Significant phorophyte (substrate) bias is not explained by fitness benefits in three epiphytic orchid species[1]

Kelli M. Gowland[2,3], Jeff Wood[4], Mark A. Clements[3], and Adrienne B. Nicotra[2,5]

[2]Division of Evolution, Ecology and Genetics, Research School of Biology, Bldg 116, Daley Road, The Australian National University, Canberra, ACT 0200, Australia; [3]Center for Plant Biodiversity Research, CSIRO—Plant Industry, GPO Box 1600, Canberra ACT 2601, Australia; and [4]Statistical Consulting Unit, John Dedman School of Mathematical Sciences, The Australian National University, Canberra ACT 0200, Australia

- *Premise*: Epiphytes rely on their phorophyte (host substrate) for support; epiphytic orchids also rely on mycorrhizal fungi for germination. Previous studies have proposed a degree of specificity in both interactions. Epiphytic orchids therefore provide an interesting system in which to examine multispecies interactions and the evolution of specialization.
- *Methods*: We examined the potential and actual distributions of three co-occurring, related epiphytic orchid species: *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *Sarcochilus parviflorus* on phorophytes in Australia's temperate dry rainforests.
- *Key results:* These three small epiphytic orchid species were all biased toward certain woody plant species, in particular, the tree *Backhousia myrtifolia*, though the extent of specificity varied. Biases toward the most common phorophyte species were not explained by increases in adult orchid fitness, nor did probability of flowering increase on *B. myrtifolia*. Indeed, individuals on this woody phorophyte tended to have fewer inflorescences than those on other woody phorophytes. Only *S. hillii* benefited from establishment on *B. myrtifolia*; it had more leaves on this phorophyte than on others.
- *Conclusions*: In many cases what appear to be simple interactions between two species may be mediated by more complex symbioses. For this system, we propose that the cause for bias in orchid distribution occurs much earlier in an orchid's life and may be due to a bias of their mycorrhizal fungi for the dominant orchid phorophytes.

Key words: Aeridinae; ecological specialization; host specificity; multispecies interactions; temperate dry rainforest.

In the absence of constraints on the ecological niche of a species, niche width typically evolves to match the amount of variation in the environment (Via and Lande, 1985; Futuyma and Moreno, 1988; Kassen, 2002). Thus, in a heterogeneous environment, one would expect selection for generalists, species that are able to use a broad range of available habitat patches. In a homogeneous environment, however, the consistency of the environment would lead to specialization on a more constrained set of conditions (Futuyma and Moreno, 1988; Kassen, 2002). Theoretically, the cost of ecological specialization is that a specialist has lower fitness outside its preferred patch type than a generalist would have. Here we examine specialization in host preferences in three species of epiphytic orchid.

Vascular epiphytes vary in their dependence on their rooting medium (Benzing, 1990). Those that are largely independent of their rooting medium use the phorophyte (the woody plant or rock substrate where the epiphyte is attached) primarily as a means of anchorage and obtain moisture and nutrients from rainwater and dust (Tremblay, 1997). Despite the separation of the epiphyte from their phorophyte's vasculature (Benzing, 1990),

some epiphytic orchid species are thought to be highly specialized with regard to their phorophyte species (Wallace, 1981; Clements, 1987; Tremblay et al., 1998). The wind-dispersed seeds of epiphytic orchids have a diversity of potential phorophytes and establishment sites in the heterogeneous environment of a rainforest, and thus evolutionary theory suggests that they should behave as ecological generalists. In such a spatially diverse environment, ecological specialists, conversely, are expected to incur a lower mean fitness across the range of phorophyte types, but a higher mean fitness on their preferred phorophyte (Futuyma and Moreno, 1988; van Tienderen, 1991; Kassen, 2002).

Twig epiphytes exemplify epiphytic plants that can be largely independent of their rooting medium. These epiphytes exist on the smallest axes of their phorophytes with minimal attachment to them (Benzing, 1990). Typically, twig epiphytes are exposed to the highest light levels and the greatest fluctuation in water availability (Chase, 1987). Often these epiphytes have a low tolerance for the high humidity that is common toward the trunk of the tree and on larger branches (Chase, 1987; Zotz, 2007). It has been predicted, therefore, that twig epiphytes are phorophyte-zone specialists (Chase, 1987), rather than phorophyte-species specialists.

Epiphytic orchids depend on one to many mycorrhizal fungi for germination. Hence, phorophyte specificity among epiphytic orchid species could reflect associations between fungal symbionts and particular woody plant species (Clements, 1987; Hietz and Hietz-Seifert, 1995b; Tremblay, 1997; Zotz and Schultz, 2008). However, among the epiphytic species of the Orchidaceae, phorophyte specificity is not common (Johansson, 1974; Sandford, 1974; Ackerman et al., 1989, 1996; Zimmerman and Olmsted, 1992; Migenis and Ackerman, 1993; Laube and Zotz, 2006; Trapnell and Hamrick, 2006; Zotz and Schultz, 2008),

and where fungal specificity has been tested for in photosynthetic epiphytic orchid species, it has only rarely been found (Tremblay et al., 1998; Otero et al., 2002).

Among the Orchidaceae of Australia many of the twig epiphytes are in the Aeridinae (syn. Sarcanthinae nom. illeg.) subtribe (Chase, 1987; Dressler, 1993). One species of the Aeridinae subtribe, *Sarcochilus hillii*, is purported to be phorophyte-specific based on field observations (Wallace, 1981; Clements, 1987). Wallace (1981) primarily found *S. hillii* on *Backhousia* spp. in the temperate, dry rainforests of southeastern Australia. In contrast, in the same investigation, two other Aeridinae species, *Plectorrhiza tridentata* and *Sarcochilus parviflorus*, were not considered to be phorophyte specific. However, Wallace's (1981) field research did not take into account the natural aggregation of some epiphyte species on individual phorophytes. Such aggregation has been recorded in other epiphytic orchid species (Yeaton and Gladstone, 1982; Hietz and Hietz-Seifert, 1995b; Tremblay, 1997; Zotz and Schultz, 2008) and is thought to be due to the leptokurtic distribution of their wind-dispersed seeds or the patchy distribution of resources such as mycorrhizal associates (Tremblay, 1997).

Detection of phorophyte species specificity is highly problematic, and there has been much criticism of the experimental approach used in studies of the distribution of epiphytic orchid species (Zotz, 2007). Logistical difficulties aside, assessing phorophyte preference requires comparing potential and actual phorophyte composition. By conducting two concurrent surveys along a single transect, we were able to describe the composition of the woody plant flora of a forest (potential phorophytes), as well as the actual phorophyte composition of an epiphytic community. We then replicated this across a range of disparate habitats to enable generality in the interpretation of our results.

The purpose of the present investigation was to determine (1) whether these three related epiphytic orchid species, *S. hillii*, *P. tridentata*, and *S. parviflorus*, prefer specific phorophyte species; (2) whether particular phorophyte/habitat characteristics are associated with the presence of these orchid species; (3) if so, whether the preferred phorophyte confers a fitness advantage on any of the orchid species; and (4) whether orchid fitness increases with particular characteristics of the location of establishment. There was no a priori reason to expect specificity, rather there is a large potential cost to specialization, and thus our null hypothesis was that these small epiphytic orchid species are distributed randomly throughout their habitat.

MATERIALS AND METHODS

Field sites and study species—*Sarcochilus hillii* (F.Muell.) F.Muell., *Sarcochilus parviflorus* Lindl. (formerly *S. olivaceous* Lindl., Jones and Clements, 2006), and *Plectorrhiza tridentata* (Lindl.) Dockr. are small, perennial, monopodial epiphytes found in the coastal ranges of eastern Australia. All three orchid species co-occur at four field sites (Table 1). The area of habitat at each site is at least 50 × 100 m; and all sites are located along creek lines. The most southerly site surveyed is Wagonga State Forest (Wagonga SF) which is 36 km south of the Wanderra State Forest (Wanderra SF) site, which, in turn, is 436 km south of two sites in Chichester State Forest that we call Chichester Hill and Chichester Creek (Chichester Ck) (Table 1). These latter two sites are separated by 30 m at their closest point, but are disparate in ecology. The Chichester Ck site is located in a flat rock creek bed and bounded by water; the other three sites are bounded by sclerophyll forest at or near the upper limits of the transect.

Survey design—A series of parallel transects, spaced 10 m apart and typically 50 m long (except where this extended beyond orchid habitat), were run perpendicular to the angle of the creek. Sampling was conducted every 4 m at

transect points. A minimum of 100 transect points were scored at each site. The number of transects sampled was increased as necessary to ensure at least 20 individuals of each orchid species were surveyed at each site.

At each transect point, a 4 × 4 × 4 m volume was searched, with the transect point at the center. Because some individuals of these orchid species occurred above this height range, we conducted preliminary investigations above 4 m. However, there was no indication that the phorophyte associations of these orchid species differed beyond this range. At each transect point, canopy cover was assessed against calibrated photographs with different percentage cover. To determine the phorophyte flora of each orchid species, we located the closest individual (of each orchid species) to the transect point and identified its phorophyte. Identification of the orchid species was confirmed by staff at the Australian National Herbarium, Canberra, with reference to numerous existing specimens; vouchers were not lodged.

To determine the woody plant composition of the forest, we identified the closest woody plant to each transect point that had a basal diameter (measured above buttressing roots, if applicable) greater than 1 cm. For all woody plants surveyed (that is, both the closest woody plant and the phorophytes of the closest orchids), the height and basal diameter were recorded; if the plant was multistemmed, only the diameter of the largest stem was recorded. Additionally, the amount of moss and lichen cover of the trunk and major branches was determined and grouped according to the following categories: 0%, 25%, 50%, 75%, and 100%.

The overall presence or absence of each orchid species was noted for each woody plant scored. In these searches for orchid presence, the determination of a nonphorophyte should be treated with some caution; established orchids may have been missed given the small size of these species and/or a location beyond easy visual range.

For the closest orchid to the transect point of each species, we recorded the following characteristics as indicators of fitness (i.e., size and reproductive potential): the number of leaves, length of longest leaf (Pino et al., 2002; Tremblay, 2006), and the total number of inflorescences (old and new) (Zotz, 1998; Tremblay, 2006). Measures of fitness such as pollinaria removal or fruit set would have proved more direct estimates of adult fitness; however, such measurements were beyond the scope of this investigation. Next, we recorded where the orchid established on its phorophyte by measuring the orchid's height above ground (height of establishment site) and the diameter of the phorophyte at the point of establishment.

Statistical analysis—A maximum likelihood method was used to determine whether each orchid species preferred particular phorophyte species (Appendix S1, see online file at http://www.amjbot.org/cgi/content/full/ajb.1000241/DC1). Sites were analyzed individually because of the disparity in woody plant species between the sites. Woody plant species that comprised less than 3% of the forest ecosystem were grouped into a category called "others". One dead tree and two woody vines could not be identified and were included in the "others" category.

Generalized linear mixed models (GLMMs) (McCulloch and Searle, 2001) were used to determine which woody plant and/or habitat characteristics might have contributed to establishment of these orchid species. The response variable was the absolute presence/absence of each orchid species. That is, each woody plant that had a particular orchid species on it, regardless of whether that orchid was the closest or not, was given the value 1, and those without were given the value 0. Site, transect, and distance along transect were fitted as random effects. Fixed effects were moss, lichen, and canopy cover; phorophyte height; and basal diameter (height and basal diameter of phorophytes were $\log_e$ transformed to meet assumptions of normality).

Rocks constituted a major component of the growth substrates of *S. parviflorus* at Wanderra SF and Chichester Ck. Orchids established on rocks were not included in any of the statistical analyses unless stated otherwise. Additionally, only seven *S. hillii* individuals were found at Chichester Hill, and so the data for this species from this site were not sufficient for statistical analysis.

Because of the abundance of *Backhousia myrtifolia* Hook. & Harv. among the phorophyte flora of all three orchid species, we tested whether this tree species conferred a fitness advantage to its epiphytic orchids. To determine whether establishment on *B. myrtifolia*, compared with other woody phorophytes, made it more likely that these orchid species would produce inflorescences we used a replicated *G*-test (Sokal and Rohlf, 1981). In these analyses, the observed number of flowering individuals of each orchid species on *B. myrtifolia* or other woody phorophytes was compared to the expected number, given the observed proportion of orchid plants flowering in the population as a whole.

We next tested whether each of these orchid species had more inflorescences, more leaves or longer leaves on their preferred phorophyte. Because the numbers of each orchid species at each site and on *B. myrtifolia* varied (the

TABLE 1.   Field site locations in eastern Australia and climatic features. Climatic features obtained from metadata sourced from Commonwealth Scientific and Industrial Research Organization, Land and Water, Canberra, Australia. Site names abbreviations: SF = State Forest; Ck = Creek; Aspect abbreviations: E = east; S = south; SE = southeast

Site	Latitude	Longitude	Aspect	Elevation (m a.s.l.)	Mean annual rainfall (mm)	Mean daily max. temp. (°C)	Mean daily min. temp. (°C)
Wagonga SF	S36°11.512′	E150°03.466′	SE	30–50	953	20	11
Wanderra SF	S35°52.519′	E149°59.229′	SE	100–130	960	21	10
Chichester Hill	S32°14.150′	E151°43.576′	E	380–400	1253	21	10
Chichester Ck	S32°14.150′	E151°43.576′	S	350–370	1253	21	10

terms were nonorthogonal), the data were analyzed using residual maximum likelihood, REML (Patterson and Thompson, 1971). Phorophyte (*B. myrtifolia* or "other woody phorophyte") and site were fitted as fixed effects. There were two individuals of *P. tridentata* at Wagonga SF whose leaf and inflorescence number were more than three standard deviations away from their respective means and had high leverage in the analyses so these individuals were excluded from analyses of these variables. All fitness characteristics were log$_e$ transformed to meet the assumption of normality; however, for each orchid species a small number (1–3) of individuals had a leaf length of <1 cm, so 1 was added to all length values before transformation.

The high number of *S. parviflorus* individuals on rock at two of the sites led us to ask whether there was a fitness advantage to this orchid species living on rock. Consequently, we looked at the response of the fitness characteristics of these orchid species growing on rock compared with those on woody plants using an additional REML model (Patterson and Thompson, 1971). Phorophyte type (woody plant or rock) and site were fitted as fixed effects; random effects were number of leaves, length of longest leaf, and number of inflorescences. The latter two characteristics were log$_e$-transformed to meet the assumption of normality (and again 1 was added to leaf lengths before transformation). Only Wanderra SF and Chichester Ck were included in these analyses because there were insufficient *S. parviflorus* individuals on rock at the other sites.

Linear mixed models (McCulloch and Searle, 2001) were used to determine whether the orchid fitness characteristics (number of leaves and inflorescences and length of longest leaf) responded to physical characteristics of the phorophyte or habitat. Site, transect, and transect points were included as random effects. For each orchid species, a separate model was fitted for each fitness characteristic measured. The explanatory variables fitted were the diameter at point of establishment, orchid height, phorophyte height, phorophyte basal diameter, phorophyte species, canopy cover, and moss and lichen cover.

The described analyses revealed that the effect of phorophyte species was significant for only one variable, the length of leaves in just one orchid species, *P. tridentata*. An additional analysis was used to investigate this effect, with the less common phorophyte species grouped according to frequency [rare, *N* = 26; moderate, *N* = 32; *B. myrtifolia*, *N* = 94; *Notelaea venosa* F.Muell., *N* = 16; and *Tristaniopsis laurina* (Sm.) Peter G.Wilson & J.T.Waterh., *N* = 15], and the model was fitted again.

The maximum likelihood model was fitted using the program S-PLUS 6 for Windows (S-PLUS, TIBCO Software, Palo Alto, California, USA) and all GLMs, GLMMs, and REMLs were fitted using the program GenStat for Windows (7th ed.) (Payne et al., 2003).

RESULTS

Sites varied in structure and composition of woody plant species (Table 2; Fig. 1). Fifty-four species of woody plants from 26 families (Appendix S2) comprised the forest and/or phorophyte flora of these orchid species across all four sites. *Backhousia myrtifolia* was the most common woody plant species at all sites except Chichester Hill. *Sarcochilus hillii*, *P. tridentata*, and *S. parviflorus* each were significantly biased toward *B. myrtifolia*, although this bias varied across the four sites (Fig. 1; Table 3). Only one other woody plant species represented more than 18% of the woody plant flora at any one site and that was *Notelaea venosa* at Wanderra SF. At this site, *N. venosa* comprised more than 28% of the woody plant flora.

Orchid distribution—This investigation of phorophyte species and characteristics revealed that *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *S. parviflorus* were distributed nonrandomly across the potential phorophytes in their habitat. *Sarcochilus hillii* was found on 15 of the 37 (40.5%) woody plant species across the three sites in which it was recorded. Most often *S. hillii* was found on the most common species at each site, *B. myrtifolia*, but only at Wagonga SF was this bias statistically significant (Fig. 1; Table 3). Occasionally *S. hillii* occurred on rock (five times) but it was never found on *Acmena smithii* (Poir.) Merr. & L. M. Perry. Despite this species being a common woody plant at both Wagonga SF and Wanderra SF.

Plectorrhiza tridentata exhibited an overall bias toward *B. myrtifolia* at all sites as well; this difference was statistically significant at two of the four sites (Fig. 1; Table 3). At Chichester Hill, *B. myrtifolia* represented only 12.6% of the woody plants, but 36.6% of *P. tridentata* individuals at this site were on *B. myrtifolia*. Other than this bias toward *B. myrtifolia*, *P. tridentata* was the most broadly distributed of these three orchid species, occurring on 27 of the 54 (50%) woody plant species identified at these four sites and without any clear biases for or against any other woody plant species. Only twice did this orchid species occur on rock.

In contrast, despite *S. parviflorus* occurring at least once on 22 of the 54 (41%) woody plant species surveyed, this orchid species had the most significantly biased association across all four sites (Fig. 1; Table 3). *Backhousia myrtifolia* comprised the bulk of the phorophyte flora at all sites excluding Chichester Hill, where *Tristaniopsis laurina* was its dominant woody

TABLE 2.   Site characteristics. (A) Composition of structural features and canopy cover are expressed as a percentage. (B) Canopy height of the closest woody plants, including shrubs and trees but not vines. Number of transect points at each site: Wagonga SF = 169; Wanderra SF = 130; Chichester Hill = 143; and Chichester Ck = 105; *N* = total number of woody plant species at each site;

Structural feature	Wagonga SF *N* = 28	Wanderra SF *N* = 12	Chichester Hill *N* = 30	Chichester Ck *N* = 17
A) Percentage composition				
Vine (%)	17	12	16	1
Shrub (%)	10	1	17	0
Tree (%)	73	82	67	99
No woody plants at transect points (%)	0 [a]	5 [a]	0	0
Mean canopy cover (SD)	62 (17)	51 (23)	66 (22)	59 (19)
B) Canopy height				
Range (m)	1–40	1–26	1.4–25	0.75–22
Mean (m)	7.3	8	5.5	7.3

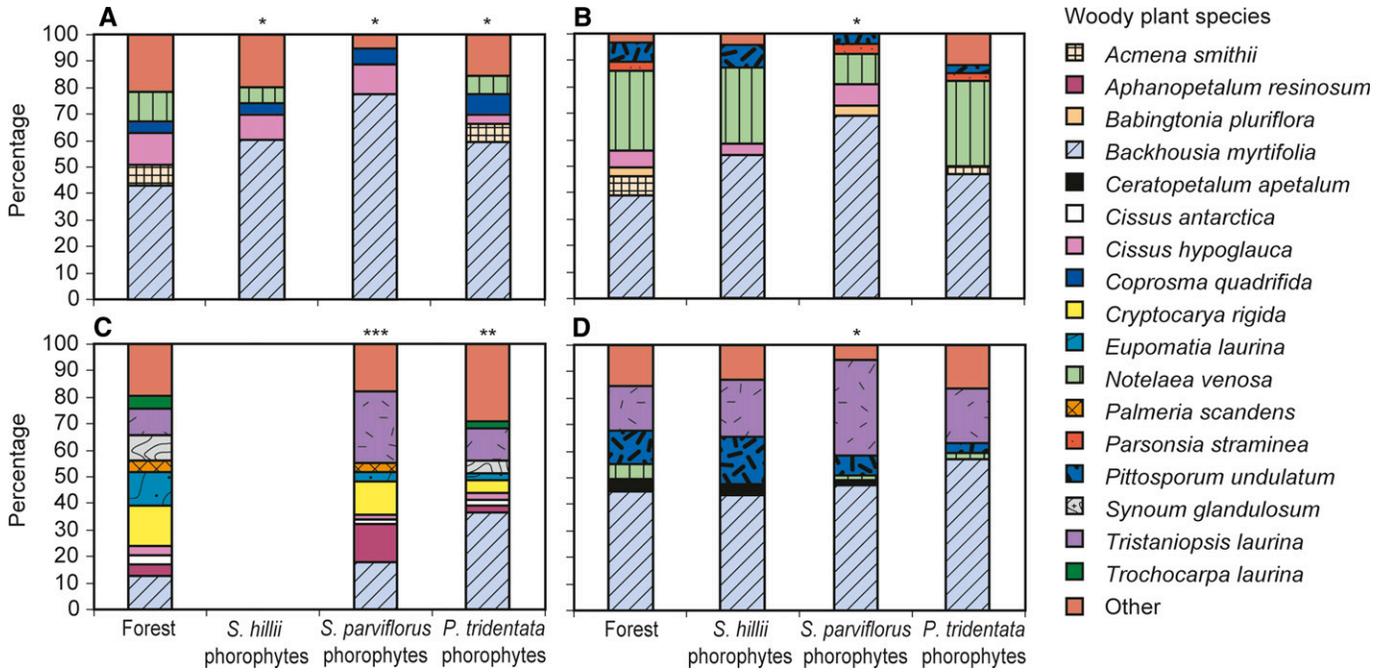[a] Orchids were present on rock at some of these transect points.

Fig. 1. Woody plant species of the forest and phorophyte flora of *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *S. parviflorus* at each site in eastern Australia. The proportion of the forest and phorophyte flora represented by each woody plant species is depicted at (A) Wagonga State Forest, (B) Wanderra State Forest, (C) Chichester Hill, and (D) Chichester Creek. Significant deviation of phorophyte species composition from the forests woody plant species composition for each species: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. There were not enough plants of *S. hillii* at Chichester Hill to include in the analysis.

phorophyte. This latter tree species was also a major component of the phorophyte flora of *S. parviflorus* at the adjacent Chichester Ck site. Additionally, *S. parviflorus* was not only more prevalent on some woody plant species than expected, but it was underrepresented on others. For example, like *S. hillii*, *A. smithii* was never a phorophyte for *S. parviflorus*. However, 67 of the 222 *S. parviflorus* individuals sampled were found on rock, comprising 59% and 31% of this species' phorophytes at Wanderra SF and Chichester Ck, respectively.

The only characteristics that differed significantly between woody plants that were and were not phorophytes were the amount of moss cover (Fig. 2) and basal diameter of the phorophytes. All three orchid species had significant biases toward woody plants that had a high (50–75%) moss cover on the trunk

(*S. hillii*: Wald statistic = 46.12, 3 df, $P <0.001$; *P. tridentata*: Wald statistic = 41.94, 3 df, $P <0.001$; and *S. parviflorus*: Wald statistic = 41.57, 3 df, $P <0.001$). Despite this preference for a high moss cover on the phorophytes of these orchid species, moss was not found exactly at the point of establishment for *S. hillii* and *P. tridentata*, but was commonly found at the establishment site of *S. parviflorus* (K. M. Gowland personal observation). The other characteristic that distinguished phorophytes of *P. tridentata* and *S. parviflorus* from other woody plants was basal diameter, both of these orchid species were more likely to be found on woody plants with a larger basal diameter (*P. tridentata*: Wald statistic = 4.52, 1 df, $P = 0.034$ and *S. parviflorus*: Wald statistic = 15.66, 1 df, $P <0.001$). No significant difference was detected between phorophytes and nonphorophytes

TABLE 3. Maximum likelihood analysis of phorophyte specificity of *Sacrochilus hillii*, *Plectorrhiza tridentata*, and *S. parviflorus* at each site in eastern Australia. Site details are in Table 1; df = $s - 1$, where s = the number of species of woody plants in a forest in which minor species (those comprising <3% of ecosystem) are combined into a category "others". Two of the closest individuals of *S. parviflorus* at Wagonga SF were found on rock and excluded from the analysis.

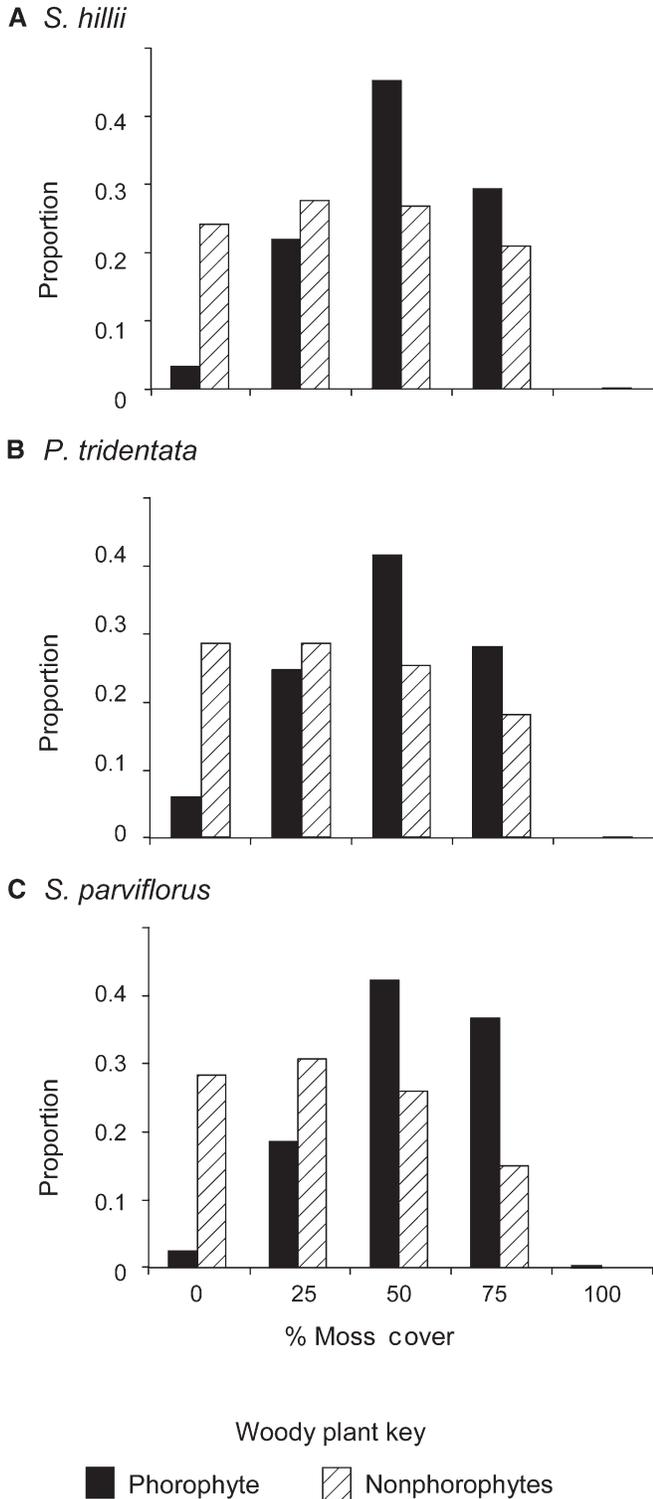| Orchid species	Site	No. of closest woody plants	No. of orchid phorophytes surveyed	Deviance change	df	Mean change	P
S. hillii	Wagonga SF	168	50	11.78	5	2.36	0.038
	Wanderra SF	123	24	7.92	7	1.13	0.34
	Chichester Ck	105	23	3.26	5	0.65	0.66
P. tridentata	Wagonga SF	168	59	11.81	5	2.36	0.038
	Wanderra SF	123	34	12.36	7	1.77	0.089
	Chichester Hill	143	41	27.82	10	2.78	0.002
	Chichester Ck	105	49	10.58	5	2.12	0.06
S. parviflorus	Wagonga SF	168	18	13.31	5	2.66	0.021
	Wanderra SF	123	26	14.54	7	2.08	0.042
	Chichester Hill	143	56	40.75	10	4.07	<0.001
	Chichester Ck	105	55	14.77	5	2.95	0.011

A *S. hillii*

B *P. tridentata*

C *S. parviflorus*

Woody plant key

■ Phorophyte   ▨ Nonphorophytes

Fig. 2. Moss cover on phorophytes (solid columns) and nonphorophytes (hatched columns) of *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *S. parviflorus*; sites have been grouped. All orchid species were biased toward woody plants with a relatively high (50–75%) moss cover ($P <$ 0.001 for all three orchid species). (A) *S. hillii*: phorophytes, $N = 150$; nonphorophytes, $N = 425$; (B) *P. tridentata*: phorophytes, $N = 269$; nonphorophytes, $N = 511$; (C) *S. parviflorus*: phorophytes, $N = 232$; nonphorophytes, $N = 548$

for any of these orchid species in relation to lichen or canopy cover or phorophyte height.

All three orchid species established primarily on the narrow axes of their phorophytes, although all were occasionally found on larger establishment sites as well (Table 4). *Sarcochilus parviflorus* established on the largest branches ranging from 0.2–60.0 cm (mean ± SE: 8.64 cm ± 0.89). At Chichester Hill, the establishment sites for *S. parviflorus* were approximately half the mean diameter of those of the other three sites (Table 4).

Effect of dominant phorophytes on orchid fitness—Having found that *S. hillii*, *P. tridentata*, and *S. parviflorus* were more likely to be found on *B. myrtifolia* than on other woody phorophytes, we used replicated *G*-tests of goodness of fit to test whether these orchid species also had a higher probability of flowering if growing on *B. myrtifolia*. We found that the probability of flowering was not significantly greater on *B. myrtifolia* than on other woody phorophytes for any of the orchid species at any site (results not shown).

We next asked whether an orchid is likely to produce more inflorescences on *B. myrtifolia* when it does flower. A total of 72% of *S. hillii*, 60% of *P. tridentata*, and 42% of *S. parviflorus* individuals on woody phorophytes had inflorescences. Among the flowering *S. hillii* individuals, inflorescence number differed significantly depending on whether the woody phorophyte was *B. myrtifolia* or not (Wald statistic = 4.25, df = 1, $P =$ 0.039). The cause of this effect appears to be largely due to one site; Wanderra SF. Counter to the other two sites, *S. hillii* individuals at Wanderra SF had substantially more inflorescences when established on *B. myrtifolia* than on other woody phorophytes (Fig. 3A). The disproportionately higher number of inflorescences on *S. hillii* individuals on *B. myrtifolia* at Wanderra SF is also the most probable cause of the significant site effect detected (Wald statistic = 12.37, df = 2, $P = 0.002$). In contrast, *P. tridentata* had fewer inflorescences on *B. myrtifolia* than other woody phorophytes (Fig. 3B; Wald statistic = 4.27, df = 1, $P = 0.039$).

Because plant size is generally correlated with fitness, we asked whether orchids were larger (had more or longer leaves) on *B. myrtifolia* than on other woody phorophytes. *Sarcochilus hillii* and *S. parviflorus* had more leaves when established on *B. myrtifolia* than on other woody phorophytes (Fig. 3D and 3F, respectively); however, only for *S. hillii* was this difference significant (Wald statistic = 5.35, df = 1, $P = 0.021$). Both *S. hillii* and *S. parviflorus* also varied significantly in leaf number

TABLE 4. Diameter of establishment for *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *S. parviflorus* across all sites surveyed. Site details are in Table 1. N = number of individual orchids sampled; SE = standard error

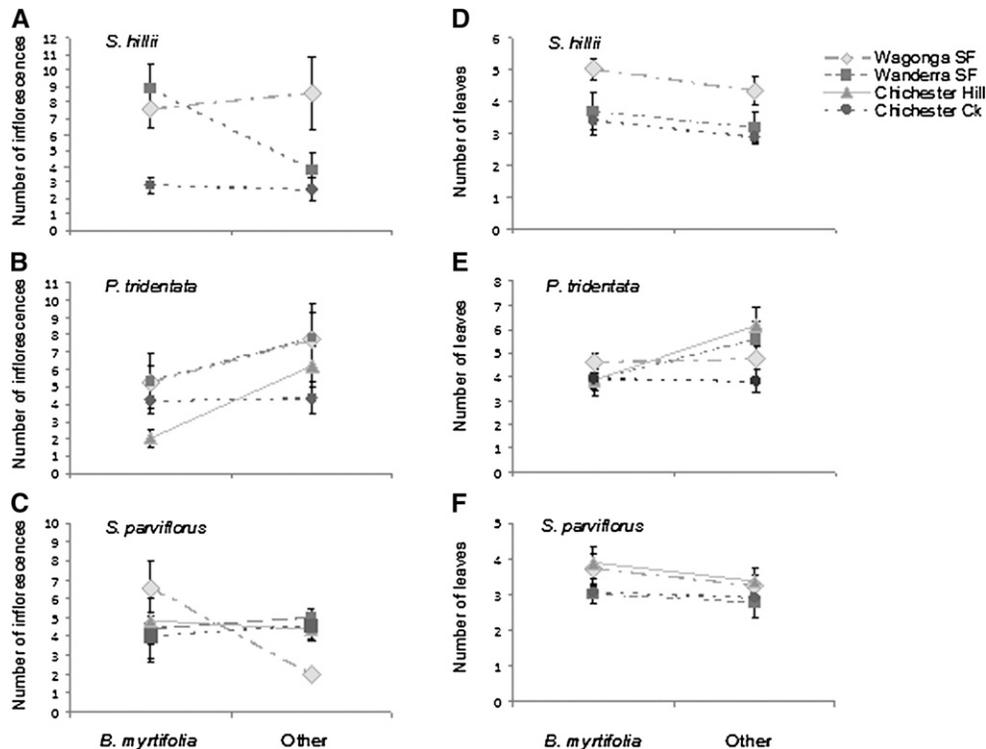| Orchid species	Site	N	Median	Mean	SE
S. hillii	Wagonga SF	50	1.6	2.6	0.46
	Wanderra SF	24	5.8	6.8	1.05
	Chichester Ck	23	2.8	3.8	0.86
P. tridentata	Wagonga SF	59	0.4	2.4	0.64
	Wanderra SF	34	1.2	2.7	0.70
	Chichester Hill	41	1.7	3.6	0.81
	Chichester Ck	49	0.8	2.2	0.38
S. parviflorus	Wagonga SF	18	6.3	11.0	3.40
	Wanderra SF	26	5.8	11.1	2.82
	Chichester Hill	56	3.4	5.1	0.81
	Chichester Ck	55	5.6	10.3	1.56

Fig. 3. Number of leaves and inflorescences on *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *S. parviflorus* on *Backhousia myrtifolia* compared to other woody phorophytes at each site in eastern Australia. Site information is in Table 1. Mean and standard error indicated by marker and error bars. Only those individuals with inflorescence stalks still attached were included in the inflorescence analyses. Typically, 5–23 individuals of each orchid species were flowering in each phorophyte category at each site; however, only one individual of *S. parviflorus* had an inflorescence stalk on other woody phorophytes at Wagonga SF and at Wanderra SF.

according to site (*S. hillii*: Wald statistic = 16.35, df = 2, *P* <0.001; *S. parviflorus*: 9.72, df = 3, *P* = 0.021). Counter to the expectation that the dominant phorophyte might confer a fitness advantage to its epiphytic orchids, *P. tridentata* individuals on *B. myrtifolia* had significantly fewer leaves than those on other woody phorophytes (Wald statistic = 4.97, df = 1, *P* = 0.026; Fig. 3E), although this primarily appears to be in response to two sites. No difference was found in leaf length for any of the orchid species on *B. myrtifolia* compared to the other woody phorophytes.

Sarcochilus parviflorus frequently established on rock, but we found that *S. parviflorus* individuals established on woody plants had significantly more inflorescences compared to those established on rock (log$_e$ inflorescences: Wald statistic = 4.81, df = 1, *P* = 0.028). Excluding those individuals without any inflorescences, the number of inflorescences on *S. parviflorus* individuals on rock is averaged (adjusted) to 2.0 (±1.3 SE) compared to 3.3 (±1.3 SE) on woody plant phorophytes. Furthermore, *S. parviflorus* individuals had significantly longer leaves on woody plants than rocks (Wald statistic = 5.68, df = 1, *P* = 0.017). Additionally, *S. parviflorus* individuals also had more leaves on woody compared to rock phorophytes; however, the latter difference was not statistically significant.

Effect of establishment site on orchid fitness—Given that establishment on a dominant phorophyte does not necessarily equate to fitness benefits to an individual orchid, we next asked whether other characteristics of an orchid's establishment site conferred a fitness advantage to the respective orchid.

Two main features of the establishment site affected the fitness characteristics of *S. hillii*: the height of the orchid's establishment site and the height of the phorophyte itself (Table 5). The average number of inflorescences on *S. hillii* individuals increased with increasing phorophyte height. Likewise, the number of leaves and length of longest leaf on *S. hillii* increased with increasing phorophyte height and increasing establishment site height. A moderate to high moss cover also had a significantly positive effect on leaf number (Table 5).

Despite the overwhelming majority of *P. tridentata* plants being established on small branches (<5 cm diameter) and having a high number of inflorescence stalks (mean = 6.5 ± 0.5 SE), there was a general increase in inflorescence and leaf number for this orchid species on larger branches (Table 5). Additionally, the number of leaves on *P. tridentata* increased with increasing canopy cover and increasing orchid height above ground (Table 5). Furthermore, the mean length of the longest leaf in *P. tridentata* (4.5 cm ± 0.13 SE) increased with increasing canopy cover and diameter at establishment point and was significantly affected by the phorophyte species (Table 5). However, the longest leaf was not on the dominant phorophyte. When the scarcer phorophyte species were grouped according to relative abundance, the model revealed that the rarer phorophyte species held *P. tridentata* individuals with the longest leaves: rare (5.5 cm ± 0.32 SE), moderate (4.4 cm ± 0.29 SE), *B. myrtifolia* (4.4 cm ± 0.17 SE), *N. venosa* (4.5 cm ± 0.41 SE), and *T. laurina* (3.6 cm ± 0.43 SE). That is, *P. tridentata* individuals on its most common phorophytes had significantly smaller leaves compared to individuals on the rarer phorophyte species.

TABLE 5.   Woody plant and habitat features affecting characteristics of *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *S. parviflorus*. Orchid height refers to height that orchid was established. Analyses were conducted using generalized linear models.

Orchid species	Response character	Term	df	Deviance ratio	P
S. hillii	No. of leaves	Moss	3	3.47	0.019
		Orchid height	1	9.67	0.002
	No. of inflorescences	Phorophyte height	1	8.36	0.005
	Longest leaf	Phorophyte height	1	5.52	0.021
		Orchid height	1	14.19	<0.001
P. tridentata	No. of leaves	Canopy cover	1	5.99	0.015
		Diameter at establishment	1	6.11	0.014
		Orchid height	1	8.21	0.005
	No. of inflorescences	Diameter at establishment	1	3.7	0.056
		Phorophyte height	1	3.82	0.052
		Orchid height	1	3.48	0.064
	Longest leaf	Canopy cover	1	12.17	<0.001
		Diameter at establishment	1	5.7	0.018
		Woody plant species	26	1.82	0.014
S. parviflorus	No. of leaves	Orchid height	1	4.75	0.031
	No. of inflorescences	Canopy cover	1	8.34	0.004
		Orchid height	1	7.9	0.006
	Longest leaf	Orchid height	1	7.36	0.007

Finally, the average number of inflorescences on *S. parviflorus* individuals (3.7 ± 1.1 SE) increased significantly with increases in canopy cover and height of establishment (Table 5). Similarly, the number of leaves and length of the longest leaf increased with increasing orchid height above ground.

DISCUSSION

Our study examined the distribution of three species of orchid, *Sarcochilus hillii*, *Plectorrhiza tridentata*, and *Sarcochilus parviflorus*, to assess whether these epiphytic species had signs of phorophyte (host) specificity. We found the three species were not distributed randomly throughout their habitat. Rather, each of these orchid species had varying degrees of ecological specificity for (and against) particular phorophyte species and phorophyte/habitat characteristics. However, counter to the prevailing theory on the evolution of specialization (Futuyma and Moreno, 1988), we found no evidence that these species have a higher mean fitness in their preferred niche. That is, no trade-off for their specialization was detected. Orchid fitness was affected by particular characteristics of establishment site; these were not characteristics associated with the most common establishment site.

Phorophyte specificity—Across the four sites sampled, each of these orchid species differed in the composition of their phorophytes (Fig. 1): *S. hillii* had the broadest phorophyte species niche with limited deviation from the forest's woody plant flora; *P. tridentata*, although having the broadest range of phorophyte species, had the most marked bias toward *B. myrtifolia* (demonstrated at Chichester Hill); and *S. parviflorus* had the narrowest phorophyte niche of the three species, predominantly occurring on a select few woody plant species at each site. *Sarcochilus parviflorus* had both the most significant bias in its phorophyte flora at each of the sites and also the most marked changes in its phorophyte bias across the four sites surveyed (Fig. 1; Table 3).

Despite these biased distributions, the probability of flowering did not increase for any of these orchid species on *B. myrtifolia* compared to other woody phorophytes. Moreover, with the exception of *S. hillii* at Wanderra SF, these orchid species

formed fewer inflorescences on *B. myrtifolia* than on other woody phorophytes, and *P. tridentata* had more leaves on rarer woody plant species. Additionally, *S. parviflorus* did not receive any fitness benefits for establishing on rock phorophytes either, despite rocks representing a substantial component of its phorophyte composition at two sites.

Site variation—Phorophyte specificity has been shown here, and previously, to vary across the geographic range of epiphyte species (Johansson, 1974; Laube and Zotz, 2006; Trapnell and Hamrick, 2006). Variability in ecological specialization is such that a widely distributed species can differentiate and become an ecological specialist in different locations (Trapnell and Hamrick, 2006). For example, normally epiphytic plants can become terrestrial in relatively dry environments (Johansson, 1974). This geographic variability may be used to identify key components of a species ecological niche. For example, *B. myrtifolia* comprised ca. 40% of the woody plants of the forest and phorophyte flora at all sites except for Chichester Hill, where it represented only 12.6% of the forest's woody flora. At this site, the distribution and establishment characteristics of these orchid species, and their phorophytes, differed from the other sites. The variation in phorophyte composition and preference (Fig. 1) was probably a response to the altered environmental conditions at this site. Chichester Hill had the highest diversity of woody plant species (Fig. 1), the highest structural diversity (Table 2) of the four sites investigated and had 25% more rain than the most structurally similar site, Wagonga SF (Table 1). Hence, we propose that these factors contribute to Chichester Hill being a more humid environment and that this increased humidity selects against establishment by *B. myrtifolia* and *S. hillii*. Both *B. myrtifolia* and *S. hillii* are more abundant at the adjacent, but more open, Chichester Ck site (Table 2). Furthermore, we expect that the higher humidity at Chichester Hill also explains the altered establishment characteristics of *S. parviflorus* at this site (where *S. parviflorus* becomes more common on narrower branches, Table 4). These results demonstrate that sampling across multiple disparate sites can better identify critical components of a species niche.

Specificity and establishment site characteristics—Desiccation is considered the primary ecological constraint of all epiphytes

(Benzing, 1998; Zotz, 1998; Annaselvam and Parthasarathy, 2001). Epiphyte distribution patterns are frequently the result of a balance between high light intensities and a tolerance for the evaporative power of the air (Johansson, 1974). These orchids are all monopodial epiphytes, and as such, they lack the substantial water and nutrient storage organs of their pseudobulbous relatives (Wallace, 1981; Ng and Hew, 2000), potentially subjecting these species to a greater desiccation threat (Johansson, 1974). Thus, the prevalence of these and other orchid species (Tremblay et al., 1998; Rasmussen, 2002) on woody plants with a high moss cover (Fig. 2) may be a consequence of higher localized humidity within the branches of such woody plants. The distinct ecological niches of these orchid species and their variability across these disparate sites provide an indication of the extent of this stress for each individual species.

The distributions of *S. hillii*, *P. tridentata*, and *S. parviflorus* were biased toward woody plants with relatively high moss cover (Fig. 2); however, it appeared that the moss was rarely at the point of establishment for *S. hillii* and *P. tridentata*. We predict that, rather than moss being a direct water or nutrient reservoir for the orchid (as suspected for other orchid species, see Tremblay et al., 1998), high moss cover is indicative of an increased local humidity in these relatively dry temperate rainforests. Therefore, we hypothesize that high moss cover reflects a suitable ecological niche for orchid mycorrhizal fungi to establish, although it is unlikely that the fungi have a specific association with the moss (Read et al., 2000; Peterson and Massicotte, 2004). Compared to *S. hillii* and *P. tridentata*, *S. parviflorus* occurs on larger establishment sites (Table 4) and with moss present at the establishment site. Therefore, we suggest that *S. parviflorus* is an orchid with a comparatively humid ecological niche. *Sarcochilus hillii* and *P. tridentata*, on the other hand, are both epiphytes of the narrowest axes (smallest branches) of the phorophyte. Epiphytes of this zone are thought to decline as humidity increases (Chase, 1987).

Nevertheless, the key features of a phorophyte for these orchid species—moss, size, and species of woody plant—do not completely explain the distributional biases of these orchid species. The dominant woody phorophytes *B. myrtifolia* and *Tristaniopsis laurina* are part of the group of woody plants that had the highest quantity of moss on them, but so are nonphorophytes such as *Acmena smithii* (data not shown). Distributional bias toward woody plants with a larger basal diameter, as detected here for *S. parviflorus* and *P. tridentata*, has also been noted among other epiphyte species (Catling et al., 1986; Hietz and Hietz-Seifert, 1995a). Larger phorophyte size is considered to be a reflection of the increased age and, hence, exposure time and available surface area, for epiphyte propagules to establish (Catling et al., 1986). Thus, larger phorophyte size is unlikely to explain the species bias detected for *P. tridentata* and *S. parviflorus* either. Rather, the distributional biases of *S. hillii*, *P. tridentata* and *S. parviflorus* might be better explained by other characteristics of their phorophyte, for example, physical and chemical characteristics of their host substrate.

Morphological and chemical characteristics of a woody plant's bark have been used to explain phorophyte preference among other epiphyte species (Frei and Dodson, 1972; Johansson, 1974; Benzing, 1990; Hietz and Hietz-Seifert, 1995a; Malizia, 2003). However, a distinct difference between bark characteristics of phorophytes and nonphorophytes was not immediately evident in this study. *Notelaea venosa*, a major phorophyte species of these orchid species, is smooth barked; however, rough bark is characteristic of both *B. myrtifolia* and *A. smithii* (Floyd, 1989). Yet, *A. smithii* is only a phorophyte to *P. tridentata*. Furthermore, both *S. hillii* and *P. tridentata* are more commonly found away from the rough bark of the trunk and larger branches, suggesting that the predominance of *B. myrtifolia* is not directly related to the morphological characteristics of its bark. Nevertheless, it remains possible that the chemical characteristics of the bark of these woody plant species not only have an effect on the establishment of these orchid species but also on their orchid mycorrhizal fungi.

Benefits of specialization—Increased fitness benefits from ecological specialization were not detected here, but this does not mean that such trade-offs do not exist (Futuyma and Moreno, 1988; Jaenike, 1990). Fry (1996) argues that even slight positive effects will encourage specialization to evolve. The comparison of the fitness characteristics measured here generally indicated a negative fitness response on the dominant phorophytes. Thus, we suggest the cause for the bias toward particular phorophytes has not been assessed here.

Greater inflorescence displays may be indicative of a greater ability to attract pollinators (Valdivia and Niemeyer, 2006; Majetic et al., 2008) and thus increase the fitness potential of an individual, especially among pollinator-limited species such as orchids. Similarly, increased vegetative size is generally considered to be indicative of increased fitness potential due to increased potential to flower (Pino et al., 2002; Tremblay, 2006). Ideally, we would have used more direct measures of fitness such as pollinaria removal or fruit set; however, these were not logistically possible. Alternatively, fitness benefits from establishment on the dominant phorophytes may be received at an earlier stage. We predict that the bias of *S. hillii*, *P. tridentata*, and *S. parviflorus* for *B. myrtifolia* reflects a benefit at an earlier stage, such as germination, in the establishment of these epiphytic orchid species.

We conducted a preliminary check for the presence of orchid mycorrhizal fungi (OMF) in an isobilateral protocorm (a structure characteristic of germinating seeds of a range of orchid taxa including the Aeridinae) found attached to a twig at Wagonga SF (Gowland, 2009). This protocorm was not only colonized by fungi in a manner characteristic of OMF colonization, but the fungi were also in the bark of the twig, suggesting an intimate multispecies association between these orchids, their OMF, and their twigs. Therefore, we propose that identification of the OMF of these orchid species may indicate that these fungi are biased toward particular woody plant species and hence explain the phorophyte preference of these orchid species.

Conclusion—Comparison across four sites differing in structural characteristics (Table 2) and woody plant species (potential phorophyte composition; Fig. 1) enabled an investigation into the degree of phorophyte specificity for these three epiphytic orchid species. Although significant logistical difficulties still need to be overcome for canopy epiphytes, we propose that this sampling strategy is a useful and generally applicable one for phorophyte specificity.

This research revealed that despite varying degrees of ecological specificity for each of these orchid species, the most common characteristics of a species' ecological niche were not consistently positively correlated with fitness proxies such as increased probability of flowering, vegetative size, or inflorescence number. Nevertheless, the results indicate that some characteristic of the tree *B. myrtifolia* makes it a more suitable

phorophyte than other woody plants. We suggest that the explanation for this bias lies in the three-way interaction between the orchid, their phorophytes, and their OMF. That is, there is an indirect benefit to the orchids from the phorophyte biases detected. Furthermore, we propose that this specificity is just an extreme case of something that may be more common—in many cases, apparently simple two-species interactions may be mediated by more complex symbioses. Therefore, we hypothesize that the cause of the distributional bias of these epiphytic orchid species is due to a bias of their mycorrhizal fungi for the dominant orchid phorophytes. Future research will identify the mycorrhizal fungi of these orchid species to determine their role in the distribution of these orchid species.

LITERATURE CITED

ACKERMAN, J. D., A. M. MONTALVO, AND A. M. VERA. 1989. Epiphyte host specificity of *Encyclia krugii*, a Puerto Rican endemic orchid. *Lindleyana* 4: 74–77.

ACKERMAN, J. D., A. SABAT, AND J. K. ZIMMERMAN. 1996. Seedling establishment in an epiphytic orchid: An experimental study of seed limitation. *Oecologia* 106: 192–198.

ANNASELVAM, J., AND N. PARTHASARATHY. 2001. Diversity and distribution of herbaceous vascular epiphytes in a tropical evergreen forest at Varagalaiar, Western Ghats, India. *Biodiversity and Conservation* 10: 317–329.

BENZING, D. H. 1990. Vascular epiphytes: General biology and related biota. Cambridge University Press, Cambridge, UK.

BENZING, D. H. 1998. Vulnerabilities of tropical forests to climate change—The significance of resident epiphytes. *Climatic Change* 39: 519–540.

CATLING, P. M., V. R. BROWNELL, AND L. P. LEFKOVITCH. 1986. Epiphytic orchids in a Belizean grapefruit orchard: Distribution, colonization, and association. *Lindleyana* 1: 194–202.

CHASE, M. W. 1987. Obligate twig epiphytism in the Oncidiinae and other neotropical orchids. *Selbyana* 10: 24–30.

CLEMENTS, M. A. 1987. Orchid–fungus–host associations of epiphytic orchids. *In* K. Saito and R. Tanaka [eds.], Proceedings of the 12th World Orchid Conference, 80–83. Tokyo, Japan. World Orchid Conference Trust, Bermuda.

DRESSLER, R. L. 1993. Phylogeny and classification of the orchid family. Dioscorides Press, Portland, Oregon, USA.

FLOYD, A. G. 1989. Rainforest trees of mainland and south-eastern Australia. Inkata Press for the Forestry Commission of N.S.W., Melbourne, Australia.

FREI, S. J. K., AND C. H. DODSON. 1972. The chemical effect of certain bark substrates on the germination and early growth of epiphytic orchids. *Bulletin of the Torrey Botanical Club* 99: 301–307.

FRY, J. D. 1996. The evolution of host specialisation: Are trade-offs overrated? *American Naturalist* 148: S84–S107.

FUTUYMA, D. J., AND G. MORENO. 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* 19: 207–233.

GOWLAND, K. M. 2009. Investigations of the phorophyte and fungal relationships of three epiphytic Aeridinae orchid species in southeastern Australia. Ph.D. dissertation, Australian National University, Canberra, Australia.

HIETZ, P., AND U. HIETZ-SEIFERT. 1995a. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science* 6: 487–498.

HIETZ, P., AND U. HIETZ-SEIFERT. 1995b. Intra- and interspecific relations within an epiphyte community in a Mexican humid montane forest. *Selbyana* 16: 135–140.

JAENIKE, J. 1990. Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics* 21: 243–273.

JOHANSSON, D. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeographica Suecia* 59: 1–136.

JONES, D. L., AND M. A. CLEMENTS. 2006. The status of *Sarcochilus olivaceous* Lindl. and *Sarcochilus parviflorus* Lindl., with a new species, *Sarcochilus argochilus*, described from Queensland. *Australian Orchid Review* 71: 21–23.

KASSEN, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology* 15: 173–190.

LAUBE, S., AND G. ZOTZ. 2006. Neither host-specific nor random: Vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* 97: 1103–1114.

MAJETIC, C. J., R. A. RAGUSO, AND T. L. ASHMAN. 2008. The impact of biochemistry vs. population membership on floral scent profiles in colour polymorphic *Hesperis matronalis*. *Annals of Botany* 102: 911–922.

MALIZIA, A. 2003. Host tree preference of vascular epiphytes and climbers in a subtropical montane cloud forest of northwest Argentina. *Selbyana* 24: 196–205.

MCCULLOCH, C., AND S. SEARLE. 2001. Generalized, linear, and mixed models. Wiley, New York, New York, USA.

MIGENIS, L. E., AND J. D. ACKERMAN. 1993. Orchid–phorophyte relationships in a forest watershed in Puerto Rico. *Journal of Tropical Ecology* 9: 231–240.

NG, C. K. Y., AND C. S. HEW. 2000. Orchid pseudobulbs—'False' bulbs with a genuine importance in orchid growth and survival! *Scientia Horticulturae* 83: 165–172.

OTERO, J. T., J. D. ACKERMAN, AND P. BAYMAN. 2002. Diversity and host specificty of endophytic *Rhizoctonia*-like fungi from tropical orchids. *American Journal of Botany* 89: 1852–1858.

PATTERSON, H. D., AND R. THOMPSON. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* 58: 545–554.

PAYNE, R., D. MURRAY, S. HARDING, D. BAIRD, D. SOUTAR, AND P. LANE. 2003. GenStat for Windows, 7th ed., version 7.1 for PC/Windows XP [computer program]. Website http://www.vsni.co.uk/downloads/genstat/. VSN International, Hemel Hempstead, UK

PETERSON, R. L., AND H. B. MASSICOTTE. 2004. Exploring structural definitions of mycorrhizas, with emphasis on nutrient-exchange interfaces. *Canadian Journal of Botany* 82: 1074–1088.

PINO, J., F. X. SANS, AND R. M. MASALLES. 2002. Size-dependent reproductive pattern and short-term reproductive cost in *Rumex obtusifolius* L. *Acta Oecologica* 23: 321–328.

RASMUSSEN, H. N. 2002. Recent developments in the study of orchid mycorrhiza. *Plant and Soil* 244: 149–163.

READ, D. J., J. G. DUCKETT, R. FRANCIS, R. LIGRONE, AND A. RUSSELL. 2000. Symbiotic fungal associations in 'lower' land plants. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 355: 815–831.

SANDFORD, W. W. 1974. The ecology of orchids. *In* C. L. Withner [ed.], The orchids: Scientific studies. John Wiley, New York, New York, USA.

SOKAL, R., AND F. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman, New York, New York, USA.

TRAPNELL, D. W., AND J. L. HAMRICK. 2006. Variety of phorophyte species colonized by the neotropical epiphyte *Laelia rubescens* (Orchidaceae). *Selbyana* 27: 60–64.

TREMBLAY, R. L. 1997. Distribution and dispersion patterns of individuals in nine species of *Lepanthes* (Orchidaceae). *Biotropica* 29: 38–45.

TREMBLAY, R. L. 2006. The effect of population structure, plant size, herbivory and reproductive potential on effective population size in a temperate epiphytic orchid, *Sarcochilus australis*. *Cunninghamia* 9: 529–535.

TREMBLAY, R. L., J. K. ZIMMERMAN, L. LEBRÓN, P. BAYMAN, I. SASTRE, F. AXELROD, AND J. ALERS-GARCÍA. 1998. Host specificity and low reproductive success in the rare endemic Puerto Rican orchid *Lepanthes caritensis*. *Biological Conservation* 85: 297–304.

VALDIVIA, C. E., AND H. M. NIEMEYER. 2006. Do floral syndromes predict specialisation in plant pollination systems? Assessment of diurnal and nocturnal pollination of *Escallonia myrtoidea*. *New Zealand Journal of Botany* 44: 135–141.

VAN TIENDEREN, P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution* 45: 1317–1331.

VIA, S., AND R. LANDE. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39: 505–522.

WALLACE, B. J. 1981. The Australian vascular epiphytes: Flora and ecology. Ph.D. dissertation, University of New England, Biddeford, Maine, USA.

YEATON, R. I., AND D. E. GLADSTONE. 1982. The pattern of colonization of epiphytes on calabash trees (*Crescentia alata* HBK.) in Guanacaste Province, Costa Rica. *Biotropica* 14: 137–140.

ZIMMERMAN, J. K., AND I. C. OLMSTED. 1992. Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. *Biotropica* 24: 402–407.

ZOTZ, G. 1998. Demography of the epiphytic orchid, *Dimerandra emarginata. Journal of Tropical Ecology* 14: 725–741.

ZOTZ, G. 2007. Johansson revisited: The spatial structure of epiphyte assemblages. *Journal of Vegetation Science* 18: 123–130.

ZOTZ, G., AND S. SCHULTZ. 2008. The vascular epiphytes of a lowland forest in Panama—Species composition and spatial structure. *Plant Ecology* 195: 131–141.