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Associations between plant growth forms and surface rockiness explain plant diversity patterns across an Afro-montane grassland landscape

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ABSTRACT

A complex set of variables may explain biodiversity patterns both locally and regionally. Evidence exists that greater plant species richness can be associated with localised areas containing a greater percentage of rock exposure. Here, we test whether this is the case at the landscape scale, using semi-natural Afro-montane grassland in southern Africa. Plants were inventoried, percentage rock exposure calculated, and each site graded according to three levels of rockiness. Soil samples from each site were then analysed for particle size, as well as for levels of carbon, nitrogen and available phosphorus. Species richness and the compositional similarity of assemblages were compared between the three rockiness categories. Plants were then categorised into their respective growth forms, and species richness within each group compared across the rockiness categories. Greater species richness in rockier landscapes was driven by two particular plant growth forms, geophytes and perennial grasses. However, no overall plant assemblage compositional changes were recorded between the various rockiness categories, indicating that very few species are not associated with rocky areas in some way in this landscape. This shows that plant species within certain functional groups are naturally more responsive to certain abiotic ecosystem elements than others across a landscape. In turn, this highlights the significance of high habitat heterogeneity in structuring plant communities. Consequently, when an abiotic feature such as rockiness is observed across a landscape, it provides a surrogate for the spatial heterogeneity of certain plant communities.

1. Introduction

Distribution patterns of species are typically influenced by ecophysiological constraints, environmental disturbances such as droughts or habitat fragmentation, and resources such as nutrients (reviewed in Guisan and Thuiller, 2005). In turn, abiotic factors often have a great influence on community dynamics, including species abundance, as opposed to compensatory interactions such as competition (Houlahan et al., 2007). However, competitive exclusion within communities is a major principle for explaining why some areas naturally display higher species richness than others (Palmer, 1994). The competitive exclusion principle suggests that greater competition within a community would mostly lead to lower species richness. Theoretically then, at a smaller spatial scale, areas of higher species richness could indicate higher habitat heterogeneity, as variable microsite conditions often exhibit more complex resource differentiation and specialisation (Auerbach and Shmida, 1987). For example, there is an important positive relationship between plant species richness and variable environmental conditions at the local or meso-scale (tens to hundreds of metres) (Bruun et al., 2003; Dufour et al., 2006). This highlights the use of environmental predictors at a landscape scale to describe biodiversity patterns, and could be of value in conservation evaluation.

Greater percentage surface rockiness in a landscape (i.e. exposed rock surface rather than soil-covered rock) is associated with higher plant species richness in Afro-montane grasslands (Crous et al., 2013). Furthermore, higher abundance of geophytic orchids is also linked to more rocky patches within grassland landscapes (Landi et al., 2009). In essence, there seems to be a link between surface rock exposure, specialised plant growth forms, and plant biodiversity patterns across the landscape. However, the reason why more plant species are specifically associated with high levels of rockiness still remains to be explained.

A review by Poesen and Lavee (1994) emphasised how rocky soils could 1) significantly influence soil hydrological processes through an intricate combination of reducing soil moisture availability in some instances, whereas allowing for better water infiltration in others (see also Ingelmo et al., 1994); 2) affect the soil temperature, which may influence plant physiological processes; 3) positively and negatively regulate soil erosion as caused by wind; and 4) significantly influence the potential of a soil to produce a certain level of plant biomass through affecting soil volumes and potential plant rooting depths. This diverse and complex array of effects of surface rocks on soils, and consequently plants, can even further be complicated by the effect of subsurface weathering patterns of rocks (Rutherford,

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1983). Rocks have also been shown as important 'abiotic nurses', providing vital shade for certain species in their early growth phases (Peters et al., 2008). In addition, rocks in a landscape also provide fire protection to plants (Kirkpatrick et al., 1988). As such, the influence of rock exposure on vegetation patterns is complex. Nonetheless, habitats with high surface rockiness can be seen as providing greater structural complexity of the landscape (greater microhabitat heterogeneity), which will ultimately influence floral composition in some way (Lambrinos et al., 2006).

In addition, soil nutrient levels of elements such as carbon and nitrogen explain variable levels of species richness among grassland vegetation, in addition to rockiness (Maccherini, 2006), indicating a probable link between rockiness and nutrients (see also Poesen and Lavee, 1994). Available phosphorus in soils also influences the proportion of plant growth forms (Dorrough and Scroggie, 2008). There is also evidence that patterns in grassland species richness could be explained by differences in soil types (a measure of habitat heterogeneity) (Bruun, 2000).

In view of insufficient information explaining why higher plant species richness is associated with rockiness, we investigate here the reasons for this in an Afro-montane grassland landscape, specifically at the meso-scale. We explore whether species distribution variation at this scale is an artefact of the inherent, indirect, ecological association of different specialist plant growth forms to heterogeneous microsite conditions, as generated by variable levels of rockiness (sensu Auerbach and Shmida, 1987; Poesen and Lavee, 1994; Thomson et al., 1996; Lambrinos et al., 2006). We also determine whether there exist edaphic correlates of rockier patches at the meso-scale, such as soil texture (which links to soil hydraulic characteristics) and soil nutrients, and whether such relationships can help explain the rockiness-plant diversity interaction. By addressing these issues, we can view the landscape not simply as a random assortment of species, but as a way of understanding the role of certain functional groups and their abiotic correlates in structuring plant biodiversity patterns (Purvis and Hector, 2000).

2. Methods

2.1. Study area

The study was undertaken within the 16 000 ha Merensky Forestry estate at Weza, near Kokstad, KwaZulu-Natal, South Africa (S 30°34.855, E 029°44.726). A map of the area is given in Crous et al. (2013). Around 4200 ha semi-natural open spaces are on the estate, the remainder being commercial plantation forestry. These remnants are classified mostly in the endangered Midlands Mistbelt Grassland vegetation type (Mucina and Rutherford, 2006). The endangered status of this vegetation type is driven mainly by the threat of landscape transformation by forestry plantations in the area. These grasslands are dominated by the grass *Themeda triandra* Forssk. All selected sites were classified as semi-natural, as all were annually burned by forestry management for >6 decades. This fire frequency produces dense productive grasslands (Tainton and Mentis, 1984), which would naturally be induced by between one and ten ground lightning flashes km^{-2} yr^{-1} (Edwards, 1984). Moreover, grazing is minimal within these remnants, and consequently fire is the main 'herbivore' in this landscape (Bond and Keeley, 2005). All sampling was done >30 m away from the commercial plantation edge so as to reduce sampling bias due to edge effects (Bieringer and Zulka, 2003; Pryke and Samways, 2012).

The geology is sand- and siltstones from the Ecca group. Weathered resistant dolerite dykes are also present. The maximum height of the mountains is 2200 m a.s.l., above an undulating landscape with minimum elevation of 900 m a.s.l. This is a summer rainfall region, where most precipitation is between November and March. Annual precipitation varies ~1000 mm per annum in the low lying areas, to 1500 mm on the mountain peaks. Mean daily maximum temperature ranges from 17.6 °C in June to 26 °C in January. Mean daily minimum temperature range from 0.1 °C in June to 13.4 °C in January.

2.2. Vegetation sampling

Thirteen vegetation sampling sites were selected within the remnant semi-natural open spaces (sites in map in Crous et al. (2013), with sites 2, 4, 5, 17 and 18 not sampled). Sampling was undertaken between January and February 2011 through a fixed grid sampling design, where samples are taken at fixed intervals along a determined gradient (Whalley and Hardy, 2000). This sampling method is relatively easy to perform in the field, and leads to rapid yet accurate acquisition of data on species distribution and abundance within a study area (Tucker et al., 2005). Within this design, we used point intercept line transects, as this method has been shown to be relevant and insightful for biodiversity studies in these grasslands (Everson and Clarke, 1987; Armstrong et al., 1994).

Field methods were similar to Hayes and Holl (2003), where a measuring tape, 50 m long, was used to record all plant species that intercept a 1.8 mm-diameter pin every 1 m (51 points per transect). For grasslands, a dense vegetation type, transects of 50 m are seen as adequate (Rich et al., 2005). A total of four 50 m transects were placed within each of the thirteen sites, each transect being 15 m away from another, effectively having 204 points per site. Surface rockiness was calculated by adding all rock pin hits (any rocky surface >10 cm in diameter) from the four transects, divided by the total number of pin hits (204), from which a percentage rockiness was then calculated for each site. In addition, a one metre belt, perpendicular to the line transect, was time-searched (15 min) after each transect measurement, as a means for recording a more comprehensive species list that could include short lived annual plants (Hayes and Holl, 2003).

To avoid pseudoreplication, sites of higher rockiness were interspersed with those of intermediate and lower rockiness across the study area, with the minimum distance between similar sites being 400 m. In addition, to make sure we capture the effect of rockiness on flora, sites were chosen to minimise possible elevation effects (exclusion of sites 2, 4, 5, 17 and 18, data not shown here). This ensured a similar plant species composition across the selected 13 sites.

2.3. Soil analysis

At each site, 10 soil samples were taken at ~5–10 cm depth, and then bulked. Bulked samples were air dried until a constant weight was achieved, and passed through a 2 mm sieve. Samples were analysed for soil texture (sand, silt and clay particle sizes) according to the pipette method (Gee and Bauder, 1986). Plant available phosphorus content was determined using the Bray 2 extraction method (Kuo, 1996). Carbon and nitrogen content was calculated by dry combustion using a EuroVector Elemental Analyzer.

2.4. Statistical analysis

All plant species ($n = 210$) were classified into six growth forms: Annual Graminoids (Poaceae and Cyperaceae), Perennial Graminoids (Poaceae and Cyperaceae), Annual Forbs (herbaceous dicots), Perennial Forbs, Geophytes (herbaceous monocots), and Shrubs (woody dicots) (classifications as per Dorrough and Scroggie, 2008). Ferns are also a separate growth form, but as only one fern species was recorded here, we omitted it from the analysis. The soil texture data were classified as percentage sand, silt and clay. Soil nutrients were percentage carbon (C) and nitrogen (N), and available phosphorus (P) ($mg \cdot kg^{-1}$). The 13 sites were then classified in three rockiness categories: <8% rocky ($n = 4$), intermediate rockiness (8–16%) ($n = 5$), and >16% rocky (maximum of 29%) ($n = 4$). To justify this classification,