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**

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6   Running title: Lineage Functional Types for vegetation models

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47   **Abstract:**

48   Plants are critical mediators of terrestrial mass and energy fluxes, and their structural and

49   functional traits have profound impacts on local and global climate, biogeochemistry,

50   biodiversity, and hydrology. Yet Earth System Models (ESMs), our most powerful tools for

51   predicting the effects of humans on the coupled biosphere-atmosphere system, simplify the

52   incredible diversity of land plants into a handful of coarse categories of 'Plant Functional Types'

53   (PFTs) that often fail to capture ecological dynamics such as biome distributions. The inclusion

54   of more realistic functional diversity is a recognized goal for ESMs, yet there is currently no

55   consistent, widely accepted way to add diversity to models, i.e. to determine what new PFTs to

56   add and with what data to constrain their parameters. We review approaches to representing

57   plant diversity in ESMs and draw on recent ecological and evolutionary findings to present an

58   evolution-based functional type approach for further disaggregating functional diversity.

59   Specifically, the prevalence of niche conservatism, or the tendency of closely related taxa to

60   retain similar ecological and functional attributes through evolutionary time, reveals that

61  evolutionary relatedness is a powerful framework for summarizing functional similarities and

62  differences among plant types. We advocate that Plant Functional Types based on dominant

63  evolutionary lineages ('Lineage Functional Types') will provide an ecologically defensible,

64  tractable, and scalable framework for representing plant diversity in next-generation ESMs, with

65  the potential to improve parameterization, process representation, and model benchmarking. We

66  highlight how the importance of evolutionary history for plant function can unify the work of

67  disparate fields to improve predictive modeling of the Earth system.

68

69  **Keywords**

70  ecosystem function, evolutionary relatedness, functional diversity, Lineage Functional Types,

71  PFTs, phylogenetic signal, Plant Functional Types, Vegetation models

72

73  **Abbreviated Abstract:**

74  Representing the enormous diversity of land plants in Earth System models remains extremely

75  challenging. Because ecological and physiological function tend to be conserved in closely

76  related species through evolutionary time, evolutionary relatedness can help summarize plant

77  functional diversity into a tractable number of 'Lineage Functional Types' that represent the

78  most functionally distinct and logically consistent vegetation groupings on the land surface. This

79  evolutionary approach holds the potential to improve model parameterization, identify areas for

80  process development, and open up new methods of model benchmarking (e.g. with remote

81  sensing data) for vegetation modeling applications across spatial scales.

82  **Introduction**

83      There are over 400,000 described vascular plant species on Earth, which collectively

84  represent a profound diversity of form, function, and life history (IPBES, 2019). Decades of

85  research into plant functional ecology, ecophysiology, and community ecology have revealed

86  many causes and consequences of this diversity. At the same time, sophisticated representations

87  of physiological, ecological, hydrological, and biogeochemical plant processes have been

88  codified in the terrestrial processes of Earth System Models (ESMs) that simulate key aspects of

89  **ecosystem function** (e.g., energy, water, and $CO_2$ fluxes). However, even as mechanistic realism

90  increases in these models, the representation of plant diversity—the evolved variation in

91  phenotypes that influences these functions—remains quite simplistic. Vegetation models use a

92   small number of vegetation 'Plant Functional Types' or **PFTs** (e.g., five to twenty) to represent

93   archetypal end members of plant functional variation that most strongly influence ecosystem

94   processes (DeFries et al., 1995). Each PFT is represented by a set of parameter values (e.g.,

95   photosynthetic capacity, canopy roughness, nutrient uptake efficiency, rooting depth, etc.), and

96   the variation in these parameters, combined with differences in process representations (e.g., C3

97   vs. C4 photosynthesis, cold hardening, drought deciduousness), gives rise to modeled plant

98   **functional diversity** (FD). In most modern models, multiple PFTs can exist in the same grid

99   cell, and often these PFTs compete for shared water and nutrient resources (Riley et al., 2018).

100  Moreover, advances in the representation of size- and age-structure with 'vegetation

101  demographic models' (Fisher et al., 2018) allow cohorts of different PFTs to compete for light.

102        The historic Plant Functional Type paradigm has proven useful to model biosphere-

103  atmosphere interactions over multiple decades of advances, but increasing ecological realism in

104  the variation among plants is an important area for model improvement. The current PFTs in

105  ESM land models remain extremely coarse, rooted in a classic biome and growth-form based

106  concept (Bonan et al., 2003; D. B. Clark et al., 2011; Lawrence et al., 2019; Sitch et al., 2003).

107  Fundamentally, these PFTs have their origins in correlative climate-vegetation models (Köppen,

108  1936), ecological 'functional guilds' (Root, 1967), and biome concepts (Raunkiær et al., 1934;

109  Whittaker, 1975). Although they were the result of much careful thought (Smith et al., 1997),

110  most current models contain fewer than 20 PFTs to represent all land plants, and the PFTs boil

111  down to growth form (e.g., trees, shrubs, grasses, forbs),  phenology (evergreen vs deciduous),

112  photosynthetic pathway, and sometimes climate (temperate vs tropical). This combination of

113  factors is thought to capture first-order global variations in plant function (DeFries et al., 1995),

114  though they necessarily assume that widespread biomes such as savannas and hyper-diverse

115  biomes like tropical rainforests can be represented by one or two PFTs each.

116        It is widely accepted that current PFTs do not capture the majority of variation along key

117  plant functional axes (e.g., Wright *et al.*, 2004), and that better representation of diversity is

118  needed (i.e. more or different functional types) in order for models to move beyond simulating

119  short-term ecosystem fluxes to predicting long-term vegetation shifts and their associated

120  vegetation-climate feedbacks (Fisher et al., 2015). Indeed, even in the early 1990s it was

121  recognized that PFTs suffered both philosophical and practical challenges that have yet to be

122  addressed (Box, 1996; Smith et al., 1997). Copious observations and experiments have proven

123    just how critical real-world diversity is for ecosystem function (Isbell et al., 2012; Liang et al.,

124    2016; Tilman, 1996). For example, diversity significantly increases ecosystem resistance to and

125    recovery from climate variability and extreme events (W. R. L. Anderegg et al., 2018; Isbell et

126    al., 2015). Yet many open questions remain about how to increase the diversity of PFTs in

127    models. How many PFTs are needed to adequately represent functional diversity within

128    communities and across the landscape? Which new PFTs are most important? What observations

129    should be used to parameterize new PFTs? And how do these answers change with model spatial

130    extent or resolution (e.g., for fine-scale regional versus coarse-scale global simulations)?

131        'Tree thinking', or approaches informed by plant **phylogeny** that consider evolutionary

132    relatedness, have been influential in a broad range of fields and have been suggested for further

133    nuancing how models represent diversity (Edwards et al., 2007). For example, new 'Lineage

134    Functional Types' (LFTs) representing three dominant global grass clades can capture

135    considerable variation in physiology, morphology, and response to disturbance that the two

136    classic grass PFTs—which differentiate only C3 vs C4 photosynthetic mechanisms – cannot

137    capture (Griffith et al., 2020). Here, we summarize the evidence for why evolutionary lineages

138    provide a natural backbone for future functional type delineation, and discuss the potential

139    benefits of 'tree thinking' for constraining model parameters, guiding model process

140    development, and expanding model benchmarking options. Closely related species share a large

141    proportion of their ancestry, such that their genomes are very similar. Consequently, when

142    integrating across all plant functions coded by their genomes, functional similarity is likely to be

143    very high. Because of this, many key aspects of plant function are evolutionarily conserved,

144    meaning closely related species are more functionally similar than distantly related species

145    (Wiens et al., 2010). This critical pattern can help the research community leverage burgeoning

146    trait databases, community surveys, biogeographic observations, remote sensing data, and ever-

147    improving plant phylogenies to inform both model process and parameter uncertainty.

148

149    *The parameterization problem*

150        Part of the issue limiting the proliferation of PFTs lies in the delicate balance that land

151    models must strike between realism and parsimony (Prentice et al., 2015). While more

152    sophisticated representations of biodiversity (i.e., more PFTs) are needed to simulate ecological

153    processes such as niche differences, land models already suffer from fundamental issues of

154     **equifinality** (many different parameter sets yield similar predictions, making more complicated

155     models more difficult to parameterize to the point where added complexity decreases model

156     predictive ability, Tang & Zhuang, 2008). It therefore remains paramount to constrain model

157     parameters to avoid the 'complexity trap' (Prentice et al., 2015). The question of how much

158     process complexity to include in vegetation models is often treated separately from the question

159     of how to represent functional diversity in those processes, but they are inextricably linked as the

160     parameterization challenge increases with both the number of model parameters and the number

161     of PFTs (or more, if interactions between PFTs are themselves parameterized).

162         To address this parameterization challenge, ecologists have made a major push to

163     constrain models with real-world observations of '**plant functional traits**' that theoretically

164     relate to model parameters (Dietze et al., 2014) that affect vegetation responses to environmental

165     change. Indeed, one of the main motivations for the creation of TRY, the largest plant trait

166     repository in the world (Kattge et al., 2011), was to improve model PFTs. However, without a

167     rigorous, internally consistent, scalable, and ecologically motivated framework for defining what

168     PFTs should represent, model developers and users are often forced to make arbitrary decisions

169     about which observations should inform the parameter values of newly developed functional

170     types.

171

172     *Existing PFT alternatives*

173         One alternative to current PFTs is 'trait-based modeling', where functional types are not

174     prescribed based on a limited number of pre-defined PFTs but either emerge from a modeled

175     competitive search through potential parameter space (Pavlick et al., 2013; Sakschewski et al.,

176     2015; Scheiter et al., 2013) or are completely absent and parameter values are applied based on

177     empirical trait-environment relationships (van Bodegom et al., 2011; Verheijen et al., 2015).

178     However, these two approaches face fundamental limitations to their implementation in ESM

179     land models. Approaches based on competitive algorithms are limited by the fact the key

180     physiological traits invoked as model parameters are not necessarily the traits that explain real,

181     ecological niche differences (Fisher et al., 2018; Kraft et al., 2015). This is a problem for all

182     dynamic vegetation models simulating competition and co-existence, but is made greater when

183     parameter variation and covariation are constrained largely by trait theory (e.g. assumed

184     functional tradeoffs, Pavlick et al., 2013). It is difficult to simulate co-existence *de novo* in land

185  models based on partially understood physiological and ecological tradeoffs, when true co-
186  existence is likely a 'high-dimensional' ecological problem (J. S. Clark et al., 2010), with
187  multiple stabilizing mechanisms not included in models (van Bodegom et al., 2011). In short,
188  unconstrained (i.e., purely 'trait-based' or PFT-free) competitive algorithms are extremely useful
189  ecological tools, but it remains hugely challenging for relatively simple physiologically-based
190  models to solve what the entire field of community ecology is still working hard to explain
191  (coexistence and the maintenance of biodiversity) in order to predict global ecosystem function
192  in a changing environment.

193       Meanwhile, approaches based on empirical trait-climate relationships face their own
194  problems, chief among them being that trait-climate relationships are extremely elusive when
195  looking across land plants as a whole (rather than among closely related species). Extensive
196  research into leaf economic traits such as leaf mass per area (LMA), nutrient concentrations, and
197  maximum assimilation rates have found that: (1) a diversity of economic strategies are present in
198  essentially all ecosystems worldwide (Wright et al., 2004); (2) average trait values show very
199  weak relationships with environmental variables (Maire et al., 2015; Ordoñez et al., 2009); and
200  (3) trait-environment relationships are not consistent across taxonomic and ecological scales (L.
201  D. L. Anderegg et al., 2018). Ultimately, trait-based approaches have greatly furthered ecological
202  knowledge but are currently limited in their scalability and applicability to ESM land models.
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204  **Box 1: Glossary**
205  **Ecosystem function** – Processes and properties that mediate fluxes of energy and matter such as
206  gross primary productivity (photosynthesis), net primary productivity (photosynthesis minus
207  respiration), evapotranspiration, cycling of macro and micro nutrients, etc.
208  **PFTs** – Plant Functional Types, the standard method of representing the diversity of plant form
209  and function in land models via a small number of archetypal plant types, currently based on
210  growth form, climate, and phenology in most models.
211  **Phylogeny** – The evolutionary history of a group of organisms, represented via a hierarchically
212  bifurcating tree, that depicts the diversification from a common ancestor and evolutionary
213  relatedness of organisms and lineages. 'Dated' phylogenies also estimate the time since
214  evolutionary divergence of lineages based on fossils, the rate of accumulation of genetic
215  mutations, or both.

216    **Functional diversity (FD)** – The amount of functional distinctiveness in a community, often

217    quantified based on the univariate or multivariate distribution of one or more functional traits

218    among community members.

219    **Equifinality** – an issue in model parameterization and structure where different

220    parameterizations yield equally accurate (probable) model predictions based on available training

221    data.

222    **Plant functional traits** – measurable morphological, chemical, phenological, and physiological

223    plant attributes that influence fitness by affecting growth, survival, and reproduction. Many

224    model parameters are related to or sometimes explicitly designed to represent measurable plant

225    functional traits such that the parameters can be constrained by observations. We note that a trait,

226    as defined in this way, need not be static or unchanging for an individual plant or species through

227    time or in response to environmental variation. Whether a model considers a particular trait to be

228    static is an important indicator of underlying model assumptions. Example functional traits used

229    in the text include: $N_{mass}$ – leaf nitrogen content per unit mass, $N_{area}$ – leaf nitrogen per unit area,

230    *LeafLife* – leaf lifespan, *LMA* – leaf mass per unit area, *WD* – wood density, *xylem $P_{50}$* – the

231    xylem pressure causing 50% loss of hydraulic conductance due to embolism, $K_s$ – xylem

232    hydraulic conductance (inverse of hydraulic resistance) per unit sapwood area, $A_L{:}A_S$ – leaf area

233    to sapwood area ratio, *R:S* – root biomass to shoot (leaf + stem) biomass ratio.

234    **LFT –** Lineage Functional Types, a method of representing plant functional diversity in

235    vegetation models based on niche conservatism (i.e., the functional relatedness of closely related

236    evolutionary lineages).

237    **Niche Conservatism** – A widely observed pattern across many taxa that close relatives maintain

238    similar ecological niches – (the combination of abiotic and biotic factors that determine where a

239    species can exist) – through evolutionary time. This ecological similarity implies that closely

240    related species have similar functional traits.

241    **Phylogenetic scale –** The breadth of evolutionary relatedness, and thus time since most recent

242    common ancestor, considered in an analysis. Genetic differences among populations within a

243    species (e.g., microevolution) or sister species within a genus would represent a finer

244    phylogenetic scale than variation among more distantly related taxa such as plant genera or

245    families (e.g., macroevolution).

246 **Phylogenetic signal** – The tendency of related species to more closely resemble each other than

247 species drawn at random from the same evolutionary tree.

248 **Community weighted mean (CWM) –** Effective trait value for a plant community, averaged

249 across species and weighted proportionally to each species' dominance in the community (often

250 given by % of basal area or % of leaf area).

251

252 **Letting evolution be our guide**

253 　　We outline below how lineage-based functional types present an ecologically defensible

254 and scalable method for integrating data on organismal abundance, functional diversity, remote

255 sensing and evolutionary relatedness in order to define, parameterize and test the next generation

256 of PFTs for vegetation modeling. We argue that explicitly making evolutionary lineage the

257 organizing principle behind future functional types will facilitate efforts to add diversity to PFT-

258 based land models.

259 *Plant function is phylogenetically linked*

260 　　Eco-evolutionary theory and observations have come a long way since the development

261 of the original physiognomy-based PFT concept. In particular, '**Niche Conservatism**' (NC), or

262 the tendency for species or clades to retain their niches and related ecological traits over time

263 (Fig. 1a), has emerged as a dominant theme of macroevolution (Crisp & Cook, 2012; Wiens et

264 al., 2010). While adaptive radiation within lineages is well documented, at broad **phylogenetic**

265 **scales** members of a lineage tend to be more similar ecologically and physiologically to each

266 other than to members of other lineages by virtue of the high proportion of their shared ancestry

267 and hence genome similarity (Cavender-Bares et al., 2006). Some aspects of species' niches are

268 particularly strongly conserved; for instance, the thermal niche is a highly conserved niche axis

269 that leads to widespread 'biome conservatism' or the tendency for clades to remain in their

270 ancestral biome and switch to new biomes only rarely (Crisp et al., 2009). NC appears to

271 underpin many ecological interactions, including competitive dynamics (Burns & Strauss, 2012)

272 and pathogen susceptibility (Gilbert & Webb, 2007).

273 　　Importantly, ecological similarity among related taxa translates into functional similarity,

274 providing a powerful framework for summarizing and ultimately parameterizing the functional

275 attributes of entire clades. Indeed, many plant traits that are related to model parameters show

276 **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 reveal that most variation occurs at broad phylogenetic scales (among plant families), with decreasing variation within families, genera, and species (Fig. 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 Fig. 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), though see (Cadotte et al., 2017; Cavender Bares et al., 2004; Gerhold et al., 2015; Mayfield & Levine, 2010) for the nuances and complications of assuming phylogenetic distance equals ecological difference for specific applications in community ecology.

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*

308  *relatedness likely ensures functional similarity within a lineage even for functions that we do not*

309  *yet fully understand* or have implemented in vegetation models. For instance, acclimation

310  responses such as those involved in cold tolerance are a modeling challenge but show strong

311  phylogenetic signal (Lancaster & Humphreys, 2020), and life history traits that might inform

312  'demographic functional types' in size-structured models (Rüger et al., 2020) are likewise

313  probably phylogenetically conserved.

314  Some important traits are conspicuous exceptions to this rule. For example, leaf nitrogen

315  per unit leaf area ($N_{area}$) and allometric traits such as root to shoot biomass ratio (R:S) or leaf area

316  to sapwood area ratio ($A_L:A_S$) vary enormously within species and over time (Fig. 1), and show

317  little fidelity to phylogenetic relationships. Indeed, the extent to which a trait shows phylogenetic

318  signal may indicate whether it is appropriate as a 'parameter' in land models. Traits that

319  consistently show little phylogenetic signal and large within-species variation may well be

320  dynamic properties that can vary through time for an individual (e.g., through acclimation) or

321  across environments for a species. Such traits are unlikely to maintain the same value for a

322  model PFT through space and time, and should be treated as emerging from underlying physical

323  and physiological processes. Allocation for instance, which can vary enormously across

324  ontogeny, may best be simulated to emerge from economic optimization (Fisher et al., 2018) or a

325  combination of gradient-based carbon and nutrient concentrations, plant transport, and nutrient

326  acquisition-related traits (Mekonnen et al., 2019; Thornley, 1997; Zhu et al., 2019). These

327  underlying processes themselves may have phylogenetically conserved parameters linked to

328  evolutionary history, and a lack of phylogenetic signal may highlight critical areas for future

329  research.

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

331  One important trait that illustrates the utility of tree thinking for model development is

332  leaf habit (evergreen vs deciduous). Deciduousness has long been recognized as a central trait for

333  capturing annual variation in biosphere-atmosphere interactions (DeFries et al., 1995). Thus, leaf

334  habit is a key component of all current PFT schemes. In some instances, lineage-based functional

335  types may result in lumping together deciduous and evergreen species in a way that classic PFTs

336  do not. However, closer investigation of leaf habit, and especially its more informative cousin,

337  leaf lifespan, reveals a number of interesting modeling-relevant observations. First, across the

338  tree of life, leaf lifespan varies primarily among deep evolutionary nodes (see Fig 1), so LFTs

339   will naturally capture much variation in leaf habit even without considering it as an explicit

340   grouping criterion. Second, patterns of leaf lifespan as a function of temperature reveal family-

341   specific responses to cold stress. Moving into colder climes, the most well sampled families in

342   the GLOPNET global trait database (Wright et al., 2004) appear to follow one of two strategies:

343   increasing longevity with decreasing temperature (Pinaceae, Ericaceae and Myrtaceae, Fig. 2a),

344   or decreasing longevity (e.g. Asteraceae, Fig. 2a). This pattern largely holds true at the genus

345   level (Fig. 2b), with members of most genera that live at mean annual temperatures below 10ºC

346   typically being either all evergreen or all deciduous. Temperature-related changes in leaf lifespan

347   even appear to hold true within individual species, at least in conifers (Fig. 2c, L. D. L. Anderegg

348   et al., 2018; Reich et al., 2014).

349         Where cold stress is absent (e.g., in the tropics), leaf lifespan is more variable within

350   clades. However, leaf phenology in the tropics is linked to plant hydraulic strategy (Xu et al.,

351   2016), and exciting developments with dynamic leaf allocation in plant hydraulics models have

352   demonstrated the ability to predict drought deciduousness and semi-deciduousness purely from

353   the interaction between hydraulic traits and the environment (Trugman et al., 2019). Thus, we

354   believe that deciduousness may eventually be predicted from lineage-specific responses to cold

355   stress and hydraulic optimizations and need not be an overriding consideration for PFT

356   delineation.

357         In another example of evolutionary insights informing model development, Griffith *et al.*

358   (2020) demonstrated both the parametric and process importance of a new LFT classification for

359   grasses worldwide. Classic grass PFTs differentiate only between $C_3$ and $C_4$ photosynthetic

360   pathway types. Yet most grasslands are dominated by three major lineages (one $C_3$-only and two

361   $C_4$-only lineages), which inhabit distinct parts of the globe and differentiate physiologically,

362   morphologically, and in their responses to disturbances (Edwards & Still, 2008; Griffith et al.,

363   2020; Lehmann et al., 2019). Thus, evolutionary lineage provides a straightforward and efficient

364   means to improve representation of grasses in land models using existing data to guide

365   parameterization. But perhaps more importantly, the two dominant $C_4$ lineages show marked

366   differences in hydraulic traits and fire-related traits, suggesting that both hydraulics and fire may

367   be critical processes to include in models in order to simulate grassland fluxes and biogeography

368   (Griffith et al., 2020).

369

*Evolution as a scalable guide for disaggregating functional diversity*

371       Evolutionary lineages provide a major benefit to vegetation modelers over growth-form

372 and biome-based approaches: they provide a theoretically consistent approach to spatial scaling.

373 Modeling studies at different spatial scales (e.g., plot, regional, global) require different levels of

374 granularity to represent functional diversity. Currently, modelers must rely on expert opinion,

375 empirical classification algorithms, and 'gut instincts' to determine how many and which PFTs

376 to simulate and which data to use to constrain parameters for those functional types. Classic

377 PFTs sometimes *de facto* represent lineages, but explicitly tying functional types to evolutionary

378 lineage provides a scalable and theoretically defensible approach to further disaggregate

379 functional diversity. Unlike biome or growth form, which are categorical, evolutionary

380 relatedness is a continuous variable that can be as coarse or granular as needed.

381       Two patterns from community and ecosystem ecology highlight first that the biggest

382 effects of function diversity can likely be captured with a tractable number of functional types

383 even at the site or landscape level and second how plot-level inventory data can be used to

384 identify important functional types across scales using an evolutionary lineage-based approach.

385 The first observations is that, supporting Grime's 'biomass ratio hypothesis' (Grime, 1998),

386 many ecosystem functions appear to be influenced by plant community members roughly in

387 proportion to their biomass (e.g. Garnier *et al.*, 2004; Finegan *et al.*, 2014). This observation

388 *does not* imply that diversity does not matter. But it does imply that true 'keystone' plant species

389 are relatively rare when considering only ecosystem fluxes, and that dominant species tend to

390 influence ecosystem function in proportion to their dominance (Avolio et al., 2019). Thus, much

391 of the variation in plant function between communities can be explained by the biomass-

392 weighted or **community-weighted mean** (CWM) functional traits of the communities.

393 Meanwhile, functional diversity within communities is typically determined by functional

394 diversity among the most dominant species in that community. These two scales (functional

395 variation among communities across space versus functional diversity within communities)

396 roughly translate to functional differences across ESM grid cells versus the diversity of PFTs

397 within a grid cell (e.g., PFTs that directly compete for light, water and nutrients, depending on

398 the specific vegetation model). The utility of the biomass ratio hypothesis suggests that a

399 tractable number of PFTs should suffice to capture first order functional variation across

400 modeling scales, both within and among communities.

401         Second, most plant communities are comprised of a few abundant and many rare species.

402 This foundational pattern in community ecology (e.g., in the 'niche vs. neutral' debate (Hubbell,

403 2001; Tilman, 2004)) holds true even in the hyper-diverse tropics, where 'hypderdominance' of a

404 few taxa (10s to 100s of taxa rather than 1000s) emerges across large geographic areas (ter

405 Steege et al., 2013). Together, these two observations (that ecosystem function is largely

406 controlled by the dominant species and that most communities are composed of a few dominant

407 species) greatly simplify the challenge of representing plant functional diversity within and

408 among communities in land models. We can simultaneously acknowledge that biodiversity really

409 matters for ecosystem function and yet not despair about needing to model all ½ million plant

410 species to capture the influences of diversity on ecosystem function.

411         Based on the logic above, defining new PFTs requires balancing functional

412 distinctiveness (to capture as much functional diversity as possible) and a focus on dominant

413 plant types (to capture the most important groups for ecosystem function). Phylogenies therefore

414 provide a ready-made and conceptually elegant backbone for aggregating observations of species

415 diversity and abundance (e.g. from biodiversity surveys and forest inventories) to identify the

416 most evolutionarily diverse (and likely most functionally diverse) and the most abundant

417 lineages at any desired spatial scale.

418 *A practical example of describing new LFTs*

419         The forests of the Pacific Northwest, USA provide an illustration of how a

420 phylogenetic approach informed by abundance data can guide the disaggregation of coarse PFTs

421 into finer LFTs. A network of 256 plots was explicitly designed to measure forest productivity

422 and modeling-relevant traits across Oregon and northern California for parameterizing ESMs for

423 regional simulations (Berner & Law, 2016; Law & Berner, 2015). Stand surveys extensively

424 quantified community composition, and trait measurements such as leaf mass per area (LMA),

425 Leaf Lifespan, and nitrogen content per unit mass ($N_{mass}$) were collected from 37 woody species

426 in these plots, approximately in proportion to their abundance. Yet two species (*Pseudotsuga*

427 *menziesii* and *Pinus ponderosa*), and more generally two clades of the Pinaceae family (the

428 abietoides and pinoids), represent the vast majority of the biomass in the region (Fig. 3). Because

429 site-specific traits were extensively sampled, we calculated the true variation in functional

430 diversity across plots based on observed community-weighted mean traits (L. D. L. Anderegg et

431 al., 2018). We also calculated the functional diversity within plots using functional diversity

432  metrics that incorporate elements of functional richness, evenness, and occupied niche space

433  (here we average results using Functional Dispersion (Laliberté & Legendre, 2010) and Rao's

434  quadratic entropy (Botta-Dukát, 2005), which can be weighted by relative abundance and can be

435  calculated for communities with fewer than three species). We then compared the efficacy of

436  different functional type groupings by comparing observed FD within and among communities

437  with FD calculated using a single mean trait value per functional type (see SI "*Methods for*

438  *Pacific North West Functional Diversity analysis*").

439  Traditionally, all of the woody species in the region would be represented by at most

440  three growth form and phenology-based PFTs, which together capture an average of only 6% of

441  the CWM variation in LMA, Leaf Lifespan, and $N_{mass}$ among communities and an average of

442  16% of the FD within communities (Fig. 3). A similar categorization based on evolutionary

443  lineage (at the family level for the gymnosperms and lumping all angiosperms together—termed

444  'Deep LFT' in Fig. 3 for how deeply the phylogenetic tree is trimmed) captures slightly more of

445  the variation in CWM traits among communities (9% on average) and slightly less diversity

446  within communities (12%). This result is expected, as classic PFTs and 'Deep LFTs' are quite

447  similar (Table S1). LFTs guided by abundance prioritize the functional distinction among

448  gymnosperms, while classic PFTs prioritize the leaf habit distinction among angiosperms that

449  happen to be quite rare in this system. And ultimately, no 3-group functional type scheme can be

450  expected to capture the true FD of even low diversity systems. However, the LFT approach

451  provides an obvious framework for further disaggregation.

452  By splitting the most evolutionarily divergent angiosperms (acknowledging extreme

453  evolutionary and therefore functional distinctiveness) and dividing the Pinaceae family into the

454  abeitoid and pinoid subfamilies (acknowledging that Pinaceae dominate 95% of the biomass), a

455  lineage-based division with only five functional types ('Mid LFT') captures 20% of the variation

456  in CWM traits and 21% of the variation within communities (Fig. 3). Further division focusing

457  on the most abundant lineages (breaking the Pinaceae into genera, 'Shallow LFT') captures an

458  average of 37% of the between-community variation and a startling 84% of the within-

459  community functional diversity with nine LFTs. The 'Mid' and 'Shallow' LFT examples

460  presented here are based on qualitative weighting of evolutionary distinctiveness and abundance,

461  but development of a quantitative weighting scheme would be feasible with appropriate

462 abundance data and a dated phylogeny, perhaps employing sensitivity tests to determine the

463 appropriate balance between weighting functional distinctiveness and dominance.

464     Low diversity temperate forests, while tractable for calculating true functional diversity

465 from extensive observations, are admittedly a relatively simple example system. However, the

466 ability of lineage- and abundance-guided LFTs to capture within- and among-site functional

467 variation in a system where intraspecific trait variation is important (L. D. L. Anderegg et al.,

468 2018) and where rare evolutionary outlier species such as the deciduous conifer *Larix*

469 *occidentalis* could be particularly troublesome provides hope for using LFTs in more diverse

470 systems.

471     Are LFTs 'better' than alternative PFT methods? One of the many difficulties in

472 answering this question is the general lack of alternative *a priori* PFT delineation methods to

473 compare against. *A posteriori* empirical clustering of observed traits can capture more trait

474 variation than essentially any *a priori* classification technique. However, the Pacific Northwest

475 forest example illustrates the limitations of empirical clustering in terms of interpretability and

476 applicability for determining model PFTs. The 'Shallow LFT' captures an average of 59% of the

477 total variation in LMA, $N_{mass}$, and Leaf Lifespan when applied to the entire database of all

478 individual trait measurements (rather than plot-level CWM traits). With nine clusters,

479 agglomerative Ward clustering can capture an average of 78% of variation in the same traits and

480 k-means clustering can capture an average of 79% of the variance. However, empirical clustering

481 approaches yield widely different groups depending on algorithm type (e.g. Table S2 for Ward

482 vs k-means clustering) and are fundamentally limited by interpretability. Clustering on the full

483 trait database invariably places measurements from most species, even rare species, in multiple

484 clusters (e.g. Table S3), meaning the clusters do not have a taxonomic interpretation and could

485 serve as 'trait-based Plant Functional Types' *only if one knows all the traits*. A regional

486 simulation using these empirical PFTs could not map the PFTs for initialization or model

487 validation, and the PFTs could not be employed for site-based simulations outside the training

488 sites. Meanwhile, clustering on CWM traits could capture more spatial variation in traits than

489 LFTs, but could not capture within-community FD (because the algorithm is classifying sites,

490 rather than individuals).

491     Finally, a useful example of how lineage naturally captures multiple (often unknown)

492 axes of functional diversity: the Shallow LFT predicts the climate-of-origin of trait

493    measurements in the PNW trait dataset, because lineages tend to have conserved biogeographic

494    niches. Empirical clustering algorithms on traits alone explain similar variation in temperature-

495    of-origin but considerably less variation in climate-of-origin along any water-related climate axis

496    compared to LFTs (Table S4). Thus, even though none of the clustering methods explicitly

497    considered biogeography, a lineage-based approach naturally captures biogeographic patterns

498    resulting from niche conservatism.

499

500    ***Implications for benchmarking model biogeography***

501        One key goal of dynamic vegetation models in ESMs is to predict vegetation shifts and

502    their attendant vegetation-climate feedbacks under climate change. We believe that evolution-

503    based PFTs could help predict shifting functional traits across the landscape without relying on

504    the empirical climate envelopes that have long been the crutch of Dynamic Global Vegetation

505    Models (Fisher et al., 2015; Sitch et al., 2003). To judge our success at simulating biogeography

506    without climate envelopes, the PFTs used in dynamic models need be relatable to observational

507    biogeographic datasets. Paleoclimate records from pollen reconstructions are typically already

508    aggregated to the genus or higher (e.g. Jackson et al., 2000), making them useful benchmarking

509    datasets if functional types are also grounded in evolutionary lineage. Species-level

510    biogeographic observations (e.g., of post-industrial range shifts) can also easily be aggregated up

511    to the relevant scale to provide model benchmarks if functional types have a taxonomic basis.

512    Thus, LFTs naturally lend themselves to biogeographic benchmarking.

513        One particularly exciting feature that may make Lineage Functional Types both easier to

514    operationalize and useful for benchmarking longer-term vegetation model dynamics is that they

515    can potentially be remotely sensed by satellite. There is considerable evidence that the spectral

516    properties of plant canopies are phylogenetically conserved, similar to physiological traits

517    (Cavender-Bares et al., 2016, 2017; Meireles et al., 2020; Schweiger et al., 2018) and that

518    phylogenetic lineages can be remotely sensed (Cavender-Bares et al., 2021). Whether

519    serendipitously or mechanistically linked to ecological niche conservatism, the phylogenetic

520    conservatism of plant spectra (Meireles et al., 2020) could allow rapidly proliferating

521    hyperspectral data to be used to map LFTs. The combination of plant or plot-scale hyperspectral

522    data from experiments (Cavender-Bares et al., 2016; Schweiger et al., 2018), landscape-scale

523    data from aircraft hyperspectral platforms such as the U.S. National Ecological Observatory

524    Network's Airborne Observation Platform (NEON, n.d.), and ultimately satellite data, hold great

525    promise for linking evolutionary relatedness to large-scale patterns of lineage presence and

526    abundance. There are many challenges for scaling from phylogenetic relationships of plants with

527    canopies of ~0.1-10 m size to satellite remote sensing pixels (e.g., ~30 m resolution for

528    upcoming hyperspectral satellites) to model grid cells (~10-100 km for most current ESMs) (Fig.

529    4). However, if approaches such as spectral unmixing can enable downscaling of sufficient

530    resolution to capture the dominant LFTs of a model grid cell, hyperspectral satellite data—soon

531    to be available from Germany's DESIS, Japan's HiSUI, and NASA's EMIT sensors on the

532    International Space Station and planned Surface Biology and Geology (SBG) satellite (Schimel

533    et al., 2020)— could be harnessed for global LFT mapping. While the use of these data to

534    directly map functional traits is promising for initializing trait-based models, the actual identity

535    of taxa at a location can tell us considerably more information about many important unobserved

536    or unobservable traits than single traits themselves (J. S. Clark, 2016), and could potentially

537    (through spectral unmixing) inform trait and LFT diversity within a grid cell. Moreover, remote

538    sensing of lineage presence and abundance through time could provide model benchmarking data

539    independent of the short-term (seasonal to interannual) flux measurements often used for model

540    benchmarking (e.g., iLAMB, Collier et al., 2018).

541

542    ***Conclusion: Future Opportunities & Challenges***

543        Actualizing a lineage-based functional type representation of plant diversity requires merging

544    multiple sources of phylogenetic, trait, and diversity data to address three key challenges:

545    1) **Find where niche conservatism breaks:** Identify which model-relevant traits show little

546        phylogenetic signal and develop theoretically defensible ways to simulate the underlying

547        processes determining these traits. Allometric traits and area-based leaf traits are

548        important current model parameters that probably fall into this category. Both groups of

549        traits are likely determined by the interactions of multiple underlying processes and

550        properties. Improved understanding of the ecological and evolutionary forces driving

551        niche conservatism and phylogenetic signal in functional traits, and functional ecology

552        studies comparing the phylogenetic signal in a diversity of traits in a diversity of taxa are

553        needed.

2) **Test phylogenetic conservatism of plant function in hyper-diverse 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

585        using hyperspectral remote sensing data to map LFTs, though numerous scaling

586        challenges must first be addressed.

587

588        Timely and societally relevant predictions of ecological change in the Anthropocene

589 require mechanistic models that apply current ecological knowledge to forecast outside the

590 training domain of today's world. We advocate for increased collaborations among vegetation

591 modelers, evolutionary biologists, community ecologists, ecophysiologists, and paleo-ecologists

592 to generate new and creative ways to represent plant diversity in models. We propose that

593 evolutionary relatedness can serve as a unifying theme for these efforts.

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608 **Author contributions:**

609 LDLA, DMG and CJS conceived the idea for the paper, all authors revised and developed the

610 idea, LDLA wrote the first draft of the manuscript, and all authors contributed to manuscript

611 revisions.

612

613 **Data Availability:** All data used in analyses are publicly available from L. D. L. Anderegg et al.,

614 2018, DOI:10.5061/dryad.c1dn34b; Falster et al., 2015, DOI:

615    10.6084/m9.figshare.c.3307692.v1; Gleason et al., 2015, available as dataset #241 through

616    https://www.try-db.org/; Law & Berner, 2015, DOI: 10.3334/ORNLDAAC/1292 ; Ledo et al.,

617    2017, DOI: 10.6084/m9.figshare.5144164.v1; Zanne et al., 2009, DOI: 10.5061/dryad.234.

618    Analysis code is available at

619    https://github.com/leanderegg/LineageFunctionalType_PNWexample.

620    **Figure Captions:**

621

622    ***Figure 1: Plant function is phylogenetically conserved*** *(a) conceptual example of phylogenetic*

623    *conservatism of both environmental niches (y-axis) and plant functional traits invoked as*

624    *parameters in Land Models (x-axis). Grey lines illustrate evolutionary relatedness (e.g.,*

625    *phylogeny) for three lineages (colors), with related species being similar in both niche and trait*

626    *values. (b) The less common alternative example of a niche axis and associated functional trait*

627    *that are not phylogenetically conserved. (c) Taxonomic variance decomposition of example*

628    *'plant functional traits' that are sometimes considered model parameters. Many leaf and stem*

629    *traits vary primarily at broad taxonomic scales (e.g., among plant families, grey bars),*

630    *suggesting that lineage is a good predictor of trait values. However, some plant traits such as*

631    *root to shoot biomass ratio (R:S) are less strongly conserved and may be best modeled as*

632    *emergent properties from underlying processes. See Box 1 for trait descriptions and SI Variance*

633    *Decomposition Methods for data descriptions.*

634

635    ***Figure 2: Lineage-specific leaf lifespan responses to temperature.*** *Leaf lifespan in months*

636    *plotted against the Mean Annual Temperature (ºC) of the sampling location. Gray points show*

637    *all species-level observations, Leaf lifespan is $\log_{12}$-transformed so 1 = one year. (a) Within-*

638    *family patterns in the seven most well-sampled families, showing either increased longevity or*

639    *increased winter deciduousness at colder temperatures. (b) Within-genus patterns are similar to*

640    *family-level patterns, with genera outside the tropics typically adopting either a universal*

641    *evergreen or deciduous strategy. (c) Qualitative schematic of the two cold response strategies*

642    *and the area where plant hydraulics plus water availability likely dictate leaf habit in the*

643    *absence of cold stress; within-species patterns in conifers are plotted in colored lines. Data from*

644    *(Law & Berner, 2015; Wright et al., 2004).*

645

646    *Figure 3: Example of Functional Types in the PNW U.S.A. Phylogeny of woody plants in a*

647    *network of 256 forest plots in the Pacific NW, USA (Law & Berner, 2015), with four example*

648    *disaggregation schemes, and the distribution of total biomass across the species showing*

649    *hyperdominance of a small number of species. Percentages indicate the average amount of*

650    *variation in Functional Diversity (FD) explained among sites (variance in community-weighted*

651    *mean LMA, Leaf Lifespan, and $N_{mass}$ (see Box 1)) and within sites (variance in Functional*

652    *Dispersion and Rao's quadratic entropy) explained by each disaggregation scheme. The 'Classic*

653    *PFT' scheme used in many land models and a coarse Lineage Functional Type (LFT) approach*

654    *('Deep', because it is divided deep in the phylogenetic tree) explain similarly low amounts of*

655    *variance, while further disaggregation breaking up the major angiosperm lineages present and*

656    *the lineages of the dominant Pinaceae family ('Mid LFT') and then dividing Pinaceae into*

657    *genera ('Shallow LFT') explain an increasing fraction of FD within and among sites. See SI*

658    *Methods for full analysis description.*

659

660    *Figure 4: Scaling LFTs from canopy to landscape. Even a relatively low species richness forest*

661    *in the Pacific Northwest, USA poses challenges both to the remote sensing of diversity with*

662    *satellites with the resolution of 10s of meters (Canopy Scale panel) and to the representation of*

663    *diversity in ESM grid cells that range from 0.05° (~5.5km in the temperate zone) to 1°. However,*

664    *the phylogenetic signal in plant spectra may facilitate the identification of dominant lineages in*

665    *pixels representing multiple plant canopies, and ultimately the identification of the dominant*

666    *Lineage Functional Types at continental scales. The explanatory value of lineages, and our*

667    *ability to detect them, may vary with scale. Dividing vegetation based on large phylogenetic*

668    *differences (Deep LFT) may be more appropriate for broader scales whereas vegetation might*

669    *be best differentiated using shorter phylogenetic distances (Shallow LFT) at high resolution.*

670    *Images from Google Earth Pro©.*

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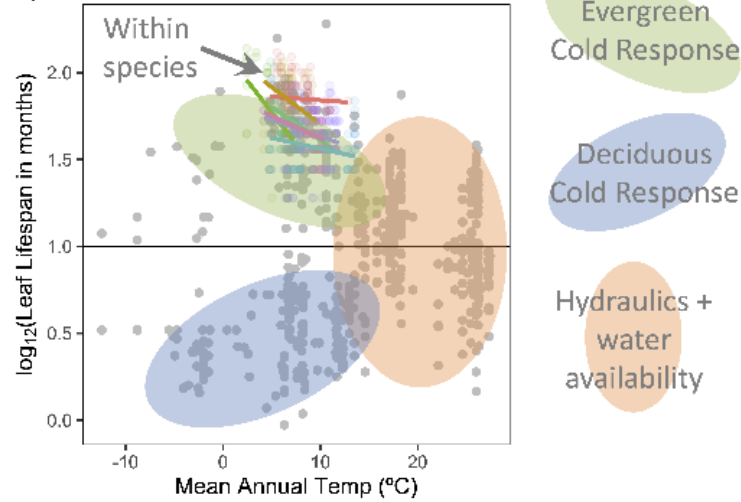978          *Systems*, *11*(7), 2238–2258. https://doi.org/10.5194/bgd-10-13455-2013

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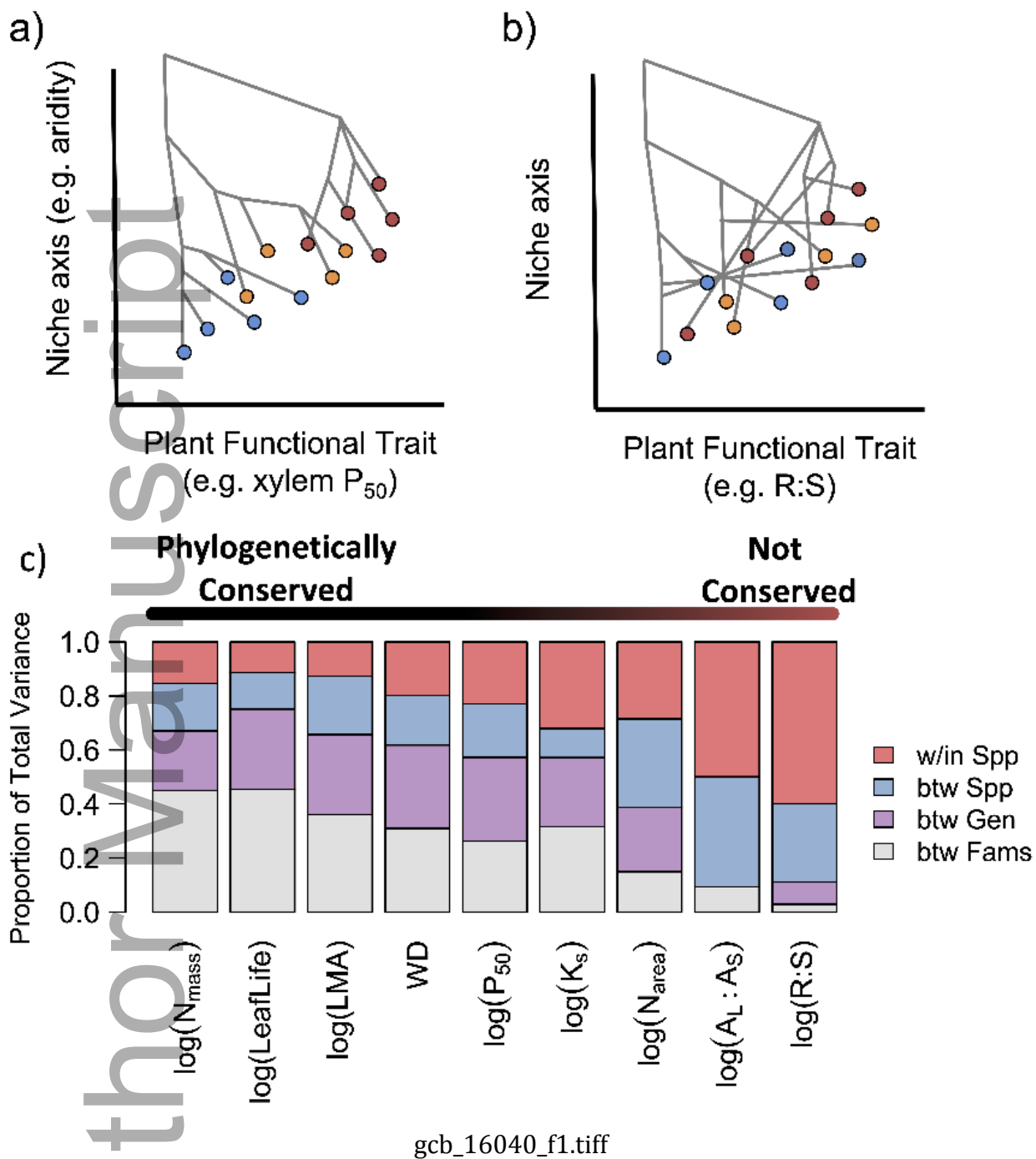
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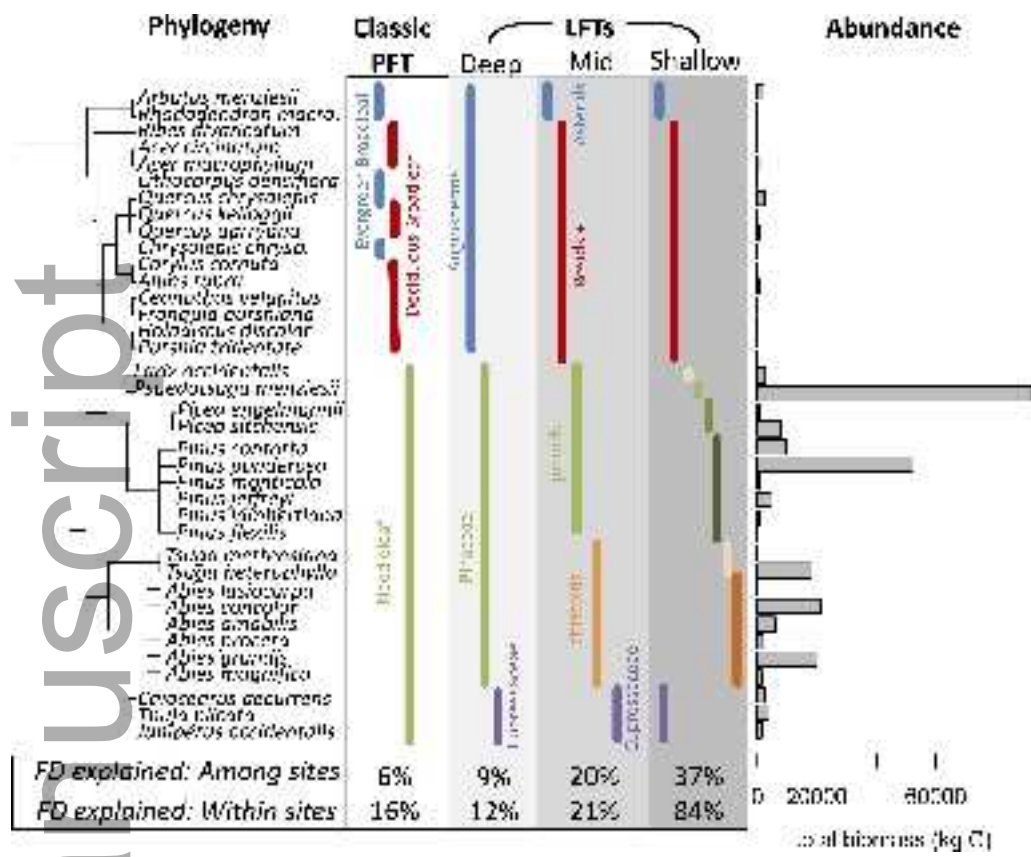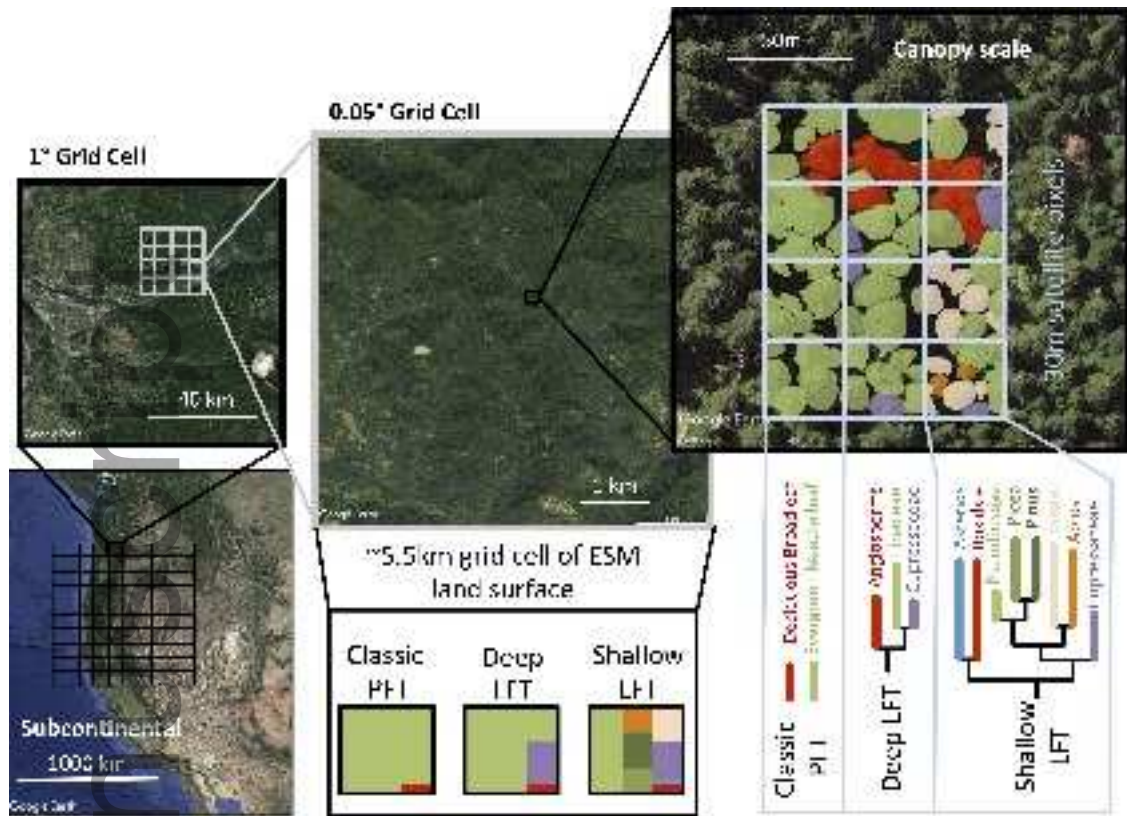
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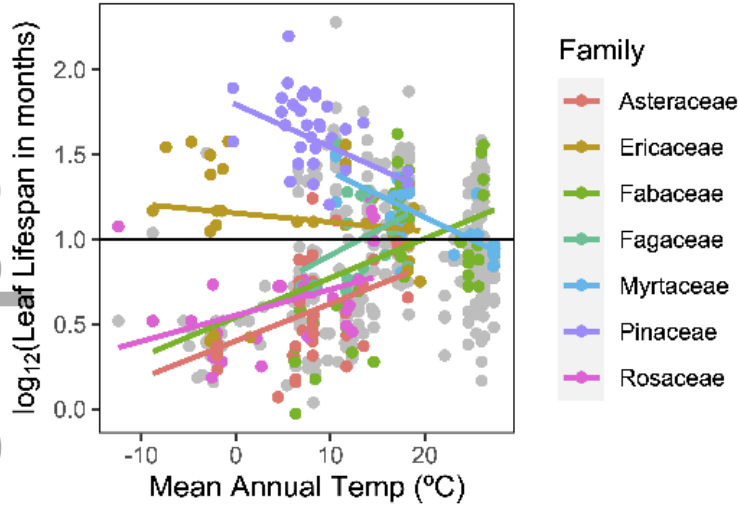
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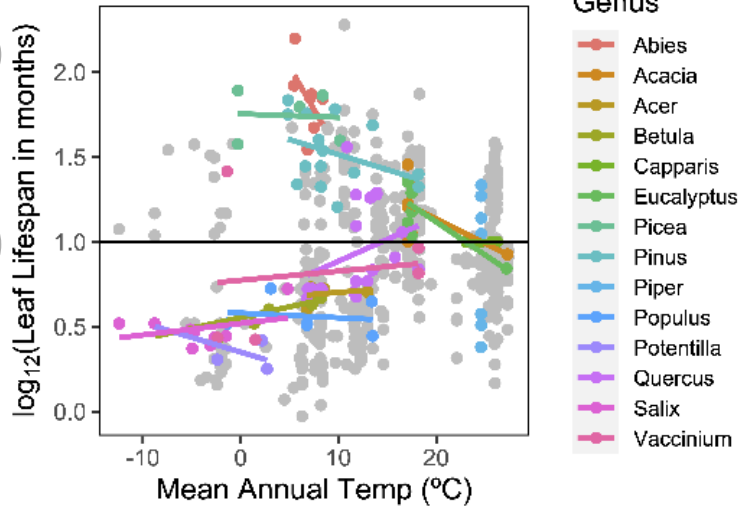
c) Theory

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