Biodiversity as a mediator of disturbance effects on carbon storage in boreal lake-margin plant communities

Introduction

At high latitudes, the effects of climate warming are expected to include increasingly frequent and intense disturbances (Soja et al. 2007). In boreal ecosystems, the primary disturbance agent is wildfire, which is a major determinant of community composition, successional dynamics and organic carbon (C) stocks (Balshi et al. 2007; Jonsson and Wardle 2010; O'Donnell et al. 2011). Warming has also been linked to reductions in lake size and abundance throughout boreal Alaska and the circumpolar north over the last 50 years (Roach et al. 2011). Lake shrinkage has been particularly pronounced in Alaskan National Wildlife Refuge lands, which contain thousands of lakes and wetlands that have been set aside to preserve their "biological integrity, diversity and health" (Meretsky et al. 2006). Shrinking trends vary across the state, but some boreal Alaskan refuges have lost an average of 3% of their surface water per year since 1980 (Roach et al. 2013). Lakes are more likely to have dried in areas that have burned in recent decades, which suggests that shrinking trends are partially an effect of changing fire regimes (Roach et al. 2013), but sustained lake shrinkage could be an important new influence on ecosystem dynamics in the surrounding landscape (Riordan et al. 2006).

Boreal lakes have strong hydrological ties with lake-margin wetlands, indicating that lake shrinkage should be associated with losses in wetland area (Whitehouse and Bayley 2005). Lakes and lake-margin wetlands provide critical breeding habitat for North American waterfowl, and reductions in their abundance are projected to drive local and regional declines in waterfowl diversity (Roach and Griffith 2015). Lakes and wetlands also contain the majority of all boreal organic carbon, one of the largest organic carbon pools in the world (Benoy et al. 2007). A significant fraction of this C can be found in surface organic layers, which are composed of

26   partially decomposed vegetation, or peat (Gorham 1991). Peat layers are strongly affected by the

27   accumulation, death, and decomposition of aboveground biomass (AGB; Chapin et al. 2009;

28   Conti and Díaz 2013), which also functions as a source of forage and/or cover for wildlife. The

29   rate of AGB production is parabolically related to soil moisture, and peat accumulation is also

30   driven by a combination of low temperatures and saturated, anoxic soils, which impede

31   decomposition (Gorham 1991; McGuire and Anderson 2009). In other words, lake shrinkage and

32   associated reductions in soil moisture have the potential to affect C budgets above and below

33   ground.

34   Shrinking lakes may also have more subtle effects on wetland communities. Boreal

35   wetlands are local plant biodiversity hotspots, including species and growth forms that cannot be

36   found in more abundant upland forest habitat (Whitehouse and Bayley 2005). Plant species

37   diversity could increase in response to lake shrinkage as lake-margin wetlands expand into newly

38   exposed bare soil, but local species losses could also occur as lake shrinkage changes the soil

39   moisture, pH, and other physical variables that govern growing conditions within existing

40   communities. The extent of the effect of lake shrinking on plant diversity is unknown, partly

41   because plant diversity is a much lower management priority than the maintenance of wildlife

42   populations and their habitat (USFWS 1987).

43   Plant diversity and community composition may be undervalued in boreal Alaskan

44   wetlands, because plant traits (such as woodiness, relative growth rate, and specific leaf area) can

45   control ecosystem properties like C storage, as well as their sensitivity to disturbance (Díaz et al.

46   2007; Cadotte et al. 2011). The ecological significance of this diversity can be captured by

47   characterizing plant communities in terms of functional diversity, which is the distribution of

48   functionally important species and traits (Tilman 2001; see Table 1 for examples of functional

49 traits). Functional diversity encompasses three components: (1) the relative abundance of

50 individual traits (functional composition), (2) the variation in trait values (functional divergence,

51 sometimes referred to as functional diversity in other studies; Mason et al. 2005), and (3) the

52 distribution of 'idiosyncratic species' that possess unique trait assemblages and may have effects

53 on ecosystem function that are disproportionate to their abundance (Conti and Díaz 2013).

54   Understanding plant communities by the basis of their functional diversity may be key to

55 improving predictions of C storage in boreal Alaskan wetlands under changing disturbance

56 regimes. Wildfires can rapidly remove massive amounts of C stored in soils and plant biomass,

57 while reduced soil moisture due to lake shrinkage could accelerate decomposition of soil organic

58 matter and reduce the potential for it to re-accumulate (Schimel et al. 2011). However, C cycling

59 may also be related to plant functional traits (De Deyn et al. 2008; Conti and Díaz 2013). For

60 example, rates of plant growth and biomass production are major determinants of soil organic

61 matter accumulation, while woodiness and tissue nutrient contents regulate litter decomposition

62 and accumulation (De Deyn et al. 2008). In addition, plant traits can moderate the effects of

63 disturbance by controlling the level of plant mortality that occurs after a disturbance event and

64 the rate of recovery by the plant community (Conti and Díaz 2013).

65   There are two primary hypotheses that link functional diversity to C storage. According

66 to the mass-balance hypothesis, ecosystem function is determined by the most abundant traits, or

67 the traits of the most abundant species. This hypothesis predicts that functional composition and

68 idiosyncratic species should be the best predictors of ecosystem processes related to the

69 accumulation and breakdown of organic matter (Grime 1998). In contrast, the niche

70 complementarity hypothesis predicts that processes like biomass production, and therefore inputs

71 to soil C, will be maximized at high functional divergence, because resources will be used more

72 efficiently when distributed among species with diverse ecological requirements and roles

73 (Trenbeith 1975). At the same time, increased diversity in rooting depth profiles could allow for

74 belowground C inputs over a larger fraction of the thawed soil profile and increased total root

75 biomass production (Steinbeiss et al. 2008). Both of these hypotheses represent mechanistic

76 pathways that would allow plant communities to mediate the effects of disturbance on above-

77 and below-ground C storage. However, their relative importance appears to be ecosystem-

78 specific, and relationships between functional diversity and disturbance effects have rarely been

79 examined in natural systems or at regional or greater spatial scales (Conti and Díaz 2013).

80   Our objective was to determine whether functional diversity mediates the effects of lake

81 shrinking and wildfire on above- and belowground C storage in boreal Alaskan wetlands, using

82 field data from a large-scale biodiversity survey combined with information on C storage in the

83 Yukon Flats National Wildlife Refuge, a 3.5 million ha wetland complex. We sought to identify

84 which of three components of functional diversity (functional composition, functional

85 divergence, and idiosyncratic species) were most influential. To accomplish this objective, we

86 followed a published framework (Díaz et al. 2007), in which the effects of environmental forces

87 and functional diversity components on ecosystem properties are assessed in three steps: 1)

88 separate models for each component, 2) a combined model to assess relative importance, and 3)

89 an investigation of nonlinear and interactive effects (referred to as 'discontinuous effects' in the

90 referenced paper). We added to that work by outlining a robust analytical approach for

91 identifying non-linear and interactive relationships between functional diversity, disturbance, and

92 above- and belowground C storage using a combination of machine learning algorithms and

93 structural equation modeling.

94   We evaluated two general alternative hypotheses (Fig. 1A): Hypothesis 1) Disturbance

95   directly alters the C sink strength of lake-margin wetlands through changes to the physical

96   environment alone (i.e. the effects of plant diversity on C storage cannot be explained by

97   intermediate changes in plant functional diversity). Mechanisms for these direct effects could

98   include removal of C through combustion as well as changes to physical variables like soil

99   moisture, which can influence rates of new biomass production, respiration, and decomposition.

100   Hypothesis 2) Disturbance effects are mediated by changes in plant community structure and the

101   distribution of functional characteristics (Fig. 1A). The concepts of disturbance and functional

102   diversity were each represented by multiple variables in our analysis, which allowed us to assess

103   the relative importance of functional composition and functional divergence as predictors of C

104   storage, and simultaneously test whether apparent effects of lake shrinking on ecosystem

105   properties could be explained by the association of shrinking trends with fire history (Fig. 1B).

106   We carried out this analysis in three lake-margin plant communities (Grass/Sedge,

107   Deciduous Shrub, and Upland Forest) that represent a gradient of increasing distance from the

108   lake edge and were expected to reflect a gradient of increasing potential functional diversity. In

109   terms of the overall relationship between disturbance and C storage, we predicted that lake

110   shrinking would lead to increased AGB in near-shore Grass/Sedge (GS) communities, with

111   similar but weaker effects in the Deciduous Shrub (SH) community, and no change in Upland

112   Forest (F) biomass (Chapin et al. 2009). We also predicted that lake shrinking would result in

113   increased decomposition and reduced near-surface soil C in the formerly saturated soils of the

114   GS community, which occurred immediately adjacent to the water's edge (Chapin et al. 2011).

115   These predictions derived from previous findings that productivity and decomposition rates show

116   parabolic responses to moisture, and that decomposition tends to respond to changes in soil

117 moisture more strongly than plant biomass production (Chapin et al. 2011). We predicted fire

118 frequency to be correlated with functional divergence and composition (Jonsson and Wardle

119 2010), and to be negatively correlated with C storage in all community types (Grosse et al.

120 2011). For our functional diversity hypotheses, we predicted that the relative importance of

121 functional diversity as a mediator of disturbance effects and the relative support for the niche

122 complementarity hypothesis would both be highest in the F community, which had the most

123 complex canopy structure and therefore the greatest potential for niche differentiation among

124 plant species (Conti and Díaz 2013).

125   As far as we know, our study is one of the first to examine the influence of functional

126 diversity in natural systems at the landscape scale. We illustrate how accounting for plant

127 community characteristics can improve our ability to predict the effects of climate-driven

128 disturbance on ecosystem dynamics. We also provide insight into the mechanisms linking spatial

129 patterns of C storage and wildlife habitat structure, which could be used to re-evaluate

130 conservation and management priorities for Alaskan National Wildlife Refuges.

131

132 **Methods**

133 *Study Area*

134   We chose the Yukon Flats National Wildlife Refuge (YFNWR) in northeastern Alaska as

135 our study area. The YFNWR encompasses 3.5 million ha surrounding the Yukon River

136 floodplain, consists of a complex mosaic of lakes, wetlands, and upland forest (Gallant 1998),

137 and is not connected to the road system. This region is uniquely appropriate for studying the

138 ecological consequences of lake shrinking in Alaska, because lake shrinking trends within the

139 refuge span the full range of variation observed across the state (Roach et al. 2013). The ~40,000

140 lakes scattered throughout YFNWR are strongly associated with the presence of discontinuous

141 permafrost, which prevents drainage and promotes ponding of surface water (Roach et al. 2011).

142 Many of these lakes are associated with concentric rings of GS fens, surrounded by shrub bog

143 communities dominated by *Salix* species.

144

145 *Diversity sampling*

146   We surveyed plant communities at 66 lakes between 2010 and 2011. We selected

147 candidate focal lake sites from a GIS layer of floatplane-landable lakes using a Generalized

148 Random Tessellation Stratified (GRTS) design, ensuring that our sample sites were a spatially

149 balanced, representative random sample of the study area (Stevens and Olsen 2004). Sampling

150 efforts were divided between two strata that had opposite regional lake area trends since 1985

151 (Roach et al. 2013). All lakes within a 1km radius of the focal lake centroid that could be

152 accessed within 14 days were sampled as satellite lakes. This design allowed us to include small,

153 unlandable lakes in our sample, and to account for the potential effects of spatial autocorrelation

154 between nearby lakes in our analyses.

155   The primary objective of our sampling campaign was to characterize vascular plant

156 diversity and community composition. We established four perpendicular 100m survey transects

157 at each site, oriented at a random azimuth to the lake centroid. Each transect began at the lake

158 edge, which we defined as the point where the soil surface was not covered by standing water.

159 We then recorded and identified all vascular species located within 5m of the transect line.

160 Specimens that could not be identified in the field were pressed and sent back to the University

161 of Alaska Fairbanks for identification. We also estimated species percent cover using a series of

162 25 5m-radius vegetation plots distributed within a 50 by 100m grid centered on a randomly

163 selected transect at each site. Finally, we delineated transitions between plant community types,

164 which occurred in concentric rings surrounding lakes, based on the plant growth form

165 (herbaceous, deciduous shrub, or tree) with >50% cover. We averaged the width of each

166 community type across the four transects, and used these measurements to generate buffers

167 around each lake in arcMap 10.0. These buffers provided an estimate of the area occupied (m2)

168 by different community types within the surveyed area at each lake.

169

170 *Fire History*

171   We estimated the time since the most recent fire at all sample lakes by overlaying lake

172 locations with a GIS map of historical fire perimeters from 1950 to the present (fire.ak.blm.gov).

173 Because only 1/3 of all sample sites had burned within that timeframe (n=35), we represented

174 fire history as an ordinal variable: 1 = < 5 years since fire, 2 = < 10 years, 3 = < 25 years, 4 = <

175 50 years, and 5 >= 50 years.

176

177 *Lake Trends*

178   We estimated trends in lake area between 1979 and the present using a time series of 22

179 Landsat satellite images. These images were converted to shapefile lake maps in ArcMap 10.0 as

180 part of a larger study on long-term lake trends in the YFNWR (Rover et al. 2012). After

181 extracting area measurements for each lake in each year where imagery could be obtained, we fit

182 linear models with the form 'Lake Area = B1*Year+B2*Day of year (Roach et al. 2011). Lakes

183 with significant model F statistics and significant negative Year coefficients were characterized

184 as shrinking. We assessed statistical significance using an alpha cutoff of 0.05. Our lake sample

185 included 16 significantly decreasing lakes, representing 12% of the total sample population. This

186 proportion was similar to the total proportion of shrinking lakes in the YFNWR, which was

187 recently estimated at ~10% using similar methodology (Rover et al. 2012). 22 lakes decreased in

188 area between 1979 and the present, but did not have significant decreasing trends due to large

189 interannual fluctuations in lake area. Because these fluctuations represent flood events that could

190 have their own effects on community composition and carbon stocks, these lakes were excluded

191 from this analysis. Three lakes had significant increasing trends, and were also excluded.

192 Increasing lakes represent a small fraction of the total landscape (<3%) in YFNWR and

193 elsewhere in Alaska (Rover et al. 2012).

194

195 *Soil C and AGB sampling*

196 Logistical constraints prevented us from collecting soil and AGB samples at all sites.

197 Instead, we selected 15 lakes for intensive sampling, and correlated measurements at these lakes

198 with remote-sensing products to generate maps of soil organic C content and AGB for the entire

199 sample population. The 15 lakes were originally selected to represent a balanced sample among

200 three lake types: Decreasing, Stable, and Fluctuating. However, the full time-series of lake areas

201 were not available prior to field sampling, and these lake-type designations were based on a pilot

202 analysis using six hand-digitized area measurements per lake. After re-analyzing lake area data

203 according to the methods described above, we found that our sample consisted of four decreasing

204 lakes, 6 stable lakes, 4 fluctuating lakes, and 1 increasing lake, which was excluded from

205 analysis as described above.

206 To sample the soil C and AGB, we visited each of these lakes within a two-week window

207 from Aug 1-Aug 14, which corresponded approximately to the period of peak biomass

208 accumulation in our study area (Mack et al. 2008). Eight lakes were sampled in 2011

209 simultaneously with our vegetation surveys, and seven lakes originally surveyed in 2010 were

210 revisited in 2012 for soil and biomass collection. We stratified soil and AGB sampling across our

211 three three community types: GS, SH, and F. Within each community type, we harvested

212 understory AGB from 5-10 randomly located 20cm x 50cm quadrats. Within each quadrat, we

213 harvested all live and dead biomass, including green moss, woody debris, and leaf litter. Samples

214 were kept cool and flown out of the field within 3 days before being frozen prior to analysis. We

215 then dried samples for 3 days at 60º C before weighing (Shaver and Chapin 1991; Mack et al.

216 2008). We also measured shrub (<3m tall) and tree stem density along a randomly located 60m

217 transect in each plant community. Transects were broken into 6 10m cells. We then counted all

218 deciduous shrub stems within 5m of the transect line in each cell, and harvested 10 randomly

219 located stems per community type. All stem material was dried for 5 days at 60º C before being

220 weighed. We also estimated tree density in each cell using a third nearest neighbor angle-order

221 estimator, which is a robust alternative to plot-based density estimates (Engeman et al. 1994;

222 Sheil et al. 2003), and calculated tree biomass using allometric equations (Bond-Lamberty et al.

223 2002; Yarie and Kane 2007).

224 We collected three 20cm soil cores from each plant community using a specially designed

225 4.4 cm diameter fitting for a Makita power drill, which minimized compression in organic

226 horizons. Horizon depths and weights were recorded in the field, and samples were kept cool in

227 permafrost pits for a maximum of 3 days before being flown out and stored at -20C prior to

228 analysis. After returning from the field, we dried samples at 60C before measuring % C and N

229 with a Costech CHN analyzer. Bulk density was estimated by measuring the dry weight of a

230 known-volume subsample for each horizon in each core. We then calculated soil C content as

231 %C * bulk density * layer thickness (Johnson et al. 2011).

232 In addition to these soil cores, we characterized soil horizons by recording the depths of

233 fibric organic, humic organic, mineral, and frozen soil layers in pits dug along the four

234 vegetation survey transects at all 130 lakes. In 2010, soil pits were dug at the lake edge and at the

235   upland forest boundary. In 2011, we also dug additional pits located in the center of each plant

236   community type (n=58).

237   We compared average biomass estimates from field sampling to estimates derived from a

238   recently published raster map of AGB for the YFNWR, which modeled biomass based on

239   spectral reflectance indices from Landsat imagery (Ji et al. 2012). We estimated mean mapped

240   AGB by averaging biomass values for all pixels that overlapped buffer polygons representing

241   plant communities after weighting values based on the degree of overlap. We then regressed field

242   biomass estimates against mapped estimates for each plant community type to validate the

243   mapped values, which we used to represent mean AGB for all communities at all 130 lakes.

244   Horizon thickness is commonly used as a proxy for soil C content per unit area (Johnson

245   et al. 2011). We used a recently published 30m-resolution map of organic layer thickness (OLT)

246   in the Yukon River Basin to estimate average C content per unit area (Pastick et al. 2014).

247   Average OLT estimates were derived and validated against field data with the same methods

248   used to determine average AGB.

249

250   *Functional diversity and functional composition*

251   We calculated plant functional trait diversity based on five effect traits and five response

252   traits (Table 1). These traits were selected based on their potential to influence rates of organic C

253   accumulation and decomposition, and on their relevance for predicting plant community

254   responses to lake-related disturbance. We developed separate trait matrices for all species found

255   in each plant community, using a combination of field data, literature searches, and a query from

256   the TRY functional trait meta-database (www.try-db.org; Kattge et al. 2011). We chose not to

257   remove species with missing trait data from our analysis. Instead, we filled data gaps using

258   multiple imputation, as implemented in the mice R package (Taugourdeau et al. 2014). Multiple

259   imputation methods have been shown to yield more robust datasets than either case deletion or

260   simple gap-filling methods in functional diversity studies, as long as the proportion of species

261   with missing data does not exceed ⅓ for each variable. We confirmed that there was sufficient

262   data to retain each functional trait variable before proceeding.

263   We estimated functional trait divergence using Rao's quadratic entropy (Rao 1982),

264   which is derived by calculating the multivariate distance between each species pair in a

265   community, and weighting these distance scores by the proportional abundance of each species

266   (Equation 1).

267

268   Equation 1: $\sum p_i \star j_i \star d_{ij}$

269   pi, ji = proportional abundance of species i, j. Dij = multivariate distance between species i, j.

270

271   Gower's distance formula was used to accommodate the presence of both continuous and

272   categorical trait variables in our dataset (Roscher et al. 2012). Functional trait composition was

273   estimated by 1) calculating the community-weighted mean (CWM) of functional trait values, for

274   all species present at a given lake and community type, and 2) extracting the first principal

275   component score from a PCA of CWM functional trait values (Roscher et al. 2012). Community-

276   weighted mean trait values were an average over all species present, weighted by species

277   abundance.

278   We used the random forest algorithm to identify potential idiosyncratic species that were

279   strong predictors of above- and belowground C (Cutler et al. 2007). We ran separate random

280   forest models for AGB and OLT in each community type, with binary presence/absence scores

281   for all plant species as independent variables. Variables were ranked based on their average

282   individual effect on model mean squared error (Archer and Kimes 2008). Since the presence of

283   many unimportant predictors can suppress model performance, we sequentially removed the 5

284   lowest-ranking variables and re-ran models until we arrived at a model with maximum predictive

285   power (Strobl et al. 2007). Model results were used to construct reduced species presence

286   matrices. We then calculated idiosyncratic species scores for each community and response

287   variable as the first principal component of a species presence/absence PCA.

288

289   *Structural equation modeling*

290   We used structural equation modeling (SEM) to evaluate hypotheses about the network of

291   causal relationships linking lake shrinking, plant community traits, and C storage. The SEM

292   modeling framework facilitates the testing of hypotheses about direct and indirect influences,

293   and makes it possible to explicitly account for causal relationships between predictor variables

294   (Grace and Anderson 2010). These features make SEM modeling a more appropriate tool for

295   addressing our research questions than more common statistical techniques like general linear

296   models in which unaccounted-for covariance between predictors can have a dramatic influence

297   on parameter estimates (Grace et al. 2014)

298   The first step in our modeling process was to graphically represent our *a priori*

299   hypotheses about the network of causal relationships that might drive variation in AGB and OLT,

300   which reflect above- and below-ground C respectively (Fig. 1B). Concepts such as disturbance,

301   functional diversity, and C storage were represented by measured variables (Table 1), producing

302   a hypothetical network of influence that could be directly compared against data. A directed

303   arrow from one variable to another (x -> y) represents the hypothesis that 'y is a linear function

304   of x' (Fig. 1B).

305   We fit this network to our data with the lavaan package in R using the LISREL method,

306   and assessed model fit by comparing the observed variance-covariance structure of the data to a

307   modeled variance-covariance matrix using a Chi-squared test (Grace and Anderson 2010;

308   Rosseel 2012). A significant test statistic implied inadequate model fit, meaning there were

309   missing structural relationships between variables. If the initial model had inadequate fit, we

310   added biologically plausible paths sequentially based on modification index values (Chaudhary

311   et al. 2009). Once we obtained a model with adequate fit, we assessed our hypotheses by

312   examining the standardized path coefficients linking variables. Standardized coefficients are

313   essentially z-transformed coefficients, and reflect the expected number of standard deviations

314   that the response will change when a predictor is changed by one standard deviation (Grace

315   2006). The product of all path coefficients in an indirect pathway (e.g. lake shrinking -> plant

316   diversity -> AGB) represents the coefficient for the entire pathway, and the sum of all indirect

317   and direct path coefficients linking two variables indicates the total influence of the predictor on

318   the response. Finally, we also assessed the predictive power of our hypotheses by examining

319   model R^2 values for each response variable.

320

321   **Results**

322   All community-specific variables were summarized by community type and by lake trend

323   (Table 2). Overall, GS communities had the highest AGB, greatest OLT, and lowest species

324   richness of any community (Table 2). SH communities contained the greatest average functional

325   divergence, but GS communities were similar (Table 2). F communities the lowest average AGB

326   and shallowest average OLT, and had substantially lower functional divergence scores than either

327   of the two lake-margin communities, despite having the highest average species richness (Table

328   2).

329

Bivariate relationships

331

Vegetation

333   AGB per unit area was significantly positively related to the length of time since the most

334   recent wildfire in all three communities (Table 3). GS and SH communities adjacent to shrinking

335   lakes also had significantly lower AGB per unit area compared to similar communities near

336   stable lakes (Table 3). Size (width of community zones surrounding lakes) was the best single

337   predictor of AGB per unit area in all communities, with R^2 values ranging from 0.33 to 0.54).

338   Size was negatively associated with AGB per unit area in GS and SH communities, but was

339   positively correlated with biomass in the F (Table 3). Lake shrinking was not significantly

340   associated with AGB per unit area in the F community (Table 3). Functional divergence (Rao's

341   quadratic entropy) was significantly positively correlated with AGB per unit area in GS and SH

342   communities, but not in the F. Functional composition, as measured by the first principal

343   component score from a PCA of community-weighted mean (CWM) functional trait values, was

344   not significantly associated with biomass in any plant community.

345   However, the first principal component from a PCA of idiosyncratic plant species

346   presence/absence was significantly correlated with AGB in all three communities (Id Spp; Table

347   3). Idiosyncratic species scores were positively correlated with the presence of most

348   idiosyncratic species for each community (Appendix 1).

349

Soils

351   OLT, a proxy for surface (0-30cm) soil C content per unit area, was significantly

352   predicted by time since fire in the GS and SH communities, negatively correlated with Size in

353   the F, and significantly correlated with idiosyncratic species scores in the SH and F communities

354   (Table 3). Idiosyncratic species scores for peat thickness were primarily associated with a suite of

355   forb and graminoid species (Appendix 1), although SH IdSpp scores were positively correlated

356   with the presence of one shrub species (*Salix glauca*), and F IdSpp scores were positively

357   correlated with the presence of one deciduous tree (*Populus tremuloides*; Appendix 1).

358

359   *Using random forest models of idiosyncratic species to predict above- and belowground C*

360   Random forest models using only community-weighted mean functional trait values were

361   poor predictors of AGB (Table 4). However, random forest models of AGB as a function of

362   species presence/absence were more successful, explaining 43% of variance in the GS

363   community, 48% in the SH community, and 61% in the F. The optimal model for each

364   community included 15 species, although the top five species accounted for over half the

365   variance explained in all cases (% variance explained = 36 for GS, 29 for shrub, and 49 for the F.

366   Species were grouped into six functional types (Table 5), which characterize growth form and are

367   expected to represent species with broadly similarly functional traits (Chapin et al. 1996).

368   *Chamerion angustifolium*, a post-disturbance colonizing forb, was the top predictor of GS AGB,

369   while the top predictor in the SH community was the dwarf deciduous shrub *Arctostaphylos*

370   *rubra*, and the best predictor of forest AGB was the forb *Galium boreale*, although a deciduous

371   shrub (*Salix pseudomonticola*) and an evergreen shrub species were also highly ranked (*Linaea*

372   *borealis*; Table 5). In general, herbaceous species were more strongly associated with variation in

373   AGB in the GS community, while woody plants had high variable importance values in the shrub

374   and forest communities (Table 5).

375   OLT, like AGB, was not well predicted by community weighted mean functional trait

376   values, with CWM random forest models explaining less than 1% of variance in peat thickness in

377   the GS and Shrub communities, and only 15% of variance in F OLT (Table 4). Id Spp random

378   forest models were more successful, explaining between 40 and 57% of variance in OLT. All top

379   predictors of GS OLT were herbaceous (gramionid or forb) species, including several plants

380   found in emergent wetlands and floating vegetation mats, such as *Calla palustris* and

381   *Menyanthes trifoliata* (Table 5). Deciduous tree and shrub species were generally not strong

382   predictors of OLT in any community, although the nitrogen fixing shrub Alnus viridis had the

383   second highest variable importance ranking of any species in the SH IdSpp model (Table 5). The

384   only woody species with high variable importance rankings in the F model were understory

385   evergreen shrubs (*Ledum palustre* and *Vaccinium oxycoccus*).

386

387   *Structural equation modeling of lake shrinking, plant community traits, and C storage*

388   *Aboveground C storage (AGB)*

389   In all communities, AGB was significantly associated with both disturbance

390   history (time since fire, lake shrinking status) and plant functional diversity variables (Rao's

391   quadratic entropy and idiosyncratic species distributions). Structural equation models (SEM)

392   explained more than half of observed variation in AGB in all communities (R^2= 0.6 for GS, 0.59

393   for SH, and 0.73 for F; Figure 2). All SEM models adequately captured the underlying variance-

394   covariance structure in the data, as indicated by non-significant X^2 tests (Figure 2).

395   Time since fire was positively correlated with AGB in all communities, although the

396   relative strength of this effect was greatest in the GS community (Table 6). Only direct pathways

397   linked fire history with AGB in the GS and F, while the effects of fire history were at least

398   partially mediated by changes in functional diversity in SH (Fig. 2).

399   Lake shrinking was significantly associated with reduced biomass per unit area in both

400   the GS and SH communities (Fig. 2). In both cases, effects of lake shrinking on biomass did not

401 appear to be mediated by functional diversity. Lake shrinking status was not significantly

402 predicted by time since fire (Fig. 2).

403   Size was the strongest direct influence on AGB per unit area in all communities (Figure

404 3). Small/narrow GS and SH community zones surrounding lakes had relatively high biomass

405 density, whereas Size and AGB were positively correlated in the F. Strong positive relationships

406 between Size and idiosyncratic species effects in the F also indicated that larger F communities

407 were more likely to include idiosyncratic species with strong influences on biomass.

408   Idiosyncratic species effects were the only components of functional diversity with direct

409 influence on AGB (Fig. 2). Idiosyncratic species scores were significantly positively correlated

410 with Rao's quadratic entropy scores, which represent functional divergence, in the GS and SH

411 communities (Fig. 2). In other words, species whose presence was positively correlated with

412 AGB were more likely to occur in communities with high functional divergence. A similar but

413 non-significant trend was produced in the F AGB SEM model (Fig. 2). Rao's quadratic entropy

414 was not consistently predicted by any variable across the three communities, but increased with

415 increasing time since fire in the SH (Fig. 2). Functional trait composition, as measured by CWM

416 scores, was not strongly associated with biomass in any community (Fig. 2).

417

418 *Peat thickness (OLT) structural equation model results*

419   Structural equation models explained close to 30% of observed variance in OLT thickness

420 in all three communities, representing approximately half the predictive power of AGB SEM

421 models (Fig. 3). The influence of disturbance and functional diversity variables, and the evidence

422 for mediation of disturbance effects by functional diversity varied between communities. When

423 direct and indirect pathways were included, organic layer thickness increased with time since fire

424 in both the GS and SH communities, but not in the F (Fig. 3). In contrast, lake shrinking was

425   only associated with OLT in the SH. The effects of lake shrinking on SH OLT included indirect

426   pathways mediated by functional composition (CWM) and idiosyncratic species (IdSpp) effects,

427   while Fire effects were mediated by Size, Rao, CWM, and IdSpp (Fig. 3).

428   Community size was not a significant predictor of GS OLT although it was positively

429   correlated with OLT in both the SH and F via direct paths (Fig. 3), In the SH, this effect was

430   countered by indirect pathways mediated by IdSpp and CWM, for a negligible net effect (Table

431   6).

432   The IdSpp variable was the strongest predictor of OLT in all communities, and was the

433   only functional diversity variable linked to OLT via direct pathways (Fig. 3). Functional

434   divergence (Rao) was only significantly correlated with OLT in the SH, with a net negative

435   relationship (Table 6). In contrast with AGB SEM models, CWM was a significant predictor of

436   SH and F OLT (Table 6). In both communities, the effect of CWM was positive and mediated by

437   relationships between functional composition and idiosyncratic species effects (Fig. 3, Table 6) .

438   PCA results indicated that these positive CWM PCA scores were linked with the dominance of

439   taller, woody, drought-tolerant species with the ability to resprout rapidly following disturbance

440   (Fig. 4).

441

442   **Discussion**

443   *Overview*

444

445   We examined relationships between disturbance, functional diversity, and above- &

446   below-ground C storage (AGB and OLT) in boreal lake-margin plant communities. We built on

447   previously-published methods (Diaz et al. 2007) by outlining an analytical framework for

448   simultaneously estimating the separate and interactive effects of functional diversity components

449 on ecosystem function. We implemented this framework using plant diversity data from an

450 intensive field survey across a 3.5 million-ha study area combined with an online plant trait

451 database (Kattge et al. 2011), to test hypotheses about the ecological role of functional diversity

452 in diverse, natural systems at a management-relevant scale.

453   Our analyses showed that lake shrinkage is a significant driver of AGB and OLT.

454 However, its effects appears limited to ecosystems in close proximity to lakes, and are often

455 overshadowed by the influence of fire history and functional diversity. We also found that the

456 relative influence of functional divergence and functional composition differed between above-

457 ground and below-ground C pools, and that correlations between functional divergence and AGB

458 could be explained at least in part by idiosyncratic species effects. In addition, our study

459 provided insight into the importance of patch size in functional diversity-ecosystem function

460 analysis. We conclude by discussing how our work could help improve representation of plant

461 biodiversity and disturbance in ecosystem models designed to predict high-latitude C dynamics,

462 and by reviewing the implications of our work for land managers tasked with preserving the

463 ecological and social value of boreal wetlands in a drying landscape.

464

465 *Disturbance effects on C storage*

466   Our findings supported the hypothesis that lake shrinking is a significant negative

467 influence on C storage in lake-margin plant communities of interior Alaska. GS and SH wetlands

468 near shrinking lakes had significantly reduced AGB per unit area relative to areas with stable

469 lakes, while drying SH communities had significantly thinner soil organic layers (Table 4).

470 Although lakes within fire scars from the past 60 years area more likely to dry than unburned

471 lakes (Roach et al. 2013), the probability of shrinking was not related to time since fire over

472 more recent time scales (Fig. 2, Fig. 3). In addition, lake shrinking appears to represents a

473   distinct form of disturbance whose influence on C stocks cannot be explained as an indirect

474   effect of increased fire frequency (Fig. 2, Fig. 3). As predicted, the effects of lake shrinking were

475   most apparent in herbaceous and shrub wetland plant communities that occur in close proximity

476   to the lake shore, whereas lake shrinking had no effect on either above- or below-ground C in the

477   F community, which was hydrologically isolated from adjacent lakes (Table 6). Overall, lake

478   shrinking appeared more tightly linked to AGB than to the much larger C stocks stored in

479   organic soil (Fig. 2, Fig. 3). Lake shrinking trends can only be calculated over a few decades

480   (Roach et al. 2011; Rover et al. 2012), and this timespan may not be sufficient to show the effects

481   of lake shrinking on soil peat accumulation.

482   In addition to being a poor predictor of belowground C, lake shrinking was a relatively

483   minor component of the local disturbance regime in our study area. Fire history was a stronger

484   predictor of both above- and belowground C stocks in the GS and SH communities, despite the

485   clear sensitivity of both communities to lake shrinking (Table 6). Wildfire is widely recognized

486   as the dominant disturbance agent in interior Alaska (Harden et al. 2000; Balshi et al. 2007) and

487   our analysis suggests that this continues to be true at the landscape scale even in regions like the

488   Yukon Flats, which show pronounced lake shrinking trends (Riordan et al. 2006; Roach et al.

489   2011). Surprisingly, the only C pool that was not significantly associated with time since fire in

490   our analysis was the F organic layer. The effects of wildfire on OLT in the boreal forest are well

491   established (Harden et al. 2000). However, our analysis used a relatively coarse measure of fire

492   history that did not include estimates of severity or timing, both of which regulate the amount of

493   surface organic material removed during boreal forest fires (Kasischke and Johnstone 2005). In

494   addition, the F community category in our analysis included a spectrum of forest types ranging

495   from pure black spruce stands to mixed aspen-birch forests, which are associated with a similar

496 diversity of soil profiles (Johnson et al. 2011), as evidenced by the significant pathways linking

497 functional trait values, idiosyncratic species distributions, and forest OLT (Fig. 3).

498

499 *Carbon storage/community size relationships*

500 Community size, which was estimated as the width of concentric vegetation bands

501 surrounding each lake, was one of the strongest predictors of both above and belowground C in

502 our analyses (Table 6). These effects could not be explained in terms of size-diversity

503 relationships, since direct pathways between area and AGB/OLT were stronger than indirect,

504 functional diversity-mediated pathways in almost all models (Table 6). In addition, when size

505 was correlated with functional divergence, the sign of this relationship was negative, as opposed

506 to the near universal phenomenon of positive species diversity-patch size relationships (Table 6;

507 Whittaker and Triantis 2012). We suggest this negative relationship, and the negative relationship

508 observed between community size and AGB in both GS and SH communities (Fig. 2), can be

509 explained as edge effects. As already noted, SH communities in the Yukon Flats are often

510 characterized by infilling of both GS and forest plant species. Similarly, the outer edges of GS

511 communities typically contain shrub propagules and spruce or aspen seedlings. The edge effect

512 hypothesis is further supported by our idiosyncratic species random forest models. These models

513 identified species that were characteristic of adjacent communities as top predictors of AGB in

514 all three communities. For example, top-ranked species in the GS community included a tree

515 *Populus tremuloides* and a deciduous shrub *Salix bebbiana*, while all top species in the F

516 biomass models were forbs (*Galium boreale*), graminoids (*Carex concinna*), or shrubs (*Linnaea*

517 *borealis*, *Salix pseudmyrsinites*) (Table 5). Patch size-diversity relationships, though seen a

518 cornerstone of species-based biodiversity research (Whittaker and Triantis 2012), have not been

519 as widely discussed in the functional diversity literature. Our findings illustrate the need to

520   explicitly consider patch size and spatial structure in analysis of functional diversity-ecosystem

521   function relationships.

522
523
524   *Functional diversity mediation*

525   The mediation hypothesis, which predicts that disturbance effects are mediated by

526   changes in plant community structure and the distribution of functional characteristics, was not

527   well-supported, with significant indirect pathways linking disturbance to C storage only being

528   detected in the SH community (Fig. 2, Fig. 3). This result was consistent with our prediction that

529   the importance of functional diversity as a mediator of disturbance effects would be positively

530   correlated with mean functional divergence, which varied significantly across plant communities

531   and was highest in the SH community ($F_{2,157}$ = 10.1, p < 0.0001; Table 2). Although we initially

532   predicted that trait divergence would play the largest role in the F community, where productivity

533   could be driven by efficient light competition across multiple canopy levels (De Deyn et al.

534   2008), the SH community tends to contain a variety of woody and non-woody growth forms due

535   to its position as a zone of transition between herbaceous fens and upland forest (Whitehouse and

536   Bayley 2005).

537   Of the two disturbance types we examined, the mediation hypothesis was only supported

538   for fire history (Fig. 2, Fig. 3). Lake drying was not significantly correlated with any functional

539   diversity variable in any community except for SH OLT functional composition scores (CWM).

540   Interaction between shrinking trends and functional diversity, particularly functional divergence,

541   was apparently not related to species diversity; GS communities near shrinking and stable lakes

542   had similar functional divergence levels, despite an average of 40% greater species richness at

543   shrinking lake sites (Table 2). This discrepancy underscores the need to consider the influence of

544 functional traits, rather than species diversity alone (Mayfield et al. 2010), when examining

545 disturbance-diversity relationships.

546
547
548 *Functional diversity hypotheses*

549 Effects of functional diversity on ecosystem processes are most commonly explained as

550 evidence for either the niche complementarity hypothesis or the mass-balance hypothesis

551 (Sandra and Cabido 2001). Our results provided support for both hypotheses depending on the

552 response variable in question. AGB increased with functional divergence scores (Rao's quadratic

553 entropy) in all communities (Table 6). The standard explanation for this pattern, according to the

554 niche complementarity hypothesis, is that a diverse array of functional niches allowed plant

555 communities to use resources more efficiently (Díaz et al. 2007). However, the pathway linking

556 functional divergence with biomass was mediated by the idiosyncratic species variable, which

557 was the only functional diversity variable that was directly correlated with AGB in any

558 community. In other words, communities with high functional trait divergence were more likely

559 to contain species with disproportionate influence on total biomass (Díaz et al. 2007).

560 Unlike AGB, soil OLT was positively correlated with CWM scores in both the shrub and forest

561 communities, which indicates that thickness was associated with the abundance of functional

562 traits associated with woody vegetation (woodiness, plant height, leaf dry matter content; Fig. 4).

563 As with apparent functional divergence effects in our biomass models, the pathways linking

564 CWM to OLT were mediated by idiosyncratic species effects. We interpret this relationship to

565 mean that the disproportionate effects of particular species on OLT can be associated with

566 individual traits, specifically those traits that help determine the decomposability and lability of

567 dead plant organic matter (Steinbeiss et al. 2008; Conti and Díaz 2013) .

568   Overall, our results highlight the importance of idiosyncratic species effects as the

569   dominant functional diversity component. Like the mass balance hypothesis, the idiosyncratic

570   species hypothesis suggests that ecosystem properties are driven by specific traits, but further

571   suggests that any one trait is less important than the unique combinations that occur in particular

572   species (Conti and Díaz 2013). Our ability to resolve the true importance of trait divergence

573   versus mean trait values could have been improved by considering within-species trait variation,

574   potentially by incorporating genetic diversity into our analysis (Albert et al. 2011). However,

575   most high-resolution studies of functional diversity deal with species-poor, often experimentally

576   constructed plant communities (Sandra and Cabido 2001). In landscape-scale field studies of

577   remote and/or diverse ecosystems, idiosyncratic species analysis may be an efficient strategy for

578   evaluating the importance of functional diversity, while also identifying particular species for

579   more detailed trait measurements or experimental work.

580

581   *Conclusions*

582   *Implications for improving representation of functional diversity in ecosystem models*

583   Accurately representing plant diversity effects in ecosystem models is a critical step

584   towards improving our ability to predict the fate of high-latitude C stocks. Boreal and arctic

585   ecosystems are undergoing rapid and widespread vegetation shifts, such as treeline movement

586   and shrub expansion, and continued lake shrinkage is likely to add to this trend by driving the

587   redistribution of peat-forming wetland communities. Our study is one of several examples

588   illustrating how these changes in plant community composition and diversity can influence C

589   balance, both directly and by mediating the effects of disturbance (Jonsson and Wardle 2010).

590   Although many existing ecosystem models incorporate plant functional diversity effects, they

591   typically rely on coarse characterizations of functional diversity, such as plant functional types.

592   Recent work has called the functional type approach into question by demonstrating that random

593   functional type designations can outperform a priori classification systems in their ability to

594   predict ecosystem properties (Wright et al. 2006). The dangers of relying on functional type-level

595   functional diversity estimates are evident in our idiosyncratic species analyses, which show that

596   even within a single plant functional type (e.g. deciduous shrubs, forbs, or graminoid; Fig. 2),

597   species differ widely in their ability to predict AGB versus OLT, and their relative

598   importance/predictive power also varied between communities.

599   There is growing interest in the development of ecosystem models that represent plant

600   functional diversity at the level of traits, rather than functional types (Wullschleger et al. 2014).

601   Empirical functional diversity analyses like ours, and the analytical methods we employ, could

602   help to inform dynamic vegetation models in several ways, whether such models incorporate

603   traditional functional types or novel trait-based dynamics. First, functional diversity analyses

604   could help improve the delineation of plant functional types, by revealing when functional types

605   do and do not correspond to species with similar ecosystem function and suites of functional

606   traits (Wright et al. 2006). Second, empirical functional diversity analyses can highlight traits or

607   species that strongly correlate with model variables, and potentially inform data collection efforts

608   for model parameterization (Wullschleger et al. 2014). Finally, studies like ours can provide

609   estimates of the responses of functional diversity metrics and trait values to changing

610   environmental conditions, and these estimates could in turn be used as targets for model

611   validation (Soranno et al. 2010). Understanding these relationships is essential for the

612   development of models in which functional traits are allowed to change dynamically, and

613   therefore allowing models to effectively capture the role that high-latitude plant communities

614   play in regulating some of the largest C stocks on the planet.

615

Management considerations

616

617   Our objectives were designed to provide relevant information for managers tasked with

618   developing appropriate land exchange plans and other management strategies for shrinking

619   boreal landscapes. In this context, two overarching messages emerge from this study. First,

620   although lake shrinking has measurable and sometimes dramatic effects on organic C

621   sequestration and other functional values provided by boreal wetland ecosystems, the biological

622   significance of these effects is related to other landscape characteristics. Specifically, fire history

623   and the diversity & composition of local plant communities are stronger predictors of above- and

624   below-ground C than shrinking trends in lake-margin plant communities, even in regions that

625   have experienced rapid and widespread shrinking over the last 30 years.

626   Our second major take-home message is that although plant diversity has historically

627   been a low management priority in Alaskan wildlife refuges and other wetland-dominated

628   landscapes (USFWS 1987), the functional diversity of plant communities appears to play an

629   important role in regulating valuable ecosystem functions, of which C sequestration is only one

630   example. AGB, although only a small component of total ecosystem C, is also related to the

631   quality of wetland plant communities as wildlife habitat, since plant biomass is related to the

632   availability of both forage and cover for herbivores (Jeffereies et al. 1994; Paragi et al. 2008;

633   Rittenhouse et al. 2012). In addition, the diversity and composition of plant functional traits

634   (woodiness, tissue nutrient concentrations, etc.) affect the type and diversity of wildlife that a

635   landscape can support (Morettie and Legg 2009). However, as the discrepancies between our

636   AGB and OLT models illustrate, ecosystem properties like OLT/belowground C, plant functional

637   diversity, and AGB do not necessarily all co-vary in space, and respond differently to changes in

638   disturbance regime. If the goal of management is to maximize multiple functional values (e.g. C

639   storage, biodiversity, and AGB/forage/cover availability) simultaneously, heterogeneous

640   landscapes containing both shrinking and stable lakes as well as a diverse range of disturbance

641   histories may provide better value than homogeneous patches dominated by large, stable lakes

642   and wetlands.

643

644

645   **Literature Cited**

646   Albert CH, de Bello F, Boulangeat I, Pellet G, Lavorel S, Thuiller W (2011) On the importance
647   of intraspecific variability for the quantification of functional diversity. Oikos 121:116–
648   126. doi: 10.1111/j.1600-0706.2011.19672.x

649   Archer KJ, Kimes R V (2008) Empirical characterization of random forest variable importance
650   measures. Comput Stat Data Anal 52:2249–2260. doi: 10.1016/j.csda.2007.08.015

651   Balshi MS, McGuire AD, Zhuang Q, Melillo J, Kicklighter DW, Kasischke E, Wirth C,
652   Flannigan M, Harden J, Clein JS, Burnside TJ, McAllister J, Kurz WA, Apps M,
653   Shvidenko A (2007) The role of historical fire disturbance in the carbon dynamics of the
654   pan-boreal region: A process-based analysis.

655   Benoy G, Cash K, McCauley E, Wrona F (2007) Carbon dynamics in lakes of the boreal forest
656   under a changing climate. Environ Rev 15:175–189. doi: 10.1139/A07-006

657   Bond-Lamberty B, Wang C, Gower S (2002) Aboveground and belowground biomass and
658   sapwood area allometric equations for six boreal tree species of northern Manitoba. Can J
659   For Res 32:1441–1450. doi: 10.1139/X02-063

660   Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the
661   maintenance of ecological processes and services. J Appl Ecol no–no. doi:
662   10.1111/j.1365-2664.2011.02048.x

663   Chapin F, McFarland J, David McGuire A, Euskirchen ES, Ruess RW, Kielland K (2009) The
664   changing global carbon cycle: linking plant-soil carbon dynamics to global consequences.
665   J Ecol 97:840–850. doi: 10.1111/j.1365-2745.2009.01529.x

666   Chapin FS, Bret-Harte MS, Hobbie SE, Zhong H (1996) Plant functional types as predictors of
667   transient responses of arctic vegetation to global change. J Veg Sci 7:347–358.

668   Chapin FS, Matson PA, Vitousek P (2011) Principles of terrestrial ecosystem ecology. Springer
669   Science & Business Media

670   Chaudhary VB, Bowker MA, O'Dell TE, Grace JB, Redman AE, Rillig MC, Johnson NC (2009)
671   Untangling the biological contributions to soil stability in semiarid shrublands. Ecol Appl
672   19:110–22.

673   Conti G, Díaz S (2013) Plant functional diversity and carbon storage--an empirical test in semi-
674   arid forest ecosystems. J Ecol 101:18–28.

675   Cutler D, Jr TE, Beard K (2007) Random forests for classification in ecology. Ecology 88:2783–
676   2792.

677   De Deyn GB, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon
678   sequestration in contrasting biomes. Ecol Lett 11:516–31. doi: 10.1111/j.1461-
679   0248.2008.01164.x

680   Díaz S, Lavorel S, de Bello F, Quetier F, Grigulis K, Robson TM (2007) Incorporating plant
681   functional diversity effects in ecosystem service assessments. Proc Natl Acad Sci U S A
682   104:20684–9. doi: 10.1073/pnas.0704716104

683   Engeman RM, Sugihara RT, Pank LF, Dusenberry WE (1994) A comparison of plotless density
684   estimators using Monte Carlo simulation. Ecology 75:1769–1779.

685   Gallant AL (1998) Ecoregions of Alaska. DIANE Publishing

686   Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic
687   warming. Ecol Appl 1:182–195.

688   Grace J, Anderson T (2010) On the specification of structural equation models for ecological
689   systems. Ecol Mono 80:67–87.

690   Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press

691   Grace JB, Adler PB, Stanley Harpole W, Borer ET, Seabloom EW (2014) Causal networks
692   clarify productivity-richness interrelations, bivariate plots do not. Funct Ecol 28:787–798.
693   doi: 10.1111/1365-2435.12269

694   Grime J (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J
695   Ecol 86:902–910.

696   Grosse G, Harden J, Turetsky M, McGuire AD, Camill P, Tarnocai C, Frolking S, Schuur EAG,
697   Jorgenson T, Marchenko S, Romanovsky V, Wickland KP, French N, Waldrop M,
698   Bourgeau-Chavez L and Striegl RG (2011) Vulnerability of high-latitude soil organic
699   carbon in North America to disturbance. J Geophys Res 116:G00K06. doi:
700   10.1029/2010JG001507

701   Harden JW, Trumbore SE, Stocks BJ, et al. (2000) The role of fire in the boreal carbon budget.
702   Glob Chang Biol 6:174–184. doi: 10.1046/j.1365-2486.2000.06019.x

703   Jefferies RL, Klein DR, Shaver GR (1994) Vertebrate Herbivores and Northern Plant
704   Communities: Reciprocal Influences and Responses. Oikos 71:193. doi:
705   10.2307/3546267

706   Ji L, Wylie BK, Nossov DR, et al. (2012) Estimating aboveground biomass in interior Alaska
707   with Landsat data and field measurements. Int J Appl Earth Obs Geoinf 18:451–461.

708   Johnson KD, Harden J, McGuire a. D, et al. (2011) Soil carbon distribution in Alaska in relation
709   to soil-forming factors. Geoderma 167-168:71–84. doi: 10.1016/j.geoderma.2011.10.006

710 Jonsson M, Wardle D a (2010) Structural equation modelling reveals plant-community drivers of

711 carbon storage in boreal forest ecosystems. Biol Lett 6:116–9. doi:

712 10.1098/rsbl.2009.0613

713 Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich

714 PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, Van BODEGOM PM, Reichstein

715 M, Enquist BJ, Soudzilovskaia N a., Ackerly DD, Anand M, et al (2011) TRY - a global

716 database of plant traits. Glob Chang Biol 17:2905–2935. doi: 10.1111/j.1365-

717 2486.2011.02451.x

718 Kasischke ES, Johnstone JF (2005) Variation in postfire organic layer thickness in a black spruce

719 forest complex in interior Alaska and its effects on soil temperature and moisture. Can J

720 For Res 35:2164–2177. doi: 10.1139/x05-159

721 Mack MC, Treseder KK, Manies KL, et al. (2008) Recovery of Aboveground Plant Biomass and

722 Productivity After Fire in Mesic and Dry Black Spruce Forests of Interior Alaska.

723 Ecosystems 209–225. doi: 10.1007/s10021-007-9117-9

724 Mason NWH, Mouillot D, Lee WG, Wilson JB, Functional JB (2005) Functional richness,

725 functional evenness and functional divergence : the primary components of functional

726 diversity. 1:112–118.

727 Mayfield MM, Bonser SP, Morgan JW, et al. (2010) What does species richness tell us about

728 functional trait diversity? Predictions and evidence for responses of species and

729 functional trait diversity to land-use change. Glob Ecol Biogeogr 19:423–431. doi:

730 10.1111/j.1466-8238.2010.00532.x

731 McGuire A, Anderson L (2009) Sensitivity of the carbon cycle in the Arctic to climate change.

732 Ecol Mono. 79:523–555.

733 Meretsky VJ, Fischman RL, Karr JR, et al. (2006) New Directions in Conservation for the

734 National Wildlife Refuge System. 56:135–143.

735 Moretti M, Legg C (2009) Combining plant and animal traits to assess community functional

736 responses to disturbance. 299–309. doi: 10.1111/j.1600-0587.2008.05524.x

737 O'Donnell J a., Harden JW, McGuire AD, Kanevskiy MZ, Jorgenson MT, Xu X (2011) The

738 effect of fire and permafrost interactions on soil carbon accumulation in an upland black

739 spruce ecosystem of interior Alaska: implications for post-thaw carbon loss. Glob Chang

740 Biol 17:1461–1474. doi: 10.1111/j.1365-2486.2010.02358.x

741 Pastick NJ, Rigge M, Wylie BK, et al. (2014) Distribution and landscape controls of organic

742 layer thickness and carbon within the Alaskan Yukon River Basin. Geoderma 230-

743 231:79–94. doi: 10.1016/j.geoderma.2014.04.008

744   Paragi TF, Seaton CT, Kellie KA (2008) Identifying and Evaluating Techniques for Wildlife
745   Habitat Management in Interior Alaska : Moose Range Assessment.

746   Rao C (1982) Diversity and dissimilarity coefficients: a unified approach. Theor Popul Biol
747   43:24–43.

748   Riordan B, Verbyla D, McGuire AD (2006) Shrinking ponds in subarctic Alaska based on 1950–
749   2002 remotely sensed images. J Geophys Res 111:G04002.

750   Rittenhouse CD, Rissman AR (2012) Forest cover, carbon sequestration, and wildlife habitat:
751   policy review and modeling of tradeoffs among land-use change scenarios. Environ Sci
752   Policy 21:94–105. doi: 10.1016/j.envsci.2012.04.006

753   Roach J, Griffith B, Verbyla D, Jones J (2011) Mechanisms influencing changes in lake area in
754   Alaskan boreal forest. Glob Chang Biol 17:2567–2583.

755   Roach JK, Griffith B (2015) Climate-induced lake shrinking causes heterogeneous reductions in
756   waterfowl species richness. Landsc Ecol 30:1005–1022. doi: 10.1007/s10980-015-0207-3

757   Roach JK, Griffith B, Verbyla D (2013) Landscape influences on climate-related lake shrinkage
758   at high latitudes. Glob Chang Biol 19:2276–84. doi: 10.1111/gcb.12196

759   Roscher C, Schumacher J, Gubsch M, et al. (2012) Using plant functional traits to explain
760   diversity-productivity relationships. PLoS One 7:e36760. doi:
761   10.1371/journal.pone.0036760

762   Rosseel Y (2012). lavaan: An R Package for Structural Equation Modeling. J Stat Software,
763   48(2), 1-36. URL: http://www.jstatsoft.org/v48/i02/.

764   Rover J, Ji L, Wylie BK, Tieszen LL (2012) Establishing water body areal extent trends in
765   interior Alaska from multi-temporal Landsat data. Remote Sens Lett 3:595–604.

766   Sandra D, Cabido M (2001) Vive la différence : plant functional diversity matters to ecosystem
767   processes. 16:646–655.

768   Schimel JP, Wetterstedt JÅM, Holden PA, Trumbore SE (2011) shrinking/rewetting cycles
769   mobilize old C from deep soils from a California annual grassland. Soil Biol Biochem
770   43:1101–1103. doi: 10.1016/j.soilbio.2011.01.008

771   Shaver G, Chapin FS (1991) Production: biomass relationships and element cycling in
772   contrasting arctic vegetation types. Ecol Monogr 61:1–31.

773   Sheil D, Ducey MJ, Sidiyasa K, Samsoedin I (2003) A new type of sample unit for the efficient
774   assessment of diverse tree communities in complex forest landscapes. J Trop For Sci
775   15:117–135.

776   Soja AJ, Tchebakova NM, French NHF, et al. (2007) Climate-induced boreal forest change:
777   Predictions versus current observations. Glob Planet Change 56:274–296. doi:
778   10.1016/j.gloplacha.2006.07.028

779   Soranno PA, Cheruvelil KS, Webster KE, Bremigan MT, Wagner T, Stow CA (2010) Using
780   Landscape Limnology to Classify Freshwater Ecosystems for Multi-ecosystem
781   Management and Conservation. Bioscience 60:440–454. doi: 10.1525/bio.2010.60.6.8

782   Steinbeiss S, Bebler H, Engels C, et al. (2008) Plant diversity positively affects short-term soil
783   carbon storage in experimental grasslands. Glob Chang Biol 14:2937–2949. doi:
784   10.1111/j.1365-2486.2008.01697.x

785   Stevens DL, Olsen AR (2004) Spatially Balanced Sampling of Natural Resources. J Am Stat
786   Assoc 99:262–278. doi: 10.1198/016214504000000250

787   Strobl C, Boulesteix A, Zeileis A, Hothorn T (2007) Bias in random forest variable importance
788   measures: illustrations, sources and a solution. BMC Bioinformatics 8:25. doi:
789   10.1186/1471-2105-8-25

790   Taugourdeau S, Villerd J, Plantureux S, et al. (2014) Filling the gap in functional trait databases:
791   use of ecological hypotheses to replace missing data. Ecol Evol 4:944–958. doi:
792   10.1002/ece3.989

793   Tilman D (2001) Functional diversity. Encycl Biodivers 3:109–120.

794   Trenbeith B (1975) Biomass productivity of mixtures. Adv Agron 26:177.

795   US Fish and Wildlife Service (1987) Final Yukon Flats National Wildlife Refuge comprehensive
796   conservation plan, environmental impact statement, and wilderness review. US Fish
797   Wildl. Serv. Anchorage, Alaska, USA

798   Whitehouse HE, Bayley SE (2005) Vegetation patterns and biodiversity of peatland plant
799   communities surrounding mid-boreal wetland ponds in Alberta, Canada. Botany 83:621–
800   637.

801   Whittaker RJ, Triantis KA (2012) The species-area relationship: an exploration of that "most
802   general, yet protean pattern"1. J Biogeogr 39:623–626. doi: 10.1111/j.1365-
803   2699.2012.02692.x

804   Wright JP, Naeem S, Hector A, et al. (2006) Conventional functional classification schemes
805   underestimate the relationship with ecosystem functioning. Ecol Lett 9:111–20. doi:
806   10.1111/j.1461-0248.2005.00850.x

807 Wullschleger SD, Epstein HE, Box EO, et al. (2014) Plant functional types in Earth system

808   models: past experiences and future directions for application of dynamic vegetation

809   models in high-latitude ecosystems. Ann Bot 114:1–16. doi: 10.1093/aob/mcu077

810 Yarie J, Kane E (2007) Aboveground biomass equations for trees of Interior Alaska. For. Sci.

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813

814 Table 1. Variable names and descriptions. A) Functional trait variables used in calculation of functional divergence (Rao) and functional
815 composition (CWM) scores. Traits are designated as 'Effect' or 'Response' traits based on whether they predict effects of plants on ecosystem
816 properties (biomass, productivity, litter decomposition, etc.) or the response of plants to changes in the environment. B) Variables used in
817 structural equation models relating disturbance, functional diversity and carbon storage in plant communities of the Yukon Flats National
818 Wildlife Refuge. Variables in Table 1B are not designated as effect or response variables to avoid confusion with the classification of effect
819 vs. response functional traits. Variables in Table 1B marked with an '*' were treated only as dependent variables in SEM models, while those
820 marked with '^' were treated only as independent variables. All others were simultaneously modeled as independent and dependent variables,
821 with pathways leading to and away from them.

A

Trait Name	Data type	Effect/Response	Units
Specific Leaf Area	continuous	Effect	cm^2/g biomass
Leaf Dry Matter Content	continuous	Effect	g/g
Leaf Nitrogen Content	continuous	Effect	%
Vegetative Height	continuous	Effect	m
Woodiness	binary	Effect	
Tolerance to fire	ordinal	Response	0-3
Tolerance to drought	ordinal	Response	0-3
Tolerance to flooding	ordinal	Response	0-3
Moisture use	ordinal	Response	0-3
Resprouting capacity post-disturbance	ordinal	Response	0-3

B

| Variable	Data Type	Abbreviation	Units
Time Since Fire^	ordinal	Fire	0-10 years, 10-25, 25-50, >50
Lake Shrinking Trend	binary	Shrink	1=shrinking, 0=stable
Community zone width surrounding lake	continuous	Size	m
Functional divergence score	continuous	Rao	none. Larger values ~ greater functional divergence
Functional composition score	continuous	CWM	none. 1st axis of CWM PCA (Fig. 5)
Idiosyncratic species score	continuous	IdSpp	none. 1St axis of idiosyncratic species PCA (Fig. 6)
Aboveground biomass*	continuous	AGB	Mg/ha
Organic layer thickness*	continuous	OLT	dm
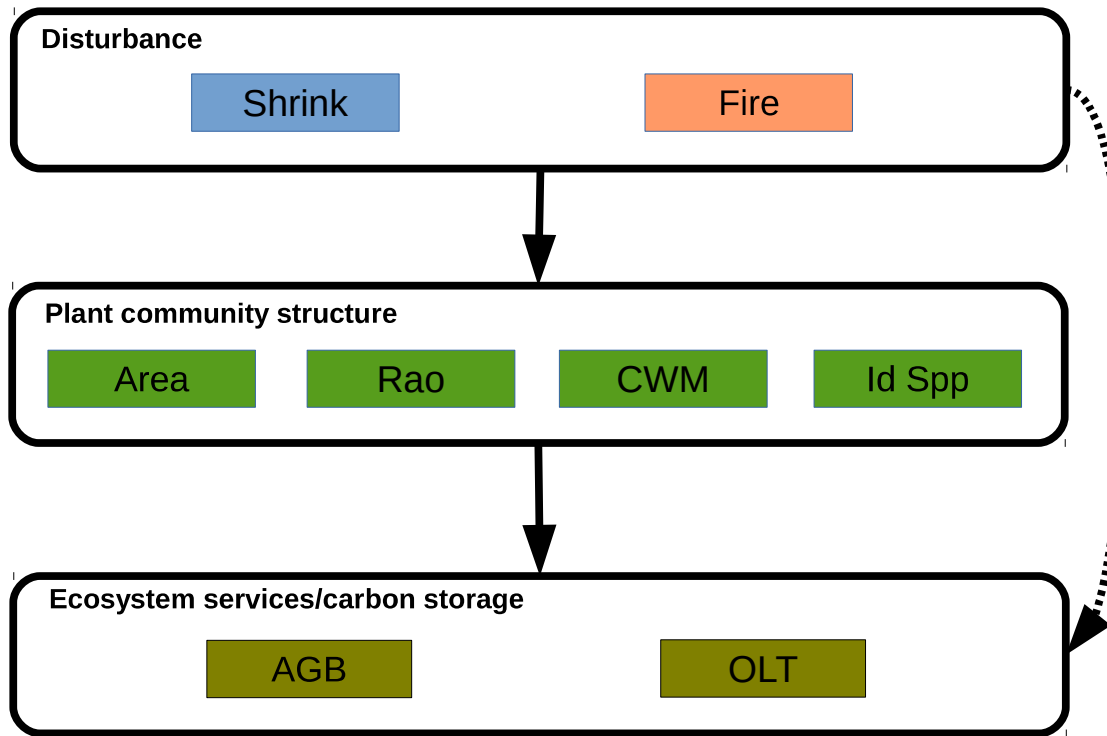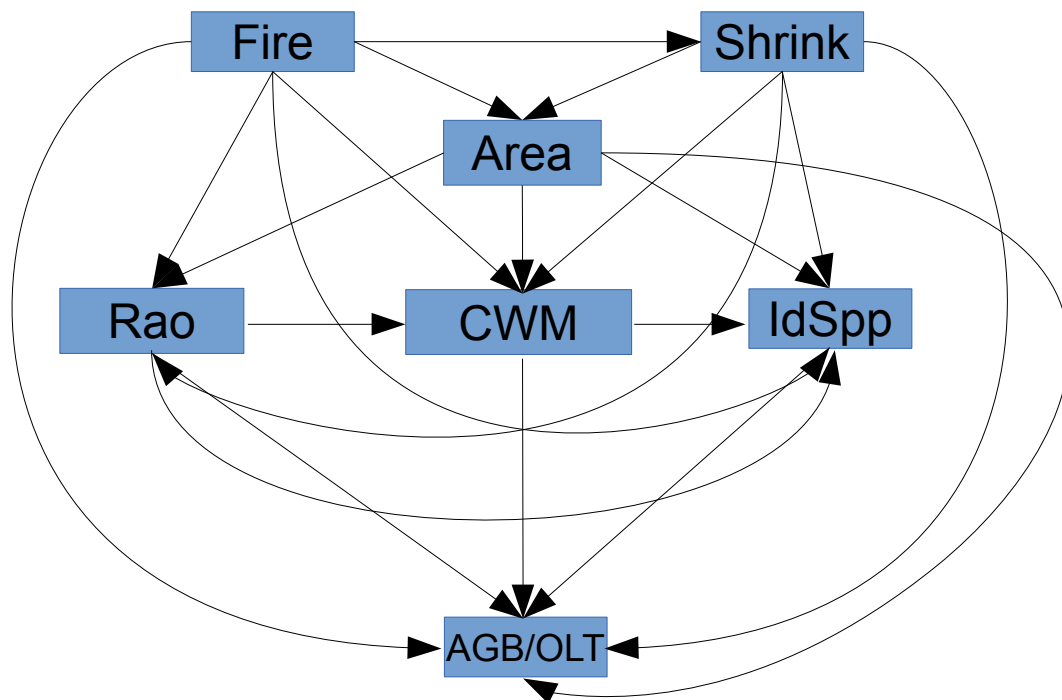
Figure 1. Conceptual diagram showing A) general hypothesized direct and indirect linkages between disturbance, plant community structure, and carbon storage, and B) hypothesized relationships between all variables. Variables include shrinking trend (Shrink) time since fire (Fire), plant community zone width (Area), functional divergence (Rao), functional composition (Func Comp), idiosyncratic species effects (Id Spp), aboveground biomass (AGB) and organic layer thickness (OLT).

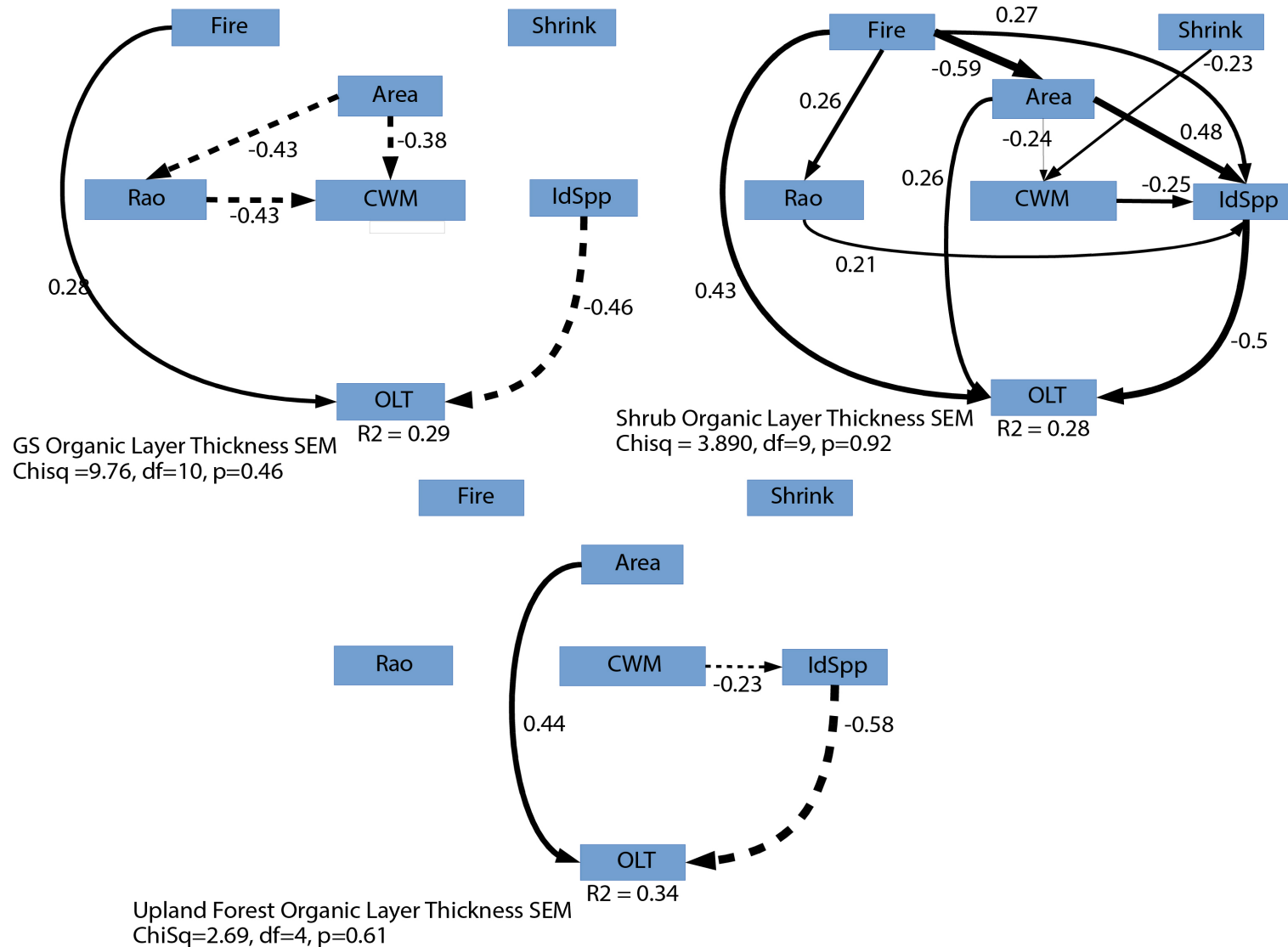| Dependent Variable	Independent	Type	Grass/Sedge			Decid. Shrub			Upland Forest		
			R2	slope	p	R2	slope	p	R2	slope	p
AGB	Time Since Fire	Ordinal (0-10,10-25,25-50,>50 years)	0.16	3.57	0.00	0.22	3.41	0.00	0.22	3.17	0.00
	Shrinking Trend	Binary (1=shrinking)	0.11	-7.77	0.02	0.08	-5.61	0.03	0.02	-2.15	0.28
	Size (m)	Continuous	0.33	-0.24	0.00	0.28	-0.18	0.00	0.54	0.14	0.00
	Rao	Continuous	0.13	0.31	0.01	0.19	0.44	0.00	0.00	-0.04	0.76
	CWM	Continuous	0.00	0.02	0.83	0.00	0.03	0.61	0.00	0.01	0.74
	Id.Spp	Continuous	0.14	5.82	0.01	0.39	7.60	0.00	0.40	4.53	0.00
OLT	Time Since Fire	Ordinal (0-10,10-25,25-50,>50 years)	0.07	0.21	0.05	0.07	0.21	0.05	0.02	-0.10	0.37
	Shrinking Trend	Binary (1=shrinking)	0.00	0.06	0.84	0.02	0.27	0.36	0.00	-0.03	0.90
	Size (m)	Continuous	0.06	-0.01	0.07	0.03	-0.01	0.21	0.15	-0.01	0.00
	Rao	Continuous	0.02	0.01	0.36	0.00	0.00	0.76	0.00	0.01	0.70
	CWM	Continuous	0.00	0.00	0.81	0.01	0.01	0.43	0.01	0.00	0.46
	Id.Spp	Continuous	0.00	-0.06	0.69	0.16	-0.56	0.00	0.34	-0.47	0.00

866 Table 3. Bivariate relationships between aboveground biomass per unit area (AGB), organic layer thickness (OLT), Fire history, Lake
867 shrinking trend (Shrink), lake-margin community zone width (Size), functional divergence (Rao), functional trait composition (CWM), and
868 the presence of idiosyncratic species (Id. Spp). CWM and Id. Spp. values are the first principal component scores from principal components
869 analysis of community-weighted mean functional trait values and presence/absence matrices for idiosyncratic species, as described in the
870 Methods section. All analysis are derived from general linear models with Gaussian errors.

Plant Functional Type	Species	AGB			OLT		
		GS	SH	F	GS	SH	F
Deciduous Tree	Populus.tremuloides	4.45	8.22				
Deciduous Shrub	Arctostaphylos.rubra		23.9				
Deciduous Shrub	Salix.bebbia	4.81	9.7				
Deciduous Shrub	Salix.pseudomyrsinites			13.03			
Deciduous Shrub	Alnus.viridis					12.3	
Evergreen Shrub	Linea.borealis			12.54			
Evergreen Shrub	Ledum.palustre						10.51
Evergreen Shrub	Vaccinium.oxycoccos						8.43
Equisetum	Equisetum.scirpoides			10.51			9.02
Forb	Chamerion.angustifolium	18.86		8.98			
Forb	Calla.palustris	12.46					
Forb	Epilobium.ciliatum	8.05					
Forb	Ranunculus.sceleratus	7.73			10.33		
Forb	Cicuta.virosa		9.04				
Forb	Eriophorum.vagitum		7.55				
Forb	Galium.boreale			13.13	11.11	18	5.64
Forb	Chenopodium.rubrum				15.68		
Forb	Bidens.cernua				10.54		
Forb	Caltha.palustris				10.26		
Forb	Rubus.arcticus					8.52	
Forb	Geum.aleppicum					6.81	
Forb	Mertensia.paniculata						11.02
Graminoid	Scolochloa.festucacea	7.51					
Graminoid	Carex.concinna			12.48		5.1	8.45
Graminoid	Carex.sp.					6.78	

871   Table 5. Variable importance scores from random forest models predicting above -ground
872   biomass (AGB) and soil organic layer thickness (OLT) based on the presence/absence of
873   vascular plant species. Species shown were ranked in the top five for at least one plant
874   community. Species are grouped into one of six plant functional types, which characterize
875   species with similar growth forms, and which are expected to be broadly similar in their
876   functional traits. Variable importance values indicate the average percent increase in model
877   mean-squared error that occurs when a predictor is omitted from the analysis. Variable
878   importance values are shown for models using data from three plant communities: Grass/Sedge
879   (GS), Deciduous Shrub (SH) and Upland Forest (F). Model results were used to generate species
880   presence/absence matrices in each community. Principal components analysis on these matrices
881   were used to generate idiosyncratic species effect scores (first principal component scores).
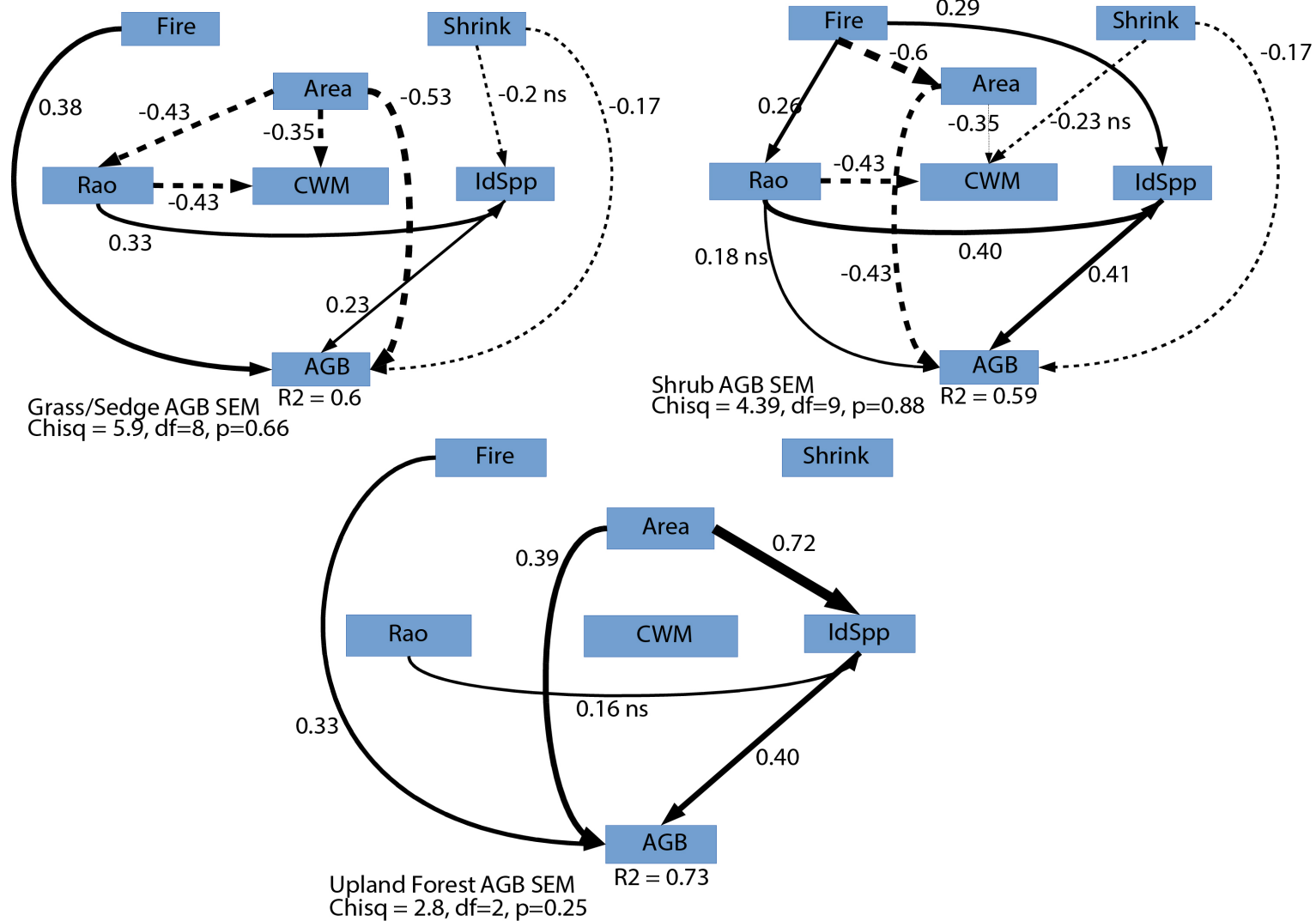
Figure 2. Path diagrams for structural equation models of relationships between shrinking trend (Shrink) time since fire (Fire), plant community zone width (Area), functional divergence (Rao), functional composition (CWM), idiosyncratic species effects (Id Spp), and aboveground biomass (AGB) in three plant communities: Grass/Sedge, Deciduous Shrub, and Upland Forest. Model variables are shown in boxes. Arrows indicate a linear causal pathway between two variables (Fire -> AGB implies that time since fire is a linear predictor of organic layer thickness). Solid arrows represent positive relationships, and dashed lines represent negative relationships. Standardized path coefficients in standard deviation units are shown for each pathway. Overall model fit was assessed with a Chi-Squared test. Non-significant test results indicate adequate model fit.

GS Organic Layer Thickness SEM
Chisq =9.76, df=10, p=0.46

Shrub Organic Layer Thickness SEM
Chisq = 3.890, df=9, p=0.92

Upland Forest Organic Layer Thickness SEM
ChiSq=2.69, df=4, p=0.61

890 Figure 3. Path diagrams for structural equation models of relationships between shrinking trend presence (Shrink) time since fire (Fire), plant community zone width
891 (Area), functional divergence (Rao), functional composition (CWM), idiosyncratic species effects (Id Spp), and organic layer thickness (OLT) in three plant
892 communities: Grass/Sedge, Deciduous Shrub, and Upland Forest. Model variables are shown in boxes. Arrows indicate a linear causal pathway between two variables
893 (Fire -> OLT implies that time since fire is a linear predictor of organic layer thickness). Solid arrows represent positive relationships, and dashed lines represent
894 negative relationships. Standardized path coefficients in standard deviation units are shown for each pathway. Overall model t was assessed with a Chi-Squared test.
895 Non-significant test results indicate adequate model fit.

Table 6. Summary of direct and indirect path coefficients for structural equation models of aboveground biomass (AGB) and organic layer thickness (OLT) (See Figure 3, Figure 4). Results are separated by plant community type: Grass/Sedge (GS), Deciduous Shrub (SH), and Upland forest (F). Values are standardized coefficients, which reflect the expected change in the response variable (in standard deviations) if the predictor is increased by one standard deviation. Direct influence values are the coefficients for direct paths between the predictor and response. Indirect influence values are the product of all path coefficients for a multi-segment path linking two variables. Finally, the total influence of a predictor is the sum of all direct and indirect coefficients. Mediating variables are the intermediate variables in a multi-segment pathway linking two variables. Predictor variables are time since fire (Fire), lake shrinking trend (Shrink), community area (Area), functional divergence (Rao), and idiosyncratic species scores (Id. Spp.). Id. Spp. values are the first principal component scores from principal components analysis of community-weighted mean functional trait values and presence/absence matrices for idiosyncratic species, as described in the Methods section.

| Community	Response	Predictor	Indirect Influence	Direct Influence	Total Influence	Mediating Variables
GS	AGB	Fire	0.00	0.38	0.38	
		Shrink	-0.05	-0.17	-0.22	Idspp
		Size	-0.03	-0.53	-0.56	Rao, Idspp
		Rao	0.08	0.00	0.08	Idspp
		Idspp	0.00	0.23	0.23	
	OLT	Fire	0.00	0.28	0.28	
		Idspp	0.00	-0.46	-0.46	
SH	AGB	Fire	1.05	0.00	1.05	Rao, Idspp, Area
		Shrink	0.00	-0.17	-0.17	
		Size	0.00	-0.43	-0.43	
		Rao	0.16	0.18	0.34	Idspp
		Idspp	0.00	0.41	0.41	
	OLT	Fire	-0.16	0.43	0.27	Area,Rao,CWM,Idspp
		Shrink	-0.03	0.00	-0.03	CWM,Idspp
		Size	-0.27	0.26	-0.01	CWM,Idspp
		Rao	-0.11	0.00	-0.11	Idspp
		CWM	0.13	0.00	0.13	Idspp
		Idspp	0.00	-0.50	-0.50	
Forest	AGB	Fire	0.00	0.33	0.33	
		Size	0.29	0.39	0.68	Idspp
		Rao	0.06	0.00	0.06	Idspp
		Idspp	0.00	0.40	0.40	
	OLT	Size	0.00	0.44	0.44	
		CWM	0.13	0.00	0.13	Idspp
		Idspp	0.00	-0.58	-0.58	
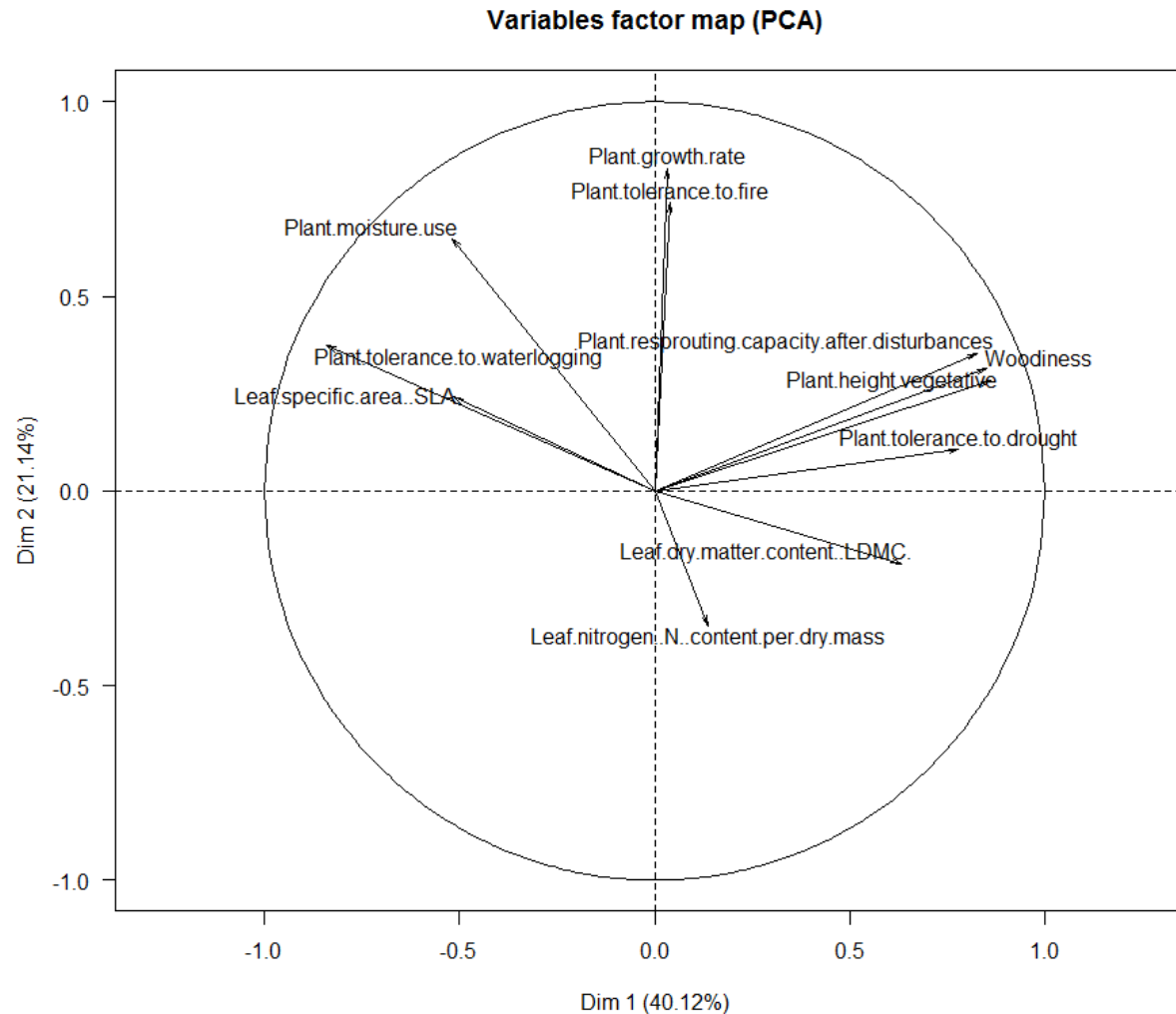
Figure 4. Community-weighted mean functional trait value PCA results. Results of a principal component analysis of community-weighted mean functional trait values for Grass/Sedge communities adjacent to lakes in the Yukon Flats National Wildlife Refuge. PCA results for Deciduous Shrub and Upland Forest communities showed similar associations between traits and axes. Axes indicate the strength of correlation between measured variables and the first (horizontal) and second (vertical) principal component scores. The horizontal and vertical locations of arrow tips indicate correlation scores for each variable. Closely-grouped arrows indicate sets of functional traits that co-vary across lakes. The first (horizontal) axis corresponds to a suit of four traits that primarily characterizes deciduous shrubs, including woodiness, rapid re-growth following disturbance, and tolerance to relatively dry conditions in the Yukon Flats floodplain.