

5-2022

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# An overview of the current research on epiphyte ecology

Honors Senior Project

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## Abstract

Epiphytes are non-parasitic, photosynthetic organisms that depend on other photosynthetic host organisms for support. Epiphytes can be found both in aquatic and terrestrial habitats. The interactions between epiphytes and their hosts can vary based on both their habitat and the features of individual hosts. This review explores the many facets of epiphyte research, including: the diversity of epiphytes in aquatic and terrestrial habitats; the effects of host-epiphyte interactions on the hosts; and the abiotic and biotic interactions that together determine epiphyte community composition.

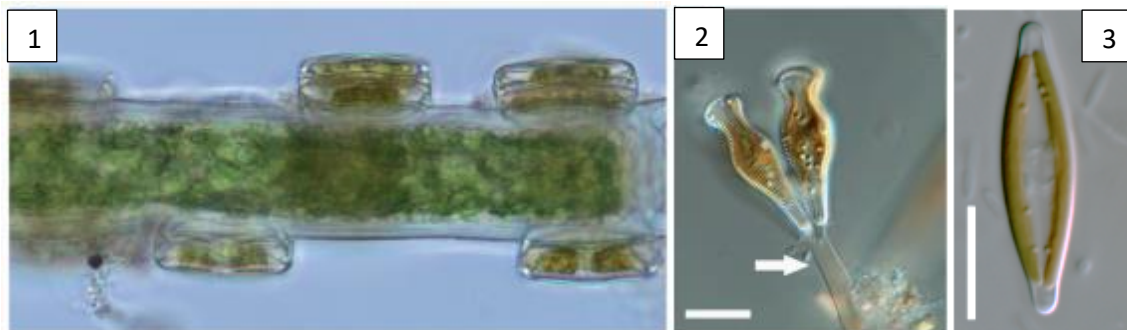
## Introduction

Epiphytes are photosynthetic organisms that grow on, and interact with, other photosynthetic organisms (Letáková et al. 2016). They are not parasitic, but their growth can affect their hosts both positively and negatively. Epiphytes range from microscopic bacteria and algae gliding along a macrophyte (Letáková et al. 2018) to large swaths of vascular plants blanketing whole forests (Taylor 2019). The habitats in which these epiphytes grow vary just as greatly as the epiphytes themselves, with some species of vascular epiphytes preferring the bark of a specific tree species and others finding themselves along the leaves of seagrass. Some epiphytes spend only a portion of their lives depending on a host for structure (Nieder et al. 2001). Two large areas of study regarding epiphytes focus on their hosts. The first involves the interactions between host and epiphyte, and how their relationship affects each of the organisms involved. The second involves the extent to which epiphytes exhibit host specificity. The purpose of this review is to provide a broad overview of the many aspects of epiphyte research. In particular, this review will focus on the diversity of epiphytes and their hosts, the interactions between epiphytes and hosts, and the factors that are at play in determining epiphytic community composition.

## Epiphyte Diversity

Epiphytes are diverse in terms of appearance, host choice, and environments, and as such they are more easily discussed when broken down into three subgroups: 1.) aquatic epiphytes; 2.) vascular terrestrial epiphytes; and 3.) non-vascular terrestrial epiphytes. The first group of epiphytes are those found in aquatic environments. One of the most abundant organisms in aquatic settings are algae, most often specifically diatoms (Azam et al. 2016). Epiphytic algae

play an important role as primary producers in aquatic systems (Letáková et al. 2018). The rate of primary production by epiphytes is comparable to, and in some cases greater than, the production of phytoplankton. Moncreiff & Sullivan (2001) found that epiphytic algae were responsible for roughly 46% of a seagrass system's primary production in the Gulf of Mexico, compared to the seagrass itself, which was responsible for only 13%. Epiphytic algae can be found on both aquatic plants and macroalgae. One of the most common hosts for epiphytic algae in freshwater systems are Charophytes. The epiphytes grow mostly on the tops of Charophyte filaments and internodes and sometimes associate with the node itself or the base of the macrophyte (Azam et al. 2016). Charophytes provide an attachment point for the epiphytes that allow them to remain in ideal conditions for growth (Letáková et al. 2018). The need for a host introduces a new level of competition for the epiphytic algae as these individuals are not only competing for nutrients and light but also for the most optimal space on their host (Letáková et al. 2018). Epiphytes can attach to their hosts using a variety of methods. Diatoms attach using stalks, pads, or adhering films and can grow as individuals or a part of a colony (Letáková et al. 2018; Figs. 1-3). Photosynthetic bacteria form thin films along their hosts (Hempel et al. 2008) and green macroalgae can form crusts or sheets on their host or form branching structures by employing holdfasts or penetrative rhizoids (Taylor 2019).



**Figures 1-3** (Letáková et al. 2018) **1.** *Cocconeis* attached to green algae by valve face **2.** *Gomphonema* attached via mucilaginous stalk **3.** *Navicula* (motile)

The second and third groups of epiphyte are found in terrestrial environments in two forms: vascular and nonvascular. Group two, vascular epiphytes, include orchids, bromeliads, aroids, and ferns. These epiphytes have their own vascular tissue despite relying on other organisms, typically trees, for support (Gradstein et al. 2003). Vascular epiphytes are common in subtropical, tropical, and even temperate rainforests and make up ~10% of the world's flora (Callaway et al. 2002), and nearly 25% of all vascular plant species in tropical environments (Nieder et al. 2001). Unlike their aquatic counterparts, vascular epiphytes do not outcompete their hosts in terms of productivity. Few studies have compared the primary production of vascular epiphytes to their host trees, but Zotz (2016) found the production of the epiphytes to be negligible. On average the epiphyte's capacity to fix carbon is lower than the capacity of tree leaves (Zotz 2016). This lower productivity is likely due to limited water and nutrient availability (Taylor 2019). Although the primary productivity of these vascular epiphytes is not high, they do play other important ecological roles. These epiphytes affect the water balance of their systems and store nutrients in large concentrations (Gradstein et al. 2003). Compared to their hosts, vascular epiphytes store nutrients in greater amounts than could be expected from their biomass alone (Zotz 2016). Outside of their role in storage, vascular epiphytes are also a source of food and habitat for many animals and microorganisms as well as useful ecological indicators of climate and forest health (Gradstein et al. 2003).

Within the vascular epiphytes there are two subclasses: holo-epiphytes and hemi-epiphytes. Holo-epiphytes (more common) use the host as a growing site throughout their life cycle (Nieder et al. 2001). Alternatively, hemi-epiphytes spend only a part of their life cycle as epiphytes while they wait for their aerial roots to reach the ground and establish themselves in the soil (Nieder et al. 2001). Some of these epiphyte species can also be found growing

independent of hosts in a non-epiphyte form (Zhang et al. 2021; Fig. 4). The community composition of these two types of epiphytes varies slightly. Holo-epiphytes exhibit a vertical gradient where different species can be found at the tops of trees compared to those near the ground. Hemi-epiphyte communities vary more between hosts than on a single host because the host tree's structure is important in determining which epiphyte species take hold there (Nieder et al. 2001).



**Figure 4.** (Zhang et al. 2021)  
Epiphytic *Briggsia longifolia*.

The overall ecological impact of vascular epiphytes is often smaller than the third group of epiphytes, the non-vascular epiphytes, though this impact can vary by forest type (Zotz 2016). Non-vascular epiphytes include mosses, liverworts, and lichens (Porada and Giordani 2021; Fig. 5), all organisms which have no vascular tissue and instead take in their water and nutrients through the air (Gradstein et al. 2003). Non-vascular epiphytes exhibit greater diversity than vascular epiphytes with liverworts representing the greatest number of non-vascular plant taxa in most environments (Affeld et al. 2008). The variation of these epiphyte communities on singular hosts and between hosts in the same habitat is complex and not easily explained by differences in the environment as neighboring trees often host completely different species of epiphytes (Wolf 1995). It is still unclear if there is a pattern to the epiphytes' spore dispersal that could lead to the high variability in community composition (Affeld et al. 2008). The areas of the host that have been established the longest have the greatest abundance of epiphytes, but greater diversity is found in the outermost limbs of the host trees while the inner branches and trunk of the tree are populated by larger patches of singular species (Wolf 1995). This may be in part because non-

vascular epiphytes are not thought to be in competitive equilibrium (described by Watson (1980) as a positive correlation between magnitude of species diversity and environmental complexity), making it easy for new or invasive species to successfully take over an area (Wolf 1995). Non-vascular epiphytes are sensitive to climate change, particularly changes in moisture and temperature (Song et al. 2012). Due to their need to draw moisture from the air rather than through vascular systems, a drier climate could be detrimental to non-vascular epiphyte communities. As such, non-vascular epiphytes in particular could be used as climate change indicators in their environments.



**Figure 5.** (Porada and Giordani 2021) A foliose lichen (*Lobaria* sp.) growing on a tree

### Host-Epiphyte Interactions

While epiphytes are not parasitic, they interact with their hosts in a variety of ways that can be either beneficial or detrimental for the health of the host. The benefits for the host, are complex. For example, particularly in aquatic systems, the presence of epiphytes may act as a protective coating by causing a grazing organism to avoid the host that they would typically consume if the grazer were averse to the epiphyte (Karez et al. 2000). Similarly, if the protective epiphyte-coating is just the right thickness it may benefit the hosts by allowing the epiphytes to absorb the majority of the UV radiation (Letáková et al. 2018). As for benefits for epiphytes, the host provides stability for the epiphytic organism, allowing it to stay in a location with optimal light and access to nutrients, and can prevent stress due to currents in aquatic systems (Letáková et al. 2018).



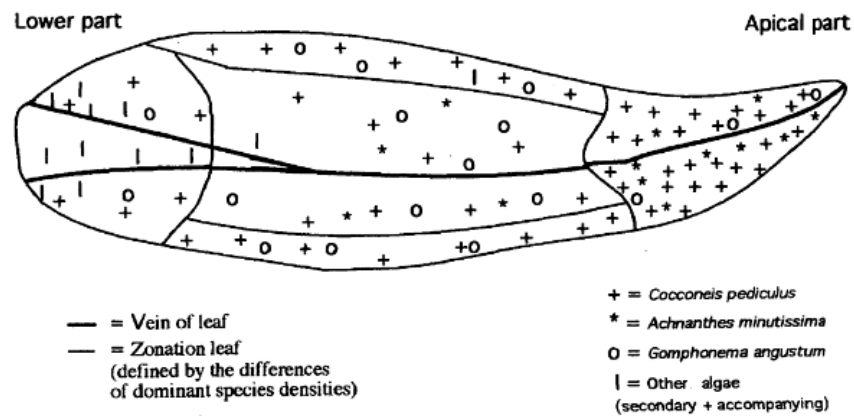
Epiphytes can cause negative effects to their hosts as well. Similar to the ability of epiphytes to ward off grazers, if a grazing organism is attracted to the epiphytes, it may draw more attention to the host, and often the host is then harmed either as a side effect or through purposeful grazing (Karez et al. 2000). Epiphytes can also have an effect on the thallus flexibility of aquatic plants as they build up along the plant, increasing the probability of breakage (Fricke et al. 2011). In aquatic systems, epiphytes can increase the pH levels, contributing to the induction of hypoxic conditions overnight, affecting the hosts' ability to grow. In both aquatic and terrestrial systems, epiphytes are known to decrease the photosynthetic activity of their hosts (Letáková et al. 2018). Although epiphytes in both aquatic and terrestrial systems are known to store nutrients in high quantities, this is especially detrimental in terrestrial environments where nutrients are often stored for a long time, making them unavailable to the host (Zotz 2016). In aquatic systems, some hosts produce allelopathic chemicals to reduce epiphyte growth (Letáková et al. 2018). Land plants have been found to produce similar effects, in addition to the rugosity of their bark playing a role in the abundance of epiphytes on their surface (Callaway et al. 2002).

### Community Composition Factors

Epiphyte community composition relies on the interactions between a number of factors, including host anatomy, nutrient availability, light, temperature gradients, and grazing patterns. Much research has been done to determine which of these factors plays the largest role in determining the make-up of epiphytic communities (e.g., Letáková et al. 2018).

Beginning with host factors, the host's anatomy plays an important role in determining the communities' make up, both in aquatic and terrestrial environments. In aquatic environments, Comte & Cazaubon (2002) found specific epiphytic species often settled in patterns that were

nearly identical from one plant to the next of their host species, suggesting that the topography of the host led to microhabitat niches for individuals to fill. For example, the most abundant of the diatom species found on the upper side of *Potamogeton densus* leaves appeared closest to the stem while less abundant species appeared denser closer to the tip of the leaves (Fig.6; Comte & Cazaubon 2002).



**Figure 6.** (Comte & Cazaubon 2002) The distribution of epiphytic diatoms on the upper side of a *Potamogeton densus* leaf.

Epiphytes found on Charophyta often exhibit homogeneity across hosts of the same species. Each species of epiphyte exists in their own microniches on the host, and these same microniches can be observed on multiple individuals of the same host species (Azam et al. 2016). Richness, diversity, and composition of epiphytic diatom communities varied greatly between the two macrophyte hosts (Letáková et al. 2016). For *Potamogeton gramineus*, there was higher species richness and diversity than in the communities found on *Chara aspera* and larger-celled, adnate diatoms were found in abundance. *C. aspera* was a host for more small-celled, motile diatom species, suggesting that host structure is likely at play in the differing community composition of different algal hosts (Letáková et al. 2016). Whereas diatoms are often found on hosts that have more complex structures, such as charophytes or *Elodeids* (a genus of aquatic plants with tightly

packed axial leaves), larger epiphytes (typically green algae) are often found on hosts that have more simple structures, such as *Nymphaea* (Messyasz et al. 2009).

In terrestrial environments, the host's structure also plays an important role in community composition. Callaway et al. (2002) found many species-specific relationships were highly correlated with the host tree's water-holding capacity in a study in a coastal forest in the southeastern United States. Also, the rugosity of the host bark was positively correlated with epiphyte abundance (Callaway et al. 2002). Similarly, larger and more established terrestrial hosts are more likely to have a higher abundance of epiphytes (Elias et al. 2021). Without considering host structure, epiphytes still show preference (or an aversion) toward certain hosts, likely due to a resource the host offers or a chemical affect that the host has on the epiphytes both in aquatic (Letáková et al. 2018) and terrestrial systems (Callaway et al. 2002).

Host factors alone are not enough to explain the variation in epiphytic communities between different host species. In aquatic communities, factors such as water clarity can have an effect on epiphyte abundance and community composition (Azam et al. 2016). Water motion, light availability, grazing pressure, and nutrient supply often have as much (if not more) effect than host complexity on the composition of epiphytic communities (Fricke et al. 2011). Differential shading, differential grazing, and interspecific competition can lead to differences in epiphytic diatom communities growing on vascular aquatic plants that otherwise experienced shared environmental factors (Millie & Lowe 1983). Epiphytes, like all aquatic communities, can also be affected by seasonality with the highest abundance from spring to autumn (Azam et al. 2016) or mid to late summer (Millie & Lowe 1983).

In terrestrial environments, water availability plays an important role in where epiphytes will successfully establish themselves (Callaway et al. 2002). Light availability is also important,

which is why epiphyte abundance typically decreases on trees with a denser leaf cover (Elias et al. 2021) and why greater diversity is typically seen in the less shaded outer branches of trees than closer to the trunk (Wolf 1995). In addition, epiphytes with a greater tolerance for a wider range of environmental factors will often outcompete specialist epiphytes, especially in habitats that have been influenced by human activity, such as pastures (Elias et al. 2021).

### Conclusion

The term epiphyte is used to describe a vast, diverse group of organisms that all share the common feature of relying on another photosynthetic organism as a structure of support, and/or as a source of nutrients or water. While these organisms range from microscopic bacteria to entire “forests” of vascular plants and can be found anywhere from the seafloor to the trunks of trees in a rainforest, they have common patterns in which they interact with their environments. These epiphytes rely on their hosts, which in many cases are affected by their presence either positively or negatively. Epiphytes interact with each other to form complex communities, typically made up of microniches, that compete with each other for nutrients and light availability. Epiphytes are unique and important to the functioning of ecosystems as a whole. The continued study of epiphytic communities, both aquatic and terrestrial, will lead to a better understanding of the ecosystems in which they are found.

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