CrossMark

Vegetation – environment relationships of the Hamersley Ranges, a mountainous desert of north-west Australia

Eddie J. B. van Etten · John E. D. Fox

Abstract Understanding environment-vegetation relationships provides important ecological insights, and here we examined such relationships for the Hamersley Ranges of North West Australia. We were particularly interested to see if such relationships were similar to those of other mountainous deserts. We used direct gradient analyses of floristic and environmental variables (constrained ordination), supplemented by identification of environmental differences between plant communities, assessment of environment-vegetation associations and partitioning of the floristic variance between environmental, climatic and spatial variables. Most communities could be differentiated from others according to environmental variables, with slope, surface stone cover, topsoil phosphorus and pH particularly good at differentiating between plant communities. There was strong association between communities and classes of landform and/or geological substrate. Gradient analysis demonstrated the primary floristic gradient was linked to a complex of several topographic, edaphic and geomorphic variables. This was interpreted as floristic change along broad toposequences from mountain/ridge tops to valley floors over which gradients in key environmental variables occur. Gradient analyses of other mountainous deserts have reported similar findings. A key distinction in the complex gradient identified for the Hamersley Ranges is the inclusion of topsoil phosphorus (rather than nitrogen) and time since last fire. The second most important floristic gradient was linked to soil pH and conductivity, which reflects floristic variation due to differences in geological substrate throughout the study area.

Keywords arid · catena · CCA · floristics · gradient analysis · ordination · vegetation

E. J. B. van Etten (✉)
Centre for Ecosystem Management, School of Natural Sciences, Edith Cowan University, 270 Joondalup Drive, Joondalup, Perth 6027, Australia
e-mail: e.van_etten@ecu.edu.au

J. E. D. Fox
Department of Environment and Agriculture, Curtin University of Technology, GPO Box U1987, Perth 6845, Australia
e-mail: johnfox10@bigpond.com

Introduction

Understanding variation in plant species composition across landscapes and the biological and environmental factors which may be driving these patterns is an important objective in ecology and can greatly inform land management and conservation planning. Gradient analysis is a common analytical approach in ecology to link floristic variation to environmental gradients and, although essentially correlative, have proven valuable in the formation of hypotheses as to the main driver(s) of plant species distribution and vegetation patterns within landscapes and regions (Enright et al. 1994; Kent 2012).

⚡ Springer

Modelling of vegetation characteristics against environmental variables has long been routine, but typically only explains a minority of total floristic variability measured across landscape to regional scales (Legendre and Legendre 1998). More recently, exploration of the role of spatial variables to explain floristic variability has been a fruitful area of research and has shown, via variance partitioning, to explain unique variability not explicitly linked to spatially-structured environmental variables (Borcard et al. 2004; Legendre et al. 2005).

Mountainous areas are common to all major desert regions of the world, with the most common type being range-and-basin systems where mountain ranges (formed via tectonic lifting and/or folding) occur between broad valley systems which have been largely infilled with sediment (Mabbutt 1977; Parsons and Abrahams 1994). Mountainous deserts in Australia are relatively limited in extent (covering about 600,000 km^2 or around 12 % of the arid zone; Williams and Calaby 1985) and are generally much lower in relief than in deserts on other continents. Despite this, their geomorphic characteristics are similar to other mountainous deserts (Mabbutt 1977; Cooke et al. 1993).

Gradient analyses of mountainous desert regions are relatively commonplace throughout the world, although not so for Australia. Not surprisingly given their dryness, gradient analyses of mountainous deserts have commonly shown strong relationships between plant species composition and indicators/measures of soil moisture or moisture holding capacity (Silvertown et al. 2015). In such regions, topographic variation results in profound differences in soil moisture status throughout the landscape due to: (1) altitudinal influences on precipitation (e.g. Abd El-Ghani 1996); (2) influence of aspect and slope on the evaporation of soil water (e.g. Parker 1991); and (3) spatial redistribution of rainfall across land surfaces at various scales (Noy-Meir 1985; Ludwig et al. 2005).

Spatial redistribution of rainfall typically has the greatest influence as surface water flow on slopes is typically substantial during and immediately following rainfall events (run-off zones). Subsequent storage of water in the soil of flats and other run-on areas results in far greater moisture availability and standing plant biomass in these areas than would be otherwise predicted from mean rainfall data (Milewski 1981; Stafford Smith and Morton 1990). With the movement of water over the surface, soil particles and nutrients are also redistributed (Noy-Meir 1985; Ludwig and Tongway 1995; Turnbull et al. 2011; Collins et al. 2014). Over the millennia, the erosion and deposition of alluvium has resulted in major differences in soil depth, structure and nutrient status across the landscape and has contributed to the formation of distinctive landforms in such environments. These soil and landform differences further enhance differences in soil moisture status, and, in turn, exacerbate the spatial and floristic distinctiveness of the vegetation (Stafford Smith and Morton 1990; Ludwig et al. 2005; Michaud et al. 2013).

Our main aim in this paper is to elucidate the relationships between vegetation, environmental and spatial variables in a large, central portion of the Hamersley Ranges, a mountainous desert of the Pilbara region of northwest Australia, using gradient analyses and variance partitioning. A secondary aim is to compare the nature of the environment-vegetation relationships of this mountainous desert with those of similar environments on other continents. This is particularly relevant given propositions regarding the ecological distinctiveness of the Australian arid zone (Stafford Smith and Morton 1990; Morton et al. 2011). The key hypothesis being tested here relate directly to the framework and propositions developed by these authors, namely that the principal environmental variables correlated with the major floristic gradients of the Hamersley Ranges will differ from that of mountainous deserts outside of Australia in terms of the importance of phosphorus (reflecting the ancient and well-sorted landscapes of arid Australia; their proposition 3), and fire (a more prevalent and important force in the Australian arid zones than elsewhere; proposition 7).

Material and methods

Study area and sites

The study area is located within the central portion of the Hamersley Ranges, in the Pilbara region, ~ 1,100 km north of Perth, Western Australia. It is 9,600 km^2 in size and centred on 23.0^o S, 118.5^o W (van Etten and Fox 2004). The area is dominated by Karijini National Park and is situated between the towns of Newman, Tom Price and Wittenoom. Most of the study area has either never been grazed by domestic livestock or only until 1969 when much of the area was gazetted as National Park. The Hamersley Ranges are located on the

extensive Hamersley Plateau which lies 600–700 m a.s.l. A series of east to west trending ranges and associated hills and mountains rise above the plateau a further 200 to 600 m. Characteristic landforms of the region are similar to those of other mountainous deserts (Cooke et al. 1993) and include: (1) slopes of hills, ridges and mountains; (2) pediment slopes at the base of hills; (3) bajada slopes (coalesced alluvial fans below pediments); (4) alluvial flats and broad drainage lines; and (5) confined streams and creeklines. The surface geology of the Ranges is dominated by ironstones (dating from the Proterozoic), including banded iron formations on the uplands and various formations of colluvium and alluvium in the broad valley systems. Archaean (basement) granites and gneiss are common in the south of the study area. Volcanic intrusions (mainly dolerite sills) are also found throughout the geological profile, particularly in the softer, dolomitic formations (Thorne and Tyler 1997).

Based on the Köppen climate classification, the study area straddles a transition from 'hot desert' (BWh) to 'hot semi-arid' (Bsh; Beard 1975; Peel et al. 2007). Rainfall is ~ 350 mm per annum on average, and decreases in a southerly direction and inter-annual rainfall variability is very high, reflecting the erratic nature of cyclonic and monsoonal rains during summer and autumn (Beard 1975; van Etten 2009; Rouillard et al. 2015). Temperatures and evaporation rates are very high in summer with the mean January and February maxima close to 40°C. Winter maximum temperatures average around 24°C, with the average winter minimum around 11°C.

Sampling design

Within the study area, we selected 139 study sites using a stratified random approach, with the landscape stratified by major units of geomorphology (geology and landform) and sites then randomly selected within these units. To avoid short-term effects of physical disturbance, newly burnt (< 3 years) areas and those adjacent to roads and tracks were avoided. At each study site we placed a 20 m × 25 m plot (with longest axis across slope) and the cover of each plant species present was estimated. Several site variables, such as slope and soil depth, were measured or estimated within plots (Table 1). We collected the top 5 cm of soil from at least three points within the plot and bulked these for further analyses in the laboratory (Table 1). Soil samples were

first dried at room temperature and then sieved to remove the soil fraction > 2 mm before analyses. Other site environmental variables (such as altitude and distance from nearest ridgeline) were generated by interpolation of a digital elevation model within a GIS and we estimated various climatic variables for each site using BIOCLIM (Busby 1991); altogether 36 explanatory variables were available for analysis (Table 1).

Data analysis

Perennial species cover data from each plot were square-root transformed (to dampen the influence of dominant species). We explicitly excluded annual/ephemeral species from analyses as the area was sampled across several years (1994–2000) and the presence and cover of these species were highly dependent of rainfall received in months before sampling. Firstly, unconstrained ordinations of sites were performed to examine the variability in the dataset and identify floristic gradients using correspondence analysis (CA) within CANOCO (v5.03; ter Braak and Šmilauer 2012). CA assumes unimodal responses to environmental gradients and was justified as gradients were long (in our case greater than 5 *SD* units). Direct gradient analysis was then performed using Canonical Correspondence Analysis (CCA) where axes are constrained to be linear combinations of the environmental variables, with only constrained axes making a significant contribution to total floristic variance used (ter Braak 1986; Šmilauer and Lepš 2014). To avoid problems of multicollinearity among environmental variables, clearly redundant variables were removed and then a forward selection procedure was used to select variables, stopping when variables no longer made a significant contribution to the cumulative variation explained (ter Braak and Šmilauer 2012; Šmilauer and Lepš 2014). Significance was determined by Monte Carlo permutation tests with a conservative probability for inclusion (< 0.005) applied to reduce the possibility of type I errors, or overfitting. CCA was then performed using the reduced number of variables (20 including binary variables). A third CCA was then run with the floristic variation associated with geographic distance removed by using the variables *geographic distance*, *northing* and *easting* as covariables; this is known as a partial constrained ordination (ter Braak 1988). These variables were used as covariables as we were primarily interested in within-landscape patterns rather than the influence of regional-scale variables.

Table 1 Details of environmental variables measured at study sites, including methodology of their measurement or estimation.

Variable	Description	Method	Unit
Stone cover	% of surface covered with stones	Visual estimation within plots	%
Stone size	Average size of surface stones	Visually estimated	cm
Stone roundness	Degree of roundness of surface stones (measure of degree of weathering)	1 – angular/platey; 2 – semi-angular; 3 – semi-rounded; 4 – well rounded	Ordinal
Gravel	% gravel in topsoil	> 2mm fraction as % of total soil mass	%
Slope	Average angle of slope across plot	Clinometer	degrees
Aspect	Horizontal direction of slope converted to degree of 'northness'	Cosine of aspect	Nil
Heat index	Heat stress due to amount of solar radiation received	= cos (aspect −315) * tan (slope) (Enright et al. 1994)	Nil
Outcropping	Degree of outcropping of surface rocks	0 – none; 1 – some; 2 – common	Ordinal
Soil depth	Depth to impenetrable layer such as hardpan	Depth to which narrow and pointed steel road could be hammered into ground	cm
Soil texture	Texture class of non-gravel fraction	Bolus test. 1 – sand; 1.5 – sand/loam; etc.	Ordinal
pH	Topsoil pH	pH electrode in 1:5 soil to water mix	
Soil colour	Degree of topsoil redness	Munsell soil colour chart. 1 – red; 2 – red/brown; 3 – brown	Ordinal
Phosphorus	Available topsoil phosphorus	Colourimetrically following $NaHCO_3$ extraction (Colwell 1963)	ppm
Nitrate	Nitrogen as nitrate in topsoil	Nitrate electrode in 1:5 soil to water mix	ppm
Ammonium	Ammonium nitrogen in topsoil	Colourimetrically following 1M KCl extraction (Rayment and Higginson 1992)	ppm
Potassium	Available potassium in topsoil	AAS following $NaHCO_3$ extraction (Rayment and Higginson 1992)	ppm
Iron	Reactive iron in topsoil	AAS following extraction with Tamm's reagent	ppm
Organic carbon	% organic carbon content of topsoil	Colourimetrically following reaction with acid dichromate (Walkley and Black 1934	%
Conductivity	Electrical conductivity of topsoil	Electrode in 1:5 soil to water mix	dS/m
Fire period	Time since last fire	National Park records or estimated from vegetation and fuel loads	years
Recent rainfall	Rainfall in three months prior to sampling	Monthly rainfall totals from nearby weather stations	mm
Average rain	Long-term average annual rainfall	Interpolation of climate data using BIOCLIM (Busby 1991)	mm
Summer rain	Long-term average summer (Jan-Mar) rainfall	Interpolation of climate data using BIOCLIM (Busby 1991)	mm
Winter rain	Long-term average winter rainfall	Interpolation of climate data using BIOCLIM (Busby 1991)	mm
Temperature	Long-term average temperature	Interpolation of climate data using BIOCLIM (Busby 1991)	°C
Distance	Distance from SW corner of study area	GPS/GIS calculation	m
Easting	Distance eastward from SW corner	GPS/GIS calculation	m
Northing	Distance northward from SW corner	GPS/GIS calculation	m
Ridge distance	Distance (m) from nearest ridge/hill top as a % of distance across ridge –valley floor catena	Calculation using DEM within GIS	% distance
Altitude	Height above sea level	GPS and DEM within GIS	m
Landform	Landform in order of sequence from ridge top to valley floor	1 – upland; 2 – scree slope; 3 – bajada/pediment; 4 – drainage line; 5 – alluvial flat	Ordinal
Calcareous	Present on volcanic and calcareous soils	1 – present; 0 – absent	Binary
Upland	Present on uplands such as ridges and hills	1 – present; 0 – absent	Binary
Pediment	Present on pediments	1 – present; 0 – absent	Binary
Bajada	Present on bajada (alluvial fans)	1 – present; 0 – absent	Binary
Alluvium	Present on alluvial soils on flats	1 – present; 0 – absent	Binary

We used the variation partitioning approach of Legendre et al. (2005) to examine the shared and unique variability, respectively, in species composition explained by three groups of explanatory variables: (1) site environmental (all soil, geomorphic and topographic variables collected or estimated at each site); (2) climate (those derived from BIOCLIM); and (3) spatial. Spatial variables were derived using PCNM (Principle Co-ordinates of Neighbouring Matrices; Borcard et al. 2004). This procedure produces a variable for each spatial scale indicated by plot locations from broad gradients across the study area down to a scale equal to the widest gap between neighbouring plots (Borcard et al. 2004). Variables were selected from all those available using the forward selection process in CCA including only those which made a significant ($P < 0.005$) contribution to the adjusted explained variation; this adjustment compensates for the number of variables in similar fashion to adjusted R^2, although in our case variation is estimated using the χ^2 statistic, as CCA assumes unimodal responses of species to environmental gradients rather than linear (Peres-Neto et al. 2006). Following forward selection, 16 site environmental, 12 spatial and 5 climate variables were used to calculate the adjusted variation. We used the programme 'eulerAPE' to draw area-proportional Venn diagrams to visually represent the adjusted variation explained and the overlaps between the three groups of explanatory variables using ellipses (Micallef and Rodgers 2014).

Classification using flexible UPGMA (Belbin et al. 1992) was performed on the Bray-Curtis dissimilarity matrix to determine plant communities. For each environmental variable, we compared averages (means or medians) for each community using one-way ANOVA for parametric variables, or the Kruskal-Wallis test for non-parametric measures, with post hoc tests (Tukey's b) to distinguish between communities.

For categorical variables such as landform and geology, the distribution of communities was compared using contingency tables and bar graphs showing % frequency of sites belonging to each category for each community. Tests of association were performed on contingency tables using the χ^2 test statistic with expected frequencies based on even spread of sites amongst each landform/geology category. The strength (or degree) of associations was calculated using the Cramér coefficient of association (C).

Results

Gradient analyses

The first two axes of correspondence analysis (CA) explained 12.6 % of the total floristic variation, the first four axes 19.3 % (Table 2) and the first eight just 31.4 %. With the ordination constrained (CCA) by all 36 environmental variables (as per Table 1), 51 % of the overall floristic variation was explained. The first axis of this CCA explained almost 20 % of the species-environment relationship and was strongly correlated with the first axis of CA (Table 2). This axis was linked to a range of variables, the most important being surface stone cover (−ve correlation), presence of alluvial soil (+ve), landform sequence from ridge top to valley floor (+ve) and both vertical and horizontal distance from nearest ridgeline (+ve). Other variables linked to topography (e.g. slope), landform type and soil structure, as well as soil nutrients (namely P and K), were also strongly correlated with this first axis (Table 2). Many species were correlated with this axis; those displaying the highest species scores were highly typical of alluvial lowlands (+ve values) or uplands (−ve values; Table 2). The second axis accounted for about 10 % of the overall species-environment relationship and was strongly associated with pH of the soil, the presence of calcareous/alkaline soils, conductivity and the presence of soil iron. Species strongly associated with either strongly alkaline or acidic soils displayed high species scores with this axis (Table 2). The third axis (explaining 8.8 % of the species-environment relationship) was positively linked to geographic distance, the amount of rain which fell in the four months previous to sampling and the presence of calcareous soils (Table 2). Species strongly associated with this axis included those common to soils derived from volcanic substrates in the south-west corner of the study area (+ve) or short-lived species found predominantly at south-eastern sites (−ve; Table 2). The fourth axis is linked to areas with outcropping of parent rock, high altitude, lower temperatures, higher rainfall and high levels of organic carbon in the topsoil (Table 2). Although not shown in Table 2, the next two axes were also significant and explained 4.9 % and 4.3 % of the species-environment relationship respectively, and were linked to: (i) soil texture and presence of sandy soils; (ii) aspect of slope and heat index.

Following forward selection to further refine the number of variables to 20 (including 5 'dummy'

Table 2 Eigenvalues, correlations between species and environmental variables, species scores and percentage of floristic variation (inertia) explained by the first four axes of a CCA of 36 environmental variables and floristic data from 139 sites. Only variables demonstrating strongest ($r > 0.4$) and significant ($P < 0.05$) correlations with axes are listed.

| Axis	1	2	3	4
Eigenvalues	0.47	0.24	0.21	0.16
Species – environmental correlations	0.95	0.89	0.88	0.87
< % Variation of species	7.1	10.8	14	16.5
< % Variation of species – environm. relation	19.1	28.8	37.6	44.3
Significance of axis	$F = 4.1, P < 0.001$	$F = 2.3, P = 0.007$	$F = 2.5, P = 0.001$	$F = 2.2, P = 0.009$
Correlation with Environmental variables	Stone cover −0.88	pH 0.75	Easting 0.60	Outcrop 0.60
	Alluvium 0.80	Calcareous 0.61	Geog. distance 0.72	Pediment −0.55
	Landform 0.73	Iron −0.52	Calcareous 0.48	Altitude 0.48
	Soil depth 0.72	Conductivity 0.44	Recent rain 0.44	Average temp 0.48
	Ridge distance 0.67	Soil colour 0.42		Average rain 0.43
	Gravel −0.63			Organic carbon 0.41
	Upland 0.63			
	Slope −0.61			
	Stone shape −0.61			
	Phosphorus 0.60			
	Fire period 0.57			
	Potassium 0.56			
	Bajada 0.54			
Species scores	*Eri. flaccida* 2.00	*M.eleuterostachya* 2.60	*E. kingsmillii* 1.58	*Tr. brizoides* 2.49
	Eulalia aurea 1.80	*E. socialis* 2.43	*A. victoriae* 1.54	*E. kingsmillii* 2.13
	E. victrix 1.79	*Tr. longiceps* 1.83	*Tr. longiceps* 1.52	*Dodonaea viscosa* 2.16
	Er. lanceolata 1.61	*E. trivalva* 1.68	*Ma. georgei* 1.45	*Pt. astrolasius* −1.46
	Eri. benthamii 1.40	*A. victoriae* 1.54	*G. stobbsiana* −1.19	*Sida* sp. 1.32
	A. citrinoviridis −1.33	*S. artemisioides* 1.53	*M.eleuterostachya* 1.14	*Cy. ambiguus* 1.02
	A. hilliana −1.29	*Er. cuneifolia* 1.49	*P. clementii* −1.11	*Sc. parvifolia* −0.96
	A. adoxa −1.22	*R. minima* 1.43	*Am. caricinus* −1.08	*Eri. mucronata* 0.89

Genera: *A – Acacia, Am – Amphipogon, Cy – Cymbopogon, G – Goodenia, E – Eucalyptus, Er – Eremophila, Eri – Eriachne, M – Melaleuca, Ma – Maireana, P – Paspalidium, Pt – Ptilotus, R – Rhynchosia, S – Senna, Sc – Scaevola, Tr – Triodia*

variables for geomorphology) and then removal of floristic variability associated with geographic distance (by setting these three variables as covariables), resulted in a biplot which more clearly demonstrated the pattern of species-environment relationships than that using all variables. This biplot (Fig. 1) accounted for 48 % of the floristic variation associated with the 17 environmental variables or 11.6 % of the total variation following fitting of covariables. Reducing the number of variables to 17 preserved 63 % of the total variation associated with all 38 environmental variables or 82 % of that present before the fitting of covariables. Most variables were strongly correlated to the first axis of the biplot (Fig. 1); this axis explained 30.7 % of the variation associated with the 17 environmental variables. The most important of these variables were linked to soil structure (cover of surface stones and the depth of soil), altitude, phosphorus concentrations, time since last fire, soil texture class, degree of outcropping and average rainfall. The second axis, which accounts for around 27 % of the relationship with environmental variables, was linked to pH and conductivity. Landform sequence along catenae was important in explaining floristic variation and was correlated with both axes (Fig. 1).

Partitioning of total floristic variation into groups of explanatory variables showed that most (19.5 % of adjusted variation) was explained by site environmental variable (i.e. edaphic, topographic and geomorphic

Fig. 1 Environment-site biplot based on a partial canonical correspondence analysis (CCA) of all 139 sites using 20 explanatory variables (chosen following forward selection) and three co-variables (relating to geographic distance). Continuous and ordinal environmental variables are shown by arrows, the length of which corresponds to the strength of correlation with axes. Nominal environmental variables are represented as asterisks, and sites as open circles.
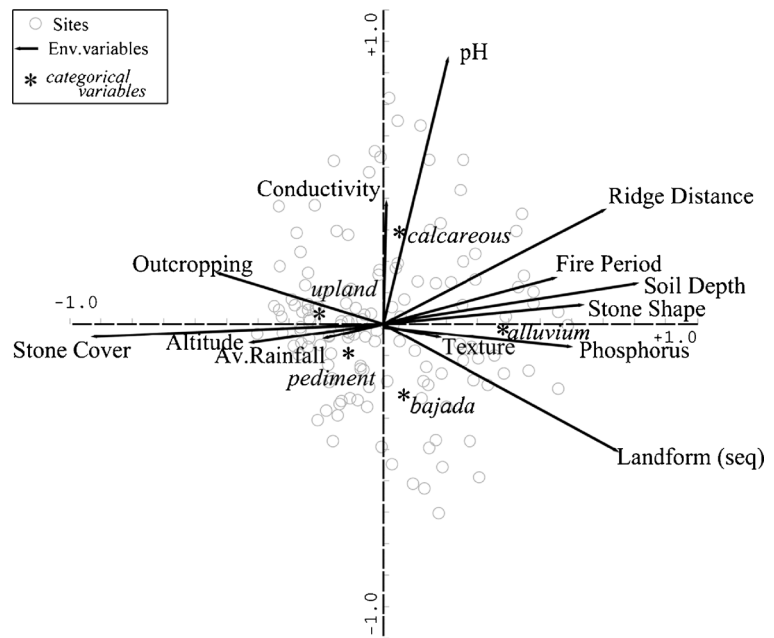
factors), with climatic and spatial variables explaining relatively small amounts (5.5 % and 8.4 %, respectively; Fig. 2). Much of the variation attributable to climatic variables overlapped with spatial and variables, with only 0.9 % of the adjusted variation being uniquely explained by climate (i.e. not also explained other variables). Similarly, only 2.8 % of the 8.4 % of adjusted variation due to spatial variables was unique, with most spatial variation also explained by site environmental (3.9 %) and climate (2.8 %; Fig. 2). Approximately three-quarters of the total floristic variation was not explained by any of the selected explanatory variables (Fig. 2).

Community comparisons and associations

Classification resulted in the delineation of 16 plant communities (Appendix 1 in Supplementary material; van Etten and Fox 2004). Significant differences were found between plant communities for all environmental variables except heat stress and aspect (Appendix 1 in Supplementary material). Many of the plant communities have a statistically significant and strong association with a particular geological substrate ($\chi^2 = 269$, $P < 0.001$; $C = 0.70$) and landform type ($\chi^2 = 446$, $P < 0.01$; $C = 0.81$). Upland communities on hill and ranges were further differentiated by geological formation (i.e. communities tended to subscribe to a particular iron

formation; Appendix 2 in Supplementary material). Communities on lower slopes also tended to favour particular geomorphic units, such as pediment slopes (Community 2A), bajada slopes (5) and unconsolidated scree (4C). Lowland communities were confined to broad alluvial flats or drainage lines of various sizes (Appendix 2 in Supplementary material). Some communities however were found on a wide mix of landforms and geological substrate (e.g. 2B).

Among environmental variables, communities were particularly well differentiated by slope angle and soil depth, pH and phosphorus concentrations (Fig. 3;
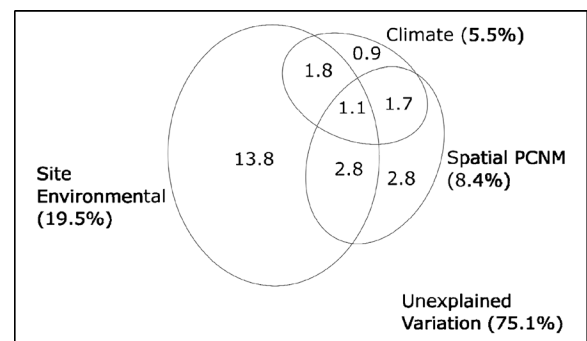

Fig. 2 Variation partitioning of species composition into three groups of explanatory variables (site environmental, climate and spatial) expressed using elliptical Venn diagram with area of ellipses and overlaps in proportion to their adjusted variation explained as constructed using the eulerAPE programme (Micallef and Rodgers 2014).
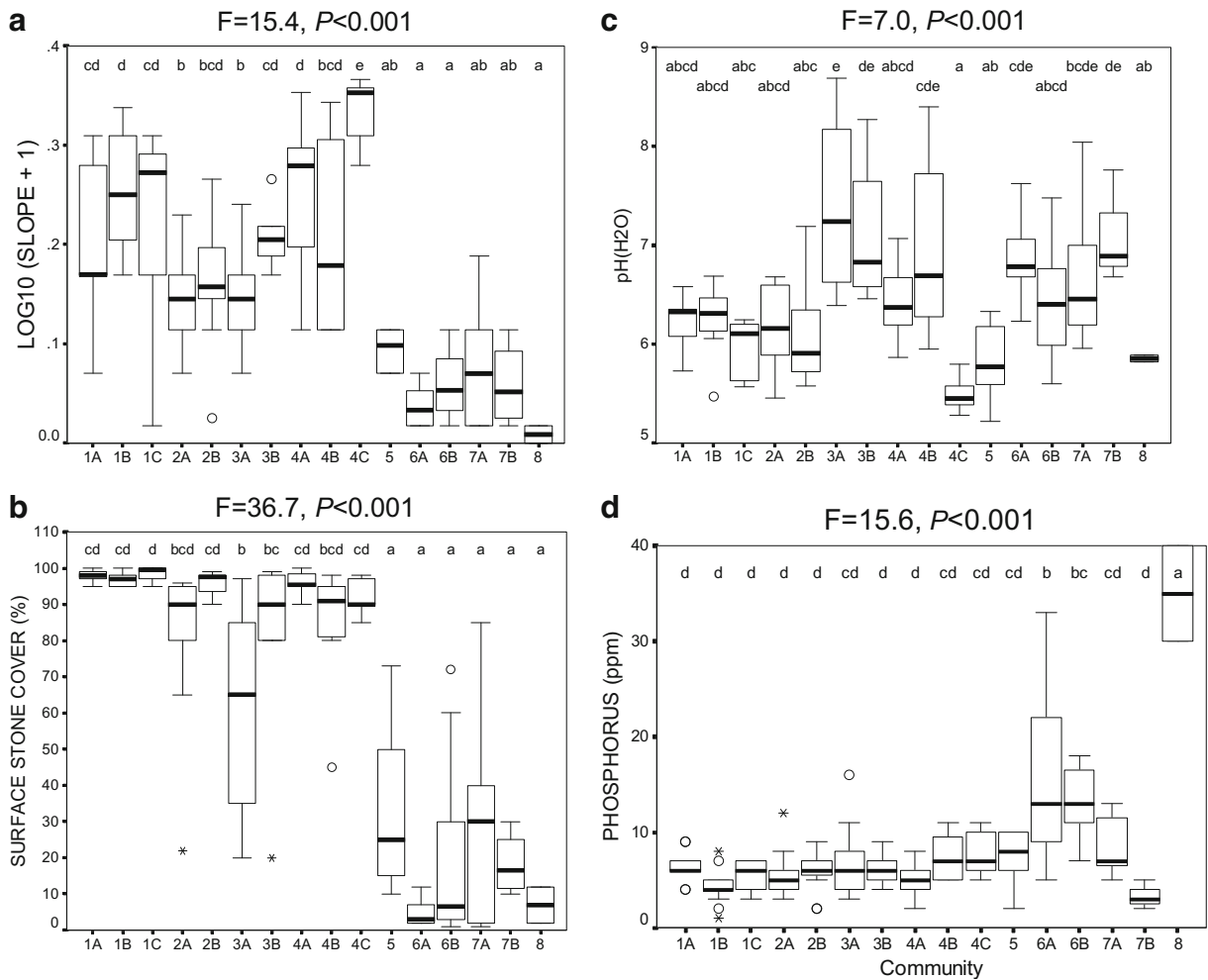
Fig. 3 Box plots for each of the 16 plant communities showing median values (horizontal line), interquartile range (box), and the total range (vertical line) excluding outliers (outliers between 1.5–3 times interquartile range indicated by ○ whereas extremes > 3 time interquartile range are indicated by *) for: **a** – slope (log-transformed); **b** – % stone cover over surface; **c** – topsoil pH (CaCl₂); and **d** – available phosphorus. Results of one-way ANOVA and Tukey's-b post-hoc tests given with communities sharing at least one letter (a,b,c etc) not significantly different. Community descriptions are given in Appendix **1** in Supplementary material.

Appendix **1** in Supplementary material). Upland and pediment communities were on shallower soil with an almost complete cover of stones on the surface (Fig. **3b**) and greater gravel content than lowland communities. Concentrations of available phosphorus were significantly higher within the surface soils of alluvial flats compared to those of upland and pediment communities (Fig. **3d**). Significant differences were also found in soil reaction (pH) with communities derived from dolomites and other volcanics (3A, 3B and 4B) having neutral to slightly basic soils and communities on pediment and bajada slopes having acidic soils (Fig. **3c**).

Climatic variables, as predicted by BIOCLIM (Busby 1991), were reasonably consistent across communities, with the exception of the high altitude community (4A) which had lower temperatures and higher annual rainfall than elsewhere, and the lowland community 6A which occurred at sites with lower rainfall than other communities (Appendix **1** in Supplementary material). Communities on uplands and pediments last experienced a fire between 5–10 years ago whereas within mulga woodland and drainage line communities the period was conservatively estimated at 20–30 years ago (Appendix **1** in Supplementary material).

Discussion

Main gradient

We have found the main floristic gradient of the Hamersley Ranges is strongly linked to a complex (*sensu* Whittaker 1967) of several topographic, edaphic, geomorphic, pyric and microclimatic variables. Importantly, this complex gradient includes distance along the topographic profile from hill/ridge/mountain top to valley floor, which demonstrates that this floristic gradient is spatially explicit. Because other environmental factors also change in a more-or-less gradual fashion along this profile, such as declines in slope and stoniness, and increases in available nutrients, alluvium and soil depth, differences in species composition across such landscapes are linked to a large number of environmental variables.

Most gradient analyses of warm/hot mountainous deserts have also found the primary floristic gradient linked to a complex of variables related to topography, landform and soil texture. Pertinent examples include: Parker (1991) for the Sonoran Desert; Cornelius et al. (1991) for the Chihuahuan Desert; Ward et al. (1993) for the Negev Desert; Abd El-Ghani (1996) for Egyptian coastal mountains; Patten and Ellis (1995) for the northern Kenya; Acebes et al. (2010) for Monte Desert, Argentina; and Zheng et al. (2013) for northeastern China. These gradient relationships support the hypothesis that landform and topographic variation indirectly control vegetation patterns through their influence on moisture and nutrient availability to plants (Noy-Meir 1985). Primarily this stems from the redistribution of water, soil and nutrients from slopes (run-off areas) to flats (run-on areas) during and immediately following intense rainfall events (Noy-Meir 1985; Ludwig et al. 2005).

Role of phosphorus

One potential new finding from our study is the central role played by soil phosphorus in the primary environmental complex gradient identified. This contrasts with published studies of mountainous deserts on other continents that show nitrogen as the important nutrient in the primary environmental complex gradient. Two explanations are possible. Firstly, this finding may support Stafford Smith and Morton's (1990) view that phosphorus has a far greater controlling influence in the Australian arid zone than those on other continents due to the ancient and well-sorted nature of its landscapes. Indeed, the phosphorus levels in soils of the Hamersley Ranges are extremely low even by Australian standards (Stafford Smith and Morton 1990), with 'available' concentrations on pediment and upland slopes around 4–6 ppm. Furthermore, there were significant differences across the landscape with concentrations of phosphorus on the flats several times greater than on uplands.

A second possibility is that phosphorus variation is generally important in mountainous deserts, but the relationships haven't been fully explored (Morton et al. 2011). Parker's (1991) vegetation study in the northern Sonoran mountainous desert is of particular relevance here as available phosphorus concentrations were measured using the same extraction technique as our study and found to vary only slightly between communities (range from 15–20 ppm) and not strongly correlated with the primary floristic gradient; however nitrogen did vary widely (available nitrate concentrations were between 4–17 ppm) and was strongly correlated. In another study, Ben-Shahar (1991) reported that phosphorus had 'marginal influence on the differential abundance of plant species' in a South African woodland savanna whereas other nutrients measured were important. Other studies have shown the importance of phosphorus to vegetation patterns in arid Australia, although across broader spatial extents and not in mountainous topography (Noy-Meir 1974; Griffin 1990). Arruda et al. (2015) showed significant phosphorus variation linked to different communities along catenary sequences of hilly semi-arid vegetation in Brazil. Like the Hamersley Ranges, these soils were old and highly weathered, especially on uplands, suggesting that acute phosphorus differentiation is more likely to develop and be a driver of vegetation distinctiveness in old, stable landscapes compared to younger landscapes (Mucina and Wardell-Johnson 2011), such as postglacial grasslands of central European; Cachovanová et al. 2012).

Fire regime

Another difference between the main environmental complex gradient identified in this study and those identified in overseas mountainous deserts is that a component of the fire regime, namely period of time since the last fire, was included in the complex for

the Hamersley Ranges. Fire is rarely mentioned as an important environmental factor in synopses of overseas mountainous deserts (e.g. Evenari et al. 1985). In contrast, fire is a regular and important feature over much of the Australian arid/semi-arid zone, including the Hamersley Ranges (Stafford Smith and Morton 1990; Nano et al. 2012). One possible interpretation of time since last fire being linked to the main floristic gradient is that the vegetation patterns reflect, at least in part, different successional stages following pyric disturbance. More likely, the link is merely a consequence of different fire regimes occurring across the catena. Fires are widespread and frequent (every 5–10 years) in the hummock grasslands of uplands and pediments (itself an unusual phenomenon for desert vegetation), and recovery from seed or vegetative buds is rapid (Nano et al. 2012). In contrast, fire rarely occurs in the mulga woodlands on the flats, due to typically low fuel levels, and many plants here are fire sensitive. The zone of interest with respect to the influence of fire lies at the transition between these two areas — that is the open mulga woodlands with hummock grass understorey found on the bajada and outwash slopes. Other studies (van Leeuwen et al. 1995; Bowman et al. 2008) have found that fire is important in shaping the structure and floristics of vegetation in this broad transition zone.

pH and conductivity patterns

The second most important floristic gradient was related to the pH and conductivity of the topsoil. This gradient effectively separated sites on soils derived from calcareous (dolomites, shales, siltstones, etc.) and volcanic substrates from those soils of ironstone formations which are typically acidic and gravelly red loams. It is relatively common for the second most important floristic gradient of desert vegetation to be linked to variation in geological substrate, especially where the study is of sufficient spatial extent and/or geological complexity to include contrasting types of substrate (Parker 1991; Ward et al. 1993; Acebes et al. 2010). Species most strongly associated with this gradient were those tolerant of alkaline soils such as *Melaleuca eleuterostachya*, *Eucalyptus socialis*, *E. trivalva* and *Acacia victoriae*.

Role of geographic distance

The floristic gradient related to geographic distance was the third most important. At least some of this is attributable to floristic changes along broad climatic gradients across the study area, and would explain the small proportion of overall floristic variance explained by both spatial and climatic variables. However, this floristic gradient was also strongly correlated, positively, with rainfall received (in the 4 months) before sampling and, negatively, to the presence of calcareous and volcanic soils. Therefore it is at least partly an artifact of uneven sampling with a disproportionately high number of sites measured: (1) following a high rainfall period in the south-east corner of the study area; and (2) within the large area of volcanic and dolomitic soils in the south-west corner. Although annual species were excluded from the floristic analysis, a large number of seedlings of shrubs, sub-shrubs and perennial grasses were found at sites in the south-east corner when sampled following well-above average rainfall.

Importance of topography and landform

In addition to redistributing rainwater and alluvium, topography can also influence soil moisture availability through its effect on microclimate. Two distinct processes appear to be operating. Firstly, the effects of altitude on air temperature and rainfall can be important, and, secondly, the effects of aspect on temperature, radiation and evaporation can be important on steeper slopes. The increases in rainfall and decreases in temperature with increasing altitude can be quite profound and appear to have a major influence on species composition in many mountainous deserts (e.g. Whittaker and Niering 1965; Abd El-Ghani 1996), not surprising given the 2000 m+ altitudinal range found in such areas. In the more topographically subdued Hamersley Ranges, where the highest mountains rise 400–500 m above the plateau surface, such an altitudinal influence was detected but constituted only a minor (fourth most important) floristic gradient. Temperatures are around 2°C cooler and annual mean rainfall around 20–40 mm higher on mountain summits of the Hamersley Ranges compared to lower slopes. Aspect and the heat index were also linked to a minor (although significant) gradient in species composition, which

suggests there are slight differences in species composition between north and south facing upland slopes. Overseas studies in similar environments have often reported distinct differences in vegetation due to aspect, although this effect seems to be more pronounced at higher latitudes (Måren et al. 2015).

A characteristic sequence of distinct landforms was found along topographic profiles most of which were found to have different plant communities. This explains why the primary floristic gradient is not smooth along the profile, but rather consists of a sequence of reasonably discrete communities, each with a fair degree of internal heterogeneity and a certain amount of spatial overlap with adjoining communities. This pattern of communities, controlled by a combination of landform patterning and broader topographic gradients, subscribes to Austin and Smith's (1989) reformulated model of the continuum concept and theories regarding spatial transitions and overlaps between communities (van der Maarel 1990). Sharp transitions, or ecotones, between plant communities are common in mountainous deserts where erosional surfaces give way to depositional zones (Wondzell et al. 1996), something we also found at the transition from pediment to bajada landforms. We found the generalized topo-sequence for the Hamersley Ranges as: (1) hummock grassland of *Triodia brizoides* with low *Eucalyptus kingsmillii* mallee on the mountain tops; (2) upland slopes dominated largely by *T. wiseana* hummock grassland and emergent *E. leucophloia* trees; (3) *T. basedowii* hummock grassland and *E. gamophylla* mallee on pediments with ironstone pavements; (4) alluvial fans and bajada landforms with a mosaic of *T. melvillei* hummock grassland and *A. aneura* woodland; (5) *A. aneura* woodland with a bunch and/or tussock grass understorey on alluvial flats.

The vast majority of the spatial variation in floristics was found to be linked to spatially-structured environmental variables rather than being linked to climatic gradients or independent in terms of its influence, as also reported by Gibson et al. (2012) for ironstone ranges of southern Western Australia. This is not surprising given the distinctiveness of landforms and soils in our area and their strong association with vegetation units. Such an association has regularly been reported for mountainous deserts (Parker 1995; McAuliffe 1994; Patten and

Ellis 1995; Whitford 2002; Michaud et al. 2013). The associations between vegetation and geomorphology are quite consistent for the Hamersley Ranges even when geological differences appear to be subtle. For instance, the community found on upland Brockman iron formation (mid Proterozoic period) differed from that of the older Marra Mamba iron formation (lower Proterozoic), and we found the latter had higher soil nutrient levels. These two iron formations are also known to differ in carbonate, manganese and silicate content of the iron-enriched layers (Morris 1993). Our findings support Parker's (1995) theory that geomorphic history plays an important role in differentiating vegetation types on particular arid landforms, as well as contributing to studies showing high beta diversity across ironstone ranges (Jacobi et al. 2007; Gibson et al. 2012).

References

Abd El-Ghani MM (1996) Vegetation along a transect in the Hijaz mountains. *J Arid Environm* 32:289–304

Acebes P, Traba J, Peco B, Reus ML, Giannoni, SM, Malo JE (2010) Abiotic gradients drive floristic composition and structure of plant communities in the Monte Desert. *Revista Chilena Hist Nat* 83:395–407

Arruda DM, Schaefer CE, Corrêa GR, Rodrigues PM, Duque-Brasil, R., Ferreira-JR WG, Oliveira-Filho AT (2015) Landforms and soil attributes determine the vegetation structure in the Brazilian semiarid. *Folia Geobot* 50:175–184.

Austin MP, Smith TM (1989) A new model for the continuum concept. *Vegetatio* 83:35–47

Beard JS (1975) *Vegetation survey of Western Australia. Sheet 5: Pilbara*. University of Western Australia Press, Nedlands

Belbin L, Faith DP, Milligan GW (1992) A comparison of two approaches to beta flexible clustering. *Multivar Behav Res* 27:417–433

Ben-Shahar R (1991) Abundance of trees and grasses in a woodland savanna in relation to environmental factors. *J Veg Sci* 2: 345–350

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832

Bowman DMJS, Boggs GS, Prior LD (2008) Fire maintains an *Acacia aneura* shrubland-*Triodia* grassland mosaic in central Australia. *J Arid Environm* 72:34–47

Busby JR (1991) BIOCLIM - A bioclimate analysis and prediction system. In Margules CR, Austin MP (eds) *Nature conservation: cost effective biological surveys and data analysis*. CSIRO, Melbourne, pp 64–68

Cachovanová L, Hájek M, Fajmonová Z, Marrs R (2012) Species richness, community specialization and soil-vegetation relationships of managed grasslands in a geologically heterogeneous landscape. *Folia Geobot* 47:349–371

Collins SL, Belnap J, Grimm NB, Rudgers JA, Dahm CN, D'Odorico P, Litvak M, Natvig DO, Peters DC, Pockman WT, Sinsabaugh RL, Wolf BO (2014) A multiscale, hierarchical model of pulse dynamics in arid-land ecosystems. *Annual Rev Ecol Evol Syst* 45: 397–419

Colwell JD (1963) The estimation of phosphorus fertilizer requirements of wheat in Southern New South Wales by soil analysis. *Austral J Exp Agric Anim Husb* 3:190–197

Cooke RJ, Warren A, Goudie A (1993) *Desert geomorphology*. UCL Press, London

Cornelius JM, Kemp PR, Ludwig JA, Cunningham GL (1991) The distribution of vascular plant species and guilds in space and time along a desert gradient. *J Veg Sci* 2:59–72

Enright NJ, Miller BP, Crawford A (1994) Environmental correlates of vegetation patterns and species richness in the northern Grampians, Victoria. *Austral J Ecol* 19:159–168

Evenari M, Noy-Meir I, Goodall DW (eds) (1985) *Ecosystems of the world, Vol. 12A & B: Hot deserts and arid shrublands*. Elsevier, Amsterdam

Gibson N, Meissner R, Markey AS, Thompson WA (2012) Patterns of plant diversity in ironstone ranges in arid south western Australia. *J Arid Environm* 77:25–31

Griffin GF (1990) Characteristics of three spinifex alliances in Central Australia. *J Veg Sci* 1:435–444

Jacobi CM, Carmo FF, Vicent RC, Stehmann JR (2007) Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodivers & Conservation* 16: 2185–2200

Kent M (2012) *Vegetation description and data analysis: a practical approach*, 2nd ed. Wiley-Blackwell, Oxford, UK

Legendre P, Legendre L (1998) *Numerical ecology*, 2nd English ed. Elsevier Science BV, Amsterdam

Legendre P, Borcard D, Peres-Neto P (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75:435–450

Ludwig JA, Tongway DJ (1995) Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. *Landscape Ecol* 10:51–63

Ludwig JA, Wilcox BP, Breshears DD, Tongway DJ, Imeson AC (2005) Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86:288–297

Mabbutt JA (1977) *Desert landforms*. MIT Press, Boston

Måren IE, Karki S, Prajapati C, Yadav RK, Shrestha BB (2015) Facing north or south: does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan valley? *J Arid Environm* 121:112–123

McAuliffe JR (1994) Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecol Monogr* 64:111–148

Micallef L, Rodgers P (2014) eulerAPE: drawing area-proportional 3-Venn diagrams using ellipses. *PLoS ONE* 9: e101717

Michaud GA, Monger HC, Anderson DL (2013) Geomorphic-vegetation relationships using a geopedological classification system, northern Chihuahuan Desert, USA. *J Arid Environm* 90:45–54

Milewski AV (1981) A comparison of vegetation height in relation to the effectiveness of rainfall in the Mediterranean and adjacent arid parts of Australia and South Africa. *J Biogeogr* 8:106–116

Morris RC (1993) Genetic modelling for banded iron-formation of the Hamersley Group, Pilbara Craton, Western Australia. *Precambrian Res* 60:243–286

Morton SR, Stafford Smith DM, Dickman CR, Dunkerley DL, Friedel MH, McAllister RR, Reid JRW, Roshier DA, Smith MA, Walsh FJ, Wardle GM, Watson IW, Westoby M (2011) A fresh framework for the ecology of arid Australia. *J Arid Environm* 75:313–329

Mucina L, Wardell-Johnson GW (2011). Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework. *Pl & Soil* 341:1–23.

Nano CE, Clarke P, Pavey CR (2012) Fire regimes in arid hummock grasslands and Acacia shrublands. In Bradstock RA, Gill AM, Williams RJ (eds) *Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world*. CSIRO Publishing, Melbourne, pp 195–214

Noy-Meir I (1974) Multivariate analysis of the semiarid vegetation in south-eastern Australia. II. Vegetation catenae and environmental gradients. *Austral J Bot* 22:115–140

Noy-Meir I (1985) Desert ecosystem structure and function. In Evenari M, Noy-Meir I, Goodall DW (eds), *Ecosystems of the world. Vol. 12 A. Hot deserts and arid shrublands*. Elsevier, Amsterdam, pp 93–103

Parker KC (1991) Topography, substrate, and vegetation patterns in the northern Sonoran Desert. *J Biogeogr* 18:151–163

Parker KC (1995) Effects of complex geomorphic history on soil and vegetation patterns on arid alluvial fans. *J Arid Environm* 30:19–39

Parsons AJ, Abrahams AD (1994). *Geomorphology of desert environments*. Springer, Dordrecht

Patten RS, Ellis JE (1995) Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. *Vegetatio* 117:69–79

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrol Earth Syst Sci* 11:1633–1644

Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625

Rayment GE, Higginson FR (1992) *Australian laboratory handbook of soil and water chemical methods*. Inkata Press, Melbourne

Rouillard A, Skrzypek G, Dogramaci S, Turney C, Grierson PF (2015) Impacts of high inter-annual variability of rainfall on a century of extreme hydrologic regime of northwest Australia. *Hydrol Earth Syst Sci* 19:2057–2078

Silvertown J, Araya Y, Gowing, D (2015) Hydrological niches in terrestrial plant communities: a review. *J Ecol* 103:93–108

Šmilauer P, Lepš J (2014) *Multivariate analysis of ecological data using CANOCO 5*, 2nd ed. Cambridge University Press, Cambridge, UK

Stafford Smith DM, Morton SR (1990) A framework for the ecology of arid Australia. *J Arid Environm* 18:255–278

ter Braak CJF (1986) Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179

ter Braak CJF (1988) Partial canonical correspondence analysis. In Bock HH (ed) *Classification and related methods of data analysis*. North-Holland, Amsterdam, pp 551–558.

ter Braak CJF, Šmilauer P (2012) *Canoco reference manual and user's guide: software for ordination, version 5.0.* Microcomputer Power, Ithaca

Thorne AM, Tyler IM (1997) *Mt Bruce 1:250 000 geological series – explanatory notes*. Geological Survey of Western Australia, Perth

Turnbull L, Wainwright J, Brazier RE (2011) Nitrogen and phosphorus dynamics during runoff events over a transition from grassland to shrubland in the south-western United States. *Hydrol Process* 25:1–17

van der Maarel E (1990) Ecotones and ecoclines are different. *J Veg Sci* 1:135–138

van Etten EJB (2009) Inter-annual rainfall variability in arid Australia: greater than elsewhere? *Austral Geogr* 40: 107–118

van Etten EJB, Fox JED (2004) Vegetation classification and ordination of the central Hamersley Ranges, Western Australia. *J Roy Soc Western Australia* 87:63–79

van Leeuwen SJ, Start A, Bromilow RB, Fuller PJ (1995) Fire and the floristics of mulga woodlands in the Hamersley Ranges, Western Australia. In Page MJ, Beutel TS (eds) *Ecological research and management in the mulgalands.* The University of Queensland, Brisbane, pp 169–175

Walkley A, Black IA (1934) An examination of the Degiareff method for determining SOM and a proposed modification of the chromic acid titration method. *Soil Sci* 37:29–38

Ward D, Olsvig-Whittaker L, Lawes M (1993) Vegetation-environment relationships in a Negev Desert erosion cirque. *J Veg Sci* 4:83–94

Whitford WG (2002) *Ecology of desert systems.* Academic Press, San Diego

Whittaker RH (1967) Gradient analysis of vegetation. *Biol Rev* 42: 207–267

Whittaker RH, Niering WA (1965) Vegetation of the Santa Catalina Mountains, Arizona. II. A gradient analysis of the south slope. *Ecology* 46:429–452

Williams OB, Calaby JH (1985) The hot deserts of Australia. In Evenari M, Noy-Meir I, Goodall DW (eds) *Ecosystems of the World. Vol. 12A. Hot deserts and arid shrublands*. Elsevier, Amsterdam, pp 269–317

Wondzell SM, Cunningham GL, Bachelet D (1996) Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert. *Landscape Ecol* 11:351–362

Zheng JG, Chen YW, Wu GX (2013) Association of vegetation patterns and environmental factors on the arid western slopes of the Helan Mountains, China. *Mountain Res Developm* 33: 323–331