VERDE: Vast Exploration and Research across Dry Forest Ecosystems

Short title: Dry Forest Phenology

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Project and Public Summary: We propose Vast Exploration and Research in Dry Forest Ecosystems (VERDE), a working group to harness environmental data science for understanding the evolutionary past and probable futures of a globally distributed and threatened biome—tropical dry forests. Tropical dry forests are defined by drought deciduousness which determines ecosystem productivity and nutrient cycling. However, the origins of deciduousness, its degree of variation, and its role in determining the impacts of climate change in tropical dry forests are unclear. To understand the evolutionary history, contemporary biogeography, and probable futures of dry forests, we propose to examine the distribution of deciduousness across evolutionary time, across geographical gradients, and to forecast the success of the deciduous trait under future climates. We will achieve this by bringing together datasets that include phylogenetic trees, functional traits, field-based phenology data, remote sensing imagery, and ecosystem modeling. Importantly, our working group will broaden the century-old and geographically biased 'temperate phenology paradigm' by identifying past, present, and future determinants of tropical phenological variation. Our team is deliberately diverse, representing a spectrum of career stages, geography, and disciplines like ecophysiology, ecology, ecosystem science, macroevolution, forecasting, and remote sensing.

Introduction and Goals: Deciduousness is ubiquitous in tropical forests, but it varies considerably. Some forests experience partial leaf loss, while others undergo complete defoliation (Quigley and Platt 2003). For this reason, deciduousness is often used for vegetation classification (Beard 1944, Box 1996). Deciduousness increases with increasing precipitation seasonality (Borchert 1998, Bohlman 2010), especially in regions with distinct wet and dry seasons, a defining feature of tropical dry forests (Gentry 1995). However, deciduousness is not a simple strategy. A complex interplay between precipitation, irradiance, soil moisture, and geology (Bohlman 2010, Seghieri et al. 2012, Xie et al. 2015, Ouédraogo et al. 2016), as well as tradeoffs between water conservation and carbon gain (Vico et al. 2017, Trugman et al. 2019) impact the timing, extent, and plasticity of deciduousness. The prevalence of deciduous species within a forest can also influence ecosystem dynamics. Forests with a higher proportion of deciduous species exhibit different patterns of carbon cycling and productivity compared to those dominated by evergreens (Bohlman 2010).

Despite the importance of deciduousness for vegetation classification and ecosystem function, there are few efforts in synthesizing generalizable mechanisms driving deciduousness in tropical dry forests. Paradoxically, leaf demography appears to be studied more in tropical wet forests compared to seasonally dry forests (Wu et al. 2016, 2017). Perhaps because the study of phenology has largely emphasized temperate ecosystems (Davis et al. 2022), there are fewer paradigms for quantifying phenological and leaf habit variation in tropical forests. Furthermore, the origins of deciduousness in tropical dry forests are unresolved. Some studies suggest that deciduousness evolved from rainforest species independently in different regions during drier glacial periods (Axelrod 1966, Pennington et al. 2004). This hypothesis is based on the observations that the dominant deciduous species in different tropical regions belong to distinct lineages (Pennington et al. 2006) and tropical dry forests are characterized by high endemism (DRYFLOR et al. 2016). Understanding the origins of deciduousness in tropical forests can also provide insight into the potential resilience or vulnerability of tropical forests in the face of ongoing global change. Because deciduousness is a key trait linked to plant function, it is a useful tool for calibrating models that simulate tropical forest responses to projected changes (Singh and Kushwaha 2016, Vico et al. 2017). What is needed, then, is to understand (1) the origins of deciduousness, (2) the interplay of factors that shape the biogeographic distribution of deciduousness across tropical forests, and (3) how to predict the success of the deciduous strategy under future climate scenarios. Specifically, comparative studies across dry forests can provide insight into the timing and evolutionary drivers of deciduousness in these ecosystems. In addition, new tools like remote sensing can quantify the degree of deciduousness across tropical forests, distinguishing these from temperate phenology paradigms. Finally, as climate regimes shift, understanding the factors influencing deciduousness will be crucial for predicting how tropical forests respond and adapt to altered temperature and precipitation regimes. We propose a data science approach to fill these gaps, providing a deeper understanding of the role of deciduousness in tropical ecosystems, identifying novel tropical phenological paradigms, and determining the implications for future tropical forests.

Aim 1: Evolutionary past and origins of tropical deciduousness

Across vast stretches of the Americas, Africa, and southern Asia, a compelling pattern emerges: as rainfall decreases and becomes more seasonal, the prevalence of evergreen rainforests gives way to deciduous dry forests, woodlands, and ultimately, deserts (Schimper 1903, Beard 1944). Furthermore, across time, the fossil record in the Americas hints at an evolutionary route from tropical rainforests, through dry forests, to North American deserts (Rzedowski 1991, Cevallos-Ferriz and Ramírez 2004). These two observations suggest deciduousness evolved as a water-saving adaptation to seasonal drought and evolved from the evergreen habit (Bews 1927). Leaf shedding during harsh conditions may have facilitated the migration of plant lineages to colder climates (e.g., *Acer*, *Celtis*, *Magnolia*, *Prunus*, *Quercus*, *Rosa*, and *Salix*), contributing to the development of temperate deciduous forests (Axelrod 1966). However, the full extent of the role of deciduousness and the influence of other adaptations remain unclear. For example, although deciduousness is considered a preadaptation to frost, freezing temperatures paradoxically constrain the northern limits of dry forest distribution (Trejo Vázquez 1999, Bojórquez et al. 2021). This raises intriguing questions about the extent that deciduousness facilitated northward expansion into colder regions. Analyzing deciduousness across diverse lineages will thus estimate its evolutionary trajectory, the selective pressures that shaped it, its impact on biogeographical formations (e.g., Van Devender et al. 2000, Lott and Atkinson 2002), and the resilience of tropical forests confronting climate change (Pérez-García and Meave 2012).

Aim 2: Defining deciduousness and its degree of variation

Tropical dry forests are a natural laboratory for defining and quantifying deciduousness. The prolonged seasonal drought that characterizes dry forests selects for different leaf habit strategies, ranging from evergreen (drought tolerant) to deciduous (drought avoidant). Although leaf habit is linked to resource-use strategies and biogeochemical cycles, emerging evidence (e.g., Brodribb and Holbrook 2005, Vargas et al. 2021) suggests that binary classifications (e.g., deciduous, evergreen) are oversimplistic. Indeed, within dry forests, trees with a range of leaf habits co-occur. Among these include evergreen, semi-deciduous, brevi-deciduous, and facultative deciduous species with varying rates of leaf flushing and leaf shedding (Eamus 1999). Even evergreen species shed leaves (Borchert 1998), and leaf phenology can be highly plastic in response to environmental cues (Wolfe et al. 2016). As a result, more nuanced classifications of leaf habits are an important, albeit overlooked, aspect of organismal responses to water availability and climate change. Yet, the study of phenology has, for more than a century, emphasized patterns that depend on large seasonal phenological drivers such as day length or dramatic temperature change (Davis et al. 2022). This limited and geographically biased perspective constrains a more detailed approach to understanding and defining tropical deciduousness where subtle changes in precipitation and topography, for example, can have dramatic effects on leaf phenology (Sakai and Kitajima 2019). To define deciduousness in tropical forests, some studies have quantified the fraction of deciduous species or stems in a flora (e.g., Webb 1968, Frankie et al. 1974, Reich 1995, Wright 1991, Bullock and Solis-Magallanes 1991, Geldenhuys 1993, Kelly et al. 1988), whereas others have quantified the fraction of canopy cover (Condit et al. 2000) or used remote sensing to map deciduousness at landscape scales (Huechacona-Ruiz et al. 2020). Some studies have shown that precipitation gradients (Bohlman 2010), soil characteristics (Ma et al. 2023), and geology (Ouédraogo et al. 2016) are important drivers of deciduousness, yet these studies are limited to a single site or region. We argue that a synthesis of the factors mediating tropical leaf phenology patterns across larger spatiotemporal scales is a necessary next step towards a generalized understanding of drought deciduousness.

Aim 3: Probable futures—remote sensing and modeling to measure the sensitivity of dry forests
Tropical dry forests are the most threatened tropical ecosystem (Miles et al. 2006) and face growing threats from climate change. Understanding their long-term response to shifting climatic conditions is critical for informing conservation efforts, tracking carbon storage, and preserving ecosystem services. While research has explored the immediate impacts of drought and warming on tropical dry forests (e.g., Maza-Villalobos et al. 2013, Powers et al. 2020), our understanding of their ability to adapt and persist over extended spatial or temporal scales remains limited. Existing studies focus on short-term observations or projections, which may not capture the complex carbon dynamics of these ecosystems over longer time scales (Swenson et al. 2020). Some studies suggest that global conditions will shift towards those that have historically supported deciduous forests (Ma et al. 2023), and thus the deciduous strategy will become more competitive under future climate scenarios (Vico et al. 2017). A shift towards more drought-deciduous communities will have cascading consequences for carbon storage and other ecosystem processes. Therefore, developing a framework to assess tropical dry forest sensitivity and the success of the deciduous strategy under future climate scenarios is crucial.

Proposed Activities & Timeline: We propose 2-in-person meetings, monthly virtual meetings, and updates to ESIIL throughout, beginning with a virtual meet-and-greet and culminating with a virtual celebration and showcase. **Workshops 1 (5/25, 4 in-person days)** and **2 (10/25, 4 virtual half-days)** will focus on data harmonization and co-designing a bilingual (English-Spanish) Tropical Phenological Monitoring Protocol (based on NEON, National Phenology Network, Phenocam, and other existing protocols, mostly designed for temperate forests) that will be implemented across our network of participants studying tropical forests. This will allow us to join Phenobase–a global database of *in situ* observatory plant phenology. We will follow the ecocomDP data design pattern (O'Brien et al. 2021) and integrate updates from ESIIL's Macrophenology group. We will harmonize phylogenetic, trait, environmental, leaf phenology, litterfall, and remote sensing data while being mindful of FAIR and CARE principles. Derived data and code will be archived with the Environmental Data Initiative and GitHub Archive. **Workshop 3 (5/26, 4 in-person days)** will feature analyses and forecasting, described below.

Aim 1 Evolutionary past: We propose a phylogenetic approach for understanding the timing, drivers, and diversification of leaf habits across dry forests. Multiple phylogenetic variance decomposition evaluates the total trait (e.g., leaf habit) variance explained by phylogeny and other factors (climate, geology) along evolutionary time (Palacio et al. 2022). It is thus a temporal analysis of variance decomposition, allowing insight into the evolution of traits. We will compile leaf habit and other trait data from flora, herbaria, trait databases (e.g., BIEN, TRY), and resident botanists. We will build a custom tree using a suite of tools (e.g., Jombart et al. 2010, Revell 2012, Jin and Qian 2019). Given the high endemism that characterizes tropical dry forests, we expect the deciduous strategy to have evolved multiple times during distinct periods (Miocene and Pleistocene; Pennington et al. 2006) and in distinct regions. On the other hand, some plant families are dominant across dry forests (e.g., Fabaceae). For these, we expect deciduousness to have had an important role early in their evolution (see Liu et al. 2024).

Aim 2 Biogeographic patterns: We will define deciduousness and its degree of variation at species, forest, and biome scales. At a species level, we will use leaf habit and trait data from digitized herbaria, floras, trait databases (e.g., BIEN, TRY), and botanists (as in *Aim 1*) and examine the extent to which leaf habit and other traits can be generalized across species, helping us move 'beyond the binary' (e.g., Roughgarden 2007). Doing so has implications for ecosystem models which rely on binary classifications of leaf habit (evergreen vs. deciduous) to model vegetation and carbon dynamics (e.g., Medvigy et al. 2009). At a forest level, we will use harmonized field-based leaf phenology and litterfall data from the literature (e.g., Borchert 1998, Reich 1995, many others) encompassing dry forests from Mexico to Colombia, and Puerto Rico to Brazil, to quantify variation in deciduousness using circular statistics and other algorithms (Tan et al. 2011). Finally, at a biogeographical scale, we will harmonize the above datasets (leaf habit, phenology) with remote sensing, climatic, and geological datasets to quantify the dominant biogeographical drivers of leaf habit variation across latitudinal, aridity, and seasonality gradients in the Neotropics. Briefly, we will use spectral mixture analysis and NDVI to predict deciduousness and how deciduousness varies across climatic gradients and geological substrates.

Aim 3 Probable futures: We will combine remote sensing and ecological modeling to estimate leaf phenological shifts and the sensitivity of dry forests to climate change. This framework leverages remote sensing to capture long-term changes in phenology, such as leaf cover and timing of leaf loss, across decadal time scales and vast spatial scales, for example, from crown to landscape to ecosystem using PlanetScope, harmonized Landsat Sentinel-2, and MODIS. By employing machine learning algorithms (e.g., k-nearest neighbor) on historical and contemporary satellite imagery, we can generate detailed leaf phenology maps capturing the spatial and temporal dynamics of dry forests. These maps can then be integrated into ecological models (e.g., ED2) that simulate the growth, competition, and mortality of different tree species with differing leaf habit strategies under various climate scenarios. By incorporating the success of the deciduous trait within the modeling framework, we can assess its projected performance under future climatic conditions. This combined approach will not only offer insights into the long-term sensitivity of tropical dry forests but also predict the potential fate of the deciduous strategy, ultimately informing targeted conservation strategies for these diverse ecosystems.

Advancing DEI: Our group is diverse by design, representing a spectrum of career stages, geographies, institutions (including Minority Serving), and disciplines, and we work across dry forests throughout the Caribbean, Mexico, Costa Rica, Ecuador, and Colombia. By bringing together early career and senior researchers, and experts in natural history and modeling, we aim to harness the collective knowledge of these dynamic ecosystems. Importantly, inclusion and accessibility (of data, data products, and an emphasis on bilingual outputs) are central foci of our work, especially in light of the unequal geographical distribution of research in the tropics (Stocks et al. 2008). Leaf habit is as equally defined by local ecological knowledge (LEK) as it is by herbaria data sheets. LEK is a natural feature of our past and ongoing work, emerging from decades of relationship-building across the diverse communities represented by our team (e.g., Arenas-Wong et al. 2024), many of whom have deep ties to the land. We bring these connections to design a more holistic phenology paradigm, helping us reflect on and integrate different ways of defining tropical drought deciduous phenology.

Rationale for ESIIL support: Video-conferencing is a part of daily life, but there is no substitute for in-person interactions that complement virtual meetings and facilitate productivity and relationships. ESIIL is centrally located within the United States and has convenient access to domain experts from NEON (e.g., plant phenology monitoring program leads and Terrestrial Plant Diversity and Phenology technical working group), NCAR (Will Weder), CIRES' EarthLab, and others, making it an ideal meeting location. Our group would also benefit from the recent SinBiose workshop to inform best practices relevant to challenges, equity, and opportunities for collaboration across countries, institutions, data providers, and synthesizers.

Collaborations with other ESIIL activities: We are working with 2024 Working Group lead Sydney Record from Macrophenology–focused on temperate North American phenology. Our group extends this phenology focus to tropical ecosystems, enabling new, cross-system, cross-American synthesis. We hope to learn from their Hackathon to harmonize phenology data, and share lessons learned. The implementation of *in situ* phenological monitoring will enable us to join Phenobase, positioning ESIIL as a connector of globally distributed phenological networks.

Anticipated IT Needs: Our three-pronged approach (evolutionary/phylogenetics, data mining, and forecasting) will result in code, harmonized data, model outputs, and protocols. We request CyVerse access (persistent storage, docker containers, cloud instances, JupyterLabs) for modeling components, parallel computing, and image processing, and Data Cubes for satellite imagery data. We also request workshop overviews of CyVerse and GitHub.

Outcomes: In addition to **peer-reviewed publications**, our meetings will have a lasting impact on the development of **distributed phenological observatory networks**, facilitating new and strengthening existing relationships across diverse teams and domains. We will **co-design system-relevant and bilingual (Spanish-English) protocols and capabilities** to detect and predict the impact of climate change on deciduousness. We will achieve this by synthesizing phenological monitoring methods in the tropics and adapting methods from temperate-focused National Phenological Network, NEON, and PhenoCam protocols. Importantly, our efforts will expand phenological data compatible with NEON. We have rich collective expertise in Guanica, Puerto Rico, a NEON tropical dry forest site (see Vargas et al. 2021, Waring et al. 2021, Beidler et al. 2023), where many species are represented across other American dry forests. Among the dry forests represented by our group, the percentage of deciduousness ranges from 10-90% (Vargas et al. 2021). Our synthesis is designed to understand this variation. An inherent understanding of phenology is intricately tied to the development of human agriculture. Our focus on phenology thus **links us to our deep past and our probable futures**. Our meetings will lay the foundation for **grant proposal submissions** related to tropical phenology, becoming part of new efforts to decolonize the study of deciduousness.

References

Arenas-Wong, R.A., Robles-Morúa, A., Bojórquez, A., Martínez-Yrízar, A., Yépez, E.A. and Álvarez-Yépiz, J.C., 2023. Climate-induced changes to provisioning ecosystem services in rural socioecosystems in Mexico. Weather and Climate Extremes, 41, p.100583.

Axelrod, D. I. 1966. Origin of deciduous and evergreen habits in temperate forests. Evolution 20:1–15.

Beard, J. S. 1944. Climax Vegetation in Tropical America. Ecology 25:127–158.

Bews, J. W. 1927. Studies in the Ecological Evolution of the Angiosperms (continued). The New Phytologist 26:209–248.

Bohlman, S. A. 2010. Landscape patterns and environmental controls of deciduousness in forests of central Panama. Global ecology and biogeography: a journal of macroecology 19:376–385.

Bojórquez, A., A. Martínez-Yrízar, and J. C. Álvarez-Yépiz. 2021. A landscape assessment of frost damage in the northmost Neotropical dry forest. Agricultural and Forest Meteorology 308-309:108562.

Borchert, R. 1998. Responses of tropical trees to rainfall seasonality and its long-term changes. Climatic change 39:381–393.

Box, E. O. 1996. Plant functional types and climate at the global scale. Journal of Vegetation Science: official organ of the International Association for Vegetation Science 7:309–320.

Brodribb, T. J., and N. M. Holbrook. 2005. Leaf physiology does not predict leaf habit; examples from tropical dry forest. Trees 19:290–295.

Condit, R., K. Watts, S. A. Bohlman, R. Pérez, R. B. Foster, and S. P. Hubbell. 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. Journal of Vegetation Science: official organ of the International Association for Vegetation Science 11:649–658.

Davis, C. C., G. M. Lyra, D. S. Park, R. Asprino, R. Maruyama, D. Torquato, B. I. Cook, and A. M. Ellison. 2022. New directions in tropical phenology. Trends in Ecology & Evolution 37:683–693.

DRYFLOR, K. Banda-R, A. Delgado-Salinas, K. G. Dexter, R. Linares-Palomino, A. Oliveira-Filho, et al. 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353:1383–1387.

Eamus, D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Trends in ecology & evolution 14:11–16.

Gentry, A. H. 1995. Diversity and floristic composition of neotropical dry forests. Pages 146–194 Seasonally Dry Tropical Forests. Cambridge University Press.

Huechacona-Ruiz, A. H., J. M. Dupuy, N. B. Schwartz, J. S. Powers, C. Reyes-García, F. Tun-Dzul, and J. L. Hernández-Stefanoni. 2020. Mapping Tree Species Deciduousness of Tropical Dry Forests Combining Reflectance, Spectral Unmixing, and Texture Data from High-Resolution Imagery. Forests, Trees and Livelihoods 11:1234.

Jin, Y., and H. Qian. 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42:1353–1359.

Jombart, T., F. Balloux, and S. Dray. 2010. adephylo: new tools for investigating the phylogenetic signal in biological traits. Bioinformatics 26:1907–1909.

Liu, H., Q. Ye, M. R. Lundgren, S. N. R. Young, X. Liu, Q. Luo, Y. Lin, N. Ye, and G. Hao. 2024. Phylogeny and climate explain contrasting hydraulic traits in different life forms of

150 woody Fabaceae species. The Journal of Ecology 112:741–754.
Lott, E. J., and T. H. Atkinson. 2002. Biodiversidad y fitogeografía de Chamela-Cuixmala, Jalisco. Historia Natural de Chamela:83–97.
Ma, H., T. W. Crowther, L. Mo, D. S. Maynard, et al. 2023. The global biogeography of tree leaf form and habit. Nature plants 9:1795–1809.
Maza-Villalobos, S., L. Poorter, and M. Martínez-Ramos. 2013. Effects of ENSO and temporal rainfall variation on the dynamics of successional communities in old-field succession of a tropical dry forest. PloS one 8:e82040.
Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. Journal of Geophysical Research 114.
Miles, L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos, and J. E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. Journal of Biogeography 33:491–505.
Ouédraogo, D.-Y., A. Fayolle, S. Gourlet-Fleury, F. Mortier, V. Freycon, N. Fauvet, S. Rabaud, G. Cornu, F. Bénédet, J.-F. Gillet, R. Oslisly, J.-L. Doucet, P. Lejeune, and C. Favier. 2016. The determinants of tropical forest deciduousness: disentangling the effects of rainfall and geology in central Africa. The Journal of Ecology 104:924–935.
Palacio, S., A. Cera, A. Escudero, and A. L. Luzuriaga. 2022. Recent and ancient evolutionary events shaped plant elemental composition of edaphic endemics: a phylogeny-wide analysis of Iberian gypsum plants. New.
Pennington, R. T., M. Lavin, D. E. Prado, C. A. Pendry, S. K. Pell, and C. A. Butterworth. 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both tertiary and quaternary diversification. Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences 359:515–537.
Pennington, R. T., G. P. Lewis, and J. A. Ratter. 2006. An Overview of the Plant Diversity, Biogeography and Conservation of Neotropical Savannas and Seasonally Dry Forests. Pages 0–1 *in* R. T. Pennington, G. P. Lewis, and J. A. Ratter, editors. Neotropical savannas and seasonally dry forests plant diversity biogeography and conservation. CRC Press.
Pérez-García, E. A., and J. A. Meave. 2012. Flora and vegetation of the seasonally dry tropics in Mexico: origin and biogeographical implications. Acta Botánica.
Powers, J. S., G. Vargas G, and T. J. Brodribb. 2020. A catastrophic tropical drought kills hydraulically vulnerable tree species. Global change biology.
Quigley, M. F., and W. J. Platt. 2003. Composition and structure of seasonally deciduous forests in the Americas. Ecological monographs 73:87–106.
Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in ecology and evolution / British Ecological Society 3:217–223.
Roughgarden, J. 2007. Challenging Darwin’s Theory of Sexual Selection. Daedalus 136:23–36.
Sakai, S., and K. Kitajima. 2019. Tropical phenology: Recent advances and perspectives. Ecological Research 34:50–54.
Seghieri, J., F. Do, J.-L. Devineau, and A. Fournier. 2012. Phenology of woody species along the climatic gradient in west tropical Africa. Phenology and climate:143–177.
Singh, K. P., and C. P. Kushwaha. 2016. Deciduousness in tropical trees and its potential as indicator of climate change: A review. Ecological Indicators 69:699–706.
Swenson, N. G., C. M. Hulshof, M. Katabuchi, and B. J. Enquist. 2020. Long-term shifts in the functional composition and diversity of a tropical dry forest: a 30-yr study. Ecological

Monographs 90.
Tan, B., J. T. Morisette, R. E. Wolfe, F. Gao, G. A. Ederer, J. Nightingale, and J. A. Pedelty. 2011. An Enhanced TIMESAT Algorithm for Estimating Vegetation Phenology Metrics From MODIS Data. IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing 4:361–371.
Trejo Vázquez, I. 1999. El clima de la selva baja caducifolia en México. Investigaciones Geograficas.
Trugman, A. T., L. D. L. Anderegg, B. T. Wolfe, B. Birami, N. K. Ruehr, M. Detto, M. K. Bartlett, and W. R. L. Anderegg. 2019. Climate and plant trait strategies determine tree carbon allocation to leaves and mediate future forest productivity. Global Change Biology 25:3395–3405.
Van Devender, T. R., A. C. Sanders, R. K. Wilson, and S. A. Meyer. 2000. Vegetation, flora, and seasons of the Río Cuchujaqui, a tropical deciduous forest near Alamos, Sonora. The tropical deciduous forest.
Vargas G, G., T. J. Brodribb, J. M. Dupuy, R. González-M, C. M. Hulshof, D. Medvigy, T. A. P. Allerton, C. Pizano, B. Salgado-Negret, N. B. Schwartz, S. J. Van Bloem, B. G. Waring, and J. S. Powers. 2021. Beyond leaf habit: generalities in plant function across 97 tropical dry forest tree species. The New Phytologist 232:148–161.
Vico, G., D. Dralle, X. Feng, S. Thompson, and S. Manzoni. 2017. How competitive is drought deciduousness in tropical forests? A combined eco-hydrological and eco-evolutionary approach. Environmental research letters: ERL [Web site] 12:065006.
Wolfe, B. T., J. S. Sperry, and T. A. Kursar. 2016. Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. The New Phytologist 212:1007–1018.
Wu, J., L. P. Albert, A. P. Lopes, N. Restrepo-Coupe, M. Hayek, K. T. Wiedemann, K. Guan, S. C. Stark, B. Christoffersen, N. Prohaska, J. V. Tavares, S. Marostica, H. Kobayashi, M. L. Ferreira, K. S. Campos, R. da Silva, P. M. Brando, D. G. Dye, T. E. Huxman, A. R. Huete, B. W. Nelson, and S. R. Saleska. 2016. Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. Science 351:972–976.
Wu, J., S. P. Serbin, X. Xu, L. P. Albert, M. Chen, R. Meng, S. R. Saleska, and A. Rogers. 2017. The phenology of leaf quality and its within-canopy variation is essential for accurate modeling of photosynthesis in tropical evergreen forests. Global Change Biology 23:4814–4827.
Xie, Y., X. Wang, and J. A. Silander Jr. 2015. Deciduous forest responses to temperature, precipitation, and drought imply complex climate change impacts. Proceedings of the National Academy of Sciences of the United States of America 112:13585–13590.

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Appointments and Positions

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Products

Products Most Closely Related to the Proposed Project

1. Ortiz-Colin P, Hulshof CM. Ecotones as Windows into Organismal-to-Biome Scale Responses across Neotropical Forests. Plants (Basel). 2024 Aug 27;13(17) PubMed Central PMCID: PMC11397621.
2. Walter JA, Atkins JW, Hulshof CM. Climate and topography control variation in the tropical dry forest–rainforest ecotone. Ecology. 2024 August 21; e4442. Available from: https://esajournals.onlinelibrary.wiley.com/doi/epdf/10.1002/ecy.4442
3. Umaña MN, Hulshof CM. Characterizing tree trait variance over spatiotemporal scales. Ecology. 2023 Aug;104(8):e4126. PubMed PMID: 37323009.
4. Hulshof CM, Waring BG, Powers JS, Harrison SP. Trait-based signatures of cloud base height in a tropical cloud forest. Am J Bot. 2020 Jun;107(6):886-894. PubMed PMID: 32500611.
5. Hulshof CM, Spasojevic M. The edaphic control of plant diversity. Global Ecology and Biogeography. 2020; 29:1634-1650.

Other Significant Products, Whether or Not Related to the Proposed Project

1. Hulshof C, Stegen J, Swenson N, Enquist C, Enquist B. Interannual variability of growth and reproduction in *Bursera simaruba* : the role of allometry and resource variability. Ecology. 2012 January; 93(1):180-190. Available from: https://esajournals.onlinelibrary.wiley.com/doi/10.1890/11-0740.1 DOI: 10.1890/11-0740.1
2. Hulshof C, Violle C, Spasojevic M, McGill B, Damschen E, Harrison S, Enquist B. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. Journal of Vegetation Science. 2013 January 28; 24(5):921-931. Available from: https://onlinelibrary.wiley.com/doi/10.1111/jvs.12041 DOI: 10.1111/jvs.12041
3. Hulshof C, Swenson N, Weiser M. Tree height–diameter allometry across the United States. Ecology and Evolution. 2015 February 20; 5(6):1193-1204. Available from: https://onlinelibrary.wiley.com/doi/10.1002/ece3.1328 DOI: 10.1002/ece3.1328
4. Swenson N, Hulshof C, Katabuchi M, Enquist B. Long-term shifts in the functional composition and diversity of a tropical dry forest: a 30-yr study. Ecological Monographs. 2020; 90:e01408.
5. Hulshof C, Ackerman J, Franqui R, Kawahara A, Restrepo C. Temperature seasonality drives taxonomic and functional homogenization of tropical butterflies. Diversity and Distributions. 2024 January 26; 30(7):-. Available from: https://onlinelibrary.wiley.com/doi/10.1111/ddi.13814 DOI: 10.1111/ddi.13814

Certification:

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I also certify that, at the time of submission, I am not a party to a malign foreign talent recruitment program.

Misrepresentations and/or omissions may be subject to prosecution and liability pursuant to, but not limited to, 18 U.S.C. §§ 287, 1001, 1031 and 31 U.S.C. §§ 3729-3733 and 3802.

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IDENTIFYING INFORMATION:

NAME: Vargas Gutiérrez, German

ORCID iD: https://orcid.org/0000-0003-1738-0014

POSITION TITLE: Assistant Professor

PRIMARY ORGANIZATION AND LOCATION: Oregon State University, Corvallis, Oregon, United States

Professional Preparation:

ORGANIZATION AND LOCATION	DEGREE (if applicable)	RECEIPT DATE	FIELD OF STUDY
University of Minnesota, Minneapolis, Minnesota, United States	PHD	11/2021	Plant Biological Sciences
Universidad Nacional de Costa Rica, Heredia, Heredia, Costa Rica	BS	11/2013	Tropical Biology

Appointments and Positions

2024 - present Assistant Professor, Oregon State University, Corvallis, Oregon, United States

2022 - 2024 NOAA Climate and Global Change Postdoctoral Fellow, University Corporation for Atmospheric Research, Salt Lake City, Utah, United States

2021 - 2022 Postdoctoral Research Associate, University of Utah, Salt Lake City, Utah, United States

2016 - 2021 Graduate Research Assistant, University of Minnesota, Minneapolis, Minnesota, United States

Products

Products Most Closely Related to the Proposed Project

1. Wang Y, Yang D, German Vargas G, Hao G, Powers J, Ke Y, Wang Q, Zhang Y, Zhang J. Leaf habit differentiation explains trait tradeoffs across savanna woody plants. Forest Ecosystems. 2024; 11:100190-. Available from: https://linkinghub.elsevier.com/retrieve/pii/S2197562024000265 DOI: 10.1016/j.fecs.2024.100190
2. Vargas G G, Kunert N, Hammond WM, Berry ZC, Werden LK, Smith-Martin CM, Wolfe BT, Toro L, Mondragón-Botero A, Pinto-Ledezma JN, Schwartz NB, Uriarte M, Sack L, Anderson-Teixeira KJ, Powers JS. Leaf habit affects the distribution of drought sensitivity but not water transport efficiency in the tropics. Ecol Lett. 2022 Dec;25(12):2637-2650. PubMed Central PMCID: PMC9828425.
3. Vargas G G, Brodribb TJ, Dupuy JM, González-M R, Hulshof CM, Medvigy D, Allerton TAP, Pizano C, Salgado-Negret B, Schwartz NB, Van Bloem SJ, Waring BG, Powers JS. Beyond leaf habit: generalities in plant function across 97 tropical dry forest tree species. New Phytol. 2021 Oct;232(1):148-161. PubMed PMID: 34171131.
4. Wu D, Vargas G G, Powers JS, McDowell NG, Becknell JM, Pérez-Aviles D, Medvigy D, Liu Y, Katul GG, Calvo-Alvarado JC, Calvo-Obando A, Sanchez-Azofeifa A, Xu X. Reduced

ecosystem resilience quantifies fine-scale heterogeneity in tropical forest mortality responses to drought. Glob Chang Biol. 2022 Mar;28(6):2081-2094. PubMed PMID: 34921474.

5. Smith-Martin CM, Muscarella R, Hammond WM, Jansen S, Brodribb TJ, Choat B, Johnson DM, Vargas-G G, Uriarte M. Hydraulic variability of tropical forests is largely independent of water availability. Ecol Lett. 2023 Nov;26(11):1829-1839. PubMed PMID: 37807917.

Other Significant Products, Whether or Not Related to the Proposed Project

1. Powers JS, Vargas G G, Brodribb TJ, Schwartz NB, Pérez-Aviles D, Smith-Martin CM, Becknell JM, Aureli F, Blanco R, Calderón-Morales E, Calvo-Alvarado JC, Calvo-Obando AJ, Chavarría MM, Carvajal-Vanegas D, Jiménez-Rodríguez CD, Murillo Chacon E, Schaffner CM, Werden LK, Xu X, Medvigy D. A catastrophic tropical drought kills hydraulically vulnerable tree species. Glob Chang Biol. 2020 May;26(5):3122-3133. PubMed PMID: 32053250.
2. Toro L, Pereira-Arias D, Perez-Aviles D, Vargas G G, Soper FM, Gutknecht J, Powers JS. Phosphorus limitation of early growth differs between nitrogen-fixing and nonfixing dry tropical forest tree species. New Phytol. 2023 Feb;237(3):766-779. PubMed Central PMCID: PMC10107181.
3. Vargas Gutiérrez G, Pérez-Aviles D, Raczka N, Pereira-Arias D, Tijerín-Triviño J, Pereira-Arias L, Medvigy D, Waring B, Morrisey E, Brzostek E, Powers J. Throughfall exclusion and fertilization effects on tropical dry forest tree plantations, a large-scale experiment. Biogeosciences. 2023 June 15; 20(11):2143-2160. Available from: https://bg.copernicus.org/articles/20/2143/2023/ DOI: 10.5194/bg-20-2143-2023
4. Becknell J, Vargas G. G, Pérez-Aviles D, Medvigy D, Powers J. Above-ground net primary productivity in regenerating seasonally dry tropical forest: Contributions of rainfall, forest age and soil. Journal of Ecology. 2021 September 29; 109(11):3903-3915. Available from: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.13767 DOI: 10.1111/1365-2745.13767
5. Vargas G. G, Werden L, Powers J. Explaining Legume Success in Tropical Dry Forests Based on Seed Germination Niches: A New Hypothesis. Biotropica. 2015 April 08; 47(3):277-280. Available from: https://onlinelibrary.wiley.com/doi/10.1111/btp.12210 DOI: 10.1111/btp.12210

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Certified by Vargas Gutiérrez, German in SciENcv on 2024-10-22 00:45:19

IDENTIFYING INFORMATION:

NAME: Powers, Jennifer S

ORCID iD: https://orcid.org/0000-0003-3451-4803

POSITION TITLE: Professor

PRIMARY ORGANIZATION AND LOCATION: University of Minnesota, Saint Paul, Minnesota, United States

Professional Preparation:

ORGANIZATION AND LOCATION	DEGREE (if applicable)	RECEIPT DATE	FIELD OF STUDY
University of Minnesota, Saint Paul, Minnesota, United States	Postdoctoral Fellow	05/2003 - 12/2005	Soil science
State University of New York-Stony Brook, Stony Brook, New York, United States	Postdoctoral Fellow	12/2001 - 04/2003	Tropical ecosystem ecology
Duke University, Durham, North Carolina, United States	PHD	05/2001	Biology
Oregon State University, Corvallis, Oregon, United States	MS	10/1995	Forest Science
Reed College, Portland, Oregon, United States	BA	05/1991	Biology

Appointments and Positions

2020 - present Professor, University of Minnesota, Saint Paul, Minnesota, United States
2013 - 2020 Associate Professor, University of Minnesota, Saint Paul, Minnesota, United States
2006 - 2013 Assistant Professor, University of Minnesota, Saint Paul, Minnesota, United States

Products

Products Most Closely Related to the Proposed Project

1. Powers JS, Vargas G G, Brodribb TJ, Schwartz NB, Pérez-Aviles D, Smith-Martin CM, Becknell JM, Aureli F, Blanco R, Calderón-Morales E, Calvo-Alvarado JC, Calvo-Obando AJ, Chavarría MM, Carvajal-Vanegas D, Jiménez-Rodríguez CD, Murillo Chacon E, Schaffner CM, Werden LK, Xu X, Medvigy D. A catastrophic tropical drought kills hydraulically vulnerable tree species. Glob Chang Biol. 2020 May;26(5):3122-3133. PubMed PMID: 32053250.
2. Brodribb TJ, Powers J, Cochard H, Choat B. Hanging by a thread? Forests and drought. Science. 2020 Apr 17;368(6488):261-266. PubMed PMID: 32299945.
3. Vargas G G, Kunert N, Hammond WM, Berry ZC, Werden LK, Smith-Martin CM, Wolfe BT, Toro L, Mondragón-Botero A, Pinto-Ledezma JN, Schwartz NB, Uriarte M, Sack L, Anderson-Teixeira KJ, Powers JS. Leaf habit affects the distribution of drought sensitivity but not water transport efficiency in the tropics. Ecol Lett. 2022 Dec;25(12):2637-2650. PubMed Central PMCID: PMC9828425.
4. Willson AM, Trugman AT, Powers JS, Smith-Martin CM, Medvigy D. Climate and hydraulic

traits interact to set thresholds for liana viability. Nat Commun. 2022 Jun 9;13(1):3332. PubMed Central PMCID: PMC9184652.

5. Vargas G G, Brodribb TJ, Dupuy JM, González-M R, Hulshof CM, Medvigy D, Allerton TAP, Pizano C, Salgado-Negret B, Schwartz NB, Van Bloem SJ, Waring BG, Powers JS. Beyond leaf habit: generalities in plant function across 97 tropical dry forest tree species. New Phytol. 2021 Oct;232(1):148-161. PubMed PMID: 34171131.

Other Significant Products, Whether or Not Related to the Proposed Project

1. Toro L, Pereira-Arias D, Perez-Aviles D, Vargas G G, Soper FM, Gutknecht J, Powers JS. Phosphorus limitation of early growth differs between nitrogen-fixing and nonfixing dry tropical forest tree species. New Phytol. 2023 Feb;237(3):766-779. PubMed Central PMCID: PMC10107181.
2. Smith-Martin CM, Xu X, Medvigy D, Schnitzer SA, Powers JS. Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. New Phytol. 2020 May;226(3):714-726. PubMed PMID: 31630397.
3. Medvigy D, Wang G, Zhu Q, Riley WJ, Trierweiler AM, Waring BG, Xu X, Powers JS. Observed variation in soil properties can drive large variation in modelled forest functioning and composition during tropical forest secondary succession. New Phytol. 2019 Sep;223(4):1820-1833. PubMed PMID: 30980535.
4. Gei M, Rozendaal DMA, Poorter L, Bongers F, Sprent JI, Garner MD, Aide TM, Andrade JL, Balvanera P, Becknell JM, Brancalion PHS, Cabral GAL, César RG, Chazdon RL, Cole RJ, Colletta GD, de Jong B, Denslow JS, Dent DH, DeWalt SJ, Dupuy JM, Durán SM, do Espírito Santo MM, Fernandes GW, Nunes YRF, Finegan B, Moser VG, Hall JS, Hernández-Stefanoni JL, Junqueira AB, Kennard D, Lebrija-Trejos E, Letcher SG, Lohbeck M, Marín-Spiotta E, Martínez-Ramos M, Meave JA, Menge DNL, Mora F, Muñoz R, Muscarella R, Ochoa-Gaona S, Orihuela-Belmonte E, Ostertag R, Peña-Claros M, Pérez-García EA, Piotto D, Reich PB, Reyes-García C, Rodríguez-Velázquez J, Romero-Pérez IE, Sanaphre-Villanueva L, Sanchez-Azofeifa A, Schwartz NB, de Almeida AS, Almeida-Cortez JS, Silver W, de Souza Moreno V, Sullivan BW, Swenson NG, Uriarte M, van Breugel M, van der Wal H, Veloso MDDM, Vester HFM, Vieira ICG, Zimmerman JK, Powers JS. Legume abundance along successional and rainfall gradients in Neotropical forests. Nat Ecol Evol. 2018 Jul;2(7):1104-1111. PubMed PMID: 29807995.
5. Xu X, Medvigy D, Powers JS, Becknell JM, Guan K. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. New Phytol. 2016 Oct;212(1):80-95. PubMed PMID: 27189787.

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