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ORIGINAL ARTICLE

High diversity and low specificity of fungi associated with seedless epiphytic plants

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Abstract

Epiphytes, which grow on other plants for support, make up a large portion of Earth's plant diversity. Like other plants, their surfaces and interiors are colonized by diverse assemblages of fungi that can benefit their hosts by increasing tolerance for abiotic stressors and resistance to disease or harm them as pathogens. Fungal communities associated with epiphytic plants and the processes that structure these communities are poorly known. To address this, we sampled seven epiphytic seedless plant taxa in a Costa Rican rainforest and examined the effects of host identity and microhabitat on external and endophytic fungal communities. We found low host specificity for both external and endophytic fungi and weak differentiation between epiphytic and neighboring epilithic plant hosts. High turnover in fungi within and between hosts and habitats reveals that epiphytic plant-associated fungal communities are highly diverse and suggests that they are structured by stochastic processes.

Abstract in Spanish is available with online material

KEYWORDS
bryophytes, Costa Rica, ferns, fungal community, host specificity

1 | INTRODUCTION

Epiphytic plants, which are plants that grow on the surfaces of other plants, make up about 10% of the land plant flora (Madison, 1977) and are especially diverse and abundant in tropical forests (Benzing, 1990; Nieder et al., 2001). Common epiphytes include liverworts, mosses, ferns, bromeliads, and orchids. Epiphytes face additional challenges compared to their counterparts that grow on the ground, including lack of access to water and nutrients stored in the soil (Zotz & Hietz, 2001). Additionally, epiphytes are highly vulnerable to climate change and land use change (Benzing, 1998; Nadkarni & Solano, 2002; Zotz & Bader, 2009). Interactions with symbiotic fungi likely help ameliorate these difficulties, such as by increasing stress tolerance or improving access to scare nutrients. Despite the prevalence and diversity of epiphytic plants, surveys of fungi associated with them have largely been focused on arbuscular mycorrhizal fungi in vascular plants (Janos, 1993; Lesica & Antibus, 1990; Michelsen, 1993) or fungi hosted by Orchidaceae (Otero et al., 2002, 2007; Yuan et al., 2008).

Plants host a broad range of fungi within their tissues and on their surfaces, and these fungi have a diverse array of ecological functions. The most widely known known are mycorrhizal fungi, which form mutualisms with plant roots and exchange nutrients scavenged from the substrate for photosynthate from the plant. Mycorrhizae and mycorrhiza-like mutualisms can be seen even in more basal plant lineages, such as ferns and liverworts (Lehnert et al., 2017; Pressel et al., 2014). Other fungi are plant pathogens that cause disease in the host plant. Some fungi are endophytes, living inside the host plant tissues without causing disease symptoms. Their functions are often mysterious, but some endophytes have been shown to increase host plant tolerance to abiotic stress (Waller et al., 2005; Wu et al., 2006) and defense against herbivores (Bamisile et al., 2018;

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Clay et al., 1985) and pathogenic microbes (Arnold et al., 2003; Liu et al., 2007; Wiewióra et al., 2015). Fungi associated with plants, be they mutualistic, pathogenic, or commensal, have been observed in all major lineages of land plants, including the seed plants, ferns, lycopods, and bryophytes.

Fungi associated with plants can vary in several ways, including among host plant species. Host specificity is seen among fungi associated with terrestrial boreal bryophytes (Kauserud et al., 2008), tree bark endophytes (Pellitier et al., 2019), and among fungi associated with roots (Shefferson et al., 2007; Toju et al., 2013) and leaves (Gange et al., 2007; Karimi et al., 2012; Kembel & Mueller, 2014; Moricca et al., 2012) of vascular plants. Within individual hosts, fungi vary among tissues, such as between roots and shoots of vascular plants (Wearn et al., 2012) and between living and dead or senescent bryophyte tissue (Cook, Sharma, et al., 2022; Davey, Heimdal, et al., 2013). Fungal variation by host can be due to differences in chemical composition among host tissues (Pellitier et al., 2019; van Bael et al., 2017). Host specificity is not universal, however. Some endophytic fungi are found in a broad range of hosts (Thomas et al., 2016), and geography was found to play a greater role that host phylogeny in explaining liverwort endophyte community composition (Davis & Shaw, 2008). Fungi can also differ within a single host species depending on the habitat of the host plant. For example, bryophyte-associated fungal communities can vary along elevation gradients (Davey, Heegaard, et al., 2013), between forests of different ages (Davey et al., 2014), and along continental-scale geographic gradients (Nelson & Shaw, 2019). Tree leaf endophytes have also been found to differ between urban and rural areas (Matsumura & Fukuda, 2013) and disturbance history (Gamboa & Bayman, 2001). These geographical differences can be driven by dispersal limitation (Higgins et al., 2014; Koide et al., 2017) or variation in environmental conditions, like rainfall and temperature (Zimmerman & Vitousek, 2012). It is unclear if fungal communities associated with epiphytic plants follow the same distribution patterns as in ground-dwelling plants. Lehnert et al. (2017) found lower colonization rates of endophytic and arbuscular mycorrhizal fungi in epiphytic ferns compared to terrestrial ones, suggesting differences between these two habitats and perhaps a greater role of dispersal limitation in the epiphytic environment.

The epiphytic plant community may host a large, unexplored diversity of fungi. Previous work using culturing (Arnold et al., 2000; Arnold & Lutzoni, 2007; Dreyfuss & Petrini, 1984) and sequence-based approaches (Donald et al., 2020) have found high diversity of Ascomycota in tropical epiphyte and tree leaf endophytes. Fungal taxa were frequently rare, with the majority being found in only one or a few leaf samples. Research on fungi in epiphytic substrates has documented high fungal species richness and spatial turnover over short, sub-meter distances (Cook, Sharma, et al., 2022), which might be explained in part by high host specificity and community variation among epiphytic plants.

In this study, we sequenced, using a metabarcode approach, fungi associated with seven co-occurring epiphytic plants, including five bryophytes and two groups of ferns, to test whether fungal communities differ among host plants. To determine if differences in fungi were greater for endophytes than for the entire fungal community and if endophytes had greater host specificity, we took subsamples of three bryophyte taxa and surface-sterilized them in order to distinguish endophytic fungi from the external or coincidental fungi found on unsterilized plants. For two of the bryophytes, we collected the same taxa on both branches and nearby rocks to assess the effect of microhabitat on fungal community composition. We expected fungal communities to segregate by host plant taxon, with particularly strong differences between fern and bryophyte hosts, and for these differences to be strongest when considering only endophytes as opposed to the full community, including taxa on surfaces. We predicted that endophytic fungi would be a nested subset of those found on the corresponding unsterilized plants. We also expected to find large differences in fungal communities between plants living in the epiphytic environment versus those on rocks.

2 | METHODS

2.1 | Sample collection and processing

This study took place in Parque Nacional Tapantí in Cartago Province, Costa Rica along a 500 m transect on the east bank of Rio Orosi (9°44′31″N, 83°47′2″W, 1300 m a.s.l), in a low montane rainforest. In July 2016 and July 2018, we collected small epiphytic plants, including liverworts (*Trichocolea* and *Plagiochila*), mosses (*Prionodon*, *Thuidium*, and *Orthostichopsis*), and ferns (*Elaphoglossum peltatum* and members of Hymenophyllaceae), from the branches of *Saurauia montana* trees. *Elaphoglossum* samples were separated into leaf and root/rhizome subsamples. In January 2019 we collected eight additional samples of *Thuidium* and *Plagiochila* and four samples of *Trichocolea*. Half of the *Thuidium* and *Plagiochila* samples were epiliths collected from nearby rocks. Each of the 2019 samples, both epiphytic and epilithic, were split into two subsamples. One subsample was rinsed thoroughly in distilled water. This treatment was aimed to remove most incidental spores and hyphae but retain a significant portion of fungal taxa growing on the plant tissues. The other halves of these samples were surface-sterilized by immersion for 30 sec in 96% ethanol, 90 sec in 10% bleach, 30 sec in 70% ethanol, and three rinses in deionized water. The goal of this treatment was to remove the bulk of incidental and external fungi, leaving primarily true endophytes. Similar procedures have been used for isolating endophytic fungi in culture (Arnold et al., 2000; U'Ren et al., 2012) and in metabarcode studies (U'ren et al., 2019). After collection and processing, samples were either stored in RNALater (Ambion, ThermoFisher) or lyophilized. For a summary of sampling design and sample sizes, see Table S1.

We extracted total DNA from each sample using DNeasy 96 Plant kits (Qiagen, Hilden, Germany). We identified host plants and confirmed our morphotypes by sequencing a portion of the chloroplast rbcL gene. We used the primers rbcL-Z1 (5'-ATGTCACCACAAACAG ARACTAAAGC-3′, modified from Kress & Erickson, 2007) and a_r (5'-

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CTTCTGCTACAAATAAGAATCGATCTC-3′, Kress & Erickson, 2007). We performed PCR amplifications in 25 µl reactions with 5 µl GoTaq reaction buffer, 0.2 µM of each primer, 200 µM of each dNTP, 1 mM $MgCl_2$, and 1.25 units of GoTaq polymerase (Promega, Madison, WI, USA) with the following thermocycler conditions: initial denaturation at 96° for 2 min, 35 cycles of 94° for 30 sec, 50° for 45 sec, and 72° for 90 sec, followed by a final elongation at 72° for 8 min. We sequenced rbcL using rbcL-Z1 as the sequencing primer.

To sequence the fungal ITS2 region in each plant sample, we used the primers 5.8S_Fun (5′ - AACTTTYRRCAAYGGATCWCT – 3′) andITS4_Fun (5′ – AGCCTCCGCTTATTGATATGCTTAART - 3′) (Tayloret al., 2016) with attached adapters (5′ – GTCTGCTGGGCT CGGAGATGTGTATAAGAGACAGAAA - 3′ and 5′ - TCGTCGGCAG CGTCAGATGTGTATAAGAGACAG - 3′ respectively). We performed PCR as described above for rbcL, with the following differences: 0.5 µM of each primer was used, the PCR annealing step was at 55° for 40 sec, the final elongation step lasted 10 min, and only 30 cycles. We cleaned the PCR products using 0.25 µl Exonuclease I (New England Biolabs, Ipswich, MA, USA) per 5 µl of sample incubated at 37° for 15 min and 80° for 15 min. We then added sample specific 6 bp barcodes and Illumina adaptors with a second, seven-cycle PCR reaction following the same procedure as above, with the exception of the primers (5′ -CAAGCAGAAGACGGCATACGAGAT-NNNNNN -GTCTCGTGGGCTCGG - 3′ and 5′ -AATGATACGGCGACCACCG AGATCTACAC-NNNNNN-TCGTCGGCAGCGTC - 3′, Ns represent variable barcode region, at 0.4 µM each). A mock community (described in Taylor et al., 2016) was added to each run to validate parameter choices in later bioinformatic steps. The barcoded samples and mock communities were quantified and pooled in equal amounts then purified with Agencourt AmPure XP beads (Beckman Coulter, Indianapolis, IN, USA) and sequenced on the Illumina MiSeq platform using the 2 × 300 bp kit.

2.2 | Bioinformatics

ITS2 data were processed in USEARCH v9.2.64 (Edgar, 2013). We merged paired-end reads and excluded sequences that did not successfully merge or had a merged length of less than 150 bp. We removed primer sequences with cutadapt (Martin, 2011) and then quality-filtered, dereplicated, and clustered reads into operational taxonomic units (OTUs) at 97% similarity. The clustering step also removed chimeric OTUs. We excluded any OTUs represented by only a single sequence. Taxonomic assignments were made using SINTAX (Edgar, 2016) with the UNITE v.8.2 (Abarenkov et al., 2020) database. Assignments with less than 80% confidence were dropped. We removed all OTUs assigned to a kingdom other than Fungi and OTUs classified as *Malassezia*, a common contaminant, and we dropped all samples with fewer than 1000 remaining sequences. *Elaphoglossum* leaf and root/rhizome subsamples were determined not to differ by organ (PERMANOVA $F = 0.135$, $p = .135$) and were combined into single samples. rbcL sequences were quality trimmed using CodonCode Aligner (CodonCode Corp., Dedham, MA, USA) and identified by searching for similar sequences in GenBank (Benson et al., 2017) using the BLAST algorithm (Altschul et al., 1990).

2.3 | Statistical analysis

All analyses were performed in R v3.5.1 (R Core Team, 2018) using the vegan (Oksanen et al., 2019) and phyloseq (McMurdie & Holmes, 2013) packages. To account for differences in sequencing depth among samples, OTU counts were transformed in two ways: relative abundance (RA) and presence-absence (PA). Analyses were done for both data transformations.

We visualized differences in fungal community composition among host plants, between surface-sterilized and un-sterilized plants, and between habitats using nonmetric multidimensional scaling (NMDS) ordinations. We tested for differences among groups using permutational multivariate analysis of variance (PERMANOVA) as implemented in the adonis2 function (McArdle & Anderson, 2001) in the vegan package, using Bray–Curtis dissimilarity for RA data and Jaccard dissimilarity for PA. To test for differences between pairs of host plant taxa, we subset the data by host and performed PERMANOVAs for each host pair. During pairwise tests, we adjusted p-values to account for multiple testing using the Holm method (Holm, 1979).

We visualized the overlap in fungal communities among unsterilized, epiphytic host taxa using Venn diagrams generated with the VennDiagram R package (Chen, 2018). We tested if the number of OTUs unique to single host plant taxa (host specific OTUs) and number of OTUs shared across all hosts (generalist OTUs) were significantly different from what would be expected by chance with a permutation test. In this test, we took each sample and randomly reassigned it to a new host taxon, keeping the numbers of samples of each host taxon constant. We then calculated the number OTUs that were specific to one of these randomized hosts and the number of those present in all the hosts. This process was repeated 1000 times, and then the actual observed values were compared to the generated distributions to assess statistical significance. This was done for all seven host taxa and for just the bryophytes (scripts for permutation tests available as supplementary material).

We tested the effects of surface-sterilization on OTU diversity using a paired t-test. We calculated alpha diversity in each sample by estimating the number of OTUs present at a sequencing depth of 1000 reads using the rarefy function in the vegan package. We tested for a difference in sample dispersion (i.e., the degree of dissimilarity among communities in a set of samples) between surface-sterilized and unsterilized samples using the PERMDISP2 procedure, as implemented in the betadisper function in vegan. We partitioned beta diversity, in the form of the Jaccard metric, between paired surface-sterilized and unsterilized samples into nestedness and turnover components using betapart (Baselga et al., 2018).

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3 | RESULTS

Fungal communities associated with epiphytes were highly diverse, with 12,773 OTUs found across all samples (n = 71). Most of these OTUs were rare and found in only one or two samples (Figure S1). The majority or plurality of fungal OTUs in every unsterilized host plant taxon belonged to Ascomycota (Figure S2), which included 5317 OTUs. The second-most abundant phylum was Basidiomycota with 2507 OTUs. In surface-sterilized samples, the percentage of Ascomycota, in particular Sordariomycetes, was even higher, making up over two thirds of all reads (Figure S2). Other phyla each made up less than one percent of all OTUs. 4822 OTUs could not be assigned to a phylum at 80% confidence. The most OTU-rich fungal family was Xylariaceae, with 143 OTUs.

Fungal community composition varied significantly by host plant (RA [relative abundance]: $F(6,58) = 1.82$, $p = .001$, $R^2 = 0.159$; PA [presence-absence]: $F(6,58) = 1.23$, $p = .001$, $R^2 = 0.113$) when only epiphytic, unsterilized samples were considered. Community composition also differed by whether the host plant was a fern or bryophyte (RA: $F(1,63) = 2.64$, $p = .001$, $R^2 = 0.04$; PA: $F(1,63) = 1.55$, $p = .001$, $R^2 = 0.0240$, Figure 1a & Figure S3). When testing differences between pairs of host plant taxa, all differences were significant when using RA data, with the exception of *Orthostichopsis-Prionodon* (Table 1). In contrast, only four of 21 pairs were significantly different when using PA data (Table S2). Ordinations suggested limited differences in fungal communities among host taxa, with high overlap among clusters (Figure 1 & Figure S4).

Each host taxon contained some unique OTUs (Figure S5). 847 OTUs were shared across all plant hosts, and 1153 were shared among all bryophyte hosts. Neither of these numbers are significantly different from what would be expected by chance based on our permutation test ($p > .05$). The number of OTUs unique to a single host taxon was not significantly different from chance when using either the entire epiphytic, unsterilized data set or just the bryophytes.

Fungal communities differed significantly but weakly between epiphytic and epilithic environments for unsterilized *Plagiochila* and *Thuidium* (RA: $F(1,30) = 1.72$, $p = .002$, $R^2 = 0.052$, PA: $F(1,30) = 1.39$, $p = .001$, $R^2 = 0.044$). When analyzing RA, the effect of host ($F(1,28) = 2.418$, $p = .001$, $R^2 = 0.073$) was stronger than the effect of habitat, and there was no significant interaction with host identity (Figure 1d). Effects of habitat were non-significant for surface-sterilized samples (Figure S6).

As expected, OTU richness was significantly lower in surface-sterilized subsamples than in their unsterilized counterparts ($t(18) = 26.915$, $p < .001$, Figure 2a). There was significantly more dispersion in unsterilized samples using both RA ($F(1,36) = 15.928$, $p < .001$) and PA ($F(1,36) = 73.072$, $p < .001$) data, and this can also be

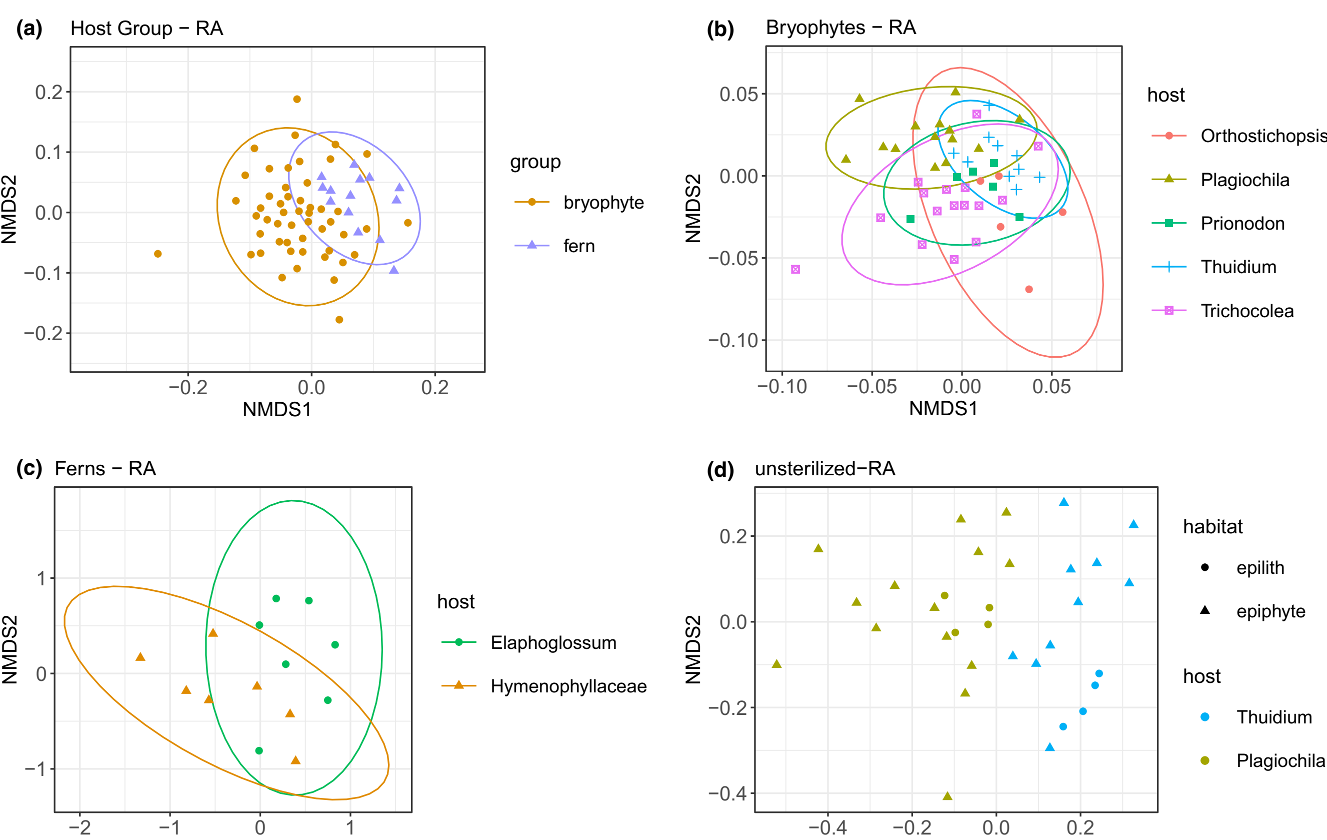

FIGURE 1 NMDS ordinations comparing unsterilized RA fungal community composition by group (a, stress = 0.272), by bryophyte taxon (b, stress = 0.266), by fern taxon (c, stress = 0.157) with 95% confidence ellipses, and by host and habitat (d, stress = 0.2044). The host plant groups and taxa form overlapping clusters. Samples cluster by host more strongly than by habitat

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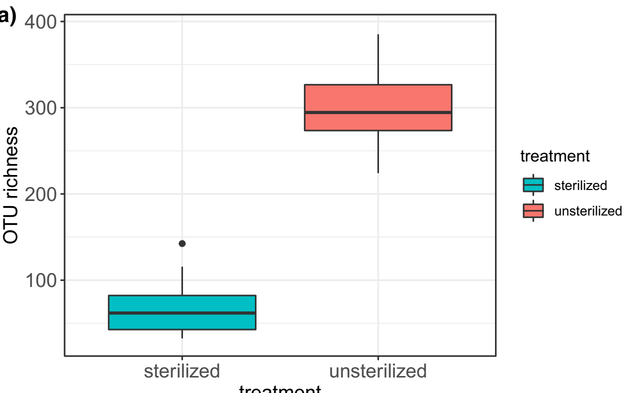
TABLE 1 Pairwise PERNMANOVA results by host plant using RA data

	Hymenophyllaceae	Elaphoglossum	Thuidium	Plagiochila	Trichocolea	Orthostichopsis
Elaphoglossum	$F(1,12) = 1.87, p = .028, R^2 = 0.135$					
Thuidium	$F(1,15) = 2.35, p = .021, R^2 = 0.135$	$F(1,15) = 1.90, p = .021, R^2 = 0.112$				
Plagiochila	$F(1,19) = 2.53\ p = .021, R^2 = 0.117$	$F(1,19) = 2.19, p = .021, R^2 = 0.103$	$F(1,22) = 1.86, p = .026, R^2 = 0.078$			
Trichocolea	$F(1,21) = 2.58, p = .021, R^2 = 0.109$	$F(1,21) = 1.88, p = .021, R^2 = 0.082$	$F(1,24) = 1.56, p = .021, R^2 = 0.078$	$F(1,28) = 2.03, p = .021, R^2 = 0.068$		
Orthostichopsis	$F(1,10) = 2.16, p = .028, R^2 = 0.177$	$F(1,10) = 1.65, p = .027, R^2 = 0.142$	$F(1,13) = 1.24, p = .028, R^2 = 0.087$	$F(1,17) = 1.69\ p = .026, R^2 = 0.090$	$F(1,19) = 1.26, p = .028, R^2 = 0.062$	
Prionodon	$F(1,11) = 2.06, p = .027, R^2 = 0.158$	$F(1,11) = 1.45, p = .026, R^2 = 0.116$	$F(1,14) = 1.34, p = .028, R^2 = 0.088$	$F(1,18) = 1.74, p = .026, R^2 = 0.088$	$F(1,20) = 1.40, p = .028, R^2 = 0.065$	$F(1,9) = 1.12, p = .17$

Note: Bolded values indicate statistically significant results.



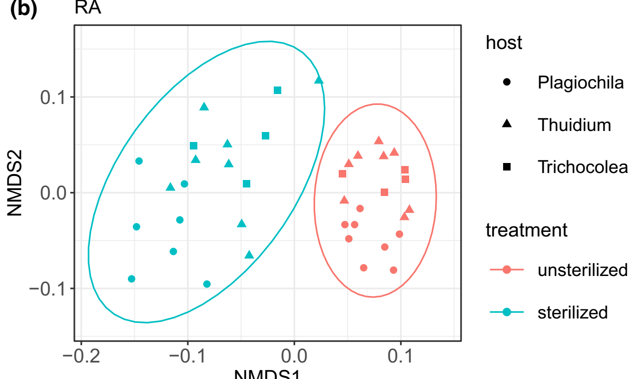


FIGURE 2 OTU richness (a) and NMDS ordination (b, stress = 0.195) of fungal communities by sterilization treatment. Richness was calculated as the expected number of OTUs at a sequencing depth of 1000 reads, in surface-sterilized and unsterilized bryophyte samples. Sterilized samples had greatly reduced diversity compared to their unsterilized counterparts. Ordination used RA data with 95% confidence ellipses based on sterilization treatment. Samples form distinct clusters based on sterilization

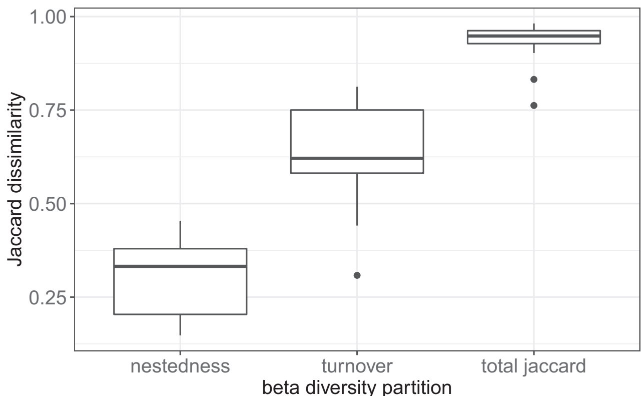


FIGURE 3 Boxplot of partitioned beta diversity among paired unsterilized and surface-sterilized bryophyte samples. Overall Jaccard dissimilarities between sample pairs were high. Turnover tended to be higher than the nestedness component, indicating lack of shared OTUs

seen in the ordinations of these samples (Figure 2b and Figure S7). Fungal communities differed significantly by host taxon in surface-sterilized samples (RA: $F(2,16) = 1.34$, $p = .003$, $R^2 = 0.095$, PA:

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$F(2,16) = 1.17$, $p = .013$, $R^2 = 0.083$), but not by habitat or the interaction between host and habitat ($p > .05$). Jaccard dissimilarity between paired sterile and unsterile samples was high, averaging 0.935, meaning there were few shared OTUs between sample pairs. When Jaccard dissimilarities were partitioned into turnover and nestedness components, turnover predominated (Figure 3).

4 | DISCUSSION

While much has been learned about endophytic and other plant-associated fungal communities, most work has focused on terrestrial seed-plants. In this study, we addressed the host- and habitat-specificity of fungi, including endophytes, associated with epiphytic spore-dispersed plants. Fungal diversity and OTU richness was high, both across all samples and within individuals, (Figure 3), though most OTUs were rare (Figure S1). Ascomycota OTUs dominated most samples, and this is consistent with past studies on endophytes (Arnold, 2007; del Olmo-Ruiz & Arnold, 2017; Rodriguez et al., 2009) and leaf-associated fungi (Davey et al., 2012; Jumpponen & Jones, 2009; Kembel & Mueller, 2014). Glomeromycota were present in some samples, though typically at levels below one percent RA. They have previously been observed in epiphytic plants (Janos, 1993; Rabatin et al., 1993) and may be forming arbuscular mycorrhizal associations with the ferns in this study, but cytological studies would be required to confirm this.

As predicted, fungal community composition did vary significantly among host plant taxa. These differences, however, were small, with high overlap among host plants and large variation among samples from the same host(Figure 1). While each host did have some unique fungal OTUs (Figure S5), the number of these unique fungi is no greater than expected by chance given the rarity of most OTUs. Similarly, most host plants did not differ in fungal community composition when using PA data, indicating a lack of strict-sense host specificity. There were greater differences when using RA data, though explanatory power of host was still small, especially among bryophytes. Greater differences in RA versus PA suggests that hosts share many fungal taxa, but these fungi differ in abundance based on host. This might reflect a fairly uniform influx of propagules, in which the more common fungal taxa are found in several hosts, but that differences in fungal biomass, and hence RA, of actively growing OTUs are related to host-fungus interactions that differ by host plant. Differences in fungal communities were larger between ferns and bryophytes, possibly due to biochemical differences between these two distantly related groups of plants. Fungal communities can also change dramatically within a host through time or over the course of the hosts' development (Cook, Taylor, et al., 2022; del olmo-Ruiz & Arnold, 2014; Younginger & Ballhorn, 2017), which could contribute to high community variation within host taxa and obscure inter-host differences.

Other researchers have documented high host specificity of endophytic or leaf-associated fungi; for example, Kembel and Mueller (2014) were able to explain over half of the variation in tropical tree leaf fungal community with host plant taxonomy. High host specificity, however, is not universal. Bayman et al. (1997), for example, found higher variation in fungal endophytes within single plants than across host orchid species. Similarly, Del Olmo-Ruiz and Arnold (2017) and Donald et al. (2020) found low host specificity of fungal endophytes in tropical ferns and tree leaves, respectively. It is possible that many fungi in this environment are generalists without strong host preferences, as has been seen in some endophytic *Xylaria* species (Laessøe & Lodge, 1994; Thomas et al., 2016). This pattern has been found with culturable angiosperm leaf endophytes, where host breadth was lower in the tropics than in temperate or boreal regions (Arnold & Lutzoni, 2007). This may be due to the high plant diversity found in the tropics, in which density of any particular host plant tends to be low, making it difficult for specialized fungi to find their preferred hosts. Specificity can also be low in polar regions, however, as has been seen in root endophytes (Botnen et al., 2014). Low specificity might also be explained by lack of differences in the traits of the host plants, particularly the bryophytes. More research on bryophyte biochemistry would be needed to tie fungal community with host chemical traits.

Contrary to our expectations, differences in fungal communities between epiphytic and epilithic bryophytes were small (Figure 1d), and these communities did not differ when only considering endophytic fungi in the surface-sterilized samples. Research on variation in fungal associations between microhabitats at the same site in the tropics are limited, so we can make few comparisons. Del Olmo-Ruiz and Arnold (2014) examined differences in fungal endophytes in various fern species and did not find a difference between epiphytic and terrestrial ferns, though this study involved different host species in each habitat. Climate, including temperature and precipitation, can have impacts on endophyte community composition (Barge et al., 2019; Giauque & Hawkes, 2016; Zimmerman & Vitousek, 2012), though the epiphytes and epiliths in our study were located at the same site and exposed to the same general climate. Plants in both habitats were likely exposed to the same species pool of airborne fungal propagules, and abiotic conditions were similar enough between the two habitats to permit some of the same plant species to grow in both. Thus, abiotic differences may have been too small for environmental filtering to have a substantial effect on fungal communities. Additional environmental factors which can impact fungal communities, such as height in the tree canopy and disturbance history (Gamboa & Bayman, 2001) or season, were not addressed here but could be considered in future studies.

Fungal diversity was much lower in surface-sterilized plants than in unsterilized plants, as expected (Figure 2a). We predicted that endophytes would be more consistent both within and between hosts due to increased specialization that is presumably needed to function as an endophyte, but we found the communities in surface-sterilized samples were more different from each other than unsterilized ones (Figure 1b). On the contrary, this finding is consistent with the idea that the community on unsterilized plants more closely resembles a homogeneous airborne propagule community than does the endophyte community. The surface-sterilized

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plants also did not contain nested subsets of the fungi recovered from their un-sterilized counterparts, but had additional fungi not found in the other (Figure 3). This may be due to the high, centimeter scale spatial turnover in fungal communities and intra-host variation previously observed in this tropical epiphyte system, in which epiphytes located even a meter or less apart from one another share few fungi in common (Cook, Sharma, et al., 2022). Our sampling method was destructive, and the exact same plant material could not be used for both sterilized and un-sterilized sampling. Thus, if endophytes in our system have high turnover within individual plants or between nearby plants (see e.g., Bayman et al., 1997; Oono et al., 2017), this could help explain the limited nestedness and high turnover between our sterile-unsterile sample pairs. It might also be that fungi are much more abundant on plant surfaces, swamping out the signal from endophytes. Also, because bryophytes lack a cuticle, we may have inadvertently killed a portion of the endophytes with our sterilization procedure.

Overall, our data suggest low specificity in plant-fungal interactions in a tropical epiphyte system. Host specificity was low in our studied bryophyte and fern taxa, even when only endophytes were considered. Abiotic environment, in the form of an epiphytic versus epilithic habitat, also had little effect on the fungal community. The community was highly diverse, with high turnover among samples that could not be explained by host or environment. This, combined with the high spatial turnover of fungi seen in this system (Cook, Sharma, et al., 2022), suggest that tropical epiphytic fungal communities are hyper-diverse with extremely stochastic community assembly and a lack of strong biotic or abiotic drivers at the local scale.

AUTHOR CONTRIBUTION

KC and DLT contributed to study design and writing of the manuscript. KC conducted the research and analyzed the data.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The raw fungal sequence data used in this study is available on NCBI SRA through accession PRJNA817531. Plant rbcL sequences are accessioned on GenBank as BankIt2475881: ON055169 – ON055243.

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