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ON THE RELATIONSHIP BETWEEN BRYOPHYTE COVER AND THE DISTRIBUTION OF *LEPANTHES* SPP.

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ABSTRACT. Epiphytic plant communities in tropical montane ecosystems are particularly vulnerable to climate change. *Lepanthes* is a large genus of primarily epiphytic orchids that is prominent in the Costa Rican flora. Generally, these orchids are very small and often occur in highly exposed habitats, thus leading to the theory that they are dependent on bryophyte cover to prevent desiccation. Accordingly, the aim of this project was to determine if the distribution of *Lepanthes* is limited by the distribution of moss cover on trees. To accomplish this, bryophyte cover was measured on phorophytes hosting *Lepanthes* spp. as well as on other unoccupied trees in the surrounding areas. The results suggest that *Lepanthes* spp. are correlated with high levels of moss cover and there is often substantially more moss cover at locations where *Lepanthes* occur than at locations where they do not occur. Accordingly, bryophytes appear to form a commensalism with this diverse group of orchids. The results of this study are in agreement with similar studies that suggest moss cover is important for orchid growth and survival. Consequently, if climate change adversely affects moss coverage on trees, *Lepanthes* orchids may suffer concomitantly.

RESUMEN. Las comunidades epífitas de plantas en los ecosistemas tropicales de montaña son particularmente vulnerables al cambio climático. *Lepanthes* es un género grande de orquídeas epífitas el cual es prominente en la flora de Costa Rica. Por lo general, estas orquídeas son muy pequeñas, y con frecuencia ocurren en hábitats altamente expuestos, lo que conduce a la teoría de que son dependientes de la cobertura de briófitos para prevenir la desecación. El objetivo de este proyecto fue determinar si la distribución de *Lepanthes* está limitada por la distribución de la cobertura de musgos en los árboles. Para lograr esto, se midió la cobertura de briófitos sobre los forófitos que hospedan *Lepanthes* spp., así como en otros árboles desprovistos de briófitos localizados en las áreas circundantes. Los resultados sugieren que *Lepanthes* spp. esta correlacionada con altos niveles de cobertura de musgos, además hubo substancialmente más cobertura de musgos en los lugares donde *Lepanthes* ocurre que en los lugares donde no ocurre. En consecuencia, parece que los briofitos forman un comensalismo con este grupo diverso de orquídeas. Los resultados de este estudio concuerdan con estudios similares que sugieren que la cobertura de musgos es importante para el crecimiento y supervivencia de las orquídeas. Por consiguiente, si el cambio climático tiene un impacto negativo en la cobertura de musgos, las orquídeas *Lepanthes* sufrirían simultáneamente.

KEY WORDS: bryophyte cover, commensalism, host trees, *Lepanthes*, microhabitat, orchid distribution

Introduction. Global climate change is adversely affecting ecosystems worldwide and empirical models indicate that over time, these changes will have an increasing impact on the earth's environment (Markham 1996, Hulme & Viner 1998, Williams *et al.* 2003, Parmesean 2006). Although there is significant variability and uncertainty in predictive climate change models, there are several noteworthy global trends and projections. Foremost, expectations are that average temperatures will increase in many regions. In addition, most models suggest that global rainfall patterns will change considerably, and in turn, fluctuations in moisture availability are anticipated for many areas (see Markham 1996, Pounds *et al.* 1999). Consequently, species that are adapted to cool, moist environments will likely be threatened by climate change.

A large body of research shows that high elevation ecosystems, particularly those in the tropics, are especially susceptible to climate change for several reasons (Foster 2001, Williams *et al.* 2003, Parmesean 2006). In these systems, changes in temperature and moisture availability can lead to a lifting of orographic cloud cover, which can subsequently lead to other changes in microclimate and community dynamics (Markham 1996, Pounds *et al.* 1999, Foster 2001, Williams *et al.* 2003). Many plant species may be unable to emigrate away from these types of environmental pressures because of their sessile nature (Foster 2001, Kelly & Goulden 2008). Over extended periods, unfavorable upslope vegetation shifts can occur that lead to a compression of important habitats (Foster 2001, Parmesean 2006). For many high elevation biotic communities, these changes can lead directly to fragmentation and mountaintop extinctions (Foster 2001, Williams *et al.* 2003).

Research consistently suggests that epiphytes will respond particularly unfavorably to climate change, resulting in range shifts and extirpations (Benzing 1998, Hietz 1999, Foster 2001, Kelly & Goulden 2008, Zotz & Bader 2009). Most epiphytes in high elevation ecosystems show high sensitivities to climatic conditions due to their direct interface with the atmospheric environment. For example, many species are dependent upon the relatively permanent fog cover in cloud forests (Benzing 1998, Hietz 1999, Zotz & Bader 2009). Even minor changes in local conditions can alter growth, phenology, reproduction, and biotic partnerships, all of which are factors contributing to reductions in species survival (Johnson & Bond 1992, Parmesean 2006, Colwell *et al.* 2008, Liu *et al.* 2010). Accordingly, epiphytic plant communities in tropical montane systems warrant immediate attention from conservation biologists.

Lepanthes Swartz (Orchidaceae) is a large and diverse genus of primarily epiphytic orchids. These orchids are distributed throughout the Neotropics with a high number of species occurring in the montane cloud forests of Costa Rica (Dressler 1993, Luer 2003). Previous research suggests that the distribution of *Lepanthes* orchids may be highly sensitive to the presence of bryophyte cover, but this relationship has only been demonstrated on a single species from Puerto Rico (Tremblay *et al.* 1998). Nevertheless, the complex associations between bryophytes and other plant species are well established, and a variety of positive and negative interactions exist (During & Van Tooren 1990). Unfortunately, however, bryophytes may also be highly susceptible to changes in climatic conditions because of their significant dependency on moisture availability (Benzing 1998, Raven *et al.* 2005, Raabe *et al.* 2010), and thus, the fate of *Lepanthes* spp. may be jeopardized directly as a result of climate change, but also indirectly via impacts to potential orchid/bryophyte commensalism. Therefore, the overall goal of this study was to determine if the local distribution of *Lepanthes* spp. is correlated with bryophyte cover. Results generated by this analysis should help to determine the potential effects that loss of bryophyte cover would have on the distribution of this diverse group of orchids. Previously, it has been predicted that bryophytes provide an important substrate for the recruitment, growth, and survival of orchids, and therefore *Lepanthes* spp. should occur on trees with substantial amounts of moss cover (Tremblay *et al.* 1998, Tremblay & Velazquez-Castro 2009). Accordingly, the hypothesis tested here is that the sections of phorophytes occupied by *Lepanthes* spp. will have significantly more moss cover than equivalent sections of un-colonized trees.

Methods. To determine if the local distribution of *Lepanthes* orchids is limited by the distribution of bryophyte cover, moss coverage was measured on phorophytes hosting *Lepanthes* spp. as well as on unoccupied trees in the immediate surrounding areas. Between 15 June and 25 July 2011, surveys were conducted in several forests among various regions of Costa Rica in an attempt to locate individuals of a variety of different species of *Lepanthes*. Specifically, two forests were surveyed in Monteverde, Puntarenas Province, two forests in Heredia Province including one in La Selva Biological Station and another at the Bijagual Reserve, a single forest at the Cuericí Field Station, San Jose Province, and two forests in Punterenas Province including one at the Las Cruces Field Station and another at the Las Alturas field station. Although *Lepanthes* have either been previously collected or reported as being present at each of these sites (Luer 2003), populations were only located at half of the survey sites. Plants were identified as members of the *Lepanthes* genus based on morphological features of flowers or by the presence of lepanthiform sheaths if flowers were unavailable (see Dressler 1993, Luer 2003).

At each site where a *Lepanthes* orchid was located, plots centered on the host tree were established. Bryophyte cover was then measured on the host tree at the position occupied by the orchid. This was accomplished by using a clear acetate sheet with a 20 x 20 cm metric grid printed on it. This grid size was chosen because it was large enough to cover the entire area surrounding each orchid, but small enough to limit sampling to the area directly interacting with it. In no instance was the plant larger than 20 cm and roots never extended outside of the grid area. To estimate moss cover on the section occupied by the orchid, the center of the grid was placed directly at the base of the orchid, and the number of 1 cm cells occupied by moss was counted. The overall number was then converted into a percentage of the maximum grid area (400 cm^2). This conversion was done mainly to accommodate different sizes of trees on which orchids were found. In cases where the circumference of the phorophyte was less than 20 cm, the entire grid could not be used. Therefore, the subset of the grid that did not overlap onto itself when placed over the orchid was used as the maximum potential grid area. In such cases, the percent cover was calculated in the same manner, but using the overall area of the usable subset of the grid as the denominator. Depth of moss cover was initially considered as a variable, but in all instances, the depth of the mat (when present) was approximately equal among sampled sections (≈1.5 cm). In most cases, more than one individual of *Lepanthes* was found on a given tree, particularly on trees with branching trunks. To avoid effects of pseudo-replication, the sampling process was only repeated for other orchids that were located on separate trunks of the original host tree or for other orchids found on the adjacent trees within the plot. Lastly, the bearing and vertical position of the orchid on the central phorophyte was measured to the nearest cm.

After data was collected at each host tree, the moss cover was measured on four non-host trees within each plot to establish a mean background moss cover. Non-host trees were selected by choosing the individual trees nearest the central host tree within each of four quadrants delineated by the cardinal directions. Only trees that were greater than 2 cm diameter at breast height were selected for sampling, as no orchids were discovered on trees smaller than this size. Moss cover on each non-host tree was measured at the same height and bearing that was recorded for the position of the orchid at the plot center. Percent cover was calculated in the same manner as for host tree sites.

Finally, the data from each site were analyzed with non-parametric Wilcoxon rank sum tests with continuity corrections to look for differences in median values of bryophyte cover between the sampled sections of host trees and non-host trees (i.e. baseline cover) at each individual site. These tests were conducted on data from each site to determine if the relationship between orchids and bryophytes was the same at each location. The Wilcoxon rank sum test was chosen mainly for its ability to handle the relatively small sample sizes that are often obtained during orchid surveys at a given site due to their patchy distributions. All statistical tests and analyses were conducted with the R version 2.13.0 computer statistical program (R Development Core Team 2011).

Results. During the course of the surveys, *Lepanthes* populations were discovered at several sites within three areas. In the Monterverde area, *Lepanthes* host trees were located at three sites within one of the forests surveyed. In Cuericí, two individual sites contained multiple host trees. Lastly, at Las Alturas, host trees were found at two additional sites. In Monteverde and Las Alturas, *Lepanthes* populations were found on at least two tree species; in Cuericí, the populations were located on a single tree species. Non-host trees at each site included individuals of the same species as the host trees, as well as other species. The results of the surveys were consistent with expected results, as *Lepanthes* orchids are often patchily distributed among several tree species and are most common in middle to high elevation sites (Tremblay 1997, Riofrío *et al.* 2007).

Considering all the trees surveyed, moss cover on sampled sections ranged from 0-100% (Fig. 1) with an average cover of 65%. Considering only the host trees, moss was always present and overall cover on sampled sections ranged from 28-100%. The mean moss cover on the sampled sections of host trees was approximately 81%. Considering only non-host trees, moss cover on the sampled sections ranged from

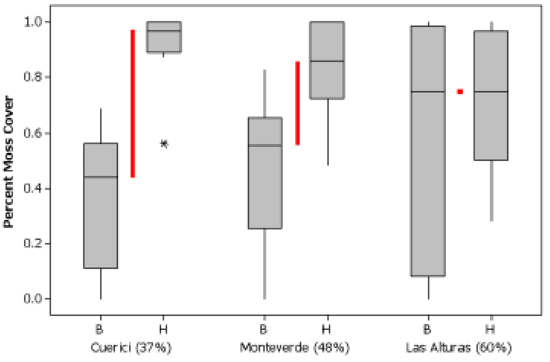

FIGURE 1. Box-plot showing differences in the percent of moss cover between sampled sections of host trees (H) and random non-host trees, i.e., baseline moss cover (B), at three sites in Costa Rica. Numbers in parentheses next to site names are the mean baseline moss coverage estimates for sampled sections on random non-host trees at each site. Boxes represent the first and third quartiles, horizontal lines within the boxes are the median values, and lines extending from the boxes represent the overall range of values. The vertical lines between the paired box plots for each site represent the difference in median moss cover on sampled sections of host trees and median baseline coverage. Asterisk (*) indicates an outlier.

0-100%, with a mean coverage of only 48% (Fig. 1). The Wilcoxon rank sum tests conducted for trees from individual sites showed that there was a difference in median moss cover on sampled sections of host trees versus non-host trees at Monteverde (W = 125, n = 12, P = 0.002373) and Cuericí (W = 62, n = 8, P = 0.001717), but not at Las Alturas (W = 35, n = 8, P = 0.7909, Fig. 1). This was likely the result of the higher mean background moss cover on non-host trees in Las Alturas (60%) than on non-host trees at the other sites (Monteverde- 47%, Cuericí- 36%). In all cases, however, orchids occupied locations with substantial amounts of moss cover (Fig. 1).

Discussion. The results of this study are in agreement with and expand upon the findings of previous research on moss cover and the presence of *Lepanthes* spp. (Tremblay *et al.* 1998, Tremblay & Velasquez-Castro 2009) and other orchids (Gowland *et al.* 2007, Watthana & Pedersen 2008, O'Malley 2009, Scheffknecht *et al.* 2010, Gowland *et al.* 2011). In short, it appears that a large number of *Lepanthes* spp. from various locations and environments form strong relationships with epiphytic bryophytes. Several theories as to why this is the case seem plausible, and indeed all may be acting in unison. First, bryophytes could provide a moist heterogeneous substrate that may be beneficial to *Lepanthes* orchids because they provide a suitable landing place for dust-like orchid seeds in an otherwise potentially smooth, dry, bare bark environment (Tremblay *et al.* 1998, O'Malley 2009, Scheffknecht *et al.* 2010). Secondly, moss beds could also support the growth of mycorrhizal fungi necessary for seed germination and transfer of nutrients that the mosses themselves may provide (Tremblay *et al.* 1998, Cornelissen *et al.* 2007, Osorio-Gil *et al.* 2008, Tremblay & Velasquez-Castro 2009). Third, moss beds could shield orchid roots from exposure to wind and sun and thus help buffer plants from desiccation during dry periods (Benzing 1998, Venturieri & Mendoza de Arbieto 2011). Finally, many moss species leach nutrients and other chemicals into water that may stimulate orchid growth (Coxson *et al.* 1992, Carlton & Read 1991, Benzing 1998, Clark *et al.* 1998) or act as fungicides (Frahm 2004), which could perhaps prevent fungal parasitism of *Lepanthes*. Certainly, these are only a subset of the potential benefits that bryophytes could provide to epiphytic *Lepanthes* and additional manipulative studies are necessary to test the theories as to why these orchids are associated with bryophyte cover.

Accordingly, it is evident that in many cases, conservation of *Lepanthes* spp. will require us to focus our attention on epiphyte communities as a whole, as opposed to only on isolated species. Scheffknecht *et al.* (2010) conclude that bryophytes are highly representative of microclimate characteristics and could thus be useful indicators of habitat quality for orchids. Even in the absence of a direct causal relationship between the distribution of orchids and bryophytes (e.g. Gowland *et al.* 2011), their dependency on similar conditions is an indication that these plants could be susceptible to the same threats. A positive corollary of the general sensitivity of many tropical montane bryophytes is that they may act as important environmental indicators and may be useful for foreshadowing oncoming threats to many orchids before their effects are realized (Gignac 2001). Recent studies of bryophyte distributions have already indicated that global warming trends are driving species upslope and are causing extinctions at lower elevations (Bergamini *et al.* 2009). If orchids are reliant upon the distribution bryophytes, we can anticipate similar trends in their distributions.

From a conservation perspective, the results presented here demonstrate that climate change could have a double impact on *Lepanthes* spp. in Costa Rica and elsewhere. A large number of species from this genus are distributed in highly susceptible montane cloud-forest environments (Hammel *et al.* 2003). No doubt, these species are adapted to, and dependant upon, the cool temperatures and the moist cloud cover that persists in these forests (Benzing 1998, Zotz & Bader 2009). Similarly, the bryophytes that these orchids associate with are equally dependent of these cool and moist conditions (Hallingbäck & Tan 2010). Changes leading to hotter and dryer conditions in montane cloud forests such as Monteverde, Cuericí, and Las Alturas could directly and indirectly eliminate the conditions necessary for the survival of numerous species. If *Lepanthes* spp. can adapt to these changing conditions, or perhaps migrate away from them (see Hietz 1999, Foster 2001), they may still be in jeopardy if their bryophyte partners cannot persist. Recent analyses indicate that loss of bryophytes could eliminate many important resources required by *Lepanthes* spp. (Tremblay *et al.* 1998, Tremblay & Velazquez-Castro 2009, Gowland *et al.* 2011). Consequently, the ability of these orchids to adapt to a changing climate may be a secondary concern if the bryophytes they depend on cannot.

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