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Characterising fine-scale variation in plant species richness and endemism across topographically complex, semi-arid landscapes

G. Di Virgilio^{a,b,*}, G.W. Wardell-Johnson^a, T.P. Robinson^c, D. Temple-Smith^d, J. Hesford^e

^a School of Molecular and Life Sciences, Curtin University, GPO Box U1987, Perth, 6845 WA, Australia

^b Climate Change Research Centre, School of Biological Earth and Environmental Sciences, University of New South Wales, Sydney, 2052, Australia

^c School of Earth and Planetary Sciences, Curtin University, GPO Box U1987, Perth, 6845 WA, Australia

^d Mineral Resources Limited, 1 Sleat Rd, Applecross, 6153 WA, Australia

e Tetris Environmental Pty Ltd, PO Box 3103, Myaree, WA 6154, Australia

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ABSTRACT

The banded ironstone formation (BIF) ranges of south-western Australia are prominent landforms in a flat landscape and host a diverse flora. Plant diversity is expected to have a positive relationship with environmental heterogeneity in these ranges. However, there has been a lack of high-resolution data to assess how fine-scale environmental variation structures changes in plant communities across these ranges. We calculated species richness and corrected weighted endemism over 659 quadrats (each 400 m²) and investigated their spatial distribution across BIFs in relation to 1 m resolution variables (microtopographic heterogeneity, solar radiation and topographic wetness) using geographically weighted regression. Microtopographic heterogeneity was most strongly related to richness and endemism, but this association was spatially variable at short distances across BIFs: relationships were negative or weakly positive on north-eastern range sections, whereas positive associations became progressively stronger further south and west on central, western and southern sections. Negative solar radiation-plant associations were reduced in these areas, likely because metre-scale surface variation moderates insolation. Topographic wetness-plant associations were negative on BIFs, but positive on the surrounding plains. The presence of fine-scale, geographically variant heterogeneity-diversity relationships in other locations would be difficult to detect if high-resolution environmental data are not used, with the implication that conservation decision-making may be compromised. Given climatic warming predicted for south-western Australia and other regions globally, a similar approach to that applied here can contribute to conservation by identifying locations likely to act as micro-buffers against warming.

1. Introduction

The link between environmental heterogeneity and plant species diversity is a long-standing fundamental ecological hypothesis (Ricklefs, 1977; Schimper, 1903) and supported by a raft of studies as reviewed by Tews et al. (2004). It assumes that heterogeneous environments have a greater number of niches within them, which are expected to support a greater range of plant species through reduced competition for the same space (Hutchinson, 1959; Rocchini et al., 2010). These environments may also serve as refuges from harsh extremes, promoting persistence and, potentially, speciation (Stein et al., 2014). These theoretical relationships are expected to hold across spatial scales (Ettema and Wardle, 2002; Tamme et al., 2010). However, at finer spatial scales the extent to which environmental

heterogeneity explains plant diversity is less clear, in part because there has been a paucity of high-resolution environmental data with which to explore this link empirically (Moeslund et al., 2013). Greater testing of the effect of environmental heterogeneity on diversity using field data is therefore needed, particularly at metre scales and in a variety of different environments (Dufour et al., 2006).

Airborne LiDAR (light detection and ranging) data can now be acquired at very high resolution (e.g. 1 m) offering extensive coverage (e.g. 1000 km²) of terrain, enabling the link between environmental heterogeneity, in the form of microtopographic heterogeneity, and field data to be explored empirically at the landscape scale. In addition to exploring microtopographic heterogeneity, various other metrics of microtopography (Brubaker et al., 2013) can also be derived from high resolution digital elevation models (DEMs) such as slope, aspect,

E-mail address: giovanni@unsw.edu.au (G. Di Virgilio).

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^{*} Corresponding author. Present address: Climate Change Research Centre, School of Biological Earth and Environmental Sciences, University of New South Wales, Sydney, 2052, Australia.



Fig. 1. (A) The low mountain ranges comprising BIFs in the study region. (B) Many BIFs have a high degree of microtopographic variation. Several plant species grow on surfaces with skeletal soil cover; the examples shown here are (C) *Tetratheca aphylla* subsp. *aphylla* (Elaeocarpaceae) and (D) *Banksia arborea* (Proteaceae).

curvature, topographic wetness and solar radiation. For example, given that moisture is vital for plant function, and the variety of adaptations to moisture stress (e.g. Chaves et al., 2016; Poot and Lambers, 2008), any fine-scale variation in surface relief and aspect that moderates incident solar radiation could cause evapotranspiration variability at metre scales (Bennie et al., 2008). Such microhabitats may be important in plant establishment and survival, particularly in semi-arid environments where surfaces can experience intense insolation and rapid moisture loss.

The banded ironstone formations (BIFs) of semi-arid, south-western Australia are island-like outcrops that constitute a highly suitable system to study the impacts of environmental heterogeneity on species diversity (Fig. 1A). They comprise a matrix of fractured rock surfaces, fissures and depressions (Fig. 1B–Mucina and Wardell-Johnson, 2011) and host a diverse flora (Hopper and Gioia, 2004). Many plant species are endemic to individual BIF ranges (Fig. 1C) or are 'BIF specialists' (Fig. 1D) in this region (Gibson et al., 2012).

Plant species composition varies between adjacent BIF ranges within relatively short distances in this area, i.e. 25–60 km (Butcher et al., 2007; Gibson et al., 2010). Hence, these patterns cannot be attributed to mesoscale climatic gradients, or to geology. While floristic patterns can be partly attributed to topographic variation (Gibson et al., 2010), data resolution has not been sufficient to analyse vegetation patterns in relation to environmental heterogeneity across an entire BIF range empirically. Understanding the potential for environmental heterogeneity to provide buffering from projected climatic warming (Delworth and Zeng, 2014) may inform plant conservation strategies in the region.

We hypothesise that environmental heterogeneity of BIFs is likely to be a key factor influencing plant establishment and hence patterns of plant species diversity and endemism. Moreover, given the complex variation of BIF surfaces, the relationship between environmental heterogeneity and patterns of plant biodiversity may vary at short distances across hillsides, i.e. at the scale of proximate microhabitats. We have three aims: 1) identify centres of high plant species richness and endemism on BIF ranges and the surrounding landscape; 2) identify the microtopographic correlates of species richness and endemism; and 3) determine the role of environmental heterogeneity in explaining patterns of plant species diversity.

2. Material and methods

2.1. Study area

The study area is adjacent to the Southwest Australian Floristic Region (SWAFR; Hopper and Gioia, 2004) and is comprised of the entire Helena and Aurora Range (HAR), Mt. Jackson Range, neighbouring, small rock formations and surrounding plains. The areas studied are delineated in red and blue (Fig. 2) and have a total area of 1593 km^2 . The 52 km^2 HAR is the largest range in this area and consists of Precambrian BIF and talus slopes surrounded by outwash and sand plains (Hocking et al., 2007). It comprises a range of low mountains, with the highest peak 702 m above sea level (ASL), approximately 200 m above the surrounding plains. Mt. Jackson (613 m ASL) is comprised of similar

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