

## Letters

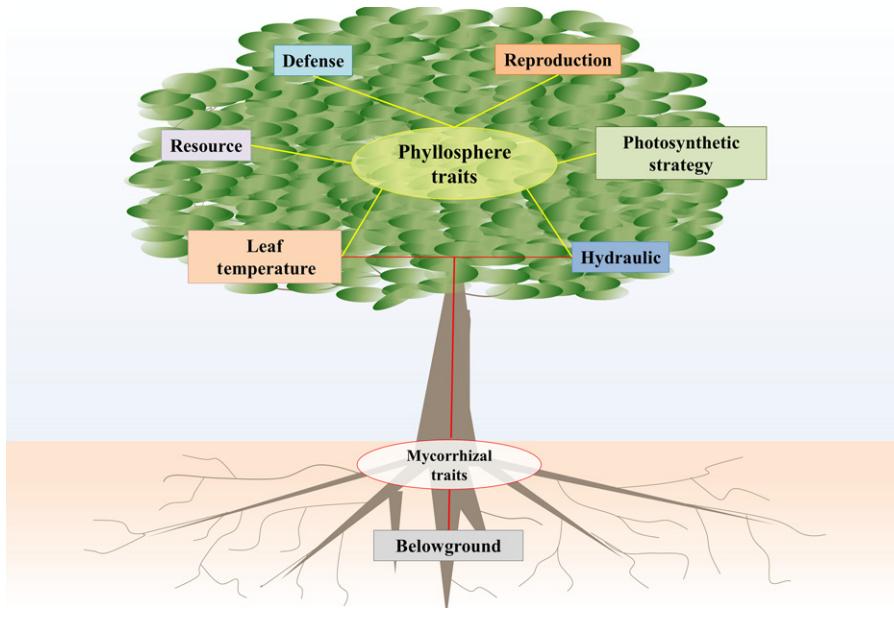
# The importance of phyllosphere on plant functional ecology: a phyllo trait manifesto

Identifying axes of plant strategies based on trait-covariance, and how these axes are connected, have been pointed out as essential to obtain a better understanding of how plant species respond to the environment and, consequently, to improve the accuracy of predictive models applied at different ecological scales (Ackerly, 2004; Reich, 2014; Walker *et al.*, 2017). There has also been a shift in plant ecology in recent years that acknowledges the plant microbiome as being intimately linked to some of these plant traits (Friesen *et al.*, 2011). For instance, advances in trait-based research indicate the importance of inclusion of mycorrhizal traits to better characterize below-ground plant strategies due to their role in resource acquisition and storage in roots (Walker *et al.*, 2017). In line with the importance of mycorrhizal traits to plant strategies (Lambers *et al.*, 2008; Ke *et al.*, 2015; Laliberté *et al.*, 2015; Walker *et al.*, 2017), we would like to further expand the importance of macro- and micro-organisms associated with plant species when defining trait schemes. We propose phyllosphere traits (from endophytic and epiphytic organisms such as liverworts, mosses, lichens, bacteria, fungi and other micro-organisms colonizing leaves) as fundamental traits linked with the aboveground trait axes such as photosynthetic strategy, hydraulics, resource acquisition, leaf temperature, reproduction as described by Walker *et al.* (2017) and plant defense (Chauvin *et al.*, 2018) (Fig. 1). Although 'root mycorrhizal associations can substantially alter the acquisitive capability of a root' (Walker *et al.*, 2017), traits related to the aboveground phyllosphere associations have not been completely unveiled and may also have important consequences at both the plant and ecosystem level. Although the interplay between phyllosphere and traits has been reported (Beattie, 2011), these studies have focused specifically on bacterial communities at the level of the cell or leaf (Remus-Emsermann & Schlechter, 2018). Few studies have shown how different organisms making up the phyllosphere may be associated to plant ecological strategies aboveground (Friesen *et al.*, 2011; Kembel *et al.*, 2014). Therefore, since the effects of phyllosphere traits on plant strategies have been overlooked, the same is true for the remaining gaps in this research field. Thus, inspired by Reich's plant trait manifesto (2014), we call for additional efforts by the scientific community to study the roles of the phyllosphere on plant functional ecology.

## Phyllosphere traits as the missing link among axes of plant strategies

Since an integrated network of plant traits is important to describe plant strategies (Messier *et al.*, 2017), phyllosphere traits may represent the understudied missing link in the network of plant traits that, finally, would allow a better characterization of plant strategies. From plant growth to reproduction, studies have shown how the phyllosphere affects traits such as seed mass, stomatal conductance and leaf longevity (Jones & Dangl, 2006; Lambers *et al.*, 2008; Friesen *et al.*, 2011; Sawinski *et al.*, 2013; Kembel *et al.*, 2014), but a main knowledge gap to be filled is related to how the net interaction of the multitude of positive and negative effects of phyllosphere traits may mediate axes describing plant strategies (Fig. 1).

For instance, leaf surfaces colonized by liverworts may have reduced photosynthetic rates due to decreased light interception (Coley *et al.*, 1993; Coley & Kursar, 1996) (Fig. 1). However, bryophytes may also play a role in leaf nitrogen balance either by reciprocally transferring nitrogen to host leaves (Wanek & Portl, 2005) or creating favorable microclimatic conditions for cyanobacteria (Bentley, 1987; Turetsky, 2003). Microbial assemblages such as biofilms harboring cyanobacteria and other nitrogen fixing bacteria, including endophytic bacteria, might also transfer nitrogen to the leaf (Coley & Kursar, 1996; Moyes *et al.*, 2016; Rigonato *et al.*, 2016; Lambais *et al.*, 2017). In this line, Laforest-Lapointe *et al.* (2017), using a tree biodiversity-ecosystem functioning experiment, have shown that plant community productivity is positively related to phyllosphere bacterial diversity indicating the importance of the interplay of plant–phyllosphere for ecosystem functioning. The combined effects of phyllosphere cover on photosynthesis and nitrogen input may affect leaf turnover rates due to changes in leaf pay-back time and ultimately impact leaf longevity (Coley & Kursar, 1996; Jones & Dangl, 2006; Friesen *et al.*, 2011). Moreover, leaf longevity may be increased by pathogens producing cytokinins (Jones & Dangl, 2006). However, it is not known how the interplay between the phyllosphere and plant traits may directly affect axes related to carbon acquisition. In terms of plant hydraulics, fungal endophytes and bacteria might have an important role in facilitating foliar water uptake (FWU) through stomata since they decrease leaf surface tension and/or act as a direct entry pathway for water, in the case of fungal hyphae growing into stomata pores (Burgess & Dawson, 2004; Burkhardt, 2010; Fernández *et al.*, 2017). FWU has been indicated as an important ecophysiological process alleviating water stress and allowing plant growth and survival under drought conditions (Burgess & Dawson, 2004; Eller *et al.*, 2013; Fernández *et al.*, 2017). Moreover, given that the magnitude of FWU may decrease



**Fig. 1** Scheme modified from Walker *et al.* (2017) adding the connection between various common axes of plant strategy aboveground and phyllosphere traits (yellow lines). Additionally, the interplay between mycorrhizal traits and axes aboveground are also presented (red lines). For simplicity, the plant traits were not included.

or even suppress daytime and nighttime transpiration (Eller *et al.*, 2015), FWU promoted by phyllosphere colonizing organisms might have an indirect effect on leaf temperature, determined by the leaf coupling to the atmosphere (Wright *et al.*, 2017). Furthermore, it could also be expected that fungal hyphae might potentially lead to water loss due to a bypass pathway. In fact, it has been shown that the phyllosphere microbiome may change leaf wettability by producing hygroscopic particles (Beattie, 2011), changing cuticle permeability (Schreiber *et al.*, 2005; Beattie, 2011; Ritpitakphong *et al.*, 2016) leading to increases in cuticular transpiration (Schreiber *et al.*, 2005). In terms of axis of plant defense, changes in plant traits, such as decreases in water potential and xylem conductivity (Beattie, 2011), stomatal closure or opening (Jones & Dangl, 2006; Friesen *et al.*, 2011; Sawinski *et al.*, 2013), biosynthesis of plant hormones, such as indole-3-acetic acid (IAA), abscisic acid (ABA) and ethylene (Lindow & Brandl, 2003; Beattie, 2011; Egamberdieva *et al.*, 2017), may either be defensive responses to pathogens or shifts promoted by them in order to increase their virulence and growth (Beattie, 2011). Consequently, such changes associated with plant defense may directly affect axes of leaf temperature, photosynthesis and hydraulics. Importantly, it must not be neglected that even axes of strategies aboveground may also be affected by mycorrhizal traits such as plant hydraulic function and leaf temperature due to changes in stomatal conductance (Fig. 1; Lambers *et al.*, 2008).

## What are phyllosphere traits?

In a functional context, the phyllosphere core microbiome may be defined according to their 'shared predicted functions' such as protein-coding genes indicating low functional uniqueness (Vandenkoornhuyse *et al.*, 2015). By expanding this definition to phyllosphere traits, we argue that it is necessary to define those

traits within the response–effect trait framework to completely understand their potential roles in shaping plant ecological strategies. The association between plants and phyllosphere organisms must be seen through the lens of the distinction between response traits (i.e. how an organism responds to an environmental driver; Lavorel *et al.*, 2013) and effect traits (i.e. traits determining ecosystems processes and the functional role of species in affecting other organisms and trophic levels; Rosado *et al.*, 2016). A response–effect functional framework is needed to disentangle the effect of species from their response to environment and the interplay between organisms from different trophic levels (Lavorel *et al.*, 2013; Rosado *et al.*, 2016; Laforest-Lapointe *et al.*, 2017). Such a distinction is essential because the ability of each organism inhabiting the phyllosphere in colonizing a given leaf/plant species is dependent on their response traits. However, the ability of phyllosphere organisms to affect plant functioning will be determined by their effect traits that are not necessarily the same traits describing their responses to a given factor. Since phyllosphere organisms may have either positive or negative effects on plant traits, phyllosphere traits may be understood as effect traits. Therefore, phyllosphere traits are a complex of traits of different organisms (e.g. fungi, bacteria, mosses) colonizing different plant tissues and affecting plant function simultaneously. Consequently, despite the remarkable advances in comprehending how microbes affect plants at the cell level (Remus-Emsermann & Schlechter, 2018), one of the main gaps that should be addressed in future studies is evaluating the net result of positive and negative effects promoted by the bulk of phyllosphere traits at the whole-plant level.

Understanding how plants control phyllosphere colonization (phyllosphere response traits) is essential for a better comprehension of how phyllosphere organisms affect plant traits (phyllosphere effect traits) at ecological (affecting plant responses in shorter

timescales) and evolutionary scales (modulating changes in plant traits and fitness due to co-evolution; Friesen *et al.*, 2011). For instance, in a recent global analysis of root functional traits, Ma *et al.* (2018) reported that mycorrhizal colonization is higher in ancestral thick roots in comparison to evolutionarily recent thin roots. Thus, plant species with thick roots, possessing a conservative resource-use strategy, and occurring in more stable and ancient environments (e.g. tropical forests), are more dependent on mycorrhizal colonization to cope with ecological factors (Ma *et al.*, 2018). Based on this evolutionary perspective, we advocate the same approach to evaluate the degree to which interactions between plants and phyllosphere organisms are dependent on phylogeny and functional traits aboveground that, similar to thick and thin roots, are associated to the fast–slow plant economic spectrum (Reich, 2014). Thus, including phylogenetic information would be important to evaluate the way in which such interaction may determine how plant species cope with ecological factors and, ultimately, may shape plant community structure at ecological and evolutionary scales.

Therefore, knowing the contribution of other organisms, mainly micro-organisms, on processes affecting plant traits aboveground and belowground is essential to model the processes shaping plant communities. Even though the concept of ‘environmental filtering’ assumes that the ability of macro-organisms (e.g. plants) to pass through a given filter is exclusively related to their traits alone, it neglects their interactions with micro-organisms (Aguilar-Trigueros *et al.*, 2017), which may change plant niches by inducing shifts in plant functional traits (Friesen *et al.*, 2011).

Due to the role of micro-organisms in mediating plant responses to environmental filtering, it was recently proposed that, due to the functional roles microbes play in facilitation and function of plant response to abiotic and biotic drivers, microbes be included as an aspect of the extended plant phenotype, also called plant holobiont (Vandenkoornhuyse *et al.*, 2015). However, their negative and neutral effects must be also considered when describing the extended phenotype of plants (Partida-Martínez & Heil, 2015). In this line, the theoretical background that may improve the understanding of including phyllosphere traits is related to the alternative functional designs (i.e. multiple phenotypes with equal fitness). Alternative functional designs are related to a hierarchy of traits (Marks, 2007) where different trade-offs of trait combinations may lead to similar responses (i.e. integrative traits; Rosado & de Mattos, 2017) at the whole plant level (Marks & Lechowicz, 2006; Marks, 2007; Laughlin & Messier, 2015; Rosado & de Mattos, 2017). Therefore, we argue that including phyllosphere traits in the hierarchy of plant traits may improve our understanding, not only of how trade-offs are mediated by phyllosphere, but also how ‘multiple extended phenotypes’ may be derived from this interplay, which remains a shortfall in plant functional ecology.

## Barking up the right tree

Including the effects of phyllosphere and rhizosphere-associated organisms on plant traits will strengthen the predictive power of

models applied from plant organs to ecosystems. Across habitats, we expect that phyllosphere organisms are especially important as modulators of plant strategies in tropical forests (Arnold & Lutzoni, 2007; Meiser *et al.*, 2014), which harbor the majority of plant species in the world. Similarly, the lower phyllosphere species richness, cover degree and abundance in small forest fragments (Zartman & Nascimento, 2006; Pereira Alvarenga & Pôrto, 2007) suggests that declines in phyllosphere colonization in more disturbed areas may directly affect plant ability to cope with environmental changes. The testing of such hypotheses, however, will need an integrative research program that merges functional ecology, physiology, microbiology, phylogeny and metagenomics. This will lead to a more defined focus on identifying phyllosphere species and their functions and interactions (i.e. phyllosphere effect traits) with host plants, comprehending the position of each organism inhabiting the phyllosphere in the mutualism–antagonism continuum (Partida-Martínez & Heil, 2015), and how their positions may change across spatio-temporal scales, among individuals, species and along plant ontogeny (Partida-Martínez & Heil, 2015; Vandenkoornhuyse *et al.*, 2015). This approach, consequently, would enable study of how the phyllosphere may affect plant functioning (from leaf to whole plant level) and plant performance. In this sense, experiments of cross-inoculation of phyllosphere core microbiomes (Ritpitakphong *et al.*, 2016) between plants with different traits and strategies to detect the role of such interactions in the hierarchy of traits will be valuable. Moreover, phylogenetic tools will be important to describe whether phyllosphere traits may be ‘heritable traits’ in plant species or only dependent on horizontal transmission among species and individuals (Rodriguez, 2009; Partida-Martínez & Heil, 2015; Rezki *et al.*, 2017). Therefore, the advancement of trait-based ecology depends on further comprehension of how plants and associated organisms inhabiting the phyllosphere (Friesen *et al.*, 2011; Aguilar-Trigueros *et al.*, 2017) and rhizosphere (Egamberdieva *et al.*, 2017) respond to environmental drivers. Such an approach may result in the discovery of another ‘loose foundation stone’ in plant functional ecology (Shipley *et al.*, 2016).

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