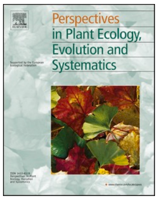
Perspectives in Plant Ecology, Evolution and Systematics 54 (2022) 125658

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



# A case for studying biotic interactions in epiphyte ecology and evolution

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ARTICLE INFO

*Keywords:*
Competition
Facilitation
Mutualism
Bryophyte
Lichen
Vascular epiphyte

ABSTRACT

Biotic interactions are widely accepted as an important driver of ecological and evolutionary patterns, contributing to the structure of systems as diverse as tropical tree seedlings, intertidal barnacles, and wildflower-pollinator networks. Species interactions within a trophic level, such as competition and facilitation, can drive patterns of community change over time, yielding both fundamental ecological theories of succession as well as insight vital to predicting biodiversity conservation priorities. One system in which biotic interactions are poorly explored is epiphytes, or structurally dependent, non-parasitic organisms. This is a topic of broad interest because epiphytes—including vascular plants, bryophytes, and lichens—exist in practically all terrestrial ecosystems throughout the world. From lichens acting as pollution-sensitive indicator species in urbanized landscapes, to the multimillion-dollar commercial market for horticultural bromeliads, to tropical orchids representing striking examples of rapid speciation, epiphytes make substantial contributions to theory, biodiversity, ecosystem services, and the global economy. This review is the first to broadly synthesize the underlying biotic interactions important to epiphyte ecology and evolution. We first draw from theory to discuss where and when biotic or abiotic processes are likely stronger drivers of epiphyte dynamics. We then systematically review the literature across the major interaction modes, highlighting areas where different groups of epiphytes (e.g., vascular versus nonvascular) and ecosystems have contrasting patterns or expectations. Throughout, we illustrate where research efforts have focused and where large gaps in knowledge exist. Our review is organized around the major biotic interactions, rather than the specific organisms interacting with the epiphytes, to highlight general processes and set epiphytism within the framework of ecological and evolutionary theory. Our review encompasses pollination and dispersal, intratrophic facilitation and competition, mycorrhizal mutualisms, epiphyte-host interactions, parasitism and pathogens, and herbivory, focusing on the impact of these interactions on the epiphyte. Finally, we provide a simple conceptual framework distilling open questions in the field, expand our findings to the community and ecosystem level, and summarize the biodiversity conservation implications of ignoring biotic interactions in epiphytes. Our synthesis brings together currently disparate literature from tropical and temperate systems on vascular and nonvascular plants and lichens. We hope our review stimulates further research and inspires cross-disciplinary collaboration.

## 1. Introduction

Biotic interactions, whether within or across trophic levels, drive critical ecological and evolutionary patterns in plants and form the foundation of ecological theories (Dobzhansky, 1950; HilleRisLambers et al., 2012; Schemske et al., 2009). For example, facilitation and competition among niche-differentiated plant species can drive successional turnover, promote coexistence, and stabilize community dynamics (e.g., Connell and Slatyer, 1977; Levine and HilleRisLambers, 2009), the presence of mycorrhizal fungi symbionts can structure the distribution of plant communities and mediate key ecosystem processes (Johnson and Gehring, 2007; Otero et al., 2005), and plant-pollinator and herbivory-defense relationships contribute to rapid speciation in the most diverse plant families (e.g., Givnish et al., 2015; Marquis et al., 2016). Specialist enemies are now known to be a major part of the answer to the age-old question of why tropical tree communities are so diverse, a concept that greatly advanced the field of diversity maintenance theory (e.g., Comita and Stump, 2020; Mangan et al., 2010). Niche theory, once focused solely on abiotic factors, such as light, water, and nutrients, now includes more cryptic axes of differentiation driven

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https://doi.org/10.1016/j.ppees.2021.125658
Received 1 April 2021; Received in revised form 27 September 2021; Accepted 27 December 2021

by biotic interactions, such as microbial endophytes (Griffin et al., 2016) and antiherbivore chemical defenses (Kursar et al., 2009; Sedio, 2017). However, much of this progress has been taxonomically and geographically biased, hindering our ability to generalize across plant groups or geographic regions (Culumber et al., 2019; Fitzjohn et al., 2014). Here, we make an argument for expanding the research effort on biotic interactions to another important plant growth form: epiphytes.

Epiphytes, or plants that grow non-parasitically on other plants, are charismatic and ecologically vital components of ecosystems across the world. They contribute to forest biodiversity and play an important role in ecosystem processes, such as mediating nutrient cycling and increasing water retention (Coxson and Nadkarni, 1995; Van Stan and Pypker, 2015). Vascular epiphytes contribute approximately 9% of vascular plant species worldwide and can make up 50 % or more of species in some tropical forests (Kelly et al., 1994; Zotz, 2013a). Nonvascular epiphytes are globally ubiquitous, can make up to four times more foliar biomass than their host trees (Nadkarni, 1984), and out-number vascular epiphytes in temperate rainforests (e.g., Hofstede et al., 1993). Because of their characteristic structural dependence, epiphytes live in a unique, three-dimensional habitat space above the ground; we use the broad definition of canopy (*sensu* Moffett, 2000) to describe this multilayered space. Light, water, and nutrient gradients exist both vertically from the understory to the upper canopy strata as well as from the inner to the outer crown in tropical (Hietz and Hietz-Seifert, 1995a; Woods et al., 2015) and temperate (Woods et al., 2019) rainforests. These abiotic variations have been the focus of numerous studies that correlate patterns of epiphyte diversity and abundance with abiotic variables for both vascular epiphytes (e.g., Cardelús, 2006; Hietz and Hietz-Seifert, 1995a, 1995b; Rosa-Manzano et al., 2017; Woods et al., 2015) and nonvascular epiphytes (McCune et al., 1997; Mellado-Mansilla et al., 2017; Woods et al., 2019); a smaller body of work also has experimentally demonstrated abiotic drivers of vascular epiphyte fitness (e.g., water, nutrients and light, Laube and Zotz, 2003; nutrients, Zotz and Asshoff, 2010). In addition to these abiotic gradients, host characteristics such as bark texture, phenology, size, age, chemical compounds, branch patterns, and structural stability vary in three-dimensional space (e.g., Callaway et al., 2002b; Einzmann et al., 2015; Hietz and Hietz-Seifert, 1995b; Rasmussen and Rasmussen, 2018). Likewise, microbial communities vary from forest floor to the canopy in tropical (Gora et al., 2019) and temperate rainforests (Dangerfield et al., 2017), as do animal communities, including pollinators, seed dispersers, and herbivores (Bawa, 1990; Neves et al., 2014; Smith, 1973; Thiel et al., 2020). These complex vertical gradients and substrate characteristics provide axes of niche differentiation and opportunities for highly diverse species interactions, perhaps even exceeding those of terrestrial plants. However, because the field of epiphyte biology is less well-developed than that of terrestrial plants, the extent to which epiphyte biotic interactions compare to similar relationships in terrestrial plant systems, or intersect with abiotic gradients, is currently unknown. Better characterization of epiphyte biotic interactions, and an examination of how biotic interactions contribute to epiphyte ecology and evolution, would bring new insights to ecological and evolutionary theory.

For this review, we define epiphytes as any vascular plant, bryophyte, or lichen that spends much of its life cycle perched on another plant, without a connection to the ground. This broad definition includes both vascular and nonvascular holoepiphytes, which germinate, grow, and reproduce in the canopy, never making a root connection to the ground (Benzing, 2008; Moffett, 2000; Zotz, 2013b). We include vascular hemiepiphytes, which germinate in the canopy and then later send down aerial roots that reach the ground because part of their life-cycle is epiphytic, unlike vines and lianas (Moffett, 2000; Zotz, 2013b; Zotz et al., 2021). Guided by the recently updated definition of epiphytic plants based on the site of germination (Zotz, 2013b; Zotz et al., 2021), we do not explicitly include nomadic vines in our review, which germinate in the ground and then climb up into higher forest strata, losing their root connection with the ground later during ontogeny (Benzing, 2008; Moffett, 2000). We include epiphytic lichens in our review (for an in-depth lichen-specific review, see Ellis, 2012), but do not include discussion of aquatic plants. However, we note that literature on aquatic epiphytes such as algae on seagrasses may have some parallels to canopy epiphytes, and would be interesting for future comparisons (e.g., Lobelle et al., 2013; Michael et al., 2008). Much of our paper will cite examples from vascular holoepiphytes, in part because these taxa make up the majority of epiphyte literature (68 % of the articles in our systematic review; **Figure S1**); however, we argue that some of the concepts we propose also extend to the diverse taxa and growth habits of the broader epiphytic community. We use the available literature to illustrate potential differences among epiphytic groups (vascular plants vs. bryophytes vs. lichens; holo- vs. hemiepiphytes).

This review has three primary goals. First, we acknowledge the importance of abiotic drivers in epiphyte ecology and evolution and make the argument for why this does not preclude the importance of biotic drivers. We briefly provide theoretical bases for when and where biotic interactions should be most important for epiphytes, and where biotic interactions could better explain extant patterns than abiotic-only explanations. Second, we highlight, and provide examples of, the diverse biotic interactions that exist for epiphytes, and show which interactions remain uncharacterized. We organize biotic interactions into two major modes from the perspective of the epiphyte: net positive interactions, such as mutualisms and facilitation, and net negative interactions, such as competition and herbivory. We also discuss where the lines between positive and negative begin to blur, whether by nature or by lack of data. Third, we synthesize the state of the field by pointing out apparent gaps in the epiphyte biotic interactions literature and suggest several areas for future research. We conclude by reminding the reader of why this area of research matters, enumerating implications for both applied conservation and management as well as for the advancement of ecological and evolutionary theory.

## 2. Methodology

We conducted an extensive literature search from September 2020-September 2021 by searching the Web of Science for articles containing “epiphyt*” AND ("biotic interaction" OR "species interaction" OR "interspecific interaction" OR "intraspecific interaction" OR mutualism OR facilitation OR commensalism OR coevolution OR co-evolution OR pollination OR "animal dispersal" OR zoochor* OR parasitism OR pathogens OR herbivory OR florivor* OR "seed predation" OR competition). This yielded 1764 articles; we narrowed the search by topic by excluding articles in the categories Marine Freshwater Biology, Agronomy, Biochemistry Molecular Biology, Oceanography, Microbiology, Biotechnology Applied Microbiology, Toxicology, Public Environmental Occupational, Cell Biology, Water Resources, Engineering, Pharmacology Pharmacy, Chemistry, Energy Fuels, Immunology, Integrative Complementary Medicine, Physics, Public Administration, and Research Experimental Medicine. The narrowed search yielded 921 articles; we read through article titles and abstracts to only include relevant literature; we excluded aquatic ecosystems, microepiphytes (fungi and bacteria), terrestrial plants, nomadic vines, strict molecular studies (e.g., chemicals competing for binding sites), articles focused on pollinator behavior (e.g., competition among pollinators, rather than plants), evolution of traits independent of biotic interactions, strict surveys (no predictor variables that included biotic interactions), papers strictly about the co-evolution of lichen components, horticultural hand-pollination only studies (no observations of plant-pollinator interactions), and articles that did not mention a biotic interaction in the abstract. We did include review articles and theoretical articles that used epiphytes as examples of biotic interactions, as well as evolutionary and phylogenetic articles that provided evidence of biotically-mediated co-evolution (e.g., pollinator and epiphyte evolution). The search ultimately resulted in 304 articles (**Figure S2**), spanning the publication years 1992–2021 (**Figure S3**). As we read the abstracts, we noted which type of biotic interaction and which type of epiphyte (vascular plant, nonvascular plant, lichen) was the focus of the research. We summarized these observations and illustrated the data in Fig. 1. Note that some articles contained multiple topics and some did not fit into the major interaction categories, so the total number of articles in Fig. 1 does not add up to 304. In some topical areas of our review (Section 4), we supplemented the systematic search by adding papers cited in the references.

## 3. The importance of abiotic drivers in epiphyte ecology and evolution

The epiphytic habitat poses particular challenges, which have historically led to epiphytes being categorized as stress-tolerators (e.g., Benzing, 2008; Lüttge, 2012). Namely, because epiphytes do not have a permanent root connection to the terrestrial soil, their water and nutrient supplies are usually more limited than those of terrestrial counterparts (Benzing, 2008). For epiphytes living in the upper and outer reaches of tree canopies, abiotic conditions can be very harsh. High light and very low humidity, combined with high winds typical of canopy locations, exert strong selection pressure for traits similar to those seen in desert habitats: leaf succulence, CAM photosynthesis, small stature, slow growth rate, water and nutrient storage capabilities, and UV protection (Bartels and Chen, 2012; Benzing, 1987; Madison, 1977; Reyes-García et al., 2012; Zhang et al., 2018; Zotz and Hietz, 2001), in addition to poikilohydry for nonvascular epiphytes and lichens (Frahm, 2003; Lakatos and Fischer-Pardow, 2013; Sillett and Antoine, 2004). At the same time, microhabitats in the inner crown of trees that are often shaded, humid, and moist are inhabited by species that are less tolerant of drought and high light (Freiberg, 1996; ter Steege and Cornelissen, 1989; Watkins et al., 2007; Woods et al., 2015). Acquiring unique traits to thrive in the canopy along with the fine-scale variation in microhabitats within canopies has been argued as evolutionary reasons why some vascular epiphyte groups have had such high speciation rates: there are few competitors in the niche space and many fine-scale niches to occupy (Benzing, 1987; Givnish et al., 2015; Gravendeel et al., 2004). Epiphytism has evolved several times and occurs in at least 73 vascular plant families (Zotz, 2013a); few specific traits are common among all epiphytes, but most share some substrate-anchorage adaptations, drought adaptations, and/or the ability to obtain nutrients in unusual ways to thrive in a range of abiotic conditions (Benzing, 2008, 1987, 1986; Gentry and Dodson, 1987; Zotz, 2016).

Epiphyte habitats likely range from very stressful to very resource-rich environments, just like terrestrial habitats do. On one extreme and rare end of drought adaptation, atmospheric bromeliads cannot survive in prolonged wet periods, because the very trichomes that can collect atmospheric water create an impenetrable film when too wet, effectively drowning the plant (Benzing, 1987; Benzing et al., 1978; Zotz and Bader, 2009). Similarly, a surplus of water reduces photosynthetic productivity in lichens (Lange et al., 1993), which may explain their higher abundance in the driest parts of the canopy (Hofstede et al., 1993;

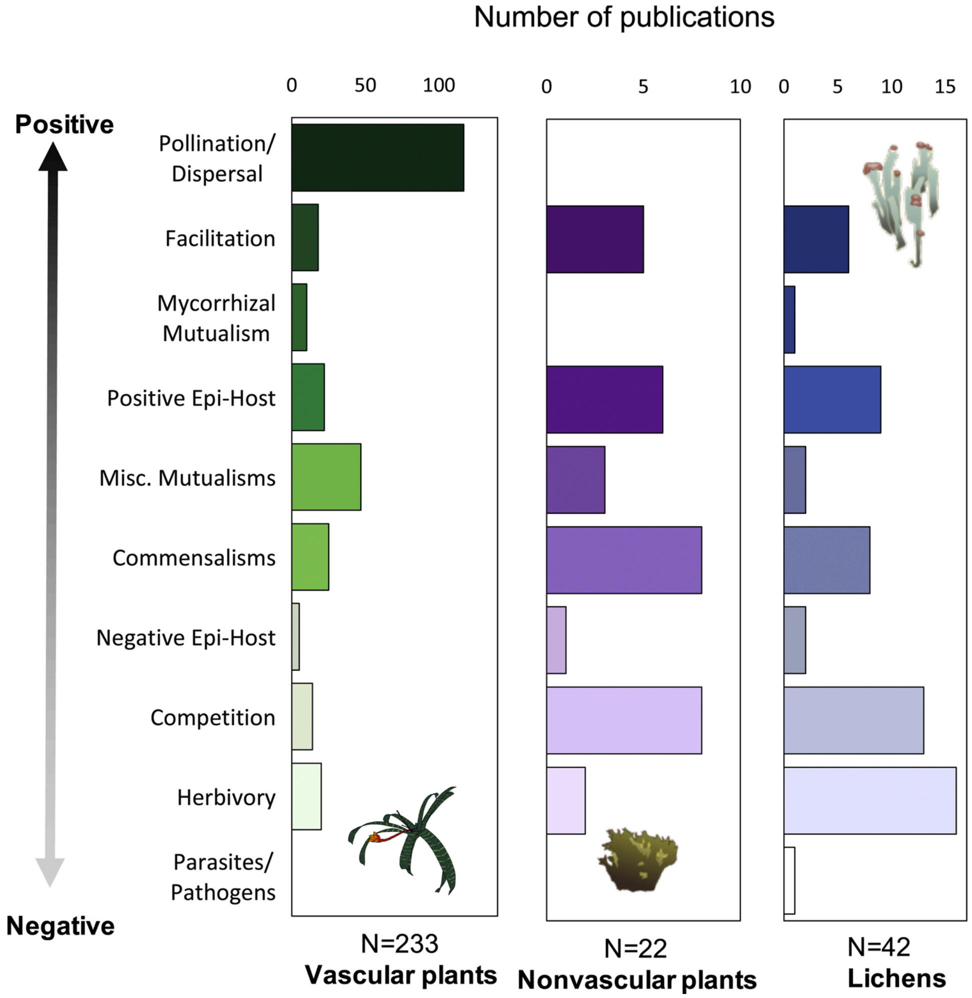


**Fig. 1.** Summary of biotic interactions focused on in the systematic literature search. 304 articles were kept in the literature review; additional literature is cited in the body of the article. Note that the scales (number of articles) are different for each epiphyte growth form.

McCune, 1993). On the other hand, some epiphytic fern species in the Hymenophyllaceae have no water-storing tissues in their leaves or rhizomes and no stomata and are, thus, restricted to the most humid locations in tree canopies (Dubuisson et al., 2009; Hietz and Briones, 1998). Moreover, primary hemiepiphtic figs were found to have higher nutrient status in their epiphytic stage than when connected to the terrestrial soil, because the canopy humus was more nutrient-rich than the forest floor (Putz and Holbrook, 1989); canopy humus was also found to be more nutrient-rich than terrestrial soil in Australian rainforests (Doyle, 2000). Thus, epiphytic habitats are not always inherently “more stressful” than terrestrial habitats.

All in all, the importance of abiotic factors to epiphyte ecology and evolution does not preclude biotic interactions from playing a major role in these patterns and processes. Stress theory allows us to make predictions about when and where epiphyte-epiphyte interactions may be important (Bertness and Callaway, 1994). In moderately high-stress, resource-poor environments, such as what we might see in the outer canopy, facilitation may dominate, because nearby individuals can ameliorate physiological stress (e.g., Callaway et al., 2002a; reviewed in Soliveres et al., 2015); this is particularly evident in studies between nonvascular epiphytes and vascular epiphytes (see section *4.1.2 Epiphyte-epiphyte facilitation* below). As conditions become more favorable, whether by abiotic variation in microsites or by the presence of other individuals, interactions can become more competitive (e.g., Choler et al., 2001; Connell and Slatyer, 1977; Maestre et al., 2009; Platt and Connell, 2003; Wilson and Agnew, 1992), particularly for high-density epiphyte communities, where space competition would predominate (see Section 4.2.3, *Direct competition* below). On the other hand, there are examples where epiphyte interactions are unlikely because epiphytes are sparsely dispersed within their environments (<10 individuals per tree in seasonally dry forest, Werner and Gradstein, 2008; average of 25 but median of 12 individuals per tree on *Annona glabra* trees surrounding BCI, Zotz et al., 1999; Bader et al., 2009). At very low plant densities, neither competitive nor facilitative interactions may be important (Benzing, 1987).

There are several areas in which biotic interactions are predicted by theory to be important to epiphyte ecology and evolution both within and across trophic levels. A major evolutionary mechanism proposed to explain the high diversity of epiphytic orchids, for example, is their close relationship with euglossine bee pollinators (Benzing, 1987; Gentry and Dodson, 1987; see Section 4.1.1*, Pollination and dispersal* below, Fig. 1A). Furthermore, island biogeography approaches to explain patterns of epiphyte colonization and diversity hinge on population dynamics of extant epiphytes, disperser and pollinator availability, and size and connectivity among host trees—all, at least in part, biotic interactions (e.g., Mallet et al., 2014; Reid et al., 2016; Snäll et al., 2003). Successional replacement driven by epiphyte-epiphyte interactions has been proposed and, more scarcely, applied to vascular epiphytes (island ontogeny framework, Taylor and Burns, 2015; species accumulation model, Woods, 2017), nonvascular epiphyte communities (similar gradient hypothesis, McCune, 1993; Ruchty et al., 2001), epiphytic lichen communities (Johansson, 1974; McCune, 1993; Nascimbene et al., 2009), and epiphyllous lichens and bryophytes (Mežaka et al., 2020). Beyond these theoretical expectations, much theory has not yet permeated the epiphyte literature, and many biotic interactions have simply not been studied or tested experimentally (Zotz, 2016; Zotz and Hietz, 2001). For example, although water shortage is surely a very important constraint for many epiphytes, competition or herbivory may be in fact more important in some scenarios, especially in lichens (e.g., Gauslaa et al., 2018; Fig. 1; see below, Sections 4.2.2 *Herbivory and 4.3.3 Direct competition*). We did not find any studies that tested these factors together. Including biotic factors in epiphyte ecological and evolutionary studies will only improve our understanding of when and how abiotic factors prevail.

## 4. What we know—and don’t know—about biotic interactions in epiphyte ecology and evolution

### *4.1. Positive interactions: Mutualisms, facilitation, commensalism, coevolution*

### *4.1.1. Pollination and seed dispersal*

The coevolution of epiphytes and their specialized pollinators is the best-studied biotic interaction in epiphyte ecology and evolution (Baguette et al., 2020; Benzing, 2008; Gentry and Dodson, 1987; Micheneau et al., 2009; Robacker et al., 1988). Pollination was the most common biotic interaction found in the abstracts in our systematic review, with approximately 36 % of articles (109) discussing pollination in the abstract (Fig. 1). Flower morphology of some epiphytic orchids mimics insect pollinators, and several examples exist of coevolution between epiphytic orchid flowers and pollinator traits, such as tongue length (Baguette et al., 2020; Micheneau et al., 2009; Wasserthal, 1997). Likewise, epiphytic and hemiepiphytic figs engage in an unusual mutualism with wasps, wherein figs attract female wasps into their closed inflorescence (the fig), which pollinate and lay an egg into the inflorescence (e.g., Harrison, 2005). The reproductive cycle is highly specialized, where only one or a few species of wasps pollinate one species of fig; the coevolution of morphologically matched traits in figs and wasps is cited as one origin of the impressive diversity of figs (over 800 species globally in the genus) (Bruun-Lund et al., 2018; Harrison, 2005). Obligate epiphytic figs may be even more specialized than hemiepiphytes, evolving an unusual fig morphology to allow re-entry of the fig wasp to maximize seed set (Mohd Hatta et al., 2021). Pollinators have been shown to be a limiting resource for epiphytes (e.g., Murren and Ellison, 1996; Vale et al., 2011), therefore mediating the classic abiotically-driven resource-limitation for epiphyte reproduction. Because most animal pollinators are volant, they are hypothesized to facilitate long-distance pollen dispersal and can allow species to be rare, contributing to the maintenance of holo- and hemiepiphyte diversity (Gentry and Dodson, 1987; Harrison, 2005). However, recent literature suggests that more research is needed to confirm these hypotheses (Janzen et al., 2020; Kessler et al., 2020).

A large body of work focuses on the fascinating mutualism between orchids and euglossine bees, which are the exclusive pollinators of nearly 700 species of orchids in the Neotropics (Fig. 2A, e.g., Pemberton and Wheeler, 2006). In this mutualism, male bees collect orchid fragrances in specialized sacs to attract female bees, erstwhile pollinating the highly unusual orchid flowers (Dodson et al., 1969; Dressler, 1986; Robacker et al., 1988). The details of the coevolutionary dynamics of this mutualism are still debated at large, due to the lack of host species specificity or dependence on the orchids in many orchid-pollinating euglossine bees; that is, the orchids need the bees but the bees seem not to need the orchids (Baguette et al., 2020; Gravendeel et al., 2004; Pemberton and Wheeler, 2006; Roubik and Ackerman, 1987). Naturalized euglossine bees outside the native range of their orchid partners, for example, substitute local fragrant compounds from non-orchid species, effectively showing facultative mutualisms (Pemberton and Wheeler, 2006). Likewise, many orchids are deceptive, attracting pollinators without providing nectar or pollen as a reward; a recent study found approximately 38 % of 34 studied epiphytic *Dendrobium* orchids to have no nectar (Jia and Huang, 2021). Still, the orchid-bee interaction is accepted as a complex coevolution in which floral mimics could be a key evolutionary innovation facilitating the rapid diversification of orchids (reviewed in Baguette et al., 2020).

Epiphytes also attract generalist pollinators. The ericoid *Disterigma sterophyllum* displays traits characteristic of bee- and hummingbird-pollinated species, in a so-called “mixed pollination syndrome” (Navarro et al., 2007). Lehnebach and Robertson (2004) and Peter and Venter (2017) reported many species of insects visiting and pollinating orchids, although orchids mainly attract one or a few specialist pollinators. Bromeliads are pollinated mostly by hummingbirds, but are also

**Fig. 2.** Photographic examples of epiphyte biotic interactions. A) Pollination of orchid by euglossine bees. B) Epiphytic bryophyte propagule dispersal is aided by banana slugs in temperate rainforests. C) Tank bromeliads collect substrate and water, which can facilitate other epiphytes. D) Epiphytic bryophyte mats can serve as safe germination sites and favored microsites for establishment of juvenile vascular epiphytes. E) Herbivory damage on epiphytic aroid leaf. F) Lichens exude chemicals that inhibit other epiphytes, but can also provide structure for subsequent epiphytes to establish upon. Bryophytes overgrow each other and epiphytic lichens, potentially competing for space. G) Epiphytes can both directly benefit and potentially compete with host trees for light, water, and nutrients. Here, a host tree collects nutrients from epiphytic bryophyte mats via abundant adventitious roots beneath the epiphytic bryophyte mat. H) A spider hunts above bromeliad phytotelmata in a tropical cloud forest. I) Nutrients can be deposited in bromeliad water tanks via amphibian use for tadpole rearing in tropical forests. Photo credits: A) David Roubik; B, G, H) Michelle Elise Spicer; C-F) Carrie Woods; I) Yusan Yang.

pollinated by insects, other birds, and bats (Aguilar-Rodríguez et al., 2014; Kessler et al., 2020). Some bromeliad species seem to have one primary pollinator, but more frequently are visited by many pollinator species (Aguilar-Rodríguez et al., 2014). Aroids have diverse pollination and reproduction strategies, including mutualisms with both specialist and generalist insects and birds (Bleiweiss et al., 2019; Gibernau and Chartier, 2010; Prieto and Cascante-Marín, 2017), and some epiphytic cacti are pollinated by bats (Tschapka et al., 1999). Pollination strategies are less well-characterized for other groups of vascular epiphytes, but most seem to rely heavily on relatively rare visits of animal pollinators (Madison, 1977; Mondragón et al., 2015). Epiphytic ferns and bryophytes are primarily wind-dispersed (Patiño and Vanderpoorten, 2018; Watkins and Cardelús, 2012); however, animals still contribute to spore and propagule dispersal (see below; Fig. 2B; Barbé et al., 2016).

Although most epiphytes have wind-dispersed seeds (84 % of angiosperms) or spores, animals play an important role in epiphyte seed and propagule dispersal, especially for lower-strata vascular epiphytes (Kelly, 1985; Madison, 1977; Mondragón et al., 2015) and hemi-epiphytes (Zotz et al., 2021). Birds, mammals, ants, and other invertebrates are known to collect and disperse several species of vascular epiphyte seeds (Celis-Diez et al., 2012; Mondragón et al., 2015; Nadkarni and Matelson, 1989; Youngsteadt et al., 2008) and hemi-epiphyte seeds (Kaufmann et al., 1991; Zotz et al., 2021), as well as disperse bryophyte propagules and fern spores (Boch et al., 2013; Chmielewski and Eppley, 2019; Kimmerer and Young, 1995; Rudolphi, 2009; Fig. 2B). Interestingly, arboreal animals may also play an important role in epiphyte-mycorrhizal interactions (Section 4.1.3., *The epiphyte-mycorrhizal mutualism*). Mangan and Adler (2000) found spores of arbuscular mycorrhizal fungi in the fecal pellets of primarily arboreal rodents and Langtimm (2000) found spores in fecal pellets of four species of climbing mice, indicating potential dispersal of the mutualistic fungi to epiphytes. Some groups of ants cultivate so-called “ant gardens” by depositing epiphyte seeds into nutrient-rich “nests” (frequently tank bromeliads, Beattie and Hughes, 2002; Davidson, 1988; Marini-Filho, 1999; Yu, 1994). Deposited epiphyte seeds germinate into a diverse arboreal epiphyte community, forming conspicuous and highly productive interconnected communities in clumps in and on tropical trees. Ants will prune or remove non-mutualistic epiphyte species from the ant nest, preferentially leaving ant-nest species; see more information on ant-defense in Section 4.1.5 *Miscellaneous mutualisms*. These complex, multi-species ant-epiphyte interactions are likely chemically-mediated (Youngsteadt et al., 2008), but the extent to which close coevolution and specialization occurred is yet unclear (but see Chomicki et al., 2017; Chomicki and Renner, 2016). Despite over a century of interest in ant-garden epiphyte systems (Benzing, 2008; Longino, 1986; Wheeler, 1910), many open questions remain, including the frequency, variation, and causes of gains and losses of the mutualism across phylogenies.

### *4.1.2. Epiphyte-epiphyte facilitation*

The stress gradient hypothesis (Bertness and Callaway, 1994) predicts that facilitation interactions contribute to plant survival and reproduction in low-resource, high-stress environments (Brooker et al., 2008; Bruno et al., 2003; McIntire and Fajardo, 2014). Although debate exists on whether and when epiphytes are, in fact, “stressed” (see discussion above, Section 2, *The importance of abiotic drivers in epiphyte ecology and evolution*), the spatial arrangement of many vascular epiphytes on a within-tree scale are consistent with positive interactions: aggregated distributions or positive density dependence, both interspecifically (Caners et al., 2010; Hietz and Hietz-Seifert, 1995b; Ravéntos et al., 2011) and to some extent intraspecifically (Gómez et al., 2006; Hietz and Hietz-Seifert, 1995b; Valencia-Díaz et al., 2012; but see Kartzinel et al., 2013). In network analyses, vascular epiphyte communities demonstrate nestedness greater than expected by chance and positive co-occurrence patterns, suggesting potential epiphyte facilitation and successional processes (Blick and Burns, 2009; Burns, 2007; Burns and Zotz, 2010; Ceballos et al., 2016). On a population level, one study found both facilitative and competitive interactions among epiphytes; for juveniles, growing in clumps rather than alone increased average growth rate, but not survival, over seven years (Zotz et al., 2005). Like alpine plants (Callaway et al., 2002a), close physical associations of epiphytes could ameliorate temperature or drought stress (Stuntz et al., 2002) and enhance survivorship. There are a few empirical demonstrations of vascular epiphytes directly benefiting other species of vascular epiphytes via nutrient or water leaching, for example with ferns in Taiwan (Chen et al., 2019; Jian et al., 2013). Epiphytes, especially those with weblike networks of roots, also provide physical structure and complexity which can facilitate subsequent epiphyte establishment, including capturing epiphyte seeds (Chaves and Rossatto, 2020) and increasing canopy soil retention (Victoriano-Romero et al., 2020). Upward-facing “trash-basket” or tank-forming epiphytes collect leaf litter and water (phytotelmata), providing substrate which other species can colonize (Fig. 2C) and buffering temperature and moisture variability (Ortega-Solís et al., 2017). Facilitative evolutionary interactions among vascular epiphytes or between vascular epiphytes and other plants include the “magnetic species effect”, wherein close presence of species with similar displays increase reproductive success (Carmona-Díaz and García-Franco, 2009).

Facilitative interactions between nonvascular and vascular epiphytes, among nonvascular epiphytes (bryophytes), and among lichens, are somewhat more well-established in the literature than vascular-vascular epiphyte facilitation (Colesie et al., 2012; Favero-Longo and Piervittori, 2010; Hietz et al., 2002; Lu et al., 2020; Sillett and Antoine, 2004; van Leerdam et al., 1990). Facilitation was the topic of 22 % of the nonvascular epiphyte literature, 14 % of lichen literature, and 8% of the vascular epiphyte literature (Fig. 1). Most empirical evidence in bryophytic epiphyte ecology is observational. Nonvascular and vascular epiphytes are spatially aggregated on trees and co-occur in specific microsites, both in temperate and tropical ecosystems (Cifuentes-García et al., 2020; Cornelissen and Steege, 1989; Lakatos and Fischer-Pardow, 2013; Mizuno et al., 2015; Zotz and Vollrath, 2003; Fig. 2D). Epiphytic bryophytes have high water holding capacities, and can, thus, create humid microhabitats and ameliorate water stress or other climate variables (Cornelissen and Steege, 1989; Mendieta-Leiva et al., 2020; Mizuno et al., 2015; Richards, 2021); higher moss cover has been correlated to increased colonization rates of orchids (Acevedo et al., 2020). Experimentally removing neighboring bryophytes can change how much ferns depend on clonal connections, thereby decreasing both the biomass and survival rate of several epiphytic fern species (Lu et al., 2020). When climate, host tree traits, and bryophyte cover were assessed together in one model from data collected from old (>120 y) shade-coffee farms and adjacent old-growth forests, bryophyte cover predicted vascular epiphyte richness even more so than tree size, which has historically been a major predictor of epiphyte richness (Richards, 2021). The structural complexity of bryophyte mats may also facilitate higher adherence and survival of vascular epiphyte juveniles (Hietz et al., 2012; Fig. 2D). One experiment demonstrated that leaving epiphytic lichens on substrates increases growth rate of bromeliads in comparison to substrates with lichens removed and that lichens increased bromeliad seed adherence in the field; they also showed that the extracts of lichen species from less-preferred trees have negative effects on bromeliad growth and survival (Callaway et al., 2001). A few observational studies have also shown patterns consistent with net competitive interactions between lichens and vascular epiphytes (Belinchón et al., 2012; John and Dale, 1995). Preliminary correlative evidence also exists for both facilitation (Jüriado et al., 2012; Sillett et al., 2000) and competition (e.g., Ruchty et al., 2001) between epiphytic lichens and bryophytes (Fig. 2F).

Several studies have shown patterns consistent with successional replacement via facilitation and competition dynamics for vascular epiphytes (Benavides et al., 2006; Nadkarni, 2000; Victoriano-Romero et al., 2020; Woods, 2017; Woods and DeWalt, 2013), nonvascular epiphytes (Ruchty et al., 2001; Wiklund and Rydin, 2004), and lichens (Ellis and Ellis, 2013; Stone, 1989), and several models have been proposed (McCune, 1993; Taylor and Burns, 2015; Woods, 2017). Some commonalities among the hypothesized models include: 1. the importance of habitat heterogeneity increasing with tree ontogeny, 2. the continuous development of “new” substrates as the tree grows (Benzing, 2008), 3. the classification of epiphyte species into “pioneer” or “early colonizing” species as well as “late-colonizing” or “competitively advanced” species, and 4. the “movement” of species from one area of the canopy to another as the tree grows due to facilitative or competitive interactions (McCune, 1993; Taylor and Burns, 2015; Wiklund and Rydin, 2004; Woods, 2017). Thus, a single tree can harbor multiple communities at different stages of succession (McCune, 1993; Woods, 2017). Despite these advances, the field of epiphyte succession is not well-developed; in fact, it has been argued that vascular epiphytes are “assemblages” rather than true communities because of their lack of interactions (Mendieta-Leiva and Zotz, 2015). Clearly, there are many important facilitative interactions among epiphytes (and competitive, see Section 4.2.3, *Direct competition*), but the extent to which these dynamics dominate community assembly or contribute to distribution patterns is unresolved. Where it used to be a minor modifying factor to largely competitive interactions, facilitation in the broad sense has recently been argued as a ubiquitous process driving biodiversity across many systems (McIntire and Fajardo, 2014). Future research in the topic will surely produce and test alternate hypotheses to the abiotic-only explanations of epiphyte distributions, as has occurred in terrestrial plant facilitation research.

### *4.1.3. The epiphyte-mycorrhizal mutualism*

One common and comparatively well-studied mutualism in epiphyte ecology and evolution is the relationship between mycorrhizal fungi and orchids. Much like in the mutualism between terrestrial plants and mycorrhizae, epiphytic orchids receive fixed carbon, other nutrients (Bermudes and Benzing, 1989; Hadley and Williamson, 1972; Zhang et al., 2018), and water (Yoder et al., 2000) from the fungi. Although the direct benefits to the fungi are still unclear, mycorrhizae obtain a protected location to establish (Dearnaley, 2007). Orchid seeds lack endosperm, and so require certain mycorrhizal strains to germinate in the wild (Arditti, 1967; Bermudes and Benzing, 1989; Porras-Alfaro and

Bayman, 2007; Pujasatria et al., 2020); the degree to which this orchid-mycorrhizal mutualism is specialized is still debated (e.g., Herrera et al., 2019). Other strains of mutualistic fungi enhance survivorship of orchids and growth (Otero et al., 2007; Porras-Alfaro and Bayman, 2007), although much less is known about the role mycorrhizae play in epiphyte life cycles after germination (Mondragón et al., 2015). Notably, orchids can germinate and grow in laboratory settings asymbiotically, but only with added nutrients (Knudson, 1922; Stewart and Kane, 2006).

Mycorrhizal fungi have also been found in many epiphytic species other than orchids, including species in the Clusiaceae, Araceae, Piperaceae and Bromeliaceae (Lesica and Antibus, 1990; Lugo et al., 2009; Rains et al., 2003; Richardson and Currah, 1995). In comparison to terrestrial plants, epiphytes with arbuscular mycorrhizal fungi seem to be less common and patchier in distribution, suggesting possible fungal spore limitation in the canopy (Bermudes and Benzing, 1989; Lesica and Antibus, 1990; Mangan and Adler, 2000; Michelsen, 1993), potentially linked to the distribution of humus or wet microsites (Lugo et al., 2009; Maffia et al., 1993). Interestingly, mycorrhizal associations have been found more commonly in facultative epiphytes than obligate holoepiphytes and have been postulated to contribute to the evolution of the epiphytic habit (Lugo et al., 2009; Maffia et al., 1993; Michelsen, 1993; Nadarajah and Nawawi, 1993). Waterman and Bidartondo (2008) suggest a potential trade-off between belowground mycorrhizal associations and aboveground pollination associations in orchids. Although their review focuses mostly on terrestrial orchids, epiphytic orchids, in their more resource-poor environment, may deal with even more potential trade-offs. Simultaneous above- and below-ground studies of diversification drivers in epiphytes are, to our knowledge, nonexistent.

One area that is starting to gain momentum in epiphyte research is that of microbial endophytes. Dark septate endophytes, a group of ascomycetous fungi found in roots, are capable of forming mutualistic associations with plants, particularly in nutrient-poor environments where it is difficult for mycorrhizal fungi to disperse (Lugo et al., 2009). Dark septate endophytes have been found in epiphyte roots in some studies (Lugo et al., 2009; Rains et al., 2003). While it has yet to be shown whether dark septate endophytes benefit epiphytes, these endophytes can facilitate plant growth and phosphorus (P) acquisition for plants in stressful environments (Li et al., 2018), which may be linked to their ability to mineralize organic forms of P (Della Monica et al., 2015). Given that P is limiting for epiphytes (e.g., Wanek and Zotz, 2011), future research could examine the influence of dark septate endophytes on P acquisition. Foliar fungal endophytes have only been examined in a handful of studies, where they vary with taxa and physiological traits in vascular epiphytes (Tellez et al., 2020; Unterseher et al., 2013). While their role in epiphytes remains unknown, fungal endophytes have been found to confer host protection against pathogens (Otero et al., 2007), provide anti-herbivory defense through the production of bioactive metabolites (Panaccione et al., 2014), broaden a species' geographic range by ameliorating drought stress (Afkhami et al., 2014), improve nutrient accumulation, biomass, and competitive ability, and influence colonization by mycorrhizae (Omacini et al., 2006). This avenue of research in epiphytes, as well as characterizing other non-mycorrhizal microbial mutualisms, could help explain how epiphytes are able to thrive under nutrient and water limitations.

#### 4.1.4. *Epiphyte-host interactions*

Generally, epiphytes are characterized as commensalists, benefiting from the host plant but not directly harming the host (Benzing, 2008; Moffett, 2000; Zotz, 2016; but see section below, ***4.2.4, Indirect competition between epiphytes and host trees***). Epiphytes lack haustorial roots, which would allow direct extraction of nutrients or water from their host, like mistletoes or parasitic vines do (Steel and Bastow Wilson, 2003; Těšitel, 2016). Instead, epiphyte roots function to structurally anchor to the host tree, to absorb water (in some species directly from the air), and in some species to contribute to photosynthesis (Benzing, 1987; Goh et al., 1983; Madison, 1977; Zhang et al., 2018). Structural dependence on trees allows the epiphyte to access light in the canopy without growing all the structural biomass needed to reach up into the canopy from the ground (Nyman et al., 1987). Epiphytes benefit from host stemflow and bark properties (such as high water-holding capacity) to indirectly obtain nutrients and water (Benzing, 1978a; Gauslaa and Goward, 2012; Mendieta-Leiva et al., 2020; Moore, 1989; Van Stan and Pypker, 2015). Exudates from trees' extrafloral nectaries can facilitate realized niche expansion for epiphytic lichens: one experimental study demonstrated increased photosynthetic rate and thallus production via uptake of exogenous carbon below *Populus* trees in an otherwise too-dry habitat (Campbell et al., 2013). Another study showed that *Populus* trees facilitate higher growth rates in epiphytic lichens on nearby trees by increasing bark pH, but not via P leaching (Gauslaa and Goward, 2012). Host species differ in these characteristics, and although strict host species specificity is not commonly observed (or "basic host specificity", ***sensu*** Naranjo et al., 2019; Wagner et al., 2015), some trees host much more diverse and abundant epiphyte communities than others (e.g., Callaway et al., 2002b; Cardelús, 2006; Wagner et al., 2015). This variability in host quality exists among species (e.g., for vascular epiphytes: Cardelús, 2006; for lichens: Esseen and Renhorn, 1996; Nascimbene et al., 2009), within-species (Mehltreter et al., 2005; Zytynska et al., 2011), as well as among trees with different traits in forest and pasture habitats (Elias et al., 2021). Intriguingly, epiphytes can also have direct positive impacts on their hosts. Epiphytes can improve host plant water use efficiency (Mendieta-Leiva et al., 2020; Stanton et al., 2014) and can directly provide nutrients via the host tree's adventitious roots (Moore, 1989; Nadkarni, 1981).

#### 4.1.5. *Miscellaneous mutualisms*

Some epiphytes have evolved mutualistic associations with ants as a means of defense; the ants protect the plant from herbivores in exchange for food, such as extrafloral nectaries, or housing (Bequaert, 1922; Janzen, 1974; Vergara-Torres et al., 2021). Koptur et al. (2013) experimentally demonstrated this evolved benefit in a Mexican cloud forest epiphytic fern; ferns with nectaries covered up experienced approximately three times higher leaf damage than those with their nectaries left intact. Another experiment demonstrated that ants associated with ant-garden epiphytes will also defend nearby non-ant-garden epiphytes with extrafloral nectaries, effectively extending their defense benefit beyond their direct mutualists (da Silva-Viana et al., 2021). In a lowland rainforest in Venezuela, 10 epiphyte species were found to contain extrafloral nectaries, all with visiting ants (Blüthgen et al., 2000). About 60 % of ant-garden epiphytes have extrafloral nectaries (Koptur, 1992), suggesting the strength of herbivory as a driver of this defense mutualism. Frogs that use bromeliads for tadpole rearing (Ferreira et al., 2019; Souza et al., 2021) are mutualists with epiphytes by hunting phytophagous insects; importantly, they preferentially avoid eating pollinators (Sabagh et al., 2021).

Epiphyte-animal mutualisms can also take the form of nutrient exchange. Ants living in specialized domatia provide nutrients to the epiphyte (Gay, 1993; Treseder et al., 1995; Zotz, 2016), including different forms of N that are not available without ant mutualists (Gegenbauer et al., 2012). A recent study showed distinct fungal communities in each of the three functional types of domatia, suggesting that this mutualism is in fact multipartite (Greenfield et al., 2021). Spiders can also provide seasonal nutrients to bromeliads in which they live and breed (Gonçalves et al., 2011; Fig. 2H).

### 4.2. *Negative interactions: Parasitism, herbivory, competition*

#### 4.2.1. *Parasitism and pathogens*

The negative interactions between microbial communities and epiphytes are still not well understood; only one article discussing epiphyte parasites or pathogens came up in our systematic literature search (Fig. 1). A few studies that cultured endophytic fungi from epiphyte roots found a wide variety of fungal species, including a few common pathogenic species (Lugo et al., 2009; Richardson and Currah, 1995). Although the majority of the epiphyte species sampled were orchids (51 species), pathogenic fungi were also found in the roots of *Anthurium* sp. (Araceae), and the authors found a genus of fungus (*Xylaria*), which includes both weak woody parasites and harmless endophytes, in *Tillandsia festucoides* (Bromeliaceae) (Richardson and Currah, 1995). Epiphytes likely host a diversity of microbial species, encompassing biotic interactions ranging from pathogens to mutualists. This area of research is ripe for future investigation, especially with more recent advances in molecular techniques and decreasing costs of genetic sequencing (Tellez et al., 2020).

One insightful experiment with implications for epiphytes has shown that microbial diversity, abundance, and community composition vary strongly among vertical strata within the host tree (Gora et al., 2019). Major differences between terrestrial and arboreal soil microbial communities have also been reported from observational epiphyte studies (Lodge and Cantrell, 1995; Looby et al., 2019; Pittl et al., 2010). Gora et al. (2019) show that putative functional groups of bacteria and fungi vary differently with height. For example, *fungal* communities were dominated by soil saprotrophs in the forest floor but turned over to endophytes and pathogens in the canopy; *bacterial* communities on the forest floor were dominated by antagonistic competitors, while unique photosynthetic and nitrogen-fixing bacteria were found in the canopy (Gora et al., 2019). These findings, although based on wood decomposition experiments, have important implications for the ecology and evolution of epiphytes. First, because the most striking differences in microbial abundance, diversity, and community were between the forest floor (terrestrial) and all other layers above (canopy), epiphytism itself may serve as an evolutionary escape from certain terrestrial soil enemies. This idea has been proposed by Spicer et al. (2020) as the Epiphyte Enemy Escape Hypothesis, but has yet to be tested. On the other hand, nitrogen-fixing bacteria in the canopy certainly could strongly benefit epiphytes by providing potentially limiting nutrients, especially because mycorrhizal associations may be less common in the canopy than in the terrestrial soil (Looby et al., 2019; see Section 4.1.4*, The epiphyte-mycorrhizal mutualism*). Second, because fungal and bacterial communities functionally contrast at the same heights (e.g., nitrogen-fixing bacteria and fungal pathogens in the canopy), epiphytes may exhibit adaptations that balance trade-offs between bacteria and fungi, an interesting parallel to pathogen-mutualist trade-offs in mycorrhizal roots of terrestrial plants (Wood et al., 2018). These potential trade-offs between parasitism and mutualism offer an excellent opportunity to investigate microbial-epiphytic coevolution.

### *4.2.2. Herbivory*

Herbivory is well-established as a major driver of plant evolution and community structure, particularly in tropical latitudes (Marquis et al., 2016), yet it is thought to be relatively unimportant in vascular epiphytes (Benzing, 2008; Zotz, 2016). We found 20 papers that mentioned herbivory and vascular epiphytes in the abstract (9% of vascular epiphyte articles; Fig. 1). The impact of herbivory on epiphyte performance seems to vary both across habitats and among epiphyte species (e.g., Fig. 2E). In Panama, herbivory was found on 26–61 % of a tank bromeliad population (*Werauhia sanguinolenta*), and leaf damage due to herbivory by the caterpillar *Napaea eucharilla* (Riodinidae, Lepidoptera) was within the range experienced by soil-rooted tropical plants (Schmidt and Zotz, 2000). However, the degree of herbivory was found to have little consequence for reproductive output in *W. sanguinolenta* over the long term (7 years, Zotz et al., 2005). In the Peruvian Amazon, herbivory resulted in leaf area loss of 10.4 % on *Aechmea nallyi,* on average twice as high a rate as host tree leaf herbivory (Lowman et al., 1999). In a humid montane forest in Mexico, leaf area loss to herbivory was low in orchids and bromeliads (<1.5 %) but reached 7–20 % in epiphytic ferns (Winkler et al., 2005). Many species of both specialist and generalist herbivores have been observed on bromeliads, including beetles, weevils, and Lepidoptera larvae as well as spectacled bears (Frank and Lounibos, 2009; Goldstein and Goldstein, 2004).

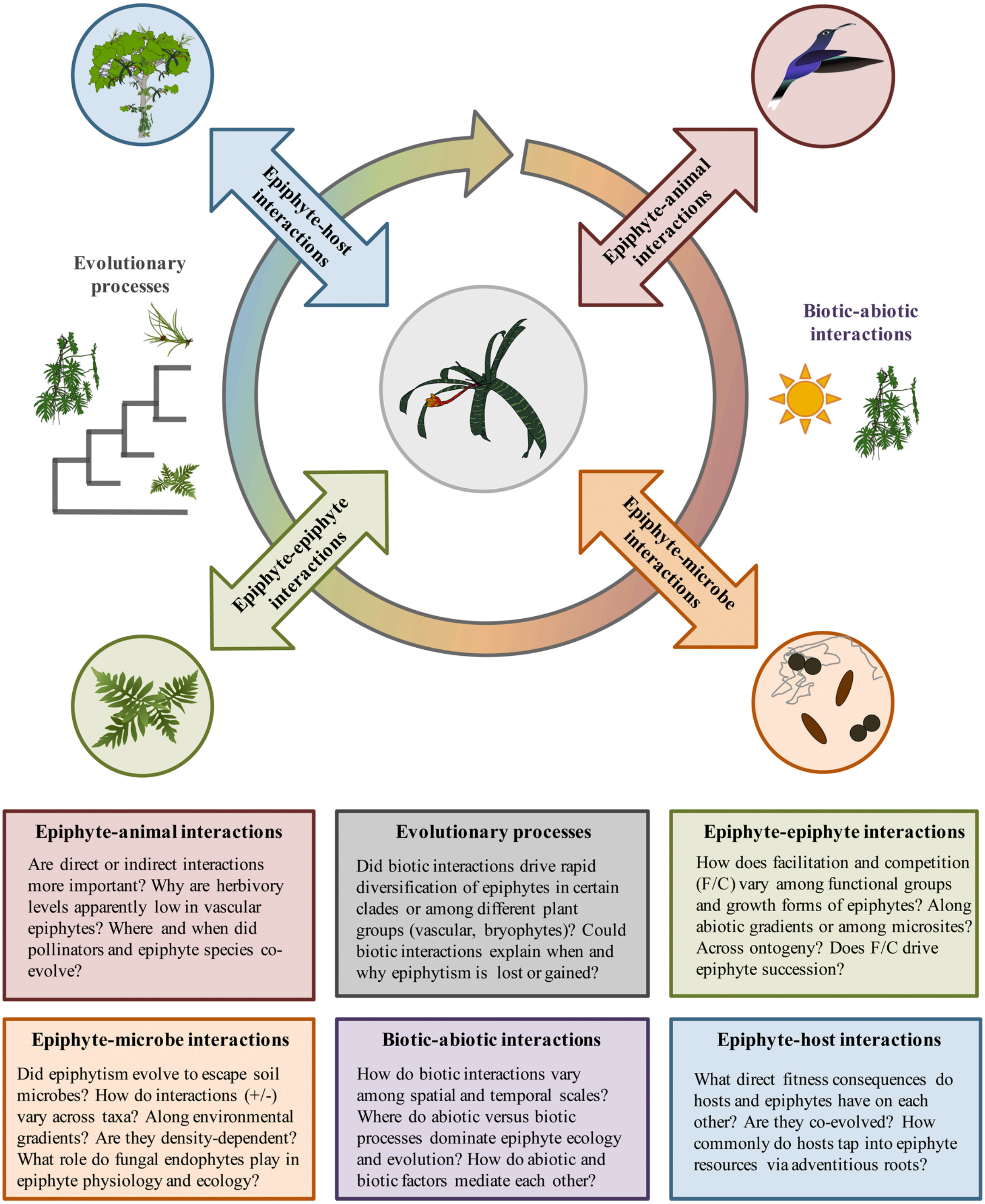
Moderate to potentially detrimental herbivory has been observed in epiphytic bryophytes and lichens. Herbivory was the most-commonly studied biotic interaction in lichen literature (38 % of articles), but only found in a few bryophyte papers (9% of nonvascular articles; Fig. 1). In northern temperate forests, species distributions of epiphytic lichens and lichen damage correlated to grazing pressure and species preferences by gastropods, suggesting that herbivory can provide top-down controls on epiphyte community structure and dynamics (Asplund et al., 2010; Clyne et al., 2019). In one experimental study, gastropod exclusion had varying effects on epiphytic lichens, bryophytes, and algae, indicating that gastropod grazing could maintain diversity in some epiphyte communities (Boch et al., 2016). High grazing pressure can also reduce performance of endangered epiphytic lichens reintroduced into the wild (Gauslaa et al., 2018); yet, in another study, lichen species moved from areas with high herbivory from snails to areas with low herbivory did not differ in growth (Gauslaa et al., 2006). Ungulate herbivore overbrowsing of terrestrial plants can also have an indirect negative effect on epiphytic bryophytes and ferns. By causing mortality of host trees, host tree debarking, or by creating more open understory conditions, herbivory indirectly causes declines in epiphyte diversity and shifts epiphyte communities towards more xerophylic species (e.g., Oishi and Doei, 2019).

Herbivores may have their largest impact on epiphytes via more difficult-to-detect pathways, rather than just via visible leaf damage. Winkler et al. (2005) found that weevil larvae (Curculionidae, Coleoptera) caused 18–31 % of ramet and shoot death in *Tillandsia puntulata* and *T. deppeana* by feeding on meristematic tissue at the ramet base. Florivory, the consumption of flower products, of epiphytes resulted in reduced fecundity for bromeliads (14–18 %) and an orchid (90 %) in humid montane forests in Mexico (Winkler et al., 2005), and caused the loss of up to 41 % of reproductive structures in a bromeliad in an arid pine-oak forest in Mexico (Palacios-Mosquera et al., 2019). In a dry forest in Cuba, 32–50 % of inflorescences of *Broughtonia lindenii* were damaged by herbivory and mechanical causes, which resulted in 18–36 % of the flowers produced not being available to pollinators (Vale et al., 2011). Because epiphytes invest up to 30 % in reproductive structures, and nutrient limitation precludes them from yearly reproduction (Zotz and Richter, 2006), florivory could have profound impacts on the ecology and evolution of vascular epiphytes. Florivory may even have implications for plant species coexistence. One study suggested florivory may be density-dependent; the most abundant species had <5 % damage, but less-abundant species had up to 40 % florivory damage (Orozco-Ibarrola et al., 2015).

Anti-herbivore defenses come in a myriad of forms, including defensive mutualists (see Section 4*.3.5. Miscellaneous mutualisms*), chemical defenses, physical barriers, and low nutrient content. Epiphytes are known for their low nutrient content and tough leaves, which can reduce herbivory (Benzing, 2012; Nomura et al., 2001). Epiphytic fig species, for example, have evolved a suite of defensive traits such as tough, tannin-rich leaves, distinct from congeneric free-standing species; the distinct evolutionary trajectory suggests coordinated defense syndromes and an evolutionary arms race between fig and herbivorous insects (Zhao et al., 2021). Epiphytes have evolved many chemical defenses to herbivory (Lawrey, 1983; Nomura et al., 2001). Phenolic compounds were higher at the site of grazing by a herbivore (Chrysomelidae, Coleoptera) in the bromeliad *Aechmea blanchetiana* (Magalhães et al., 2012), and phenolic compounds were higher in juvenile *Macaranga* myrmecophytes in Borneo prior to them gaining their mutualistic ants (Nomura et al., 2001), showing a highly plastic and concentrated response of chemical defenses to herbivory. Some epiphytic lichens also produce chemicals that act as effective herbivory deterrents; in one experiment, snails preferred to eat certain lichens, especially less common species, after their chemical compounds were removed (Boch et al., 2015). However, there is a dearth of research on herbivory in epiphytes. Whether lack of research is because of less conspicuous modes, such as florivory (Winkler et al., 2005) or genuinely low levels of herbivory as suggested previously (e.g., Benzing, 2008), still remains an open question. Given the contribution of herbivory-defense relationships to the massive diversification of the angiosperms (e.g., Givnish et al., 2015; Marquis et al., 2016) and their contribution to species coexistence (e.g., Kursar et al., 2009), research into herbivore-epiphyte relationships could be fruitful (see related questions, Fig. 3). At later ontogenic stages, animal-epiphyte interactions may also have negative consequences, but we only found one paper on seed predation in epiphytes. In epiphytic bromeliads, post-dispersal seed predation by small mammals can cause seed removal rates of up to 90 % (Chilpa-Galván et al., 2017).

### 4.2.3. Direct competition

Competition among vascular epiphytes is not seen as a major driving force governing patterns of epiphyte diversity, abundance, or community assembly (Benzing, 2008; Zotz, 2016). This assumption is based upon numerous observations that vascular epiphytes are not in very close proximity spatially and generally do not show patterns of negative



**Epiphyte-animal interactions**

Are direct or indirect interactions more important? Why are herbivory levels apparently low in vascular epiphytes? Where and when did pollinators and epiphyte species co-evolve?

**Evolutionary processes**

Did biotic interactions drive rapid diversification of epiphytes in certain clades or among different plant groups (vascular, bryophytes)? Could biotic interactions explain when and why epiphytism is lost or gained?

**Epiphyte-epiphyte interactions**

How does facilitation and competition (F/C) vary among functional groups and growth forms of epiphytes? Along abiotic gradients or among microsites? Across ontogeny? Does F/C drive epiphyte succession?

**Epiphyte-microbe interactions**

Did epiphytism evolve to escape soil microbes? How do interactions (+/-) vary across taxa? Along environmental gradients? Are they density-dependent? What role do fungal endophytes play in epiphyte physiology and ecology?

**Biotic-abiotic interactions**

How do biotic interactions vary among spatial and temporal scales? Where do abiotic versus biotic processes dominate epiphyte ecology and evolution? How do abiotic and biotic factors mediate each other?

**Epiphyte-host interactions**

What direct fitness consequences do hosts and epiphytes have on each other? Are they co-evolved? How commonly do hosts tap into epiphyte resources via adventitious roots?

**Fig. 3.** Open questions surrounding the role of biotic interactions in epiphyte ecology and evolution, including interactions between epiphytes and animals, between epiphytes and microbes, between epiphytes and host trees, and among epiphytes, as well as how biotic-abiotic interactions and evolutionary process contribute to epiphyte biotic interactions. Rather than being independent, these processes are interrelated (represented by the central rainbow arrow).

density dependence, as well as upon theoretical expectations due to stress-growth tradeoffs (Blick and Burns, 2009; Gómez et al., 2006). This is particularly true for dry or seasonally dry forests, ecosystems where many epiphytic studies come from. Perhaps because of this assumption, very few studies exist that address competition among vascular epiphytes (only 5% of vascular epiphyte articles mentioned competition in the abstract; Fig. 1). In ecosystems such as cloud forests where vascular epiphyte density is very high, competition may be at play. One study suggested this competitive mechanism to explain why several bromeliad species coexisted in more open, less-abundant epiphyte habitats, but barely had any range overlap in areas of a cloud forest where epiphyte density was very high (Sugden and Robins, 1979). A recent modeling study predicted that competitive exclusion among epiphytes may be an important process when epiphyte communities are saturated and forests have extremely low-turnover rates (Petter et al., 2021). Competition could lead to successional turnover, which has been suggested in tropical lowland forests heavy with epiphytes (Woods, 2017). In another example from a wet forest, patterns of epiphyte distributions were consistent with competition and successional replacement (Catling and Lefkovitch, 1989). At least one species of bromeliad (*Tillandsia recurvata*) is known to exude allelopathic chemicals that inhibit the germination of other *Tillandsia* species (Valencia-Díaz et al., 2012), despite this not completely explaining their distribution patterns in the field. In another experiment with three *Tillandsia* species, close association of conspecifics or heterospecifics decreased the survival and seed germination of *T. pohliana* (Chaves and Rossatto, 2020).

Like facilitation interactions, competition is somewhat more accepted as an important contributor to community development in nonvascular epiphytic plants and lichens than in vascular epiphytes (e.g., Armstrong and Welch, 2007; Peck and Frelich, 2008). Competition was the topic of 35 % of epiphytic bryophyte studies and 31 % of epiphytic lichen studies (Fig. 1). Although very few direct experimental tests of competitive interactions in epiphytic communities exist, competition has been demonstrated a few times in epiphytic lichen communities (John, 1992; Mikhailova, 2007) and terrestrial bryophytes (e.g., Doxford et al., 2013; Udd et al., 2016). One *in situ* transplant experiment showed contracted realized niches for epiphytic lichens in comparison to fundamental niche space (Antoine and McCune, 2004), and another study found that a less-competitive lichen species thrived when the competitive dominant lichen population was reduced by pollution (Mikhailova, 2007). Bates (1998) suggested that certain life-forms of bryophytes, in particular dendroid forms with high colonization potential via spreading, could be adapted for superior competition, forming thick mats and local monocultures. Spreading, dense genera such as *Rhytiadelphus* and *Isothecium* show patterns consistent with this model in temperate rainforests (Peck and Frelich, 2008; Woods et al., 2019). Successional replacement consistent with competition is found in epiphytic bryophytes in temperate rainforests (Peck and Frelich, 2008; Ruchty et al., 2001; Stone, 1989) and in epiphytic lichen communities (Armstrong and Welch, 2007; Ellis, 2012) where some species overgrow and exclude earlier species (Fig. 2F). McCune (1993) proposed the "similar gradient hypothesis" for successional replacement in epiphytes, wherein lichens are pushed towards the tops of coniferous trees because of competition with bryophytes. Lichens, in turn, leach allelopathic chemicals and inhibit germination of vascular and nonvascular plants (Callaway et al., 2001; Lawrey, 1986; Sillett and Antoine, 2004). Increased competition by epiphytic bryophytes has even been proposed as an evolutionary mechanism for why tropical epiphytic fern gametophytes are long-lived in comparison to terrestrial fern gametophytes (Watkins et al., 2007). Still, much debate surrounds the prevalence of competition among nonvascular epiphytes in various ecosystems, and several studies present data countering any important role of competition in structuring communities (e.g., Patiño and Vanderpoorten, 2018). Most likely, competition and facilitation both occur in epiphyte communities, but the strength of each process depends on the ecosystem, microhabitat conditions, and presence of other epiphytes (Michalet et al., 2014). Where and when competition and facilitation dominate, if at all, remains relatively unexplored in epiphyte ecology, in particular in vascular systems (Francisco et al., 2018; Fig. 1).

### *4.2.4. Indirect competition between epiphytes and host trees*

Epiphytes have been suggested to be "structural parasites", directly decreasing growth rates or viability of host tree branches (Montaña et al., 1997; Ruinen, 1953); this term originated mainly from the observational pattern that dead branches and dead trees host very high numbers of epiphytes (e.g., Montaña et al., 1997). These correlations have since been upheld by experimental data to some extent with epiphytic bromeliads in the *Tillandsia* genus (Pérez-Noyola et al., 2020; Soria et al., 2014). *in situ* comparisons of *Tillandsia*-laden and epiphyte-free branches show negative epiphyte-host water interactions, in which epiphytes limit water flux in host trees and cause structural damage to the phloem and xylem (Páez-Gerardo et al., 2005; Pérez-Noyola et al., 2020). In a different experiment (also with a *Tillandsia* species), shade, rather than epiphyte presence itself, decreased host branch shoot survival (Flores-Palacios, 2016). Tree fern skirts (persistent dead fronds around the upper trunk) were thought to be an adaptation to avoid epiphyte damage (Brock and Burns, 2021; Page and Brownsey, 1986), but a recent New Zealand study did not find any epiphyte envelopment of the growing crown of 1912 studied tree ferns; the authors suggest that the skirts are instead an adaptation to protect the tree from freezing (Brock and Burns, 2021). Benzing (1979) proposed several alternative explanations for why host branch vitality is negatively correlated with epiphyte abundance that did not include direct competition between the host and the epiphyte. For example, tree branch and epiphyte successional processes may be occurring simultaneously but independently, resulting in the correlation of older branches and greater epiphyte loads. It is still difficult to pinpoint causal relationships without experiments and long-term controls, and thus the structural parasite concept remains an open debate.

Another suggested negative interaction between tree host and epiphyte is competition for nutrients or "nutritional piracy" (Benzing and Seemann, 1978). For example, upward-facing "trash-basket epiphytes" that capture leaf litter and stemflow can lead to a reduction of nutrients on the forest floor, preventing uptake for the host tree and indirectly competing for nutrients (Benzing and Seemann, 1978; Coxson and Nadkarni, 1995). Direct competition for nutrients may also occur between the host tree and epiphytes via host adventitious roots (Fig. 2G; Orlovich et al., 2013). As mentioned above (Section 4.1.4*, Epiphyte-host interactions*), trees uptake nutrients from arboreal soil maintained and enhanced by epiphytes (Nadkarni, 1981; Orlovich et al., 2013). Although this on a large scale could be categorized as a mutualism (epiphytes get access to light via host structure; trees get extra nutrients), on the smaller scale (within branch), the vascular epiphytes and tree roots may be seen as competitors as well (Orlovich et al., 2013). To our knowledge, no study exists that compares the distribution of arboreal adventitious roots in relation to epiphyte abundance or identifies why and how this relationship evolved (or did not; see Herwitz, 1991); this may be an interesting area for future exploration.

Host trees themselves may not all be interacting with epiphytes in a net positive direction. Based on interaction network analyses, which model expected epiphyte abundance in comparison to empirical data, some species of trees have much *fewer* epiphytes than expected by chance (Cortés-Anzúres et al., 2020). Lower-than-chance establishment of epiphytes suggests a potential ammensalism in the direction of host to epiphyte; that is, hosts may be actively defending themselves against epiphyte colonization or establishment. For example, organic bark extracts from host trees with very few epiphytes inhibited seed germination and development in bromeliads (Valencia-Díaz et al., 2010) and orchids (Frei and Dodson, 1972), and have been suggested to inhibit moss growth (Fojcik and Chmura, 2020). High bark exfoliation rate has also been suggested as a host adaptation to decrease epiphyte colonization (Benzing, 1978b), but the few studies that explicitly test this hypothesis do not show strong effects of peeling rate on epiphyte germination (e.g., Jiménez-Salmerón et al., 2017). Interestingly, epiphytes can also exude chemicals that inhibit host tree seedlings (Flores-Palacios et al., 2014). The relative importance of various types of host defenses for the establishment of epiphytes is not well characterized, and epiphyte species likely vary in their susceptibility or resilience to host defenses.

## 5. Conclusions

### *5.1. Opportunities for the advancement of epiphyte ecology and evolution*

Overall, our understanding of epiphyte ecology and evolution has increased substantially in recent years. Biotic interactions, in their various forms, are still not a major point of attention in the field. Recent studies characterizing the trophic interactions among epiphytes and other plants and animals demonstrate the depth and complexity of epiphyte biotic interactions (Angelini and Silliman, 2014; Hammill et al., 2014; Thomsen et al., 2018). Although a few interactions—namely between epiphytes and pollinators, and epiphytes and their host tree—have a well-established body of literature, the vast majority of biotic interactions remain largely unexplored. To date, most epiphyte research is observational, so the mechanisms underlying patterns we see are, for the most part, speculative. As mentioned in Mendieta-Leiva and Zotz (2015), our understanding of vascular epiphyte assemblages comes from relatively short-term studies. Many biotic interactions, in contrast, work indirectly and may only be apparent at longer time scales. Moreover, epiphyte biotic interaction literature is heavily taxonomically biased, just like epiphyte abiotic literature. Certain families, in particular orchids and bromeliads for vascular epiphytes, have been the focus of much epiphyte research to date. To generalize among the diverse array of epiphytes, we must expand our studies to a broader taxonomic and functional level, and foster collaborations among researchers of diverse taxa and systems. The potential to expand this area of research is great, and we list several questions ready for investigation in Fig. 3.

To synthesize the opportunities for advancement in understanding the importance of biotic interactions in epiphytes, we categorized the epiphyte biotic interaction literature into six major areas (delineated in Fig. 3). While much of the research on **epiphyte-animal** interactions has focused on pollination (36 % of publications reviewed; Fig. 1), testing hypotheses of the role of pollinators in driving diversity maintenance, speciation rates, and co-evolution remain largely unexplored. Furthermore, the low levels of herbivory and its evolutionary history remain, as yet, unresolved, potentially due to the taxonomic bias or the assumption that the current adaptations seen in many vascular epiphytes (low nutrition, thick leaves) were driven more by abiotic factors than biotic ones. It is entirely possible that these adaptations evolved in response to herbivory pressure that has since been reduced (*i.e.,* the ghost of anti-herbivory defense of the past). One of the most promising areas of biotic interactions research for the ecology and evolution of epiphytes is in **epiphyte-microbe** interactions, including the role of dark-septate endophytes in stress-tolerance, herbivore defense, and nutrient acquisition, the potential driver of epiphytism as an escape from microbial enemies in the forest floor (*i.e.*, epiphyte enemy escape hypothesis), and how these interactions vary across taxa and environmental gradients (**biotic-abiotic** interactions). Experimental and theoretical research in terrestrial plant communities has illuminated the importance of competition and facilitation in determining patterns of diversity, succession, and evolution of traits in co-existing plant communities, yet these remain virtually untested in vascular epiphyte communities (see **epiphyte-epiphyte** interactions). It has been argued that epiphytes do not compete with each other because they are in a stressful environment with low densities (e.g., slow growth has been hypothesized to be an adaptation to low competition pressure; Zotz and Bader, 2009). However, growth rates of epiphytes have not been measured in a wide enough range of taxa from a diverse enough array of environments to definitively conclude this. Furthermore, for those with confirmed slow growth, it could be an adaptation to avoid competition (as suggested for epiphytic fern gametophytes; Watkins et al., 2007), and this remains a gap in knowledge. Moreover, competition and facilitation have been demonstrated several times in nonvascular epiphytes and lichens; the stage is therefore set for additional experiments testing intratrophic interactions as drivers of community change and successional turnover.

Digging into epiphytic biotic interactions also offers an excellent opportunity to contribute to advancing ecological and evolutionary theory. Diversity maintenance theories such as, for example, conspecific negative density dependence (CNDD), have not been tested in the epiphyte system; neither have microbially-mediated mechanisms for epiphyte community spatial patterns. If CNDD turns out *not* to be a major mechanism for epiphytes, as was found for lianas (e.g., Ledo and Schnitzer, 2014), CNDD may be less of a general rule for maintenance of plant diversity and more of a tree-specific or habitat-specific theory. Understanding this difference is imperative, especially considering that trees make up a minority of the plant diversity of the world (e.g., Spicer et al., 2020). The characteristic association between epiphytes and host trees provides the opportunity to test spatial theories of arrival, dispersal, and biogeography within a three-dimensional, biotically-mediated habitat. Because epiphytism has evolved and been lost several times across an incredibly diverse array of taxa, evolutionary questions comparing biotic and abiotic drivers of diversification could well be tested in the epiphyte system. Even the ultimate cause of epiphytism, and whether this evolutionary root differs among taxonomic groups, remains an open theoretical question (see **evolutionary processes**).

Finally, while a recently updated definition of epiphytic plants is based on the site of germination (Zotz, 2013b), and therefore excludes nomadic vines, we encourage future work to be inclusive of this group. Nomadic vines still spend part of their lifecycle embodying the essence of the epiphytic habit: living disconnected from the forest floor. We argue that understanding the similarities and differences among the different ways of being epiphytic could provide more insight into the ecology and evolution of epiphytes than excluding any one form. For example, at early life-stages, holoepiphytes and hemiepiphytes certainly experience similar abiotic and biotic challenges of germinating in the canopy and surviving while disconnected from the forest floor that are different from the challenges facing nomadic vines that germinate in the forest floor. However, at later life-stages, holoepiphytes and nomadic vines arguably face more similar challenges of the epiphytic lifestage compared to those of a hemiepiphyte that has gained a connection to the forest floor. The aerial roots of holoepiphytic orchids and nomadic vine aroids, for example, are analogous and likely both evolved in response to the epiphytic habit for a similar purpose: to aid in nutrient and water uptake when wet while preventing desiccation when dry (Benzing, 2008; Gill, 1969; Watkins and Cardelús, 2012); Zotz et al. (2021) argued that the hydraulic architecture of a nomadic vine was likely comparable to that of a hemiepiphyte. Layered on this is the variation in biotic interactions that occur along a vertical gradient from the understory to the canopy (e.g., microbes, Gora et al., 2019; pollinators, Bawa, 1990; fungal mutualists, Lugo et al., 2009; herbivores, Neves et al., 2014), which could provide different selection pressures for epiphytes at different life stages or different areas of the canopy. Furthermore, casting a wide net to include nomadic vines may offer some insights into the evolution of holoepiphytism, which may have occurred through a hemiepiphytic intermediary (Watkins and Cardelús, 2012).

### *5.2. Ecosystem implications of epiphyte biotic interactions*

Apart from the importance of biotic interactions to epiphyte ecology and evolution outlined above, epiphyte biotic interactions have many ecosystem implications. Epiphytes create habitat and provide essential resources for arboreal invertebrates and vertebrates (Hedges and Thomas, 1992; Nadkarni and Matelson, 1989; Phillips et al., 2020; Seidl et al., 2020), making them the secondary foundation species in facilitation cascades (e.g., Angelini and Silliman, 2014). In fact, a single epiphytic fern in Borneo was found to contain an invertebrate biomass similar to the rest of the tree crown in which it was found (Ellwood and Foster, 2004). These invertebrates are then used by vertebrates, such as birds (Nadkarni, 1994; Zotz, 2016). The importance of epiphytes to birds as food sources (e.g., nectar, fruits, seeds, invertebrates), as sources for nest materials and nests, and as reservoirs of water for drinking and bathing, has led them to be deemed "keystone" structures (Fontúrbel et al., 2021; Nadkarni, 1994; Nadkarni and Matelson, 1989). Experimentally removing epiphytes from a shade-coffee farm resulted in reduced bird abundance and shifts in bird community composition, wherein 18 bird species were more common in epiphyte plots than in removal plots (Cruz-Angón and Greenberg, 2005). Dendrobatid frogs and their use of tank bromeliads as brooding sites is one of the most charismatic relationships of epiphytes with animals (Fig. 2I; Benzing, 1998; Poelman et al., 2013; Stynoski et al., 2014). In this system, female parents transport tadpoles to phytotelmata in tank bromeliads and feed them an obligate diet of eggs full of alkaloids sequestered from terrestrial arthropods as a means of increasing tadpole survival through chemical defense (Stynoski et al., 2014).

These epiphyte-animal interactions can have downstream effects on epiphyte community structure and ecosystem processes. Hummingbirds that nest in epiphyte-laden trees in Valdivian rainforests in Chile have been found to choose particular epiphytes as nest substrates because of their antifungal properties, which then influences the distribution of epiphytes within tree crowns (Fontúrbel et al., 2021). In tropical moist forests in Belize, epiphyte diversity was higher on trees that contained ant nests than those that did not, even for non-obligate ant-garden epiphytes (Catling, 1997). These ants associated with epiphytes in turn influence the host tree in a facilitation cascade. In inundated sub-humid forest in Mexico, trees that hosted epiphytes had less foliar herbivory from chrysomelid beetles and leaf-cutter ants than trees without epiphytes (Dejean et al., 1995), and in an orange plantation in Guanacaste, Costa Rica, herbivory of orange tree leaves was reduced when close to bromeliads that hosted predacious ants (Hammill et al., 2014). Canopy herbivory can contribute to ecosystem processes, such as nutrient addition through frass, which can influence forest floor microbial abundance and feedbacks between plants and the soil microbiota (Reynolds et al., 2003), and epiphytes themselves fall and contribute to forest floor nutrient loads (e.g., lichen, Esseen and Renhorn, 1998). Thus, epiphytes could influence ecosystem processes directly through nutrient and water absorption or indirectly through their influence on host-tree herbivores.

### 5.3. *Biodiversity conservation implications*

Epiphytes, and their associated symbioses, are currently threatened by climate change and anthropogenic disturbance. Rising temperatures and shifting cloud cover puts atmospheric-water-dependent epiphytes at particular risk (Gotsch et al., 2015; Porada et al., 2018). Warming mountainous regions leave epiphytes at the limits of their physiological constraints, with no higher up the mountain to go (Colwell et al., 2008). Rare old-growth forests provide unique and irreplaceable habitats for epiphyte communities—communities that can take hundreds of years to develop (e.g., Woods and DeWalt, 2013). These forests are still being fragmented and logged, and will experience novel combinations of anthropogenic and natural disturbance in the future (e.g., Laurance et al., 2012). As we have demonstrated throughout this narrative, these problems are likely exacerbated by interrupted biotic interactions, including loss of pollinator networks, seed dispersers, and defensive mutualisms, although biotic interactions can also buffer negative climate change impacts to epiphyte populations (e.g., Morales-Linares et al., 2021). By considering these interactions, we have many opportunities to galvanize conservation efforts and efficiently use limited resources to manage for biodiversity and resilience (Phillips et al., 2020). A few examples give hope for proactive biodiversity management. Applying mutualistic mycorrhizal fungi to urban trees can be used as "orchid bait" to increase urban plant diversity and bolster native orchid populations in degraded landscapes (Izuddin et al., 2019). Leaving epiphytes in coffee plantations can increase the bird abundance and community diversity (Cruz-Angón and Greenberg, 2005). Bryophytes can enhance vascular plant growth and success on green roofs (Heim et al., 2014) as well as buffer vascular epiphytes from climatic change in managed landscapes (Richards, 2021). Quantifying complex interactions among orchids, foraging ants, and weevil herbivores can contribute to preventing the spread of an invasive orchid species (Ackerman et al., 2014) and improve predictions of non-native orchid range expansion in future climate scenarios (Foster and Ackerman, 2021).

Epiphytes are a critical component of ecosystems across the world and are of great conservation concern. As we have demonstrated, epiphytes engage in a wide variety of biotic interactions across the parasitism-to-mutualism spectrum. These biotic interactions have important implications not only for the advancement of ecological and evolutionary theory, but also for forest management and biodiversity conservation. Although abiotic drivers are no doubt important for epiphyte diversity, we argue that a full understanding of epiphyte ecology and evolutionary processes requires consideration of biotic interactions as well.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

This article was written while MES was supported by the NSF Postdoctoral Research Fellowship in Biology under Grant # 1907190. Discussions with Walter Carson, Corlett Wolfe Wood, and Teng-Chiu Lin facilitated the development of the ideas. Jackie Spicer contributed some of the digital art for Figs. 1 and 3. Comments from Glenda Mendieta-Leiva and anonymous reviewers greatly improved the writing of the manuscript.

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ppees.2021.125658.

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