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Domatia morphology and mite occupancy of *Psychotria horizontalis* (Rubiaceae) across the Isthmus of Panama

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Abstract Leaf domatia are small plant structures in vein axials on the undersides of leaves that are often inhabited by mites of several species. The mites are presumed to benefit the plant because they are predatory or fungivorous. The domatia are thought to provide the mites shelter from predators and changes in relative humidity, and in exchange, the mites protect the plant from small herbivores and fungal spores. Differences in relative humidity can affect food availability, changing the interaction between plants and mites. We examined domatium morphology of the shrub *Psychotria horizontalis* (Rubiaceae) and its associated mite diversity at three sites along the rainfall gradient of the Isthmus of Panama, during the dry and wet seasons. The dry forest had a domatium morphology consistent with providing greater desiccation protection, with trichomes and a smaller domatium opening relative to domatium size (size/opening ratio). Additionally, this size/opening ratio was significantly higher in the dry season than in the wet season at all three sites. Mite diversity was highest at the intermediate rainfall site with a large degree of overlap with the other sites, whereas the dry site and wet site shared few mite species. More fungivorous mites were

present in the moist forests and more facultative feeders on fungal spores and small mites in the dry forest. The average mite size at each site matched the average domatium size at each site. The dry forest had small mites in small domatia, whereas the moist forests had larger mites in larger domatia. While these data are primarily observational, the site and seasonal differences in domatium morphology and mite diversity are consistent with two main hypotheses: (1) that protection from changes in humidity would be particularly important when humidity was low, such as in the dry forest and during the dry season (2) more fungivorous mites would be found in domatia of the moist forests. The data presented here further highlight the close adaptive relationship between leaf domatia on plants and the mites that inhabit them.

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Introduction

Plants worldwide have leaf domatia that are often occupied by mites (Grostal and O'Dowd 1994; O'Dowd and Willson 1989; Pemberton and Turner 1989; Rozario 1995). Despite the widespread geographic and phylogenetic occurrence of domatia, the functional relationship between domatia and mites has received little attention. Leaf domatia structure varies from a simple tuft of hair to a pouch of plant tissue located on the underside of leaves at the vein axials (O'Dowd and Willson 1989, 1991). The relationship between mites and plants with domatia is thought to be a mutualism (Agrawal 1997; Grostal and O'Dowd 1994; Norton et al. 2000). The mites occupying domatia are

primarily beneficial to the plant as predators and/or fungivores (Pemberton and Turner 1989). In return, the domatia are thought to shelter mites from larger predators and fluctuations in relative humidity, which is particularly important for mite eggs and post-molt individuals (Grostal and O'Dowd 1994; Norton et al. 2001). Grostal and O'Dowd (1994) found higher mite fitness in the presence of domatia, particularly under conditions of low humidity. Many previous studies on the interactions between mites and domatia have focused on identifying how widespread this relationship is (O'Dowd and Willson 1989; Pemberton and Turner 1989; Rozario 1995) and testing to what degree it is a mutualism (Agrawal 1997; Grostal and O'Dowd 1994; Kasai et al. 2005; Norton et al. 2000; O'Dowd and Pemberton 1997; Walter and O'Dowd 1992; Rozario 1995).

We hypothesized that differences in seasonal rainfall and relative humidity between sites could affect the relationship between mites and domatia. Under the hypothesis that mites receive protection from changes in relative humidity, one would expect domatia morphology to some degree vary with the macro environment. The few previous studies investigating this proposal found that the benefits domatia provide in desiccation protection are mainly under conditions of low humidity (Grostal and O'Dowd 1994; Rowles and O'Dowd 2009). In this respect, the importance of domatia to mites would be greatest in drier habitats. However, fungal spore abundance is often positively correlated with humidity (Lim et al. 1998). Thus, the relationship between mites and domatia could vary along a humidity gradient and across seasons.

In this study, we compared mite diversity and domatia morphology of a common understory shrub, *Psychotria horizontalis* (Rubiaceae), along a natural rainfall gradient across the Isthmus of Panama. The Atlantic side receives almost twice the rainfall as the Pacific side, 80 km away. We predicted there would be more fungivorous mites in domatia in the wet site and that domatia morphology would provide more protection from low humidity in the dry site.

Materials and methods

Study system

This study was conducted at three sites across the Isthmus of Panama operated by the Smithsonian Tropical Research Institute. These included the moist forest of Fort Sherman (FS) on the Atlantic coast (9°17′N, 79°58′30″), Barro Colorado Island (BCI) in the middle of Gatun Lake (9°10′N, 79°33′W), and the dry forest of Parque Metropolitano (PM) in Panama City on the Pacific coast (8°56′N, 79°33′W). The average annual rainfall at these sites is 3.02,

2.62, and 1.85 m, respectively, and the average annual relative humidity is 95, 90.3, and 87.9%, respectively (Patton 2001–2003). We collected data in multiple seasons over several years. The forests at all three sites experience a dry season from mid December to the end of April. Although there is no difference in the length of the dry season between the sites, the amount of rainfall they receive during the dry season does differ (0.3, 0.28, and 0.14 m in FS, BCI and PM, respectively; (Patton 2001–2003), as well as relative humidity (91.8% in FS, 79.8% in BCI, and 74.0% in PM).

Psychotria horizontalis (Rubiaceae) is an understory shrub (1.5–3 m tall) found from Mexico to Ecuador (Croat 1978) and is common across the Isthmus. *P. horizontalis* produces leaves continuously all year with a peak of synchronous leaf flush in May at the end of the dry season (Aide 1993). The leaves are short-lived, being dropped after 1 year. At the terminal ends of the branches, there are one or two opposite pairs of leaves with characteristic pouch-like domatia at the secondary vein axial (Croat 1978).

Sampling and data collection

We collected one terminal leaf off multiple branches of haphazardly selected *P. horizontalis* plants in all three sites. We collected leaves from each site in the late wet season (Oct. 2001, 10 leaves from 10 plants; Nov. 2003, 5 leaves from 10 plants), the early wet season (Jul. 2002, 10 leaves from 10 plants), and the dry season (Apr 2003, 5 leaves from 19 plants). The leaves were immediately placed in a ziplock bag and placed on ice in a cooler in the field and stored in the refrigerator at the lab until processing (within 36 h). This technique was successful in keeping the mites alive while reducing their movement after collection.

We examined each leaf under a dissecting scope and recorded any mites on the phylloplane. Then we carefully opened each domatium with a needle and recorded mite occupancy. We measured all the mites' length, grouped them by morphological species and placed them in 95% ethanol. The mites were identified to the minimum level needed to determine the trophic guild (suborder or family level). We compared mite morphospecies and feeding guilds across sites and between seasons. These data included the early rainy season 2002, dry season 2003, and late rainy season 2003.

In October 2001 and April 2003, we also recorded data on domatium morphology. Before opening up the domatia, we measured the size of the domatium and the opening. The domatium size was measured as the distance bisecting the domatium from the leaf axial to the end of the domatium pocket. The size of the domatium opening was

calculated by multiplying the length and width of the hole on the top of the domatia. As an index of possible level of protection from desiccation and predation, we calculated the domatium size divided by the area of the opening (size/open). For a given domatium size, large ratios indicate a smaller opening and potentially more protection, whereas small ratios indicate a larger opening and potentially less protection to the mite. A smaller opening compared to the total domatium size would reduce airflow in the domatium increasing humidity and it would reduce access from predators.

In addition, we recorded the incidence of damage to the domatium and leaf area. The damage mainly included browning of part or the entire domatium pouch, apparently due to pathogens. After the leaves were processed, we measured the leaf area (LI-COR Biosciences, Lincoln, Nebraska).

Common garden experiments

We measured domatium morphology of leaves from two experimental gardens with plants from three origins (FS, BCI, and PM). During September to December of 2001, we collected seeds from each site. The seeds germinated in January 2002 and were transplanted into local soil and maintained in the greenhouse until they were planted at each garden in the shaded understory in December 2002, one in Buena Vista (BV), which is part of the Barro Colorado Island Natural Monument and one on the dry side in the forest of Clayton, located about 6 km from Parque Metropolitano. In April 2006, we collected two mature leaves of 10 plants of each origin and garden site combination. The leaves were sent overnight to the US, and we measured domatium morphology traits as mentioned earlier. Information on the mites is not presented, as the collection methods and time of processing of the leaves were inconsistent.

Statistical analysis

We analyzed the data using plant averages as our replicate. All the data were tested for the assumptions of parametric analysis. If the data did not meet the assumptions, even after log transformation, appropriate non-parametric tests were used. We tested the effect of site and season on mite occupancy of domatia and domatium morphology using an ANOVA or a Kruskal–Wallis test. We tested the effect of site and origin for domatium morphology traits from the common garden experiments using an ANOVA.

We compared mite morphospecies diversity and feeding guilds across sites and between seasons. These data included the early rainy season 2002, dry season 2003, and late rainy season 2003. We calculated the Shannon index of diversity for each site [$H' = -\Sigma (p_i) (\log_2 p_i)$, where p_i is the proportion of the total individuals for species i]. We also calculated the Sørensen's coefficient [$Sø = 2S_c/(S_a + S_b + 2S_c)$ where S_a and S_b are the species unique to locations a and b and S_c is the number of shared species]. The coefficient is between zero and one, where zero indicates two completely different groups of species and one indicates the exact same group of species. In all the calculations, we excluded singleton morphospecies. We analyzed differences between feeding guilds and mite size using Kruskal–Wallis tests.

To explore further the differences in mite diversity across sites and seasons, we used non-metric multidimensional scaling (NMDS) of the Bray–Curtis dissimilarity distances (Quinn and Keough 2002). Bray–Curtis dissimilarity distances between two site and season combinations (for example, BCI late season vs. FM late season, variable i and j) were calculated as $\sum |x_{ik} - x_{jk}|/\sum (x_{ik} + x_{jk})$, where x is the abundance of mite species k. The dissimilarity index is between zero and one, opposite to the Sørensen's coefficient, zero indicates two sites with the exact same mite diversity (both in terms of species present and abundance) and one indicates completely different mite diversity. We calculated a dissimilarity matrix between all site and season combinations and analyzed it with NMDS (using ALSCAL procedure in PASW Statistics 17, SPSS Inc., Chicago IL). Non-metric analysis is often used with ordinal data like dissimilarity indices. In the analysis, the rows and columns of the dissimilarity matrix represent points in a Euclidean space, and thus mite diversity that are more similar are close together on the plot and those that are less similar are farther apart. ALSCAL adjusts the positions of the points on the ordination space (iteration) until the S-stress (a measure of goodness of fit) improvement is less than 0.001.

Results

More mites were found in domatia than on the phylloplane of the host leaves at all three sites. No seasonal difference was detected in the percent of mites found in domatia ($\chi^2 = 0.61$, $df = 2$, $P = 0.435$). However, there was a difference between sites ($\chi^2 = 11.52$, $df = 2$, $P = 0.003$). Of the total mites collected in all seasons, 91, 86, and 82% (FS, BCI, and PM, respectively) were in domatia. Overall, mites occupied less than 20% of the domatia, with the highest percentage in the dry forest ($14.6 \pm 1.74\%$ in PM, compared to $9.2 \pm 1.09\%$ at FS and $6.4 \pm 0.76\%$ at BCI, Kruskal–Wallis, $\chi^2 = 15.88$, $df = 2$, $P < 0.001$). In addition, some domatia were occupied by other organisms (6.8% of the domatia in FS, 4.5% BCI and 1.3% PM), including insect eggs, larvae or adults.

Leaf and domatium morphology varied among sites and seasonally. There were significant season, site and interaction effects on leaf area (ANOVA, $F_{3,134} = 11.27$, $F_{2,134} = 44.57$, $F_{6,134} = 3.46$, respectively, $P < 0.01$, Fig. 1). Leaves at PM were smaller than at BCI and FS (LSD, $P < 0.001$). Leaf area of leaves collected in the two late wet seasons were not significantly different, neither were leaves collected in the early wet season different from leaves collected in the dry season. However, leaves collected in the early wet and dry season were smaller than leaves collected in the wet seasons (LSD, $P < 0.001$). PM had more domatia per leaf than BCI and FS (11.07 ± 0.24 domatia/leaf in PM compared to 9.61 ± 0.35 BCI and

9.59 ± 0.27 FS. ANOVA, $F_{2,134} = 6.13$, $P = 0.003$), with no seasonal effect. A significant main effect of site and season was detected on domatia size (ANOVA, $F_{2,82} = 78.40$, $F_{1,82} = 7.50$, $P < 0.01$, Fig. 1), but no significant interaction. Domatia size increased from the Pacific to the Atlantic along the rainfall gradient (LDS, $P < 0.001$, Fig. 1). Domatia were larger on leaves collected in the dry season than the late wet season (LDS, $P < 0.01$). To ensure that the site and seasonal differences were due to differences in domatia and not leaf area, we normalized domatia size by dividing by leaf area. There was still a significant difference between sites and seasons (ANOVA, $F_{2,82} = 20.81$, $F_{1,82} = 38.58$, $P < 0.001$ Fig. 1). In addition, there was a significant interaction between site and season (ANOVA, $F_{2,82} = 5.33$, $P < 0.01$). Thus, the wettest site (FS) had disproportionately larger domatia and the dry site (PM) disproportionably smaller ones. Although the leaf area was less in the dry season, domatia size in FS remained the same and increased in BCI and PM. Domatia size on BCI leaves was proportionally similar to FS in the dry season and PM in the late wet season (Fig. 1).

The ratio between domatium size and opening area (size/open) also varied among sites, in the opposite pattern as domatium size (ANOVA, $F_{2,82} = 61.84$, $P < 0.001$, Fig. 2). In the dry site (PM), where the domatia were smaller, the opening was disproportionably smaller, and in the wettest site (FS) the domatia had disproportionately larger openings. In addition, there were trichomes around the domatia opening in PM that were not present in the other two sites. The domatium size/opening ratio was significantly higher in the dry season (ANOVA, $F_{1,82} = 40.94$,
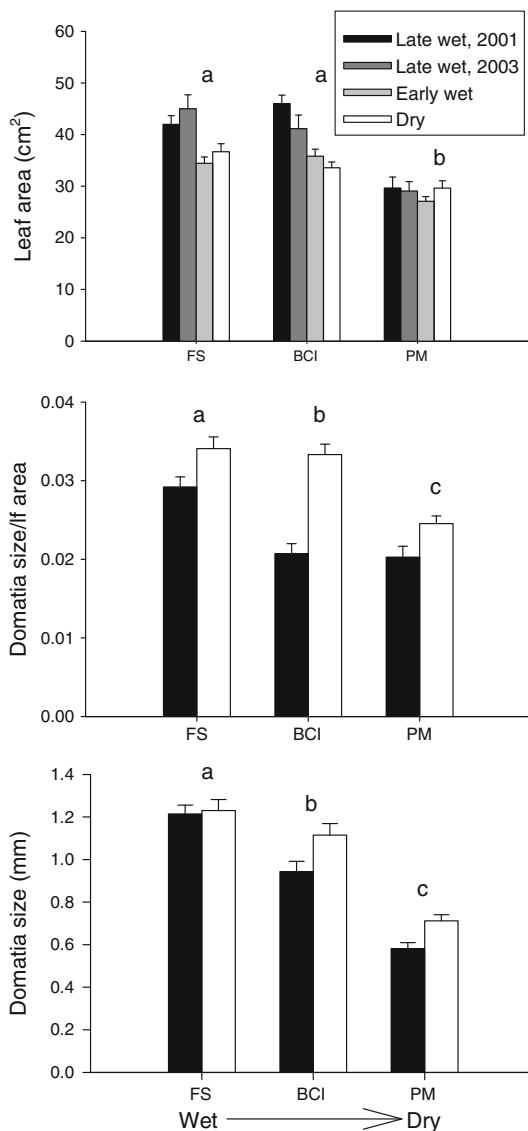

Fig. 1 Mean (±SE) leaf area and domatium size at the three sites along a humidity gradient, from the wet site of Fort Sherman (FS) to Barro Colorado Island (BCI) and the dry forest of Parque Metropolitano (PM). The *letters* represent significant differences between sites (LSD *post hoc*, $P < 0.05$); see text for further statistical details
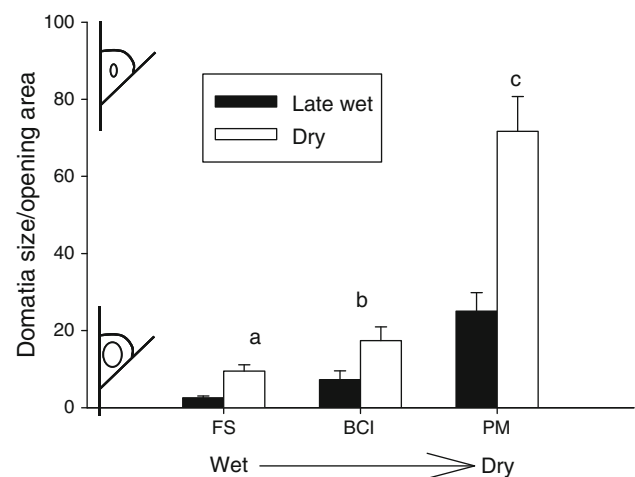

Fig. 2 Mean (±SE) ratio of domatium size to domatia opening area on leaves collected in the late wet and dry seasons. For a given domatium size, a higher ratio indicates a smaller opening and a smaller ratio a larger opening. The *letters* represent significant differences between sites (LSD *post hoc*, $P < 0.05$)

$P < 0.001$, Fig. 2). The percentage of domatia that was damaged was higher at the wetter sites (13.43 ± 1.99, 16.22 ± 2.79 and 1.88 ± 0.38 percent in FS, BCI and PM, respectively, $\chi^2 = 44.02$, $df = 2$, $P < 0.001$). The bulk of the damage was more characteristic of fungal attack than herbivore damage. Domatium damage did not vary across seasons ($\chi^2 = 2.66$, $df = 2$, $P = 0.264$)

We found a total of 30 morphospecies of mites and 20 were identified to suborder or family (Table 1). BCI had the highest species richness and diversity index, in part due to the high degree of overlap with both FS and PM, which had different mite assemblages from each other (Table 2). PM had more site-specific morphospecies (7) than the other two sites. Only two species were found in considerable abundance in all three sites (Ta1 and St1). Mite abundance peaked in the dry season (Kruskal–Wallis, $\chi^2 = 106.90$, $df = 4$, $P < 0.001$). BCI had lower mite densities than the other two sites (1.33 ± 0.24 mites/leaf at BCI, 1.95 ± 0.39 at FS and 2.68 ± 0.37 at PM, Kruskal–Wallis, $\chi^2 = 14.10$, $df = 2$, $P = 0.001$). Mite size differed significantly between sites (Kruskal–Wallis, $\chi^2 = 7.19$, $df = 2$, $P = 0.007$) with the smallest mites at PM (121 ± 4.54 μm) and

the largest at BCI (238 ± 4.54 μm, mites in FS were 194 ± 5.93 μm). Fungivorous mites were more abundant in the wettest site, FS (Kruskal–Wallis, $\chi^2 = 12.09$, $df = 2$, $P = 0.002$, Fig. 3). Omnivores, which feed on small mites and fungi, were primarily found in the dry site, PM (Kruskal–Wallis, $\chi^2 = 47.37$, $df = 2$, $P < 0.001$). Predatory species were found in all sites ($\chi^2 = 278$, $df = 2$, $P = 0.249$). There was no significant difference in mite feed guilds between seasons. We found only three individuals of a single phytophagous mite species during this study. The mite assemblages were different at all three sites with BCI and FS more similar to each other and PM considerably different from the other sites (Fig. 4). A NMDS of the Bray–Curtis dissimilarity matrix in two dimensions resulted in a configuration after 5 iterations with the stress value of 0.13 and a r^2 of 0.94.

The common garden experiment showed some effects of origin, but no differences between the garden sites. There was a significant origin effect on the number of domatia per leaf (ANOVA, $F_{2,38} = 5.62$, $P = 0.007$, Fig. 5). There was no difference in leaf area and domatia size between sites or origin; however, domatia size was significantly

Table 1 Mite morphospecies collected in the study, including juvenile mites that could not be sorted into morphospecies
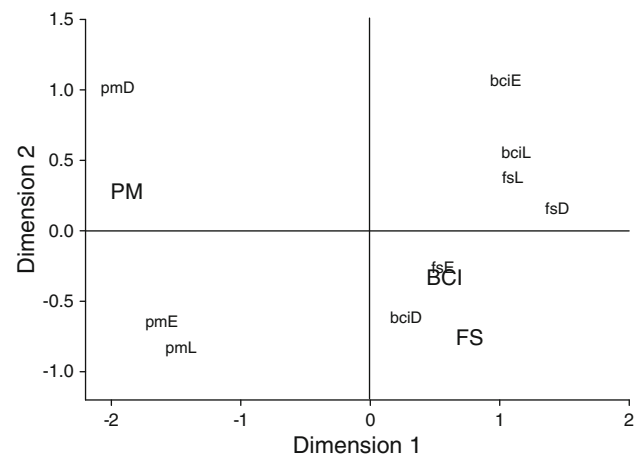
Suborder	Family	Feeding guild	Morpho *Spp*. code	Total collected
Astigmata		Fungivore	As1	165
			As2	8
			As3	25
Mesostigmata	Ologamasidae	Predator	Ol1	33
			Ol2	15
	Phytoseiidae	Predator	Ph1	8
			Ph2	8
			Ph3	85
			Ph4	2
Orbatida		Fungivore	Or1	4
Prostigmata	Tarsonemidiae	Fungivore/small mites	Ta1	163
	Tydeidae	Fungivore/small mites	Ty1	33
			Ty2	3
			Ty3	104
	Tetranychidae	Phytophagous	Te1	3
	Bdellidae	Predator	Bd1	54
	Stigmaeidae	Predator	St1	82
			St2	138
			St3	8
			St4	59
Unknown		Juveniles	UnJ	302
			Un1	4
			Un2	5
			Un3	3
			Un4	2
			Un5	2

Table 2 Mite diversity at each site for all seasons and comparisons of diversity indices between sites

Site	Species richness	Shannon index (H')	Paired sites for community comparisons	Sorensen's coefficient
FS	15	1.92	FS-BCI	0.84
BCI	17	2.30	BCI-PM	0.64
PM	14	1.80	PM-FS	0.15
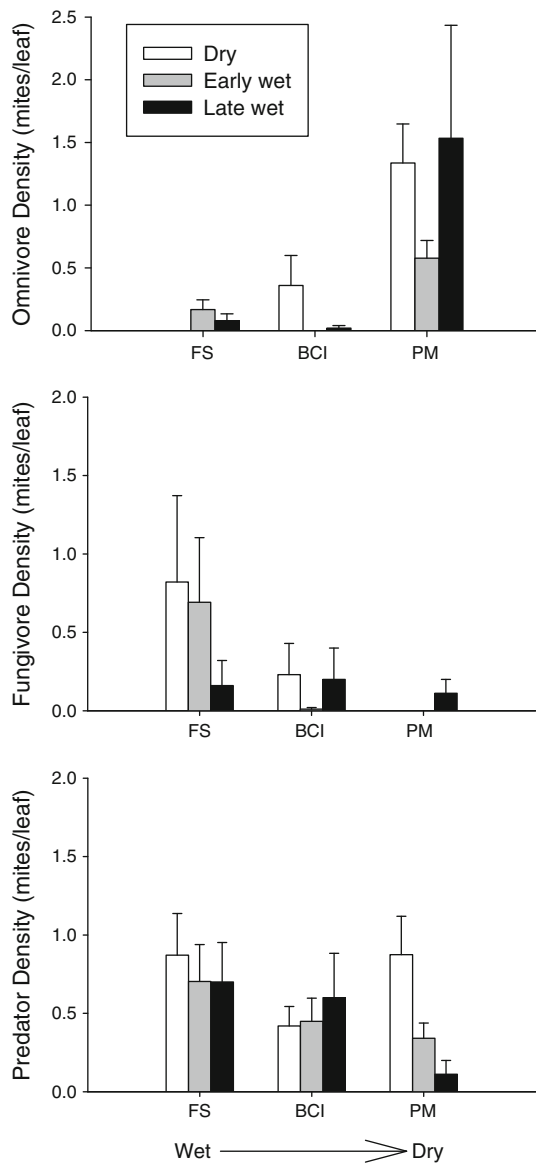
Fig. 3 Seasonal and site differences in mite trophic guilds (Mean ± SE)

Fig. 4 NMDS of the Bray–Curtis dissimilarities between each season and site. The *suffix* on the *lowercase labels* indicates the seasons as early wet (*E*), dry (*D*), and late wet (*L*). *Large font* PM, BCI, and FS represent the combined site dissimilarities. The stress value is 0.13 after 5 iterations and r^2 is 0.94

Discussion

P. horizontalis demonstrated a high degree of variation in domatium morphology. Previous studies have shown a remarkable variety of domatia morphologies across species, but only a few have shown variation within a species (Nishida et al. 2005). We found variation not only between different sites, but also within sites between seasons. Interestingly, the domatia size/opening ratio decreased with increasing average rainfall. We discuss three interpretations of this pattern later, including humidity differences, predator protection, and differences in mite size. Regardless of how we interpret the differences in size/opening ratio, this morphology appears to be adaptive relative to the environmental conditions at each site. A significant origin effect in the common garden experiment, but no location effect (BV vs. Clayton) supports the adaptive explanation because phenotypic plasticity was not detected.

Mites are sensitive to small changes from the relative humidity (Castagnoli and Simoni 1994; Wharton and Kanungo 1962). Rowles and O'Dowd (2009) found that mite reproductive output increased while inhabiting domatia only under low-humidity treatments. Therefore, a 14% decrease in relative humidity in PM during the dry season compared to only a 5% decrease in FS (Calculated from Patton 2001–2003) may result in domatia being
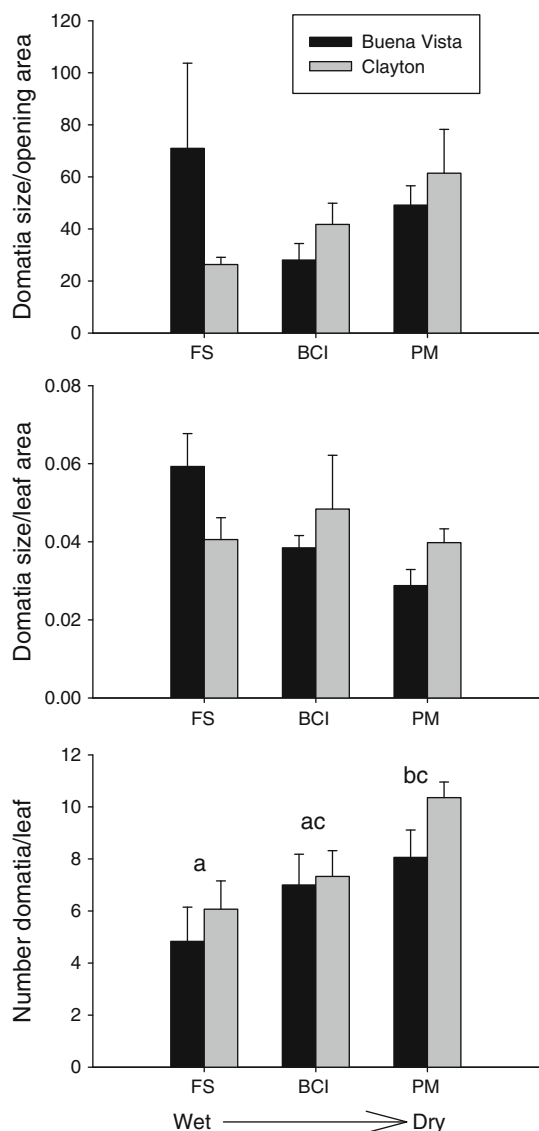
correlated with leaf area ($r^2 = 0.24$, $F_{1,42} = 13.64$, $P = 0.001$). There was no site or origin effect on domatia size/leaf area, but there was an interaction between site and origin (ANOVA, $F_{2,38} = 3.16$, $P = 0.05$, Fig. 5). We found a significant origin effect on the ratio of domatia size and opening area (Kruskal–Wallis, $\chi^2 = 6.64$, $df = 2$, $P = 0.036$, Fig. 5).

Fig. 5 Domatia morphology of plants from three origins (*FS, BCI*, and *PM*) growing in two experimental gardens [Intermediate rainfall (Buena Vista) and Dry (Clayton)]. The *letters* represent significant differences between sites (LSD *post hoc, P < 0.05*)

especially important in buffering from humidity fluctuations for mite reproduction in PM. A smaller opening relative to domatium size may provide more protection from fluctuations in humidity by reducing the air flow in the domatia. Domatia found in PM had the largest size/open, plus additional trichomes around the domatia opening would further reduce airflow. This interpretation is also consistent with the differences we found between seasons, with domatia in the dry season providing greater protection from desiccation than domatia in the wet season.

Alternatively, domatia have been found to protect mites from predators (Norton et al. 2001) and insect eggs from parasitism (Agrawal et al. 2000). Not only would a smaller

opening limit access from natural enemies, but a smaller opening compared to the total domatium size would provide more refugia for mites around the edge of the domatium. However, further investigations are required to determine the differences in predator pressure on mites between the different forest sites and seasons.

Mite diversity differed between each site. At the intermediate site, BCI, there was overlap of mite species that were found in either the wet forest or the dry forest, leading to higher diversity. Mite feeding guild composition may be dictated by differences in overall food availability and seasonality between sites. As predicted, we found that differences in fungivore densities coincided with differences in humidity. Fort Sherman (FS) with the highest humidity year round had the most fungivores. Although we found no significant seasonal effects on fungivore densities, FS and BCI had higher densities in the dry season, which corresponds with the peak in airborne fungal spores in Panama (Hutton and Rasmussen 1970). Additionally, higher fungal damage to domatia in the wetter sites indicates higher fungal growth or spore densities. Dry forests have greater seasonal differences in rainfall, which can translate into greater seasonal differences in small arthropod and fungal spore abundance. Therefore, in the dry forest a strict predator or fungivore may experience times of food shortages, where omnivores would be able to feed more opportunistically. This could explain why we found more omnivores in PM. In comparison, the wetter forests have less dramatic seasonal differences creating more reliable food sources.

The different mite communities at each site varied in average mite size, which coincided with domatia morphology. Nishida et al. (2005) were among the first to show that different mite species occupied domatia of different morphologies. PM had small domatia inhabited by small mites, whereas FS and BCI had larger domatia with larger mites. It is unclear from our data whether mite size is restricted by domatium size or domatium size is adapted to mite size. However, this does pose another interpretation of the size/opening ratio patterns we observed. Perhaps the larger mites require larger openings and as adults they may be less susceptible to desiccation and predation.

Similar to previous studies (Agrawal 1997; Grostal and O'Dowd 1994; Norton et al. 2000; Pemberton and Turner 1989), the mites we found on *P. horizontalis* were almost exclusively fungivores and/or predators, which therefore should be beneficial to the plant. Additionally, phenotypic differences we found in domatium morphology indicate that the relationship between mites and *P. horizontalis* may be mutually beneficial. While the results of the study are primarily observational, the patterns we found in mite diversity relative to domatium morphology were consistent with our initial expectations based on differences in forest

humidity and seasonal rainfall patterns. Domatia in the dry site and during the dry season provide more protection from desiccation and the marked differences in species composition and trophic guilds were consistent with variation in food resources. However, there may be alternative explanations to the patterns we found. Thus with future experimental investigations, we would gain insight to the dynamics between mite, plant and environmental factors.

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