1 **Defining a spectrum of integrative trait-based vegetation canopy structural types**

2 Running title: Defining canopy structural types

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30 data and conducted initial analyses to support inclusion of data in the analysis framework. RTF

31 wrote the initial manuscript draft and all authors contributed substantially to final revisions.

32

35

36 **Abstract**

37 Vegetation canopy structure is a fundamental characteristic of terrestrial ecosystems that defines

38 vegetation types and drives ecosystem functioning. We use the multivariate structural trait

39 composition of vegetation canopies to classify ecosystems within a global canopy structure

40 spectrum. Across the temperate forest subset of this spectrum we assess gradients in canopy

41 structural traits, characterize canopy structural types (CST), and evaluate drivers and functional

42 consequences of canopy structural variation. We derive CSTs from multivariate canopy structure

43 data, illustrating variation along three primary structural axes and resolution into six largely

44 distinct and functionally relevant CSTs. Our results illustrate that within-ecosystem successional

45 processes and disturbance legacies can produce variation in canopy structure similar to that

46 associated with sub-continental variation in forest types and ecoclimatic zones. The potential to

47 classify ecosystems into CSTs based on suites of structural traits represents an important advance

48 in understanding and modeling structure-function relationships in vegetated ecosystems.

49

50 **Introduction**

51   The structural characteristics of vegetation canopies are a defining feature of terrestrial

52 ecosystems and a fundamental driver of ecosystem functioning (Ishii *et al.* 2004). Canopy

53 structure is an emergent property of the organization of vegetation elements, at leaf to crown

54 scales, by plant individuals and communities with variable crown architecture and shade

55 tolerance (Parker *et al.* 1989; Hardiman *et al.* 2013a; Fotis *et al.* 2018). The development of

56 these emergent canopy structures is driven by optimization of leaf to canopy resource use

57 efficiency and by competition among individuals, within the biotic and abiotic constraints

58 determined by the broader context in which the ecosystem is situated (Niinemets 2007; Ishii &

59 Asano 2010). As an emergent property of vegetated ecosystems, canopy structure integrates

60 ecologically important characteristics of individuals, species, communities, ecosystems, and

61　biophysical regions (e.g., Aber *et al.* 1982; Ellsworth & Reich 1993; Ishii *et al.* 2004). For this

62　reason, characterization of broad, readily categorizable vegetation structural types has been a

63　focus of the foundational work of biogeography, ecology, and remote sensing (Whittaker 1970;

64　Running *et al.* 1995; Box 1996).

65　　Quantification of canopy structure is highly important in studying terrestrial ecosystems both

66　because of its role as an integrator of ecological factors, and as a basis for studying fundamental

67　structure-function relationships. Canopy structure is most commonly quantified using the density

68　metric "leaf area index" (LAI), which has become ubiquitous because of its combination of

69　relative simplicity (in quantification and application) and potential for predicting ecosystem

70　functioning (e.g., Reich 2012). However, vegetation canopies are inherently three-dimensional

71　and the integrated vertical and horizontal arrangement of canopy elements provides additional

72　predictive capacity on ecosystem processes and functions such as light harvesting and light use

73　efficiency (Ellsworth & Reich 1993; Ishii & Asano 2010; Fotis & Curtis 2017; Atkins *et al.*

74　2018b), air movement (Reich *et al.* 1990; Parker *et al.* 2004b; Maurer *et al.* 2015), vertical

75　temperature and humidity gradients (Niinemets 2007), productivity (Hardiman *et al.* 2011;

76　Cushman & Kellner 2019; Gough *et al.* 2019), and disturbance resilience (Gough *et al.* 2013;

77　Hardiman *et al.* 2013b; Fahey *et al.* 2016). There is not a widely accepted framework or set of

78　metrics to characterize the 3D structure of vegetation canopies (Nadkarni *et al.* 2008). This fact

79　is not surprising given that a broad definition of canopy structure incorporates several disparate

80　concepts describing the spatial positioning of canopy elements or open space, and also because

81　there has been limited work pairing functional data with integrative measures as a way of testing

82　their functional significance (Atkins *et al.* 2018c).

83　　The wide variety of canopy structure metrics that have been described (including LAI) can be

84　viewed as structural "traits" of vegetation canopies (Reich 2012). However, recognizing that

85　individual aspects of canopy structure (e.g., height, LAI) do not fully describe functionally-

86　relevant variation in structure among canopies, we propose a multivariate, trait-based approach

87　to the study of variation in canopy structure among vegetated ecosystems. The multivariate

88　structural trait composition of a canopy can be used to place vegetated ecosystems within a

89　hypothesized global canopy structure spectrum (Fig. 1). Characterization of terrestrial vegetation

90　types has long been strongly focused on vegetation structure (alongside aspects of phenology and

91　general physiognomy; Bailey 2009), and the general canopy structural types that make up this

92   spectrum are the basis for global to regional scale vegetation classifications (e.g., grasslands vs.

93   savannas vs. tropical forests; Fig. 1a; Whittaker 1970). These vegetation structural types can be

94   viewed as an agglomeration of canopy traits describing the arrangement of vegetation elements

95   in canopy space and generally relate to three primary components of variation; canopy height,

96   vertical layering, and horizontal openness/patchiness (Aber *et al.* 1982; Brokaw & Lent 1999;

97   Ehbrecht *et al.* 2016; Paynter *et al.* 2018; Cushman & Kellner 2019), as well as higher order

98   metrics that combine or describe variation in these traits to characterize the arrangement of

99   canopy elements in 2D or 3D space (Hardiman *et al.* 2011; Chen *et al.* 2012; Seidel *et al.* 2016).

100   The structure of vegetation canopies has an inherent spatial dimension constrained by several

101   biotic factors (e.g., crown form, plant height, and leaf angles; Horn 1971; Givnish 1982; Anten

102   2004; Verbeeck *et al.* 2019), but is perhaps most fundamentally defined by the scale of

103   individual leaves, which are ultimately the unit of allocation for organisms exploring canopy

104   space and optimizing light capture and resource use (Hikosaka & Anten 2012; Niinemets 2012).

105   Leaf size is relatively consistent across plants that vary in overall size by several orders of

106   magnitude, and so is the amount of space that can be filled or explored by those leaves (Fotis &

107   Curtis 2017). Variation among ecosystems in total height, vertical layering, and horizontal

108   openness, therefore, affects the potential for complex arrangement of leaf area in space and

109   differentiation in canopy structural characteristics (Ishii *et al.* 2004; Fotis *et al.* 2018). Less

110   complex (i.e., shorter, more horizontally and vertically uniform) canopies inherently have less

111   canopy space that can be explored to promote optimal light harvesting and drive differential

112   interception of diffuse radiation (Montgomery & Chazdon 2001; Fotis & Curtis 2017).

113   Therefore, a framework separating ecosystems based on total canopy height and vertical layering

114   has grounding in allocation and optimization theories (Anten 2004; Hikosaka & Anten 2012;

115   Niinemets 2012), as well as copious evidence to support functional importance (e.g., Ishii &

116   Asano 2010; Hardiman *et al.* 2011).

117   A canopy structural trait-based classification system can be viewed as analogous to other trait-

118   focused frameworks for classifying vegetated ecosystems, such as plant functional types (PFT;

119   Box 1996; Bugmann 1996) or the global leaf economics, wood economics, and leaf size

120   spectrums (Westoby & Wright 2003; Wright *et al.* 2004; Chave *et al.* 2009; Wright *et al.* 2017).

121   Canopy structural traits and types likely embody functional information not currently represented

122   by conventional forest types (which are often qualitatively assigned), PFTs based on growth

123   forms/leaf habits, or non-integrative leaf and plant traits. A quantitative framework for

124   characterizing canopy structure could aid in isolating the role that physical structure plays in

125   mediating ecosystem functional responses and thus has direct implications not only for

126   vegetation and ecosystem modeling (Hurtt *et al.* 2010), but also for testing underlying basic

127   ecological assumptions of structure-function relationships (Ishii *et al.* 2004).

128   Differentiation of broad vegetation structural types is driven by biophysical and

129   environmental factors such as seasonality and temperature gradients (Fig. 1a) and characteristics

130   of the regional-scale biota (e.g., gamma diversity; Prentice *et al.* 1992; Box 1996). However, the

131   arrangement of ecosystems among and within these broad categories of canopy structural types

132   is also likely to be related to fine-scale environmental variation (e.g., soil water holding capacity,

133   topography; Aber *et al.* 1982; Jucker *et al.* 2018), species, crown type, plant functional type, and

134   trait composition of the local community (Ishii & Asano 2010; Verbeeck *et al.* 2019), stand to

135   landscape-level community characteristics (e.g., alpha and beta diversity; Dial *et al.* 2004; Jucker

136   *et al.* 2015), and historical factors such as successional processes and disturbance legacies

137   (Scheuermann *et al.* 2018). Understanding how canopy structural types develop and how they

138   vary within and among vegetation types and ecoclimatic domains is essential to assessing

139   structure-function relationships broadly and modeling the distribution of these relationships

140   across landscapes.

141   Here we explore the foundational ecological topic of conceptualizing and characterizing

142   vegetation canopy structure, using novel analytic methods and an extensive, sub-continental-

143   scale data set that combines detailed canopy structure data with information on environmental

144   gradients, community composition, and ecosystem processes and functions. Our overall research

145   goal was to quantify a spectrum of potential canopy structural types (CST) that characterize

146   hypothesized variation among temperate forest ecosystems as a subset of a global canopy

147   structure spectrum (Fig. 1b). Our specific research objectives were to: 1) describe variation

148   among a broad suite of canopy structural traits across large, heterogeneous data sets, 2)

149   implement and test a novel method and framework for deriving synthetic canopy structure

150   gradients and CSTs, and 3) assess potential drivers and importance of variation in canopy

151   structure by relating CSTs to environmental gradients, community composition, and ecosystem

152   functioning. To address this goal we developed and tested multivariate analytical frameworks for

153   deriving synthetic canopy structural complexity gradients and generalized CSTs, based on

154 approaches adopted from analysis of ecological communities. We utilized datasets representing a

155 range of spatial scales (sub-continental, landscape, and stand) and different dominant gradients

156 driving variation in vegetation characteristics (ecoclimatic domains, landscape ecosystems,

157 successional stages, and disturbance severity).

158

159 **Material and methods**

160 *Study systems and sampling methods*

161   To analyze patterns of variation in canopy structure we utilized four data sets spanning

162 different dominant gradients (environmental, successional, and disturbance) and a range of

163 spatial scales (stand to sub-continental). Three data sets were focused on the University of

164 Michigan Biological Station (UMBS) in northern lower Michigan, USA. The UMBS area has a

165 mean annual temperature of 5.5°C and a mean annual precipitation of 817 mm. Forests in the

166 area are primarily ~100 years old, but old forest (200+ years) remnants are also present (Gough

167 *et al.* 2007). The first UMBS data set ("UMBS-LE") was a landscape-scale (~4000ha) plot

168 network originally utilized to characterize Landscape Ecosystem types (Pearsall 1995). The

169 second UMBS data set ("UMBS-Chrono") included three experimental chronosequences

170 consisting of 15 forest stands varying from 17 to 180 years of age and differing in type and

171 severity of establishing disturbance (clear-cut vs. clear-cut and burned) and forest type

172 (deciduous broadleaf dominated vs. evergreen needle-leaf dominated; Scheuermann *et al.* 2018).

173 The third UMBS data set ("UMBS-FASET") was a 39 ha experimental disturbance where 39%

174 of pre-treatment basal area (range of 9-69% at the plot-level) was removed through stem-girdling

175 of early-successional species (Gough *et al.* 2013).

176   The final data set was a sub-continental-scale network of study areas primarily focused on

177 National Ecological Observatory Network (NEON) sites, but also including a mixture of Long

178 Term Ecological Research (LTER) sites, AmeriFlux sites, and university field stations (hereafter

179 referred to as "LQ-NEON") (Atkins *et al.* 2018b). For this data set 13 sites were sampled across

180 the eastern US (Table 1) spanning broad gradients in latitude (29.7 – 46.3°N), climate (mean

181 annual temperature: 4.5 – 20.0°C, mean annual precipitation: 800 – 1475mm yr^{-1}), forest type

182 (USDA Forest Service Types: oak-pine, oak-hickory, maple-beech-birch, aspen-birch, longleaf-

183 slash pine, loblolly-shortleaf pine; Ruefenacht *et al.* 2008) and 6 NEON ecoclimatic domains:

184 Northeast, Great Lakes, Mid-Atlantic, Appalachians and Cumberland Plateau, Ozarks Complex,

185 and Southeast (Kao *et al.* 2012).

186   The number and characteristics of previously established sample plots varied among data sets

187 (Table 1), but canopy structure sampling was conducted with a consistent methodology. Canopy

188 structure was analyzed using below-canopy lidar scan data collected using the portable canopy

189 lidar system (PCL; Parker *et al.* 2004a). PCL transects of 30-50m in length were located in each

190 plot; total transect length and number of transects were specific to plot type (Table S1), but were

191 sufficient to characterize canopy structural variability based on prior work (Hardiman *et al.*

192 2018). We utilized the *forestr* package (Atkins *et al.* 2018a) in *R* (v. 3.5.0) to process raw PCL

193 scan data into 1 x 1m grids of vegetation area index (VAI) from which we derived canopy

194 structure metrics. In prior work we developed a suite of 23 structural metrics (Table S2) that

195 span a gradient of dimensionality and encompass the range of canopy structural descriptions

196 found in the literature, describing functionally meaningful aspects of canopy density, cover,

197 arrangement, height, and variability (Ehbrecht *et al.* 2017; Atkins *et al.* 2018b). These canopy

198 structural traits are relatable to the canopy structure spectrum proposed in Fig. 1, with 6 traits

199 describing vertical complexity (e.g., effective number of layers, rugosity), 10 conveying canopy

200 density or openness (e.g., vegetation area index, gap fraction), and 8 describing measures of

201 canopy height (maximum canopy height, mean vegetation height; Table S2). We used the multi-

202 variate composition of these canopy structural traits for each plot to describe canopy

203 characteristics and derive canopy structural types as described below. Additional data on

204 environmental factors, community characteristics, and stand structure were used as predictors in

205 analyzing drivers of canopy structure and assessing relationships with ecosystem functioning

206 (Table S3).

207

208 *Data analysis*

209   Our analysis utilized techniques often applied to understanding ecological communities,

210 recognizing that analysis of multi-factor canopy structure data, canopy traits, and derivation of

211 CSTs has much in common with analysis of species traits and delineation of vegetation

212 communities – namely high dimensionality and strong intercorrelations. To better understand the

213 primary gradients in canopy structure within and across data sets, we performed ordination

214 analysis on matrices of all 24 canopy structure metrics. Ordination was conducted using Non-

215 metric Multidimensional Scaling (NMS) in PC-ORD v.5.31 (McCune & Mefford 2006) with
216 Sorensen's distance measure and the ''slow-and-thorough'' auto-pilot setting, using 250 runs of
217 real data and 250 Monte Carlo randomizations to assess the robustness of the solution (McCune
218 & Grace 2002). Ordination was conducted on a matrix with all canopy structure metrics first
219 relativized to the maximum value that the metric obtained to scale all metrics equivalently. We
220 also included a second matrix of environmental and site information to enable creation of bi-plot
221 and categorical overlays. We tested for differences among groupings in each data set (Landscape
222 Ecosystem types, Ecoclimatic Domains, stand ages, and disturbance severity groups; Table S3)
223 in multivariate suites of canopy structure metrics using Multiple Response Permutation
224 Procedure (MRPP) with Sorensen's distance measure in PC-ORD (McCune & Grace 2002).
225   To produce data-driven CSTs we performed hierarchical agglomerative clustering on matrices
226 of canopy structure metrics. Clustering was performed with PC-ORD using Ward's Method and
227 Euclidean distance measures (McCune & Grace 2002). Optimal cluster grouping level was
228 determined by conducting Indicator Species Analysis and deriving mean p-values for indicator
229 values across all metrics for each level of grouping (McCune & Grace 2002). The grouping level
230 with the lowest mean p-value was selected as the optimal grouping level for the data set and
231 clusters identified at this grouping level were utilized as the CSTs. We then evaluated which
232 metrics were most strongly associated with each CST based on the results of the Indicator
233 Species analysis for the final grouping level. Plant Functional Type (PFT) classifications were
234 produced for the LQ-NEON plots using an equivalent methodology and based on published
235 species PFT classifications (Bugmann 1996; see Supporting Information 1)
236   To evaluate how CSTs were related to the primary gradients (community, environmental,
237 successional, disturbance) represented in each data set, we conducted a classification tree
238 analysis. We evaluated which predictors (Table S3) were most influential on the separation of
239 plots into distinct CSTs for each data set using the Random Forest algorithm (Breiman 2001),
240 which produces a series of iterative decision trees using binary, recursive partitioning based on
241 predictor values and known classes (Cutler *et al.* 2007). We evaluated the classification accuracy
242 of the models based on the out of bag error calculation (OOB) and evaluated the relative strength
243 of individual predictors based on the mean decrease in accuracy associated with trees from which
244 each predictor was removed. The predictors with greatest influence on accuracy across all trees

245   were considered the most influential factors in driving CST differentiation. All analyses were

246   conducted using the *randomForest* package (Liaw & Wiener 2018) in R (v. 3.5.0).

247   To explore relationships of CSTs with ecosystem processes and functioning we utilized plot-

248   level light interception (fraction of photosynthetically active radiation absorbed by the canopy;

249   fPAR), wood net primary productivity (NPPw), and light use efficiency (LUE, as NPPw/fPAR;

250   Hardiman *et al.* 2013b) data that were available for a subset of the NEON plots (Supporting

251   Information 2; also Atkins *et al.* 2018b). We utilized generalized linear models to evaluate

252   variation in these factors across CSTs and to assess the effect that adding CSTs and PFTs to a

253   model including only Ecoclimatic Domain had on model performance. All analysis was

254   conducted using PROC GLM in SAS v. 9.4 (SAS-Institute 2013).

255

256   **Results**

257   *Multivariate analysis of canopy structure metrics*

258   Concurrent ordination of all four data sets illustrated strong gradients in canopy structure that

259   aligned primarily along two axes associated with canopy density/openness (VAI and gap

260   fraction) and vertical heterogeneity (Fig. 2). The NMS ordination had a three dimensional

261   solution that was highly significant relative to randomized data (p = 0.004, mean stress = 6.56)

262   and explained a large majority of the variance in the original data matrix (98.1%; mostly on axes

263   1 and 2 - 54.1 and 28.6% respectively). Axis 1 was strongly related to metrics associated with

264   canopy area/density (e.g., mean VAI: r = -0.85; full list of correlations in Table S5) and canopy

265   cover/openness (e.g., sky fraction: r = 0.90). Axis 2 was strongly related to metrics relating

266   canopy vertical heterogeneity (e.g., SD of vertical return height: r = -0.86) and canopy height

267   distribution (e.g., height of maximum return density: r = -0.77). Axis 3 explained a minor

268   component of the variation in the original data matrix (15.4%), and was most strongly related to

269   maximum canopy height (r = -0.93).

270   Patterns within the individual data sets illustrated distinct variation across analysis scales and

271   in relation to environmental, disturbance, and successional gradients (Fig. 3). Although there was

272   some evidence of separation among ecoclimatic domains in multivariate structure space (MRPP:

273   A = 0.33, p < 0.001), there was also significant overlap of domains within the ordination (Fig.

274   3a). For the landscape-scale UMBS-LE data set, there was significant but weak (A = 0.13, p

275   <0.001) evidence of separation among the primary geomorphic landforms (Fig. 3b) and stronger

276   separation among the more specific Landscape Ecosystem types (MRPP: A = 0.26, p < 0.001).

277   Within the UMBS-Chrono data set there was very strong evidence for differentiation among age

278   classes (MRPP: A = 0.64, p < 0.001), but the chronosequence types (disturbance type, forest

279   type) were not as strongly separated (MRPP; A = 0.28, p < 0.001; Fig. 3c). For the experimental

280   FASET disturbance there was little evidence of separation among disturbance severity groups in

281   the ordination space (Fig. 3d; MRPP: A = 0.11, p = 0.02).

282

283   *Derivation of canopy structural types*

284   Cluster analysis for the combined data sets indicated six relatively distinct canopy structural

285   types (CSTs), each represented across multiple data sets, and which generally aligned with the

286   hypothesized canopy structure spectrum presented in Fig. 1. Incremental Indicator Analysis on

287   the agglomerative clustering results suggested pruning the dendrogram at 6 clusters based on the

288   minimum mean p-value in the set (across cluster levels 2-7; mean p = 0.0002; Table S4).

289   Clusters generally aligned with those predicted in Fig. 1, with the exception being that no forests

290   were found to have very high openness/low density and high vertical heterogeneity. Three of the

291   CSTs (clusters 1, 78, and 166) had strong indicator traits in the Indicator Analysis (standard

292   deviation >1.0; Table S6).

293

294   *Relationships between CST and environmental and community characteristics*

295   The strongest environmental and community predictors of CSTs differed among the data sets

296   and largely matched the gradients represented by the data sets. For the LQ-NEON data set the

297   estimated error rate for classification (OOB error rate) was 52.2%, indicating limited potential to

298   predict CSTs at the sub-continental scale. The most important predictors of CSTs in the NEON

299   data were species composition and annual growing degree day accumulation, reflecting macro-

300   scale differentiation in forest type and eco-climatic domains (Fig. 4a). For the UMBS-LE data

301   the error rate was estimated at 26.7%, with Landscape Ecosystem type, elevation, and soil

302   drainage as the most important predictors, reflecting variation in physiographic factors across a

303   landscape with limited differentiation in composition and diversity among stands (Fig. 4b;

304   Pearsall 1995). For the UMBS-Chrono data the error rate was estimated at 6.9% and CSTs were

305   most strongly predicted by stand age, which reflects the strong impact of successional

306   development on stand structure (Fig. 4c). Finally, for UMBS-FASET the classification error rate

307 was estimated as 31.6% and the most important predictor was species composition, and to a

308 lesser extent disturbance severity, reflecting the limited impact of the moderate severity

309 disturbance on overall canopy structure (Fig. 4d). In the NEON data set CSTs were significantly

310 associated with plant functional types based on contingency table analysis ($X^2_{df=16}$ = 99.8, p

311 <0.001). However, there was representation of multiple CSTs across all but one of the PFTs, and

312 all but one of the CSTs likewise included multiple PFTs (Supplement; Table S8).

313

314 *Forest productivity in relation to CSTs, PFTs, and Ecoclimatic Domains*

315   Plot-level wood NPP ($F_{4,92}$ = 7.39, p < 0.001), light interception (fPAR; $F_{4,56}$ = 21.76, p <

316 0.001), and light use efficiency ($F_{4,56}$ = 2.93, p =0.029) all differed significantly across CSTs

317 (Table 2). For NPPw the model that included only Domain explained 49% of the variation in

318 plot-level NPPw, and the addition of CSTs increased the explanatory power to 59%. A Domain-

319 only model explained 79% of the variance in fPAR and the addition of CSTs improved the

320 model slightly (R^2 = 0.82). For LUE a Domain-only model explained 49% of the variance and

321 the addition of CSTs to the model increased the explanatory power substantially (R^2 = 0.66). In

322 each case the addition of CSTs added equivalent or greater explanatory power relative to the

323 addition of PFTs (Table 2). Also, for each factor models that included interactions of PFTs and

324 CSTs alongside Domains had the greatest explanatory power (Table 2).

325

326 **Discussion**

327   Our findings demonstrate the potential for deriving functionally relevant canopy structural

328 types and gradients from multivariate canopy structural data, using temperate mixed coniferous-

329 deciduous forests as a model system. The broad range of forests represented by our sub-

330 continental data set represent a subset of a global spectrum of vegetation structural types (Fig. 1),

331 and were characterized by 2-3 primary gradients in canopy structure variability. These gradients

332 were driven by variation not only in canopy density (i.e., LAI), but also vertical canopy layering,

333 horizontal heterogeneity in canopy density, and the integrative three-dimensional arrangement of

334 canopy elements in vertical and horizontal space (Fig. 2). The multi-variate canopy structural

335 types derived here delineate forests based on integration of these characteristics and capture

336 variation in canopy structure not characterized by conventional categories of structure based on

337 PFTs, canopy density, or vertical layering.

338   The most important canopy structure gradient driving separation among forests was
339   associated with vegetation density and horizontal heterogeneity in canopy openness (Fig. 2). This
340   finding illustrates that, although canopy density is an important factor separating canopy
341   structural types, additional variation associated with horizontal heterogeneity in the placement of
342   leaf area is necessary to describe even the first axis of variation in canopy structure. This pattern
343   aligned with our hypothesized canopy structure spectrum (Fig. 1), and is indicative of
344   fundamental differences in vegetation density and gap fraction among forest types ranging from
345   dense, closed-canopy forests to open savannas/barrens. Our results also illustrate strong
346   separation related to vertical variability in canopy density and layering (Fig. 2), but also
347   demonstrate that these integrative traits are not redundant with canopy height (Parker & Brown
348   2000; Ehbrecht *et al.* 2016). The importance of the vertical dimension generally matched our
349   expectation, but separation of this variation into two somewhat orthogonal axes (~70%
350   orthogonal) did not entirely match the hypothesized framework for temperate forests (Fig. 1b).
351   Data-driven classification of canopy structure produced 6 relatively distinct canopy structural
352   types (CSTs), which were largely consistent with expectations (Fig. 1), demonstrating expected
353   separation of open-canopied forests from dense, closed canopy forests and tall, many-layered
354   forests from those with shorter, single-layered canopies (Leiterer *et al.* 2015; Moran *et al.* 2018).
355   However, the actual CSTs suggested by the data were somewhat more nuanced than the broad
356   characterization represented in Fig. 1. For example, the separation of tall forests into top-heavy,
357   two-layered canopies and similarly tall, broadly vertically stratified forests was not represented
358   in Fig. 1, but is a tenet of forest stand dynamics and silviculture (Franklin & Van Pelt 2004).
359   There were also some "missing" CSTs, most notably the lack of differentiation of open canopied
360   forests based on vertical variability (i.e., along Axis 2 or 3), which could be related to the
361   absence of very tall or very short open-canopied forests (represented in the upper and lower left
362   quadrants of Fig. 1b) in our data set (e.g., no scrub barrens).
363   Our findings highlight the variable role of factors such as climatic gradients, disturbance
364   history, and community assembly in driving the development of canopy structure across scales
365   and ecosystems (Ishii & Asano 2010; Jucker *et al.* 2015; Scheuermann *et al.* 2018). At the sub-
366   continental-scale, there was significant multivariate separation among ecoclimatic zones and
367   forest types in canopy structure, likely reflecting a combination of regional environmental
368   variation and species pools (Prentice *et al.* 1992), and supporting the basis for hierarchical

369   ecosystem classifications defined according to these factors (e.g., Bailey 2004). A large body of

370   prior work has recognized linkages between species composition and diversity and canopy

371   structure (e.g., Dial *et al.* 2004; Vojtech *et al.* 2008; Fahey *et al.* 2015; Jucker *et al.* 2015; Fotis

372   *et al.* 2018), but the distinct role of community assembly of species and related functional traits

373   in driving multidimensional canopy structural variability is largely unresolved (Ishii *et al.* 2004;

374   Hikosaka & Anten 2012; Jucker *et al.* 2015).

375   However, although CSTs varied across ecoclimatic domains, our results also illustrated

376   substantial variation in canopy structure within domains and plant functional types (PFTs; Fig.

377   3a; Table S8). Such variation is not currently represented in broad scale PFT-based frameworks

378   for classifying vegetation structure or models that rely on these frameworks (Hurtt *et al.* 2010).

379   Landscape scale variation in canopy structure was of relatively similar magnitude to that

380   observed at the sub-continental scale (Fig. 3). For example, plots in the landscape-scale UMBS-

381   LE data set showed separation into four different CSTs (Fig 3b), reflecting the strong influence

382   that fine-grain variation in physiographic factors can have on canopy structural development and

383   that CSTs are integrators of these environmental factors (Aber *et al.* 1982; Dial *et al.* 2004; Kane

384   *et al.* 2010; Nave *et al.* 2017; Jucker *et al.* 2018). In addition, the successional chronosequences

385   at UMBS spanned 5 CSTs and included variation, largely driven by stand age, equivalent to that

386   present in the entire subcontinental LQ-NEON data set. There was a consistent successional

387   trajectory in canopy structure (and sequence of CSTs) across forest types and severities of

388   initiating disturbance (Fig. 3c), and our findings support several prior studies that have illustrated

389   disturbance legacies on stand to landscape-level canopy structure (Kane *et al.* 2010; Hardiman *et*

390   *al.* 2013a; Scheuermann *et al.* 2018). However, the effects of the moderate FASET disturbance

391   on forest canopy structure were highly variable (Fig. 3d), and did not generally override pre-

392   disturbance variation in canopy structure (Gough *et al.* 2013; Stuart-Haëntjens *et al.* 2015).

393   Our results indicate that CSTs can provide additional explanatory power beyond that of broad

394   ecoclimatic domains and forest functional types in predicting ecosystem processes and functions.

395   The importance of CSTs was especially apparent when assessed within domains, suggesting that

396   variation in canopy physical structure could be an particularly important predictor of functioning

397   at the landscape scale within regions (Cushman & Kellner 2019). Although individual canopy

398   traits have previously been shown to be highly influential on ecosystem functions (Reich 2012;

399   Atkins *et al.* 2018b; Jucker *et al.* 2018), a focus on multivariate suites of canopy traits could help

400 further elucidate fundamental ecological mechanisms underpinning ecosystem structure-function

401 relationships and isolate the distinct role of physical structure (e.g., relative to species and

402 functional diversity and environmental gradients) in driving ecosystem functioning. However,

403 further research is needed to fully characterize the potential relevance of CSTs across multiple

404 vegetation types and ecosystem functions.

405   The characterization of CSTs and their role in fundamental structure-function relationships

406 provides a basis for studying the mechanistic underpinnings of these relationships (Gough *et al.*

407 2016; Fotis & Curtis 2017; Atkins *et al.* 2018b) and could, thus, be highly useful to terrestrial

408 ecosystem modeling (Hurtt *et al.* 2010; Shugart *et al.* 2010). Canopy structural traits or types

409 could be incorporated alongside (or in place of) conventional measures of structure such as LAI,

410 leaf traits, and PFTs in ecosystem models or integrated with these factors (e.g., vertical

411 heterogeneity in SLA or leaf N; Niinemets 2007). The inclusion of derived CSTs in ecosystem

412 models could also improve mechanistic fidelity without requiring ingestion of computationally

413 intractable spatially explicit canopy structural data. In addition, understanding and

414 characterization of the effects of disturbances that do not significantly alter total leaf area or

415 species and trait composition could be greatly improved by analyzing shifts in canopy structural

416 traits or CSTs (Seidl *et al.* 2014; Gough *et al.* 2016; Scheuermann *et al.* 2018).

417   Derivation of canopy structural traits and CSTs is also an important step in fully utilizing data

418 being provided by emerging and rapidly expanding technologies such as terrestrial laser scanning

419 and aerial and satellite waveform lidar (Ilangakoon *et al.* 2018; Paynter *et al.* 2018). In the near

420 term, lidar-based canopy structural data will have increasing geographic coverage and

421 availability from a variety of sources including the NASA Global Ecosystem Dynamics

422 Investigation satellite, NEON Aerial Observation Platform, and UAV platforms. Widespread

423 adoption of technologies and analysis techniques focused on quantifying and classifying canopy

424 structure across vegetated ecosystems could represent a paradigm shift in terrestrial ecosystem

425 ecology (Danson *et al.* 2018), and implementation of canopy trait-based framework for

426 describing canopy structural variation is an important step in that direction.

427

428 **Conclusions**

429   Implementation of a multivariate, quantitative structural trait-based framework to describe

430 canopy structure variation across vegetated ecosystems represents an important advance in

understanding the functional role of canopy structure, evaluating factors that drive emergence of canopy structures and forest functional types, and meaningfully representing canopy structure in models. Augmenting traditional descriptors of vegetation structure and composition with an integrative canopy trait framework that describes functionally relevant characteristics of the canopy provides a foundation for testing the functional significance of canopy structure via empirical and modeling approaches (Hurtt *et al.* 2010). Use of CSTs as a basis for future work could substantially improve our ability to elucidate basic structure-function relationships in terrestrial ecosystems (Atkins *et al.* 2018b), predict ecosystem functions such as wildlife habitat (e.g., Barnes *et al.* 2016) and carbon sequestration (Gough *et al.* 2016), and design and implement management practices focused on promoting ecosystem complexity and resilience (Fahey *et al.* 2018).

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659   **Tables**

660   Table 1. Characteristics of individual data sets, including component study sites within sub-continental

661   data set (LQ-NEON dataset) collected at National Ecological Observatory Network (NEON) and other

662   university (UNIV) or USDA Forest Service (USFS) sites, and three plot networks at the University of

663   Michigan Biological Station (UMBS).

Data set/Site	Domain	# Plots	Type	Citation
LQ-NEON		156		Atkins et al. 2018b
Arnot Forest	Northeast	10	UNIV	
Bartlett EF	Northeast	15	NEON*^	
Fernow EF	Appalachian	13	USFS	
Great Smoky Mtns.	Appalachian	10	NEON*^	
Harvard Forest	Northeast	19	NEON*^	
Mountain Lake BS	Appalachian	10	NEON	
Ordway Swisher BS	Southeast	24	NEON*^	
Smithsonian CBI	Mid-Atlantic	6	NEON*^	

|			
Smithsonian ERC	Mid-Atlantic	13	NEON*
Talladega NF	Ozarks	12	NEON*^
Treehaven	Great Lakes	10	NEON*^
Univ. Notre Dame ERC	Great Lakes	8	NEON*^
UVA Obs. Hill	Mid-Atlantic	6	UNIV
UMBS LE	Great Lakes	91	Pearsall 1995
UMBS FASET	Great Lakes	19	Gough et al. 2013
UMBS Chrono	Great Lakes	41	Scheuermann et al. 2018

664 * NPPw data available

665 ^ fPAR and LUE data available

666

667 Table 2. Results of generalized linear modeling analysis on relationships of wood net primary

668 productivity (NPPw), light interception (fraction of photosynthetically active radiation absorbed; fPAR),

669 and light use efficiency (LUE as NPPw/fPAR) with ecoclimatic domains, plant functional types (PFT),

670 and canopy structural types (CST) for a subset of the National Ecological Observatory Network sites

671 included in the overall analysis. All analysis was conducted using PROC GLM in SAS v9.4.

Model - NPP	R^2	RMSE	F	df	p
Domain	0.49	4.13	7.39	5,91	<0.001
CST	0.24	3.26	7.20	4,92	<0.001
CST (Domain)	0.59	3.41	17.52	16,80	<0.001
PFT	0.44	3.56	17.88	4,92	<0.001
PFT (Domain)	0.59	3.20	9.19	13,83	<0.001
CST*PFT (Domain)	0.68	3.11	5.40	27,69	<0.001
Model - fPAR	R^2	RMSE	F	df	p
Domain	0.79	0.13	40.75	5,55	<0.001
CST	0.61	0.17	21.76	4,56	<0.001
CST (Domain)	0.82	0.12	14.97	12,48	<0.001
PFT	0.67	0.16	28.44	4,56	<0.001
PFT (Domain)	0.83	0.12	19.44	12,48	<0.001
CST*PFT (Domain)	0.85	0.13	10.09	22,38	<0.001
Model - LUE	R^2	RMSE	F	df	p
Domain	0.49	3.24	10.77	5,55	<0.001
CST	0.17	4.11	2.93	4,56	0.029
CST (Domain)	0.66	2.89	6.44	12,48	<0.001
PFT	0.39	3.51	9.17	4,56	<0.001
PFT (Domain)	0.60	3.07	6.06	12,48	<0.001

|				
CST*PFT (Domain)	0.75	2.73	5.25	22,38	<0.001

672

Figures

673
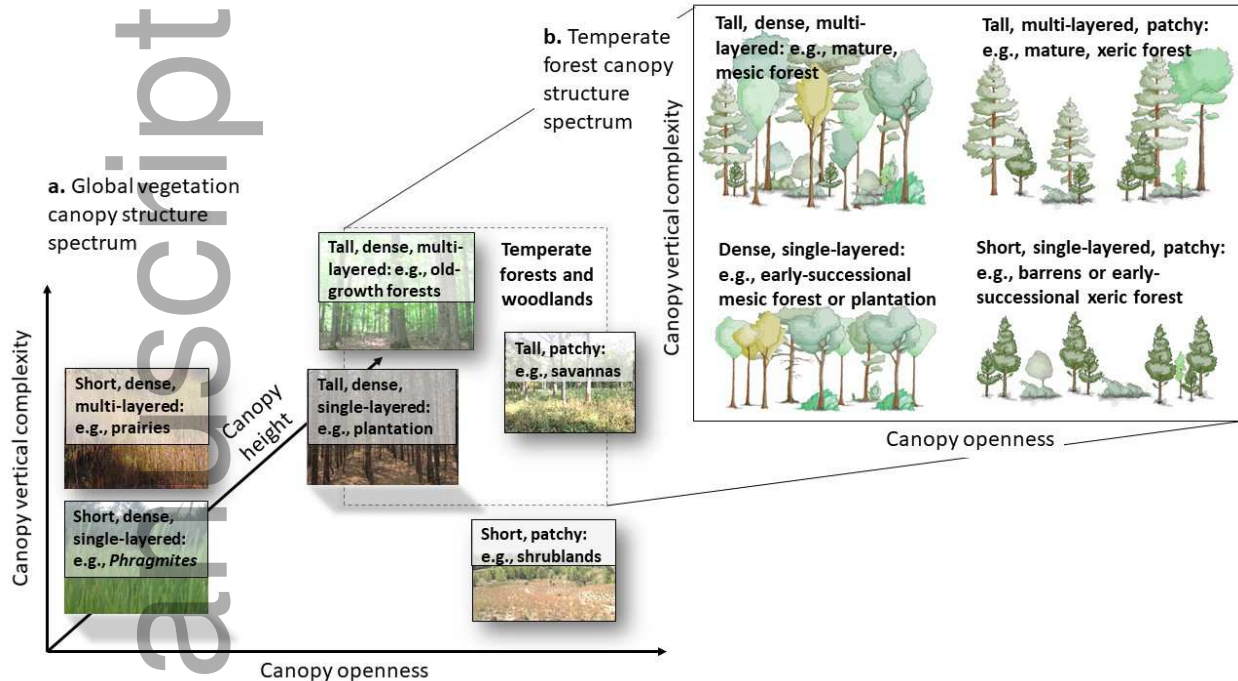
674

675 Figure 1. Illustration of the proposed (a) global canopy structure spectrum and (b) the sub-set of

676 temperate forest canopy structure that was evaluated in the present study with hypothesized canopy

677 structural types represented by forest illustrations. The conceptual model presented here separates

678 ecosystems based on canopy height and horizontal and vertical complexity because these factors are most

679 commonly used to delineate vegetation types and have been previously related to ecosystem functioning.

680 The characterization of canopies as more or less complex focuses on the interspersion of open space

681 within the canopy volume that allows transmission/movement of energy or material and also provides

682 potentially explorable space for placement of new leaf area. The temperate forest subset is depicted

683 without canopy height as an axis to reflect the expected lower importance of this variable as a delineating

684 factor among temperate tree-dominated ecosystems, which all have relatively similar total canopy height

685 (vs. a prairie-forest comparison).

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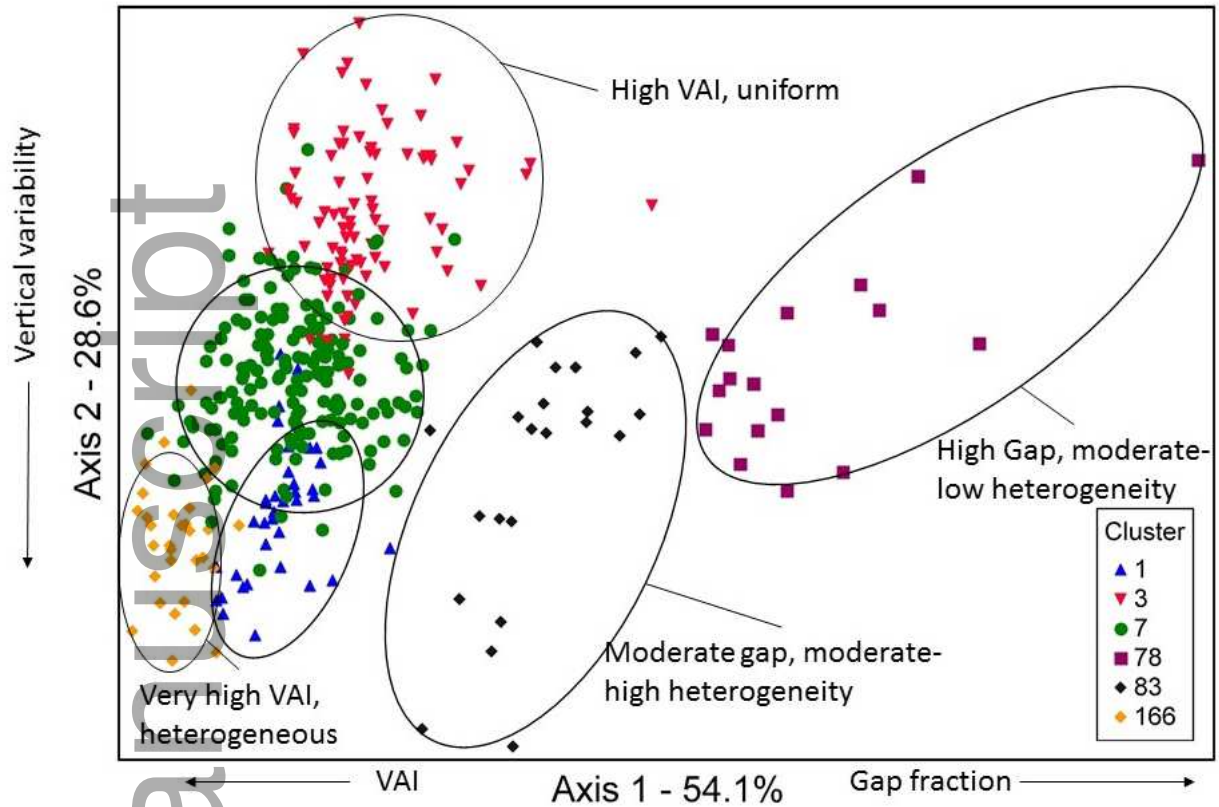
Figure 2. Graphic illustrating position of all study plots in multidimensional canopy structure space based
on non-metric multidimensional scaling ordination with overlay of canopy structural types resulting from
hierarchical agglomerative clustering. Dominant traits driving separation among plots are indicated for
each axis (full list of correlations between traits and axes included in Supplementary Material Table S5).

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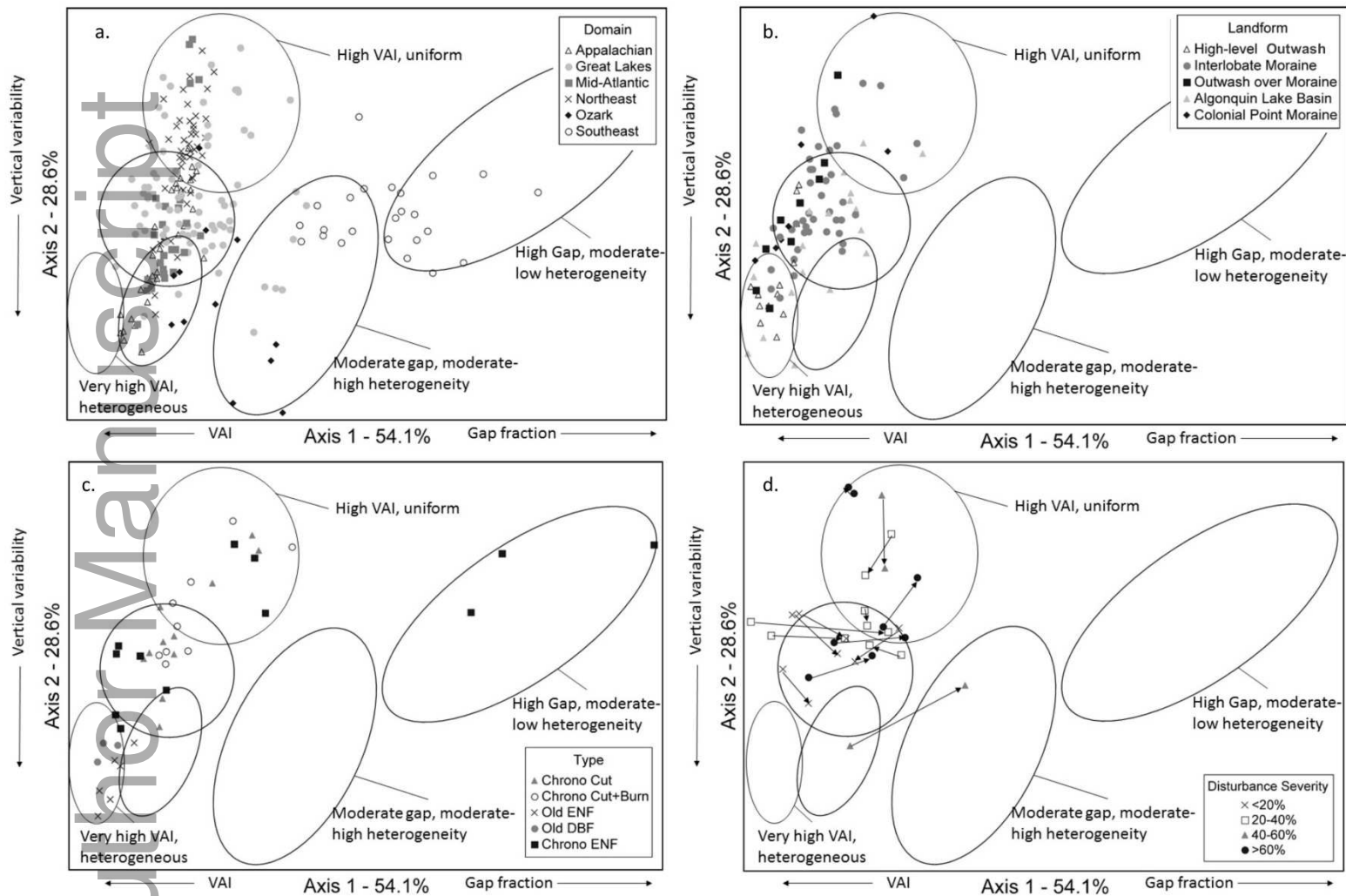
Figure 3. Illustration of plots for each individual data set indicating position of plots in multidimensional canopy structure space. Each panel

indicates the same non-metric multidimensional scaling ordination result, but with only the plots for specific data sets illustrated: a) sub-

continental LQ-NEON data set with plot symbols coded by NEON ecoclimatic domain, b) landscape-scale UMBS-LE data set with plot symbols

coded by geomorphic landform, c) successional chronosequences in the UMBS-Chrono data set with plot symbols coded by chronosequence type,

697   and d) experimental disturbance of the UMBS-FASET data set with symbols coded by disturbance severity and pre – and post-disturbance plots
698   locations connected by vectors. Details of individual data sets and groupings included in text.

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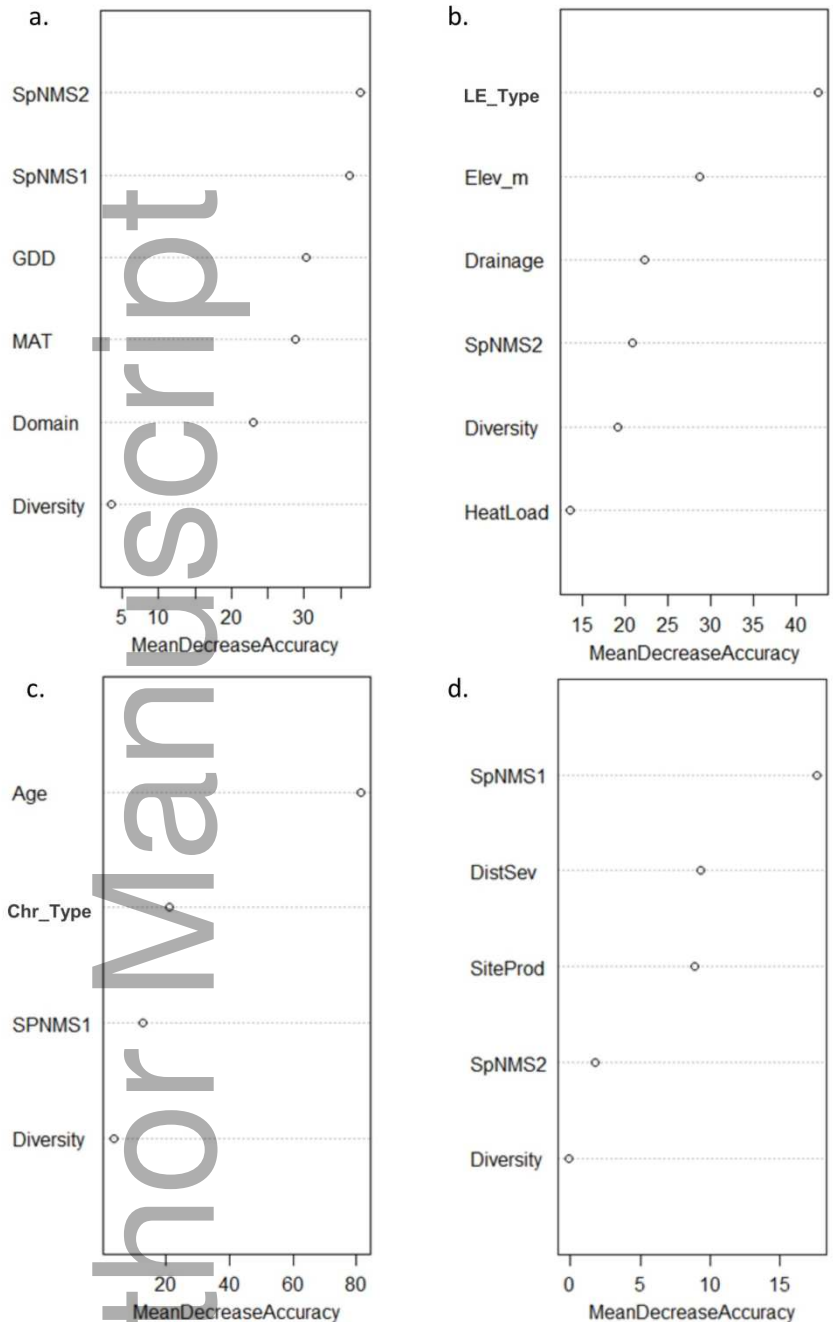
Figure 4. Ranking of predictors in random forest classification tree models for classifying individual plots from four primary data sets (panels a-d same as Fig. 3) into canopy structural types based on mean decrease in accuracy associated with trees from which each predictor was removed. "SPNMS" refers to axes from ordinations of plots by species composition, "GDD" – annual growing degree day accumulation, "MAT" – mean annual temperature, "Diversity" - Simpson's Index of species diversity, "Domain" – NEON ecoclimatic domain, "LE_Type" – Landscape Ecosystem type for plots from Pearsall (1995), "Drainage" – NRCS soil drainage class, "Heatload" – heat load index calculated using slope and

707   aspect based on methods of McCune and Keon (2002), "Chr_Type" – refers to chronosequence type as

708   described in text, "DistSev" – disturbance severity based on proportion of basal area removed, "SiteProd"

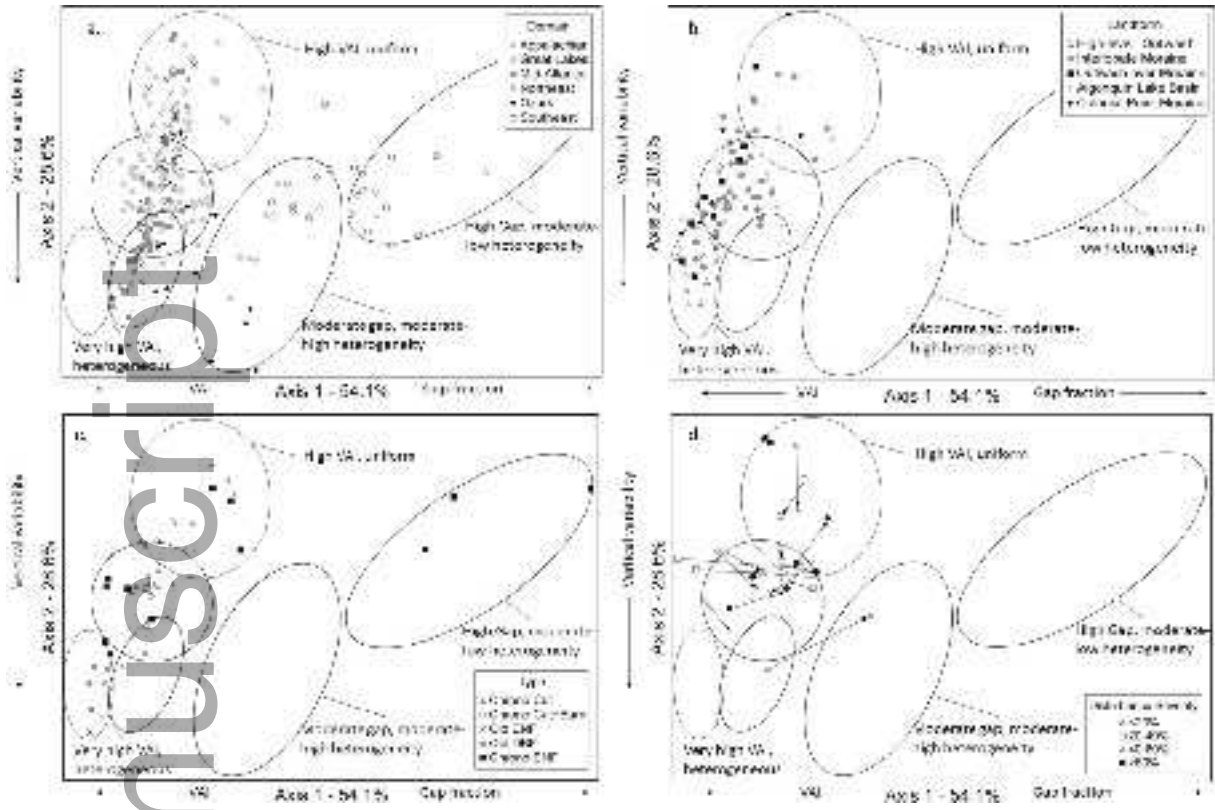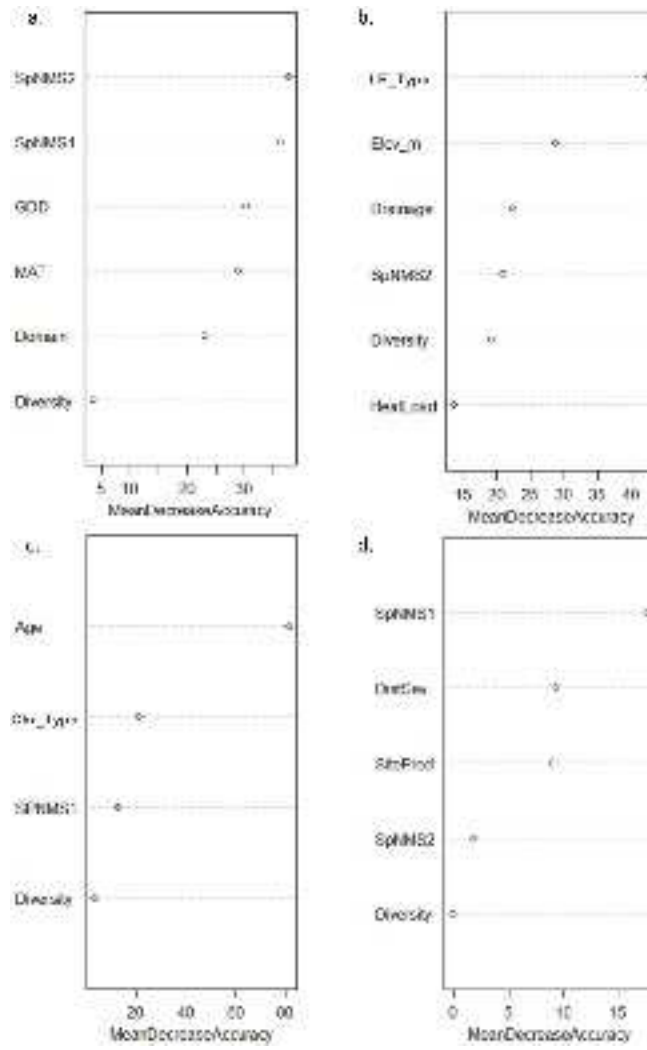709   – pre-disturbance net primary productivity.

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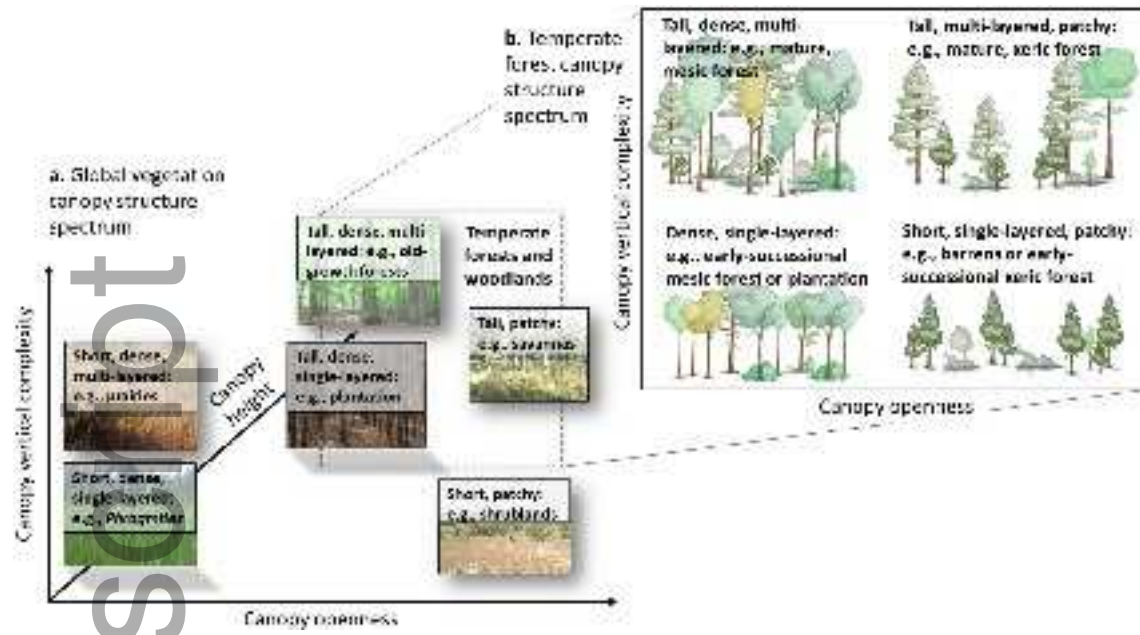
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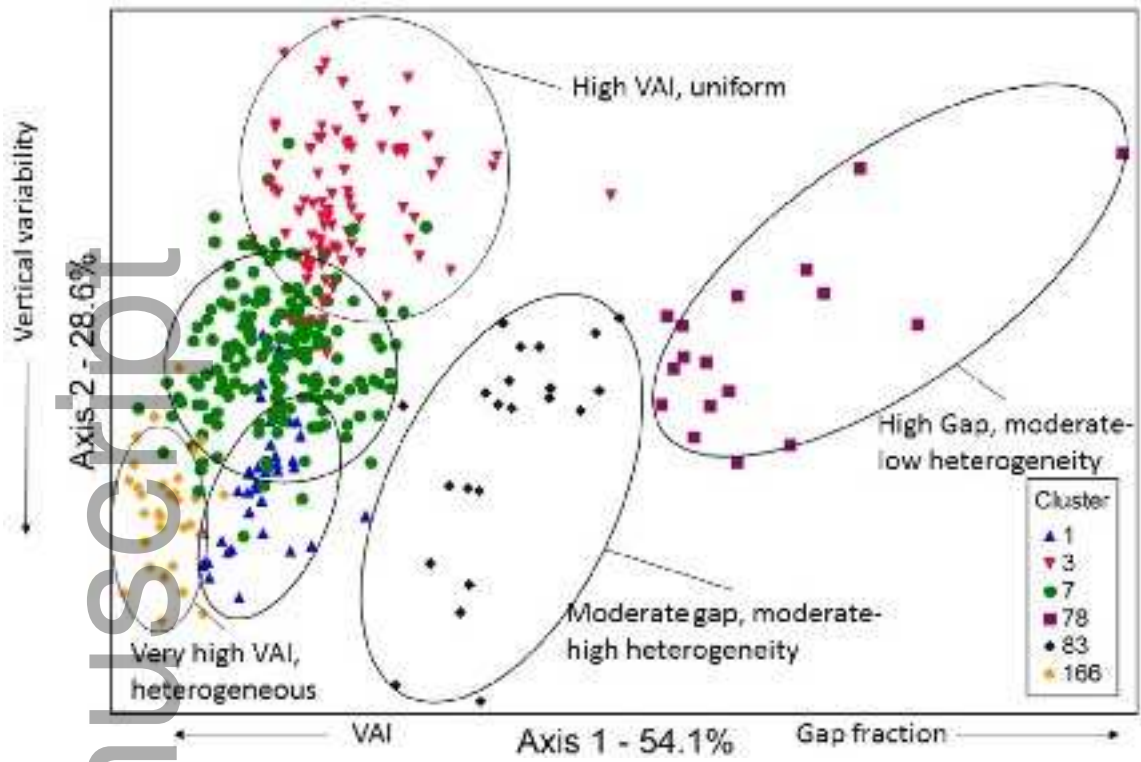
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