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MINI REVIEW

The Plant Ecology of Nature-Based Solutions

Plant traits, microclimate temperature and humidity: A research agenda for advancing nature-based solutions to a warming and drying climate

A. J. Wright[1] | R. M. Francia[2]

[1]Department of Biological Sciences, California State University Los Angeles, Los Angeles, California, USA
[2]Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois, USA

Correspondence
A. J. Wright
Email: awrigh20@calstatela.edu

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Abstract

1. Climate models predict at least another 1.5°C warming in the next 75 years. This warming drives increased atmospheric drying and a global increase in the severity and duration of ecological drought. Vegetation has the capacity to reduce microclimate temperatures and atmospheric aridity.
2. All species of plants create shade, move water, evapotranspire, humidify the air around them, and affect the temperature and vapour pressure deficit of the environment. Vegetation can thus act as a nature-based solution to warming and atmospheric drying.
3. These microclimate modifications likely depend on the traits, functional groups and diversity of the plant community. Vegetative feedbacks on microclimate are strong enough to buffer some plants against the negative impacts of warming and drying (e.g. facilitation).
4. *Synthesis*: Here we present, for the first time, a trait-based framework that can be applied across study systems for assessing microclimate temperature and humidity under vegetation. This framework includes multiple new hypotheses for future work in this area. We emphasize that a systematic examination of trait–microclimate relationships will enable us to use vegetation as a nature-based solution to warming and atmospheric drying in a changing climate.

KEYWORDS
diversity, facilitation, feedbacks, humidity, nature-based solutions, temperature, vegetative microclimate, VPD

1 | CLIMATE CHANGE AND VEGETATIVE BUFFERING

Anthropogenic climate change has already caused more than 1.1°C warming since the beginning of the industrial revolution (Lenssen et al., 2019). Current climate models predict a further increase of at least 1.5°C before the end of this century (IPCC, 2021). Climate warming has deleterious effects on many individual plants, communities, and ecosystems (Walther, 2010). More specifically, warming reduces productivity in tropical and some temperate regions (Boisvenue & Running, 2006) and can drive shifts in plant community composition, dominance and diversity of ecosystems

(Wright et al., 2018). Even when warming leads to increases in productivity, temperature changes drive species outside their temperature optima and alter competitive hierarchies within communities (Niskanen et al., 2019; Parmesan & Yohe, 2003; Richter et al., 2022). Some species may be driven extinct by warming temperatures (IPBES, 2019) and this can ultimately lead to ecosystem type transitions as dominant species shift from one type to another (e.g. from forests to non-forests following a change in wildfire regime, Coop et al., 2020).

Beyond this, warming temperatures also increase the water holding capacity of the atmosphere and accelerate the water cycle (Zhou et al., 2019). Recent work demonstrates that increased temperatures are decreasing relative humidity and increasing the vapour pressure deficit (VPD) of the atmosphere (Novick et al., 2024). Plants usually respond to rising VPD by closing their stomata, which can limit carbon capture and decrease productivity of ecosystems, sometimes even when soil moisture is not limiting (Fu et al., 2022; Schönbeck et al., 2022). While precipitation is expected to shift globally, resulting in some areas receiving less rainfall and some areas receiving more (IPCC, 2021), VPD is increasing at a global scale (Yuan et al., 2019). Increased VPD can also drive changes in agricultural yields (López et al., 2021), species composition (Wang & Wen, 2022), species diversity (Aguirre-Gutiérrez et al., 2020) and wildfire risk (Rao et al., 2022). Both warming and atmospheric drying pose large-scale risks for the systems upon which humans depend.

While technological solutions to warming and drying are a major area of policy concern, ecologists have proposed natural climate solutions or "nature-based solutions" as a ready-made approach to mitigate the future consequences of climate change (Fargione et al., 2018; Griscom et al., 2017). Nature-based solutions include restoration, conservation and other land management strategies that can be applied to increase carbon capture to mitigate future global warming (Fargione et al., 2018). While most nature-based solutions are focused on carbon capture, vegetation can also be used as a nature-based solution to directly mitigate warming (Chakraborty et al., 2022) and atmospheric drying (Ellison et al., 2024).

There is now widespread evidence that vegetation modifies microclimate temperatures in every ecosystem on earth (Lembrechts et al., 2020). Data from eddy covariance flux tower networks support these claims in terms of vegetative effects on temperature and relative humidity, and thus VPD as well (Novick & Barnes, 2023). More specifically, plants can reduce local temperatures by as much as 10–20°C (usually in warmer temperate ecosystems) and increase local temperatures by up to 10°C (usually in colder ecosystems and at higher latitudes, DeFrenne et al., 2019; Lembrechts et al., 2020). Beyond this, plants can also increase humidity of the microclimate by over 10% in grasslands (Wright et al., 2015), and potentially more in forests (Anderegg et al., 2018; Barbera et al., 2023). These changes in temperature and humidity can lower the VPD of the microclimate by up to 1.5 kPa in grasslands (Wright et al., 2015) and over 2 kPa in forests (Barbera et al., 2023).

2 | MECHANISMS FOR PLANT TEMPERATURE AND HUMIDITY MODIFICATIONS

The theory that links plant morphology to near-surface temperature and VPD is nearly 30 years old (Geiger et al., 1995). Specifically, plants affect microclimates through two classes of mechanisms: (1) sensible heat flux: the physical structures of leaves, branches, stems and canopies can either increase or decrease the rate of heat exchange between the atmosphere and vegetation. Plants can create shade (blocking surface irradiation), absorb solar radiation proportional to leaf area and albedo, and block or increase turbulent wind (Figure 1, Table 1). (2) Latent heat flux: plants also modify the microclimate through evaporative cooling. Plants can move water from the soil and cool the air around them as they transpire this water from their leaves. Rates of transpiration for an individual or a community can vary, likely due to changes in functional composition, functional diversity and species-specific traits (e.g. leaf area, stomatal density, stomatal responses to heating or drying, rates of surface evaporation, and rooting depth; Figure 1, Table 1).

Despite a strong theoretical underpinning, and an emerging body of evidence demonstrating the degree of microclimate temperature, humidity and VPD modification that happens below vegetation, there is not yet a framework that pairs the strength of microclimate modification with particular plant functional traits. In fact, to our knowledge there are only a handful of studies that specifically examine plant traits and how they affect microclimate temperature or VPD (Bruner et al., 2023; Gao et al., 2022; Guimarães-Steinicke et al., 2021; Mallen-Cooper et al., 2021; Richter et al., 2022; Zhang et al., 2022). There are several recent studies that examine the inverse relationship (e.g. how microclimate conditions can drive changes in plant traits, Govaert et al., 2024; Kemppinen & Niittynen, 2022), though this is not what we explore here. There is also a larger focus on plant traits or species-specific temperature relationships in urban contexts (Speak et al., 2020), but these studies usually focus on management regimes (e.g. asphalt + tree vs. lawn + tree), as opposed to advancing a universal trait-based framework that can be applied as a nature-based solution to climate change across study systems.

To advance such a framework, we review recent literature on microclimate effects under particular plant functional groups or ecosystem types (e.g. shrublands, forests and grasslands). This research, often utilizing data from flux tower networks, has allowed for broad cross-ecosystem comparisons that yield empirical insights into how different types of vegetation can affect temperature and humidity (Ellison et al., 2024; Lin et al., 2022; Novick et al., 2024; Novick & Barnes, 2023; Schlesinger & Jasechko, 2014; van Heerwaarden & Teuling, 2014). These authors *hypothesize* underlying trait relationships that may explain why, for instance, grasslands cool microclimates less than forests. However, this work again does not explicitly or experimentally examine the impact of species-specific traits on microclimate conditions. We emphasize that this type of trait-based work will be essential if we want to utilize and manage plants as a

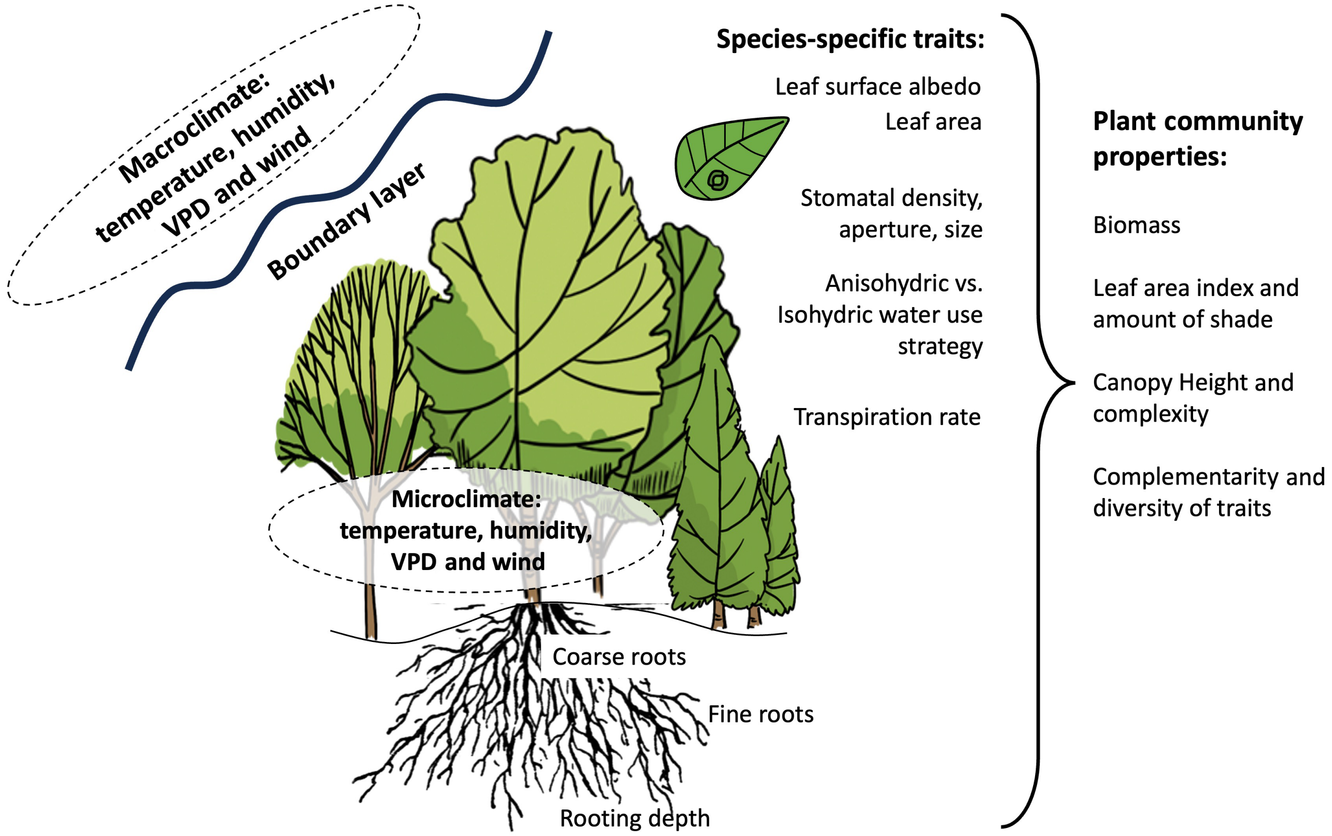

FIGURE 1 Microclimate cooling, humidification, and modification of vapour pressure deficit under vegetation is driven by plant functional traits (e.g. stomatal traits, transpiration and rooting depth), functional types (e.g. grasses vs. trees) and community properties (e.g. biomass production, leaf area index and trait complementarity).

nature-based solution to warming and drying. We combine this research with data from a small number of trait-based studies, to propose a trait-based framework for examining vegetative microclimates. Many of these trait-based relationships are not yet tested, and instead should serve as a research agenda for testing novel hypotheses about how plants, and plant communities, affect microclimate temperatures and VPD.

3 | DIFFERENCES IN MICROCLIMATE EFFECTS BETWEEN PLANT FUNCTIONAL TYPES, COMMUNITIES AND BIOMES

Overall, vegetative effects on microclimate temperature, humidity and VPD are likely stronger in forests, and weaker in grasslands and croplands (Novick & Barnes, 2023, Table 1). Within shrublands, microclimate effects are likely strongly dependent on water availability and whether the shrublands are open or closed-canopy (Lortie et al., 2022). Within forests, microclimate effects will differ between coniferous and deciduous forests (Balandier et al., 2022; Muller et al., 2021), depending on the composition and diversity of traits described throughout this paper (e.g. Richter et al., 2022), and depending on macroclimate context (DeFrenne et al., 2019). Because vegetative effects on microclimate temperature and VPD can be divided into sensible heat flux (direct heat exchange) and latent heat flux (changes in temperature due to evapotranspiration), we propose a framework that also divides plant traits into latent heat flux traits and sensible heat flux traits, though there are undoubtedly some traits that fall into both categories (Table 1, Muller et al., 2021; Novick & Barnes, 2023; Richter et al., 2022).

For example, on average, forests have higher leaf area index (LAI) than grasslands (Asner et al., 2003; Hill et al., 2006), this means greater surface area through which solar radiation can be absorbed and thus greater warming of the upper canopy (sensible heat flux). This can also be associated with greater shading and thus cooling of the lower canopy (Muller et al., 2021; Richter et al., 2022, more on canopy position below). Similarly, crown diameter and canopy height will affect the amount of light intercepted (and solar radiation absorbed), the degree to which air is trapped by vegetation and the amount of shade cast on the ground (Guimarães-Steinicke et al., 2021; Mallen-Cooper et al., 2021; Speak et al., 2020), thus also affecting sensible heat flux (Table 1). Leaf albedo also affects microclimate cooling (e.g. Speak et al., 2020), as plants with darker coloured leaves and thus lower albedo will absorb more solar radiation and be warmed more by the sun (Hollinger et al., 2010; Mallen-Cooper et al., 2021, Table 1).

Traits associated with greater water movement and thus latent heat flux may also shift in predictable ways between plant functional

TABLE 1 There is an abundance of research on the ecosystem types that influence latent and sensible heat flux, though the traits that drive these differences are mostly not yet examined with empirical work.

	Traits and system descriptions	Bareground	Forest	Grassland	Shrubland	Citations
Sensible heat flux traits	Albedo	Lowest (darkest surfaces)	Medium	High	Highest (lightest surfaces)	Hollinger et al. (2010)[a] and Mallen-Cooper et al. (2021)[a]
	LAI	—	Highest	Low	Low	Hill et al. (2006)[b], Asner et al. (2003)[b]; Guimarães-Steinicke et al. (2021)[a]
	Aerodynamic resistance	None	Highest	Low	Low	Rigden et al. (2018)[b]
	Canopy height	—	Highest	Lowest	Medium	Speak et al. (2020)[a], Mallen-Cooper et al. (2021)[a] and Guimarães-Steinicke et al. (2021)[a]
	Crown diameter/shade cast	None	Highest	Lowest	Lowest	Speak et al. (2020)[a], Richter et al. (2022)[a], Zhang et al. (2022) and Mallen-Cooper et al. (2021)[a]
	Sensible heat flux	Lowest	Medium	Low	Highest	Lin et al. (2022)[b]
Latent heat flux traits	Stomatal sensitivity to drought	—	Fast closure	Slow closure	Medium	van Heerwaarden and Teuling (2014)[b] and Teuling et al. (2010)[b]
	Transpiration	—	Highest on average	Lower, but can be higher during drought	Lower	Schlesinger and Jasechko (2014)[b], Gao et al., 2022[b], Mallen-Cooper et al. (2021)[a] and Bruner et al. (2023)[a]
	Sap flow					Richter et al. (2022)[a]
	Evaporation	Highest	Low	High	Low	Schlesinger and Jasechko (2014)[b], Gao et al. (2022)[b] and Mallen-Cooper et al. (2021)[a]
	Rooting depth	—	Depends on water limitation	Depends on water limitation	Deepest (in Mediterranean regions	Schenk and Jackson (2002)[b] and Fan et al. (2017)[b]
	Stomatal density/aperture/size	—	Medium	Lowest, but increases with increasing light	Medium	Kelly and Beerling (1995) and Muir (2018)[b]
	Latent heat flux	Lowest	Highest, especially for broadleaf forests, except during short-term drought	Medium, except during short-term drought	Lowest	van Heerwaarden and Teuling (2014)[b] and Lin et al. (2022)[b]

Note: This table is a first attempt at identifying trait relationships that are hypothesized in the literature, organizing these traits into sensible and latent heat flux categories, and associating these traits into predictions based on ecosystem type. The listed citations relate to two categories of studies.

[a] Trait-based studies that associate plant traits to microclimate cooling or humidifying.

[b] Studies that examine how particular traits vary by ecosystem type (but not necessarily any link to microclimate temperature or humidity).

groups (Mallen-Cooper et al., 2021), though these types of traits are underrepresented in global trait databases (Flo et al., 2021). Some shrubs may transpire more water than herbaceous species, and past work has shown that this is associated with greater microclimate cooling (Bruner et al., 2023). During dry periods, or in water-limited soils, rooting depth can affect transpiration rates (Li et al., 2021) and thus likely also affects cooling and humidification of the microclimate. Past work has shown differences in average rooting depth between ecosystem types (Fan et al., 2017; Schenk & Jackson, 2002, Table 1), though, to date there have been no experimental examinations of the relationship between rooting depth and microclimate cooling.

Stomatal traits and drought response strategies will also play a role in microclimate temperature and VPD effects. For example, grasslands may be able to cool the microclimate via transpiration more efficiently than deciduous forests during a heatwave (Teuling et al., 2010). This is attributed to differences in stomatal behaviour wherein herbaceous species can sometimes maintain higher stomatal conductance despite water stress (anisohydricity, Teuling et al., 2010). Conversely, most deciduous tree species respond rapidly to water stress by closing their stomates (isohydricity). During non-heatwave events, and when soil moisture is not limiting, average transpiration and the latent cooling effects of grasslands versus forests are often reversed (Lin et al., 2022). Stomatal density, aperture and size could thus also affect microclimate cooling and humidifying effects under different vegetation types. While past work has proposed differences in stomatal density between ecosystem types (e.g. Muir, 2018), there are no studies examining how variation in stomatal traits affects microclimate cooling via latent heat flux.

The cooling effects of vegetation also vary strongly depending on position within a plant canopy. Canopy leaf surface temperatures tend to be higher than the surrounding air due to the absorption of solar radiation by the leaf surface (Muller et al., 2021). Canopy leaf surface cooling is thus important, and improved by factors that increase mixing between the macroclimate air and the boundary layer air (Muller et al., 2021). Conversely, understorey air and leaf surface temperature can be cooler than the surrounding air (controlling for distance from the ground surface) due to shade cast by the overstorey and evaporative cooling due to transpiration (Richter et al., 2022; Wright et al., 2014). In these understorey conditions, larger and less turbulent boundary layers can protect cooler and more humid conditions from getting remixed into macroclimate bodies of air (Meinzer, 1993). Forests tend to have larger boundary layers than grasslands, and thus greater decoupling of microclimate conditions between the understorey and macroclimate air. This also indicates that anything driving greater decoupling of the macroclimate and microclimate could potentially lead to greater vegetative effects on air temperatures (Figure 1).

Diversity of functional traits also affects microclimate cooling and humidification. In grasslands, past work has shown that cooler microclimate temperatures in higher diversity communities are strongly driven by LAI and mean canopy height which both increase with increasing herbaceous species diversity (Guimarães-Steinicke et al., 2021). Higher diversity herbaceous communities may be able to decrease microclimate temperatures by up to 2°C, increase relative humidity of the microclimate by 10% and decrease understorey VPD by 1.5 kPa (Wright et al., 2014, 2015, 2021). These effects are strongest on hot/dry days (Wright et al., 2014). These effects are also emergent and do not appear to be merely the additive result of individual species traits (Mallen-Cooper et al., 2021; Wright et al., 2021). Within and among forests, diversity of plant hydraulic traits, particularly those that affect water transport are better at decoupling forest microclimates from macroclimate conditions during drought (Anderegg et al., 2018). Experimental forests and natural variation in older forests can drive changes in microclimate conditions: higher diversity forests can be up to 1.5°C cooler than lower diversity forests (Zhang et al., 2022), and forest management type (e.g. clear cutting vs. gap cutting) can change microclimate RH by 2% (Kovács et al., 2020).

4 | VEGETATIVE FEEDBACKS ON OTHER PLANTS: FACILITATION IN A CHANGING CLIMATE

Facilitative effects between plant neighbours have been examined across a broad range of ecosystems and positive interaction types (e.g. legume effects, mycorrhizal associations, plant–pollinator networks). However, the facilitative effects of vegetative microclimate temperature and humidity on plant neighbours are not widely examined (reviewed in Brigham & Suding, 2023). It is clear that plants affect the microclimate, and microclimate effects on temperature and humidity are stronger at hotter sites (DeFrenne et al., 2019) and when the macroclimate is drier (Wright et al., 2015). But for those constituent species that are growing in the cooler or more humid conditions provided by trees, shrubs or herbaceous species, how do microclimate conditions feedback and affect plant performance? There is an exceedingly small number of studies that examine plant microclimates and their impacts on neighbouring plant performance (Brigham & Suding, 2023).

DeFrenne et al. (2013) demonstrated how denser forests may buffer against understorey warming and can thus protect cool-adapted species from extirpation as the macroclimate warms. In Minnesota, USA, higher diversity grasslands decreased the VPD of the microclimate and this fed back and improved growth and water status of small tree seedlings (Wright et al., 2014, 2015). Similar patterns have been shown for focal grass species (*Poa secunda*) growing in higher diversity native grass communities in the Mediterranean climate of southern California (Aguirre et al., 2021). Filazzola et al. (2017) demonstrated that mid-day temperatures under shrubs in southern California could be over 5°C cooler than in open micro-sites, with over 10% increases in RH. This was associated with increases in the abundance of desert benefactor species (mostly small herbaceous species), suggesting positive facilitative effects near neighbours. Maestre et al. (2001)

demonstrated that 1–3°C cooling under grass tussocks, in a semi-arid steppe, was associated with less negative leaf water potential and higher survival for shrub seedlings planted under the canopy of grasses. Abdallah et al. (2016) demonstrated that 4°C cooling and a decrease of 4 kPa VPD under savanna trees in Tunisia was associated with a fourfold increase in herbaceous understorey growth. While these results are compelling, they are not numerous. Future work should focus on the role of facilitation due to vegetative cooling and humidifying for structuring plant community composition and diversity in a warming and drying climate (Brigham & Suding, 2023).

5 | CONCLUSIONS

Vegetation has the capacity to be a nature-based solution to the warming and atmospheric drying effects of climate change. We caution that many traits are a product of their environment (as well as feeding back and affecting their environment); thus selecting species with particular traits is not something that can be done by simply moving any species from one ecoregion to another. For example, many sage scrub species have a high albedo, likely due to evolutionary pressures that favoured lighter leaves that can stay cooler in Mediterranean climates (e.g. Martin-Sanchez et al., 2024). Due to these evolutionary forces, some ecoregions will have an inherent capacity for greater microclimate effects than others. Further, species not ecologically suited to a particular ecoregion should not be planted in unsuitable habitats due merely to their microclimate cooling or humidifying capacity.

Barring this, the specific degree of cooling and humidification depends on shading, absorption of solar radiation, insulation and evapotranspiration. This means that plant functional groups, traits, community properties and environmental conditions (e.g. soil moisture) control the strength of vegetative microclimate effects. However, more work is needed to make these effects prescriptive: we do not yet know which species, traits or communities could be best applied to provide a certain set of microclimate modifications in a given environment. Here we present a trait-based framework for studying vegetative effects on microclimate temperature and humidity. To advance a research agenda, we have identified the following trait-based questions that have strong theoretical underpinnings, but little to no examination in the published literature:

1. How does rooting depth affect microclimate cooling and humidification? How does rooting depth interact with precipitation, temperature and VPD to affect microclimates?
2. How do stomatal density, aperture and size influence microclimate cooling and humidification?
3. How do anisohydric versus isohydric drought strategies affect microclimate temperature and humidity? Do herbaceous species have the capacity to cool microclimates more than woody species during drought (e.g. van Heerwaarden & Teuling, 2014)?
4. What proportion of microclimate effects are due to latent versus sensible heat flux? How much does this vary by ecosystem type? How much does this vary as a result of particular functional traits?
5. At the whole community level, do multiple traits (e.g. aerodynamic resistance, mean canopy height, LAI and crown diameter) contribute to canopy complexity? Does whole community canopy complexity help explain differences in microclimate cooling and VPD? Do these canopy complexity-microclimate relationships vary based on precipitation, temperature and VPD in different regions?
6. How much does the built environment in cities modify these trait relationships?

We also identify other areas where some research has been conducted, but more empirical trait-based work is needed:

1. For traits like albedo, LAI, canopy height, crown diameter, transpiration and evaporation, how do these traits and the trait-microclimate relationships vary by ecoregion, species composition and species diversity?
2. There is evidence for emergent effects of diversity on microclimate humidity and VPD (though not as much evidence for microclimate temperature, Mallen-Cooper et al., 2021; Wright et al., 2021). Do diverse traits explain these relationships, or is there a form of trait complementarity that is needed to explain how diverse plant communities are uniquely capable of ameliorating microclimate conditions?

We present this research agenda as a way to move the field of community ecology forward, and also identify practical recommendations for how to use vegetation as a nature-based solution to a warming and drying climate.

AUTHOR CONTRIBUTIONS

A. J. Wright and R. M. Francia conceived the idea, outlined the paper and contributed substantially to revisions. A. J. Wright wrote the first draft of paper. R. M. Francia conducted a thorough literature review for the paper.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to report.

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DATA AVAILABILITY STATEMENT

This mini-review did not use data.

ORCID

A. J. Wright https://orcid.org/0000-0002-5205-8576
R. M. Francia https://orcid.org/0000-0002-6612-4239

REFERENCES

Abdallah, F., Michalet, R., Maalouf, J., Ouled-Dhaou, S., Touzard, B., Noumi, Z., & Chaieb, M. (2016). Disentangling canopy and soil effects of a savanna tree species on its understorey. *Journal of Vegetation Science*, *27*(4), 771–779. https://doi.org/10.1111/jvs.12402

Aguirre, B. A., Hsieh, B., Watson, S. J., & Wright, A. J. (2021). The experimental manipulation of atmospheric drought: Teasing out the role of microclimate in biodiversity experiments. *Journal of Ecology*, *109*(5), 1986–1999. https://doi.org/10.1111/1365-2745.13595

Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S. L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T. R., Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemińska, K., Phillips, O. L., & Oliveras, I. (2020). Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity. *Nature Communications*, *11*(1), 3346. https://doi.org/10.1038/s41467-020-16973-4

Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K., Bowling, D. R., Gabbitas, R., Karp, D. S., Pacala, S., Sperry, J. S., Sulman, B. N., & Zenes, N. (2018). Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, *561*(7724), 538–541. https://doi.org/10.1038/s41586-018-0539-7

Asner, G. P., Scurlock, J. M. O., & Hicke, J. A. (2003). Global synthesis of leaf area index observations: Implications for ecological and remote sensing studies. *Global Ecology and Biogeography*, *12*(3), 191–205. https://doi.org/10.1046/j.1466-822x.2003.00026.x

Balandier, P., Gobin, R., Prévosto, B., & Korboulewsky, N. (2022). The contribution of understorey vegetation to ecosystem evapotranspiration in boreal and temperate forests: A literature review and analysis. *European Journal of Forest Research*, *141*(6), 979–997. https://doi.org/10.1007/s10342-022-01505-0

Barbera, I., Paritsis, J., Ammassari, L., Morales, J. M., & Kitzberger, T. (2023). Microclimate and species composition shape the contribution of fuel moisture to positive fire-vegetation feedbacks. *Agricultural and Forest Meteorology*, *330*, 109289. https://doi.org/10.1016/j.agrformet.2022.109289

Boisvenue, C., & Running, S. W. (2006). Impacts of climate change on natural forest productivity—Evidence since the middle of the 20th century. *Global Change Biology*, *12*(5), 862–882. https://doi.org/10.1111/j.1365-2486.2006.01134.x

Brigham, L. M., & Suding, K. N. (2023). Cross-scale facilitation: A framework for microclimate moderation of climate change. *Oikos*. https://doi.org/10.1111/oik.10241

Bruner, S. G., Palmer, M. I., Griffin, K. L., & Naeem, S. (2023). Planting design influences green infrastructure performance: Plant species identity and complementarity in rain gardens. *Ecological Applications*, *33*, e2902. https://doi.org/10.1002/eap.2902

Chakraborty, T., Biswas, T., Campbell, L. S., Franklin, B., Parker, S. S., & Tukman, M. (2022). Feasibility of afforestation as an equitable nature-based solution in urban areas. *Sustainable Cities and Society*, *81*, 103826. https://doi.org/10.1016/j.scs.2022.103826

Coop, J. D., Parks, S. A., Stevens-Rumann, C. S., Crausbay, S. D., Higuera, P. E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B. M., Davis, K. T., Dobrowski, S., Falk, D. A., Fornwalt, P. J., Fulé, P. Z., Harvey, B. J., Kane, V. R., Littlefield, C. E., Margolis, E. Q., … Rodman, K. C. (2020). Wildfire-driven Forest conversion in Western North American landscapes. *BioScience*, *70*(8), 659–673. https://doi.org/10.1093/biosci/biaa061

DeFrenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(46), 18561–18565. https://doi.org/10.1073/pnas.1311190110

DeFrenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*(5), 744–749. https://doi.org/10.1038/s41559-019-0842-1

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. In S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, … C. N. Zayas (Eds.), *IPBES secretariat* (p. 56). Bonn, Germany. https://doi.org/10.5281/zenodo.3553579

Ellison, D., Pokorný, J., & Wild, M. (2024). Even cooler insights: On the power of forests to (water the earth and) cool the planet. *Global Change Biology*, *30*(2), e17195. https://doi.org/10.1111/gcb.17195

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(40), 10572–10577. https://doi.org/10.1073/pnas.1712381114

Fargione, J. E., Bassett, S., Boucher, T., Bridgham, S. D., Conant, R. T., Cook-Patton, S. C., Ellis, P. W., Falcucci, A., Fourqurean, J. W., Gopalakrishna, T., Gu, H., Henderson, B., Hurteau, M. D., Kroeger, K. D., Kroeger, T., Lark, T. J., Leavitt, S. M., Lomax, G., McDonald, R. I., … Griscom, B. W. (2018). Natural climate solutions for the United States. *Science Advances*, *4*(11), eaat1869. https://doi.org/10.1126/sciadv.aat1869

Filazzola, A., Liczner, A. R., Westphal, M., & Lortie, C. J. (2017). The effect of consumer pressure and abiotic stress on positive plant interactions are mediated by extreme climatic events. *New Phytologist*, *217*(1), 140–150. https://doi.org/10.1111/nph.14778

Flo, V., Martínez-Vilalta, J., Mencuccini, M., Granda, V., Anderegg, W. R. L., & Poyatos, R. (2021). Climate and functional traits jointly mediate tree water-use strategies. *New Phytologist*, *231*(2), 617–630. https://doi.org/10.1111/nph.17404

Fu, Z., Ciais, P., Prentice, I. C., Gentine, P., Makowski, D., Bastos, A., Luo, X., Green, J. K., Stoy, P. C., Yang, H., & Hajima, T. (2022). Atmospheric dryness reduces photosynthesis along a large range of soil water deficits. *Nature Communications*, *13*(1), 989. https://doi.org/10.1038/s41467-022-28652-7

Gao, G., Wang, D., Zha, T., Wang, L., & Fu, B. (2022). A global synthesis of transpiration rate and evapotranspiration partitioning in the shrub ecosystems. *Journal of Hydrology*, *606*, 127417. https://doi.org/10.1016/j.jhydrol.2021.127417

Geiger, R., Aron, R. H., & Todhunter, P. (1995). The climate near the ground. https://doi.org/10.1007/978-3-322-86582-3

Govaert, S., Meeussen, C., Vanneste, T., Bollmann, K., Brunet, J., Calders, K., Cousins, S. A. O., Pauw, K. D., Diekmann, M., Graae, B. J., Hedwall, P., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., Ponette, Q., Plue, J., Sanczuk, P., Selvi, F., … Frenne, P. D. (2024). Trait–micro-environment relationships of forest herb communities across Europe. *Global Ecology and Biogeography*, *33*(2), 286–302. https://doi.org/10.1111/geb.13789

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(44), 11645–11650. https://doi.org/10.1073/pnas.1710465114

Guimarães-Steinicke, C., Weigelt, A., Proulx, R., Lanners, T., Eisenhauer, N., Duque-Lazo, J., Reu, B., Roscher, C., Wagg, C., Buchmann, N., & Wirth, C. (2021). Biodiversity facets affect community surface temperature via 3D canopy structure in grassland communities. *Journal of Ecology*, *109*, 1969–1985. https://doi.org/10.1111/1365-2745.13631

Hill, M. J., Senarath, U., Lee, A., Zeppel, M., Nightingale, J. M., Williams, R. (Dick) J., & McVicar, T. R. (2006). Assessment of the MODIS LAI product for Australian ecosystems. *Remote Sensing of Environment*, *101*(4), 495–518. https://doi.org/10.1016/j.rse.2006.01.010

Hollinger, D. Y., Ollinger, S. V., Richardson, A. D., Meyers, T. P., Dail, D. B., Marin, M. E., Scott, N. A., Arkebauer, T. J., Baldocchi, D. D., Clark, K. L., Curtis, P. S., Davis, K. J., Desai, A. R., Dragoni, D., Goulden, M. L., Gu, L., Katul, G. G., Pallardy, S. G., K. T. Paw, U., … Verma, S. B. (2010). Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. *Global Change Biology*, *16*(2), 696–710. https://doi.org/10.1111/j.1365-2486.2009.02028.x

IPCC. (2021). Climate change 2021—The physical science basis. *Journal Chemistry International*, *43*(4), 22–23. https://doi.org/10.1515/ci-2021-0407

Kelly, C. K., & Beerling, D. J. (1995). Plant life form, stomatal density and taxonomic relatedness: A reanalysis of Salisbury (1927). *Functional Ecology*, *9*(3), 422–431.

Kemppinen, J., & Niittynen, P. (2022). Microclimate relationships of intraspecific trait variation in sub-Arctic plants. *Oikos*, *2022*(12), e09507. https://doi.org/10.1111/oik.09507

Kovács, B., Tinya, F., Németh, C., & Ódor, P. (2020). Unfolding the effects of different forestry treatments on microclimate in oak forests: Results of a 4-yr experiment. *Ecological Applications*, *30*(2), e02043. https://doi.org/10.1002/eap.2043

Lembrechts, J. J., Aalto, J., Ashcroft, M. B., Frenne, P. D., Kopecký, M., Lenoir, J., Luoto, M., Maclean, I. M. D., Roupsard, O., Fuentes-Lillo, E., García, R. A., Pellissier, L., Pitteloud, C., Alatalo, J. M., Smith, S. W., Björk, R. G., Muffler, L., Backes, A. R., Cesarz, S., … Nijs, I. (2020). SoilTemp: A global database of near-surface temperature. *Global Change Biology*, *26*(11), 6616–6629. https://doi.org/10.1111/gcb.15123

Lenssen, N. J. L., Schmidt, G. A., Hansen, J. E., Menne, M. J., Persin, A., Ruedy, R., & Zyss, D. (2019). Improvements in the GISTEMP uncertainty model. *Journal of Geophysical Research: Atmospheres*, *124*(12), 6307–6326. https://doi.org/10.1029/2018jd029522

Li, H., Ma, X., Lu, Y., Ren, R., Cui, B., & Si, B. (2021). Growing deep roots has opposing impacts on the transpiration of apple trees planted in subhumid loess region. *Agricultural Water Management*, *258*, 107207. https://doi.org/10.1016/j.agwat.2021.107207

Lin, H., Li, Y., & Zhao, L. (2022). Partitioning of sensible and latent heat fluxes in different vegetation types and their spatiotemporal variations based on 203 FLUXNET sites. *Journal of Geophysical Research: Atmospheres*, *127*(21), e2022JD037142. https://doi.org/10.1029/2022jd037142

López, J., Way, D. A., & Sadok, W. (2021). Systemic effects of rising atmospheric vapor pressure deficit on plant physiology and productivity. *Global Change Biology*, *27*(9), 1704–1720. https://doi.org/10.1111/gcb.15548

Lortie, C. J., Filazzola, A., Westphal, M., & Butterfield, H. S. (2022). Foundation plant species provide resilience and microclimatic heterogeneity in drylands. *Scientific Reports*, *12*(1), 18005. https://doi.org/10.1038/s41598-022-22579-1

Maestre, F. T., Bautista, S., Cortina, J., & Bellot, J. (2001). Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications*, *11*(6), 1641–1655. https://doi.org/10.1890/1051-0761(2001)011[1641:pfufbg]2.0.co;2

Mallen-Cooper, M., Graae, B. J., & Cornwell, W. K. (2021). Lichens buffer tundra microclimate more than the expanding shrub *Betula nana*. *Annals of Botany*, *128*(4), 407–418. https://doi.org/10.1093/aob/mcab041

Martin-Sanchez, R., Sancho-Knapic, D., Alonso-Forn, D., Lopes-Ballesteros, A., Ferrio, J. P., Hipp, A. L., Peguero-Pina, J. J., & Gil-Pelegrin, E. (2024). Oak leaf morphology may be more strongly shaped by climate than by phylogeny. *Annals of Forest Science*, *81*, 14.

Meinzer, F. C. (1993). Stomatal control of transpiration. *Trends in Ecology & Evolution*, *8*(8), 289–294. https://doi.org/10.1016/0169-5347(93)90257-p

Muir, C. D. (2018). Light and growth form interact to shape stomatal ratio among British angiosperms. *New Phytologist*. https://doi.org/10.1111/nph.14956

Muller, J. D., Rotenberg, E., Tatarinov, F., Oz, I., & Yakir, D. (2021). Evidence for efficient nonevaporative leaf-to-air heat dissipation in a pine forest under drought conditions. *New Phytologist*, *232*(6), 2254–2266. https://doi.org/10.1111/nph.17742

Niskanen, A. K. J., Niittynen, P., Aalto, J., Väre, H., & Luoto, M. (2019). Lost at high latitudes: Arctic and endemic plants under threat as climate warms. *Diversity and Distributions*, *25*(5), 809–821. https://doi.org/10.1111/ddi.12889

Novick, K. A., & Barnes, M. L. (2023). A practical exploration of land cover impacts on surface and air temperature when they are most consequential. *Environmental Research: Climate*, *2*(2), 025007. https://doi.org/10.1088/2752-5295/accdf9

Novick, K. A., Ficklin, D. L., Grossiord, C., Konings, A. G., Martínez-Vilalta, J., Sadok, W., Trugman, A. T., Williams, A. P., Wright, A. J., Abatzoglou, J. T., Dannenberg, M. P., Gentine, P., Guan, K., Johnston, M. R., Lowman, L. E. L., Moore, D. J. P., & McDowell, N. G. (2024). The impacts of rising vapour pressure deficit in natural and managed ecosystems. *Plant, Cell & Environment*. https://doi.org/10.1111/pce.14846

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42.

Rao, K., Williams, A. P., Diffenbaugh, N. S., Yebra, M., & Konings, A. G. (2022). Plant-water sensitivity regulates wildfire vulnerability. *Nature Ecology & Evolution*, *6*(3), 332–339. https://doi.org/10.1038/s41559-021-01654-2

Richter, R., Ballasus, H., Engelmann, R. A., Zielhofer, C., Sanaei, A., & Wirth, C. (2022). Tree species matter for forest microclimate regulation during the drought year 2018: Disentangling environmental drivers and biotic drivers. *Scientific Reports*, *12*(1), 17559. https://doi.org/10.1038/s41598-022-22582-6

Rigden, A., Li, D., & Salvucci, G. (2018). Dependence of thermal roughness length on friction velocity across land cover types: A synthesis analysis using AmeriFlux data. *Agricultural and Forest Meteorology*, *249*, 512–519.

Schenk, H. J., & Jackson, R. B. (2002). The global biogeography of roots. *Ecological Monographs*, *72*(3), 311. https://doi.org/10.2307/3100092

Schlesinger, W. H., & Jasechko, S. (2014). Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, *189*, 115–117. https://doi.org/10.1016/j.agrformet.2014.01.011

Schönbeck, L. C., Schuler, P., Lehmann, M. M., Mas, E., Mekarni, L., Pivovaroff, A. L., Turberg, P., & Grossiord, C. (2022). Increasing temperature and vapor pressure deficit lead to hydraulic damages in the absence of soil drought. *Plant, Cell & Environment*, *45*(11), 3275–3289. https://doi.org/10.1111/pce.14425

Speak, A., Montagnani, L., Wellstein, C., & Zerbe, S. (2020). The influence of tree traits on urban ground surface shade cooling. *Landscape and Urban Planning*, *197*, 103748. https://doi.org/10.1016/j.landurbplan.2020.103748

Teuling, A. J., Seneviratne, S. I., Stöckli, R., Reichstein, M., Moors, E., Ciais, P., Luyssaert, S., van den Hurk, B., Ammann, C., Bernhofer, C., Dellwik, E., Gianelle, D., Gielen, B., Grünwald, T., Klumpp, K., Montagnani, L., Moureaux, C., Sottocornola, M., & Wohlfahrt, G. (2010). Contrasting response of European forest and grassland energy exchange to heatwaves. *Nature Geoscience*, *3*(10), 722–727. https://doi.org/10.1038/ngeo950

van Heerwaarden, C. C., & Teuling, A. J. (2014). Disentangling the response of forest and grassland energy exchange to heatwaves under idealized land–atmosphere coupling. *Biogeosciences*, *11*(21), 6159–6171. https://doi.org/10.5194/bg-11-6159-2014

Walther, G. R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *365*(1549), 2019–2024. https://doi.org/10.1098/rstb.2010.0021

Wang, J., & Wen, X. (2022). Increasing relative abundance of C4 plants mitigates a dryness-stress effect on gross primary productivity along an aridity gradient in grassland ecosystems. *Plant and Soil*, *479*(1–2), 371–387. https://doi.org/10.1007/s11104-022-05529-8

Wright, A., Schnitzer, S. A., & Reich, P. B. (2014). Living close to your neighbors-the importance of both competition and facilitation in plant communities. *Ecology*, *95*, 2213–2223.

Wright, A., Schnitzer, S. A., & Reich, P. B. (2015). Daily environmental conditions determine the competition–facilitation balance for plant water status. *Journal of Ecology*, *103*(3), 648–656. https://doi.org/10.1111/1365-2745.12397

Wright, A. J., Barry, K. E., Lortie, C. J., & Callaway, R. M. (2021). Biodiversity and ecosystem functioning: Have our experiments and indices been underestimating the role of facilitation? *Journal of Ecology*, *109*(5), 1962–1968. https://doi.org/10.1111/1365-2745.13665

Wright, A. J., Fisichelli, N. A., Buschena, C., Rice, K., Rich, R., Stefanski, A., Montgomery, R., & Reich, P. B. (2018). Biodiversity bottleneck: Seedling establishment under changing climatic conditions at the boreal–temperate ecotone. *Plant Ecology*, *219*(6), 1–14. https://doi.org/10.1007/s11258-018-0827-1

Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A. K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J. E., Qin, Z., Quine, T., … Yang, S. (2019). Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Science Advances*, *5*(8), eaax1396. https://doi.org/10.1126/sciadv.aax1396

Zhang, S., Landuyt, D., Verheyen, K., & Frenne, P. D. (2022). Tree species mixing can amplify microclimate offsets in young forest plantations. *Journal of Applied Ecology*, *59*(6), 1428–1439. https://doi.org/10.1111/1365-2664.14158

Zhou, S., Williams, A. P., Berg, A. M., Cook, B. I., Zhang, Y., Hagemann, S., Lorenz, R., Seneviratne, S. I., & Gentine, P. (2019). Land–atmosphere feedbacks exacerbate concurrent soil drought and atmospheric aridity. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(38), 18848–18853. https://doi.org/10.1073/pnas.1904955116

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