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OPINION

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Representing plant diversity in land models: An evolutionary approach to make "Functional Types" more functional

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Abstract

Plants are critical mediators of terrestrial mass and energy fluxes, and their structural and functional traits have profound impacts on local and global climate, biogeochemistry, biodiversity, and hydrology. Yet, Earth System Models (ESMs), our most powerful tools for predicting the effects of humans on the coupled biosphere–atmosphere system, simplify the incredible diversity of land plants into a handful of coarse categories of "Plant Functional Types" (PFTs) that often fail to capture ecological dynamics such as biome distributions. The inclusion of more realistic functional diversity is a recognized goal for ESMs, yet there is currently no consistent, widely accepted way to add diversity to models, that is, to determine what new PFTs to add and with what data to constrain their parameters. We review approaches to representing plant diversity in ESMs and draw on recent ecological and evolutionary findings to present an evolution-based functional type approach for further disaggregating functional diversity. Specifically, the prevalence of niche conservatism, or the tendency of closely related taxa to retain similar ecological and functional attributes through evolutionary time, reveals that evolutionary relatedness is a powerful framework for summarizing functional similarities and differences among plant types. We advocate that Plant Functional Types based on dominant evolutionary lineages ("Lineage Functional Types") will provide an ecologically defensible, tractable, and scalable framework for representing plant diversity in next-generation ESMs, with the potential to improve parameterization, process representation, and model benchmarking. We highlight how the importance of evolutionary history for plant function can unify the work of disparate fields to improve predictive modeling of the Earth system.

KEYWORDS
ecosystem function, evolutionary relatedness, functional diversity, Lineage Functional Types, phylogenetic signal, Plant Functional Types, vegetation models

1 | INTRODUCTION

There are over 400,000 described vascular plant species on Earth, which collectively represent a profound diversity of form, function, and life history (IPBES, 2019). Decades of research into plant functional ecology, ecophysiology, and community ecology have revealed many causes and consequences of this diversity. At the same time, sophisticated representations of physiological, ecological, hydrological, and biogeochemical plant processes have been codified in the terrestrial processes of Earth System Models (ESMs) that simulate key aspects of **ecosystem function** (e.g., energy, water, and CO_2 fluxes). However, even as mechanistic realism increases in these models, the representation of plant diversity—the evolved variation in phenotypes that influences these functions—remains quite simplistic. Vegetation models use a small number of vegetation “Plant Functional Types” or **PFTs** (e.g., 5–20) to represent archetypal end members of plant functional variation that most strongly influence ecosystem processes (DeFries et al., 1995). Each PFT is represented by a set of parameter values (e.g., photosynthetic capacity, canopy roughness, nutrient uptake efficiency, rooting depth), and the variation in these parameters, combined with differences in process representations (e.g., C3 vs. C4 photosynthesis, cold hardening, drought deciduousness), gives rise to modeled plant **functional diversity** (FD). In most modern models, multiple PFTs can exist in the same grid cell, and often these PFTs compete for shared water and nutrient resources (Riley et al., 2018). Moreover, advances in the representation of size- and age-structure with “vegetation demographic models” (Fisher et al., 2018) allow cohorts of different PFTs to compete for light.

The historic Plant Functional Type paradigm has proven useful to model biosphere–atmosphere interactions over multiple decades of advances, but increasing ecological realism in the variation among plants is an important area for model improvement. The current PFTs in ESM land models remain extremely coarse, rooted in a classic biome and growth-form-based concept (Bonan et al., 2003; Clark et al., 2011; Lawrence et al., 2019; Sitch et al., 2003). Fundamentally, these PFTs have their origins in correlative climate–vegetation models (Köppen, 1936), ecological “functional guilds” (Root, 1967), and biome concepts (Raunkiær et al., 1934; Whittaker, 1975). Although they were the result of much careful thought (Smith et al., 1997), most current models contain fewer than 20 PFTs to represent all land plants, and the PFTs boil down to growth form (e.g., trees, shrubs, grasses, forbs), phenology (evergreen vs. deciduous), photosynthetic pathway, and sometimes climate (temperate vs. tropical). This combination of factors is thought to capture first-order global variations in plant function (DeFries et al., 1995), though it necessarily assumes that widespread biomes such as savannas and hyperdiverse biomes like tropical rainforests can be represented by one or two PFTs each.

It is widely accepted that current PFTs do not capture the majority of variation along key plant functional axes (e.g., Wright et al., 2004), and that better representation of diversity is needed (i.e., more or different functional types) in order for models to move beyond simulating short-term ecosystem fluxes to predicting long-term vegetation shifts and their associated vegetation–climate feedbacks (Fisher et al., 2015). Indeed, even in the early 1990s, it was recognized that PFTs suffered both philosophical and practical challenges that have yet to be addressed (Box, 1996; Smith et al., 1997). Copious observations and experiments have proven just how critical real-world diversity is for ecosystem function (Isbell et al., 2012; Liang et al., 2016; Tilman, 1996). For example, diversity significantly increases ecosystem resistance to and recovery from climate variability and extreme events (Anderegg, Konings, et al., 2018; Isbell et al., 2015). Yet, many open questions remain about how to increase the diversity of PFTs in models. How many PFTs are needed to adequately represent functional diversity within communities and across the landscape? Which new PFTs are most important? What observations should be used to parameterize new PFTs? And how do these answers change with model spatial extent or resolution (e.g., for fine-scale regional versus coarse-scale global simulations)?

“Tree thinking,” or approaches informed by plant **phylogeny** that consider evolutionary relatedness, has been influential in a broad range of fields and has been suggested for further nuancing how models represent diversity (Edwards et al., 2007). For example, new “Lineage Functional Types” (LFTs) representing three dominant global grass clades can capture considerable variation in physiology, morphology, and response to disturbance that the two classic grass PFTs—which differentiate only C3 vs. C4 photosynthetic mechanisms—cannot capture (Griffith et al., 2020). Here, we summarize the evidence for why evolutionary lineages provide a natural backbone for future functional type delineation, and discuss the potential benefits of “tree thinking” for constraining model parameters, guiding model process development, and expanding model benchmarking options. Closely related species share a large proportion of their ancestry such that their genomes are very similar. Consequently, when integrating across all plant functions coded by their genomes, functional similarity is likely to be very high. Because of this, many key aspects of plant function are evolutionarily conserved, meaning closely related species are more functionally similar than distantly related species (Wiens et al., 2010). This critical pattern can help the research community leverage burgeoning trait databases, community surveys, biogeographic observations, remote sensing data, and ever-improving plant phylogenies to inform both model process and parameter uncertainty.

1.1 | The parameterization problem

Part of the issue limiting the proliferation of PFTs lies in the delicate balance that land models must strike between realism and parsimony (Prentice et al., 2015). While more sophisticated representations of biodiversity (i.e., more PFTs) are needed to simulate ecological processes such as niche differences, land models already suffer from fundamental issues of **equifinality** (many different parameter sets yield similar predictions, making more complicated models more difficult to parameterize to the point where added complexity decreases model predictive ability; Tang & Zhuang, 2008). It therefore remains paramount to constrain model parameters to avoid the “complexity trap” (Prentice et al., 2015). The question of how much process complexity to include in vegetation models is often treated separately from the question of how to represent functional diversity in those processes, but they are inextricably linked as the parameterization challenge increases with both the number of

BOX 1 Glossary

Ecosystem function: Processes and properties that mediate fluxes of energy and matter such as gross primary productivity (photosynthesis), net primary productivity (photosynthesis minus respiration), evapotranspiration, cycling of macronutrients and micronutrients, etc.

PFTs: Plant Functional Types, the standard method of representing the diversity of plant form and function in land models via a small number of archetypal plant types, currently based on growth form, climate, and phenology in most models.

Phylogeny: The evolutionary history of a group of organisms, represented via a hierarchically bifurcating tree, which depicts the diversification from a common ancestor and evolutionary relatedness of organisms and lineages. "Dated" phylogenies also estimate the time since evolutionary divergence of lineages based on fossils, the rate of accumulation of genetic mutations, or both.

Functional diversity (FD): The amount of functional distinctiveness in a community, often quantified based on the univariate or multivariate distribution of one or more functional traits among community members.

Equifinality: An issue in model parameterization and structure where different parameterizations yield equally accurate (probable) model predictions based on available training data.

Plant functional traits: Measurable morphological, chemical, phenological, and physiological plant attributes that influence fitness by affecting growth, survival, and reproduction. Many model parameters are related to or sometimes explicitly designed to represent measurable plant functional traits such that the parameters can be constrained by observations. We note that a trait, as defined in this way, need not be static or unchanging for an individual plant or species through time or in response to environmental variation. Whether a model considers a particular trait to be static is an important indicator of underlying model assumptions. Example of functional traits used in the text include the following: N_{mass}—leaf nitrogen content per unit mass, N_{area}—leaf nitrogen per unit area, *LeafLife*—leaf lifespan, *LMA*—leaf mass per unit area, *WD*—wood density, *xylem* P_{50}—the xylem pressure causing 50% loss of hydraulic conductance due to embolism, K_s—xylem hydraulic conductance (inverse of hydraulic resistance) per unit sapwood area, A_L:A_S—leaf area to sapwood area ratio, R:S—root biomass to shoot (leaf + stem) biomass ratio.

LFT: Lineage Functional Types, a method of representing plant functional diversity in vegetation models based on niche conservatism (i.e., the functional relatedness of closely related evolutionary lineages).

Niche Conservatism: A widely observed pattern across many taxa that close relatives maintain similar ecological niches (the combination of abiotic and biotic factors that determine where a species can exist) through evolutionary time. This ecological similarity implies that closely related species have similar functional traits.

Phylogenetic scale: The breadth of evolutionary relatedness, and thus time since most recent common ancestor, considered in an analysis. Genetic differences among populations within a species (e.g., microevolution) or sister species within a genus would represent a finer phylogenetic scale than variation among more distantly related taxa such as plant genera or families (e.g., macroevolution).

Phylogenetic signal: The tendency of related species to more closely resemble each other than species drawn at random from the same evolutionary tree.

Community-weighted mean (CWM): Effective trait value for a plant community, averaged across species and weighted proportionally to each species' dominance in the community (often determined by % of basal area or % of leaf area).

model parameters and the number of PFTs (or more, if interactions between PFTs are themselves parameterized).

To address this parameterization challenge, ecologists have made a major push to constrain models with real-world observations of "**plant functional traits**" that theoretically relate to model parameters (Dietze et al., 2014) that affect vegetation responses to environmental change. Indeed, one of the main motivations for the creation of TRY, the largest plant trait repository in the world (Kattge et al., 2011), was to improve model PFTs. However, without a rigorous, internally consistent, scalable, and ecologically motivated framework for defining what PFTs should represent, model developers and users are often forced to make arbitrary decisions about which observations should inform the parameter values of newly developed functional types.

1.2 | Existing PFT alternatives

One alternative to current PFTs is "trait-based modeling," where functional types are not prescribed based on a limited number of pre-defined PFTs but either emerge from a modeled competitive search through potential parameter space (Pavlick et al., 2013; Sakschewski et al., 2015; Scheiter et al., 2013) or are completely absent and parameter values are applied based on empirical trait–environment relationships (van Bodegom et al., 2011; Verheijen et al., 2015). However, these two approaches face fundamental limitations to their implementation in ESM land models. Approaches based on competitive algorithms are limited by the fact the key physiological traits invoked as model parameters are not necessarily the traits that explain real, ecological niche differences (Fisher et al., 2018; Kraft et al., 2015). This is a problem for all dynamic vegetation models simulating competition and coexistence, but is made greater when parameter variation and covariation are constrained largely by trait theory (e.g., assumed functional tradeoffs, Pavlick et al., 2013). It is difficult to simulate coexistence *de novo* in land models based on partially understood physiological and ecological tradeoffs, when true coexistence is likely a "high-dimensional" ecological problem (Clark et al., 2010), with multiple stabilizing mechanisms not included in models (van Bodegom et al., 2011). In short, unconstrained (i.e., purely "trait-based" or PFT-free) competitive algorithms are extremely useful ecological tools, but it remains hugely challenging for relatively simple physiologically based models to solve what the entire field of community ecology is still working hard to explain (coexistence and the maintenance of biodiversity) in order to predict global ecosystem function in a changing environment.

Meanwhile, approaches based on empirical trait–climate relationships face their own problems, chief among them being that trait–climate relationships are extremely elusive when looking across land plants as a whole (rather than among closely related species). Extensive research into leaf economic traits such as leaf mass per area (LMA), nutrient concentrations, and maximum assimilation rates have found that (1) a diversity of economic strategies are present in essentially all ecosystems worldwide (Wright et al., 2004); (2) average trait values show very weak relationships with environmental variables (Maire et al., 2015; Ordoñez et al., 2009); and (3) trait–environment relationships are not consistent across taxonomic and ecological scales (Anderegg, Berner, et al., 2018). Ultimately, trait-based approaches have greatly furthered ecological knowledge but are currently limited in their scalability and applicability to ESM land models.

2 | LETTING EVOLUTION BE OUR GUIDE

We outline below how lineage-based functional types present an ecologically defensible and scalable method for integrating data on organismal abundance, functional diversity, remote sensing, and evolutionary relatedness in order to define, parameterize, and test the next generation of PFTs for vegetation modeling. We argue that explicitly making evolutionary lineage the organizing principle behind future functional types will facilitate efforts to add diversity to PFT-based land models.

2.1 | Plant function is phylogenetically linked

Eco-evolutionary theory and observations have come a long way since the development of the original physiognomy-based PFT concept. In particular, "**Niche Conservatism**" (NC), or the tendency for species or clades to retain their niches and related ecological traits over time (Figure 1a), has emerged as a dominant theme of

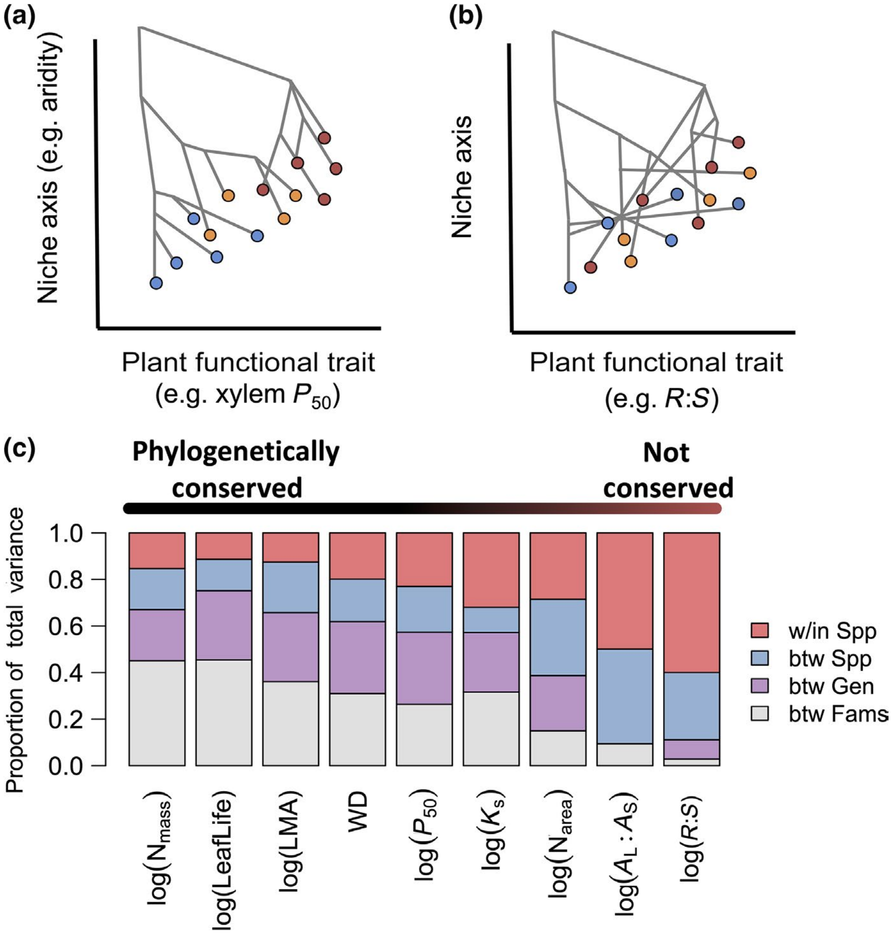

FIGURE 1 Plant function is phylogenetically conserved: (a) conceptual example of phylogenetic conservatism of both environmental niches (*y*-axis) and plant functional traits invoked as parameters in Land Models (*x*-axis). Gray lines illustrate evolutionary relatedness (e.g., phylogeny) for three lineages (colors), with related species being similar in both niche and trait values. (b) The less common alternative example of a niche axis and associated functional trait that are not phylogenetically conserved. (c) Taxonomic variance decomposition of example "plant functional traits" that are sometimes considered model parameters. Many leaf and stem traits vary primarily at broad taxonomic scales (e.g., among plant families, gray bars), suggesting that lineage is a good predictor of trait values. However, some plant traits such as root to shoot biomass ratio (R:S) are less strongly conserved and may be best modeled as emergent properties from underlying processes. See Box 1 for trait descriptions and SI "*Methods for variance decomposition*" for data descriptions [Colour figure can be viewed at wileyonlinelibrary.com]

macroevolution (Crisp & Cook, 2012; Wiens et al., 2010). While adaptive radiation within lineages is well documented, at broad **phylogenetic scales** members of a lineage tend to be more similar ecologically and physiologically to each other than to members of other lineages by virtue of the high proportion of their shared ancestry and hence genome similarity (Cavender-Bares et al., 2006). Some aspects of species' niches are particularly strongly conserved; for instance, the thermal niche is a highly conserved niche axis that leads to widespread "biome conservatism" or the tendency for clades to remain in their ancestral biome and switch to new biomes only rarely (Crisp et al., 2009). NC appears to underpin many ecological interactions, including competitive dynamics (Burns & Strauss, 2012) and pathogen susceptibility (Gilbert & Webb, 2007).

Importantly, ecological similarity among related taxa translates into functional similarity, providing a powerful framework for summarizing and ultimately parameterizing the functional attributes of entire clades. Indeed, many plant traits that are related to model parameters show **phylogenetic signal** (Ackerly, 2009; Swenson, 2013). Variance decomposition of numerous leaf and stem traits attributing the percent of total variation to levels of the taxonomic hierarchy typically reveals that most variation occurs at broad phylogenetic scales (among plant families), with decreasing variation within families, genera, and species (Figure 1c, see SI "*Methods for variance decomposition*"). This pattern even appears to hold for less well-sampled hydraulic traits that are increasingly incorporated into models (e.g., xylem P_{50} and K_s in Figure 1c, see Box 1, Sanchez Martinez et al., 2020).

While the taxonomic hierarchy is a coarse stand-in for well-supported and dated phylogenies, the explanatory power of deep evolutionary divergences supports lineage as a defensible approach to assign trait values for a group of plants. The evolutionary null hypothesis that closely related species are more functionally similar than distantly related species is rarely disproven. Indeed, 20th-century ecology has a long history of describing the clade-based ecological characteristics of plant families (a simplification still employed in the hyperdiverse tropics where species-specific natural history knowledge is rare), implicitly acknowledging the power of niche conservatism. In fact, the strength of phylogenetic signal in many traits has led some to use phylogeny to "gap fill" missing trait values in trait databases (e.g., Swenson, 2013; Schrodt et al., 2015).

Niche conservatism can arise from a number of ecological and evolutionary processes (Crisp & Cook, 2012), and thus phylogenetic signal in functional traits does not necessarily imply anything about trait lability or canalization (how evolvable a trait is). But the widespread phylogenetic signal observed does suggest that evolutionary history is a strong predictor of modern ecology. Indeed, in community ecology, functional niche conservatism has been so widely accepted that phylogenetic diversity is often used as a proxy for hard-to-measure functional diversity (Srivastava et al., 2012). We note, however, that there are many nuances and complications in assuming phylogenetic distance equals ecological niche difference for specific ecological applications (Cadotte et al., 2017; Cavender Bares et al., 2004; Gerhold et al., 2015; Mayfield & Levine, 2010).

The implications of niche conservatism for vegetation modeling are twofold. First, *PFTs rooted in evolutionary relationships could defensibly allow estimation of model parameters from sparse observations* (essentially leveraging phylogenetic signal to "gap fill" model parameterization). Second, lineage-based functional types probably will not need to be revisited every time a new functional axis is incorporated into model structure, because *evolutionary relatedness likely ensures functional similarity within a lineage even for functions that we do not yet fully understand* or have implemented in vegetation models. For instance, acclimation responses such as those involved in cold tolerance are a modeling challenge but show strong phylogenetic signal (Lancaster & Humphreys, 2020), and life-history traits that might inform "demographic functional types" in size-structured models (Rüger et al., 2020) are likewise probably phylogenetically conserved.

Some important traits are conspicuous exceptions to this rule. For example, leaf nitrogen per unit leaf area (N_{area}) and allometric traits such as root to shoot biomass ratio (R:S) or leaf area to sapwood area ratio (A_L:A_S) vary enormously within species and over time (Figure 1), and show little fidelity to phylogenetic relationships. Indeed, the extent to which a trait shows phylogenetic signal may indicate whether it is appropriate as a "parameter" in land models. Traits that consistently show little phylogenetic signal and large within-species variation may well be dynamic properties that can vary through time for an individual (e.g., through acclimation) or across environments for a species. Such traits are unlikely to maintain the same value for a model PFT through space and time, and should be treated as emerging from underlying physical and physiological processes. Allocation for instance, which can vary enormously across ontogeny, may best be simulated to emerge from economic optimization (Fisher et al., 2018) or a combination of gradient-based carbon and nutrient concentrations, plant transport, and nutrient acquisition-related traits (Mekonnen et al., 2019; Thornley, 1997; Zhu et al., 2019). These underlying processes themselves may have phylogenetically conserved parameters linked to evolutionary history, and a lack of phylogenetic signal may highlight critical areas for future research.

2.2 | Tree thinking to inform process as well as parameterization

One important trait that illustrates the utility of tree thinking for model development is leaf habit (evergreen vs. deciduous). Deciduousness has long been recognized as a central trait for capturing annual variation in biosphere–atmosphere interactions (DeFries et al., 1995). Thus, leaf habit is a key component of all current PFT schemes. In some instances, lineage-based functional types may result in lumping together deciduous and evergreen species in a way that classic PFTs do not. However, closer investigation of leaf habit, and especially its more informative cousin, leaf lifespan, reveals a number of interesting modeling-relevant

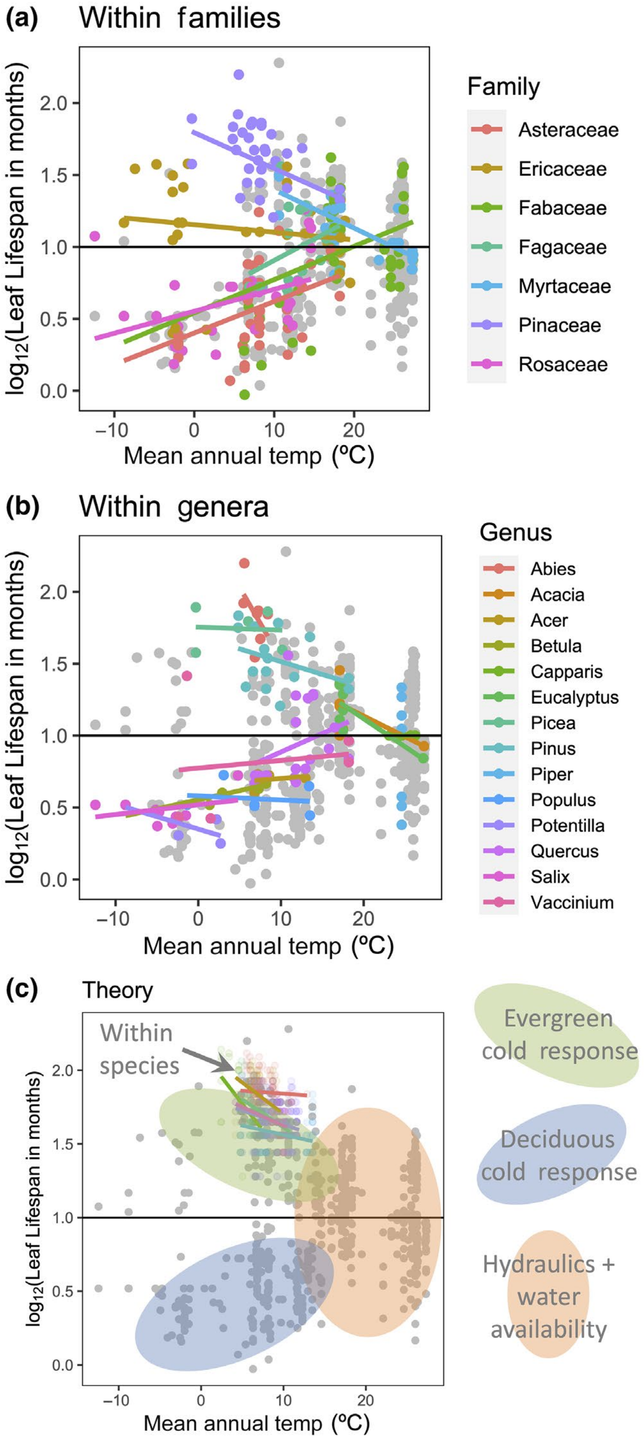

FIGURE 2 Lineage-specific leaf lifespan responses to temperature. Leaf lifespan in months plotted against the Mean Annual Temperature (°C) of the sampling location. Gray points show all species-level observations, Leaf lifespan is $\log_{12}$-transformed so 1 = one year. (a) Within-family patterns in the seven most well-sampled families, showing either increased longevity or increased winter deciduousness at colder temperatures. (b) Within-genus patterns are similar to family-level patterns, with genera outside the tropics typically adopting either a universal evergreen or deciduous strategy. (c) Qualitative schematic of the two cold response strategies and the area where plant hydraulics plus water availability likely dictate leaf habit in the absence of cold stress; within-species patterns in conifers are plotted in colored lines and transparent points. Data from Law and Berner (2015) and Wright et al. (2004) [Colour figure can be viewed at wileyonlinelibrary.com]

observations. First, across the tree of life, leaf lifespan varies primarily among deep evolutionary nodes (see Figure 1), so LFTs will naturally capture much variation in leaf habit even without considering it as an explicit grouping criterion. Second, patterns of leaf lifespan as a function of temperature reveal family-specific responses to cold stress. Moving into colder climes, the most well-sampled families in the GLOPNET global trait database (Wright et al., 2004) appear to follow one of the two strategies: increasing longevity with decreasing temperature (Pinaceae, Ericaceae, and Myrtaceae, Figure 2a) or decreasing longevity (e.g., Asteraceae, Figure 2a). This pattern largely holds true at the genus level (Figure 2b), with members of most genera that live at mean annual temperatures below 10°C typically being either all evergreen or all deciduous. Temperature-related changes in leaf lifespan even appear to hold true within individual species, at least in conifers (Figure 2c; Anderegg, Berner, et al., 2018; Reich et al., 2014).

Where cold stress is absent (e.g., in the tropics), leaf lifespan is more variable within clades. However, leaf phenology in the tropics is linked to plant hydraulic strategy (Xu et al., 2016), and exciting developments with dynamic leaf allocation in plant hydraulics models have demonstrated the ability to predict drought deciduousness and semi-deciduousness purely from the interaction between hydraulic traits and the environment (Trugman et al., 2019). Thus, we believe that deciduousness may eventually be predicted from lineage-specific responses to cold stress and hydraulic optimizations and need not be an overriding consideration for PFT delineation.

In another example of evolutionary insights informing model development, Griffith et al. (2020) demonstrated both the parametric and process importance of a new LFT classification for grasses worldwide. Classic grass PFTs differentiate only between C_3 and C_4 photosynthetic pathway types. Yet, most grasslands are dominated by three major lineages (one C_3-only and two C_4-only lineages), which inhabit distinct parts of the globe and differentiate physiologically, morphologically, and in their responses to disturbances (Edwards & Still, 2008; Griffith et al., 2020; Lehmann et al., 2019). Thus, evolutionary lineage provides a straightforward and efficient means to improve representation of grasses in land models using existing data to guide parameterization. But perhaps more importantly, the two dominant C_4 lineages show marked differences in hydraulic traits and fire-related traits, suggesting that both hydraulics and fire may be critical processes to include in models in order to simulate grassland fluxes and biogeography (Griffith et al., 2020).

3 | EVOLUTION AS A SCALABLE GUIDE FOR DISAGGREGATING FUNCTIONAL DIVERSITY

Evolutionary lineages provide a major benefit to vegetation modelers over growth-form- and biome-based approaches: they provide a theoretically consistent approach to spatial scaling. Modeling studies at different spatial scales (e.g., plot, regional, global) require different levels of granularity to represent functional diversity. Currently, modelers must rely on expert opinion, empirical classification algorithms, and "gut instincts" to determine how many and which PFTs to simulate and which data to use to constrain parameters for those functional types. Classic PFTs sometimes *de facto* represent lineages, but explicitly tying functional types to evolutionary lineage provides a scalable and theoretically defensible approach to further disaggregate functional diversity. Unlike biome or growth form, which are categorical, evolutionary relatedness is a continuous variable that can be as coarse or granular as needed.

Two patterns from community and ecosystem ecology highlight first that the biggest effects of function diversity can likely be captured with a tractable number of functional types even at the site or landscape level and second how plot-level inventory data can be used to identify important functional types across scales using an evolutionary lineage-based approach. The first observation is that, supporting Grime's "biomass ratio hypothesis" (Grime, 1998), many ecosystem functions appear to be influenced by plant community members roughly in proportion to their biomass (e.g., Finegan et al., 2014; Garnier et al., 2004). This observation *does not* imply that diversity does not matter. But it does imply that true "keystone" plant species are relatively rare when considering only ecosystem fluxes, and that dominant species tend to influence ecosystem function in proportion to their dominance (Avolio et al., 2019). Thus, much of the variation in plant function between communities can be explained by the biomass-weighted or **community-weighted mean** (CWM) functional traits of the communities. Meanwhile, functional diversity within communities is typically determined by functional diversity among the most dominant species in that community. These two scales (functional variation among communities across space versus functional diversity within communities) roughly translate to functional differences across ESM grid cells versus the diversity of PFTs within a grid cell (e.g., PFTs that directly compete for light, water, and nutrients, depending on the specific vegetation model). The utility of the biomass ratio hypothesis suggests that a tractable number of PFTs should suffice to capture first-order functional variation across modeling scales, both within and among communities.

Second, most plant communities are comprised of a few abundant and many rare species. This foundational pattern in community ecology (e.g., in the "niche vs. neutral" debate (Hubbell, 2001; Tilman, 2004)) holds true even in the hyperdiverse tropics, where "hypderdominance" of a few taxa (10s to 100s of taxa rather than 1000s) emerges across large geographic areas (ter Steege et al., 2013). Together, these two observations (that ecosystem function is largely controlled by the dominant species and that most communities are composed of a few dominant species) greatly simplify the challenge of representing plant functional diversity within and among communities in land models. We can simultaneously acknowledge that biodiversity really matters for ecosystem function and yet not despair about needing to model all ½ million plant species to capture the influences of diversity on ecosystem function.

Based on the logic above, defining new PFTs requires balancing functional distinctiveness (to capture as much functional diversity as possible) and a focus on dominant plant types (to capture the most important groups for ecosystem function). Phylogenies therefore provide a ready-made and conceptually elegant backbone for aggregating observations of species diversity and abundance (e.g., from biodiversity surveys and forest inventories) to identify the most evolutionarily diverse (and likely most functionally diverse) and the most abundant lineages at any desired spatial scale.

3.1 | A practical example of describing new LFTs

The forests of the Pacific Northwest, USA provide an illustration of how a phylogenetic approach informed by abundance data can guide the disaggregation of coarse PFTs into finer LFTs. A network of 256 plots was explicitly designed to measure forest productivity and modeling-relevant traits across Oregon and northern California for parameterizing ESMs for regional simulations (Berner & Law, 2016; Law & Berner, 2015). Stand surveys extensively quantified community composition, and trait measurements such as leaf mass per area (LMA), Leaf Lifespan, and leaf nitrogen content per unit mass (N_{mass}) were collected from 37 woody species in these plots, approximately in proportion to their abundance. Yet, two species (*Pseudotsuga menziesii* and *Pinus ponderosa*), and more generally two clades of the Pinaceae family (the abietoides and pinoids), represent the vast majority of the biomass in the region (Figure 3). Because site-specific traits were extensively sampled, we calculated the true variation in functional diversity across plots based on observed community-weighted mean traits (Anderegg, Berner, et al., 2018). We also calculated the functional diversity within plots using functional diversity metrics that incorporate elements of functional richness, evenness, and occupied niche space (here we average results using Functional Dispersion (Laliberté & Legendre, 2010) and Rao's quadratic entropy (Botta-Dukát, 2005), which can be weighted by relative abundance and can be calculated for communities with fewer than three species). We then compared the efficacy of different functional type groupings by comparing observed FD within and among communities with FD calculated using a single mean trait value per functional type (see SI "*Methods for Pacific North West Functional Diversity analysis*").

Traditionally, all of the woody species in the region would be represented by at most three growth-form and phenology-based PFTs, which together capture an average of only 6% of the CWM variation in LMA, Leaf Lifespan, and N_{mass} among communities and an average of 16% of the FD within communities (Figure 3). A similar categorization based on evolutionary lineage (at the family level for the gymnosperms and lumping all angiosperms together—termed "Deep LFT" in Figure 3 for how deeply the phylogenetic tree is trimmed) captures slightly more of the variation in CWM traits among communities (9% on average) and slightly less diversity within communities (12%). This result is expected, as classic PFTs and "Deep LFTs" are quite similar (Table S1). LFTs guided by abundance prioritize the

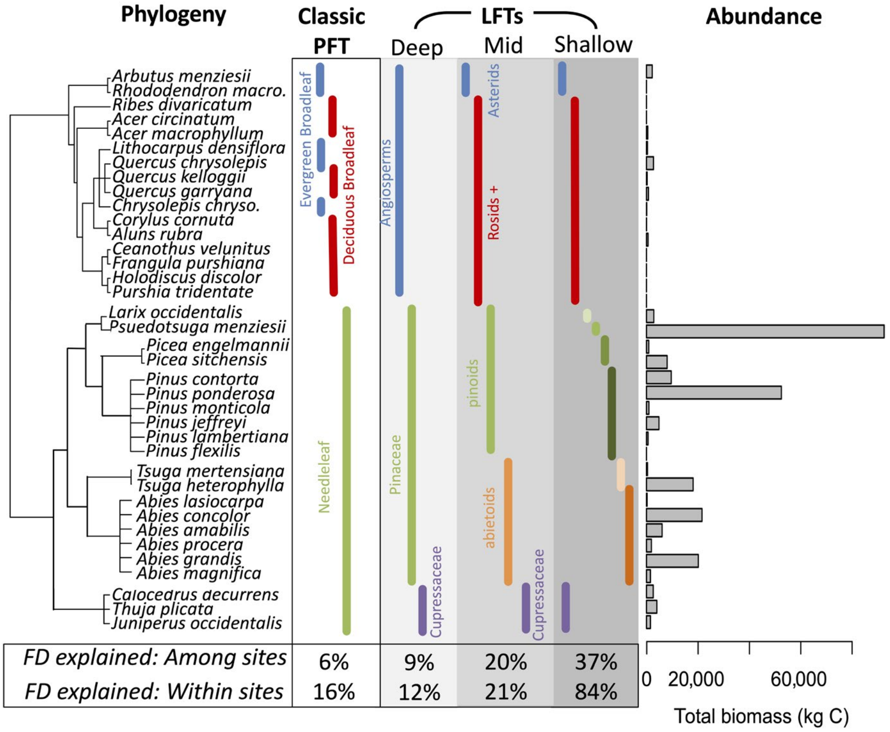

FIGURE 3 Example of Functional Types in the PNW U.S.A. Phylogeny of woody plants in a network of 256 forest plots in the Pacific NW, USA (Law & Berner, 2015), with four example disaggregation schemes, and the distribution of total biomass across the species showing hyperdominance of a small number of species. Percentages indicate the average amount of variation in Functional Diversity (FD) explained among sites (variance in community-weighted mean LMA, Leaf Lifespan, and N_{mass}; see Box 1) and within sites (variance in Functional Dispersion and Rao's quadratic entropy) explained by each disaggregation scheme. The "Classic PFT" scheme used in many land models and a coarse Lineage Functional Type (LFT) approach ("Deep," because it is divided deep in the phylogenetic tree) explain similarly low amounts of variance, while further disaggregation breaking up the major angiosperm lineages present and the lineages of the dominant Pinaceae family ("Mid LFT") and then dividing Pinaceae into genera ("Shallow LFT") explain an increasing fraction of FD within and among sites. See SI "*Methods*" for full analysis description [Colour figure can be viewed at wileyonlinelibrary.com]

functional distinction among gymnosperms, while classic PFTs prioritize the leaf habit distinction among angiosperms that happen to be quite rare in this system. And ultimately, no three-group functional type scheme can be expected to capture the true FD of even low diversity systems. However, the LFT approach provides an obvious framework for further disaggregation.

By splitting the most evolutionarily divergent angiosperms (acknowledging extreme evolutionary and therefore functional distinctiveness) and dividing the Pinaceae family into the abeitoid and pinoid subfamilies (acknowledging that Pinaceae dominate 95% of the biomass), a lineage-based division with only five functional types ("Mid LFT") captures 20% of the variation in CWM traits and 21% of the variation within communities (Figure 3). Further division focusing on the most abundant lineages (breaking the Pinaceae into genera, "Shallow LFT") captures an average of 37% of the between-community variation and a startling 84% of the within-community functional diversity with nine LFTs (see Table S1 for example parameter values). The "Mid" and "Shallow" LFT examples presented here are based on qualitative weighting of evolutionary distinctiveness and abundance, but development of a quantitative weighting scheme would be feasible with appropriate abundance data and a dated phylogeny, perhaps employing sensitivity tests to determine the appropriate balance between weighting functional distinctiveness and dominance.

Low diversity temperate forests, while tractable for calculating true functional diversity from extensive observations, are admittedly a relatively simple example system. However, the ability of lineage- and abundance-guided LFTs to capture within- and among-site functional variation in a system where intraspecific trait variation is important (Anderegg, Berner, et al., 2018) and where rare evolutionary outlier species such as the deciduous conifer *Larix occidentalis* could be particularly troublesome provides hope for using LFTs in more diverse systems.

Are LFTs "better" than alternative PFT methods? One of the many difficulties in answering this question is the general lack of alternative *a priori* PFT delineation methods to compare against. *A posteriori* empirical clustering of observed traits can capture more trait variation than essentially any *a priori* classification technique. However, the Pacific Northwest forest example illustrates the limitations of empirical clustering in terms of interpretability and applicability for determining model PFTs. The "Shallow LFT" captures an average of 59% of the total variation in LMA, N_{mass}, and Leaf Lifespan when applied to the entire database of all individual trait measurements (rather than plot-level CWM traits). With nine clusters, agglomerative Ward clustering can capture an average of 78% of variation in the same traits and *k*-means clustering can capture an average of 79% of the variance. However, empirical clustering approaches yield widely different groups depending on algorithm type (e.g., Table S2 for Ward vs. *k*-means clustering) and are fundamentally limited by interpretability. Clustering on the full trait database invariably places measurements from most species, even rare species, in multiple clusters (e.g., Table S3), meaning the clusters do not have a taxonomic interpretation and could serve as "trait-based Plant Functional Types" *only if one knows all the traits*. A regional simulation using these empirical PFTs could not map the PFTs for initialization or model validation, and the PFTs could not be employed for site-based simulations outside the training sites. Meanwhile, clustering on CWM traits could capture more spatial variation in traits than LFTs can, but could not capture within-community FD (because the algorithm is classifying sites, rather than individuals).

Finally, a useful example of how lineage naturally captures multiple (often unknown) axes of functional diversity: the Shallow LFT predicts the climate-of-origin of trait measurements in the PNW trait dataset, because lineages tend to have conserved biogeographic niches. Empirical clustering algorithms on traits alone explain similar variation in temperature-of-origin but considerably less variation in climate-of-origin along any water-related climate axis compared to LFTs (Table S4). Thus, even though none of the clustering methods explicitly considered biogeography, a lineage-based approach naturally captures biogeographic patterns resulting from niche conservatism.

4 | IMPLICATIONS FOR BENCHMARKING MODEL BIOGEOGRAPHY

One key goal of dynamic vegetation models in ESMs is to predict vegetation shifts and their attendant vegetation–climate feedbacks under climate change. We believe that evolution-based PFTs could help predict shifting functional traits across the landscape without relying on the empirical climate envelopes that have long been the crutch of Dynamic Global Vegetation Models (Fisher et al., 2015; Sitch et al., 2003). To judge our success at simulating biogeography without climate envelopes, the PFTs used in dynamic models need be relatable to observational biogeographic datasets. Paleoclimate records from pollen reconstructions are typically already aggregated to the genus or higher (e.g., Jackson et al., 2000), making them useful benchmarking datasets if functional types are also grounded in evolutionary lineage. Species-level biogeographic observations (e.g., of post-industrial range shifts) can also easily be aggregated up to the relevant scale to provide model benchmarks if functional types have a taxonomic basis. Thus, LFTs naturally lend themselves to biogeographic benchmarking.

One particularly exciting feature that may make Lineage Functional Types both easier to operationalize and useful for benchmarking longer term vegetation model dynamics is that they can potentially be remotely sensed by satellite. There is considerable evidence that the spectral properties of plant canopies are phylogenetically conserved, similar to physiological traits (Cavender-Bares et al., 2016, 2017; Meireles et al., 2020; Schweiger et al., 2018) and that phylogenetic lineages can be remotely sensed (Cavender-Bares et al., 2021). Whether serendipitously or mechanistically linked to ecological niche conservatism, the phylogenetic conservatism of plant spectra (Meireles et al., 2020) could allow rapidly proliferating hyperspectral data to be used to map LFTs. The combination of plant or plot-scale hyperspectral data from experiments (Cavender-Bares et al., 2016; Schweiger et al., 2018), landscape-scale data from aircraft hyperspectral platforms such as the U.S. National Ecological Observatory Network's Airborne Observation Platform (NEON, n.d.), and ultimately satellite data, hold great promise for linking evolutionary relatedness to large-scale patterns of lineage presence and abundance. There are many challenges for scaling from phylogenetic relationships of plants with canopies of ~0.1–10 m size to satellite remote sensing pixels (e.g., ~30 m resolution for upcoming hyperspectral satellites) to model grid cells (~10–100 km for most current ESMs) (Figure 4). However, if approaches such as spectral unmixing can enable downscaling of sufficient resolution to capture the dominant LFTs of a model grid cell, hyperspectral satellite data—soon to be available from Germany's DESIS, Japan's HiSUI, and NASA's EMIT sensors on the International Space Station and planned Surface Biology and Geology (SBG) satellite (Schimel et al., 2020)—could be harnessed for global LFT mapping. While the use of these data to directly map functional traits is promising for initializing trait-based models, the actual identity of taxa at a location can tell us considerably more information about many important unobserved or unobservable traits than single traits themselves (Clark, 2016), and could potentially (through spectral unmixing) inform trait and LFT diversity within a grid cell. Moreover, remote sensing of lineage presence and abundance through time could provide model benchmarking data independent of the short-term (seasonal to interannual) flux measurements often used for model benchmarking (e.g., iLAMB, Collier et al., 2018).

5 | CONCLUSION: FUTURE OPPORTUNITIES AND CHALLENGES

Actualizing a lineage-based functional type representation of plant diversity requires merging multiple sources of phylogenetic, trait, and diversity data to address three key challenges:

1. **Find where niche conservatism breaks:** Identify which model-relevant traits show little phylogenetic signal and develop theoretically defensible ways to simulate the underlying processes determining these traits. Allometric traits and area-based leaf traits are important current model parameters that probably fall into this category. Both groups of traits are likely determined by the interactions of multiple underlying processes and properties. Improved understanding of the ecological and evolutionary forces driving niche conservatism and phylogenetic signal in

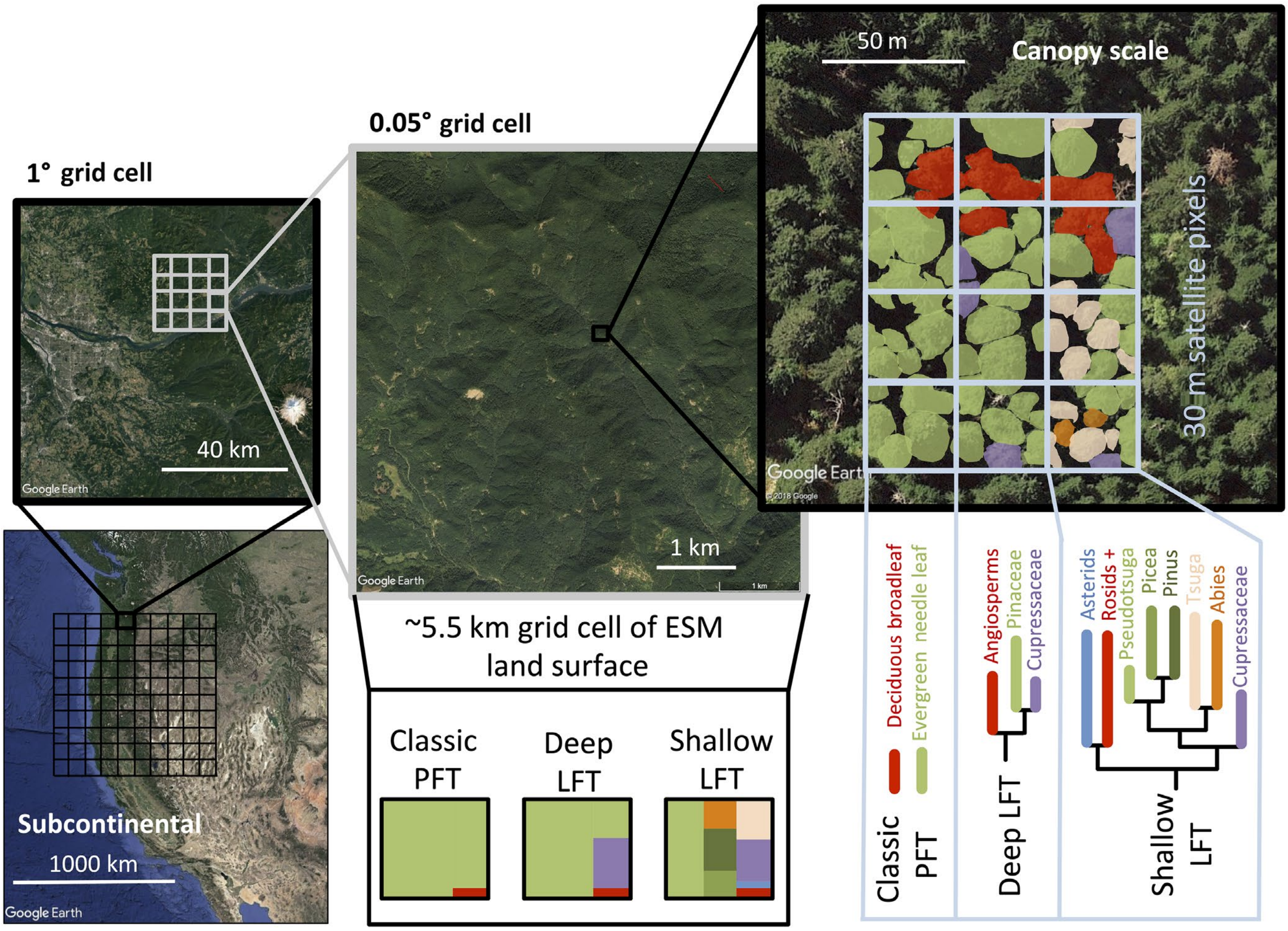

FIGURE 4 Scaling LFTs from canopy to landscape. Even a relatively low species richness forest in the Pacific Northwest, USA poses challenges both to the remote sensing of diversity with satellites with the resolution of 10s of meters (Canopy Scale panel) and to the representation of diversity in ESM grid cells that range from 0.05° (~5.5 km in the temperate zone) to 1°. However, the phylogenetic signal in plant spectra may facilitate the identification of dominant lineages in pixels representing multiple plant canopies, and ultimately the identification of the dominant Lineage Functional Types at continental scales. The explanatory value of lineages, and our ability to detect them, may vary with scale. Dividing vegetation based on large phylogenetic differences (Deep LFT) may be more appropriate for broader scales, whereas vegetation might be best differentiated using shorter phylogenetic distances (Shallow LFT) at high resolution. Images from Google Earth Pro© [Colour figure can be viewed at wileyonlinelibrary.com]

functional traits, and functional ecology studies comparing the phylogenetic signal in a diversity of traits in a diversity of taxa are needed.

2. **Test phylogenetic conservatism of plant function in hyperdiverse systems such as the tropics:** Comparative ecophysiology such as congeneric contrasts is a staple of tropical ecology, yet even in the tropics, functional traits show at least some phylogenetic signal at broad phylogenetic scales (Baraloto et al., 2012). Can the habitat preference or successional strategy of dominant lineages (e.g., the "hyperdominants" like *Eschweilera*, ter Steege et al., 2013) be generalized at large enough phylogenetic scales based on the traits of their most dominant members? We suspect so, but rigorous empirical tests are required. Given the coarse representation of tropical plants in current global models (often comprising only 1–3 PFTs), new ways of identifying and parameterizing tropical PFTs are greatly needed. If hyperspectral remote sensing can capture phylogenetic information, backbone phylogenies can be used to identify, map, and parameterize tropical LFTs that capture dominant lineages using limited existing functional data. This approach would leverage the power of evolutionary relatedness to overcome data scarcity, and may prove more tractable and possibly more effective than trying to create new PFTs from *a priori* ecological strategies in the tropics.
3. **Identify and map global LFTs:** Functional type maps are prescribed model inputs for some models, and are critical benchmarks for the emergent structure of dynamic vegetation models that allow PFTs to compete. Defining these maps for LFTs poses the dual challenge of identifying the globally most dominant evolutionary lineages and determining how to map those lineages. The growing coverage and quality of large-scale inventories (e.g., national forest inventories such as the US Forest Inventory and Analysis, global plot networks; Liang et al., 2016) and prevalence

of well-resolved phylogenies makes the identification of dominant lineages increasingly tractable. Paleo-ecological data and theory could also help identify the phylogenetic lineages whose dominance is consistent through time and pinpoint potentially important lineages that may not be dominant today but have previously been dominant and thus could be dominant in future climates (Birks, 2019; Jackson et al., 2000; Mekonnen et al., 2019). In many cases, mapping LFTs may actually be tractable with existing phylogeographic knowledge (e.g., for grasses: Griffith et al., 2020), and from bottom-up syntheses of biodiversity inventories and species distribution maps (Jetz et al., 2012). Finally, the phylogenetic signal in plant spectra (Meireles et al., 2020) also holds great promise for using hyperspectral remote sensing data to map LFTs, though numerous scaling challenges must first be addressed.

Timely and societally relevant predictions of ecological change in the Anthropocene require mechanistic models that apply current ecological knowledge to forecast outside the training domain of today's world. We advocate for increased collaborations among vegetation modelers, evolutionary biologists, community ecologists, ecophysiologists, and paleo-ecologists to generate new and creative ways to represent plant diversity in models. We propose that evolutionary relatedness can serve as a unifying theme for these efforts.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

LDLA, DMG, and CJS conceived the idea for the paper, all authors revised and developed the idea, LDLA wrote the first draft of the manuscript, and all authors contributed to manuscript revisions.

DATA AVAILABILITY STATEMENT

All data used in analyses are publicly available from Anderegg, Berner, et al. (2018), https://doi.org/10.5061/dryad.c1dn34b; Falster et al. (2015), https://doi.org/10.6084/m9.figshare.c.3307692.v1; Gleason et al. (2015), available as dataset #241 through https://www.try-db.org/; Law & Berner (2015), https://doi.org/10.3334/ORNLDAAC/1292; Ledo et al. (2018), https://doi.org/10.6084/m9.figshare.5144164.v1; Zanne et al. (2009), https://doi.org/10.5061/dryad.234. Analysis code is available at https://github.com/leanderegg/LineageFunctionalType_PNWexample.

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