated with ectomycorrhizae, sclerophyllous leaves with effective nutrient resorption, recovery of nutrients by lichen and algae, and herbivore-deterrence by C-rich secondary compounds.

Wilson and Agnew (1992) proposed several different ecological switches leading to alternative vegetation states that are stable in time or space. Each successive vegetation state makes the environment more suitable for itself and less suitable for another vegetation state resulting in a divergence of vegetation by a process of positive feedbacks. They also suggested that such ecological switches can produce different communities separated by sharp boundaries depending on the type of switch from an initially uniform environment. One type of switch that may give rise to a temporarily stable boundary is a soil-element-mediated switch; temporarily stable because one vegetation type can keep expanding into another (Wilson and Agnew, 1992). Here, a new niche is created such as trees invading an area thereby increasing the soils N, P, and K which in turn favors those species with lower nutrient use efficiencies, and consequently soil fertility is biotically determined. This modification of an environment by organisms has been described as “niche construction” and “ecosystem

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engineering" (Odling-Smee et al., 1996; Laland et al., 1999; Crain and Bertness, 2006). Niche construction by plants goes beyond changes in nutrient cycling, and includes changes in the chemical nature, the temperature, humidity, fertility, acidity and salinity of soils, and patterns of shade (Laland et al., 1999). Niche construction can also result from vegetation's opposition to or tolerance of disturbance.

Woodward et al. (2004) define biomes as areas of vegetation that are characterized by the same life-form (bound to a specific climatic envelope) interacting with various forms of disturbance. The mosaic of biomes present in the southern Cape of South Africa offers an ideal opportunity to explore a number of questions concerning forest and fynbos biomes and their boundaries. What limits the distribution of afro-temperate forest, which occurs patchily in a fynbos (chaparral-like, fire-prone vegetation) matrix, is not that clear. Two lines of thought emerge from the literature; the soils of the southern Cape of South Africa are generally low in certain soil nutrients and the low incidence of closed forests has been hypothesized to be correlated with low soil P (Cowling and Campbell, 1980; Specht and Moll, 1983). An alternative hypothesis is that the distribution of forest is driven by fire patterns in the landscape rather than by soil nutrient availability (Geldenhuys, 1994; Bond, 2010). Afromontane forests in the Cape have become considerably more fragmented since the development of pyrophytic fynbos vegetation in association with increased aridity, which started 6–8 million years ago (McDonald and Daniels, 2012). Elsewhere, 'alternative biome states' of savanna and forest are maintained by fire resistance/tolerance (e.g. Bowman, 2000; Warman and Moles, 2009; Staver et al., 2011; Hirota et al., 2011; Lehmann et al., 2011).

Our study addresses two main questions. Firstly, are soil properties responsible for the distribution limits of a specific biome? Fynbos plants are thought to be particularly well adapted to nutrient poor soils and many fynbos species possess specialized root adaptations such as root clusters and mycorrhizae for enhanced P acquisition (Marschner and Dell, 1994; Smith and Read, 2008; Lambers et al., 2003, 2006). Root clusters are common in species from the Cyperaceae (dauciform), Proteaceae (cluster/proteoid) and Restionaceae (capillaroid) (Lamont, 1982; Lambers et al., 2006). Are fynbos species restricted to areas with nutrient-poor soils where their resource conserving traits are best suited? In contrast, forest soils in this region have been shown to have a higher nutrient content (e.g. K and Ca) than fynbos soils have (Van Daalen, 1981; Coetsee and Wigley, 2013). Can forest grow on low nutrient soils?

Secondly, we ask whether fynbos and forest have traits that reflect nutrient status of soils. Globally, plant traits can be arranged on a main axis of separation according to nutrient capture, usage and release. For example, 'acquisitive type' vs. 'conservative/retentive type' according to Diaz et al. (2004) or the 'leaf economics spectrum' according to Wright et al. (2004). Fynbos species fall mostly into the conservative/retentive end of the spectrum with long-lived sclerophyllous leaves with slow decomposition rates, slow rates of nutrient cycling and high nutrient efficiency with highly specialized root systems (e.g. cluster roots). In contrast to fynbos, do forest species have traits that enhance nutrient uptake and faster cycling?

2. Materials and methods

2.1. Study area

Soil sampling was undertaken at seven paired sites in the Southern Cape, South Africa. We chose sites where forest and fynbos (evergreen, sclerophyllous, fire-adapted heathland and shrubland, see Fig. 1a for distribution of sites in the Cape and Fig. 1b for example of distribution in the landscape) were found to be growing adjacent to each other, less than 50 m apart and at similar topographical positions in the landscape. At Platbos the fynbos site occurred slightly above the forest site but the slope was fairly gradual (<5°).

Mean annual rainfall varies between 500 and 1200 mm for the study area. Mean daily temperatures for February and July are 27.3 °C and 7.3 °C, respectively (Taylor, 1961; Mucina and Rutherford, 2006). The Goukamma (Groenvlei) and Tsitsikamma sites (Covie and Plateau) are situated on old dunes which give rise to very deep undifferentiated sandy soils (Entisols according to the WRB; IUSS Working Group WRB 2006 in Fey, 2010). Kranshoek has sandy shallow surface soils overlying clay-rich subsoil with signs of podzolization (Podzols according to the WRB; IUSS Working Group WRB 2006 in Fey, 2010). See Geldenhuys (1981, 1991) for an extensive environmental description of the area. The sandy topsoil at the Groenkop sites is between 40 and 50 cm deep and overlays poorly-drained subsoil with indications of a fluctuating water level. The underlying rock formation at Platbos is predominantly Table Mountain group quartzite overlaid by calcium rich dune sands several meters thick (McKenzie et al., 1990).

The forests of Groeneweide (Groenkop 1 and 2), Kranshoek and Tsitsikamma fall within the Southern Afrotemperate forest vegetation type (Mucina and Rutherford, 2006). These forests are dominated by *Afrocarpus falcatus* (Thunb.) R.Br. ex Mirb., *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb., *Olea capensis* subsp. *macrocarpa* (CH Wright) I.Verd. and *Pterocelastrus tricuspidatus* Lam. Sond. (Mucina and Rutherford, 2006). The forest at Goukamma (Groenvlei) is Southern Coastal Forest and although the forest type at Platbos has been classified as Southern Coastal Forest (Mucina and Rutherford, 2006), McKenzie et al. (1990) describe it as transitional with floristic attributes of both the Afromontane (i.e. temperate) and Tongaland-Pondoland (i.e. sub-tropical) phytochoria. Important taxa for this vegetation type include *Sideroxylon inerme* L., *Myroxylon aethiopicum* (Thunb.) Loes., and *Celtis africana* Burm.f. Important taxa shared among the fynbos types (see Appendix A for types) include various *Cliffortia* spp., *Erica* spp., *Leucadendron* spp., *Leucospermum* spp., *Metalasia* spp., *Phyllica* spp., and *Protea* spp. (Mucina and Rutherford, 2006). See Coetsee and Wigley (2013) for further descriptions of the Groeneweide and Tsitsikamma sites.

2.2. Methods

2.2.1. Soil sampling and analyses

We assumed that any modification of the soil by vegetation would be at the surface layers and that the deeper layers would represent the soil's intrinsic geological characteristics (see e.g. Jobbágy and Jackson, 2001; Wigley et al., 2013). Thus, to compare soil properties, we compared nutrients at the surface and at deeper layers in forests versus fynbos. By comparing trends across biome boundaries at seven different sites, general versus local trends in soil modification could be evaluated.

One soil pit per site (1 × 0.5 m × 1 m in depth) was dug to ascertain depths of soil horizons and bulk densities. Five randomly distributed repeats were taken with a soil auger in each biome pair according to the methods described by Wigley et al. (2013). Soil samples were collected at four depths; 0–10 cm, 10–20 cm, and depending on soil depth at 40–50 cm or 90–100 cm. After collection, soils were sieved through a 2 mm sieve to remove organic material and roots then air-dried for several days.

All of the soil samples were analyzed for organic carbon (C), total soil N, extractable phosphorus (P), calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K), as well as pH and soil texture. All analyses, except N, were performed at the Elsenburg Laboratory, Institute for Plant Production, Stellenbosch, South Africa. Soil C was analyzed by a rapid dichromate oxidation method using the Walkley–Black procedure (Walkley, 1947). Repeatedly run samples analyzed for C had a standard deviation of 0.03%, coefficient of variation (CV) of 0.07. Extractable P, Ca, Mg, Na and K were extracted with 1% citric acid and analyzed by using a Thermo ICP iCAP 6000 Series Spectrometer (ThermoFisher Scientific, Surrey, UK). Soil pH was determined in KCl (McLean, 1982). Repeatedly

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