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Patterns of morphological and physiological traits of epiphytes within trees and between elevations in subtropical Australian rainforest

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Abstract: Taxonomically dissimilar epiphyte species can have comparable morphological and physiological traits in similar environmental conditions. However, the degree of trait similarity has not been examined in a comparison of bryophytic and vascular epiphytes across elevational and tree gradients. We assess whether epiphyte species that occupy comparable realised niche spaces within host tree and landscape scale gradients have similarities in taxonomy, morphology or physiology. Vascular and moss epiphytes were surveyed within four height zones at five elevations (300-1100 m asl) in the sub-tropical rainforest of Australia. Epiphyte species distributions were agglomeratively classified using Ward's method. Chi square tests were used to test for differences in the incidences of taxonomic groups, life forms, leaf thickness, photosynthetic pathways and other drought resistant morphologies between these distributional groups. These traits were also tested for correlation with light and humidity. Six groups were identified based on distribution. Vascular epiphytes with CAM, thickened leaves and other drought-mitigating morphologies were common in the groups that occupied the most xeric situations. All drought resistant traits were associated with high light and low humidity. Vascular species with few to no drought-mitigating characteristics were common in groups that occupied moister situations. Moss morphology was less congruent with environmental conditions than vascular plant morphology, suggesting that moss life forms are responding to a different scale of environmental variation.

Key words: Drought, Micro-habitat, Morphology, Moss, Vascular epiphytes

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Introduction

Epiphytes use other plants for mechanical support and have no direct connection to the ground, relying on moisture and nutrient inputs from fog and rainfall (Benzing 1990). Hence, epiphytes tend to be more limited by moisture availability than most terrestrial plants (Zotz & Hietz 2001). Lack of water is postulated to be the greatest stress on vascular and bryophytic epiphytes (Zotz & Hietz 2001; Sillett & Antoine 2004; Romanski *et al.* 2011; Bartels & Chen 2012).

Many vascular epiphytes exhibit physiological and morphological characteristics which help them survive drought. Some have Crassulacean Acid Metabolism (CAM) photosynthetic pathways, which help reduce water loss through nocturnal uptake of CO₂ (Winter 1985). Many vascular epiphytes have specialised morphologies that assist with water retention, such as thickened or succulent leaves, or rhizomes and specialised water storage tissue (Hietz & Briones 1998; Benzing 2004; Higgins 2004; Reyes-Garcia *et al.* 2008; Zhang *et al.* 2015).

Epiphytic bryophytes have adapted to drought in different ways to vascular epiphytes. All bryophytes, except one order of hornworts (Anthocerotales), use the C₃ pathway for photosynthesis, a process which is less water efficient than CAM (Smith & Winter 1996; Raven *et al.* 1998; Hanson & Rice 2013). Instead, bryophytes, and some pteridophyte species (such as resurrection plants), are poikilohydric, in that they can rehydrate upon wetting from a desiccated state (Proctor 1990; Bates 1998; Sillett & Antoine 2004). Bryophytes also have a range of forms, which can assist in water storage (ver Leerdam *et al.* 1990; Hedenäs 2001; Frahm 2003; Sillett & Antoine 2004). For example, bryophytes that form dense mats can store water in the capillary spaces between the leaves (Bates 1998; Frahm 2003; Sporn *et al.* 2010).

Within the host tree, light, temperature, wind, and moisture vary from the moist, shaded base of the trunk to the more arid and exposed outer branches (Wallace 1981; Théry 2001; Bartels & Chen 2012). Distinct patterns in the distributions of morphological and physiological traits of epiphytes occur within the host tree (Pittendrigh 1948; Johansson 1974; Hietz & Briones 1998; Reyes-Garcia *et al.* 2012). Vascular epiphytes inhabiting the shadier and more humid lower zones of the tree tend to have fewer traits associated with drought resistance, while species with traits such as CAM, succulence, thickened and smaller leaves are common in the sun-exposed outer crown (Johansson 1974; Winter *et al.* 1983; Hietz & Briones 1998). Bryophytes adapted to water storage, such as mats, occur in the exposed parts of the canopy, while light-gathering bryophytes, such as dendroids (fan shaped mosses), are more common in the shady bases of host trees (Bates 1998; Acebey *et al.* 2003; Silva & Porto 2013).

At the landscape scale, moisture and temperature vary with elevation, and montane environments are frequently shrouded in cloud, resulting in high levels of humidity and rainfall (Chantanaorrapint 2010; Strong *et al.* 2011; Ding *et al.* 2016). There are distinct distributions of morphological

traits in both epiphytic and terrestrial ferns with elevation in Hawaii, with more divided fronds at higher elevation (a function to collect more moisture from fog), longer blades in shaded habitats, and fronds with shorter stipes and fewer pinnae in drier habitats (Creese *et al.* 2011). Macro-lichens have a high level of branchiness at higher elevations, which is inferred to be a response to high levels of fog, as increased branchiness assists with fog interception (Stanton & Horn 2013). Many studies which describe the distributions of epiphyte morphologies and physiologies are restricted to within the host tree. There are few that cover landscape gradients (e.g. Mantovani 1999) and none that cover both gradients.

There are approximately 400 epiphyte species in Australia (Wallace 1981) and they are a prominent feature in rainforests, yet few comprehensive epiphyte studies have been conducted. In recent years, the distribution of Australia's epiphyte species have been examined over host tree and elevation gradients (Sanger & Kirkpatrick 2015, 2017). Other studies on the ecology of Australia's vascular epiphytes are limited to a few studies (Wallace 1981; Cummings *et al.* 2006; Freiberg and Turton 2007), as are studies on epiphytic bryophytes (Fensham and Streimann 1997; Franks and Bergstrom 2000; Ramsay and Cairns 2004). With one exception (Sanger & Kirkpatrick 2015), studies of epiphytic bryophytes in tropical and subtropical rainforest in Australia have been limited to the lower trunk of the host.

In the present study, we assess which vascular and moss epiphytes share similar niche spaces within the host tree and across elevational zones in the subtropical rainforests of Australia. We determine whether species with morphological and physiological similarities are found in the same habitats. We expect that species that are common in more xeric situations will have morphologies and physiologies that assist with drought resistance. Finally, we determine whether there are differences between mosses and vascular plants in the strength of the relationship between morphology and environment.

Methods

Study Area

The study was conducted in the Border Ranges National Park (28°21'35"S, 152°59'10"E), a World Heritage-listed subtropical rainforest that covers 3,600 km² in northern New South Wales, Australia. A set of long term monitoring plots, along a transect ranging from 300 to 1100 m in elevation, with plots at 200 m intervals, is located on the western side of the Border Ranges National Park (Kitching *et al.* 2011). Further details of the study site and general patterns of epiphyte distribution on this transect can be found in Sanger & Kirkpatrick (2015).

There are limited climate data (temperature only) available for the Border Ranges; however, more detailed climate information exists for a transect of similar design at Lamington National Park, which is located 20 km from

the Border Ranges transect in the same mountain range. Temperature measurements for the two transects indicate a similar environmental lapse rate for median temperatures (Fig. 1; Maunsell *et al.* 2015). At Lamington, temperature and humidity data loggers were installed in the canopy and understory (Strong *et al.* 2011). The average annual temperature decreased by 0.75 °C with every 100 m gain in elevation, equating to a difference of 6–7 °C between 300 and 1100 m (Strong *et al.* 2011). During the dry season (August and September), relative humidity at midday increased linearly from the 300 m site (canopy: 25%; understory: 45%) to the 1100 m site (canopy: 60%; understory: 80%; Strong *et al.* 2011). There was little difference in humidity during the wet season (February and March), with humidity levels at close to 100 percent within the canopy and understory at most elevations (Strong *et al.* 2011). Any climatic differences between the Lamington and Border Ranges areas are likely to be small, as the hot drying weather comes from the northwest, and the two areas from which data were collected are north-facing (Lamington) and west-facing (Border Ranges) and have similar altitudinal vegetation zonation patterns.

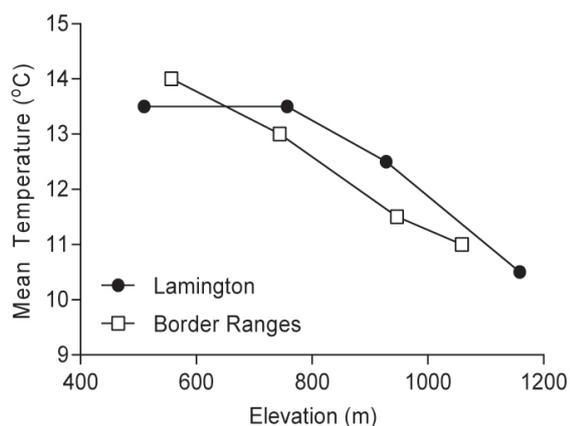


Fig. 1: Median temperatures calculated from data loggers, which recorded temperature every 3 h from July 2012 to Feb 2013 and April to July 2013 (data from Maunsell *et al.* 2015). The lowest elevation Lamington site is subject to cold air drainage.

Epiphyte sampling

We collected our data between May and July 2013. Within each of the five elevations, ten suitable large trees closest to the centre of the plot were selected. Trees were selected for their suitability for climbing (healthy trees with no obvious signs of rot, with large sturdy branches within 30 m of the ground, unobstructed by large woody vines). Approximately a quarter of trees within the plots had large woody vines in the inner canopy. These vines can alter the microclimate and may negatively affect the abundance of epiphytes. We chose not to climb trees with large woody vines, because of their lack of safety, and we acknowledge that this choice may have affected our results. Trees were climbed using a combination of single and double rope techniques (Lowman & Moffett 1993). The species, height, tree diameter at breast height (DBH - measured at a height of 1.3 m), and the elevation

and GPS location were recorded for each host tree. Fifteen tree species from ten families were sampled (see Table 2.1). Average tree diameter at breast height was 54.5 ± 15 cm at 300 m, 66.6 ± 16 cm at 500 m, 62 ± 19 cm at 700 m, 50.2 ± 15 cm at 900 m and 72.2 ± 32 cm at 1100 m.

Each tree was divided into height zones, adapted from the zonation system used by Johansson (1974). Following ter Steege & Cornelissen (1989), Romanski *et al.* (2011) and Gehrig-Downie *et al.* (2011), we divided the trunk into two zones, as the upper trunk often had a very different microclimate to the lower trunk. Four height zones were surveyed: inner canopy (the inner third of the branches in the crown), the upper trunk (the mid-point of the trunk to the first bifurcation), the lower trunk (two metres above the base of the trunk to the mid-point of the trunk), and the base (from the ground to 2 m). The outer and mid-canopy were not surveyed as these zones are often difficult to access safely. In each height zone of each tree, the number of individuals of each species of vascular epiphytes was recorded. Clumped or rhizomatous plants were counted as one individual, following Sanford (1967). Specimens that could not be identified in the field were collected and taken to the Queensland Herbarium (BRI) for identification.

We wished to produce a list of moss taxa for each zone on each tree. Due to the patchiness of bryophytes within the host trees, randomly placed quadrats (Gradstein *et al.* 1996) were not used, as richness would have been underestimated. Following Wolf (1993), subsamples were collected from different microenvironments within the zone or wherever there appeared to be a distinct change in bryophyte species composition. Ten to 15 subsamples were normally collected from each zone. Samples were taken to the Queensland Herbarium for sorting into morphospecies and identified to either genus or species level where possible. No cover estimates or abundance data were recorded. We focused on mosses to reduce the likelihood of missing rare or inconspicuous cryptogam species. Nomenclature for both vascular and non-vascular species follows the Catalogue of Life (Roskov *et al.* 2015). Herbarium vouchers were deposited in the Queensland Herbarium, Brisbane.

The life form of each epiphyte was noted. Vascular epiphytes were placed into one of three categories: holo-epiphytes, primary hemi-epiphytes and nomadic vines. Holo-epiphytes spend their entire life cycle on the host tree without connection to the ground or the vascular system of the host (Kelly 1985; Benzing 1990). Primary hemi-epiphytes are plants that begin their life cycle as true epiphytes but later send feeder roots down the trunk of the host tree and connect to the ground (Kress 1986; Benzing 1990). Nomadic vines (also known as secondary hemi-epiphytes), such as species belonging to the genera *Phymatosorus*, *Arthropteris* and *Pothos*, are semi-epiphytic climbers which are functionally similar to epiphytes, as their adventitious roots are often used for nutrient and water uptake and they occasionally lose their connection to the ground (Wallace 1981; Moffett 2000; Zotz 2013). Five types of moss life form were identified: dendroid, pendant, mat, tuft and weft, based on Bates (1998), Kürschner *et al.* (1999) and Frahm (2003).

For each epiphyte species, leaf thickness was measured on specimens collected in the field and also reconfirmed from herbarium vouchers at the Queensland Herbarium. Due to the difficulties with examining the thickness of the dried leaves of specimens, species were divided into two leaf thickness classes: thick (≥ 1 mm) and thin (< 1 mm). Features such as glossy, leathery or reduced leaves, pseudobulbs, and the presence of detritus-collecting baskets were also recorded for each species as ‘other drought morphologies’, as determined from field observations and from Wilson (1990) and Bernhardt (1993). Glossy and leathery help prevent water loss due to a thicker cuticle and reduced leaves prevent water loss due to a decrease in surface area (Benzing 2004, Higgins 2004). Detritus-collecting baskets are able to store water in the soil and hummus collected in the basket (Wallace 1981). The presence of CAM in vascular species or the presence of poikilohydry in mosses and some fern species was noted. For the vascular species, the presence of CAM or C_3 pathways followed Winter *et al.* (1983), who assessed the CAM status of 157 vascular epiphytes from Australia by examining the stable carbon isotope ratio ($\delta^{13}C$) values and the absence of Kranz anatomy. Species are said to have CAM pathway if $\delta^{13}C$ values were less than -20 ‰. Twelve species found in the current study were not assessed by Winter *et al.* (1983), with most of these species being nomadic vines. All moss species are known to use the C_3 pathway (Smith & Winter 1996; Raven *et al.* 1998; Hanson & Rice 2013).

Light was estimated using hemispherical canopy photography. This is a widely used method to calculate total transmitted light for a particular point (Frazer *et al.* 1999). A Cannon 5D mark III digital camera (Ohta-ku, Tokyo, Japan) with a Rokinon 8mm f/3.5 HD Fisheye Lens (Gangnamgu, Seoul, Korea) was used to take three to five hemispherical photos within each height zone, on both the north and south side of each tree. It is recommended to take photos on uniformly overcast conditions in order to remove the effect of direct solar irradiance; however, due to our limited time in the field, this was unachievable. Instead, to control for direct solar irradiance, all photos were taken in manual mode with adjusted shutter speed and aperture to best suit light conditions. To standardize the photos and to reduce highlights from around the edge of leaves, light levels were balanced using a standardised histogram reference in Photoshop (Adobe, San Jose, CA, USA). Photos were then analysed using Gap Light Analyser (Frazer *et al.* 1999) which calculates the percentage of total transmitted light for each image over an entire year by transforming the image pixel positions into angular coordinates (Frazer *et al.* 1999).

Data analysis

The presence/absence of each vascular and moss species was noted for each height zone for each tree surveyed. The data were then summed across the ten tree replicates at each site to create a frequency of species occurrence within each of four height zones over each of the five elevations ($n = 20$). Ward’s technique for agglomerative cluster analysis (Ward 1963) was used on a Euclidean distance matrix to identify groups of species with similar distributions in the

20 elevation by tree zone samples. These groups were plotted in three dimensions (stress = 0.14) using global non-metric multidimensional scaling (MDS) with Bray-Curtis distance values, 25 iterations and a 0.1 (10%) stress stopping rule.

Chi square was used to test whether the numbers of species in each of the distributional groups differed from the rest of the species at $p < 0.05$ in photosynthetic pathway (CAM and C_3), leaf thickness (thin and thick), life form (holoepiphyte, nomadic vine, dendroid, pendant, mat, tuft and web), the presence of other drought morphologies (pseudobulbs, leathery leaves, glossy leaves, basket forming) or taxonomic group (vascular and mosses). The expected values were calculated from the proportions of the types within the species list as a whole. Rank order correlation was used to assess whether the above mentioned traits were related to humidity and/or light. The percentage of species with a particular trait was calculated for each zone/elevation and was rank order correlated with the humidity and light averages for each zone/elevation. Classification and correlation tests were performed using Minitab 16.1.0 (MINITAB, Pennsylvania, USA). MDS plots were created using Primer v.6 with PERMANOVA+ add-on software (Primer-E Ltd, Plymouth, UK).

Results

Thirty-four species of vascular epiphytes (17 species of pteridophytes, 13 species of Orchidaceae and four species of Dicotyledonae) and 42 morphospecies of moss were recorded. There were six distinct distributional groups of species (Figs. 2, 3, 4). The species in Group 1 occupied some of the more humid locations, as they inhabited the lower tree height zones and had a broad distribution over the elevation gradient (Fig. 3). The species in Group 2 occurred in the more xeric ends of the two gradients: the upper height zones and lower elevations (Fig. 3). Group 3 consisted of species that had distributions over the mid to upper height zones and were distributed mainly around the mid elevations (Fig. 3). Group 4 had species which occurred in the upper height zones and the high elevations (Fig. 3). Group 5 contained species that were concentrated in the higher elevations and occurred over the entire tree height gradient (Fig. 3), thus, were mostly in humid environments (Table 1). Group 6 contained species that occurred in the upper height zones across all elevations (Fig. 3). Each group occupied a largely distinct part of ordination space (Fig. 4).

Group 6 had more pteridophyte species ($Chi^2 = 7.06$; $df = 1$; $P = 0.008$) and fewer mosses ($Chi^2 = 4.40$; $df = 1$; $P = 0.034$) than would be expected by chance (Table 1). Group 2 had a significantly higher proportion of orchids than the rest ($Chi^2 = 7.86$; $df = 1$; $P = 0.005$). Groups 1, 2 and 4 had an even mix of mosses and vascular species, while groups 3 and 5 were dominated by mosses. The five species of nomadic vine all belonged to Group 1 ($Chi^2 = 10.16$; $df = 1$; $P = 0.001$). Six of the nine species in group 5 were tuft mosses ($Chi^2 = 11.39$; $df = 1$; $P < 0.001$). There were a higher proportion of holoepiphytes in groups 6 than expected by chance ($Chi^2 = 11.39$; $df = 1$; $P < 0.001$).

Table 1: The percentage of species in each group with particular attributes. Int = intermediate moistness.

Group	1	2	3	4	5	6
<i>Moistness</i>	<i>Humid</i>	<i>Dry</i>	<i>Int</i>	<i>Int</i>	<i>Humid</i>	<i>Int</i>
<i>Taxonomic</i>						
Moss	19	14.3	19	26.2	16.7	4.8
Vascular	17.6	32.4	5.9	14.7	5.9	23.5
<i>Life form</i>						
Mat	25	33.3	16.7	25	0	0
Weft	33.3	0	33.3	33.3	0	0
Tuft	0	0	0	7.7	46.2	46.2
Dendroid	40	10	20	0	10	20
Pendant	0	25	50	25	0	0
Nomadic vine	100	0	0	0	0	0
Holo-epiphyte	0	40	8	16	4	32
Primary hemi-epiphyte	0	100	0	0	0	0
Filmy Fern	33.3	0	0	33.3	33.3	0
<i>Photosynthetic pathway</i>						
C ₃	15.8	14	15.8	22.8	14	17.5
CAM	0	66.7	11.1	11.1	0	11.1
Unknown	30.8	30.8	23.1	7.7	7.7	0
<i>Leaf thickness</i>						
Thin	22.6	16.1	14.5	22.6	14.5	9.7
Thick	0	50	7.1	21.4	0	21.4
<i>Other morphology</i>						
Basket-forming	0	66.7	0	0	0	33.3
Leathery leaves	55.6	0	11.1	22.2	0	11.1
Pseudobulb	0	28.6	28.6	28.6	0	14.3
Glossy leaves	0	25	0	0	0	75
Reduced leaves	0	100	0	0	0	0

Table 2: The correlation of attributes with humidity and light. Spearman's rank order correlation co-efficient (r) and p values are shown. Significant p values are shown in bold.

<i>Attribute</i>	<i>Humidity</i>		<i>Light</i>	
	<i>r</i>	<i>p-value</i>	<i>r</i>	<i>p-value</i>
<i>Taxonomic</i>				
Moss	-0.021	0.928	0.139	0.558
Vascular	-0.441	0.051	0.48	0.032
<i>Life form</i>				
Dendroid	0.282	0.229	-0.448	0.048
Filmy fern	0.145	0.541	-0.088	0.712
Holo-epiphyte	-0.658	0.002	0.745	< 0.001
Mat	-0.059	0.805	-0.078	0.743
Nomadic vine	0.769	< 0.001	-0.65	0.002
Pendant	-0.859	< 0.001	0.596	0.006
Tuft	0.228	0.333	0.417	0.067
Weft	0.689	0.001	-0.621	0.003
<i>Photosynthetic pathway</i>				
CAM	-0.75	< 0.001	0.693	0.001
C ₃	-0.122	0.609	0.252	0.284
<i>Leaf thickness</i>				
Thick leaves	-0.725	< 0.001	0.778	< 0.001
thin leaves	-0.113	0.634	0.152	0.523
<i>Other morphology</i>				
Basket forming	-0.646	0.002	0.642	0.002
Pseudobulb	-0.583	0.007	0.599	0.005
Leathery leaves	-0.76	< 0.001	0.773	< 0.001
Glossy leaves	-0.544	0.013	0.633	0.003

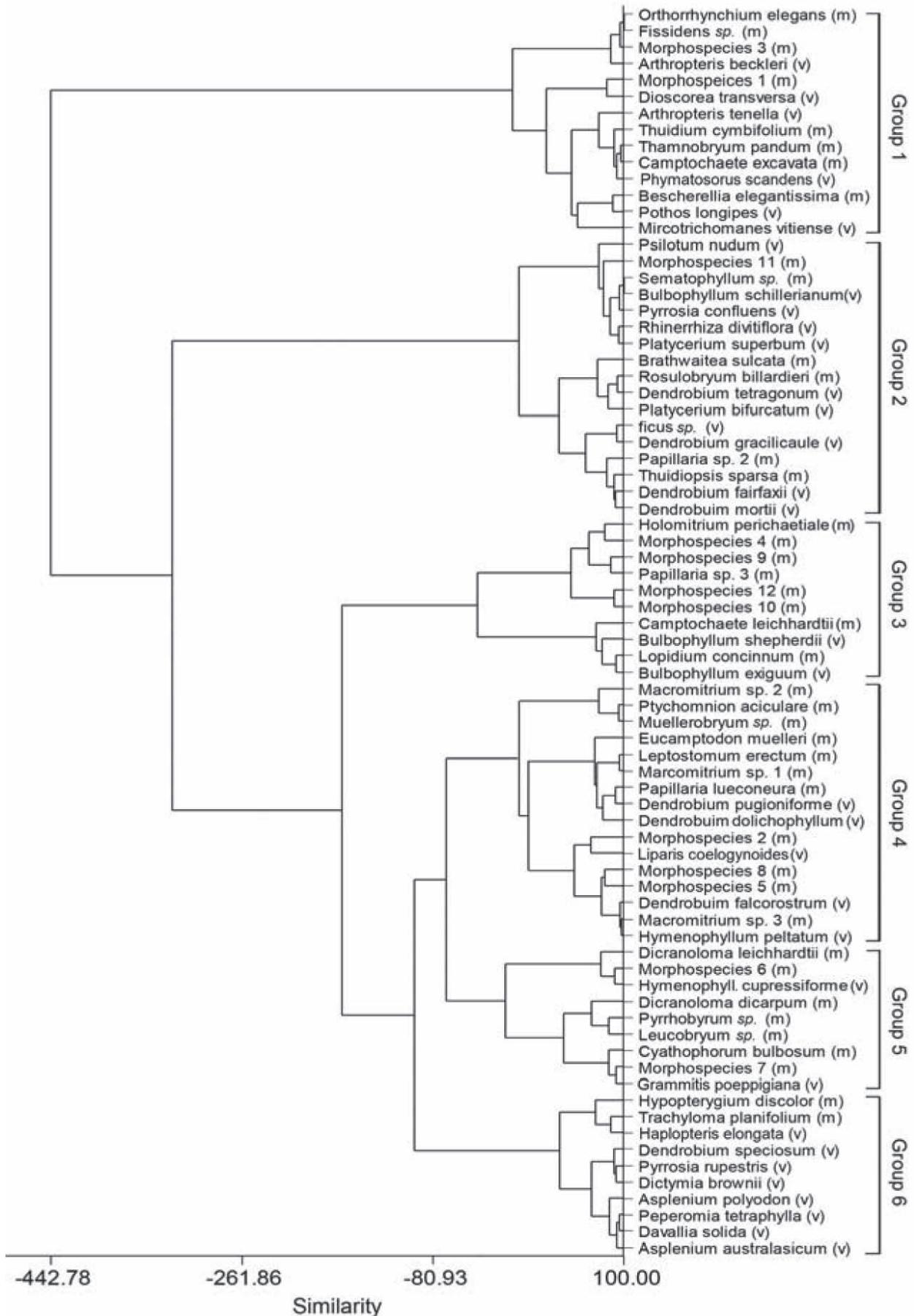


Fig. 2: Dendrogram showing the six groups of vascular (v) and moss (m) species with similar distributions over the two gradients: tree height and elevation.

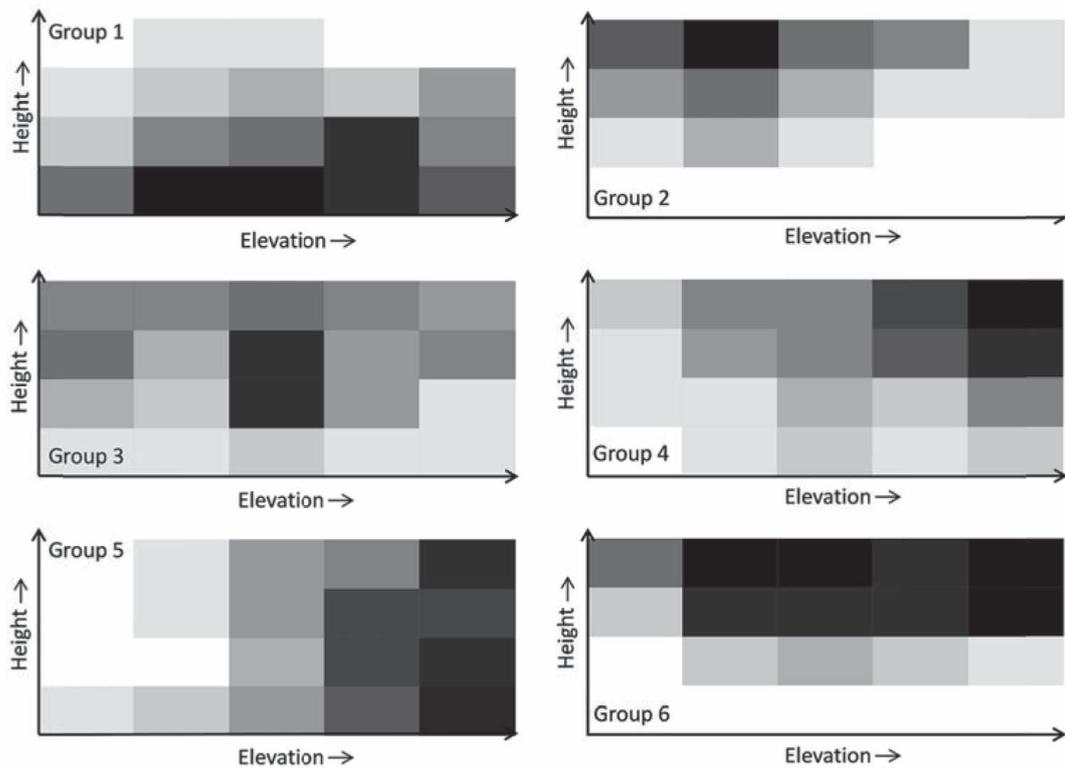


Fig. 3: The epiphyte species richness over the height and elevation gradients for each group. Shading represents the number of species in each height zone / elevation, with the lightest shade of grey representing one species and black representing all species in the group.

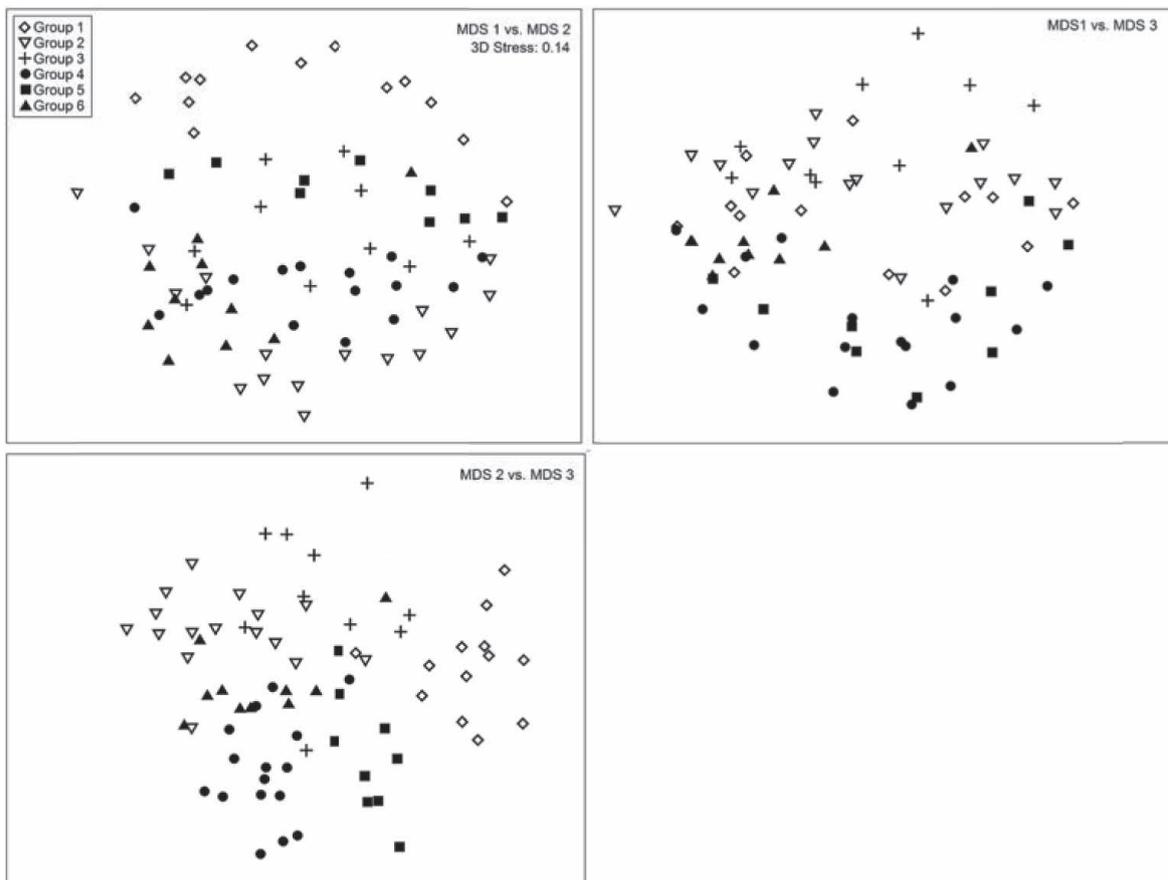


Fig. 4: MDS plots depicting the distributions of epiphyte species in the six groups.

Group 2 had a significantly higher proportion of known CAM species than the rest ($\text{Chi}^2 = 5.45$; $\text{df} = 1$; $P = 0.02$). All other groups either had no species exhibiting CAM (groups 1 and 5) or contained only one or two CAM species (groups 3, 4 and 6). For leaf thickness, only group 2 had a significantly higher proportion of thick leaved species ($\text{Chi}^2 = 5.72$; $\text{df} = 1$; $P = 0.02$). Groups 1 and 5 only contained species with thin leaves. Species in Group 2 ($\text{Chi}^2 = 9.24$; $\text{df} = 1$; $P = 0.002$) and Group 6 ($\text{Chi}^2 = 4.31$; $\text{df} = 1$; $P = 0.04$) had a higher proportion of species with other drought resistant morphologies, while Group 1 ($\text{Chi}^2 = 5.58$; $\text{df} = 1$; $P = 0.02$) and Group 5 ($\text{Chi}^2 = 5.38$; $\text{df} = 1$; $P = 0.02$) contained no species with other drought-mitigating morphologies (Table 1).

CAM, thick leaves, leathery leaves, glossy leaves and pseudobulbs were positively correlated with light and negatively correlated with humidity, as were the holopiphyte, basket forming, and pendants lifeforms (Table 2). Nomadic vines and the weft life form showed the opposite pattern, with a negative correlation with light and a positive correlation with humidity (Table 2). Vascular epiphytes were positively correlated with light and the dendroid life form was negatively correlated with light (Table 2).

Discussion

There was a strong correlation of drought-resistant traits in high light, low humidity conditions. Furthermore, species with these traits were most commonly located in the upper tree zones and lower elevations, where conditions are generally drier. The group (2) that occupied the driest habitats had a high concentration of species with CAM, an adaptation possessed by approximately two-thirds of Australia's orchid species (Winter *et al.* 1983; Holtum & Winter 1999). *Pyrosia confluens*, one of the few Australian pteridophyte species to exhibit CAM (Winter *et al.* 1983) was also in the group. The occupation of the driest and most exposed habitats by CAM epiphyte species is widespread, having been noted in lowland forest in Panama (Zotz & Ziegler 1997), Trinidad (Griffiths & Smith 1983) and in Australia (Winter *et al.* 1983). CAM has also been found to be more prevalent in vascular epiphytes at low elevations where climatic conditions are drier (Earnshaw *et al.* 1987; Silvera *et al.* 2009).

In addition to a high concentration of species with CAM, this dry habitat group had a high proportion of species with thick leaves, a trait which was also found to be correlated with low humidity and high light conditions. Thickened leaves assist in water retention and are commonly associated with dry microsities (Pittendrigh 1948; Johansson 1974; Hietz & Briones 1998; Mantovani 1999). Other drought-mitigating features had a strong correlation with low humidity and high levels of light, and a high proportion of species with these traits were present in Group 2. For example, *Platyserium bifurcatum* and *Platyserium superbum* are nest-forming pteridophytes which accumulate litter and dead fronds that assist in retaining moisture around the roots (Wallace 1981). *Platyserium bifurcatum* also has specialised water-storage

tissue (Kreier & Schneider 2006) and the epidermis of the sporotrophophyll leaves are covered by hairs which decrease water loss (Rut *et al.* 2008). The orchids in Group 2 possessed other morphological characteristics that would help them resist drought, such as specialised root systems and pseudobulbs (Benzing 2004; Higgins 2004).

The majority of the vascular species that had no obvious characteristics to cope with drought occurred in groups distributed over the more humid ends of the two gradients, a pattern which has been observed elsewhere (Johansson 1974; Hietz & Briones 1998). In Groups 1 and 5, which were concentrated at high elevations or in the lower zones of the tree, thin leaves, C_3 pathway, and a lack of apparent morphological adaptations to drought were almost ubiquitous. The ordination of species further highlights the distribution of the groups over the moisture gradient, with Groups 1 and 2 being the most separate in ordination space.

Some of the vascular epiphytes in the groups that occupied sites with deduced intermediate moisture levels exhibited apparent drought adaptations. The species in Group 6 were likely to be subject to some drought stress, as they were restricted to the upper height zones. While there was not a significantly higher proportion of either CAM or thickened leaves in this group, there were a high proportion of other apparent drought adaptations. This group was dominated by pteridophytes, which generally occupy wetter habitats than orchids (Wallace 1983; Benzing 2004) and have features such as leathery or glossy leaves or basket formations.

As expected, mosses were dominant in groups which were distributed in the mid to upper elevations, where humidity is high and temperatures are mild (Wolf 1994; Benzing 1998; Sillett & Antoine 2004). However, there were also moss species present in the group which occupied the driest habitat, a pattern which highlights the wide ecological range of mosses (Holz *et al.* 2002; Acebey *et al.* 2003; Romanski *et al.* 2011; Silva & Pôrto 2013). While we found clear distribution patterns in the morphology and physiology of vascular species related to moisture, not all of the moss life forms conformed to the pattern expected from the literature. Only dendroids and wefts, which were correlated with low light conditions, were closely consistent with previous observations. These life forms have been described as adaptations to gather more light (Frahm 2003; Sporn *et al.* 2010). The pendant life form is usually found at higher elevations where their narrow feathery stems can facilitate the uptake of atmospheric water (Bates 1998; Kürschner *et al.* 1999; Romero 1999; Frahm 2003; Parolly & Kürschner 2004); however, this life form was found in the most xeric sites and was correlated with low humidity. Tufts were concentrated in the high elevation group (Group 5) where humidity levels are generally higher, which is consistent with previous research (Frahm 2003), yet this life form had no significant correlation with humidity. Additionally, mats occurred in shady and moist environments; however, this life form is very effective at storing water in the capillary spaces created between the individuals, making them characteristic of light-intensive, dry microclimates (Bates 1998; Acebey *et al.* 2003; Frahm 2003).

We hypothesise that this seemingly poor fit between moss morphology and microclimate, compared to that of the vascular species, may be a reflection of differences in scale of occupancy between the two taxonomic groups. For example, mosses, being much smaller than the vascular species, may be able to occupy tiny areas of moisture within dry habitats, like the shady undersides of branches or small fissures in the bark, whereas the size of vascular plants might preclude such occurrence. Vascular species could also alter the microclimate of patches of the inner canopy by creating shade, which could easily be exploited by smaller organisms, such as mosses. A test of the above hypotheses would require detailed mapping of species distributions and microhabitats on trees, rather than the broad zonal approach we have adopted.

We acknowledge that there are some limitations in using physiology and morphology data from other studies. For instance, other methods to test for CAM or testing species under drought conditions may yield different results to that reported by Winter *et al.* (1983). Two basket fern species present in the group occupying the most xeric habitat, *Platyserium bifurcatum* and *Platyserium superbum*, were not identified as having a CAM when tested under non-drought conditions using carbon isotope ratios (Winter *et al.* 1983). However, CAM is often more easily detected in drought-stressed individuals (Cushman & Borland 2002; Rut *et al.* 2008). Subsequent studies measuring CAM in *Platyserium bifurcatum* under drought conditions have found that CAM was present in the cover leaves (Rut *et al.* 2008). Weak CAM has also been found in closely related *Platyserium veitchii* by testing for nocturnal increases in titratable acidity rather than using carbon isotope ratios (Holtum & Winter 1999).

By using objective classification of species groups and by testing the correlation of drought resistance features with light and humidity, we have reinforced the generalisation that vascular epiphyte species have sets of morphological and physiological characteristics that are congruent with within tree and elevational variation in environment, which represents strong gradients in moisture and humidity. We found that, at our scale of inquiry, many moss species had morphological characteristics that appeared inappropriate for the environments occupied by their group. This has led us to propose the hypothesis that they were responding to a different scale of habitat variation than the zone. There is a need to focus on the distribution of mosses at this finer scale and to determine how climatic change is likely to impact on future distributions of these cryptic species.

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