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Increasing climate seasonality controls functional trait distribution in a montane bog system, New England Tableland Bioregion, Northern New South Wales

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Abstract

The northern distributional limit of bog communities in Australia is in the New England Tableland Bioregion in northern New South Wales (NSW). An analysis of select functional trait expression using Community weighted means and redundancy analysis (CWM-RDA) tested the effects of physiographic and climatic variables of plant taxa within these bogs. Two aspects of climate seasonality (precipitation and temperature seasonality) and one spatial variable (easting) were found to be of significance in the distribution of expressed functional traits.

Anthropogenic climate change in the New England Tableland Bioregion is predicted to increase both these seasonal variables. Under these predicted conditions species with smaller geographic ranges will dominate and are likely to include shrub taxa with larger fruits and seeds and storage organs (tubers, culms, bulbs).

Key words: Bog, CWM, Wetland, Geographic range, Fruit, Seed, Storage organs

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Introduction

The occurrence of montane wetlands is limited worldwide. In few regions of the world is the rarity of these systems more acute than in Australia. Montane wetlands are restricted largely to southeastern Australia along the Great Dividing Range (Figure 1) (Jarman *et al*. 1988; Whinam & Hope 2005; Hunter & Bell 2007; Hunter & Bell 2009). Here they are under threat from land use practices such as draining, grazing, burning, peat and mining as well as climate change (Benson & Ashby 2000; Whinam *et al*. 2001; Whinam & Chilcott 2002; Whinam *et al*. 2003; Hope & Kershaw 2005; Hunter & Bell 2007; Hunter & Bell 2009; Benson & Baird 2012). This has led to montane wetland types being listed under State and National Legislative Acts as endangered ecological communities.

The New England Tableland Bioregion (>3,000,000 ha in area) includes three listed Endangered Freshwater Montane Wetland community types that are all at their northern geographic limits of distribution (Hunter & Bell 2007; Bell *et al*. 2008; Hunter & Bell 2009; Hunter & Bell 2013). Montane Bogs, one of these threatened wetland systems, is listed under the NSW *Biodiversity Conservation Act* 2016 as 'Montane Peatlands and Swamps of the New England Tableland, NSW North Coast, Sydney Basin, South East Corner, South Eastern Highlands and Australian Alps bioregion. Montane bogs occur with inflowing nutrient-poor waters with at least minor traces of peat and high acidity (Whinam & Chilcott 2002; Hunter & Bell 2007; Bonser *et al*. 2010). These bogs can form a hummock and hollow system due to differential *Sphagnum* growth as described in other world regions, where shrubs dominate the hummocks and herbaceous and semi-aquatic species occur in the hollows. These seems to be restricted to the most eastern higher rainfall occurrences in the region (Hunter & Bell 2007) and though structurally they appear to be dominated by shrubs, the predominant lifeform composition is generally cyperaceous and restionaceous (Hunter & Bell 2007; 2013).

Montane bog community occurrence is fundamentally tied to regional climate and can only develop where there is an annual moisture balance (the ratio of total precipitation and evapotranspiration) greater than zero (Ingram 1983; Jarman *et al*. 1988; Gignac *et al*. 2000; Whinam *et al*. 2003; Bragazza *et al*. 2005). Understanding how a positive moisture balance is maintained requires a more nuanced approach than an analysis of yearly climatic averages and is best studied by investigating aspects of climate seasonality (Slik *et al*. 2010; Banin *et al*. 2012; Hunter & Bell 2013; Schultz *et al*. 2014; Hunter 2015ab). Hunter and Bell (2013) investigated the floristics of these most northerly bog communities and discovered that aspects of climate seasonality provided the greatest explanatory power in regard to floristic composition. Hunter (2016) tested differences between functional trait distributions between three different mire communities (fens, bogs and lagoons) and found northern NSW bog community composition favoured species with longer-lived polycarpic life histories, woody taxa, increased seed size and local dispersal.

How species persist, disperse, compete and coexist is dependent on the capture of resources; how such resources are distributed is reliant on individual and combined functional traits (Aiba & Nakashizuka 2009, Carmona *et al*. 2010; Kleyer *et al*. 2012; Adler *et al*. 2014; Hunter 2015ab). By investigating the distribution of functional traits within a community, insight can be gained into the evolutionary, environmental and competitive pressures of that system. Such pressures are likely to be more pronounced at the edge of a community's geographic range, due to reductions in population sizes, changes in recovery potential (source-sink dynamics) and competitive regimes (Travis 2004; Guo *et al*. 2005; Holt & Kiett 2005; Thuiller *et al*. 2005; Reino *et al*. 2006; Hunter & Bell 2013). While functional trait investigations are increasingly common, those specifically undertaken at the edge of a community's geographic range are lacking. The northern-most montane bogs of eastern Australia provide an opportunity to investigate, at a regional level, the factors that affect the expression of select functional traits in a less-than-optimal environment. Such investigations should shed greater light on the effects of predicted anthropogenic climate change than those conducted within the centre of a community's distribution. This investigation is an extension and reduction of focus (to functional trait level) from that of Hunter and Bell (2007) who conducted species and family level composition research.

Methods

Study area

The New England Tableland Bioregion encounters a predominantly easterly airflow from the Pacific Ocean and the effects of tropical cyclones from the northeast; snow occurs occasionally at higher altitudes (Resource and Conservation Assessment Council 1996). There is a strong east to west gradient in rainfall due to orographic influences in the east; the western parts of the Divide receive from 600-1000 mm annually, with 1000-2500 mm along the eastern escarpment (Resource and Conservation Assessment Council 1996). The El Niṅo Southern Oscillation (ENSO) strongly affects eastern Australia, increasing the range of extreme physiological conditions vegetation in this region encounters (Pohlman *et al*. 2005). Due to the shape of the continent the New England Tableland Bioregion montane environment trends south-east to north-west with seasonality of climate increasing northward and westward, as the orographic influences in the east ameliorate, increasing seasonality.

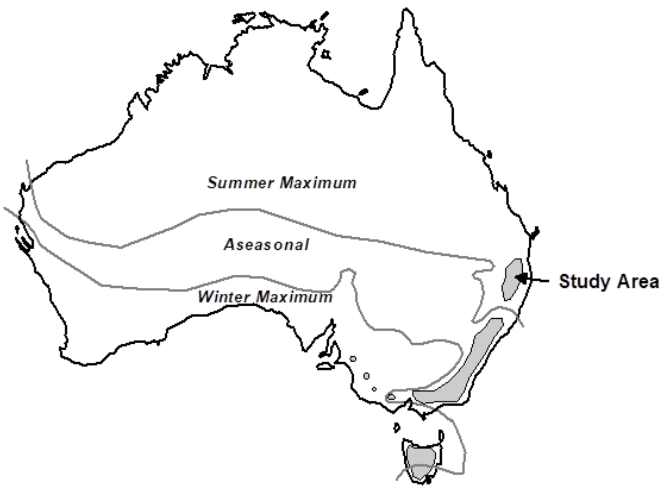

Figure 1. Map of Australia showing highly generalised areas containing montane freshwater wetland environments (grey shading) and macro-changes in the seasonality of rainfall (solid grey lines). The New England study area is indicated.

The areas sampled occurred on four rock types: basalt, metasediments, acid volcanics and granite; altitudes ranged from 850-1370 m above sea level. The most northerly sampled bog was 262 km from the most southerly; 127 km lie between the most eastern and most western samples. More detailed descriptions of the landscapes and vegetation in these threatened wetlands are given by Hunter *et al*. (1999), Whinam and Chilcott (2002), Hunter (2004), Hunter (2005a), Hunter and Bell (2007), Bell *et al*. (2008), Hunter and Sheringham (2008), Hunter (2013), Hunter and Bell (2013), Hunter (2016), Hunter & Hunter (2020) and Hunter (2026).

Site survey

Data for bog communities was gathered by sampling 62 full floristic 20 x 20 m survey plots within 11 sub-regional locations in the New England study area (Figure 1) (Hunter and Bell 2007). Species cover-abundance data using a modified Braun-Blanquet scale. Cover scores: 1: <5% and uncommon; 2: <5% and common; 3: 6-20%; 4: 21-50%; 5: 51-75%; 6: 76-100%) were collected for all vascular plants (Westhoff and Maarel 1978). Sample plots were placed at random within intact and minimally anthropogenically disturbed locations. Conservation reserves managed by the NSW Office of Environment and Heritage (now DCCEEW) were given priority for site placement. These reserves are managed for their continued biological and landscape processes; stock grazing is not permitted, and feral animals and introduced weeds are controlled. 438 native plant taxa in 72 families and 215 genera have been recorded in these bogs (Hunter and Bell 2007).

Explanatory variables

ANUCLIM 6.1.1 (Xu & Hutchinson 2011) was used to model 35 bioclimatic parameters based on the climate variables maximum temperature, minimum temperature, rainfall, solar radiation and pan evaporation. Altitude at each site was used to increase the accuracy of the modelled bioclimatic parameters. Geographic position of Easting and Northing (Australia Mag Grid 94: Zone 56) were used as variables in analyses, along with altitude (elevation above sea-level in metres); physiography (crest to open depression; scored 1-6); soil depth (deep to skeletal, scored 1-3); and drainage (waterlogged to well-drained, scored 1-4). Indices for severity of disturbance 0-5 were given for anthropogenic clearing and grazing. In each case '0' indicated no discernable occurrence of the disturbance attribute and '5' represented the most severe impacts. 42 variables were calculated or scored for each site.

Statistical analyses

Taxon-related tables including information on species Braun-Blanquet scores within each quadrat, and functional traits for each species were created. Functional traits scores were based on available regional and state floras. Where information was missing, measurements of herbarium specimens were undertaken by the author. The community-based technique of Community Weighted Means of traits (Garnier et al. 2007; Adler et al. 2013) was applied to assess the response of functional traits. Trait expressions of all species were weighted by their Braun-Blanquet scores.

A redundancy analysis (RDA) was performed on the plot by weighted trait matrix via the CANOCO5 package (ter Braak & Šmilauer 2012). Significant environmental variables were chosen by the manual forward selection procedure in CANOCO5, followed by Monte Carlo permutation tests (1000 iterations). Forward selection allows the removal of collinear/redundant variables from the regression model, and subsequent reanalysis of the contribution of the remaining unselected variables, as each new variable is added to the model (ter Braak & Šmilauer 2012). Holm's correction was used in order to adjust the significance values for potential inflated family-wise type I errors, thus reducing the chances of collinearity and false significance. Only variables which achieved a *P* value of less than 0.05, after Holm's correction, were included in the model. To further test the unique and combined influence of each significant factor, partitioning of variance was used. Variation partitioning allows an objective quantification of how the relative influence of variable sets changes over a range of scales (Borcard *et al*. 1992; Reino *et al*. 2006; ter Braak & Šmilauer 2012). Individual trait response curves, to the most significant individual environmental variable, were further tested and graphed, based on generalized additive models (GAM) using a Poisson distribution and stepwise Akaike Information Criteria (AIC) (ter Braak & Šmilauer 2012).

The final analysis was restricted to native species only. Traits recorded for each of the 438 native vascular species included: plant height (maximum height obtainable); specific leaf area (SLA); fruit size (length by width); fruit type (dry dehiscent, dry indehiscent, succulent); seed size (length by width); monocarpic or polycarpic; presence or absence of storage organs (e.g. bulbs, tubers, swollen taproots, corms, lignotubers); and vegetative spread capacity (e.g. rhizomes, runners, stolons, suckering, rooting at nodes).

Occupancy within each of the 97 Australian 'ecological regions' (Hnatiuk 1990) was chosen as a measure of geographic range size (Hunter 2003a; Hunter 2005b). The regions adopted are those recognized by State and Territory herbaria (Oakwood *et al*. 1993).

Results

Community weighted means and redundancy analysis CWM-RDA using forward selection highlighted six significant variables: precipitation seasonality, easting, temperature seasonality, aspect, annual mean moisture index, and highest period of radiation. After applying Holm's correction only precipitation seasonality, easting, and temperature seasonality, remained as significant variables. The final model accounted for 22.6% of the variance (18.4% adjusted) in the dataset. The first two axes cumulatively explaining 20.1% of variance (Table 1; Figure 2).

Table 1. Codes and descriptions of significant variables (P ≤ 5%) listed in order of decreasing importance (contribution) from forward selection in plot/hollow biplot analysis.

Variable explanation	Per cent Contribution	Per cent Explained	*P* -value	*Holm's Correction*
Precipitation Seasonality	10.5	8.9	0.001	0.04196
Australian Map Grid: Eastness (Zone 56)	7.7	6.6	0.001	0.04196
Temperature Seasonality	8.4	7.1	0.001	0.04196

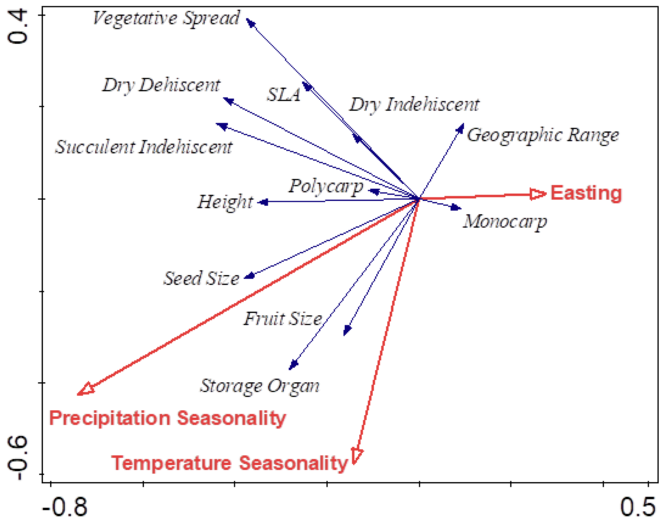

Figure 2. Community weighted means and redundancy analysis (CWM-RDA) plot: Select functional traits in bogs communities at the limit of their geographic range, against significant environmental variables.

Variation partitioning (*P* = 0.001) has highlighted the unique conditional effects of each significant variable, but also indicates the shared fractions between each of the three significant variables are negative (Figure 3). Negative values in shared fractions indicate that the joint effect of two groups of variables is more than the sum of their individual marginal effects (ter Braak & Šmilauer 2012). Though the strongest unique variance is explained by precipitation seasonality, it is the combined effects of temperature seasonality and easting (-20.3%), followed by precipitation and temperature seasonality (-18.8%), that have the greatest influence on the current model.

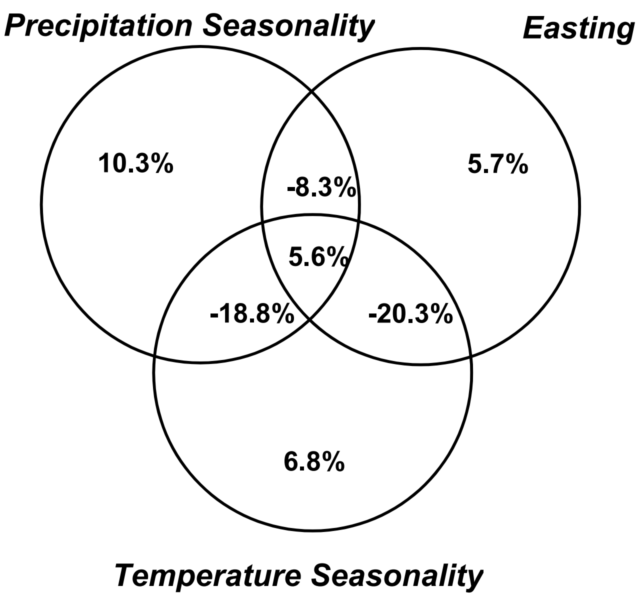

Figure 3. Variation partitioning of the three significant environmental variables within the chosen model.

Fruit size was positively influenced by all significant environmental variables (Figures 4-6), thus likely increasing due to combinatorial effects of precipitation and temperature seasonality (Figure 3). Seed size and the possession of storage organs were positively influenced greatest by the combination of increased precipitation and temperature seasonality. Geographic range was negatively associated with each of the variables within the model and monocarpy was only positively associated with an increase in temperature seasonality. All other functional traits were positively associated with an increase in precipitation seasonality and negatively with easting and temperature seasonality.

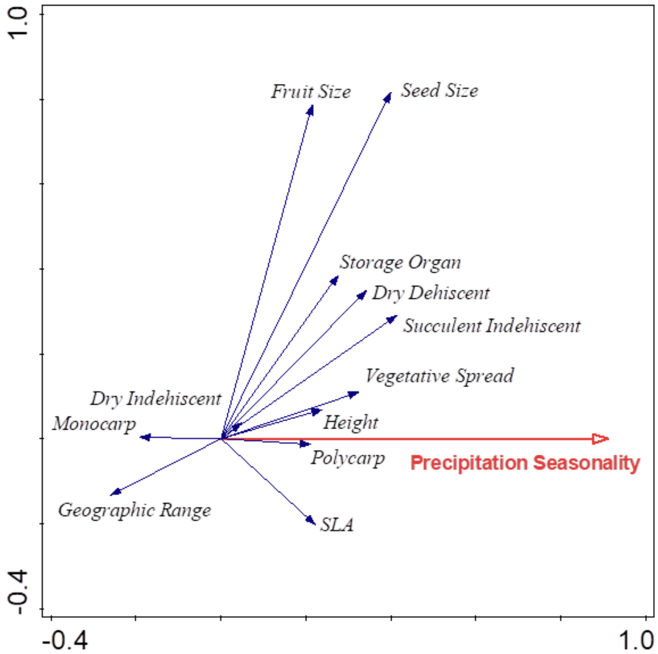

Figure 4. Conditional effects of precipitation seasonality on functional traits on the first and second axis of the Community weighted means redundancy analysis.

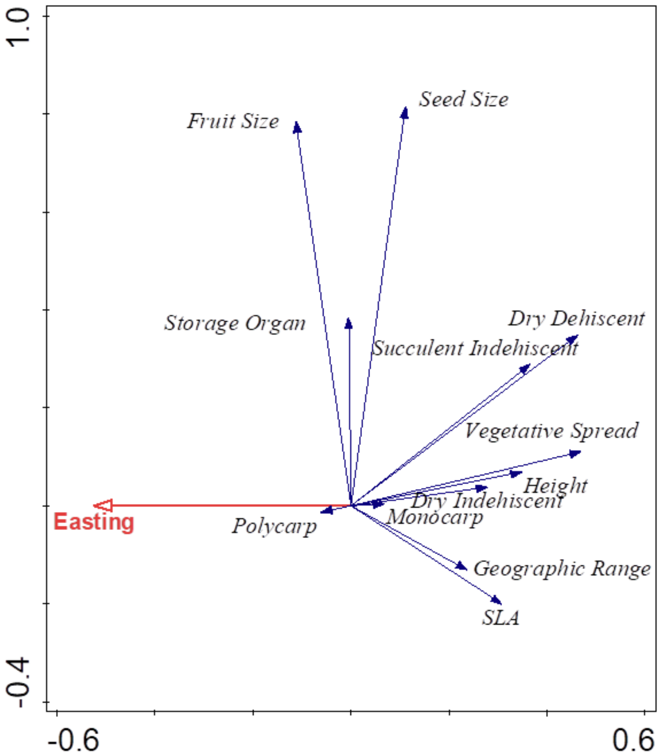

Figure 5. Conditional effects of easting on functional traits on the first and second axis of the Community weighted means redundancy analysis.

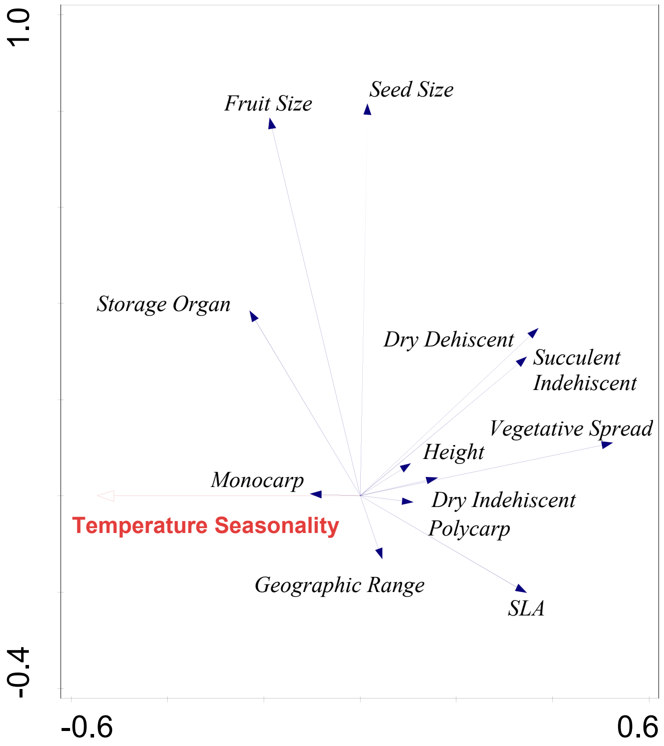

Figure 6. Conditional effects of temperature seasonality on functional traits on the first and second axis of the Community weighted means redundancy analysis.

Generalized additive model based (GAM) response curves for the functional traits; fruit size (10.4%; *P* = 0.04195); seed size (24.2%; *P* = 0.0032); vegetative spread (26.1%; P < 0.00001); and storage organs (10.2%; *P* = 0.00651) are given in Figures 7 and 8. These results indicate that the change in seed size and the increase in the prominence of storage organs have a slight and gradual change with an increase in precipitation seasonality, but there is a dramatic point of inflexion and increase, with increasing precipitation seasonality for fruit size, and ability to spread vegetatively .

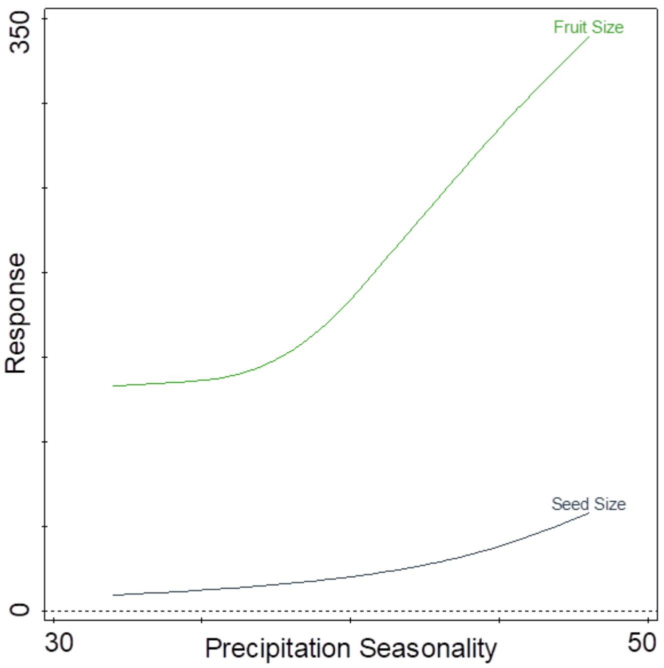

Figure 7. Functional trait response curves for seed and fruit size against precipitation seasonality using generalised additive modelling.

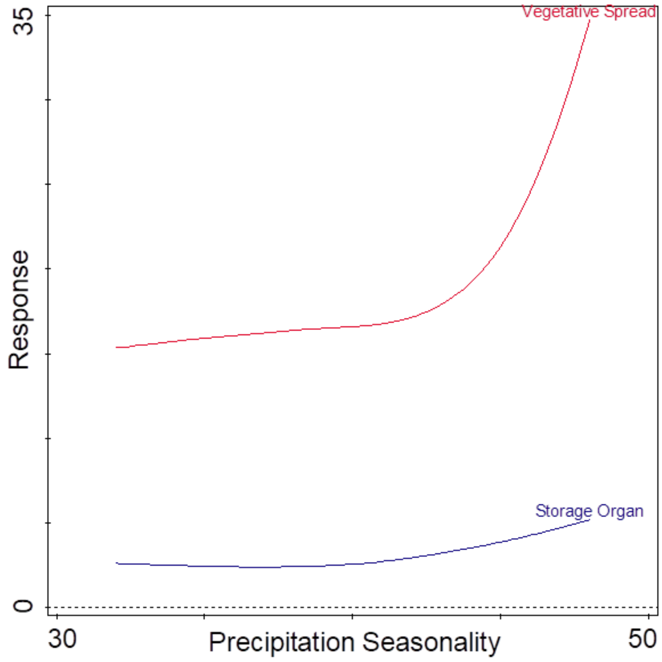

Figure 8. Functional trait response curves for vegetative spread and storage organs against precipitation seasonality using generalised additive modelling.

Discussion

Seasonality of climate has the greatest influence on the expression of important plant functional traits in montane bog communities at the geographic limits of their distribution in the New England Tableland Bioregion. Aspects of climate seasonality have previously been shown to be the most significant factors influencing species composition, allometric traits and vital attributes important for ecosystem function and species survival (Hunter & Bell 2013; Hunter 2015ab). This is not surprising as fundamentally bog communities require year-round wetness for persistence (Hunter & Bell 2013). An increase in precipitation seasonality is likely to increase the chances of extended dry periods for part of the year, and temperature seasonality to increase the difference between summer and winter temperatures, affecting the ability of the system to retain moisture. Broader temperature amplitudes would require species to have wider tolerances.

Eastness (easting) within the model is likely to be accounting for unmeasured environmental and/or various combinations of tested variables that are better explained by a single measure. Considering the strong gradients west to east across the Tableland region it is not surprising eastness has been highlighted as significant. Such surrogate variables are often found significant in multivariate analysis (Chave *et al.* 2006; Culmsee *et al.* 2010; Zhang *et al.* 2011; Larjavaara & Mueller-Landau 2012; Lines *et al.* 2012; Hunter 2015ab).

All measured functional traits, apart from geographic range and monocarpy, increased with precipitation seasonality. Thus, under increasingly extended dry periods over winter, increasingly favoured species are taller perennials, with larger leaves, fruits, and seeds, a variety of fruit types, and possess storage organs or are vegetatively spread. This agrees with Hunter and Bell (2013) who showed an increase in the representation of shrub lifeforms from Ericaceae, Fabaceae and Myrtaceae with increasing precipitation seasonality, and a decrease in Proteaceae taxa with easting. Larger fruits and an increase in the predominance of dry dehiscent fruits reflect the greater variety of polycarpic shrub species with no seedbank dormancy mechanisms. Rather than seedbank longevity and stratified germination, seed longevity is likely transferred to the canopy (serotiny) (Capon & Brock 2006) where seeds from dry dehiscent fruits (e.g. *Banksia, Callistemon, Grevillea, Hakea, Leptospermum*) can be released over extended periods as a response to increased fire risk.

Correlations between specific leaf area (SLA) and fruit size, indicate that larger leaves are required in order to capture sufficient resources for larger fruit production (Bonser *et al.* 2010), though there was no distinct link between SLA and fruit size. Restionaceous and Cyperaceous taxa dominate the bog environment (Hunter & Bell 2013), with scale leaves compensated for by photosynthetic stems, and possess comparatively large nuts. This has likely decoupled the correlation between leaf size and fruit size with stems replacing leaves and capturing sufficient light to enable large fruit and seed sizes. Large leaves require sufficient nutrient resources for their production and replacement. Bog environments are generally nutrient poor with high acidity which restricts the availability of nutrients likely leading to a reduction in leaf size (Bonser *et al.* 2010). The replacement of large leaves with longer-lived photosynthetic stems may equate to resource conservancy, similar to that obtained through sclerophylly, and allowing accumulation of resources needed to produce larger fruits and seeds.

Benwell (1998) and Clarke (2002) proposed that resprouting and clonality strategies in stable heathland sites were more likely to occur in locations of high stress and high recruitment risk. Bogs are waterlogged rather than mesic and are low nutrient environments with high acidity (Hunter & Bell 2007; Hunter & Bell 2013). Vegetative spread, particularly by monocots (rhizomes, runners, stolons) allows species to rapidly capture space within temporarily available habitats and/or quickly recovery from moderately frequent disturbances, particularly those that involve biomass removal (Hunter 2003; Cowling *et al.* 2005; Croft *et al.* 2007; Croft *et al.* 2010; Clarke *et al.* 2015). Fire is the most frequent biomass removing disturbance event within these systems (Hunter & Bell 2013) and would increase in frequency in areas which have a more prolonged drier seasonal period.

The dramatic increase in the presence of larger fruits, and vegetative spread, in response to increasing precipitation seasonality suggests a fundamental shift in the competitive advantage of these two traits with extended seasonal dry periods (Figure 7 and 8). Increases in temperature and precipitation seasonality acting in concert particularly advantaged fruit and seed size, and the occurrence of storage organs. From the perspective of the bog environment an increase in precipitation and temperature seasonality reflects less optimal conditions. Thus, in less hospitable locales species that have larger fruits and seeds, and also possession of storage organs, are increasingly favoured. Larger fruits and seeds allow species to put more resources into establishment at the time of germination, in particular, below-ground parts. Storage organs (bulbs, corms, lignotubers), like diaspore dormancy, can be a method of avoiding disadvantageous times by allowing above ground parts to die, yet allowing survival below ground and enabling a rapid response when optimal conditions recur. This would be a beneficial trait during extended dry periods.

Geographic range was found negatively associated with all three significant environmental variables. Larger geographic ranges were associated consistently in the full and partial analyses with other functional traits, in particular, larger leaf size, and possibly smaller stature, fruit and seed sizes. Life form has been correlated with differences in geographic range size (Rapoport 1982; Kelly 1996). Small seed size has been associated with larger geographic ranges by other researchers (Snell & Aarssen 2005). On acid rocky outcrops of the New England Tableland Bioregion, Hunter (2003b) found shrubs and trees had the most restricted geographic range sizes. As has already been indicated there is an increase in the prominence of shrub-dominated families with an increase in precipitation seasonality and a decrease in eastness (Hunter & Bell 2013) which may account for the decrease in geographic range size.

Predictions of impacts of global climate change in the New England Tableland Bioregion (Hughes 2003; Hennessy 2004; PMSEIC 2007) indicate that mean diurnal range is likely to increase, as is maximum temperature of the wettest period; precipitation of the driest quarter will decrease, thus increasing both temperature and precipitation seasonality in concert. Based on these changes it is likely shrub taxa will become more prominent and that functional traits such as an increase in seed and fruit size, and the possession of storage organs, will be favored. It is difficult to predict how traits such as height, leaf size and fruit type may vary under anthropogenic climate change as these traits were positively associated with an increase in precipitation seasonality, but negatively to temperature seasonality.

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