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Matos Ilaine S. (Orcid ID: 0000-0001-5557-5133)

Binks Oliver (Orcid ID: 0000-0002-6291-3644)

Rosado Bruno Henrique Pimentel (Orcid ID: 0000-0002-8924-8672)

Title

Revisiting plant hydrological niches: the importance of atmospheric resources for ground-rooted plants

Authors details

Ilaine Silveira Matos ^{1,2*}

Oliver Binks ³

Cleiton B. Eller ⁴

Bianca B. Zorger ⁵

Patrick Meir ⁶

Todd E. Dawson ^{2,7},

Bruno H. P. Rosado ⁵

* Corresponding author: ilaine.matos@gmail.com, +1 9259224385

¹ Macrosystems Ecology Laboratory, University of California Berkeley, CA, USA.

² Department of Environmental Science, Policy & Management, University of California Berkeley, CA, USA.

³ Research School of Biology, The Australian National University, Canberra, 2601 ACT, Australia.

⁴ Department of Plant Biology, University of Campinas, Campinas 13083-862, Brazil.

⁵ Department of Ecology, IBRAG, Universidade do Estado do Rio de Janeiro (UERJ), 524 PHLC 220, Rio de Janeiro, Brazil.

⁶ School of Geosciences, University of Edinburgh UK EH9 3FF.

⁷ Department of Integrative Biology, University of California Berkeley, Berkeley, CA, USA.

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Abstract

1. Occult precipitation events (fog, dew, light-rain) can alter plant water and nutritional status, both directly through the aerial uptake of surface water and nutrients, and indirectly via redistribution of atmospheric resources to the soil. However, current frameworks that explain niche segregation, species interactions, and coexistence still consider that ground-rooted plants obtain resources almost exclusively via root absorption from soil.

2. Here, we expand the plant hydrological niches model to incorporate both soil and atmospheric resource-axes, thus providing a more complete picture of how ground-rooted terrestrial plants obtain, remobilize, share, and compete for water and soluble nutrients.

3. First, we describe how plants with different water acquisition strategies access directly or indirectly atmospheric resources. Then, we discuss how the use of such resources may promote spatiotemporal niche segregation, contributing to shape species distribution and abundance within plant communities. We illustrate this argument with examples from arid, mesic, and wet vegetation types. Finally, we examine how climate and land-use changes may influence plant hydrological niches, potentially altering community structure.

4. *Synthesis*: Understanding how available atmospheric resources influences niche segregation in plant communities is a crucial step towards better predictions of species responses (e.g., changes in distribution, abundance and interactions) to climate change.

Keywords: climate change, drought, fog-drip, foliar water uptake, hydraulic redistribution, leaf-wetting, niche partitioning, occult precipitation.

Resumo

1. Eventos de precipitação oculta (neblina, orvalho, garoa) podem alterar o balanço hídrico e nutricional das plantas, tanto diretamente através da absorção aérea de água e nutrientes, quanto indiretamente através da redistribuição de recursos atmosféricos para o solo. Contudo, esquemas teóricos vigentes que explicam a segregação de nicho, as interações e a coexistência de espécies ainda consideram que as plantas não-epifíticas obtêm recursos somente através da absorção radicular no solo.

2. Aqui nós propomos uma versão expandida dos nichos hidrológicos das plantas, que incorpora tanto o solo como a atmosfera como eixos de recursos, e assim proporciona uma visão mais

completa de como as plantas não-epifíticas terrestres obtém, remobilizam, compartilham, e competem por água e nutrientes solúveis.

3. Primeiro, nós descrevemos as diferentes estratégias que as plantas usam para, direta ou indiretamente, acessar água e nutrientes de origem atmosférica. Segundo, nós argumentamos que o uso de recursos atmosféricos pelas plantas pode promover segregação de nicho (tanto espacial como temporal), e assim contribuir na distribuição e abundância das espécies nas comunidades vegetais. Nós ilustramos esses argumentos com exemplos em comunidades vegetais áridas, méxicas, e úmidas. Finalmente, nós examinamos como as mudanças climáticas e as perturbações antrópicas podem influenciar o nicho hidrológico das plantas, potencialmente alterando a estrutura das comunidades vegetais.

4. *Synthesis*: Entender como o uso de recursos atmosféricos pelas plantas influencia a segregação de nichos é um passo crucial para melhor predizermos a respostas das espécies (e.g., mudanças na distribuição, abundância e interações) às mudanças climáticas.

Palavras-chave: absorção foliar de água, molhamento foliar, mudanças climáticas, neblina, partição de nicho, precipitação oculta, redistribuição hidráulica, seca.

Introduction

Competitive interactions between species favours the emergence of diverse strategies for acquiring resources, resulting in niche differentiation. The hydrological niche segregation theory (HNS; Walter, 1939; Silvertown et al., 2015) is one of the best-supported models for explaining coexistence of ground-rooted plants in water-limited communities (e.g., savannas and deserts). It states that two or more species can coexist if they are able to reduce competition for water by obtaining this resource from different locations (spatial niche segregation) or at different times (temporal niche segregation). Spatial HNS has been documented in many biomes (**Fig. S1**) and ground-rooted vascular species (>1000 species, **Table S1, Appendix S1**), and it is typically attributed to differences in root distribution allowing spatial segregation throughout the soil profile (Walter, 1939; Brum et al., 2019; Kulmatiski et al., 2019). In contrast, temporal HNS is usually related to phenological differences (e.g., deciduous vs. evergreen) enabling plants to exploit soil-water resources during distinct seasons (Holdo, 2013; Schwinning & Kelly, 2013; Ward et al., 2013).

Although it has been known for more than a century that vascular epiphytes rely on atmospheric resources for their survival and growth (Grisebach, 1872; Zotz et al., 2021), only recently has the scale and potential importance of atmospheric inputs for ground-rooting plants become recognized in the literature (e.g., Dawson & Goldsmith, 2018; Berry et al., 2019; Binks et al., 2021). There is now mounting evidence suggesting that ground-rooted plants (> 380 species, **Table S2**) in almost all biomes (**Fig. S1**) can capture water and soluble nutrients from dew, fog, and light rain. Collectively referred to as occult precipitation (Rutter, 1975), such events tend to wet plant canopies without a direct and significant increase in soil water content.

By focusing on niche partitioning along the soil profile, and largely neglecting these occult precipitation events, the current HNS framework is providing an incomplete picture of how ground-rooted plants obtain, remobilize, share, and compete for water. To better understand niche partitioning amongst vascular plants, and its impact on species coexistence and diversity in plant communities, we propose an expanded version of the HNS theory that more explicitly incorporates the use of atmospheric resources by terrestrial plants. In this review, we (1) examine the different strategies by which ground-rooted plants obtain resources from occult precipitation events, (2) discuss how this capacity to access atmospheric resources can influence plant hydrological niches in space and time, and (3) explore how climate and land-use changes in the hydrological environment (soil and atmosphere) may affect species-specific hydrological niches, potentially altering species' relative abundance and distribution within communities. Lastly, we identify critical knowledge gaps that future studies should address to effectively expand the HNS framework.

Although we recognize that atmospheric resources are essential for the establishment and growth of poikilohydric autotrophs (e.g., Lange & Ziegler, 1986; Stanton & Horn, 2013), in this review we focus on the hydrological niches of homoiohydric and vascular plants.

How do plants access atmospheric resources?

Plants can access water and nutrients in the atmosphere through a variety of direct and indirect strategies (**Fig. 1**).

Direct strategies: involve the interception and absorption of water and nutrients from the atmosphere via plant aerial organs (i.e., aerial uptake), such as leaves (**Figs 1A-B**), stem bark (**Fig. 1C**) or aerial roots (e.g., Oliveira et al., 2005; Zotz & Winkler, 2013). One possible explanation for aerial uptake, that we refer to as ‘leaky cuticle/rhytidome hypothesis’, is that the external barrier of plant aerial organs (cuticle or rhytidome) is equally permeable to water in both directions, resulting in water gain or loss depending on the water potential gradient between the plant and its surroundings (Binks et al. 2020). Under this scenario, the contribution of aerial water uptake would be negligible compared to the water lost, because: (1) the atmosphere-plant water potential gradient is more commonly in a direction favourable to water loss, and (2) the gradients favouring water loss are typically far more extreme than the gradients favouring water gain (Schreel & Steppe, 2019; Binks et al., 2020). However, even in this scenario, there may still be a net gain in nutrients (Ferraretto et al., 2022); thus, plants may effectively trade water for nutrients. Nevertheless, the existence of special structures that facilitate aerial uptake (e.g., lenticels, trichomes, hydathodes, mucilage plugs, salt glands, cork warts, Berry et al., 2019; Raux et al., 2020) might suggest that in some cases this physical trade-off is, or can be, avoided. There are also experimental and theoretical studies suggesting that contact with liquid water or ambient humidity (e.g., Schönherr, 2000; Eller et al., 2013), as well as interactions with endophytic and epiphytic organisms (lichens and fungi, Burgess & Dawson, 2004; Rosado & Almeida, 2020), can alter the surface permeability of aerial organs which may facilitate aerial uptake, possibly via regulation of aquaporins (Laur & Hacke, 2014; Yan et al., 2015). If so, then aerial uptake may well be a strategy to increase uptake of water and/or soluble nutrients, rather than a passive mechanism resulting from leaky cuticles and rhytidome.

The notable differences across sites and species in the amount of resources acquired via aerial uptake (e.g., Berry et al., 2019; Fernandez et al., 2021; Matos et al., 2021) suggests that not all individuals benefit equally from occult precipitation events. However, identifying the relative contribution of atmospheric resources to different species (and across studies) is still challenging mainly due to the absence of standardised methods for measuring aerial uptake (Berry et al., 2019; Fernandez et al., 2021), and the lack of data on conductance to aerial uptake (e.g., Guzmán-Delgado et al., 2018; Binks et al., 2019). Moreover, few studies (e.g., Binks et al., 2019) attempted to contextualise aerial uptake in relation to climate (e.g., do lowland species with higher

conductance to aerial uptake acquire less atmospheric resources than montane species with lower conductance but more frequent exposition to fog events?), whole-plant water budgets (e.g., could small amounts of aerial-absorbed water have a substantial contribution to the whole-plant water budget for species growing in water-limited environments?), and potential negative effects (e.g., under which environmental circumstances do the benefits of aerial uptake overcome the potential negative effects related to reduced CO₂ uptake, increased fungal infection, and increased pollutants absorption?).

Indirect strategies: involve the redistribution of atmospheric resources to the soil via three potential strategies. First, atmospheric resources can be added to the soil via dewfall (**Fig. 1D**) and adsorption (**Fig. 1E**). Although small (Agam & Berliner, 2006; McHugh et al., 2015), the amount of water added to the soil via those two processes can be ecologically relevant for some ground-rooted plants in arid ecosystems (e.g., Ramirez et al., 2007; Matimati et al., 2013). Second, atmospheric resources intercepted by plant aerial organs that are not absorbed, nor evaporated, may eventually exceed the canopy surface water-storage capacity and reach the soil as throughfall (**Fig. 1G**) or stemflow (**Fig. 1H**). Both throughfall and stemflow are important processes to redistribute to the soil the atmospheric resources that otherwise would not be available for root uptake (Dawson, 1998; Aboal et al., 2000; Katata et al., 2010). Fog-water, for example, typically has higher concentration of nutrients than comparable rainwater (Saxena & Lin, 1990), but it is constituted by droplets too small to spontaneously precipitate to the soil. In montane forests with frequent fog events, each tree may be able to intercept and drip-off up to 1,200 litres of fog per year, which represents ca. 10% of the total net precipitation (Bittencourt et al., 2019). More studies are still needed (1) to quantify the amount of atmospheric resources that are intercepted, stored or redistributed to the soil in different ecosystems (Crockford & Richardson, 2000), (2) identify key factors (e.g., landscape heterogeneity, canopy structure, droplet size distribution, density of epiphytes, Katata, 2014; Hargis et al., 2019) influencing this resource partitioning, and (3) investigate potential trade-offs, as increments in soil resources via throughfall and stemflow might be sometimes achieved at the cost of leaching of nutrients from the plant canopy (Tukey, 1970). For example, in areas where atmospheric pollution is producing acid rain, fog, and dew (e.g., Paoletti et al., 1989; Turner & Tingey, 1990) foliar leaching can lead to plant nutrient deficiency (Igawa et al., 2002), especially of cations (e.g., Ca⁺², Mg⁺², K⁺, Mn⁺²), which are supposedly

exchanged by H^+ ions from leaching solutions (Tukey, 1970). Interestingly, acid fog and dew have stronger leaching power than acid rain, producing H^+ concentrations 10 to 100 times higher (Tukey, 1970).

The third way plants could divert atmospheric resources to the soil is via hydraulic redistribution of aerial-absorbed water (**Fig. 1F**). Such a reversal in the normal direction of flow can take place when root water potential exceeds (is less negative than) soil water potential, as plants can rehydrate more rapidly than the soil during occult precipitation events (Nadezhdina et al., 2010; Prieto et al., 2012). Using sap-flow methods that allow the detection of small and reverse flows (e.g., Burgess et al., 2001; Nadezhdina et al., 2010), studies have quantified this phenomenon (Burgess & Dawson, 2004; Cassana et al., 2016; Schreel et al., 2019; Zhang et al., 2019) and demonstrated that it can reach ca. 25% of the maximum daily transpiration rate in certain tree species (Eller et al., 2013). Most of those studies, however, have used methods that do not differentiate water released to the soil from water stored in fine roots (Eller et al., 2013; Cassana et al., 2016). Therefore, the costs and gains of water moving from the roots into the soil are still uncertain. On the one hand, an individual may lose water to neighbouring plants in competitive interactions. On the other hand, ‘leaked’ water may serve to remobilise nutrients from the rhizosphere (Prieto et al., 2012); thus, the plant could effectively trade water for nutrients, which would result in a competitive advantage, particularly in nutrient-limited environments. Quantifying root tissue water-storage capacity would enable estimates of the extent to which redistributed water remains in the roots versus being ‘lost’ to the soil.

The relative contribution of those direct versus indirect strategies for atmospheric-resources acquisition may differ among species and across sites, depending on characteristics of the (1) occult precipitation events (e.g., duration, frequency, intensity, and spatiotemporal variation; Dawson & Goldsmith, 2018; Binks et al., 2021); (2) vegetation (e.g., forest structure and plant individual traits related to interception, absorption, storage, and mobilisation of water; Fernández & Brown 2013; Eller et al., 2013; Matos et al., 2021); (3) soil type (e.g., texture, depth, and conductivity; Prieto et al., 2012); and (4) climate (e.g., air temperature, wind speed, topography; del-Val et al., 2006; Borthagaray et al., 2010). Nevertheless, few studies have investigated the combined influence of those factors on community ecology, as they either focus on a single

strategy of resource acquisition (Table S2), or quantify the total contribution of atmospheric resources to plant communities without discriminating between different strategies involved (e.g., Dawson, 1998; Scholl et al., 2011; Binks et al., 2019).

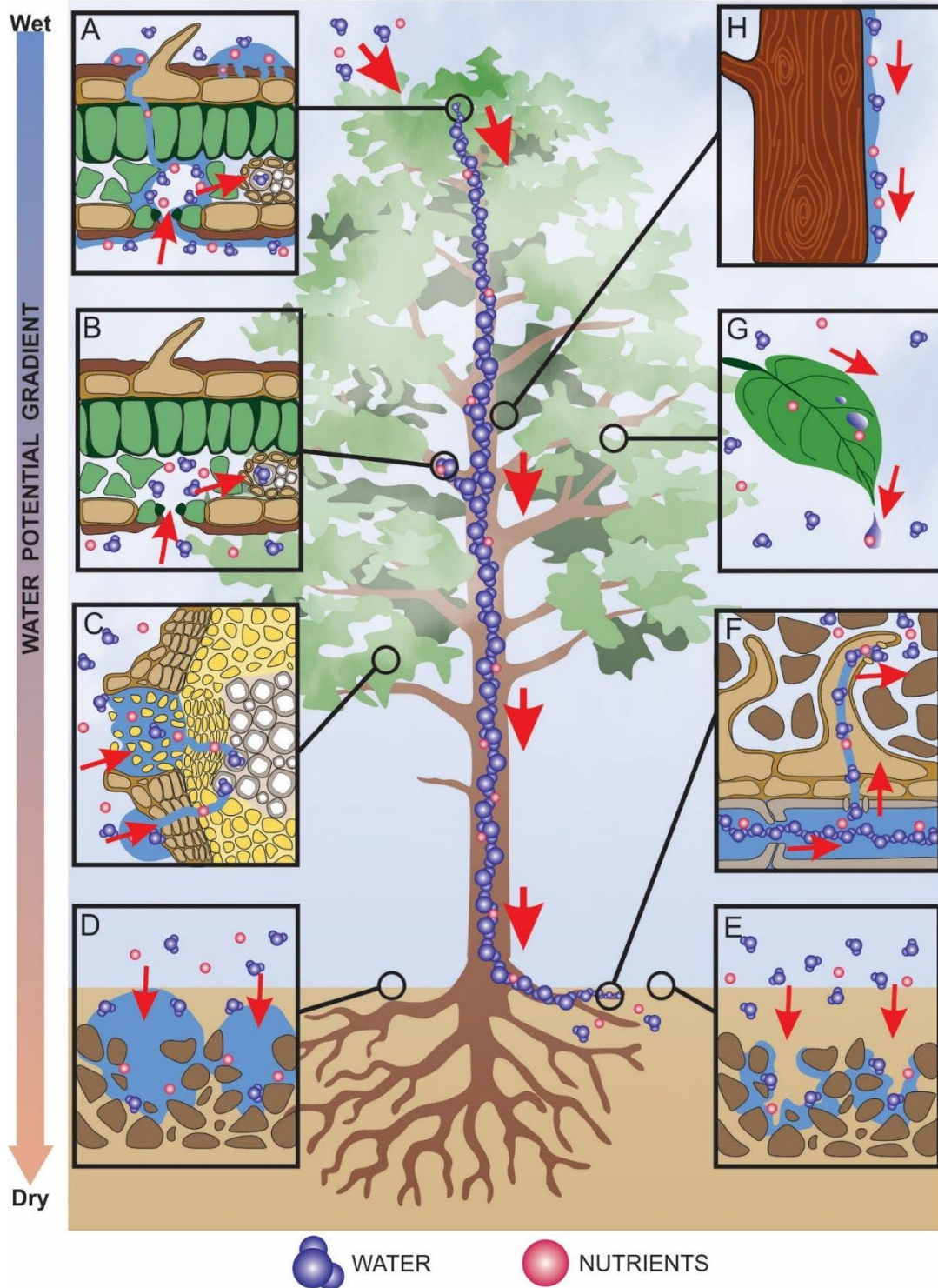


Figure 1. Direct (A-C) and indirect (D-H) strategies of atmospheric resources acquisition in ground-rooted plants. A. Foliar water/nutrient uptake: liquid water and soluble nutrients from the atmosphere enter the leaf through open stomata, cuticular pores, or other specialised structures. B. Foliar reverse transpiration: water vapour and gaseous nutrients from the air enter the leaf through open stomata. C. Stem bark water/nutrient uptake: liquid water and soluble nutrients from the atmosphere enter the stem bark through lenticels or hydrophilic capillary spaces. D. Soil dew condensation: water vapour from the air in contact with cold soil surfaces condenses to form dew. E. Soil water adsorption: water vapour from the air is adsorbed in soil pores forming liquid water. F. Root hydraulic redistribution of aerial-absorbed water: atmospheric water and nutrients absorbed by aerial organs is redistributed downwards to the roots and then may leak to the soil. G. Throughfall: atmospheric resources intercepted by plant aerial organs that exceed the canopy surface storage capacity drip-off to the soil. H. Stemflow: atmospheric resources intercepted by plant aerial organs are channelled over the trunk towards the soil.

How does accessing atmospheric resources contribute to hydrological niche segregation?

Several studies have shown that water and nutrients obtained from the atmosphere can increase whole-plant photosynthesis, growth, and survival rates (e.g., Eller et al., 2013; Berry et al., 2019; Weathers et al., 2020). These factors are also potentially important at the scale of ecosystem-level water and carbon budgets (Burgess & Dawson, 2004; Hildebrandt & Eltahir, 2007; Binks et al., 2019; Cavallaro et al., 2020). However, the extent to which access to atmospheric resources influences plant-plant interactions, and hence contributes to the hydrological niches and coexistence of ground-rooted plant species, is still largely unknown.

Silvertown et al. (2015) define hydrological niche segregation as the “(i) *partitioning of space on fine-scale soil-moisture gradients, (ii) partitioning of water as a resource through different acquisition strategies, and/or (iii) partitioning of recruitment opportunities among years caused by species specialising on particular patterns of temporal variance of water supply*”. Although this definition recognizes that niche partitioning can occur via different water-acquisition strategies, most of the studies conducted so far have only considered strategies related to soil-water acquisition, thus largely neglecting any potential role of the atmospheric axis. A literature review (**Appendix S1**) revealed that although many studies (N = 123) about hydrological niches published in the last 50 years (**Table S1**) were conducted in areas where the use of atmospheric resources by

ground-rooted plants has already been demonstrated (see **Fig. S1, Table S2**), only three of them (Liu et al., 2010; Schachtschneider & February, 2010; Francis et al., 2020) investigated strategies of atmospheric-resource acquisition.

We now present an expanded version of the HNS framework, which considers niche segregation of ground-rooting plants as occurring along both soil and atmospheric resource-axes, and involving both temporal and spatial resource partitioning.

Spatial hydrological niche segregation

One of the most influential examples of spatial niche segregation is the two-layer model (**Fig. 2A**; Schimper, 1898; Walter, 1939; Walker & Noy-Meir, 1982). Originally formulated to explain tree-grass coexistence in savannas, and later applied to many other vegetation types (Ward et al., 2013; Silvertown et al., 2015), this model suggests that although shallow-rooted grasses are superior competitors for water in the topsoil (second-layer), they can coexist with deep-rooted trees, because trees have exclusive access to the water stored in deeper soil layers (first-layer). In our expanded version of the HNS framework, we include a third layer, i.e., an atmospheric resource-axis, to account for ground-rooted plants' capacity to also obtain resources from occult precipitation events. In this three-layer model, interspecific differences in root distribution and in the capacity to exploit atmospheric resources can all contribute to niche partitioning (**Fig. 2B**).

Vascular epiphytes, particularly common in montane cloud forests (Bruijnzeel et al., 2011; Gotsch et al. 2015 Eller et al., 2020), are the classical example of plant functional type whose hydrological niche segregates exclusively along the third layer, i.e., completely disconnected from the soil resource-axis (Grisebach, 1872). Such plants display a variety of morpho-physiological traits to acquire, store, and conserve water and nutrients from rain, dew and fog (Hargis et al., 2019; Zotz et al., 2021). For example, bromeliads have evolved specialised foliar trichomes that enable aerial water uptake during fog events, while also preventing evaporation when the plant is exposed to dryer atmospheric conditions (Zotz, 2016; Raux et al., 2020). As a result of this dependency on the third layer, epiphytic biomass and diversity are frequently higher in humid montane forests characterised by frequent occult precipitation events and relatively low evaporative demand (Zotz, 2016). Another example of segregation along the atmospheric resource-axis comes from hyper-

arid areas, such as the Atacama and Namib deserts, where rainfall events are sporadic and may wet plant canopies, but rarely result in a substantial increase in soil moisture (Hill et al., 2015, 2021). Many ground-rooted plant species growing in such environments appear to obtain both water and nutrients primarily from fog and dew rather than from rainwater (e.g., del-Val et al., 2006; Hill et al., 2015; Gottlieb et al., 2019; but see Henschel et al., 2018).

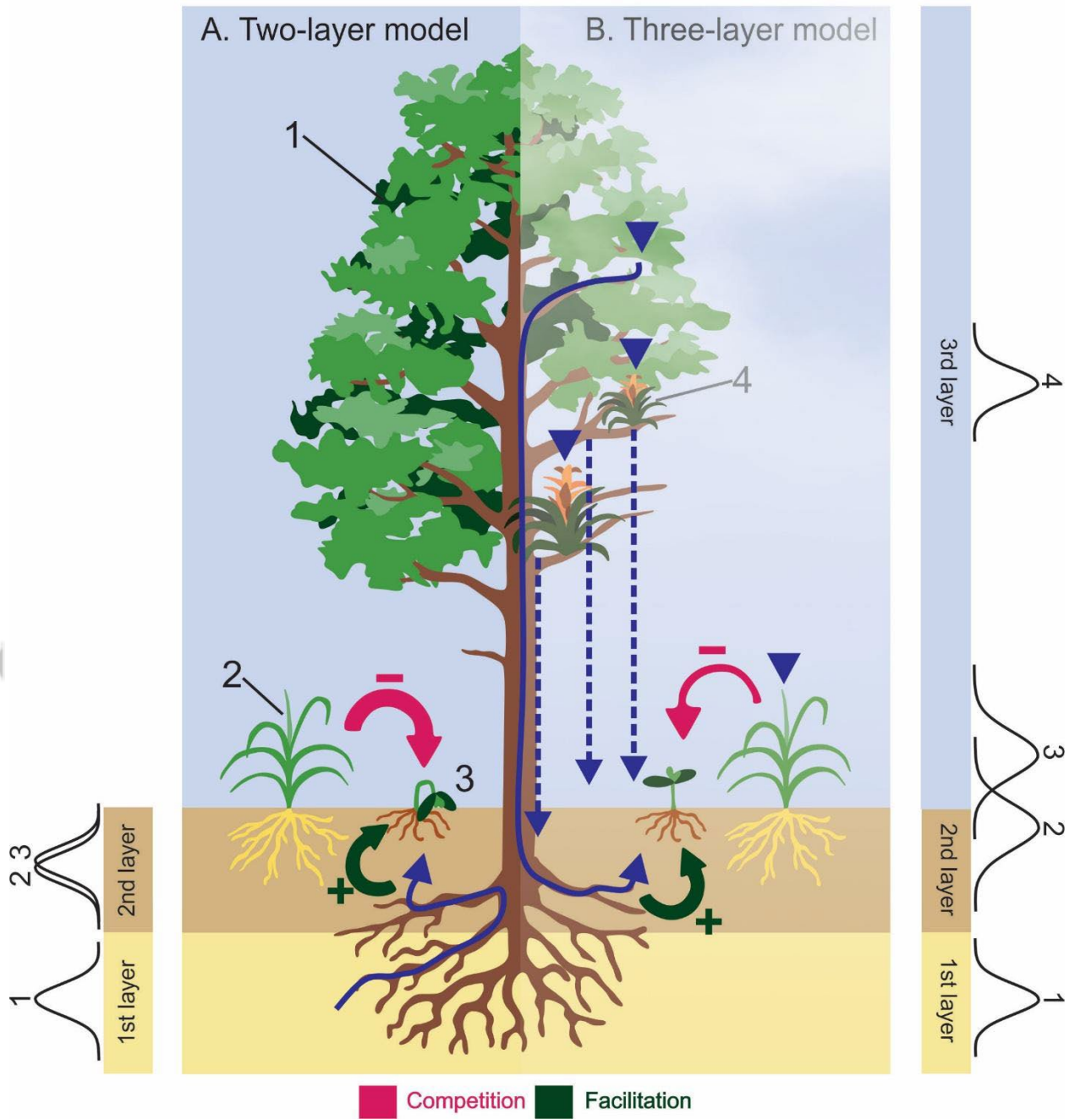


Figure 2. Two models of spatial hydrological niche segregation. (A) In the two-layer model, soil is the only source of water and nutrients for plants. Due to their exclusive access to deep-soil water (first-layer), deep-rooted trees (1) are able to coexist with shallow-rooted species (2-3). Shallow-rooted species compete strongly (thick pink arrow) for the topsoil water (second-layer), so only the superior competitive species (2) persists. However, species unable to directly access deeper soil layers, such as shallow-rooted seedlings (3) can be benefited (green arrows) by neighbouring species that remobilize resources from deep to shallow soil layers via hydraulic lift (blue solid arrow). (B) In the three-layer model, the resource-axis is expanded to include atmospheric water and nutrients (third-layer) from occult precipitation events. Some species (4) can persist in the community via their capacity to directly access atmospheric resources (blue triangles). Shallow-rooted species (2-3) may compete less strongly (thin pink arrow) for the topsoil water and hence may coexist in the community, as they can also obtain additional resources from the atmosphere. Moreover, species unable to directly access the third layer (3) can be benefited (green arrows) by neighbouring species that remobilize resources from the atmosphere to the soil either via hydraulic redistribution (blue solid arrow) or via stemflow and throughfall (blue dashed arrow). Curves (1-4) indicate species hydrological niche segregation along the three layers.

For most ground-rooted plant species, rather than being a primary source of water and nutrients, the third layer constitutes an additional resource-axis, which allows plants to temporarily and partially decouple themselves from belowground competition (**Fig. 2B**). Therefore, species more capable of acquiring atmospheric-resources may have a competitive advantage (for survival and growth), especially under conditions of low soil water availability (Eller et al., 2013; Schreel et al., 2019). Coastal redwood trees (*Sequoia sempervirens*), for example, are known to have relatively shallow roots, high levels of water stress due to their prodigious height (e.g., some > 100 m tall), and are consequently thought to be dependent on atmospheric water supply from summertime fog events (Burgess & Dawson, 2004). According to stable isotope-based estimates, 8–42% of the water used by redwood trees is acquired from fog (Dawson, 1998), possibly explaining their constrained distribution to fog-inundated coastlines (Francis et al., 2020). Redwood trees obtain fog-water either directly via foliar (Burgess & Dawson, 2004) and stem bark uptake (Earles et al., 2016), or indirectly via throughfall and stemflow (Dawson, 1998; Ewing et al., 2009). As a result, fog can contribute to more than 30% of the annual water input and up to

21% of the annual nitrogen inputs to the forest floor (Ewing et al., 2009; Templer et al., 2015; Earles et al., 2016). This increment in soil resources improves not only the redwood trees water and nutrient status but may well facilitate neighbour species. It has been shown that some understory plants (e.g., *Polystichum munitum*) are almost entirely dependent on fog-drip delivered to the forest floor by redwood trees (Dawson, 1998).

Similar positive interactions between fog-drip-producing trees (nurse or benefactor plants) and plant species growing beneath their canopies (beneficiary plants) have been reported in other plant communities, such as in fog-oases in the Atacama desert (Squeo et al., 2016; Sotomayor & Drezner, 2019) and coniferous forests in fog-inundated mountains (Rigg et al., 2002). Those facilitative effects might be particularly important for plant regeneration (Baguskas et al., 2016; del-Val et al., 2006) as without the benefactor species, seedling recruitment can be impaired by the strong competition for water in the topsoil. Hydraulic redistribution of aerial-absorbed water may play a similar positive role by increasing topsoil water content, comparable to the effects of hydraulic lift (i.e., the upward movement of water from deep-wet to shallow-dry soil layers via plant roots; Nadezhdina et al., 2010) by deep-rooting species. Although several studies have reported that plants exhibiting hydraulic lift can act as nurse species by aiding seedling recruitment during dry periods (Muñoz et al., 2008; Prieto et al., 2012), we are not aware of any study showing comparable positive effects via redistribution of atmospheric-sourced water.

Temporal hydrological niche segregation

Due to temporal variation in patterns of resource availability and/or in plant phenology, the relative competitive advantage of acquiring resources from a specific layer in the HNS model can shift over time, resulting in temporal niche segregation (e.g., Holdo, 2013; Schwinning & Kelly, 2013). For example, beyond the spatial root partitioning, tree-grass coexistence has an important temporal component in which shallow-rooted annual grasses are favoured during the wet growing season, while deep-rooted trees have the advantage during the dry season when grasses are dormant and rainfall water has recharged deep-soil layers (Schwinning & Kelly, 2013; Ward et al., 2013).

As occult precipitation events exhibit large daily, seasonal, and interannual variation (Berry et al., 2014; Dawson & Goldsmith, 2018; Bittencourt et al., 2019), which can differ from the temporal

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distribution of rainfall (Binks et al., 2021), differences in species' capacity to access the third layer may also contribute to temporal niche segregation. This contribution might be particularly important in plant communities where occult precipitation events coincide with soil dry periods, such as in Mediterranean coastal ecosystems (Burgess & Dawson, 2004; Corbin et al., 2005), temperate steppes (Cavallaro et al., 2020) and in the eastern Amazon Forest (Binks et al., 2021). In saline and freshwater wetlands, although soil water is abundant year-round, the excessive salinity or insufficient oxygenation levels in the soil can impair root water and nutrient uptake, thus likely increasing the relative advantage accrued via aerial uptake (Nguyen et al., 2017; Bryant, Fuenzalida, Zavafer, et al., 2021). In those ecosystems, the competitive advantage of accessing the third layer may vary seasonally, and possibly diurnally, according to the interaction between tidal flows and evaporative demand (Bryant, Fuenzalida, Brothers, et al., 2021). For instance, in coastal arid vegetations aerial uptake might be particularly important during the low-tide period when soil salinity levels are higher; while the opposite might be true in some tidal estuaries (e.g., mangroves), where high-tide can be associated with higher salt-water inputs. As high-tide periods in mangroves are also associated with higher risk of inundation of low hanging mature leaves and entire saplings, species in this environment may require ecologically appropriate foliar water uptake pathways (possibly involving active regulation; Bryant, Fuenzalida, Zavafer, et al., 2021) in order to benefit from occult precipitation events without leading to an unregulated ion entry into leaves.

The examples described above demonstrate that access to atmospheric resources can contribute to spatiotemporal partitioning of plant hydrological niches. However, the existence of distinct hydrological niches is not in itself evidence that niche segregation promotes species coexistence (Wilson, 2011). Confirmation of the main mechanisms leading to coexistence requires either experimental manipulation of resources, to demonstrate that coexistence depends upon the presence of spatiotemporal niche differences, or parameterization of community models that can be manipulated to determine which processes stabilise community composition (Silvertown et al., 2015). So far, experimental manipulations have used mesocosms composed of species with different rooting depths and subjected to varying levels of soil-water availability to assess the role of root partitioning in driving species coexistence (Bartelheimer et al., 2010). Future studies should expand those experiments to also investigate the role of atmospheric resources, by including treatments with different levels of atmospheric water and nutrient availability, in addition to

species with different strategies to access the atmospheric-resources axis. Likewise, modelling approaches that up to now have only used species' vertical rooting profiles and soil moisture dynamics to investigate soil water competition and species coexistence (Holdo, 2013; Letten et al., 2015) should be expanded to incorporate the complex atmospheric moisture dynamics and the different mechanisms of atmospheric-resource acquisition. Such models could also be used to better understand the impacts of climate and land-use changes on hydrological niche segregation.

How might climate and land-use changes affect hydrological niche segregation?

Climate change models predict a global increase in air temperatures and vapour pressure deficits (IPCC, 2021), which alter the conditions for fog, dew, and rain formation. Changes in hydrological regime have already been detected in some ecosystems, with trends of reduced dew formation in Mediterranean regions (Tomaszkiewicz et al., 2016), decreased summertime fog advection along coastlines (Johnstone & Dawson, 2010), altered rainfall seasonality in the tropics (Easterling, 2000), and a declining frequency of orographic fog in mountains due to the rise of the cloud ceiling height (Hu & Riveros-Iregui, 2016). Land-use changes are further impacting the atmospheric resource-axis, as deforestation can decrease both the occurrence of fog and dew events (Lawton et al., 2001) and the amount of atmospheric resources intercepted by the remaining vegetation (Dawson, 1998; Sotomayor & Drezner, 2019).

There is currently insufficient information on the individual- to species-level variation in the capacity to exploit atmospheric resources to make quantitative predictions about how such alterations in the third layer of the hydraulic model will influence species distribution and community composition. A few studies have indicated that species particularly reliant on aerial uptake for maintaining cell turgor may be at disproportionate risk of water stress as both the soil and atmosphere dries out (e.g., Eller et al., 2016; Matos et al., 2021). This is likely because such species currently benefit from occult precipitation events by having 'leaky' aerial organs, and so they are unable to prevent water loss under drought. Conversely, species that can more selectively obtain water from the atmosphere may receive proportionally more water via aerial uptake due to higher fluxes into aerial organs arising from increasingly negative plant water potentials under drier conditions (Breshears et al., 2008). Thus, as long as the frequency and intensity of occult precipitation events are not significantly reduced and the soil water stress is not severe enough to

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result in a blockage of the pathways used for aerial uptake (Berry et al., 2019), it is conceivable that for some species access to the third layer will increase, and contribute proportionally more to their water budget in the near future.

Changing hydrological regimes will also almost certainly influence the interactions between plants. But it is still unclear whether the degree to which hydrological niches are segregated would increase or decrease under drier conditions. Some studies using the classic two-layer model have shown that niche segregation for soil-water sources may become particularly evident as soil moisture declines (e.g., Volkmann et al., 2016; Brinkmann et al., 2018; Grossiord, 2020). In contrast, there is evidence that when soil resources are scarce, species that previously partitioned water and nutrient-use among different soil layers, or across different seasons, may converge on common sources (McLaughlin et al., 2017). More experimental studies are needed to evaluate how niche segregation along both soil and atmospheric resource-axes are responding to climate and land-use changes. For instance, mesocosm experiments combining species with different root distribution and different strategies of atmospheric-resources acquisition that monitor changes in species spatiotemporal niche segregation across water and/or nutrient availability gradients (in both soil and atmosphere) will be crucial to verify if niche overlap tends to increase or decrease as resources become more limiting, and whether there is a coordinated response along both resource-axes (i.e., soil and atmosphere). It is also uncertain how the outcome of interactions between benefactor-beneficiary plants, potentially mediated by hydraulic redistribution of aerial-absorbed water, would shift in response to the level of water stress that plants are exposed to. Although positive effects are usually observed when plants experience some extent of stress (e.g., greater water stress can lead to higher rates of aerial uptake due to an increased water potential gradient), highly stressful conditions may result in the collapse of facilitative interactions (Holmgren & Scheffer, 2010), which may impair seedling recruitment and decrease the long-term capacity of plant communities to regenerate after drought (Michalet et al., 2006).

Conclusion

Our expanded version of the HNS framework potentially provides a more complete understanding of the underlying mechanisms structuring plant communities in response to resource acquisition.

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It emphasises that, beyond the classical conception of supply from the soil, the hydrological niche of many ground-rooted plants extends into the atmospheric-axis, thus contributing to niche spatiotemporal segregation. The access to atmospheric resources influences not only the water and nutritional status of the individual plant but, importantly, may also impact the interactions (competitive or facilitative) with neighbouring species. We identify the following topics as research priorities to enable further understanding of how HNS will interact with future climate regimes to influence ecological communities:

- (1) Standardise a method for measuring conductance to aerial uptake in order to compare species and to model changes in uptake relative to water supply and demand;
- (2) Identify which plant traits favour direct versus indirect strategies of atmospheric resources acquisition;
- (3) Quantify the relative contribution of direct versus indirect strategies to water and carbon budgets in different vegetation types under current and future climate scenarios.
- (4) Investigate how alterations in the frequency and intensity of occult precipitation events influence trade-offs between aerial water uptake/loss and nutrient acquisition/leaching.
- (5) Examine whether the hydraulic redistribution of aerial-absorbed water can lead to facilitative interactions, and how those interactions may shift under different levels of water stress.
- (6) Incorporate the atmospheric-resource axis into experimental manipulations and models of hydrologic niche segregation.

Addressing these questions will provide fundamental insights into the structuring of ecological communities with implications to land management and understanding the impacts of climate change on terrestrial plant communities.

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Conflict of Interest

We have no conflict of interest to declare.

Authors' contributions

I.S.M. drafted the manuscript and prepared the figures. All authors provided supplementary ideas, contributed critically to the drafts, and gave final approval for publication.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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Supplementary Material

Appendix S1. Literature on hydrological niches and on atmospheric resource-use by plants: data search, inclusion criteria, metadata extraction, and preliminary results.

Table S1. List of 123 studies that investigated hydrological niches in plant communities and their associated metadata.

Table S2. List of 156 studies that reported the use of atmospheric resources by vascular plants and their associated metadata.