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Determinants of the Fynbos/Succulent Karoo biome boundary: Insights from a reciprocal transplant experiment

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ABSTRACT

Boundaries between Fynbos and Succulent Karoo vegetation in the Greater Cape Floristic Region are frequently characterised by sharp transitions from sandy, dystrophic to loamy, mesotrophic soils, together with a more gradual climate transition from cooler, wetter conditions typical of Fynbos at higher elevations to warmer, drier conditions at lower elevations typical of Succulent Karoo. There is very high species turnover across these boundaries, providing an opportunity to disentangle the relative roles of climate and soil type in determining the biome boundary. A fully reciprocal transplant approach was employed here to investigate this question, using three species from each biome occurring naturally in close proximity at Jonaskop, Western Cape. Greenhouse-germinated and established seedlings of all species were planted into both sandy, dystrophic and loamy, mesotrophic soils typical of each biome at four sites along an elevational transect (elevations 545 m, 744 m, 953 m, 1303 m) at Jonaskop, and their growth and survivorship monitored for 7 months.

At least one site on the elevation gradient represented annual climate rainfall and temperature conditions during the experimental period typical of the range edge for each of the selected species, this typically being the lowest elevation site (warm × dry) for Fynbos species (*Protea humiflora*, *P. magnifica* and *P. amplexicaulis*), and the highest elevation site (cool × wet) for Succulent Karoo species (*Ruschia lineolata*, *Drosanthemum speciosum* and *Pteronia incana*). Fynbos species showed significant adverse responses to loamy mesotrophic soil, with highly significant reductions in growth and high and rapid rates of mortality relative to their native soil. Fynbos species showed somewhat reduced growth and survival at the lowest elevation when grown in native soils, but demonstrated significant interaction between soil type and elevation with much lower growth and survival at the lowest elevation on the loamy soils. Surprisingly, all the Fynbos species showed reductions in growth and survival at the highest elevation, with significant reductions in two of the three species. Succulent Karoo species, by contrast, showed very few significant performance differences between soil types and few significant soil × elevation interactive effects, but did show significant growth and survival responses to elevation, with high growth and survival at mid-level elevations, far higher than their natural extent at the site.

These results suggest that the selected Succulent Karoo species are neither edaphically nor climatically constrained from establishing and growing in sandy dystrophic soils and cool climates typical of the Fynbos vegetation along this elevation gradient, but that Fynbos species are strongly limited both edaphically and climatically from growing under conditions typical of the Succulent Karoo. We propose that Succulent Karoo elements may be excluded competitively or through disturbance from colonising sandy dystrophic soils at higher elevations in Fynbos vegetation, with fire regime most likely responsible for maintaining the sharply delineated boundaries between these biomes. This is because fire would strongly exclude non-fire adapted Succulent Karoo species at and above the biome boundary, while loamy soils and climate together would strongly exclude Fynbos species from the heavier soils of the Succulent Karoo. The relative climate and soil affinities of these biomes, accentuated by the role of fire, could therefore provide a coherent explanation for biome boundaries in the Greater Cape Floristic Region. We note however that the limited species selection in this study precludes a conclusive general result, and that several interesting questions remain about soil, climate and disturbance determinants across this biome boundary.

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1. Introduction

Both Fynbos and Succulent Karoo Biomes are renowned for their exceptional plant species diversity (Goldblatt, 1997; Cowling et al., 1999). However, apart from sharing similarities in climate seasonality and the virtual absence of C_4 grasses, these biomes are distinct in most other biophysical, ecological and phylogeographic respects (Mucina et al., 2006; Rebelo et al., 2006). The boundary between these biomes, most often characterised by a discontinuous transition from sandy, dystrophic to loamy, mesotrophic soils, and a more continuous climate transition from cooler wetter to warmer drier conditions, is therefore biologically and ecologically interesting. A large amount of literature exists on the determinants of southern African biomes, as well as on the boundaries of the Fynbos Biome in particular (Cowling and Holmes, 1992; Rutherford and Westfall, 1994; Rutherford, 1997; Lechmere-Oertel and Cowling, 2001; Bond et al., 2003). The observed high species turnover across Fynbos-Succulent Karoo boundaries has variously been ascribed to temperature and rainfall variation, associated with aspect and elevation, as well as different soil conditions (Lechmere-Oertel and Cowling, 2001), and the result of differences in fire regime (Oliver et al., 1983; Cowling and Holmes, 1992; Goldblatt, 1997). Geology and soil type have widely been invoked as determinants of the biome boundary (Cowling and Holmes, 1992; Cowling et al., 1997; Milton et al., 1997; Lechmere-Oertel and Cowling, 2001). However, the factors that determine this boundary have rarely been explored using field reciprocal transplant experiments.

Fynbos and Succulent Karoo biomes make up the majority of the Greater Cape Floristic Region (Bergh et al., 2014) which is characterised bioclimatically by winter rainfall and summer drought, except at high elevations where summer precipitation may match that received in winter (Agenbag et al., 2008), and towards its eastern reaches. The Succulent Karoo is associated with drier and warmer conditions, and is found on plains and lower slopes with annual rainfall between 20 and 300 mm and summer temperatures reaching up to 44 °C during summer, while Fynbos is found on sandy lowland coastal plains as well as mountains, but not in areas where annual rainfall is below 200 mm, and less comonly on shale-derived loamy mesotrophic substrates (Low and Rebelo, 1996; Mucina et al., 2006; Rebelo et al., 2006). Shale derived loamy mesotrophic soils have distinct soil water holding and release characteristics from sand derived soils more typical of Fynbos, potentially providing an explanation for the lack of success of fynbos elements on shales. Indeed, at higher elevations – with cooler air temperature and higher rainfall – distinct fynbos vegetation types can be found on heavier soils typical of shale bands (Mucina and Rutherford, 2006), suggesting that high enough rainfall could overcome the water limitations imposed by shale soils on fynbos elements under drier conditions.

Apart from the water relations differences between these soil types due to the effects of higher clay content, soil differences could also be responsible for nutrient limitations and/or toxicity effects. However, this seems to be less likely as a potential biome boundary determinant, as the Cape Floristic Region is characterized by a diversity of geological formations and soil types (Bradshaw and Cowling, 2014), and Fynbos is found on a variety of soil types, ranging from derivatives of ancient, highly leached sandstone formations in the mountains, to moderately fertile finer-grained soils derived from shales and granite (mostly on the lowlands) and complex sequences of nutrient poor acidic and alkaline sands of Aeolian and marine origin along the coast (Cowling et al., 1997). Most of the underlying geological formations of the Fynbos Biome extend beyond the biome borders (Partridge, 1997), and adjacent biomes share many of the sandy soil types. Therefore, at the biome level, underlying geology seems to have an inconsistent level of importance in delimiting biome boundaries, possibly due to interactions with climate.

The role of soil type *per se* has been explored experimentally at both biome and community levels. In a controlled greenhouse experiment specifically concerned with the Fynbos-Succulent Karoo boundary, Lechmere-Oertel and Cowling (2001) found that a combination of soil type and moisture levels controlled seedling growth and survival. Fynbos seedlings survived on sandstone as well as shale derived soils under mesic conditions, but died rapidly under xeric conditions in both soil types. Succulent Karoo seedlings survived well in both soil types and under both moisture regimes. Euston-Brown (1995) performed one of the very few reciprocal transplants of this type, encompassing eight vegetation types in the Kouga Mountains, Eastern Cape, and found that Fynbos plants survived well at all sites except in the most arid areas, which were associated with shale derived soils. Succulents grew well at all sites except at the highest elevations.

At the level of plant community, many species assemblages are associated with specific soil types (Low and Rebelo, 1996). For example Richards et al. (1997a) found that soil type, rather than competition, explains replacement of Proteaceae species pairs on a sandstone-limestone edaphic gradient, and further showed how community boundaries are associated with variations in soil nutrient levels (Richards et al., 1997b). Mustart and Cowling (1993a), however, in a reciprocal transplant experiment found that soil type did not limit the germination and growth of seedlings and did not explain the distribution of edaphically restricted Proteaceae species on the Agulhas Plain. Latimer (2006) and Latimer et al. (2009) used reciprocal transplant experiments to show that species turnover across large scale climatic gradients in high-elevation white Proteas was determined less by abiotic and competitive effects, but more by dispersal limitation, and that these species both grew well and were projected to maintain positive population growth rates well outside of the bioclimatic limits suggested by their observed geographic ranges.

Apart from climate, geology and soil, disturbance is considered one of the main sculptors of vegetation patterns in southern Africa (Bond, 1997; Bond et al., 2003). In the Fynbos Biome, fire drives ecological processes such as regeneration, succession and vegetation dynamics, and because tolerance of fire requires adaptive responses in plants (Bond and Van Wilgen, 1996; Keeley et al., 2012), fire would be a critical factor in preventing species from other biomes from colonizing Fynbos. Succulent Karoo species are intolerant of fire, but it has been found that in the absence of fire, thicket and succulents have successfully invaded Fynbos (Cowling and Pierce, 1988). Wildfire is also thought to play a critical role in differentiating the biomes, but is likely an emergent property of vegetation type, due both to fuel accumulation and flammability traits. Wildfire is generally limited to Fynbos vegetation, and rarely burns into Succulent Karoo (though Renosterveld vegetation does burn on heavier soils under arid conditions, and the dominant renosterbos, *Elytropappus rhinocerotis*, has long been recognized as favouring the spread of fire (Levyns, 1929a,b,c, 1935, 1956)). A few exceptions of wildfire occurring in the Succulent Karoo have been recorded, but had devastating impacts especially on succulent components of the flora (Forrester, 1988; Rahlao et al., 2009).

Climate, soil type and wildfire need to be disentangled to develop a full and general explanatory understanding of the determinants of boundaries between Fynbos and Succulent Karoo. This would be especially useful to project how this boundary might respond, if at all, to climate change, both in the past and into the future. Bioclimatic modeling of biome distributions under future climate scenarios indicate a contraction of Fynbos and a southward shift of Succulent Karoo into areas currently occupied by Fynbos (Hannah et al., 2002; Midgley et al., 2003). These models however consider only climatic limitations to biome distributions, and ignore other biotic and abiotic factors involved in shaping biome boundaries.

The boundary between the Fynbos and Succulent Karoo biomes, with high rates of species and growth form turnover, occurs over short distances (sometimes as little as a few tens to hundreds of metres). This is especially evident on dry, equator-facing slopes of the Cape Floristic Region (Cowling and Holmes, 1992). This natural situation lends itself to a reciprocal transplant experimental approach to