**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 partially decomposed vegetation, or peat (Gorham 1991). Peat layers are strongly affected by the accumulation, death, and decomposition of aboveground biomass (AGB; Chapin et al. 2009; Conti and Díaz 2013), which also functions as a source of forage and/or cover for wildlife. The rate of AGB production is parabolically related to soil moisture, and peat accumulation is also driven by a combination of low temperatures and saturated, anoxic soils, which impede decomposition (Gorham 1991; McGuire and Anderson 2009). In other words, lake shrinkage and associated reductions in soil moisture have the potential to affect C budgets above and below ground.

Shrinking lakes may also have more subtle effects on wetland communities. Boreal wetlands are local plant biodiversity hotspots, including species and growth forms that cannot be found in more abundant upland forest habitat (Whitehouse and Bayley 2005). Plant species diversity could increase in response to lake shrinkage as lake-margin wetlands expand into newly exposed bare soil, but local species losses could also occur as lake shrinkage changes the soil moisture, pH, and other physical variables that govern growing conditions within existing communities. The extent of the effect of lake shrinking on plant diversity is unknown, partly because plant diversity is a much lower management priority than the maintenance of wildlife populations and their habitat (USFWS 1987).

Plant diversity and community composition may be undervalued in boreal Alaskan wetlands, because plant traits (such as woodiness, relative growth rate, and specific leaf area) can control ecosystem properties like C storage, as well as their sensitivity to disturbance (Díaz et al. 2007; Cadotte et al. 2011). The ecological significance of this diversity can be captured by characterizing plant communities in terms of functional diversity, which is the distribution of functionally important species and traits (Tilman 2001; see Table 1 for examples of functional traits). Functional diversity encompasses three components: (1) the relative abundance of individual traits (functional composition), (2) the variation in trait values (functional divergence, sometimes referred to as functional diversity in other studies; Mason et al. 2005), and (3) the distribution of 'idiosyncratic species' that possess unique trait assemblages and may have effects on ecosystem function that are disproportionate to their abundance (Conti and Díaz 2013).

Understanding plant communities by the basis of their functional diversity may be key to improving predictions of C storage in boreal Alaskan wetlands under changing disturbance regimes. Wildfires can rapidly remove massive amounts of C stored in soils and plant biomass, while reduced soil moisture due to lake shrinkage could accelerate decomposition of soil organic matter and reduce the potential for it to re-accumulate (Schimel et al. 2011). However, C cycling may also be related to plant functional traits (De Deyn et al. 2008; Conti and Díaz 2013). For example, rates of plant growth and biomass production are major determinants of soil organic matter accumulation, while woodiness and tissue nutrient contents regulate litter decomposition and accumulation (De Deyn et al. 2008). In addition, plant traits can moderate the effects of disturbance by controlling the level of plant mortality that occurs after a disturbance event and the rate of recovery by the plant community (Conti and Díaz 2013).

There are two primary hypotheses that link functional diversity to C storage. According to the mass-balance hypothesis, ecosystem function is determined by the most abundant traits, or the traits of the most abundant species. This hypothesis predicts that functional composition and idiosyncratic species should be the best predictors of ecosystem processes related to the accumulation and breakdown of organic matter (Grime 1998). In contrast, the niche complementarity hypothesis predicts that processes like biomass production, and therefore inputs to soil C, will be maximized at high functional divergence, because resources will be used more efficiently when distributed among species with diverse ecological requirements and roles (Trenbeith 1975). At the same time, increased diversity in rooting depth profiles could allow for belowground C inputs over a larger fraction of the thawed soil profile and increased total root biomass production (Steinbeiss et al. 2008). Both of these hypotheses represent mechanistic pathways that would allow plant communities to mediate the effects of disturbance on above- and below-ground C storage. However, their relative importance appears to be ecosystem-specific, and relationships between functional diversity and disturbance effects have rarely been examined in natural systems or at regional or greater spatial scales (Conti and Díaz 2013).

Our objective was to determine whether functional diversity mediates the effects of lake shrinking and wildfire on above- and belowground C storage in boreal Alaskan wetlands, using field data from a large-scale biodiversity survey combined with information on C storage in the Yukon Flats National Wildlife Refuge, a 3.5 million ha wetland complex. We sought to identify which of three components of functional diversity (functional composition, functional divergence, and idiosyncratic species) were most influential. To accomplish this objective, we followed a published framework (Díaz et al. 2007), in which the effects of environmental forces and functional diversity components on ecosystem properties are assessed in three steps: 1) separate models for each component, 2) a combined model to assess relative importance, and 3) an investigation of nonlinear and interactive effects (referred to as ‘discontinuous effects’ in the referenced paper). We added to that work by outlining a robust analytical approach for identifying non-linear and interactive relationships between functional diversity, disturbance, and above- and belowground C storage using a combination of machine learning algorithms and structural equation modeling.

We evaluated two general alternative hypotheses (Fig. 1A): Hypothesis 1) Disturbance directly alters the C sink strength of lake-margin wetlands through changes to the physical environment alone (i.e. the effects of plant diversity on C storage cannot be explained by intermediate changes in plant functional diversity). Mechanisms for these direct effects could include removal of C through combustion as well as changes to physical variables like soil moisture, which can influence rates of new biomass production, respiration, and decomposition. Hypothesis 2) Disturbance effects are mediated by changes in plant community structure and the distribution of functional characteristics (Fig. 1A). The concepts of disturbance and functional diversity were each represented by multiple variables in our analysis, which allowed us to assess the relative importance of functional composition and functional divergence as predictors of C storage, and simultaneously test whether apparent effects of lake shrinking on ecosystem properties could be explained by the association of shrinking trends with fire history (Fig. 1B).

We carried out this analysis in three lake-margin plant communities (Grass/Sedge, Deciduous Shrub, and Upland Forest) that represent a gradient of increasing distance from the lake edge and were expected to reflect a gradient of increasing potential functional diversity. In terms of the overall relationship between disturbance and C storage, we predicted that lake shrinking would lead to increased AGB in near-shore Grass/Sedge (GS) communities, with similar but weaker effects in the Deciduous Shrub (SH) community, and no change in Upland Forest (F) biomass (Chapin et al. 2009). We also predicted that lake shrinking would result in increased decomposition and reduced near-surface soil C in the formerly saturated soils of the GS community, which occurred immediately adjacent to the water's edge (Chapin et al. 2011). These predictions derived from previous findings that productivity and decomposition rates show parabolic responses to moisture, and that decomposition tends to respond to changes in soil moisture more strongly than plant biomass production (Chapin et al. 2011). We predicted fire frequency to be correlated with functional divergence and composition (Jonsson and Wardle 2010), and to be negatively correlated with C storage in all community types (Grosse et al. 2011). For our functional diversity hypotheses, we predicted that the relative importance of functional diversity as a mediator of disturbance effects and the relative support for the niche complementarity hypothesis would both be highest in the F community, which had the most complex canopy structure and therefore the greatest potential for niche differentiation among plant species (Conti and Díaz 2013).

As far as we know, our study is one of the first to examine the influence of functional diversity in natural systems at the landscape scale. We illustrate how accounting for plant community characteristics can improve our ability to predict the effects of climate-driven disturbance on ecosystem dynamics. We also provide insight into the mechanisms linking spatial patterns of C storage and wildlife habitat structure, which could be used to re-evaluate conservation and management priorities for Alaskan National Wildlife Refuges.

**Methods**

*Study Area*

We chose the Yukon Flats National Wildlife Refuge (YFNWR) in northeastern Alaska as our study area. The YFNWR encompasses 3.5 million ha surrounding the Yukon River floodplain, consists of a complex mosaic of lakes, wetlands, and upland forest (Gallant 1998), and is not connected to the road system. This region is uniquely appropriate for studying the ecological consequences of lake shrinking in Alaska, because lake shrinking trends within the refuge span the full range of variation observed across the state (Roach et al. 2013). The ~40,000 lakes scattered throughout YFNWR are strongly associated with the presence of discontinuous permafrost, which prevents drainage and promotes ponding of surface water (Roach et al. 2011). Many of these lakes are associated with concentric rings of GS fens, surrounded by shrub bog communities dominated by *Salix* species.

*Diversity sampling*

We surveyed plant communities at 66 lakes between 2010 and 2011. We selected candidate focal lake sites from a GIS layer of floatplane-landable lakes using a Generalized Random Tessellation Stratified (GRTS) design, ensuring that our sample sites were a spatially balanced, representative random sample of the study area (Stevens and Olsen 2004). Sampling efforts were divided between two strata that had opposite regional lake area trends since 1985 (Roach et al. 2013). All lakes within a 1km radius of the focal lake centroid that could be accessed within 14 days were sampled as satellite lakes. This design allowed us to include small, unlandable lakes in our sample, and to account for the potential effects of spatial autocorrelation between nearby lakes in our analyses.

The primary objective of our sampling campaign was to characterize vascular plant diversity and community composition. We established four perpendicular 100m survey transects at each site, oriented at a random azimuth to the lake centroid. Each transect began at the lake edge, which we defined as the point where the soil surface was not covered by standing water. We then recorded and identified all vascular species located within 5m of the transect line. Specimens that could not be identified in the field were pressed and sent back to the University of Alaska Fairbanks for identification. We also estimated species percent cover using a series of 25 5m-radius vegetation plots distributed within a 50 by 100m grid centered on a randomly selected transect at each site. Finally, we delineated transitions between plant community types, which occurred in concentric rings surrounding lakes, based on the plant growth form (herbaceous, deciduous shrub, or tree) with >50% cover. We averaged the width of each community type across the four transects, and used these measurements to generate buffers around each lake in arcMap 10.0. These buffers provided an estimate of the area occupied (m2) by different community types within the surveyed area at each lake.

*Fire History*

We estimated the time since the most recent fire at all sample lakes by overlaying lake locations with a GIS map of historical fire perimeters from 1950 to the present (fire.ak.blm.gov). Because only 1/3 of all sample sites had burned within that timeframe (n=35), we represented fire history as an ordinal variable: 1 = < 5 years since fire, 2 = < 10 years, 3 = < 25 years, 4 = < 50 years, and 5 >= 50 years.

*Lake Trends*

We estimated trends in lake area between 1979 and the present using a time series of 22 Landsat satellite images. These images were converted to shapefile lake maps in ArcMap 10.0 as part of a larger study on long-term lake trends in the YFNWR (Rover et al. 2012). After extracting area measurements for each lake in each year where imagery could be obtained, we fit linear models with the form ‘Lake Area = B1\*Year+B2\*Day of year (Roach et al. 2011). Lakes with significant model F statistics and significant negative Year coefficients were characterized as shrinking. We assessed statistical significance using an alpha cutoff of 0.05. Our lake sample included 16 significantly decreasing lakes, representing 12% of the total sample population. This proportion was similar to the total proportion of shrinking lakes in the YFNWR, which was recently estimated at ~10% using similar methodology (Rover et al. 2012). 22 lakes decreased in area between 1979 and the present, but did not have significant decreasing trends due to large interannual fluctuations in lake area. Because these fluctuations represent flood events that could have their own effects on community composition and carbon stocks, these lakes were excluded from this analysis. Three lakes had significant increasing trends, and were also excluded. Increasing lakes represent a small fraction of the total landscape (<3%) in YFNWR and elsewhere in Alaska (Rover et al. 2012).

*Soil C and AGB sampling*

Logistical constraints prevented us from collecting soil and AGB samples at all sites. Instead, we selected 15 lakes for intensive sampling, and correlated measurements at these lakes with remote-sensing products to generate maps of soil organic C content and AGB for the entire sample population. The 15 lakes were originally selected to represent a balanced sample among three lake types: Decreasing, Stable, and Fluctuating. However, the full time-series of lake areas were not available prior to field sampling, and these lake-type designations were based on a pilot analysis using six hand-digitized area measurements per lake. After re-analyzing lake area data according to the methods described above, we found that our sample consisted of four decreasing lakes, 6 stable lakes, 4 fluctuating lakes, and 1 increasing lake, which was excluded from analysis as described above.

To sample the soil C and AGB, we visited each of these lakes within a two-week window from Aug 1-Aug 14, which corresponded approximately to the period of peak biomass accumulation in our study area (Mack et al. 2008). Eight lakes were sampled in 2011 simultaneously with our vegetation surveys, and seven lakes originally surveyed in 2010 were revisited in 2012 for soil and biomass collection. We stratified soil and AGB sampling across our three three community types: GS, SH, and F. Within each community type, we harvested understory AGB from 5-10 randomly located 20cm x 50cm quadrats. Within each quadrat, we harvested all live and dead biomass, including green moss, woody debris, and leaf litter. Samples were kept cool and flown out of the field within 3 days before being frozen prior to analysis. We then dried samples for 3 days at 60º C before weighing (Shaver and Chapin 1991; Mack et al. 2008). We also measured shrub (<3m tall) and tree stem density along a randomly located 60m transect in each plant community. Transects were broken into 6 10m cells. We then counted all deciduous shrub stems within 5m of the transect line in each cell, and harvested 10 randomly located stems per community type. All stem material was dried for 5 days at 60º C before being weighed. We also estimated tree density in each cell using a third nearest neighbor angle-order estimator, which is a robust alternative to plot-based density estimates (Engeman et al. 1994; Sheil et al. 2003), and calculated tree biomass using allometric equations (Bond-Lamberty et al. 2002; Yarie and Kane 2007).

We collected three 20cm soil cores from each plant community using a specially designed 4.4 cm diameter fitting for a Makita power drill, which minimized compression in organic horizons. Horizon depths and weights were recorded in the field, and samples were kept cool in permafrost pits for a maximum of 3 days before being flown out and stored at -20C prior to analysis. After returning from the field, we dried samples at 60C before measuring % C and N with a Costech CHN analyzer. Bulk density was estimated by measuring the dry weight of a known-volume subsample for each horizon in each core. We then calculated soil C content as %C \* bulk density \* layer thickness (Johnson et al. 2011).

In addition to these soil cores, we characterized soil horizons by recording the depths of fibric organic, humic organic, mineral, and frozen soil layers in pits dug along the four vegetation survey transects at all 130 lakes. In 2010, soil pits were dug at the lake edge and at the upland forest boundary. In 2011, we also dug additional pits located in the center of each plant community type (n=58).

We compared average biomass estimates from field sampling to estimates derived from a recently published raster map of AGB for the YFNWR, which modeled biomass based on spectral reflectance indices from Landsat imagery (Ji et al. 2012). We estimated mean mapped AGB by averaging biomass values for all pixels that overlapped buffer polygons representing plant communities after weighting values based on the degree of overlap. We then regressed field biomass estimates against mapped estimates for each plant community type to validate the mapped values, which we used to represent mean AGB for all communities at all 130 lakes.

Horizon thickness is commonly used as a proxy for soil C content per unit area (Johnson et al. 2011). We used a recently published 30m-resolution map of organic layer thickness (OLT) in the Yukon River Basin to estimate average C content per unit area (Pastick et al. 2014). Average OLT estimates were derived and validated against field data with the same methods used to determine average AGB.

*Functional diversity and functional composition*

We calculated plant functional trait diversity based on five effect traits and five response traits (Table 1). These traits were selected based on their potential to influence rates of organic C accumulation and decomposition, and on their relevance for predicting plant community responses to lake-related disturbance. We developed separate trait matrices for all species found in each plant community, using a combination of field data, literature searches, and a query from the TRY functional trait meta-database (www.try-db.org; Kattge et al. 2011). We chose not to remove species with missing trait data from our analysis. Instead, we filled data gaps using multiple imputation, as implemented in the mice R package (Taugourdeau et al. 2014). Multiple imputation methods have been shown to yield more robust datasets than either case deletion or simple gap-filling methods in functional diversity studies, as long as the proportion of species with missing data does not exceed ⅓ for each variable. We confirmed that there was sufficient data to retain each functional trait variable before proceeding.

We estimated functional trait divergence using Rao's quadratic entropy (Rao 1982), which is derived by calculating the multivariate distance between each species pair in a community, and weighting these distance scores by the proportional abundance of each species (Equation 1).

Equation 1:

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

Gower's distance formula was used to accommodate the presence of both continuous and categorical trait variables in our dataset (Roscher et al. 2012). Functional trait composition was estimated by 1) calculating the community-weighted mean (CWM) of functional trait values, for all species present at a given lake and community type, and 2) extracting the first principal component score from a PCA of CWM functional trait values (Roscher et al. 2012). Community-weighted mean trait values were an average over all species present, weighted by species abundance.

We used the random forest algorithm to identify potential idiosyncratic species that were strong predictors of above- and belowground C (Cutler et al. 2007). We ran separate random forest models for AGB and OLT in each community type, with binary presence/absence scores for all plant species as independent variables. Variables were ranked based on their average individual effect on model mean squared error (Archer and Kimes 2008). Since the presence of many unimportant predictors can suppress model performance, we sequentially removed the 5 lowest-ranking variables and re-ran models until we arrived at a model with maximum predictive power (Strobl et al. 2007). Model results were used to construct reduced species presence matrices. We then calculated idiosyncratic species scores for each community and response variable as the first principal component of a species presence/absence PCA.

*Structural equation modeling*

We used structural equation modeling (SEM) to evaluate hypotheses about the network of causal relationships linking lake shrinking, plant community traits, and C storage. The SEM modeling framework facilitates the testing of hypotheses about direct and indirect influences, and makes it possible to explicitly account for causal relationships between predictor variables (Grace and Anderson 2010). These features make SEM modeling a more appropriate tool for addressing our research questions than more common statistical techniques like general linear models in which unaccounted-for covariance between predictors can have a dramatic influence on parameter estimates (Grace et al. 2014)

The first step in our modeling process was to graphically represent our *a priori* hypotheses about the network of causal relationships that might drive variation in AGB and OLT, which reflect above- and below-ground C respectively (Fig. 1B). Concepts such as disturbance, functional diversity, and C storage were represented by measured variables (Table 1), producing a hypothetical network of influence that could be directly compared against data. A directed arrow from one variable to another (x -> y) represents the hypothesis that ‘y is a linear function of x’ (Fig. 1B).

We fit this network to our data with the lavaan package in R using the LISREL method, and assessed model fit by comparing the observed variance-covariance structure of the data to a modeled variance-covariance matrix using a Chi-squared test (Grace and Anderson 2010; Rosseel 2012). A significant test statistic implied inadequate model fit, meaning there were missing structural relationships between variables. If the initial model had inadequate fit, we added biologically plausible paths sequentially based on modification index values (Chaudhary et al. 2009). Once we obtained a model with adequate fit, we assessed our hypotheses by examining the standardized path coefficients linking variables. Standardized coefficients are essentially z-transformed coefficients, and reflect the expected number of standard deviations that the response will change when a predictor is changed by one standard deviation (Grace 2006). The product of all path coefficients in an indirect pathway (e.g. lake shrinking -> plant diversity -> AGB) represents the coefficient for the entire pathway, and the sum of all indirect and direct path coefficients linking two variables indicates the total influence of the predictor on the response. Finally, we also assessed the predictive power of our hypotheses by examining model R2 values for each response variable.

**Results**

All community-specific variables were summarized by community type and by lake trend (Table 2). Overall, GS communities had the highest AGB, greatest OLT, and lowest species richness of any community (Table 2). SH communities contained the greatest average functional divergence, but GS communities were similar (Table 2). F communities the lowest average AGB and shallowest average OLT, and had substantially lower functional divergence scores than either of the two lake-margin communities, despite having the highest average species richness (Table 2).

*Bivariate relationships*

*Vegetation*

AGB per unit area was significantly positively related to the length of time since the most recent wildfire in all three communities (Table 3). GS and SH communities adjacent to shrinking lakes also had significantly lower AGB per unit area compared to similar communities near stable lakes (Table 3). Size (width of community zones surrounding lakes) was the best single predictor of AGB per unit area in all communities, with R2 values ranging from 0.33 to 0.54). Size was negatively associated with AGB per unit area in GS and SH communities, but was positively correlated with biomass in the F (Table 3). Lake shrinking was not significantly associated with AGB per unit area in the F community (Table 3). Functional divergence (Rao's quadratic entropy) was significantly positively correlated with AGB per unit area in GS and SH communities, but not in the F. Functional composition, as measured by the first principal component score from a PCA of community-weighted mean (CWM) functional trait values, was not significantly associated with biomass in any plant community.

However, the first principal component from a PCA of idiosyncratic plant species presence/absence was significantly correlated with AGB in all three communities (Id Spp; Table 3). Idiosyncratic species scores were positively correlated with the presence of most idiosyncratic species for each community (Appendix 1).

*Soils*

OLT, a proxy for surface (0-30cm) soil C content per unit area, was significantly predicted by time since fire in the GS and SH communities, negatively correlated with Size in the F, and significantly correlated with idiosyncratic species scores in the SH and F communities (Table 3). Idiosyncratic species scores for peat thickness were primarily associated with a suite of forb and graminoid species (Appendix 1), although SH IdSpp scores were positively correlated with the presence of one shrub species (*Salix glauca*), and F IdSpp scores were positively correlated with the presence of one deciduous tree (*Populus tremuloides*; Appendix 1).

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

Random forest models using only community-weighted mean functional trait values were poor predictors of AGB (Table 4). However, random forest models of AGB as a function of species presence/absence were more successful, explaining 43% of variance in the GS community, 48% in the SH community, and 61% in the F. The optimal model for each community included 15 species, although the top five species accounted for over half the variance explained in all cases (% variance explained = 36 for GS, 29 for shrub, and 49 for the F. Species were grouped into six functional types (Table 5), which characterize growth form and are expected to represent species with broadly similarly functional traits (Chapin et al. 1996). *Chamerion angustifolium*, a post-disturbance colonizing forb, was the top predictor of GS AGB, while the top predictor in the SH community was the dwarf deciduous shrub *Arctostaphylos rubra*, and the best predictor of forest AGB was the forb *Galium boreale*, although a deciduous shrub (*Salix pseudomonticola*) and an evergreen shrub species were also highly ranked (*Linaea borealis*; Table 5). In general, herbaceous species were more strongly associated with variation in AGB in the GS community, while woody plants had high variable importance values in the shrub and forest communities (Table 5).

OLT, like AGB, was not well predicted by community weighted mean functional trait values, with CWM random forest models explaining less than 1% of variance in peat thickness in the GS and Shrub communities, and only 15% of variance in F OLT (Table 4). Id Spp random forest models were more successful, explaining between 40 and 57% of variance in OLT. All top predictors of GS OLT were herbaceous (gramionid or forb) species, including several plants found in emergent wetlands and floating vegetation mats, such as *Calla palustris* and *Menyanthes trifoliata* (Table 5). Deciduous tree and shrub species were generally not strong predictors of OLT in any community, although the nitrogen fixing shrub Alnus viridis had the second highest variable importance ranking of any species in the SH IdSpp model (Table 5). The only woody species with high variable importance rankings in the F model were understory evergreen shrubs (*Ledum palustre* and *Vaccinium oxycoccus*).

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

*Aboveground C storage (AGB)*

In all communities, AGB was significantly associated with both disturbance

history (time since fire, lake shrinking status) and plant functional diversity variables (Rao's quadratic entropy and idiosyncratic species distributions). Structural equation models (SEM) explained more than half of observed variation in AGB in all communities (R2= 0.6 for GS, 0.59 for SH, and 0.73 for F; Figure 2). All SEM models adequately captured the underlying variance-covariance structure in the data, as indicated by non-significant Χ2 tests(Figure 2).

Time since fire was positively correlated with AGB in all communities, although the relative strength of this effect was greatest in the GS community (Table 6). Only direct pathways linked fire history with AGB in the GS and F, while the effects of fire history were at least partially mediated by changes in functional diversity in SH (Fig. 2).

Lake shrinking was significantly associated with reduced biomass per unit area in both the GS and SH communities (Fig. 2). In both cases, effects of lake shrinking on biomass did not appear to be mediated by functional diversity. Lake shrinking status was not significantly predicted by time since fire (Fig. 2).

Size was the strongest direct influence on AGB per unit area in all communities (Figure 3). Small/narrow GS and SH community zones surrounding lakes had relatively high biomass density, whereas Size and AGB were positively correlated in the F. Strong positive relationships between Size and idiosyncratic species effects in the F also indicated that larger F communities were more likely to include idiosyncratic species with strong influences on biomass.

Idiosyncratic species effects were the only components of functional diversity with direct influence on AGB (Fig. 2). Idiosyncratic species scores were significantly positively correlated with Rao's quadratic entropy scores, which represent functional divergence, in the GS and SH communities (Fig. 2). In other words, species whose presence was positively correlated with AGB were more likely to occur in communities with high functional divergence. A similar but non-significant trend was produced in the F AGB SEM model (Fig. 2). Rao's quadratic entropy was not consistently predicted by any variable across the three communities, but increased with increasing time since fire in the SH (Fig. 2). Functional trait composition, as measured by CWM scores, was not strongly associated with biomass in any community (Fig. 2).

*Peat thickness (OLT) structural equation model results*

Structural equation models explained close to 30% of observed variance in OLT thickness in all three communities, representing approximately half the predictive power of AGB SEM models (Fig. 3). The influence of disturbance and functional diversity variables, and the evidence for mediation of disturbance effects by functional diversity varied between communities. When direct and indirect pathways were included, organic layer thickness increased with time since fire in both the GS and SH communities, but not in the F (Fig. 3). In contrast, lake shrinking was only associated with OLT in the SH. The effects of lake shrinking on SH OLT included indirect pathways mediated by functional composition (CWM) and idiosyncratic species (IdSpp) effects, while Fire effects were mediated by Size, Rao, CWM, and IdSpp (Fig. 3).

Community size was not a significant predictor of GS OLT although it was positively correlated with OLT in both the SH and F via direct paths (Fig. 3), In the SH, this effect was countered by indirect pathways mediated by IdSpp and CWM, for a negligible net effect (Table 6).

The IdSpp variable was the strongest predictor of OLT in all communities, and was the only functional diversity variable linked to OLT via direct pathways (Fig. 3). Functional divergence (Rao) was only significantly correlated with OLT in the SH, with a net negative relationship (Table 6). In contrast with AGB SEM models, CWM was a significant predictor of SH and F OLT (Table 6). In both communities, the effect of CWM was positive and mediated by relationships between functional composition and idiosyncratic species effects (Fig. 3, Table 6) . PCA results indicated that these positive CWM PCA scores were linked with the dominance of taller, woody, drought-tolerant species with the ability to resprout rapidly following disturbance (Fig. 4).

**Discussion**

*Overview*

We examined relationships between disturbance, functional diversity, and above- & below-ground C storage (AGB and OLT) in boreal lake-margin plant communities. We built on previously-published methods (Diaz et al. 2007) by outlining an analytical framework for simultaneously estimating the separate and interactive effects of functional diversity components on ecosystem function. We implemented this framework using plant diversity data from an intensive field survey across a 3.5 million-ha study area combined with an online plant trait database (Kattge et al. 2011), to test hypotheses about the ecological role of functional diversity in diverse, natural systems at a management-relevant scale.

Our analyses showed that lake shrinkage is a significant driver of AGB and OLT. However, its effects appears limited to ecosystems in close proximity to lakes, and are often overshadowed by the influence of fire history and functional diversity. We also found that the relative influence of functional divergence and functional composition differed between above-ground and below-ground C pools, and that correlations between functional divergence and AGB could be explained at least in part by idiosyncratic species effects. In addition, our study provided insight into the importance of patch size in functional diversity-ecosystem function analysis. We conclude by discussing how our work could help improve representation of plant biodiversity and disturbance in ecosystem models designed to predict high-latitude C dynamics, and by reviewing the implications of our work for land managers tasked with preserving the ecological and social value of boreal wetlands in a drying landscape.

*Disturbance effects on C storage*

Our findings supported the hypothesis that lake shrinking is a significant negative influence on C storage in lake-margin plant communities of interior Alaska. GS and SH wetlands near shrinking lakes had significantly reduced AGB per unit area relative to areas with stable lakes, while drying SH communities had significantly thinner soil organic layers (Table 4). Although lakes within fire scars from the past 60 years area more likely to dry than unburned lakes (Roach et al. 2013), the probability of shrinking was not related to time since fire over more recent time scales (Fig. 2, Fig. 3). In addition, lake shrinking appears to represents a distinct form of disturbance whose influence on C stocks cannot be explained as an indirect effect of increased fire frequency (Fig. 2, Fig. 3). As predicted, the effects of lake shrinking were most apparent in herbaceous and shrub wetland plant communities that occur in close proximity to the lake shore, whereas lake shrinking had no effect on either above- or below-ground C in the F community, which was hydrologically isolated from adjacent lakes (Table 6). Overall, lake shrinking appeared more tightly linked to AGB than to the much larger C stocks stored in organic soil (Fig. 2, Fig. 3). Lake shrinking trends can only be calculated over a few decades (Roach et al. 2011; Rover et al. 2012), and this timespan may not be sufficient to show the effects of lake shrinking on soil peat accumulation.

In addition to being a poor predictor of belowground C, lake shrinking was a relatively minor component of the local disturbance regime in our study area. Fire history was a stronger predictor of both above- and belowground C stocks in the GS and SH communities, despite the clear sensitivity of both communities to lake shrinking (Table 6). Wildfire is widely recognized as the dominant disturbance agent in interior Alaska (Harden et al. 2000; Balshi et al. 2007) and our analysis suggests that this continues to be true at the landscape scale even in regions like the Yukon Flats, which show pronounced lake shrinking trends (Riordan et al. 2006; Roach et al. 2011). Surprisingly, the only C pool that was not significantly associated with time since fire in our analysis was the F organic layer. The effects of wildfire on OLT in the boreal forest are well established (Harden et al. 2000). However, our analysis used a relatively coarse measure of fire history that did not include estimates of severity or timing, both of which regulate the amount of surface organic material removed during boreal forest fires (Kasischke and Johnstone 2005). In addition, the F community category in our analysis included a spectrum of forest types ranging from pure black spruce stands to mixed aspen-birch forests, which are associated with a similar diversity of soil profiles (Johnson et al. 2011), as evidenced by the significant pathways linking functional trait values, idiosyncratic species distributions, and forest OLT (Fig. 3).

*Carbon storage/community size relationships*

Community size, which was estimated as the width of concentric vegetation bands surrounding each lake, was one of the strongest predictors of both above and belowground C in our analyses (Table 6). These effects could not be explained in terms of size-diversity relationships, since direct pathways between area and AGB/OLT were stronger than indirect, functional diversity-mediated pathways in almost all models (Table 6). In addition, when size was correlated with functional divergence, the sign of this relationship was negative, as opposed to the near universal phenomenon of positive species diversity-patch size relationships (Table 6; Whittaker and Triantis 2012). We suggest this negative relationship, and the negative relationship observed between community size and AGB in both GS and SH communities (Fig. 2), can be explained as edge effects. As already noted, SH communities in the Yukon Flats are often characterized by infilling of both GS and forest plant species. Similarly, the outer edges of GS communities typically contain shrub propagules and spruce or aspen seedlings. The edge effect hypothesis is further supported by our idiosyncratic species random forest models. These models identified species that were characteristic of adjacent communities as top predictors of AGB in all three communities. For example, top-ranked species in the GS community included a tree *Populus tremuloides* and a deciduous shrub *Salix bebbiana*, while all top species in the F biomass models were forbs (*Galium boreale*), graminoids (*Carex concinna*), or shrubs (*Linnaea borealis*, *Salix pseudmyrsinites*) (Table 5). Patch size-diversity relationships, though seen a cornerstone of species-based biodiversity research (Whittaker and Triantis 2012), have not been as widely discussed in the functional diversity literature. Our findings illustrate the need to explicitly consider patch size and spatial structure in analysis of functional diversity-ecosystem function relationships.

*Functional diversity mediation*

The mediation hypothesis, which predicts that disturbance effects are mediated by changes in plant community structure and the distribution of functional characteristics, was not well-supported, with significant indirect pathways linking disturbance to C storage only being detected in the SH community (Fig. 2, Fig. 3). This result was consistent with our prediction that the importance of functional diversity as a mediator of disturbance effects would be positively correlated with mean functional divergence, which varied significantly across plant communities and was highest in the SH community (F2,157 = 10.1, p < 0.0001; Table 2). Although we initially predicted that trait divergence would play the largest role in the F community, where productivity could be driven by efficient light competition across multiple canopy levels (De Deyn et al. 2008), the SH community tends to contain a variety of woody and non-woody growth forms due to its position as a zone of transition between herbaceous fens and upland forest (Whitehouse and Bayley 2005).

Of the two disturbance types we examined, the mediation hypothesis was only supported for fire history (Fig. 2, Fig. 3). Lake drying was not significantly correlated with any functional diversity variable in any community except for SH OLT functional composition scores (CWM). Interaction between shrinking trends and functional diversity, particularly functional divergence, was apparently not related to species diversity; GS communities near shrinking and stable lakes had similar functional divergence levels, despite an average of 40% greater species richness at shrinking lake sites (Table 2). This discrepancy underscores the need to consider the influence of functional traits, rather than species diversity alone (Mayfield et al. 2010), when examining disturbance-diversity relationships.

*Functional diversity hypotheses*

Effects of functional diversity on ecosystem processes are most commonly explained as evidence for either the niche complementarity hypothesis or the mass-balance hypothesis (Sandra and Cabido 2001). Our results provided support for both hypotheses depending on the response variable in question. AGB increased with functional divergence scores (Rao’s quadratic entropy) in all communities (Table 6). The standard explanation for this pattern, according to the niche complementarity hypothesis, is that a diverse array of functional niches allowed plant communities to use resources more efficiently (Díaz et al. 2007). However, the pathway linking functional divergence with biomass was mediated by the idiosyncratic species variable, which was the only functional diversity variable that was directly correlated with AGB in any community. In other words, communities with high functional trait divergence were more likely to contain species with disproportionate influence on total biomass (Díaz et al. 2007).

Unlike AGB, soil OLT was positively correlated with CWM scores in both the shrub and forest communities, which indicates that thickness was associated with the abundance of functional traits associated with woody vegetation (woodiness, plant height, leaf dry matter content; Fig. 4). As with apparent functional divergence effects in our biomass models, the pathways linking CWM to OLT were mediated by idiosyncratic species effects. We interpret this relationship to mean that the disproportionate effects of particular species on OLT can be associated with individual traits, specifically those traits that help determine the decomposability and lability of dead plant organic matter (Steinbeiss et al. 2008; Conti and Díaz 2013) ⁠.

Overall, our results highlight the importance of idiosyncratic species effects as the dominant functional diversity component. Like the mass balance hypothesis, the idiosyncratic species hypothesis suggests that ecosystem properties are driven by specific traits, but further suggests that any one trait is less important than the unique combinations that occur in particular species (Conti and Díaz 2013). Our ability to resolve the true importance of trait divergence versus mean trait values could have been improved by considering within-species trait variation, potentially by incorporating genetic diversity into our analysis (Albert et al. 2011). However, most high-resolution studies of functional diversity deal with species-poor, often experimentally constructed plant communities (Sandra and Cabido 2001). In landscape-scale field studies of remote and/or diverse ecosystems, idiosyncratic species analysis may be an efficient strategy for evaluating the importance of functional diversity, while also identifying particular species for more detailed trait measurements or experimental work.

*Conclusions*

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

Accurately representing plant diversity effects in ecosystem models is a critical step towards improving our ability to predict the fate of high-latitude C stocks. Boreal and arctic ecosystems are undergoing rapid and widespread vegetation shifts, such as treeline movement and shrub expansion, and continued lake shrinkage is likely to add to this trend by driving the redistribution of peat-forming wetland communities. Our study is one of several examples illustrating how these changes in plant community composition and diversity can influence C balance, both directly and by mediating the effects of disturbance (Jonsson and Wardle 2010). Although many existing ecosystem models incorporate plant functional diversity effects, they typically rely on coarse characterizations of functional diversity, such as plant functional types. Recent work has called the functional type approach into question by demonstrating that random functional type designations can outperform a priori classification systems in their ability to predict ecosystem properties (Wright et al. 2006). The dangers of relying on functional type-level functional diversity estimates are evident in our idiosyncratic species analyses, which show that even within a single plant functional type (e.g. deciduous shrubs, forbs, or graminoid; Fig. 2), species differ widely in their ability to predict AGB versus OLT, and their relative importance/predictive power also varied between communities.

There is growing interest in the development of ecosystem models that represent plant functional diversity at the level of traits, rather than functional types (Wullschleger et al. 2014). Empirical functional diversity analyses like ours, and the analytical methods we employ, could help to inform dynamic vegetation models in several ways, whether such models incorporate traditional functional types or novel trait-based dynamics. First, functional diversity analyses could help improve the delineation of plant functional types, by revealing when functional types do and do not correspond to species with similar ecosystem function and suites of functional traits (Wright et al. 2006). Second, empirical functional diversity analyses can highlight traits or species that strongly correlate with model variables, and potentially inform data collection efforts for model parameterization (Wullschleger et al. 2014). Finally, studies like ours can provide estimates of the responses of functional diversity metrics and trait values to changing environmental conditions, and these estimates could in turn be used as targets for model validation (Soranno et al. 2010). Understanding these relationships is essential for the development of models in which functional traits are allowed to change dynamically, and therefore allowing models to effectively capture the role that high-latitude plant communities play in regulating some of the largest C stocks on the planet.

*Management considerations*

Our objectives were designed to provide relevant information for managers tasked with developing appropriate land exchange plans and other management strategies for shrinking boreal landscapes. In this context, two overarching messages emerge from this study. First, although lake shrinking has measurable and sometimes dramatic effects on organic C sequestration and other functional values provided by boreal wetland ecosystems, the biological significance of these effects is related to other landscape characteristics. Specifically, fire history and the diversity & composition of local plant communities are stronger predictors of above- and below-ground C than shrinking trends in lake-margin plant communities, even in regions that have experienced rapid and widespread shrinking over the last 30 years.

Our second major take-home message is that although plant diversity has historically been a low management priority in Alaskan wildlife refuges and other wetland-dominated landscapes (USFWS 1987), the functional diversity of plant communities appears to play an important role in regulating valuable ecosystem functions, of which C sequestration is only one example. AGB, although only a small component of total ecosystem C, is also related to the quality of wetland plant communities as wildlife habitat, since plant biomass is related to the availability of both forage and cover for herbivores (Jeffereies et al. 1994; Paragi et al. 2008; Rittenhouse et al. 2012). In addition, the diversity and composition of plant functional traits (woodiness, tissue nutrient concentrations, etc.) affect the type and diversity of wildlife that a landscape can support (Morettie and Legg 2009). However, as the discrepancies between our AGB and OLT models illustrate, ecosystem properties like OLT/belowground C, plant functional diversity, and AGB do not necessarily all co-vary in space, and respond differently to changes in disturbance regime. If the goal of management is to maximize multiple functional values (e.g. C storage, biodiversity, and AGB/forage/cover availability) simultaneously, heterogeneous landscapes containing both shrinking and stable lakes as well as a diverse range of disturbance histories may provide better value than homogeneous patches dominated by large, stable lakes and wetlands.

**Literature Cited**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Gallant AL (1998) Ecoregions of Alaska. DIANE Publishing

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

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

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

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

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

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

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

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

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

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

Jonsson M, Wardle D a (2010) Structural equation modelling reveals plant-community drivers of carbon storage in boreal forest ecosystems. Biol Lett 6:116–9. doi: 10.1098/rsbl.2009.0613

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, Van BODEGOM PM, Reichstein M, Enquist BJ, Soudzilovskaia N a., Ackerly DD, Anand M, et al (2011) TRY - a global database of plant traits. Glob Chang Biol 17:2905–2935. doi: 10.1111/j.1365-2486.2011.02451.x

Kasischke ES, Johnstone JF (2005) Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture. Can J For Res 35:2164–2177. doi: 10.1139/x05-159

Mack MC, Treseder KK, Manies KL, et al. (2008) Recovery of Aboveground Plant Biomass and Productivity After Fire in Mesic and Dry Black Spruce Forests of Interior Alaska. Ecosystems 209–225. doi: 10.1007/s10021-007-9117-9

Mason NWH, Mouillot D, Lee WG, Wilson JB, Functional JB (2005) Functional richness, functional evenness and functional divergence : the primary components of functional diversity. 1:112–118.

Mayfield MM, Bonser SP, Morgan JW, et al. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Glob Ecol Biogeogr 19:423–431. doi: 10.1111/j.1466-8238.2010.00532.x

McGuire A, Anderson L (2009) Sensitivity of the carbon cycle in the Arctic to climate change. Ecol Mono. 79:523–555.

Meretsky VJ, Fischman RL, Karr JR, et al. (2006) New Directions in Conservation for the National Wildlife Refuge System. 56:135–143.

Moretti M, Legg C (2009) Combining plant and animal traits to assess community functional responses to disturbance. 299–309. doi: 10.1111/j.1600-0587.2008.05524.x

O’Donnell J a., Harden JW, McGuire AD, Kanevskiy MZ, Jorgenson MT, Xu X (2011) The effect of fire and permafrost interactions on soil carbon accumulation in an upland black spruce ecosystem of interior Alaska: implications for post-thaw carbon loss. Glob Chang Biol 17:1461–1474. doi: 10.1111/j.1365-2486.2010.02358.x

Pastick NJ, Rigge M, Wylie BK, et al. (2014) Distribution and landscape controls of organic layer thickness and carbon within the Alaskan Yukon River Basin. Geoderma 230-231:79–94. doi: 10.1016/j.geoderma.2014.04.008

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Wullschleger SD, Epstein HE, Box EO, et al. (2014) Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. Ann Bot 114:1–16. doi: 10.1093/aob/mcu077

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

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

A.

B.

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).

Table 3. Bivariate relationships between aboveground biomass per unit area (AGB), organic layer thickness (OLT), Fire history, Lake shrinking trend (Shrink), lake-margin community zone width (Size), functional divergence (Rao), functional trait composition (CWM), and the presence of idiosyncratic species (Id. Spp). CWM and 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. All analysis are derived from general linear models with Gaussian errors.

Table 5. Variable importance scores from random forest models predicting above -ground biomass (AGB) and soil organic layer thickness (OLT) based on the presence/absence of vascular plant species. Species shown were ranked in the top five for at least one plant community. Species are grouped into one of six plant functional types, which characterize species with similar growth forms, and which are expected to be broadly similar in their functional traits. Variable importance values indicate the average percent increase in model mean-squared error that occurs when a predictor is omitted from the analysis. Variable importance values are shown for models using data from three plant communities: Grass/Sedge (GS), Deciduous Shrub (SH) and Upland Forest (F). Model results were used to generate species presence/absence matrices in each community. Principal components analysis on these matrices were used to generate idiosyncratic species effect scores (first principal component scores).

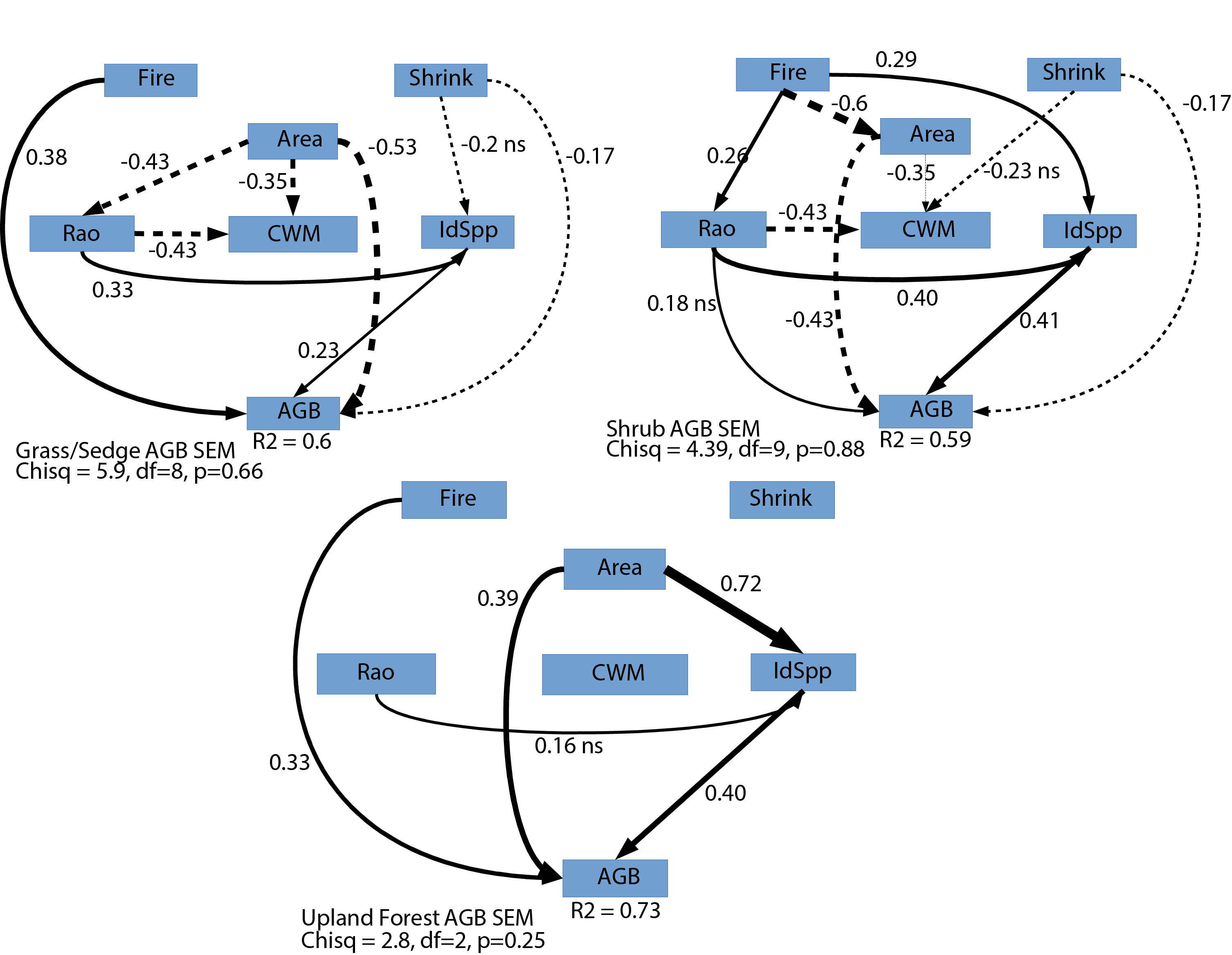


Figure 2. Path diagrams for structural equation models of relationships between shrinking trend (Shrink) time since fire (Fire), plant community zone width (Area), functional divergence (Rao), functional composition (CWM), idiosyncratic species effects (Id Spp), and aboveground biomass (AGB) in three 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.

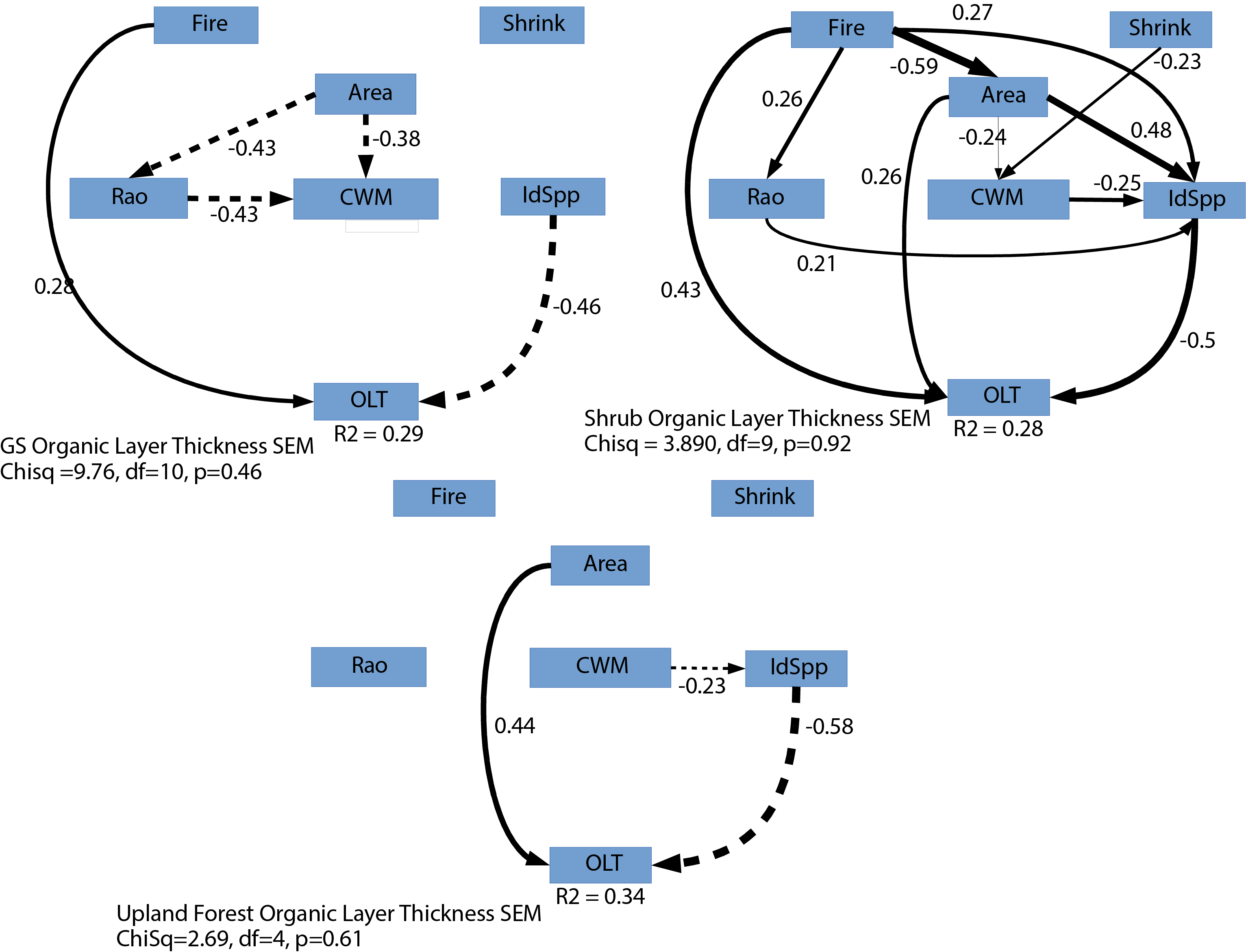


Figure 3. Path diagrams for structural equation models of relationships between shrinking trend presence (Shrink) time since fire (Fire), plant community zone width (Area), functional divergence (Rao), functional composition (CWM), idiosyncratic species effects (Id Spp), and organic layer thickness (OLT) 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 -> OLT 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 t was assessed with a Chi-Squared test. 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.

OLE-object



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.