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

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1 Main Manuscript for:

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3           **Representing plant diversity in land models: An evolutionary approach to make**  
4           **'Functional Types' more functional**

5

6           Running title: Lineage Functional Types for vegetation models

7

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27

28           **Word Count: 5594**

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39     **Abstract:**

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

60

61     **Keywords**  
62     ecosystem function, evolutionary relatedness, functional diversity, Lineage Functional Types,  
63     PFTs, phylogenetic signal, Plant Functional Types, Vegetation models

64

65     **Plain Language Summary:**

66     Land plants exhibit enormous functional variation across the globe, and this variation strongly  
67     influences water, energy, and carbon transfers between the land surface and the atmosphere and  
68     vegetation responses to disturbances and climate. However, it is extremely difficult to capture  
69     the vast diversity of land plants in state-of-the-art global Earth System Models, which synthesize  
70     understanding of ecological, physical, and biogeochemical processes, to predict the effects of

71 human activities on the Earth system. Because ecological and physiological function tend to be  
72 conserved in closely related species through evolutionary time, evolutionary relatedness can help  
73 summarize plant functional diversity into a tractable number of ‘Lineage Functional Types’ that  
74 represent the most functionally distinct and logically consistent vegetation groupings on the land  
75 surface.

76     **Introduction**

77           There are over 400,000 described vascular plant species on Earth, which collectively  
78       represent a profound diversity of form, function, and life history (IPBES, 2019). Decades of  
79       research into plant functional ecology, ecophysiology, and community ecology have revealed  
80       many causes and consequences of this diversity. At the same time, sophisticated representations  
81       of physiological, ecological, hydrological, and biogeochemical plant processes have been  
82       codified in the terrestrial processes of Earth System Models (ESMs) that simulate key aspects of  
83       **ecosystem function** (e.g., energy, water, and CO<sub>2</sub> fluxes). However, even as mechanistic realism  
84       increases in these models, the representation of actual plant diversity remains quite simplistic.  
85       Vegetation models use a small number of vegetation ‘Functional Types’ (e.g., five to twenty) to  
86       represent archetypal end members of plant functional variation that most strongly influence  
87       ecosystem processes (DeFries et al., 1995). Each Functional Type is represented by a set of  
88       parameter values (e.g., photosynthetic capacity, canopy roughness, nutrient uptake efficiency,  
89       rooting depth, etc.), and the variation in these parameters, combined with differences in process  
90       representations (e.g., C3 vs. C4 photosynthesis, cold hardening, drought deciduousness), gives  
91       rise to modeled plant **functional diversity** (FD). In most modern models, multiple Functional  
92       Types can exist in the same grid cell, and often these Functional Types compete for shared water  
93       and nutrient resources (Riley et al., 2018). Moreover, advances in the representation of size- and  
94       age-structure with ‘vegetation demographic models’ (Fisher et al., 2018) allow cohorts of  
95       different Functional Types to compete for light.

96           The historic Functional Type paradigm has been highly successful in modeling  
97       biosphere-atmosphere interactions, and yet significant modeling efforts to add trait distributions  
98       and species level information suggest that increasing ecological realism is an important area for

99 model improvement. However, the current Functional Types in ESM land models remain  
100 extremely coarse, rooted in a classic biome and growth-form based concept of ‘Plant Functional  
101 Types’ or **PFTs** (Bonan et al., 2003; D. B. Clark et al., 2011; Lawrence et al., 2019; Sitch et al.,  
102 2003). Fundamentally, these PFTs have their origins in correlative climate-vegetation models  
103 (Köppen, 1936), ecological ‘functional guilds’ (Root, 1967), and biome concepts (Raunkiær et  
104 al., 1934; Whittaker, 1975). Although they were the result of much careful thought (Smith et al.,  
105 1997), most current models contain fewer than 20 PFTs to represent all land plants, and the PFTs  
106 boil down to growth form (e.g., trees, shrubs, grasses, forbs), phenology (evergreen vs  
107 deciduous), photosynthetic pathway, and sometimes climate (temperate vs tropical). This  
108 combination of factors are thought to capture first-order global variations in plant function  
109 (DeFries et al., 1995), though they necessarily assume that widespread biomes such as savannas  
110 and hyper-diverse biomes like tropical rainforests can be represented by one or two PFTs each.

111 It is widely accepted that current PFTs do not capture the majority of variation along key  
112 plant functional axes (e.g., Wright *et al.*, 2004), and that better representation of diversity is  
113 needed (i.e. more or different functional types) in order for models to move beyond simulating  
114 short-term ecosystem fluxes to predicting long-term vegetation shifts and their associated  
115 vegetation-climate feedbacks (Fisher et al., 2015). Indeed, even in the early 1990s it was  
116 recognized that PFTs suffered both philosophical and practical challenges that have yet to be  
117 addressed (Box, 1996; Smith et al., 1997). Copious observations and experiments have proven  
118 just how critical real-world diversity is for ecosystem function (Isbell et al., 2012; Liang et al.,  
119 2016; Tilman, 1996). For example, diversity significantly increases ecosystem resistance to and  
120 recovery from climate variability and extreme events (W. R. L. Anderegg et al., 2018; Isbell et  
121 al., 2015). Yet many open questions remain about how to increase the diversity of Functional

122 Types in models. How many Functional Types are needed to adequately represent functional  
123 diversity within communities and across the landscape? Which new Functional Types are most  
124 important? What observations should be used to parameterize new Functional Types? And how  
125 do these answers change with model spatial extent or resolution (e.g., for fine-scale regional  
126 versus coarse-scale global simulations)?

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

144

145 *The parameterization problem*

146 Part of the issue limiting the proliferation of Functional Types lies in the delicate balance  
147 that land models must strike between realism and parsimony (Prentice et al., 2015). While more  
148 sophisticated representations of biodiversity (i.e., more Functional Types) are needed to simulate  
149 ecological processes such as competition, land models already suffer from fundamental issues of  
150 **equifinality** (many different parameter sets yield similar predictions, making more complicated  
151 models more difficult to parameterize to the point where added complexity decreases model  
152 predictive ability, Tang & Zhuang, 2008). It therefore remains paramount to constrain model  
153 parameters to avoid the ‘complexity trap’ (Prentice et al., 2015). The question of how much  
154 process complexity to include in vegetation models is often treated separately from the question  
155 of how to represent functional diversity in those processes, but they are inextricably linked as the  
156 parameterization challenge increases with both the number of model parameters and the number  
157 of Functional Types (or more, if interactions between Functional Types are themselves  
158 parameterized).

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

168

169 *Existing PFT alternatives*

170 One alternative to current PFTs is ‘trait-based modeling’, where Functional Types are not  
171 prescribed based on a limited number of pre-defined PFTs but either emerge from a modeled  
172 competitive search through potential parameter space (Pavlick et al., 2013; Sakschewski et al.,  
173 2015; Scheiter et al., 2013) or are completely absent and parameter values are applied based on  
174 empirical trait-environment relationships (van Bodegom et al., 2011; Verheijen et al., 2015).  
175 However, these two approaches face fundamental limitations to their implementation in ESM  
176 land models. Approaches based on competitive algorithms are limited by the fact the key  
177 physiological traits invoked as model parameters are not necessarily the traits that explain real,  
178 ecological niche differences (Fisher et al., 2018; Kraft et al., 2015). This is a problem for all  
179 dynamic vegetation models simulating competition and co-existence, but is made greater when  
180 parameters are constrained purely by trait theory rather than observations. It is difficult to  
181 simulate co-existence *de novo* in land models based on partially understood physiological and  
182 ecological tradeoffs, when true co-existence is likely a ‘high-dimensional’ ecological problem (J.  
183 S. Clark et al., 2010), with multiple stabilizing mechanisms not included in models (van  
184 Bodegom et al., 2011). In short, unconstrained (i.e., purely ‘trait-based’ or Functional Type free)  
185 competitive algorithms are extremely useful ecological tools, but it remains hugely challenging  
186 for relatively simple physiologically-based models to solve what the entire field of community  
187 ecology is still working hard to explain (coexistence and the maintenance of biodiversity) in  
188 order to predict global ecosystem function in a changing environment.

189 Meanwhile, approaches based on empirical trait-climate relationships face their own  
190 problems, chief among them being that trait-climate relationships are extremely elusive when

191 looking across land plants as a whole (rather than among closely related species). Extensive  
192 research into leaf economic traits such as leaf mass per area (LMA), nutrient concentrations, and  
193 maximum assimilation rates have found that: (1) a diversity of economic strategies are present in  
194 essentially all ecosystems worldwide (Wright et al., 2004); (2) average trait values show very  
195 weak relationships with environmental variables (Maire et al., 2015; Ordoñez et al., 2009); and  
196 (3) trait-environment relationships are not consistent across taxonomic and ecological scales (L.  
197 D. L. Anderegg et al., 2018). Ultimately, trait-based approaches have greatly furthered ecological  
198 knowledge are currently limited in their scalability and applicability to ESM land models.

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#### 200 **Box 1: Glossary**

201 **Ecosystem function** – Processes and properties that mediate fluxes of energy and matter such as  
202 gross primary productivity (photosynthesis), net primary productivity (photosynthesis minus  
203 respiration), evapotranspiration, cycling of macro and micro nutrients, etc.

204 **PFT** – Plant Functional Types, the current standard method of representing the diversity of plant  
205 form and function in land models based on growth form, climate, and phenology.

206 **Phylogeny** – The evolutionary history of a group of organisms, represented via a phylogenetic  
207 tree that depicts the evolutionary relatedness of various lineages of organisms. ‘Dated’  
208 phylogenies also estimate the time since evolutionary divergence of lineages based on fossils, the  
209 rate of accumulation of genetic mutations, or both.

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

213   **Equifinality** – an issue in model parameterization and structure where different  
214   parameterizations yield equally accurate (probable) model predictions based on available training  
215   data.

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

228   **LFT** – Lineage Functional Types, a method of representing plant functional diversity based on  
229   niche conservatism (i.e., the functional relatedness of closely related evolutionary lineages).

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

234   **Phylogenetic scale** – The breadth of evolutionary relatedness, and thus time since most recent  
235   common ancestor, considered in an analysis. Genetic differences among populations within a

236 species (e.g., microevolution) or sister species within a genus would represent a finer  
237 phylogenetic scale than variation among more distantly related taxa such as plant genera or  
238 families (e.g., macroevolution).

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

241 **Community weighted mean (CWM)** – Effective trait value for a plant community, averaged  
242 across species and weighted proportionally to each species' dominance in the community (often  
243 given by % of basal area or % of leaf area).

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244

#### 245 **Letting evolution be our guide**

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

#### 252 *Plant function is phylogenetically linked*

253 Eco-evolutionary theory and observations have come a long way since the development  
254 of the PFT concept. In particular, '**Niche Conservatism**' (NC), or the tendency for species or  
255 clades to retain their niches and related ecological traits over time (Fig. 1a), has emerged as a  
256 dominant theme of macroevolution (Crisp & Cook, 2012; Wiens et al., 2010). While adaptive  
257 radiation within lineages is well documented, at broad **phylogenetic scales** members of a lineage  
258 tend to be more similar ecologically and physiologically to each other than to members of other

259 lineages (Cavender-Bares et al., 2006). Some aspects of species' niches are particularly strongly  
260 conserved; for instance, the thermal niche is a highly conserved niche axis that leads to  
261 widespread 'biome conservatism' or the tendency for clades to remain in their ancestral biome  
262 and switch to new biomes only rarely (Crisp et al., 2009). NC appears to underpin many  
263 ecological interactions, including competitive dynamics (Burns & Strauss, 2012) and pathogen  
264 susceptibility (Gilbert & Webb, 2007).

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

275 While the taxonomic hierarchy is a coarse stand-in for well-supported and dated  
276 phylogenies, the explanatory power of deep evolutionary divergences supports lineage as a  
277 defensible approach to assign trait values for a group of plants. The evolutionary null hypothesis  
278 that closely related species are more functionally similar than distantly related species is rarely  
279 disproven. Indeed, 20<sup>th</sup> century ecology has a long history of describing the clade-based  
280 ecological characteristics of plant families (a simplification still employed in the hyperdiverse  
281 tropics where species-specific natural history knowledge is rare), implicitly acknowledging the

282 power of niche conservatism. In fact, the strength of phylogenetic signal in many traits has led  
283 some to use phylogeny to ‘gap fill’ missing trait values in trait databases (e.g., Swenson, 2013;  
284 Schrodt *et al.*, 2015).

285 Niche conservatism can arise from a number of ecological and evolutionary processes  
286 (Crisp & Cook, 2012), and thus phylogenetic signal in functional traits does not necessarily  
287 imply anything about trait lability or canalization (how evolvable a trait is). But the widespread  
288 phylogenetic signal does suggest that evolutionary history is a strong predictor of modern  
289 ecology. Indeed, in community ecology, functional niche conservatism has been so widely  
290 accepted that phylogenetic diversity is often used as a proxy for hard-to-measure functional  
291 diversity (Srivastava *et al.*, 2012).

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

303 Some important traits are conspicuous exceptions to this rule. For example, leaf nitrogen  
304 per unit leaf area ( $N_{\text{area}}$ ) and allometric traits such as root to shoot biomass ratio (R:S) or leaf area

305 to sapwood area ratio ( $A_L:A_S$ ) vary enormously within species and over time (Fig. 1). Indeed, the  
306 extent to which a trait shows phylogenetic signal may indicate whether it is appropriate as a  
307 ‘parameter’ in land models. Traits that consistently show little phylogenetic signal and large  
308 within-species variation may well be dynamic properties that can vary through time for an  
309 individual (e.g., through acclimation) or across environments for a species. Such traits are  
310 unlikely to maintain the same value for a model Functional Type through space and time, and  
311 should be treated as emerging from underlying physical and physiological processes. Allocation  
312 for instance, which can vary enormously across ontogeny, may best be simulated to emerge from  
313 economic optimization (Fisher et al., 2018) or a combination of gradient-based carbon and  
314 nutrient concentrations, plant transport, and plants’ nutrient acquisition-related traits (Mekonnen  
315 et al., 2019; Thornley, 1997; Zhu et al., 2019). These underlying processes themselves may have  
316 phylogenetically conserved parameters linked to evolutionary history, and a lack of phylogenetic  
317 signal may highlight critical areas for future research.

318 *Tree thinking to inform process as well as parameterization*

319 One important trait that illustrates the utility of tree thinking for model development is  
320 leaf habit (evergreen vs deciduous). Deciduousness has long been recognized as a central trait for  
321 capturing annual variation in biosphere-atmosphere interactions (DeFries et al., 1995). Thus, leaf  
322 habit is a key component of all current PFT schemes. In some instances, a lineage-based  
323 Functional Type may result in lumping together deciduous and evergreen species in a way that  
324 classic PFTs do not. However, closer investigation of leaf lifespan reveals a number of  
325 interesting modeling-relevant observations. First, across the tree of life, leaf lifespan varies  
326 primarily among deep evolutionary nodes (see Fig 1), so LFTs will naturally capture much  
327 variation in leaf habit even without considering it as an explicit grouping criterion. Second,

328 patterns of leaf lifespan as a function of temperature reveal family-specific responses to cold  
329 stress. Moving into colder climates, the most well sampled families in the GLOPNET global trait  
330 database (Wright et al., 2004) appear to follow one of two strategies: increasing longevity with  
331 decreasing temperature (Pinaceae, Ericaceae and Myrtaceae, Fig. 2a), or increasing  
332 deciduousness (e.g. Asteraceae, Fig. 2a). This pattern largely holds true at the genus level (Fig.  
333 2b), with members of most genera that live at mean annual temperatures below 10°C typically  
334 being either all evergreen or all deciduous, and at the species level, at least in conifers (Fig. 2c,  
335 L. D. L. Anderegg et al., 2018; Reich et al., 2014).

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

344 In another example of evolutionary insights informing model development, Griffith *et al.*  
345 (2020) demonstrated both the parametric and process importance of a new LFT classification for  
346 grasses worldwide. Classic grass PFTs differentiate only between C<sub>3</sub> and C<sub>4</sub> photosynthetic  
347 pathway types. Yet most grasslands are dominated by three major lineages (one C<sub>3</sub>-only and two  
348 C<sub>4</sub>-only lineages), which inhabit distinct parts of the globe and differentiate physiologically,  
349 morphologically, and in their responses to disturbances (Edwards & Still, 2008; Griffith et al.,  
350 2020; Lehmann et al., 2019). Thus, evolutionary lineage provides a straightforward and efficient

351 means to improve representation of grasses in land models using existing data to guide  
352 parameterization. But perhaps more importantly, the two dominant C<sub>4</sub> lineages show marked  
353 differences in hydraulic traits and fire-related traits, suggesting that both hydraulics and fire may  
354 be critical processes to include in models in order to simulate grassland fluxes and biogeography  
355 (Griffith et al., 2020).

356

### 357 ***Evolution as a scalable guide for disaggregating functional diversity***

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

368 Two patterns from community and ecosystem ecology highlight the tractability of scaling  
369 plot-level functional diversity to a relatively small number of Functional Types even at the site or  
370 landscape level using evolutionary lineage-based approaches. First, supporting Grime’s ‘biomass  
371 ratio hypothesis’ (Grime, 1998), many ecosystem functions appear to be influenced by plant  
372 community members roughly in proportion to their biomass (e.g. Garnier *et al.*, 2004; Finegan *et*  
373 *al.*, 2014). This observation *does not* imply that diversity does not matter. But it does imply that

374 true ‘keystone’ plant species are relatively rare when considering only ecosystem fluxes, and that  
375 dominant species tend to influence ecosystem function in proportion to their dominance (Avolio  
376 et al., 2019). Thus, much of the variation in plant function between communities can be  
377 explained by the biomass-weighted or **community-weighted mean** (CWM) functional traits of  
378 the communities. Meanwhile, functional diversity within communities is typically determined by  
379 functional diversity among the most dominant species in that community. These two scales  
380 (functional variation among communities across space versus functional diversity within  
381 communities) roughly translate to functional differences across ESM grid cells versus the  
382 diversity of Functional Types within a grid cell (e.g., Functional Types that directly compete for  
383 light, water and nutrients, depending on the specific vegetation model). The utility of the  
384 biomass ratio hypothesis suggests that a tractable number of Functional Types should suffice to  
385 capture first order functional variation across modeling scales, both within and among  
386 communities.

387 Second, most plant communities are comprised of a few abundant and many rare species.  
388 This foundational pattern in community ecology (e.g., in the ‘niche vs. neutral’ debate (Hubbell,  
389 2001; Tilman, 2004)) holds true even in the hyper-diverse tropics, where ‘hyperdominance’ of a  
390 few taxa (10s to 100s rather than 1000s) emerges across large geographic areas (ter Steege et al.,  
391 2013). Together, these two observations (that ecosystem function is largely controlled by the  
392 dominant species and that most communities are composed of a few dominant species) greatly  
393 simplify the challenge of representing plant functional diversity within and among communities  
394 in land models. We can simultaneously acknowledge that biodiversity really matters for  
395 ecosystem function and yet not despair about needing to model all ½ million plant species to  
396 capture the influences of diversity on ecosystem function.

397     *A practical example of describing new FTs*

398                 Based on the logic above, defining new Functional Types requires balancing functional  
399                 distinctiveness (to capture as much functional diversity as possible) and a focus on dominant  
400                 plant types (to capture the most important groups for ecosystem function). The forests of the  
401                 Pacific Northwest, USA provide an illustration of how a phylogenetic approach informed by  
402                 abundance data can guide the disaggregation of coarse PFTs into finer LFTs. A network of 256  
403                 plots was explicitly designed to measure forest productivity and modeling-relevant traits across  
404                 Oregon and northern California for parameterizing ESMs for regional simulations (Berner &  
405                 Law, 2016; Law & Berner, 2015). Stand surveys extensively quantified community composition,  
406                 and trait measurements such as leaf mass per area (LMA), Leaf Lifespan, and nitrogen content  
407                 per unit mass ( $N_{mass}$ ) were collected from 37 woody species in these plots, approximately in  
408                 proportion to their abundance. Yet two species (*Pseudotsuga menziesii* and *Pinus ponderosa*),  
409                 and more generally two clades of the Pinaceae family (the abietoides and pinoids), represent the  
410                 vast majority of the biomass in the region (Fig. 3). Because site-specific traits were extensively  
411                 sampled, we calculated the true variation in functional diversity across plots based on observed  
412                 community-weighted mean traits (L. D. L. Anderegg et al., 2018). We also calculated the  
413                 functional diversity within plots using functional diversity metrics that incorporate elements of  
414                 functional richness, evenness, and occupied niche space (here we average results using  
415                 Functional Dispersion (Laliberté & Legendre, 2010) and Rao's quadratic entropy (Botta-Dukát,  
416                 2005), which can be weighted by relative abundance and can be calculated for communities with  
417                 fewer than three species). We then compared the efficacy of Functional Type groupings by  
418                 comparing observed FD within and among communities with FD calculated using a single mean

419 trait value per Functional Type (see SI “*Methods for Pacific North West Functional Diversity*  
420 *analysis*”).

421 Traditionally, all of the woody species in the region would be represented by at most  
422 three PFTs, which together capture an average of only 6% of the CWM variation in LMA, Leaf  
423 Lifespan, and N<sub>mass</sub> among communities and an average of 16% of the FD within communities  
424 (Fig. 3). A similar categorization based on evolutionary lineage (at the family level for the  
425 gymnosperms and lumping all angiosperms together—termed ‘Deep LFT’ in Fig. 3 for how  
426 deeply the phylogenetic tree is trimmed) captures slightly more of the variation in CWM traits  
427 among communities (9% on average) and slightly less diversity within communities (12%). This  
428 result is expected, as classic PFTs and ‘Deep LFTs’ are quite similar (Table S1). LFTs guided by  
429 abundance prioritize the functional distinction among gymnosperms, while classic PFTs  
430 prioritize the leaf habit distinction among angiosperms that happen to be quite rare in this  
431 system. And ultimately, no 3-group FT scheme can be expected to capture the true FD of even  
432 low diversity systems. However, the LFT approach provides an obvious framework for further  
433 disaggregation.

434 By splitting the most evolutionarily divergent angiosperms (acknowledging extreme  
435 evolutionary and therefore functional distinctiveness) and dividing the Pinaceae family into the  
436 abeitoid and pinoid subfamilies (acknowledging that Pinaceae dominate 95% of the biomass), a  
437 lineage-based division with only five functional types captures 20% (‘Mid LFT’) of the variation  
438 in CWM traits and 21% of the variation within communities (Fig. 3). Further division focusing  
439 on the most abundant lineages (breaking the Pinaceae into genera) captures an average of 37%  
440 (‘Shallow LFT’) of the between-community variation and a startling 84% of the within-  
441 community functional diversity with nine LFTs. The ‘Mid’ and ‘Shallow’ LFT examples

442 presented here are based on qualitative weighting of evolutionary distinctiveness and abundance,  
443 but development of a quantitative weighting scheme would be feasible with appropriate  
444 abundance data and a dated phylogeny.

445 Low diversity temperate forests, while tractable for calculating true functional diversity  
446 from extensive observations, are admittedly a relatively simple example system. However, the  
447 ability of lineage- and abundance-guided FTs to capture within- and among-site functional  
448 variation in a system where intraspecific trait variation is important (L. D. L. Anderegg et al.,  
449 2018) and where rare evolutionary outlier species such as the deciduous conifer *Larix*  
450 *occidentalis* could be particularly troublesome provides hope for using LFTs in more diverse  
451 systems.

452 Are LFTs ‘better’ than alternative FT methods? One of the many difficulties in  
453 answering this question is the general lack of alternative *a priori* FT delineation methods to  
454 compare against. *A posteriori* empirical clustering of observed traits can capture more trait  
455 variation than essentially any *a priori* classification technique. However, the Pacific Northwest  
456 forest example illustrates the limitations of empirical clustering in terms of interpretability and  
457 applicability for determining model FTs. The ‘Shallow LFT’ captures an average of 59% of the  
458 total variation in LMA, N<sub>mass</sub>, and Leaf Lifespan when applied to the entire database of all  
459 individual trait measurements (rather than plot-level CWM traits). With nine clusters,  
460 agglomerative Ward clustering can capture an average of 78% of variation in the same traits and  
461 k-means clustering can capture an average of 79% of the variance. However, empirical clustering  
462 approaches yield widely different groups depending on algorithm type (e.g. Table S2 for Ward  
463 vs k-means clustering) and are fundamentally limited by interpretability. Clustering on the full  
464 trait database invariably places measurements from most species, even rare species, in multiple

465 clusters (e.g. Table S3), meaning the clusters do not have a taxonomic interpretation and could  
466 serve as ‘trait-based Functional Types’ *only if one knows all the traits*. A regional simulation  
467 using these empirical FTs could not map the FTs for initialization or model validation, and the  
468 FTs could not be employed for site-based simulations outside the training sites. Meanwhile,  
469 clustering on CWM traits could capture more spatial variation in traits than LFTs, but could not  
470 capture within-community FD (because the algorithm is classifying sites, rather than  
471 individuals).

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

480

#### 481 ***Implications for benchmarking model biogeography***

482 One key goal of dynamic vegetation models in ESMs is to predict vegetation shifts and  
483 their attendant vegetation-climate feedbacks under climate change. We believe that evolution-  
484 based Functional Types could help predict shifting functional traits across the landscape without  
485 relying on the empirical climate envelopes that have long been the crutch of ‘Dynamic Global  
486 Vegetation Models’ (Fisher et al., 2015; Sitch et al., 2003). To judge our success at simulating  
487 biogeography without climate envelopes, the FTs used in dynamic models need be relatable to

488 observational biogeographic datasets. Paleoclimate records from pollen reconstructions are  
489 typically already aggregated to the genus or higher (e.g. Jackson et al., 2000), making them  
490 useful benchmarking datasets if functional types are also grounded in evolutionary lineage.  
491 Species-level biogeographic observations (e.g., of post-industrial range shifts) can also easily be  
492 aggregated up to the relevant scale to provide model benchmarks if functional types have a  
493 taxonomic basis. Thus, LFTs naturally lend themselves to biogeographic benchmarking.

494 One particularly exciting feature that may both make Lineage Functional Types easier to  
495 operationalize and useful for benchmarking longer-term vegetation model dynamics is that they  
496 can potentially be remotely sensed by satellite. There is considerable evidence that the spectral  
497 properties of plant canopies are phylogenetically conserved, similar to physiological traits  
498 (Cavender-Bares et al., 2016, 2017; Meireles et al., 2020; Schweiger et al., 2018). Whether  
499 serendipitously or mechanistically linked to ecological niche conservatism, the phylogenetic  
500 conservatism of plant spectra (Meireles et al., 2020) could allow rapidly proliferating  
501 hyperspectral data to be used to map LFTs. The combination of plant or plot-scale hyperspectral  
502 data from experiments (Cavender-Bares et al., 2016; Schweiger et al., 2018), landscape-scale  
503 data from aircraft hyperspectral platforms such as the U.S. National Ecological Observatory  
504 Network's Airborne Observation Platform (NEON, n.d.), and ultimately satellite data, hold great  
505 promise for linking evolutionary relatedness to large-scale patterns of lineage presence and  
506 abundance. There are many challenges for scaling from phylogenetic relationships of plants with  
507 canopies of ~0.1-10 m size to satellite remote sensing pixels (e.g., ~30 m resolution for  
508 upcoming hyperspectral satellites) to model grid cells (~10-100 km for most current ESMs) (Fig.  
509 4). However, if approaches such as spectral unmixing can enable downscaling of sufficient  
510 resolution to capture the dominant LFTs of a model grid cell, hyperspectral satellite data—soon

511 to be available from Germany’s DESIS, Japan’s HiSUI, and NASA’s EMIT sensors on the  
512 International Space Station and planned Surface Biology and Geology (SBG) satellite (Schimel  
513 et al., 2020)— could be harnessed for global LFT mapping. While the use of these data to  
514 directly map functional traits is promising for initializing trait-based models, the actual identity  
515 of taxa at a location can tell us considerably more information about many important unobserved  
516 or unobservable traits than single traits themselves (J. S. Clark, 2016), and could potentially  
517 (through spectral unmixing) inform trait and LFT diversity within a grid cell. Moreover, remote  
518 sensing of lineage presence and abundance through time could provide model benchmarking data  
519 independent of the short-term (seasonal to interannual) flux measurements often used for model  
520 benchmarking (e.g., iLAMB, Collier et al., 2018).

521

### 522 ***Conclusion: Future Opportunities & Challenges***

523 Actualizing a lineage-based Functional Type representation of plant diversity requires  
524 merging multiple sources of phylogenetic, trait, and diversity data to address three key  
525 challenges:

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

533 studies comparing the phylogenetic signal in a diversity of traits in a diversity of taxa are  
534 needed.

535 **2) Test phylogenetic conservatism of plant function in hyper-diverse systems such as**  
536 **the tropics:** Comparative ecophysiology such as congeneric contrasts is a staple of  
537 tropical ecology, yet even in the tropics, functional traits show at least some phylogenetic  
538 signal at broad phylogenetic scales (Baraloto et al., 2012). Can the habitat preference or  
539 successional strategy of dominant lineages (e.g., the ‘hyperdominants’ like *Eschweilera*,  
540 ter Steege *et al.*, 2013) be generalized at large enough phylogenetic scales based on the  
541 traits of their most dominant members? We suspect so, but rigorous empirical tests are  
542 required. Given the coarse representation of tropical plants in current global models  
543 (often comprising only 1-3 PFTs), new ways of identifying and parameterizing tropical  
544 FTs are greatly needed. If hyperspectral remote sensing can capture phylogenetic  
545 information, backbone phylogenies can be used to identify, map, and parameterize  
546 tropical LFTs that capture dominant lineages using limited existing functional data. This  
547 approach would leverage the power of evolutionary relatedness to overcome data  
548 scarcity, and may prove more tractable and possibly more effective than trying to create  
549 new PFTs from *a priori* ecological strategies in the tropics.

550 **3) Identify and map global LFTs:** Functional type maps are prescribed model inputs for  
551 some models, and are critical benchmarks for the emergent structure of dynamic  
552 vegetation models that allow functional types to compete. Defining these maps for LFTs  
553 poses the dual challenge of identifying the globally most dominant evolutionary lineages  
554 and determining how to map those lineages. The growing coverage and quality of large-  
555 scale inventories (e.g., national forest inventories such as the US Forest Inventory and

556 Analysis, global plot networks (Liang et al., 2016)) and prevalence of well-resolved  
557 phylogenies makes the identification of dominant lineages increasingly tractable. Paleo-  
558 ecological data and theory could also help identify the phylogenetic lineages whose  
559 dominance is consistent through time and pinpoint potentially important lineages that  
560 may not be dominant today but have previously been dominant and thus could be  
561 dominant in future climates (Birks, 2019; Jackson et al., 2000; Mekonnen et al., 2019). In  
562 many cases, mapping LFTs may actually be tractable with existing phylogeographic  
563 knowledge (e.g., for grasses: Griffith *et al.*, 2020), and from bottom-up syntheses of  
564 biodiversity inventories and species distribution maps (Jetz et al., 2012). Finally, the  
565 phylogenetic signal in plant spectra (Meireles et al., 2020) also holds great promise for  
566 using hyperspectral remote sensing data to map LFTs, though numerous scaling  
567 challenges must first be addressed.

568

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

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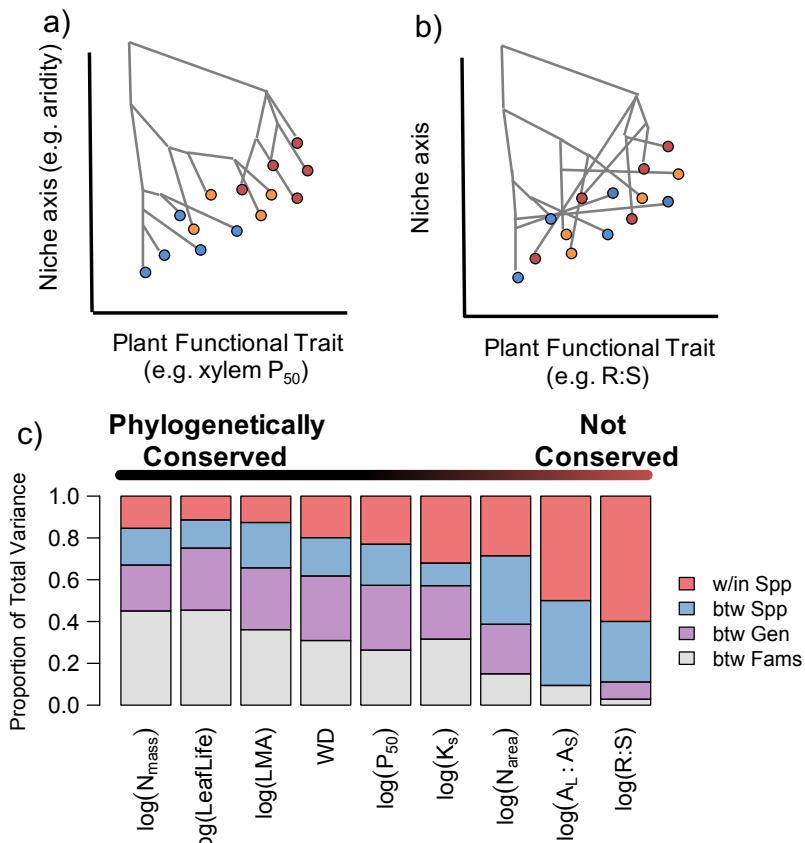
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587 **Author contributions:**

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

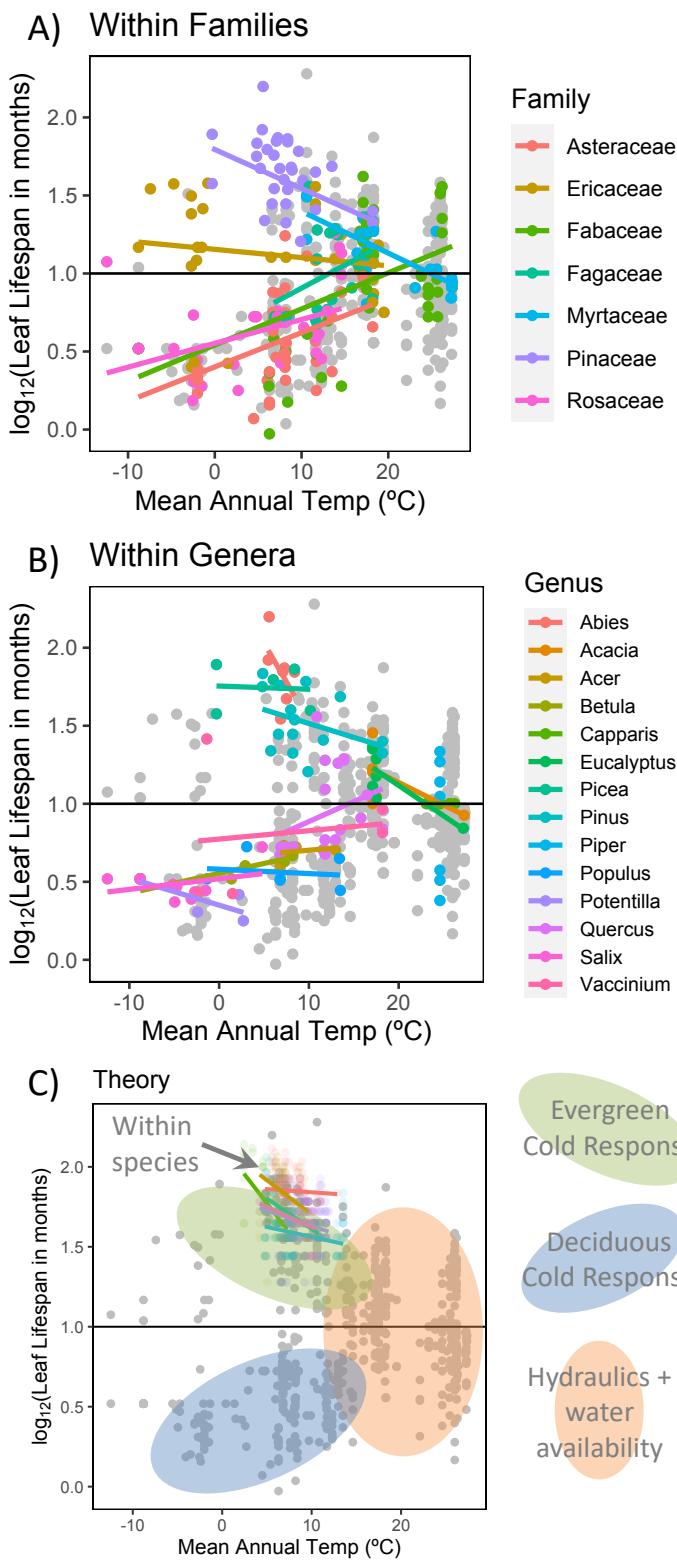
591

592 **Data Availability:** All data used in analyses are publicly available from (L. D. L. Anderegg et  
593 al., 2018; Falster et al., 2015; Gleason et al., 2015; Law & Berner, 2015; Ledo et al., 2017;  
594 Zanne et al., 2009). Analysis code is available at  
595 [https://github.com/leanderegg/LineageFunctionalType\\_PNWexample](https://github.com/leanderegg/LineageFunctionalType_PNWexample).

596 **Figure Captions:**

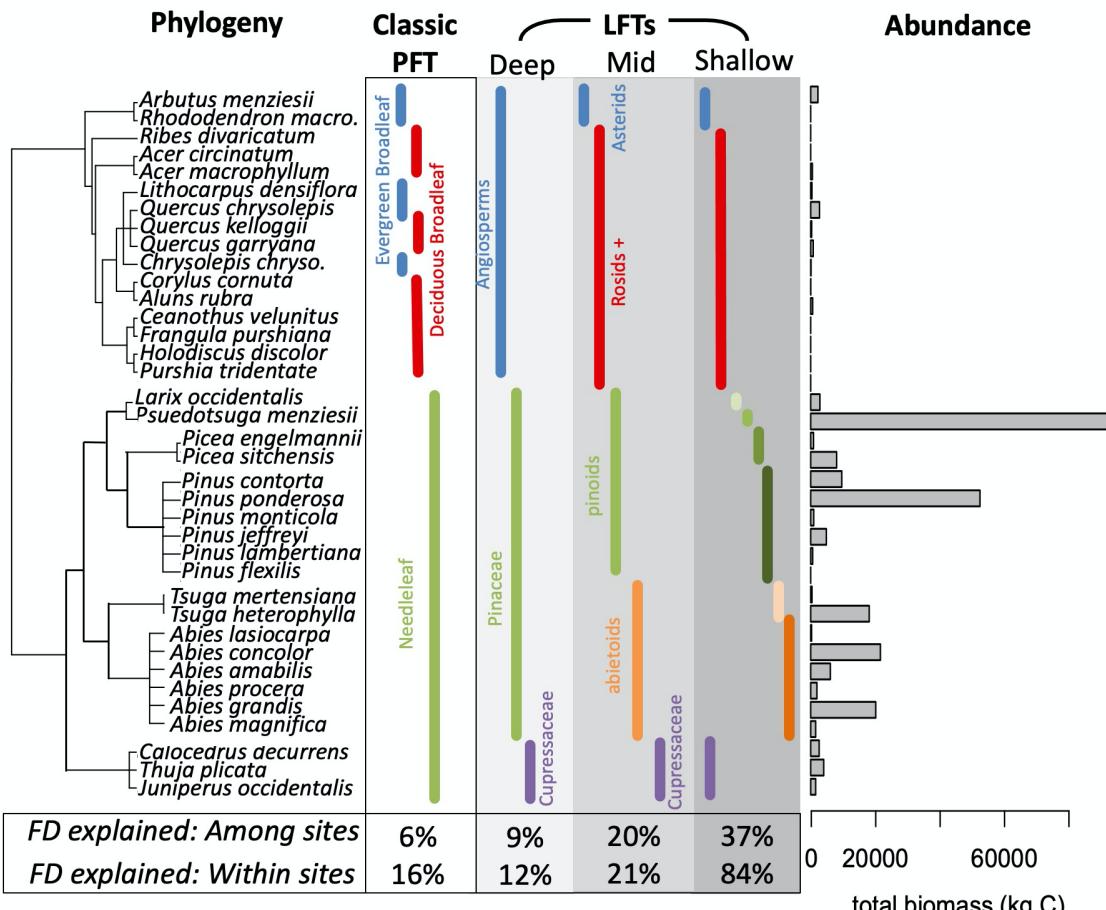
597  
598 **Figure 1: Plant function is phylogenetically conserved** (a) conceptual example of phylogenetic  
599 conservatism of both environmental niches (y-axis) and plant functional traits invoked as  
600 parameters in Land Models (x-axis). Grey lines illustrate evolutionary relatedness (e.g.,  
601 phylogeny) for three lineages (colors), with related species being similar in both niche and trait  
602 values. (b) The less common alternative example of a niche axis and associated functional trait  
603 that are not phylogenetically conserved. (c) Taxonomic variance decomposition of example  
604 'plant functional traits' that are sometimes considered model parameters, or less frequently are  
605 predicted as emergent features resulting from underlying 'lower-level' traits. Many leaf and  
606 stem traits vary primarily at broad taxonomic scales (e.g., among plant families, grey bars),  
607 suggesting that lineage is a good predictor of trait values. However, some plant traits such as  
608 root to shoot biomass ratio (R:S) are less strongly conserved and may be best modeled as  
609 emergent properties from underlying processes. See Box 1 for trait descriptions and SI Variance  
610 Decomposition Methods for data descriptions.  
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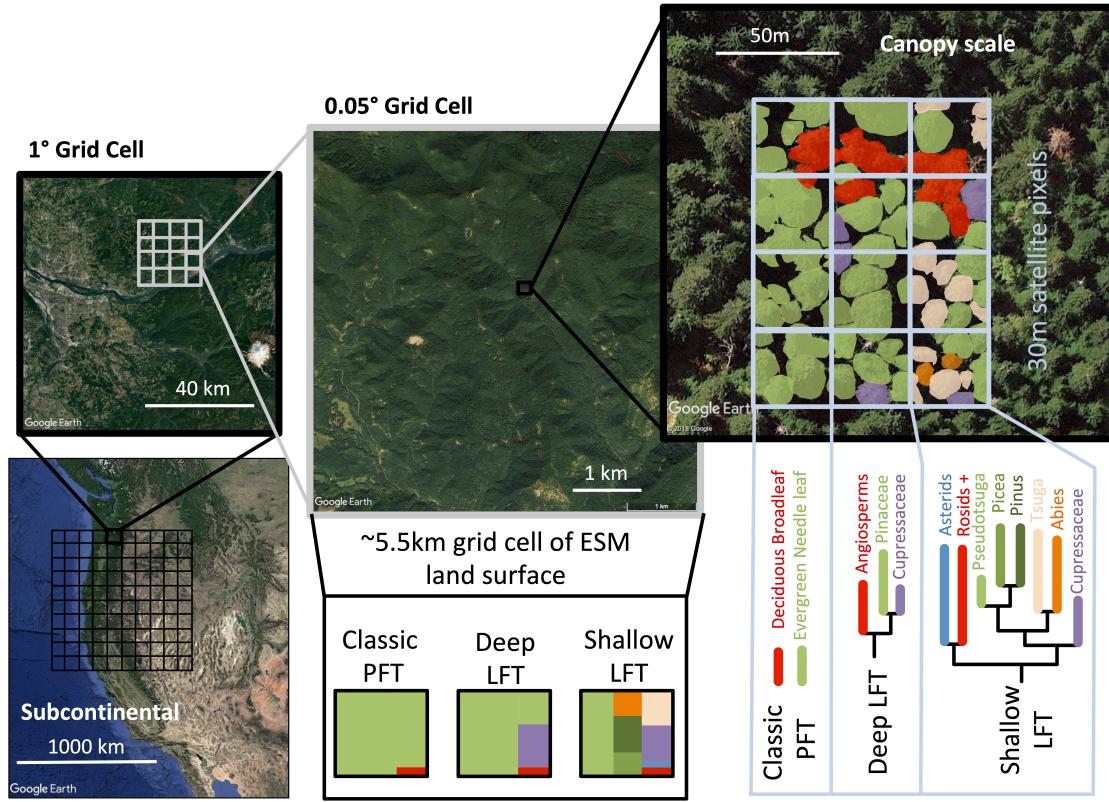
**Figure 2: Lineage-specific leaf lifespan responses to temperature.**

Leaf lifespan in months plotted against the Mean Annual Temperature ( $^{\circ}\text{C}$ ) 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. Data from (Law & Berner, 2015; Wright et al., 2004).



662  
663 **Figure 3: Example of Functional Types in the PNW U.S.A.** Phylogeny of woody plants present  
664 in a network of 256 forest plots in the Pacific NW, USA (Law & Berner, 2015), with four  
665 example disaggregation schemes, and the distribution of total biomass across the species  
666 showing hyperdominance of a small number of species. Percentages indicate the average  
667 amount of variation in Functional Diversity (FD) explained among sites (variance in community-  
668 weighted mean LMA, Leaf Lifespan, and  $N_{mass}$  (see Box 1)) and within sites (variance in  
669 Functional Dispersion and Rao's quadratic entropy) explained by each disaggregation scheme.  
670 The 'Classic PFT' scheme used in many land models and a coarse Lineage Functional Type  
671 (LFT) approach ('Deep', because it is divided deep in the phylogenetic tree) explain similarly  
672 low amounts of variance, while further disaggregation breaking up the major angiosperm  
673 lineages present and the lineages of the dominant Pinaceae family ('Mid LFT') and then dividing  
674 Pinaceae into genera ('Shallow LFT') explain an increasing fraction of FD within and among  
675 sites. See SI Methods for full analysis description.  
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687 **Figure 4: Scaling LFTs from canopy to landscape.** Even a relatively low species richness forest  
688 in the Pacific Northwest, USA poses challenges both to the remote sensing of diversity with  
689 satellites with the resolution of 10s of meters (Canopy Scale panel) and to the representation of  
690 diversity in ESM grid cells that range from 0.05° (~5.5km in the temperate zone) to 1°. However,  
691 the phylogenetic signal in plant spectra may facilitate the identification of dominant lineages in  
692 pixels representing multiple plant canopies, and ultimately the identification of the dominant  
693 Lineage Functional Types at continental scales. The explanatory value of lineages, and our  
694 ability to detect them, may vary with scale. Dividing vegetation based on large phylogenetic  
695 differences (Deep LFT) may be more appropriate for broader scales whereas vegetation might  
696 be best differentiated using shorter phylogenetic distances (Shallow LFT) at high resolution.  
697 Images from Google Earth Pro©.

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701   **References**  
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