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Radial distributions of air plants: a comparison between epiphytes and mistletoes

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Abstract. Vertical gradients of light and humidity within forest canopies are major predictors of air plant distributions. Although this pattern was first recognized over 120 years ago, few studies have considered an additional axis of resource availability, which exists radially around the trunks of trees. Here, we explored the radial distributions of mistletoes and epiphytes in relation to gradients of light and humidity around the trunks of their south-temperate host trees. Additionally, we correlated microclimate occupancy with plant physiological responses to shifting resource availability. The radial distributions of mistletoes and epiphytes were highly directional, and related to the availability of light and humidity, respectively. Mistletoes oriented northwest, parallel to gradients of higher light intensity, temperature, and lower humidity. Comparatively, epiphytes oriented away from the sun to the southeast. The rate of CO_2 assimilation in mistletoes and photochemical efficiency of epiphytes was highest in plants growing in higher light and humidity environments, respectively. However, the photosynthetic parameters of mistletoes suggest that they are also efficient at assimilating CO_2 in lower light conditions. Our results bridge a key gap in our understanding of within-tree distributions of mistletoes and epiphytes, and raise further questions on the drivers of air plant distributions.

Key words: epiphytes; microclimate; mistletoes; radial distribution.

INTRODUCTION

Microclimate (i.e., light, water, temperature) is a long-recognized driver of plant distributions. Plant assemblages at forest edges, for example, are reflective of a microclimate with lower relative humidity, greater wind speeds, solar radiation, and soil temperatures (Gehlhausen et al. 2000). Likewise, rapid changes in microclimate from canopy disturbances have direct effects on plant recruitment and growth (Denslow et al. 1990). One of the most conspicuous microclimate gradients occurs within the vertical column of forest canopies, where light and humidity vary with the height of a tree. Distributed in relation to these gradients are a specialized group of plants that utilize trees as substrate to grow on: air plants (Benzing 1990). Schimper (1888) first described the vertical distributions of air plants in his seminal monograph on the epiphytic floras of the Americas. However, a wealth of literature has since followed, and mechanisms behind the vertical distributions of air plants are well-established (Krömer et al. 2007). Despite more than a century of recognizing air plant distributions as they occur vertically within the canopy; few studies have explored spatial patterns of air plants as they occur radially around the trunks of trees, which may be equally subject to variation in microclimate. Additionally, studies that do consider the cardinal orientations of air plants are either observational (e.g., Tremblay and Castro 2009), related to a single explanatory variable (e.g., Botto-Mahan et al. 2000), or more commonly, cardinal orientation is measured but never discussed (e.g., Wyse and Burns 2011). By considering microclimate gradients that exist not only vertically within the canopy, but radially around the trunks of trees, our knowledge of within-tree distributions of air plants (hereafter specifically referred to as epiphytes or mistletoes) will be more complete.

Vascular epiphytes, which utilize their host trees solely for structural support, are almost exclusively dependent on microclimate humidity to meet their water requirements (Zotz et al. 2001). However, as a response to a discontinuous water supply, selection pressures have enabled epiphytes to exploit different parts of the canopy.

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Filmy ferns (Hymenophyllaceae), for example, lack a differentiated epidermis and stomata, and are therefore inefficient at conserving water (Krömer et al. 2007). As such, filmy ferns are often restricted to the lower trunks or branches of their host trees (Proctor 2012). Tank-forming epiphytes, however, store water in modified leaf bases, which allows them to persist in the outer reaches of the canopy (Reyes-García et al. 2008). In comparison, hemiparasitic mistletoes divert water and some mineral nutrients away from the xylem of their host trees, and are more reliant on host tree water potential rather than microclimate humidity to meet their water requirements (Ehleringer et al. 1986). Similar to epiphytes, mistletoes are postulated to partition resources within the canopy environment, although studies testing this hypothesis are rare (Shaw and Weiss 2000). Indeed, it is intuitive that mistletoes are most restricted by the canopy light environment, considering they must produce their own photoassimilates (Hull and Leonard 1964).

Although the effect of host tree aspect on epiphyte and mistletoe distributions has received little attention in the literature, the effect of aspect on terrestrial plant distributions is well established. Forest edges oriented toward the sun, for example, have more pronounced edge effects that travel further into the forest (Gehlhausen et al. 2000). Likewise, slope aspect has significant effects on floristic competition (Kutiel 1992), the radial growth of trees (Fekedulegn et al. 2003), and plant species associations (Badano et al. 2005). Here, we explore the radial position of mistletoes and epiphytes in relation to gradients of light and humidity around the trunks of trees in a south-temperate forest. First, we use circular statistics to test the null hypothesis that epiphytes and mistletoes are distributed uniformly around the trunks of their host trees. Second, we test whether epiphytes and mistletoes are distributed in relation to the availability of their most limiting resources; working under the assumption that mistletoes are light limited and epiphytes are water limited. Lastly, we test the physiological responses of mistletoes and epiphytes to changes in their most limiting resources, to determine if the responses are consistent with their distribution patterns.

METHODS

Study site and species

The study was conducted in the Nelson Lakes National Park (41°48′ S, 172°50′ E), situated in the upper region of New Zealand's South Island. The climate is subalpine and rarely deviates from 1000 mm of precipitation annually, and an average daily temperature of 10°C. Three southern beeches of the family Nothofagaceae; *Fuscospora fusca*, *F. cliffortioides*, and *Lophozonia menziesii*, dominate the higher strata of the forest. Two species of mistletoe from the family Loranthaceae parasitize the trunks of these southern beeches; *Peraxilla colensoi* and *P. tetrapetala*. Strict host specificity is prominent among *Peraxilla* mistletoes, which makes them highly dependent on their host ranges (Norton and De Lange 1999). *Peraxilla tetrapetala* parasitize *F. cliffortioides* and to a lesser extent *F. fusca*, however, the preferred host of *P. colensoi* is *L. menziesii*. Also occurring in the region are three epiphytic ferns; *Asplenium flaccidum* (Aspleniaceae), *Hymenophyllum multifidum* (Hymenophyllaceae), and *Notogrammitis billardierei* (Polypodiaceae). Unlike *Peraxilla* mistletoes, strict host specificity in epiphytes is rare, although it does occur (review in Wagner et al. 2015). In Nelson Lakes National Park, however, vascular epiphytes are often restricted to *L. menziesii* hosts, presumably because they offer the most suitable bark substrate.

Sampling

Fieldwork was carried out over a 3-yr period between April 2012 and April 2015. We sampled along 19 km of trapping lines, which traverse distinct bands of all three southern beech hosts. All trees >10 cm diameter at breast height (dbh, 1.3 m) were searched for epiphytes and mistletoes within 5 m of each trapping line. Because the trapping lines follow natural contours within the forest (i.e., trees were not felled to make the trails), edge effects were not considered to influence epiphyte and mistletoe distributions. To determine if epiphytes and mistletoes exhibited a directional bias, we quantified their cardinal orientation (in degrees) using a mirrored compass. In addition, we measured the height at which epiphytes and mistletoes occurred on their host trees. Filmy ferns have rhizomatous structures that allow plants to move laterally around the host trunk. The locality of mat-forming fronds is assumed to be the optimum habitat selected by these plants, similar to the spread of vegetation by mistletoes. As such, the cardinal orientations of mistletoes and filmy ferns were obtained by taking the angle at the midpoint between the minimum and maximum spread of vegetation. Six *P. colensoi* mistletoes were omitted from this study as they wrapped completely around their host trunks.

Microclimate measurements

We quantified the microclimatic variables hypothesized to most restrict mistletoe and epiphyte distributions: light and water, respectively. In our study region, tree aspects oriented northwest receive more sunlight than those oriented southeast. Thus, all microclimate measurements were taken on the northwest and southeast aspects of host trees. We quantified the amount of photosynthetically active radiation (PAR) that may be intercepted by mistletoe foliage by characterizing the light environment on 15 randomly selected *F. cliffortioides* trees and 15 *L. menziesii* trees between 30 and 35 cm dbh. We did not quantify the light environment on *F. fusca* because mistletoe infections were uncommon on this host. We characterized the light environment using hemispherical photography. All photographs were taken within the

Table 1. Results of Rayleigh's test of uniformity that determined whether epiphytes and mistletoes exhibited a cardinal bias in their distribution around host tree trunks.

Arboreal plants	n	Cardinal mean (degrees)	95% CI	Height (m)
Asplenium flaccidum	65	161.72 ± 1.18	159.25, 164.88	2.74 ± 0.02
Hymenophyllum multifidum	182	174.49 ± 1.06	171.62, 177.75	1.41 ± 0.02
Notogrammitis billardierei	263	146.4 ± 1.37	144.08, 149.20	0.91 ± 0.01
Peraxilla colensoi	67	331.02 ± 2.10	330.03, 331.03	3.49 ± 0.05
Peraxilla tetrapetala	70	330.47 ± 2.22	330.60, 331.1	3.44 ± 0.03

Notes: All cardinal means were significant to $P < 0.001$, which is indicative of a nonuniform distribution. Confidence limits following the parameters of a von Mises distribution and average height data are also shown. Error measurements are SE.

hour before sundown in April 2014 using a digital camera with a 180° fisheye lens attachment (Nikon 950, FC-E8, Tokyo, Japan). The resulting 60 digital images were analyzed using Canopy Gap Analyzer 2.0 (Frazer et al. 1999). In addition, we measured the relative humidity and temperature on 15 randomly selected *L. menziesii* hosts between 30 and 35 cm dbh. Measurements were made every April (2013–2015), over 10 consecutive days (following Parra et al. 2009), at 10-min intervals using HOBO temperature/relative humidity data-loggers (Onset, Bourne, Massachusetts, USA).

Plant stress measurements

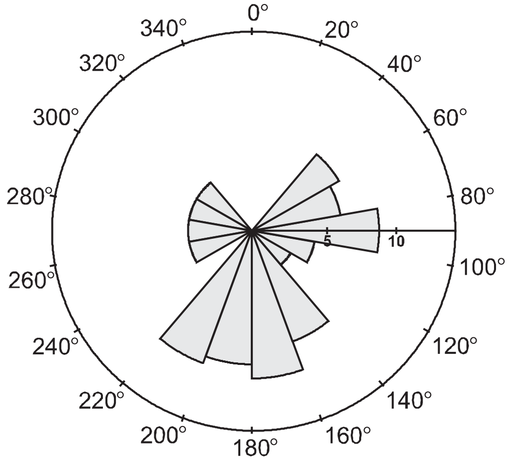
We experimentally assessed the physiological responses of mistletoes and epiphytes to reductions in light and water availability, respectively, to determine if the responses were consistent with their distribution patterns. Photosynthetic parameters of mistletoe leaves were obtained using a Li-6400 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). Field measurements were made in April 2014 using two fully expanded leaves; one oriented northwest, and one oriented southeast. Leaf temperature remained constant, relative humidity was maintained at approximately 80% and ambient CO_2 was fixed at 400 μL. Photosynthetic light response curves were created by increasing levels of photosynthetic photon flux density (PPFD) from 0 to 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Measurements were made on five plants per species. Prior to each measurement, photosynthesis was allowed to stabilize for five minutes. Chlorophyll fluorescence was used to determine the photochemical efficiency of 30 *N. billardierei* epiphytes split into two conditions of experimentally induced water stress and one control ($n = 10$ for each condition), over an experimental period of 98 d. Chlorophyll fluorescence measurements were made every 7 d using a chlorophyll fluorometer (PAM-2000; Heinz Walz GmbH, Effeltrich, Germany). Prior to taking measurements, all epiphytes were dark acclimated for 45 min.

Data analyses

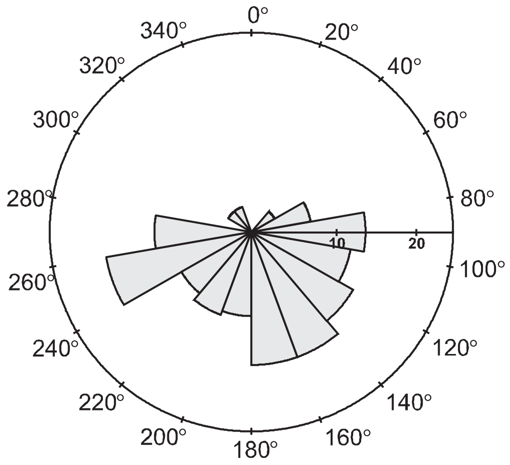
Rayleigh's test of uniformity was used to test the null hypothesis that mistletoes and epiphytes are distributed uniformly around the trunks of their host trees. Bootstrap confidence limits were obtained for the directional means following the parameters of a von Mises distribution (the circular normal distribution). Additionally, a Watson-William's two-sample test of homogeneity was used to compare the directional means of mistletoes and epiphytes. Differences in microclimate measurements between the northwest and southeast aspects of host trees were compared with Mann-Whitney U tests and Student's t tests. The photosynthetic parameters of mistletoe leaves were analyzed by fitting a light response curve. Fitting a linear regression with points below the asymptote derived the point at which light-limited CO_2 fixation occurred and the rate of CO_2 assimilation. Photosynthetic capacity was derived from the asymptote of the curve. Repeated-measures analysis of variance (RMANOVA) tested for changes in the photochemical efficiency of *N. billardierei* under two water deficit conditions and one control. We allocated "water deficit condition" as the between-subject factor and "time" as the within-subject factor. All statistical analyses were conducted in R v 3.1.2 (R Development Team 2014), with the add-on libraries CircStats v 0.2-4 (Agostinelli and Agostinelli 2009) and circular v 0.4-7 (Lund et al. 2013).

RESULTS

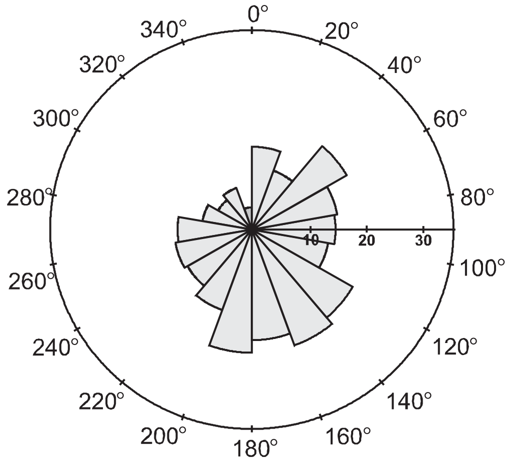
Mistletoe ($n = 137$) and epiphyte ($n = 510$) distributions were highly directional (Rayleigh's test $P < 0.001$ in all cases; Table 1). Mistletoes exhibited a cardinal bias for the northwest while epiphytes exhibited a cardinal bias for the southeast (Fig. 1). Additionally, the cardinal means of mistletoes and epiphytes were significantly different (Watson's test, $P < 0.001$). Average percent PAR was significantly higher on the northwest (33.34 ± 0.48 [mean ± SE]) compared to the southeast (28.83 ± 0.49, Mann-Whitney U test, $P = 0.006$) aspects of host trees. Mean temperatures ranged from 10.20°C on the northwest aspect to 9.61°C on the southeast aspect and did not significantly differ (Student's t test, $P = 0.29$). Average daily relative humidity (RH, %) was significantly higher on the southeast aspect (96.06 ± 0.61) compared with the northwest (90.66 ± 0.47, Mann-Whitney U test $P = 0.007$). Light-limited CO_2 fixation of mistletoe leaves occurred below a PPFD of 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in all cases except for



a) *Asplenium flaccidum, n = 65*

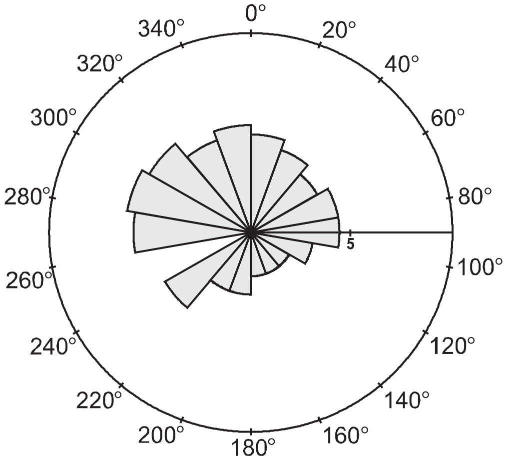


b) *Hymenophyllum multifidum, n* = 182

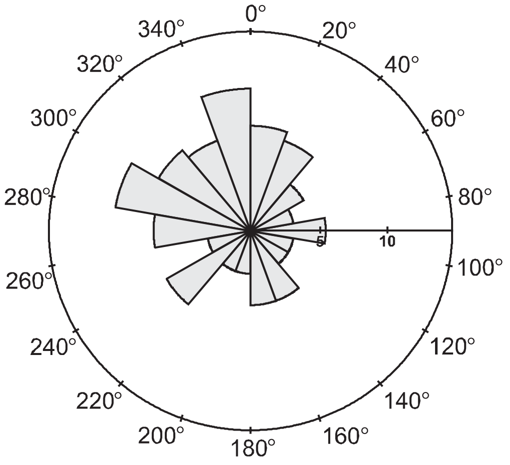


c) *Notogrammitis billardierei, n* = 263

Epiphytes



d) *Peraxilla colensoi, n* = 67



e) *Peraxilla tetrapetala, n* = 70

Mistletoes

Fig. 1. Rose diagrams illustrating the cardinal orientation (measured in degrees) of epiphytes and mistletoes as they occur radially around their host tree trunks. The length of the "petals" are proportional to the frequency of species occurrences at each cardinal direction.

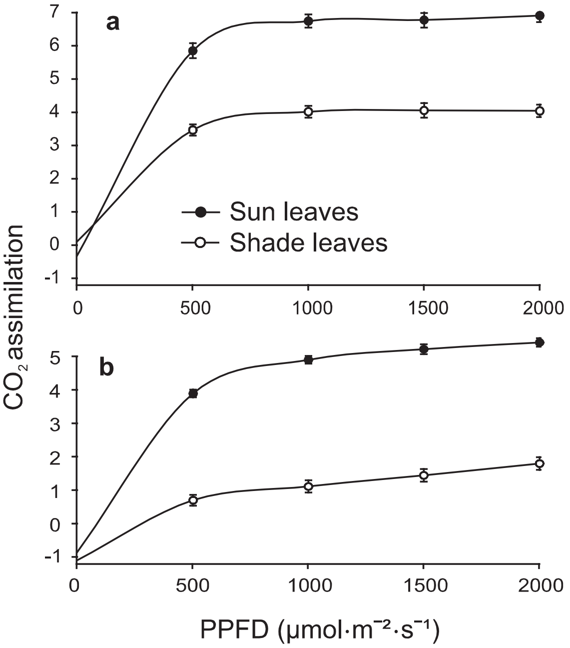


FIG. 2. Light response curve showing the relationship between CO$_2$ assimilation and photosynthetic photon flux density (PPFD) in (a) *Peraxilla tetrapetala* and (b) *P. colensoi* leaves growing on the northwest aspect (sun leaves) and southeast aspect (shade leaves) of their respective hosts. Values are averages of 10 measurements (five on sun leaves and five on shade leaves) taken on five plants of each species.

the southeast oriented leaves of *P. colensoi*, which occurred below a PPFD of 600 μmol·m^{-2}·s^{-1} (Fig. 2). *Peraxilla tetrapetala* and *P. colensoi* leaves oriented northwest assimilated CO$_2$ more efficiently than those oriented southeast, as depicted by the regression slope below the asymptote of the light response curve (northwest slope = 0.013, 0.010 and southeast slope = 0.007, 0.004, respectively). Similarly, photosynthetic capacity (A_{max}) was highest for *P. tetrapetala* and *P. colensoi* leaves growing on the northwest aspect compared with leaves growing on the southeast (northwest $A_{\max}$ = 6.91 μmol·m^{-2}·s^{-1}, 5.52 μmol·m^{-2}·s^{-1} and southeast $A_{\max}$ = 4.04 μmol·m^{-2}·s^{-1}, 1.90 μmol·m^{-2}·s^{-1}, respectively). Repeated-measures analysis of variance indicated significant effects of water deficit condition (RMANOVA, $F_{2,14}$ = 1440, $P < 0.001$) and time (RMANOVA, $F_{2,14}$ = 6.287, $P < 0.001$) on the photochemical efficiency of *N. billardierei* ferns. A significant interaction between the two factors (RMANOVA, $F_{14,28}$ = 33.642, $P < 0.001$, Fig. 3) was also observed.

DISCUSSION

To our knowledge, this is the first study to document the systematic distribution of vascular epiphytes and mistletoes in relation to a pronounced resource gradient, which exists around the trunks of trees. Mistletoes oriented northwest, parallel to gradients with higher PAR, temperature, and lower humidity. Additionally, comparisons of mistletoe photosynthetic parameters showed differences in photosynthetic capabilities both between leaves oriented to opposite cardinal orientations and between species. Perhaps the most striking was the result of *P. colensoi* leaves oriented southeast, which showed a 66% decrease in the maximum capacity to exploit light energy for photosynthesis relative to leaves oriented northwest. Comparatively, *P. tetrapetala* showed only a 44% decrease, which suggests a higher plasticity of *P. colensoi* mistletoes in response to light availability within the canopy.

While our results agree with previous observations that mistletoe occurrences are correlated with the availability of light (Shaw and Weiss 2000), the effect of light may be indirect. Mistletoes occurring at forest edges, for example, grow faster, produce more fruit, and have longer flowering times relative to mistletoes growing in forest interiors (review in Burgess et al. 2006). However, Montgomery et al. (2003), among others, attributed this positive effect to pollinator behavior rather than light availability. Similarly, mistletoe distributions may be

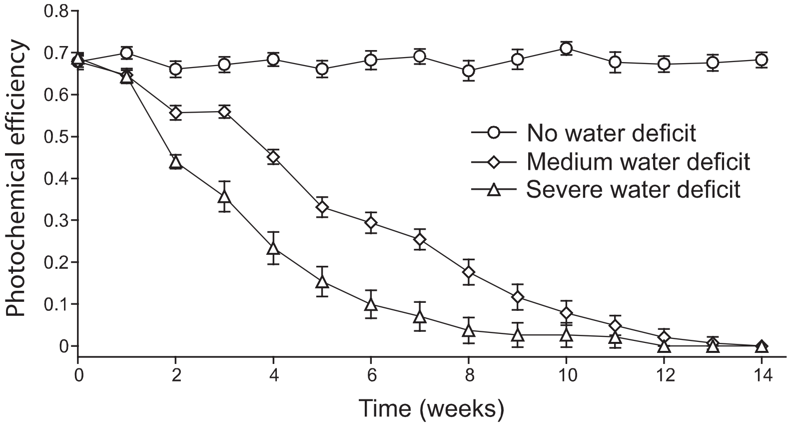


FIG. 3. Photochemical efficiency (a ratio; mean ± SE) of 30 *Notogrammitis billardierei* ferns exposed to two conditions of water deficit (medium and severe) and one control ($n = 10$ for each condition), over a 14-week experimental period.

limited by temperature. In the northern hemisphere, mistletoe range shifts to higher altitudes are attributed to rising temperatures (Dobbertin et al. 2005). Likewise, mistletoes growing in semiarid regions reportedly germinate on the cooler aspects of their hosts (Botto-Mahan et al. 2000). Thus, it is reasonable to consider that germination success of mistletoes in cooler temperate forests increases on host aspects oriented toward the sun.

Unlike mistletoes, epiphytes oriented southeast, which correlated with lower PAR, temperature, and higher humidity. Moreover, decreased photochemical efficiency was observed in water stressed plants just 10 d into a 98-d water deficit experiment. Indeed, water availability is an important determinant of epiphyte distributions (Zotz et al. 2001), and interspecific differences in desiccation tolerance may influence cardinal orientation. Previous studies comparing the effect of slope aspect on poikilohydric bryophytes and lichens at forest edges found intensified edge effects when oriented toward the sun (Hylander 2005). While poikilohydric plants make up just 0.2% of the world's vascular flora, the strategy is common among the Hymenophyllaceae, and is present in some *Asplenium* species (review in Proctor and Tuba 2002). In terms of the light environment, epiphytes that are physiologically adapted to humidity also tend to be adapted to lower light intensities (Graham and Andrade 2004). Parra et al. (2009), for example, observed that filmy ferns did not inhabit microclimates exceeding 30% light intensity. Thus, rather than selecting for habitats with high humidity, epiphytes may be selecting for lower PAR. Similar to mistletoes, temperature may also influence the cardinal orientation of epiphytes. For one, increased temperatures may induce water stress in epiphytes by evapotranspiration (Zotz and Hietz 2001). On the contrary, low temperatures may increase incidences of frost, thus limiting epiphyte distributions (Kreft et al. 2004). Bryophytes, which *N. billardierei* were found exclusively growing on, may retain water and regulate temperature (Zotz and Vollrath 2003), and may facilitate the establishment of these ferns.

This study emphasizes the importance of microclimates that exist radially around the trunks of trees as potential drivers of air plant distributions. It is important to note, however, that our findings are only representative of adult plants and neglects other life stages. Whether or not aspect effects germination and establishment of epiphytes and mistletoes, for example, needs further scrutiny. Likewise, competition for substrate space may limit epiphyte and mistletoe distributions, although evidence for this is rare (Burns and Zotz 2010). In our study, the two mistletoes *P. colensoi* and *P. tetrapetala* varied in cardinal orientation by <1°, and height by 0.05 m yet parasitized different hosts. Comparatively, all three epiphytic ferns and *P. colensoi*, which shared the same *L. menziesii* host species, differed in cardinal orientation by at least 13° and height by at least 0.5 m, which suggests subtle niche partitioning by these species. Nevertheless, due to the patchiness of suitable substrate on host trees, dispersal and establishment limitations are surely more important than competition for resources (Bennett 1987).

We believe that our study bridges a key gap in our understanding of within-tree distributions of epiphytes and mistletoes, and raises further questions on the drivers of air plant distributions. For example, what is the influence of non-vascular bryophytes on vascular epiphyte position within the canopy? At what latitudes do air plants exhibit a directional bias? How does cardinal orientation interact with other drivers of air plant within-tree distributions? By considering microclimate gradients that exist radially around the trunks of trees in other localities, further general patterns in the mechanisms behind air plant distributions may be identified.

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