

HISTORICAL CONTINGENCY AND BIOTIC DETERMINISM IN COMMUNITY
ASSEMBLY: A LONG-TERM EXPERIMENT OF GRASSLAND DYNAMICS

By

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ABSTRACT

Starting with studies about ecological succession over a century ago, ecologists have been interested in the extent to which community assembly is predictable and the degree to which assembly is influenced by colonization history and initial conditions. Today, ecologists agree that there are two general processes by which communities may assemble. The first is deterministic assembly, in which environmental conditions determine the outcomes of species interactions, and thus under common environmental conditions communities converge in composition over time. The second is historically contingent assembly, in which colonization history - regardless of environmental conditions - create unique biotic conditions and unique assembly trajectories that produce divergent communities, driven by stochastic community drift or by priority effects. It is recognized that these processes are not mutually exclusive but work in concert to produce observed, mature communities in nature.

To tease apart the roles and influences of these two processes, a field experiment in experiment was established in eastern Kansas that experimentally manipulated grassland communities to a wide variety of initial conditions in terms of species richness, species composition, and the relative abundances of constituent species. The subsequent convergence or divergence of these communities over eight years of community development was assessed not only in terms of species composition but also in functional trait and phylogenetic composition in order to integrate information on the niche requirements of coexisting species, which influences the intensity of those interactions. Furthermore, analyses of community composition were conducted using abundance-weighted and presence/absence data in order to emphasize abundance dynamics and occupancy dynamics over the course of community assembly.

These analyses revealed that assembly processes varied both among different levels of community organization (i.e. species, functional trait, or phylogenetic composition) and among weighting schemes

within a level of community organization: species abundance is strongly deterministic while species occupancy is historically contingent; functional trait abundance is historically contingent while functional trait occupancy dynamics are strongly deterministic; phylogenetic dynamics are historically contingent regardless of weighting scheme. When functional trait analyses were broken down into individual traits, it was found that dynamics in among-plot dissimilarity varied widely, converging with respect to some and diverging with respect to others. This indicated that the broad trends in aggregate functional trait composition may belie the variable dynamics of different traits during assembly.

Overall, these results provide a comprehensive and in-depth experimental study of plant community assembly processes by including and comparing both functional trait and phylogenetic composition in the assessment of community convergence or divergence, and also by considering abundance dynamics separately from occupancy dynamics. In doing so, the varied influences of deterministic and historically-contingent assembly processes are better understood. It is worth noting, however, that despite a relatively long-term experimental dataset, eight years is a fairly short timespan on an ecological scale. As such, these results only characterize dynamics at the very onset of community assembly, which may crucially impact later dynamics, but may still be species- and context-dependent and in flux, with a capacity to change over time. However, these results are still valuable to our overall understand of the long-term processes of community assembly, with the potential to improve restoration and conservation efforts in the face of habitat degradation and global climate change.

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INTRODUCTION

Community assembly describes the general theoretical framework of how local assemblages form from larger species pools (Drake 1991, Luh & Pimm 1993, Fukami 2010). This includes, for instance (but is not limited to), the process of ecological succession, in which community assembly is initiated by a major disturbance. The assembly of ecological communities is driven by the basic processes of species gain (i.e. colonization), species loss (due to biotic and abiotic interactions), and fluctuations in species abundance (which is influenced by both colonization and interaction dynamics) (Luh & Pimm 1993). Species colonization is understood to have a large stochastic component, which may produce varied colonization histories and initial states of community composition among local communities (Drake 1990, Law & Morton 1993). The impact of colonization history – including the role of species interactions associated with initial conditions – on subsequent community assembly is still poorly understood (Samuels & Drake 1997, Belyea & Lancaster 1999, Chase 2003, Fukami et al. 2005, Fukami & Nakajima 2011, Vannette & Fukami 2014) and remains a major goal in ecology (Morin 1999).

The theoretical roots of the deterministic view of community assembly date back a hundred years to Clements's (1916) theory that vegetation succession proceeds towards a well-defined climax community. Under deterministic assembly, species assemblages are formed through nonrandom interactions, driven by niche differences among species with outcomes determined by environmental conditions (e.g. Grime 1973, Diamond 1975, Tilman 1986, Fukami et al. 2005, Cavender-Bares et al. 2004, Wilson & Stubbs 2012). Under strongly deterministic assembly, and with enough time for sufficient dispersal and interactions to play out, persistent differences in community composition observed among sites directly result from environmental heterogeneity and are independent of initial differences in colonization history (e.g. Tilman et al. 1986, Sommer 1991, Fukami 2010).

In contrast, community assembly may be strongly influenced by colonization history, with little impact from interspecific interactions, a concept pioneered by Gleason (1927) in response to Clements' popular theory. Here, sites of initially different species composition will potentially assemble along different trajectories, diverging in community composition towards alternative stable states (Lewontin 1969, Fukami & Nakajima 2011), regardless of environmental conditions. Community divergence driven by differences in colonization history may be simply due to demographic stochasticity (i.e. ecological drift) (e.g. Hubbell 2001), but interspecific interactions may also play a role through *priority effects*, in which the success of a colonizer is impacted by the particular species already present in a community (Drake 1991). For instance, a species may be unable to colonize a site because its niche is already largely occupied by an established species (i.e. limiting similarity; MacArthur & Levins 1967), because limiting resources are already being utilized by several different species (i.e. niche preemption; Kardol et al. 2008), or because the local environment has been altered by early-arriving species (i.e. niche modification; Peterson 1984, D'Antonio & Vitousek 1992, Fukami & Nakajima 2013). However, it is possible for constituent species to facilitate the establishment of others as well (Holt & Polis 1997, Knowlton 2004).

While these fundamental theories of assembly are well-defined, progress in understanding the relative influences of historically-contingent and deterministic processes and how they may interact has been limited. This is owed, in part, to an underuse of long-term field experiments (Fukami et al. 2005), specifically those involving species-rich communities. By manipulating the initial identity, richness, and abundance of propagules in a community, and varying these factors widely over many environmentally similar sites, observed assembly patterns can be compared to what would be expected under either historically-contingent or deterministic assembly. Under assembly that is predominately deterministic, sites in a common environment would become more compositionally similar over time – i.e. sites would converge in composition – as superior competitors become more abundant and spread among sites to

cause poor competitors to go locally extinct. Under historically contingent assembly, the unique initial compositional states of each site would result in unique assembly trajectories along alternative stable states, and as such, sites would be expected to maintain compositional differences over time (Beisner et al. 2003, Perry et al. 2003, Chase 2010).

Assessing convergence and divergence among locations can be achieved by calculating the mean beta diversity among sites. Originally conceived as a scaling factor between local (i.e. alpha) and regional (i.e. gamma) diversity (Whitaker 1960, Whitaker 1972), beta diversity can measure compositional turnover among two locales (Anderson et al. 2006). By calculating the beta diversity between every pairwise combination of sites, the average compositional difference – that is, the average dissimilarity – among sites can be measured. With multiple years of data, convergence would be reflected in a decrease in mean beta diversity among sites. Many different methods for measuring beta diversity have been proposed (see Tuomisto 2010 and Anderson et al. 2011 for reviews), but beta diversity measured as compositional dispersion in multivariate space is ideal in an experimental setting as a multivariate test of homogeneity in dispersion can be used to test for significant differences in beta diversity among years (Anderson 2006).

Another, perhaps more important, issue faces ecologists looking to tease apart the processes that impact community assembly: the natural world is complex. For instance, it may be difficult, if not impossible, to differentiate between truly alternative stable states and alternative transient states in assembling communities (Fukami & Nakajima 2011), particularly in communities that contain organisms with generational times on the order of decades. Additionally, deterministic and historical processes can – and very likely do – work in conjunction during assembly (e.g. Fukami et al. 2005, Caruso et al. 2011, Helsen et al. 2012, Guo et al. 2013), but understanding the exact nature of this interaction can be exceptionally challenging.

To help rectify the complex interactions between processes that drive community assembly, it has been proposed that historically-contingent and deterministic processes function simultaneously during assembly, but that each is predominate at different levels of community organization. Specifically, it has been hypothesized that trait-based functional composition is deterministic, while species composition is historically contingent (Fox 1987, Temperton et al. 2004). Fukami et al. (2005) were the first to experimentally test this hypothesis and found that plots converged in functional-group composition, but remained divergent in species composition, indicating functionally-deterministic assembly and historically-contingent species assembly.

Combining species into a select number of functional groups is a coarse means of integrating functional trait information into analyses, however. By reducing species into an arbitrary number of functional groups, all species of the same group are considered ecologically identical (and members of different groups perfectly dissimilar), and potentially important information is lost. So how can we more accurately address the problem of quantifying highly complex ecological niches (Hutchinson 1957) for species? One solution has been to use values of functional traits for species, as greater overlap among species in functional trait values would theoretically result in greater competition for resources. To completely characterize a species' niche, *every* functional trait must be quantified, and to measure total functional composition of a community, this must be done for every species in that community; this is prohibitively difficult (Baraloto et al. 2012). To make this approach feasible, researchers must often choose a limited set of traits *a priori* that is particularly important to the outcome of species interactions and that accurately characterizes niche differentiation among the species in question. While there is some evidence that a handful of easily-measured traits may indeed predict the overall ecological function of species (e.g. Díaz et al 2004), the specific list of appropriate traits may be unique to particular regions, pools of species, or research question (Weiher et al. 1999, Cornelissen et al. 2003) and thus potentially difficult to define.

In order to account for a much larger and more complex suite of traits, it has been suggested that the phylogenetic relatedness of species in a community can be used as a proxy for ecological similarity (e.g. Webb et al. 2002, Cavender-Bares et al. 2009). It has been observed that closely related species tend to be more similar than to distantly-related species at least since Darwin noted it in *On the Origin of Species* (1859). This observation has been developed extensively in the past decades and is generally referred to as niche conservatism, which asserts that species become more ecologically distinct over time as they evolve independently of one another, and so ecological differentiation among species is proportional to phylogenetic differentiation (Lord et al. 1995). While many complex characters support a Brownian motion model of evolution (Cooper & Purvis 2010, Harmon et al. 2010), which is assumed in niche conservatism (Webb et al. 2002), some research has suggested that many important ecological traits exhibit little (Baraloto et al. 2012) or perhaps no (Pavoine et al. 2013) phylogenetic signal (defined as the significant pattern of evolutionarily related organisms possessing similar traits or trait values [Blomberg et al. 2002]). Despite this, both trait-based and phylogenetic-based approaches to accounting for ecological differentiation are complementary (Cadotte et al. 2013) and when used together, the assumption of phylogenetic signal among traits can be tested as well.

In short, the simultaneous influence of initial conditions and deterministic assembly processes may be better disentangled by considering the relative influence of these processes on different levels of community organization (i.e. species, functional, and phylogenetic). Along the same lines, it may be useful to consider in isolation the broader dynamics that influence overall community composition. Specifically, the influence of colonization and extinction dynamics are revealed through long-term species occupancy patterns, analyzed by weighting species equally using presence/absence data. The compositional influence of interactions among constituent individuals is revealed by weighting species occupancy by relative abundance. Thus, by analyzing overall assembly patterns under different weighting schemes, the relative influence of historically-contingent and deterministic processes on

these different compositional dynamics (i.e. colonization/extinction and biotic interactions) can be uncovered.

In this study we explore the relative roles of ecological determinism and historical-contingency influencing grassland community assembly at the patch (within-community) scale, using a long-term field experiment conducted in northeastern Kansas. In this experiment, we varied initial community states among field plots by first removing the existing vegetation and then seeding the plots with different numbers and relative abundances of plant species in 2007. From these initial conditions that varied widely in species richness, composition, and relative abundances, we analyzed convergence and divergence of community composition among plots over the first eight years of the study. With a species pool of very high richness and large initial compositional differences among plots, and by using a multivariate measure of beta diversity among different levels of community organization and weighting schemes, this experiment may provide the best and most thorough test of the role of assembly processes to date.

Specifically, the objectives of the study were as follows:

- 1) Assess changes in mean beta diversity (i.e. community dissimilarity) among plots over time. A significant decrease in beta diversity indicates a convergence in composition, suggesting the predominance of deterministic processes in guiding assembly dynamics. A failure to converge (either no change or a significant increase in beta diversity) suggests strong historical contingency, though it may also indicate that too little time has passed for deterministic impacts to become substantial.
- 2) Assess the congruency of changes in beta diversity across species, functional, and phylogenetic compositions.

3) Compare patterns of compositional change when abundance of species is included to that when only species' presence is considered.

4) Develop a phylogenetic tree of species used in this experiment and assess the congruency of phylogenetic and functional trait distances among species to test the assumption of niche conservatism.

METHODS

Study Site and Experimental Design

The site of the community assembly experiment is located at the Nelson Environmental Study Area (NESA) in northeast Kansas, a part of the University of Kansas Field Stations (KUFS) (Jefferson County, Kansas; 39°03` N, 95°12` W). The site was previously a hayfield and dominated by *Bromus inermis* when it was acquired by KUFS in 1971. Between the early 1970s until the early 1990s, the site was utilized for small mammal research, which include the erection of three fenced enclosures (~1 ha each) and a light fertilization application in May 1985; mowing and burning were not a part of the management regime during this time, except for the regular mowing of a two-foot strip around each enclosure. The site was burned in 2005, and the enclosures were removed in 2006.

In 2007, the site was prepared by a combination of herbicide, mowing, and scarification. The experiment is arranged in a factorial design, consisting of a total of 270 2x2-meter plots, arranged in blocks and clusters: one block consists of 15 plots (arranged in a 3- x 5-plot grid), and one cluster consists of 3 blocks (arranged in a 9- x 5-plot grid) (fig. 1). Within a cluster, plots are separated by one-meter walkways; each of the 6 clusters is separated by a 3-meter walkway.

There were a total of five sowing treatments and three nitrogen treatments; every combination of which was represented in each block. The sowing treatments were designed to experimentally manipulate

initial species composition, richness, and abundance in order to create a wide variety of initial community conditions at the onset of the experiment. From a pool of 48 native and naturalized species (table 1), plots were sown with: 1) 16 species, each at a random abundance (16r); 2) 32 species, each at a random abundance (32r); 3) all 48 species, each at a random abundance (48r); 4) all 48 species of equal abundances (48e); or 5) no species, and the natural seed bank was allowed to emerge (0). All plots that received seeds were sown with the same total mass of seed – 264 g – to account for differences among species in germination rate and vigor. In the random-abundance sowing treatments (16r, 32r, and 48r), sowing abundances within each plot were drawn randomly and without replacement for each species from a set lognormal distribution of possible sowing rates. In the 16r and 32r treatments, the 16 or 32 species (respectively) that were assigned to a plot were drawn randomly from the pool of species. At no point were plots weeded. Annual nitrogen treatments of 0, 4, or 12 g N/m² were initiated in 2010; five random plots within each block were assigned to each of these treatments. The experiment was first burned in 2009, and continues biennially.

This study only utilizes data from experimental plots sown with random abundances of species (the 16, 32, and 48r treatments) in order to maximize initial differences among plots, which allows for the best assessment of the impact of historical contingencies on community assembly. Furthermore, plots that received fertilizer were also removed in order to maximize the environmental homogeneity of the plots analyzed. In all, this study considered 54 total experimental plots.

Data Collection

Every year, beginning in 2008, the same 1.5 m x 0.75 m quadrat in each plot (one half the plot, minus 0.25 m on each of three walkway sides) was sampled for species presence and abundance in late June and early July. Abundance was estimated independently for each species, such that the total cover of each plot could exceed one hundred percent if multiple canopy-levels were present. One species

(Hesperis matronalis) failed to germinate and was never observed in the experiment. As such, it has been left out of all analyses and calculations.

To examine plant community composition from a functional trait perspective, ten functional traits shown to be ecologically important (e.g. Weiher et al. 1999, Fukami et al. 2005, Kraft et al. 2008, Helsen et al. 2012, Sonnier et al. 2012) were selected for analyses: leaf nitrogen content, specific leaf area (SLA), nitrogen fixation ability, photosynthetic pathway, maximum vegetative height, seed mass, life history, growth habit, floral initiation, and floral senescence. These traits were obtained for as many species in the 48-species pool as possible, from literature searches and the TRY Plant Trait Database (Kattge et al. 2011). To fill in missing SLA data, measurements were made from leaves collected from the experiment following the methods from Cornelissen et al. (2003). For one rare species, an SLA value was missing; this value was estimated using the mean of all other values. Leaf nitrogen data were missing for eleven of the species, and these missing values were interpolated based on the correlation between existing SLA and leaf nitrogen values (table 1).

A phylogenetic tree among species in the experiment was constructed with branch lengths proportional to evolutionary distances among taxa. Sequence data for all 140 plant species found in the experiment across all years were obtained for the ITS1-5.8s-ITS2 nuclear gene region from Genbank (Benson et al. 2009). If sequence data were not available, leaf tissue was collected from undamaged, fully mature leaves and stored at -20°C until sequencing could occur. Genes were amplified using the C26A/Nnc18S10 (Wen & Zimmer 1996) and ITS4/ITS1 (Hsiao et al. 1995) primers. Sequence data was aligned using the program MUSCLE (Edgar 2004). BEAST v1.8.0 (Drummond et al. 2012) was used to construct an ultrametric tree using an HKY substitution model, a coalescent tree prior of constant size (Kingman 1982), and a strict clock model, using an MCM of length 10,000,000. The analyses in this study

were conducted on a subset of these species (i.e. only species experimentally sown), and so this phylogenetic tree was pruned for these analyses to include just the sown species (fig. 2).

Alpha and Gamma Richness and Diversity Calculations

Alpha richness was calculated as the number of species in a given experimental plot, and gamma richness was the total number of species observed among all experimental plots. Alpha diversity was calculated as the Shannon's diversity index of a given experimental plot. To calculate gamma diversity, Shannon's diversity index was calculated using the sum of absolute abundances of each species among all experimental plots.

Beta Diversity Calculations

The term "beta diversity" has been used in different contexts, each with subtly different meanings. Originally, beta diversity was used as a scaling factor between local (α) and regional (γ) diversity (Whitaker 1960, Whitaker 1972). In this strict definition, $\beta = \gamma/\bar{\alpha}$ (although there has been some debate about whether beta should describe the additive or multiplicative relationship between mean alpha diversity and gamma diversity; see Jost 2007). Following this, if mean alpha diversity is very close to gamma (i.e. if individual sites, on average, exhibit diversity that approaches that encompassed by all sites) – and therefore beta is low – then many more species will be shared between sites than if mean alpha diversity is much lower than gamma. This characteristic of beta diversity led to the implication that it could also be defined in terms of inter-site similarity (within the same regional species pool, at least) (Anderson et al. 2006).

In addition to measures of beta diversity developed from this original definition (as a scaling factor between local and regional diversity), the idea of beta diversity as a measure of turnover among sites has also prompted the development of a multidimensional definition of beta diversity (see Anderson et

al. 2011 for an overview of these different classes of beta diversity measures), which utilizes measures of inter-site resemblance measurements (e.g. dissimilarity).

In this study, multidimensional beta diversity is measured as the mean distance from each site to the centroid of all sites (also called mean dispersion) in multidimensional species, functional, or phylogenetic space – greater mean distance from the centroid is equated with a greater the dissimilarity among sites, and therefore greater β -diversity. This requires a site-by-site distance matrix, which represents the pairwise differences among plots in terms of species, functional, or phylogenetic composition. For species composition, this matrix was filled using either the Jaccard dissimilarity index (for binary data) or the Bray-Curtis dissimilarity index (for abundance-weighted data) calculated using the *vegan* package (Oksanen et al. 2015) in R (R Core Team 2015). For functional and phylogenetic composition, an inter-site distance matrix first requires a species-by-species dissimilarity matrix, which represents the pairwise differences between species in terms of functional traits or phylogenetic relatedness. Because it allows for multiple data types, functional distances between species were calculated using Gower dissimilarity values (Gower 1971) modified to manage ordinal variables as described by Podani (1999). These dissimilarity values were calculated using the ‘*gowdis*’ function from the *FD* package in R (Laliberté & Legendre 2010). To measure interspecific phylogenetic dissimilarity, cophenetic distances were calculated from the branch lengths of the phylogeny of species (Sokal & Rolf 1962). These species-by-species dissimilarity matrices were then used to calculate the mean pairwise distance between each species present among every pairwise combination of plots using the ‘*comdist*’ function from the R package *Picante* (Kembel et al. 2010), thus creating plot-by-plot dissimilarity matrices from which to calculate the mean dispersion (i.e. beta diversity) among plots. Differences among each year’s centroid were assessed using a permutational MANOVA (McArdle & Anderson 2001, Anderson 2001) of 999 permutations, using the ‘*betadisper*’ and ‘*permtest*’ functions from the *vegan* package in R (Oksanen et al. 2015).

Multidimensional (species, functional, and phylogenetic) beta diversity values were calculated for sites when composition was defined when species were both unweighted and weighted by abundance across all years of the study (eight years, from 2008 through 2015). Sites were considered to be significantly converging or diverging when both of two conditions are met: 1) significant differences between multivariate dispersion values of the first and last years of the study (less for convergence, greater for divergence) as assessed with a permutation test of multivariate homogeneity of group dispersions (using 999 permutations) (Anderson 2006); and 2) dispersion values are significantly predicted by year in a linear model to ensure significant changes are consistent over time.

Individual Trait Analysis

The mean dispersion of plots with regards to individual traits was analyzed similar to overall functional dispersion, except dissimilarity matrices were calculated for single traits (still using the Gower dissimilarity coefficient). Analyses were conducted using both unweighted and abundance-weighted data. Convergence and divergence are assessed as with overall species, functional, and phylogenetic composition.

Phylogenetic Signal of Traits

In order to determine the degree to which similarities among species in functional trait data are represented by phylogenetic distances, Abouheif's C_{mean} (Abouheif 1999) was used to evaluate the phylogenetic signal of the trait data. This is an autocorrelation approach and has been shown to perform strongly when testing for a significant phylogenetic signal of traits within a single phylogeny (Münkemüller et al. 2012). To assess the hypothesis that the observed value is significantly different than would be expected by chance, a distribution of values is achieved by randomly shuffling the tips of the phylogeny 9999 times and calculated a value for each. The observed value is compared to this

distribution to obtain a p-value. This analysis was conducted using the adephylo package in R (Jombart & Dray 2009).

Graphs

Graphs were created using the R packages ggplot2 (Wickham 2009) and ape (Paradis et al. 2004).

RESULTS

Compositional Change

A permutational multivariate analysis of variance indicated a significant change in community composition over time for every level of community organization and whether using unweighted or abundance-weighted data: species composition (unweighted: pseudo-F = 8.959, $R^2 = 0.129$, $p < 0.001$ [fig. 3a]; abundance-weighted: $F = 8.063$, $R^2 = 0.117$, $p < 0.001$ [fig. 3b]), functional composition (unweighted: $F = 2.251$, $R^2 = 0.036$, $p < 0.001$ [fig. 3c]; abundance-weighted: $F = 6.039$, $R^2 = 0.091$, $p < 0.001$ [fig. 3d]), and phylogenetic composition (unweighted: $F = 1.97$, $R^2 = 0.022$, $p < 0.001$ [fig. 3e]; abundance-weighted: $F = 6.132$, $R^2 = 0.092$, $p < 0.001$ [fig. 3f]). Correlations between centroid positions on NMDS axis 1 (x-axes in fig. 3) and year indicated that these changes were also significantly progressive among all levels of community organization and data: species composition (unweighted: $r = 0.941$, $p < 0.001$; abundance-weighted: $r = 0.879$, $p < 0.005$), functional composition (unweighted: $r = 0.939$, $p < 0.001$; abundance-weighted: $r = 0.918$, $p < 0.005$), and phylogenetic composition (unweighted: $r = 0.921$, $p < 0.005$; abundance-weighted: $r = 0.879$, $p < 0.005$).

Species Alpha and Gamma Diversities

Mean alpha richness decreased significantly (repeated measures ANOVA: $F = 114.5$, $p < 0.001$) and substantially over time, with a maximum mean of 22.48 species per plot in 2008 and a minimum of

12.41 in 2012. Mean richness in 2015, the final year of data, was 13.07, which marks an average of 41.9% loss of species per plot over the course of the study. Similarly, gamma richness decreased from a maximum of 45 species in 2008, to a minimum of 33 species in 2012 and 2014, with an overall decrease of 24.4% from 2008 to 2015 (from 45 to 34 species). This change was also significantly negatively correlated with year ($r = -0.902$, $p < 0.005$) (fig. 4a, fig. 5).

Mean alpha diversity (calculated as Shannon's diversity index), on the other hand, increased significantly over time (repeated measures ANOVA: $F = 6.242$, $p < 0.001$), with a minimum of 1.71 in 2009 and a maximum of 1.91 in 2014. The change in gamma diversity was significantly negatively correlated with time ($r = -0.708$, $p < 0.05$) (fig. 4b, fig. 6).

Phylogenetic Signal in Traits

A phylogenetic tree among all species found in the experiment (sown and not) was produced from the ITS1-5.8s-ITS2 nuclear gene region and pruned to include just the sown species (fig. 2). The broad topography of the resulting tree, including the relationships among and the taxa contained within Poaceae, Fabaceae, and the Asterids, is well supported (e.g. Stevens 2001, Soltis et al. 2005, The Angiosperm Phylogeny Group 2009). Within *Poaceae*, the relationships among the C4 taxa of Panicoideae (e.g. *Panicum virgatum*, *Sorghastrum nutans*, *Andropogon gerardii*) and Chloridoideae (genus *Bouteloua*) agree with that of current literature, although the relationships among the other grasses are questionable, specifically between *Bromus inermis* (tribe Bromeeae)/*Elymus canadensis* (tribe Triticeae), *Dactylis glomerata* (tribe Poeae, subtribe Dactylidinae)/*Schedonorus arundinaceus* (tribe Poeae, subtribe Loliinae), and the other taxa, which are members of the tribe Poeae (Soreng et al. 2015). The relationships among taxa within Fabaceae are well supported, exhibiting an early divergence of the Cassieae and Mimosoideae clades from the Faboideae subfamily, and accepted relationships among the tribes Galegeae, Trifolieae, Desmodieae, and Amorpeae therein (Bruneau et al. 2008, Cardoso et al.

2013). Within the Asterids, there is a clear division between the euasterids I clade (specifically, order Lamiales, represented here by members of Verbenaceae, Scrophulariaceae, and Lamiaceae) and the euasterids II clade (orders Apiales – represented by one taxon in this experiment, and Asterales) (Angiosperm Phylogeny Group 2009). The division within Asterales between the supertribes Asterodae (containing tribes Asterea and Anthemideae) and Helianthodae (containing tribes Coreopsidae and Heliantheae) also agrees with recent classifications (e.g. Robinson 2004, Kadereit & Jeffery 2007).

Randomizations tests of Abouheif's C_{mean} (Abouheif 1999) indicate a lack of significant phylogenetic signal in SLA ($p > 0.1$), seed mass ($p > 0.5$), floral senescence ($p > 0.1$), and marginally so in life history ($p = 0.056$). A significant phylogenetic signal was observed in leaf nitrogen content ($p < 0.001$), nitrogen fixation ($p < 0.001$), photosynthetic pathway ($p < 0.001$), vegetative height ($p < 0.05$), growth habit ($p < 0.001$), and floral initiation ($p < 0.01$) (fig. 7).

Beta Diversity

Permutation tests and linear models indicated that species composition failed to significantly converge (become more dissimilar) or diverge (become more dissimilar) when unweighted (permutation test: $t = 0.557$, $p > 0.05$; linear model: $F = 0.796$, $p > 0.05$) (fig. 8a), but significantly converged when weighted by species abundance (permutation test: $t = 2.694$, $p < 0.01$; linear model: $F = 16.57$, $p < 0.001$) (fig. 8b).

Plots significantly converged in functional composition when species were unweighted (permutation test: $t = 2.803$, $p < 0.01$; linear model: $F = 13.87$, $p < 0.001$) (fig. 8c) and significantly diverged when species were weighted by abundance (permutation test: $t = -4.174$, $p < 0.001$; linear model: $F = 46.13$, $p < 0.001$) (fig. 8d). For phylogenetic composition unweighted by species abundance, dispersion differed significantly among years (permutation test: $t = 2.577$, $p < 0.05$), but did not show a monotonic trend of convergence or divergence (linear model: $F = 2.57$, $p > 0.05$) (fig. 8e). However, when species were

weighed by abundance, communities diverged in phylogenetic composition (permutation test: $t = -6.075$, $p < 0.001$; linear model: $F = 106.7$, $p < 0.001$) (fig. 8f).

Dispersion of Individual Traits

The change in mean dispersion was measured for all individual traits (fig. 9). Sites converged in terms of leaf nitrogen when species are unweighted (permutation test: $t = 15.11$, $p < 0.001$; linear model: $F = 434.3$, $p < 0.001$) and weighted by species-abundance (permutation test: $t = 11.31$, $p < 0.001$; linear model: $F = 196.1$, $p < 0.001$) (fig. 9a). With respect to SLA, sites converged significantly when species were unweighted (permutation test: $t = 5.01$, $p < 0.01$; linear model: $F = 72.3$, $p < 0.001$) and also when weighted by abundance (permutation test: $t = 3.27$, $p < 0.001$; linear model: $F = 33.38$, $p < 0.001$) (fig. 9b). With respect to nitrogen fixation, sites converged significantly when species were unweighted (permutation test: $t = 3.74$, $p < 0.001$; linear model: $F = 10.04$, $p < 0.05$) but failed to converge when species were weighted by abundance (permutation test: $t = 0.37$, $p > 0.05$; linear model: $F = 1.62$, $p > 0.05$) (fig. 9c). With respect to photosynthetic pathway, sites significantly diverged when species were unweighted (permutation test: $t = -6.54$, $p < 0.001$; linear model: $F = 104.4$, $p < 0.001$) and also when weighted by abundance (permutation test: $t = -10.64$, $p < 0.001$; linear model: $F = 250.3$, $p < 0.001$) (fig. 9d). With respect to vegetative height, sites failed to converge when species were unweighted (permutation test: $t = -1.79$, $p > 0.05$; linear mode: $F = 7.134$, $p < 0.01$) and also when weighted by abundance (permutation test: $t = 2.4$, $p < 0.05$; linear model: $F = 3.635$, $p > 0.05$) (fig. 9e). With respect to seed mass, sites significantly diverged when species were unweighted (permutation test: $t = -5.723$, $p < 0.001$; linear model: $F = 56.72$, $p < 0.001$) and also when weighted by abundance (permutation test: $t = -6.365$, $p < 0.001$; linear model: $F = 111.4$, $p < 0.01$) (fig. 9f). With respect to life history, sites converged significantly when species were unweighted (permutation test: $t = 5.062$, $p < 0.001$; linear model: $F = 66.66$, $p < 0.001$) and also when weighted by abundance (permutation test: $t = 7.768$, $p < 0.001$; linear

model: $F = 100.9$, $p < 0.001$) (fig. 9g). With respect to growth habit, sites failed to converge when species were unweighted (permutation test: $t = 0.14$, $p > 0.05$; linear model: $F = 1.939$, $p > 0.05$) but diverged significantly when species were weighted by abundance (permutation test: $t = -10.342$, $p < 0.001$; linear model: $F = 241$, $p < 0.001$) (fig. 9h). With respect to floral initiation, sites converged when species were unweighted (permutation test: $t = 2.139$, $p < 0.05$; linear model: $F = 30.97$, $p < 0.001$) and also when weighted by abundance (permutation test: $t = 5.138$, $p < 0.001$; linear model: $F = 67.25$, $p < 0.01$) (fig. 9i). With respect to floral senescence, sites converged significantly when species were unweighted (permutation test: $t = 6.158$, $p < 0.001$; linear model: $F = 99.11$, $p < 0.001$) but failed to converge when species were weighed by species abundance (permutation test: $t = 0.792$, $p > 0.05$; linear model: $F = 6.772$, $p < 0.01$) (fig. 9j).

Plots converged on dominance of species of lower SLA and leaf N (regardless of species weighting), on occupancy of nitrogen-fixing species, on dominance by perennial plants and plants delayed in floral initiation (regardless of species weighting), and on occupancy of species with later floral senescence (table 2).

Comparing the absolute changes in individual trait dispersion reveals that most of the patterns of convergence and divergence are similar but slightly exaggerated when species are weighted by abundance. The obvious and important exceptions are photosynthetic pathway, the divergence of which is substantially larger when species are weighted by abundance, and growth habit, which doesn't diverge at all when species are unweighted (fig. 10)

DISCUSSION

The overarching goal of this experiment is to explore the extent to which plant community dynamics at the within-community scale conform to deterministic or historically-contingent models of community

assembly. Here inferences are drawn from community dynamics observed over the first eight years of community assembly in a perennial plant system that is still highly dynamic, undergoing successional change, and far from stabilization. Indeed, the data show that there were significant changes in species diversity, substantial losses of species from plots, and major directional shifts in species, functional and phylogenetic composition over the course of this study. These drastic changes in composition indicate that these experimental communities have undergone substantial community assembly, but say nothing about driving forces behind that assembly, particularly those related to planting history.

The impact of deterministic and historically-contingent processes on assembly is reflected in the degree to which plots converged or remained divergent in composition, respectively, and was measured as mean among-plot beta diversity. A convergence in among-plot compositional similarity (i.e. a decrease in beta diversity) would indicate that deterministic processes such as competition are principal drivers of compositional shifts through consistent and nonrandom changes over time in species presence and/or abundances, despite initial compositional differences. On the other hand, if initial differences persist over time and sites fail to converge, it would indicate that the impact of initial conditions – species richness, composition, or relative abundances – is of primary importance in directing the dynamics and trajectory of assembly. Non-convergence may be due to completely stochastic processes, such as in ecological drift (Hubbell 2001), or result from priority effects that lead to persistent alternative stable states that are robust to shifts toward other states, except in the presence of substantial disturbance (Lewontin 1969, Law 1999). However, it is also possible for communities to be diverging into states that are transient – those that are fluctuating, and thus not truly stable, and often kept so by disturbance (Fukami & Nakajima 2011).

Convergence and divergence, which relate to predominance of deterministic and historically-contingent assembly processes, respectively, was assessed for functional trait as well as phylogenetic composition –

in addition to species composition – in order to integrate information about species' niche requirements. Additionally, analyses were conducted using both abundance-weighted data, to highlight dynamics of those dominant species that overwhelmingly contribute to community dynamics (Grime 1998), and unweighted (presence/absence) data, which emphasizes colonization and extinction dynamics that contribute to species richness and composition and may be impacted by assembly processes differently than assembly dynamics.

Species Composition

Beta diversity analyses indicated that when species are unweighted, plots showed no convergence in species composition (fig. 8a). A significant decrease in mean alpha richness overtime (fig. 4a) indicates that compositional shifts were almost exclusively due to extinctions and impacted little if at all by colonization dynamics (fig. 5). While the decrease in gamma richness (fig. 4a) means that a handful of these species' extinctions were consistent throughout the experiment (and therefore largely deterministic), a failure of plots to converge in overall species occupancy is consistent with expectations of stochastic local extinctions resulting from initial abundance (i.e. species of initially lower abundance are more likely to go locally extinct than species of higher initial abundance), made possible by experimentally manipulating species' sowing rates among plots.

When species were weighted by relative abundance, however, plots converged (fig. 8b), which is a pattern consistent with deterministic community assembly. Abundance-weighted patterns are driven predominately by those species that are of a disproportionately-high relative abundance. A failure to converge in abundance-weighted species composition would indicate that plots exhibited unique combinations of dominant species, that were initiated by the sowing treatments and that persisted over the course of assembly. The significant convergence that was observed, however, means that dominant species among plots grew more similar over time, regardless of initial community states. Over time, the

species that dominate plots are increasingly from the same small pool of native perennial prairie species that have either consistently increased in abundance over time (e.g. *Andropogon gerardii*, *Sorghastrum nutans*, *Schizachyrium scoparium*, *Silphium laciniatum*) or have maintained high abundance over the entire time frame (e.g. *Helianthus maximiliani* and *Ratbida pinnata*) (fig. 6).

Overall, these results signify that species occupancy dynamics are so far largely contingent upon initial conditions. Abundance dynamics of some species, however, within those historically-contingent assemblages, are strongly deterministic – the same species are growing to occupy a large proportion of the community despite initial sowing rates.

Functional Composition

Plots converged in occupancy-based (unweighted) functional composition (fig. 8c), signifying strong impacts of deterministic assembly, and suggests that species loss (or persistence) was functionally non-random. When individual traits were analyzed (figs. 9 & 10a, table 2), plots converged on smaller values of leaf nitrogen, smaller values of SLA, fewer nitrogen-fixing species, longer-lived species, and species of later floral initiation and senescence. Lower values of leaf nitrogen content and SLA correspond with slower growth rates and better retention of nutrients in unproductive systems (Grime et al. 1997) and coupled with the life history and floral phenology patterns suggests that this pattern largely reflects the loss of annual species and persistence of slow-growing, competitive, later-blooming perennial species – in short, functional occupancy patterns show a strong signal of ecological succession.

When species were weighted by abundance, functional composition diverged among plots (fig. 8d), revealing a strong impact of historical contingency. The traits most responsible for this divergence (fig. 10b, table 2) were photosynthetic pathway and growth habit, with a strong impact of seed mass as well, and plots thus appear to be diverging to those either dominated by C4 grasses or C3 forbs. The species that drove abundance-weighted species-composition dynamics are also members of these two broad

functional groups (*A. gerardii*, *S. nutans*, and *S. scooparium* are C4 grasses; *S. laciniatum*, *H. maximiliani*, and *R. pinnata* are C3 forbs), indicating that the same species, not surprisingly, are responsible for the functional divergence of these plots while also causing plots to converge in (abundance-based) species composition.

In all, functional occupancy among plots was convergent, which reflected, at least in part, the process of ecological succession. Abundance dynamics, on the other hand, caused plots to diverge functionally, and was strongly linked to the functional variation exhibited by the deterministically-dominant group of species.

Individual Trait Dispersions

An interesting and important pattern was revealed when dispersion among plots was analyzed for individual traits (figs. 9 & 10): there was no consistency among plots in convergence or divergence patterns among traits, although there was often consistency in those patterns among weighting schemes: for both presence/absence and abundance-weighted data, plots converged on smaller values of leaf nitrogen, converged on smaller values of SLA, diverged in photosynthetic pathway, remained divergence in vegetative height, diverged in seed mass, converged on longer-lived species, converged on delayed floral initiation (plots exhibited a convergence in nitrogen fixation for presence/absence data but no change for abundance-weighted data, no change in growth habit for presence/absence data but divergence for abundance-weighted data, and convergence in floral senescence for presence/absence data but no change for abundance-weighted data [table 2]).

Therefore, not only do deterministic and historically-contingent processes differ in predominance among different levels of community organization, but also within levels of community organization - in this case, with respect to individual traits that make up the aggregate measure of functional trait composition. Looking at overall functional trait dynamics may belie the greater complexity of

community assembly dynamics and may therefore lead to gross oversimplification in the least and complete misunderstanding at the worst.

Furthermore, it is important to note that, even though each of these functional traits have been shown to be important in ecological processes, they are not independent of one another. For instance, in this study, growth habit and photosynthetic pathway were shown to be strongly responsible for the significant pattern of functional divergence. However, while these traits are ecologically important, they were substantially correlated in this study: the only species that exhibited C4 photosynthesis were grasses. Thus, the pattern in overall functional composition may be inappropriately skewed towards divergence due to the covariance among traits related to divergence. For this reason, traits should be subject to orthogonal transformation (e.g. principle component analysis) prior to analyses.

Phylogenetic Composition

Plots failed to converge significantly in phylogenetic-occupancy composition (fig. 8e) over time. While this pattern was fairly dynamic, with initial convergence of plots from 2008 to 2011 and subsequent re-divergence through 2015, the lack of overall directionality indicates a predominance of historically-contingent processes.

The significant divergence of abundance-weighted phylogenetic composition largely reflects those of functional composition, and appears to be closely related to the divergence in C4-grass-dominated plots (which are all members of Poaceae, specifically the PACMAD clade [Soreng et al. 2015]) and C3-forb-dominated plots (the members of which are almost all from the Heliantheae tribe of the family Asteraceae) (fig. 6). So while several traits did not show a significant phylogenetic signal (SLA, seed mass, floral senescence, or, marginally, life history), those that were of the most important in this divergence pattern (photosynthetic pathway and growth habit) did.

Niche Conservatism

This study allowed the opportunity to compare how trait values vary among a phylogenetic tree, thereby testing the assumption of niche conservatism and overall usefulness of phylogenetic analyses in studies of community ecology. Of the ten traits that were measured, just over half exhibited a significant phylogenetic signal. This provides an argument against niche conservatism and therefore the use of phylogenetic analyses in this context, but there are a few important caveats to this. First, only ten traits were analyzed in this experiment and tested for phylogenetic signal, which is not enough to draw strong conclusions about a larger range and variety of traits. Second, it has not been tested (and is difficult to test in general) and therefore cannot be concluded that any of these traits are actually responsible for species interactions that structure communities during assembly – no tests have been conducted to support any causal relationships among traits and assembly processes. So while the present results suggest tentatively that phylogenetic distances can be used as a univariate measure of multivariate functional distances in limited and tenuous capacity among species in ecological studies, much more thorough research must be conducted in this area.

Synthesis

The overarching goal of this study was to examine patterns of compositional convergence and divergence among different levels of community organization to better understand the inter-relationships between historically-contingent and deterministic processes in community assembly. Overall, the results suggest that these processes do indeed function simultaneously but at different levels of community organization (i.e. with respect to species, functional, and phylogenetic composition), and they may affect occupancy dynamics and abundance dynamics differently.

This latter point, that assembly process differ not only among levels of community organization but also within them, is novel to this experiment. This conclusion is supported not only by individual trait

analyses, as mentioned earlier, that suggest plots converge and diverge with respect to different traits, but also by the differences in convergence and divergence patterns that emerge when weighting species by abundance or by presence. Occupancy patterns appear to be driven by stochastic local extinctions (driven by randomized initial conditions) and deterministic functional interactions; abundance dynamics appear to be largely deterministic in terms of species, but functionally historically-contingent.

The previous study of Fukami et al. (2005) agrees with the conclusion that assembly processes function simultaneously but at different levels of community organization, but their results differed completely from these: using abundance-weighted data, Fukami et al. found plots to remain divergent in species composition and to converge in functional composition; the present study found species convergence and functional trait divergence.

Rectifying these opposing results is a difficult task and may be linked to multiple different sources. One may simply be a matter of study sites and organisms – the heathlands of the Netherlands where the experiment of Fukami et al. was conducted differs in many ways from the grasslands of Eastern Kansas, including temperature, precipitation, and soil fertility. There are many theories and hypotheses about how species interactions vary across environmental conditions (e.g. the stress gradient hypothesis [Bertness & Callaway 1994]; CSR strategy theory [Grime 2007]; resource-ratio hypothesis [Tilman 1985]), but it is generally accepted that they do, and as such, different systems may exhibit different durations of time for species interactions to be revealed in among-plot dynamics. In the present study, for instance, species interactions may be stronger, with outcomes therefore occurring more quickly, leading to convergence in species composition more quickly. Intensity of species interactions related to environmental conditions may be further impacted by differences among studies in sowing densities (it should be noted that Fukami et al. defined sowing rates in number of seeds per square meter, with a total of 3500 seeds added per square meter in each plot; the present experiment, on the other hand, did

so in grams of seeds per square meter, with 116 grams of seeds added per square meter, and this makes the actual comparisons of sowing densities difficult), or size and composition of species pools (different pools of species may be more apt to producing species-level priority effects)

Perhaps the most glaring difference in methodology among these two studies was the difference in measuring functional composition – Fukami et al. utilized functional trait groups, while the present study incorporated a multidimensional measure of trait dispersion based on actual trait values. While using functional trait groups – even those based on trait values – is a rather coarse way of quantifying functional composition (e.g. combining species into a smaller number of groups – often by more than half – reduces the complexity of the community and treats all species with a group as functionally identical and all species among groups as completely disparate), using transformed trait values, especially those of different data types (i.e. continuous vs. categorical), can lead to other drawbacks (e.g. covariance within the data). However, the pattern of phylogenetic divergence, which is a univariate measurement and thus cannot be affected by covariation in data, may help to reaffirm those results.

In addition to the contradictions between the present results and those from other studies, the present results themselves – abundance-weighted species convergence and functional divergence – appear to be contradictory in nature. This may be explained by drawing ties between the patterns of deterministic dynamics of dominant species, historically-contingent species occupancy dynamics, and the large functional variance among dominant species: the same small group of species has grown to dominate plots across the experiment, reducing the dissimilarity among plots in highly abundant species; however, the presence of these species is contingent on sowing treatments (they are not colonizing plots in which they were not sown), and so variability exists among plots in which dominant species are present; and these species are functionally disparate, and so small differences in dominant species composition

among plots can result in large differences – which increase as the abundance of these species do – in functional trait composition.

If this pattern of functional divergence is maintained over time, it would indicate that, despite the presence of a deterministic competitive hierarchy, varying initial conditions in community membership create a biotic and abiotic environment unique to assemblages that cannot be invaded by other species (Law 1999, Fukami 2015). However, it is quite important to note that the results from this and the previous experiments are/were from quite early in the assembly process – less than a single generation for many of the species. Early dispersal limitation among sites may emphasize high levels of variation inherent to early assemblages (Hurtt & Pacala 1995, Fukami & Nakajima 2011) – particularly these assemblages that were sown to be intentionally variable – producing a temporary pattern of initial functional divergence that reflects sowing treatments. If this pattern of divergence represents transient alternative states, plots would be expected to eventually converge in species occupancy as well as in abundance-weighted functional and phylogenetic composition with sufficient dispersal, and would thus demonstrate assembly to be only temporarily historically-contingent and overall strongly deterministic in the long-term.

It is also significant to note that that, despite eight years of data, the conclusions from this experiment are possibly premature; the patterns of community assembly still have the capacity to change substantially over the course of decades, and this highlights the importance of maintaining long-term community assembly experiments. The results from these experiments are important not only to grassland communities, but also apply to many other communities – microbial communities in the human gut, for instance, which may have substantial health implications. Furthermore, the necessity of understanding these processes is becoming more urgent in the face of global climate change and its increasing impacts on natural communities, and is compounded by the continual devastation of high-

integrity ecosystems. By improving our knowledge of the processes that drive community assembly, it may improve our ability to cope – in terms of maintaining biodiversity, agriculture, and crucial ecosystem functions – with a rapidly, irreversibly changing world.

FIGURES

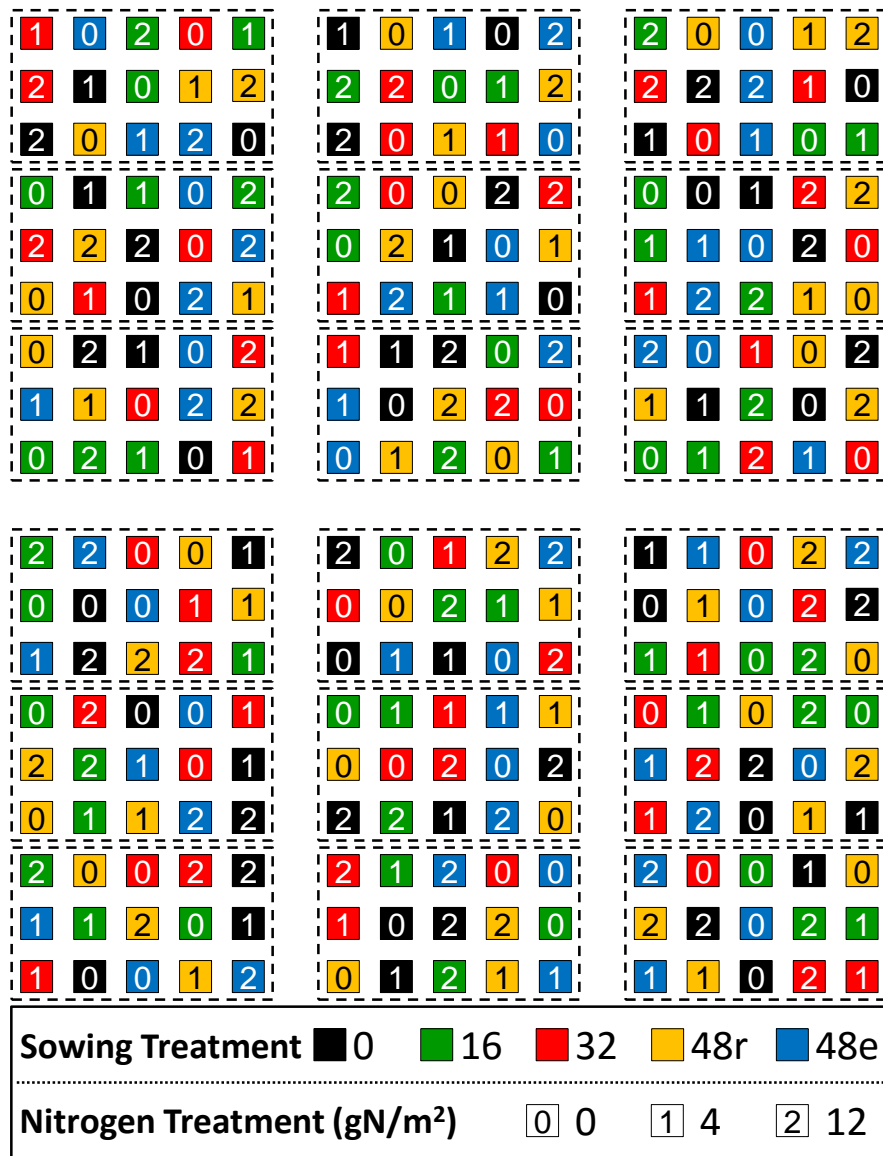


Figure 1: Experimental layout. Dotted lines separate blocks. Colors of plots indicate sowing treatment; numbers indicate fertilizer treatment.

Species	Species Code	Leaf N	SLA	N Fix.	N Photo. Path.	Veg. Height	Seed Mass	Life Hist.	Growth Habit	Floral Initiation	Floral Senescence
Achillea millefolium	Achmil	26.522	17.971	0	0	0.397	0.163	3	forb/herb	5	6
Agrostis hyemalis	Agrhye	18.429	13.315	0	0	0.539	0.055	3	graminoid	4	7
Amorpha canescens	Amocan	24.980	16.149	1	0	0.797	1.936	3	woody	5	8
Andropogon gerardii	Andger	11.557	19.439	0	1	1.201	2.348	3	graminoid	7	10
Astragalus canadensis	Astcan	39.451	17.586	1	0	0.489	1.812	3	forb/herb	5	8
Bouteloua curtipendula	Boucur	17.312	17.064	0	1	0.505	1.570	3	graminoid	6	8
Bouteloua gracilis	Bougra	18.074	17.433	0	1	0.283	0.396	3	graminoid	6	8
Bromus inermis	Broine	20.631	20.326	0	0	0.790	2.815	3	graminoid	5	7
Chamaecrista fasciculata	Chafas	14.580	9.125	1	0	0.556	8.501	1	forb/herb	5	10
Coreopsis lanceolata	Corlan	35.683	31.120	0	0	0.605	1.242	3	forb/herb	3	7
Coreopsis palmata	Corpal	20.835	12.560	0	0	0.499	1.989	3	forb/herb	6	7
Coreopsis tinctoria	Cortin	14.703	14.400	0	0	0.552	0.252	2	forb/herb	6	9
Dactylis glomerata	Dacglo	24.933	25.244	0	0	0.583	0.852	3	graminoid	5	10
Dalea candida	Dalcan	16.200	10.760	1	0	0.466	2.014	3	forb/herb	5	8
Dalea purpurea	Dalpur	24.300	12.653	1	0	0.542	2.456	3	forb/herb	5	8
Desmanthus illinoensis	Desill	24.500	20.608	1	0	0.898	5.865	3	forb/herb	6	8
Dracopis amplexicaulis	Draamp	30.878	18.657	0	0	0.610	0.283	1	forb/herb	5	7
Echinacea purpurea	Echpur	15.931	10.035	0	0	0.633	2.919	3	forb/herb	6	8
Elymus canadensis	Elycan	32.940	20.683	0	0	1.166	3.921	3	graminoid	6	8
Eryngium yuccifolium	Eryyuc	8.400	6.714	0	0	0.430	3.270	3	forb/herb	6	9
Helianthus maximiliani	Helmax	16.700	11.193	0	0	1.524	2.001	3	forb/herb	7	9

Table 1: List of sown species and respective trait values. Interpolated data in italics. Details are as follows:

Leaf N: mg nitrogen per gram of dry plant tissue (continuous variable); **SLA:** specific leaf area, mm² per mg of dry leaf tissue (continuous variable); **N Fix:** nitrogen fixation ability (0 = not able; 1 = able) (asymmetrical binary variable); **Photo. Path:** photosynthetic pathway (0 = C3; 1 = C4) (binary variable); **Veg Height:** maximum vegetative height in meters (continuous variable); **Seed Mass:** mean mass of a single seed in mg (continuous variable); **Life Hist.:** life history of plant (1 = annual; 2 = biennial or variable annual/short-lived perennial; 3 = perennial) (ordinal categorical variable); **Growth Habit:** (categorical variable); **Floral Initiation:** initiation of floral blooming, number indicates month (1 = January, 2 = February, etc.) (ordinal categorical variable); **Floral Senescence:** final month of floral blooming (ordinal categorical variable).

Species	Species Code	Leaf N	SLA	N Fix.	N Path.	Veg. Height	Seed Mass	Life Hist.	Growth Habit	Floral Initiation	Floral Senescence
<i>Heliopsis helianthoides</i>	Helhel	25.700	21.527	0	0	1.282	4.462	3	forb/herb	7	10
<i>Koeleria macrantha</i>	Koemac	17.406	13.220	0	0	0.203	0.286	3	graminoid	5	8
<i>Lespedeza capitata</i>	Lescap	24.096	16.154	1	0	1.026	2.783	3	forb/herb	6	8
<i>Medicago sativa</i>	Medsat	44.466	19.824	1	0	0.675	2.266	3	forb/herb	5	9
<i>Melilotus officinalis</i>	Meloff	34.800	19.375	1	0	1.300	2.676	1	forb/herb	5	10
<i>Monarda fistulosa</i>	Monfis	18.367	20.933	0	0	0.939	0.355	3	forb/herb	6	8
<i>Oenothera macrocarpa</i>	Oenmac	17.010	11.700	0	0	0.600	4.512	3	forb/herb	5	7
<i>Panicum virgatum</i>	Panvir	15.082	23.563	0	1	1.023	1.105	3	graminoid	7	9
<i>Penstemon digitalis</i>	Pendig	16.000	9.840	0	0	1.219	1.132	3	forb/herb	4	7
<i>Phleum pratense</i>	Phlpra	19.278	22.918	0	0	0.616	0.409	3	graminoid	5	8
<i>Poa pratensis</i>	Poapra	21.084	19.640	0	0	0.363	0.267	3	graminoid	5	8
<i>Ratibida columifera</i>	Ratcol	21.000	16.081	0	0	0.945	0.818	3	forb/herb	6	9
<i>Ratibida pinnata</i>	Ratpin	8.600	15.236	0	0	0.924	0.681	3	forb/herb	6	9
<i>Rudbeckia hirta</i>	Rudhir	31.131	19.815	0	0	0.587	0.793	2	forb/herb	5	9
<i>Salvia azurea</i>	Salazu	16.200	10.850	0	0	0.914	2.777	3	forb/herb	7	10
<i>Schedonorus arundinaceus</i>	Scharu	25.733	17.738	0	0	0.698	2.329	3	graminoid	5	10
<i>Schizachyrium scoparium</i>	Schsco	13.020	20.944	0	1	0.732	1.484	3	graminoid	7	10
<i>Silphium laciniatum</i>	Sillac	22.000	3.885	0	0	0.502	56.907	3	forb/herb	6	9
<i>Solidago rigida</i>	Solrid	11.975	11.612	0	0	1.205	0.542	3	forb/herb	8	10
<i>Sorghastrum nutans</i>	Sornut	13.780	17.000	0	1	1.454	1.759	3	graminoid	8	10
<i>Symphotrichum novae-angliae</i>	Symnov	24.100	23.328	0	0	0.911	0.487	3	forb/herb	9	10
<i>Trifolium pratense</i>	Tripra	40.119	23.532	1	0	0.412	1.579	3	forb/herb	5	9
<i>Trifolium repens</i>	Trirep	41.934	28.588	1	0	0.190	0.549	3	forb/herb	5	10
<i>Tripsacum dactyloides</i>	Tridac	19.200	14.100	0	1	1.524	63.116	3	graminoid	5	10
<i>Verbena hastata</i>	Verhas	23.084	18.030	0	0	0.971	0.217	3	forb/herb	6	10
<i>Verbena stricta</i>	Verstr	10.600	13.783	0	0	0.822	1.010	3	forb/herb	5	9

Table 1: continued

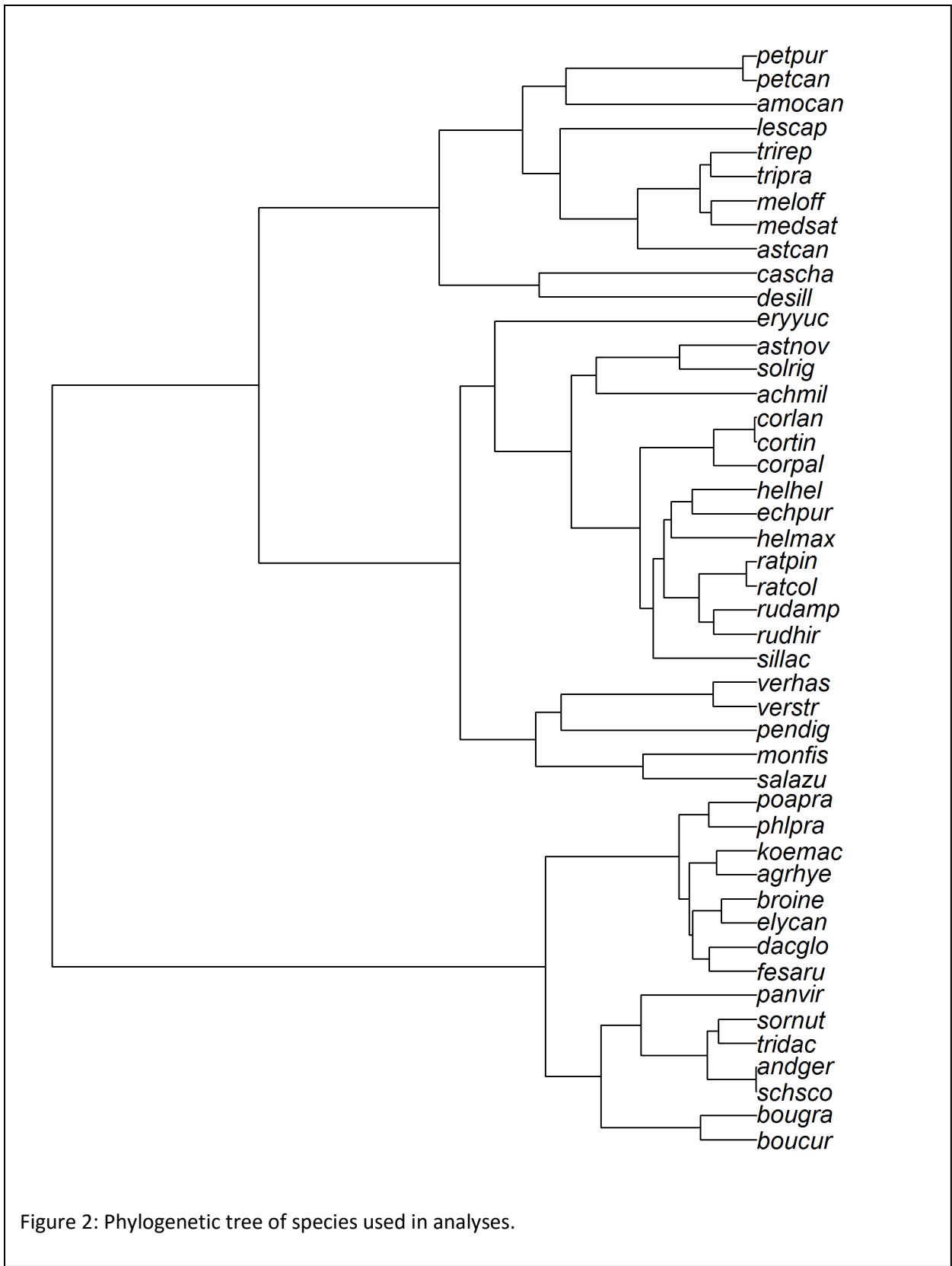
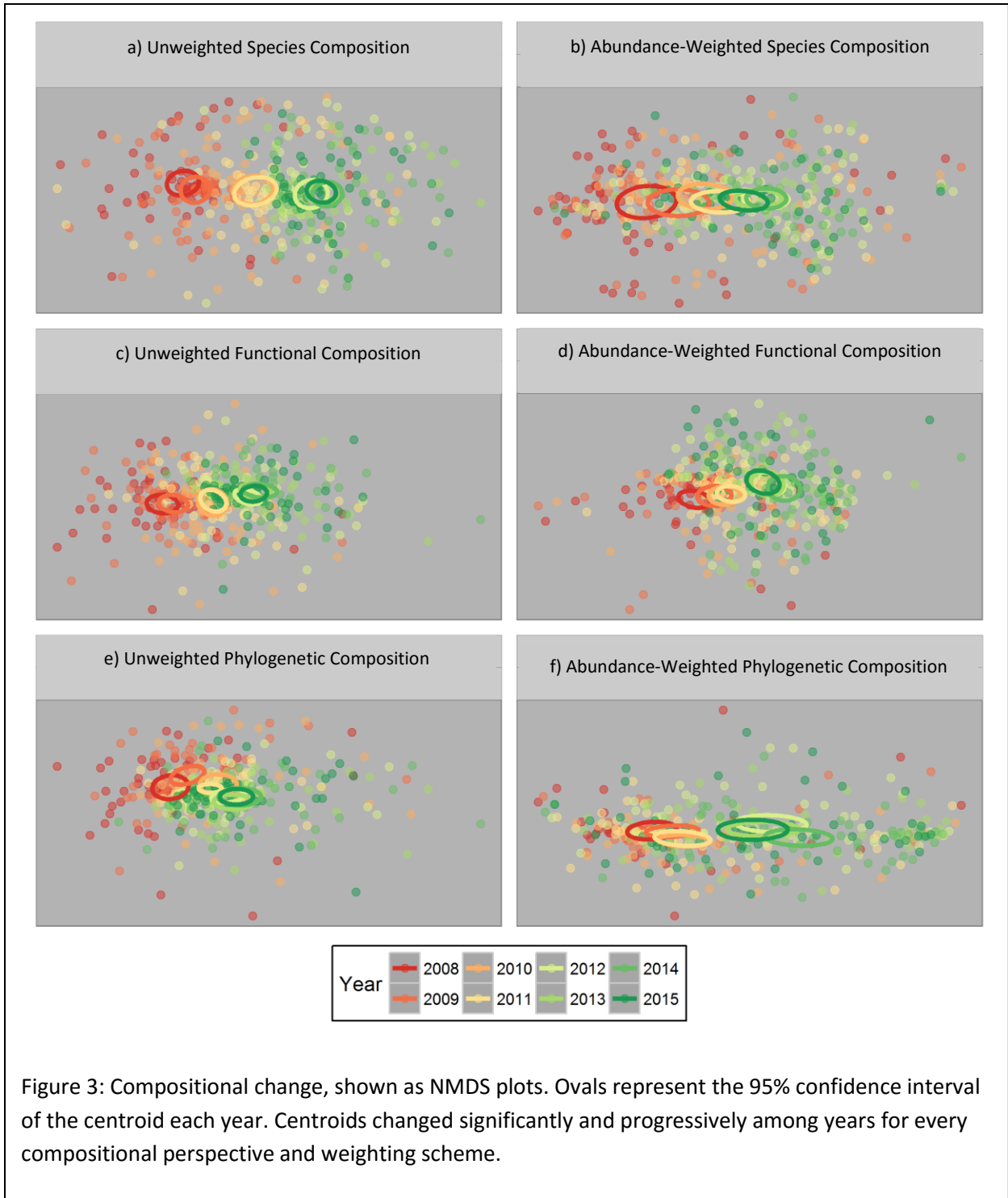


Figure 2: Phylogenetic tree of species used in analyses.



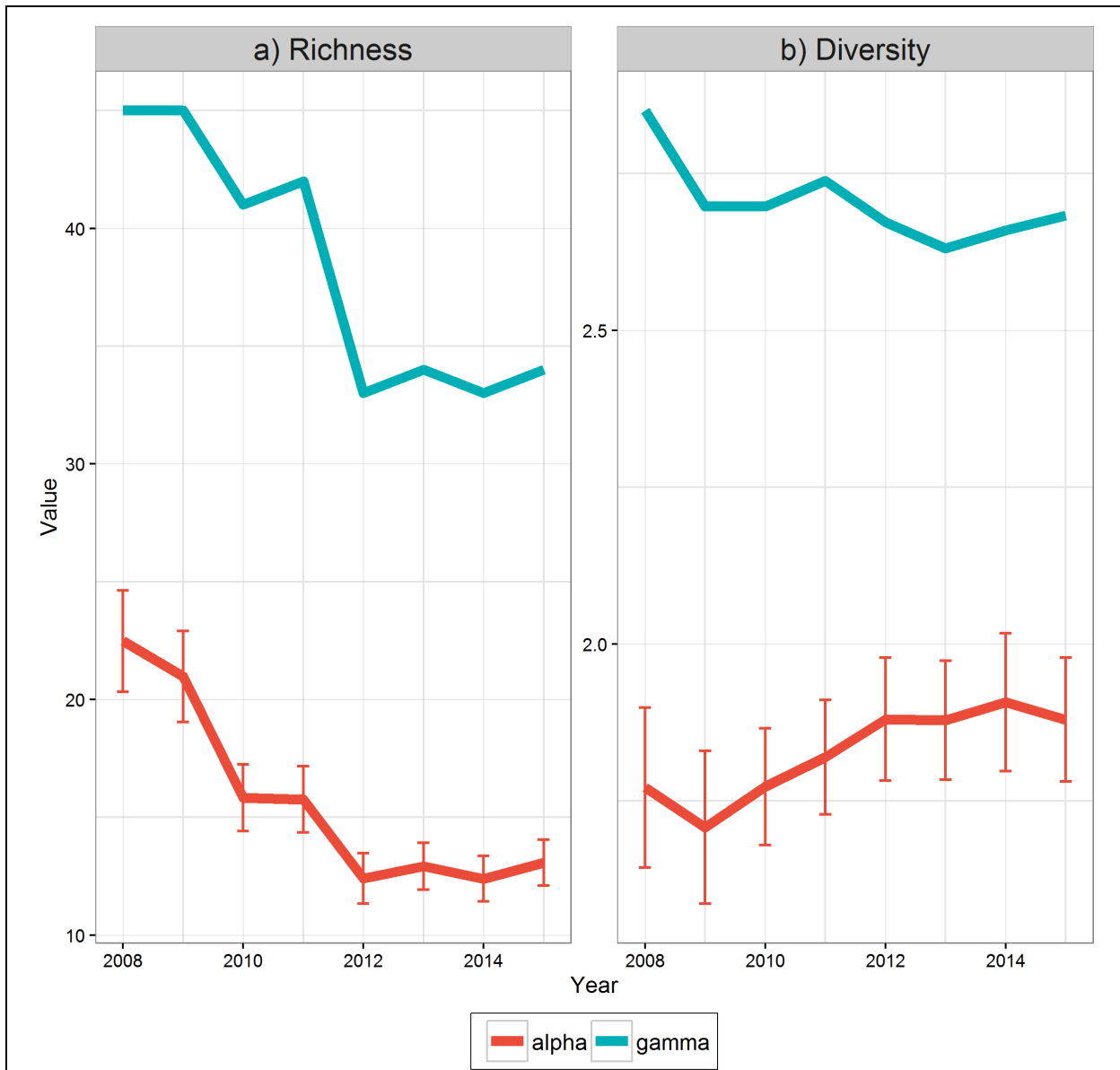


Figure 4: Species gamma and mean alpha (a) richness and (b) diversity. Error bars are 95% confidence intervals. Mean alpha richness decreased significantly over time (repeated measures ANOVA: $F = 114.5$, $p < 0.001$) and the decline was significantly and negatively correlated with time ($r = -0.888$, $p < 0.005$). The decline of gamma richness was also significantly and negatively correlated with time ($r = -0.902$, $p < 0.005$). Mean alpha diversity increased significantly over time (repeated measures ANOVA: $F = 6.242$, $p < 0.001$) and this increase was significantly and positively correlated with time ($r = 0.879$, $p < 0.005$). The decline of gamma diversity was significantly and negatively correlated with time ($r = -0.708$, $p < 0.05$)

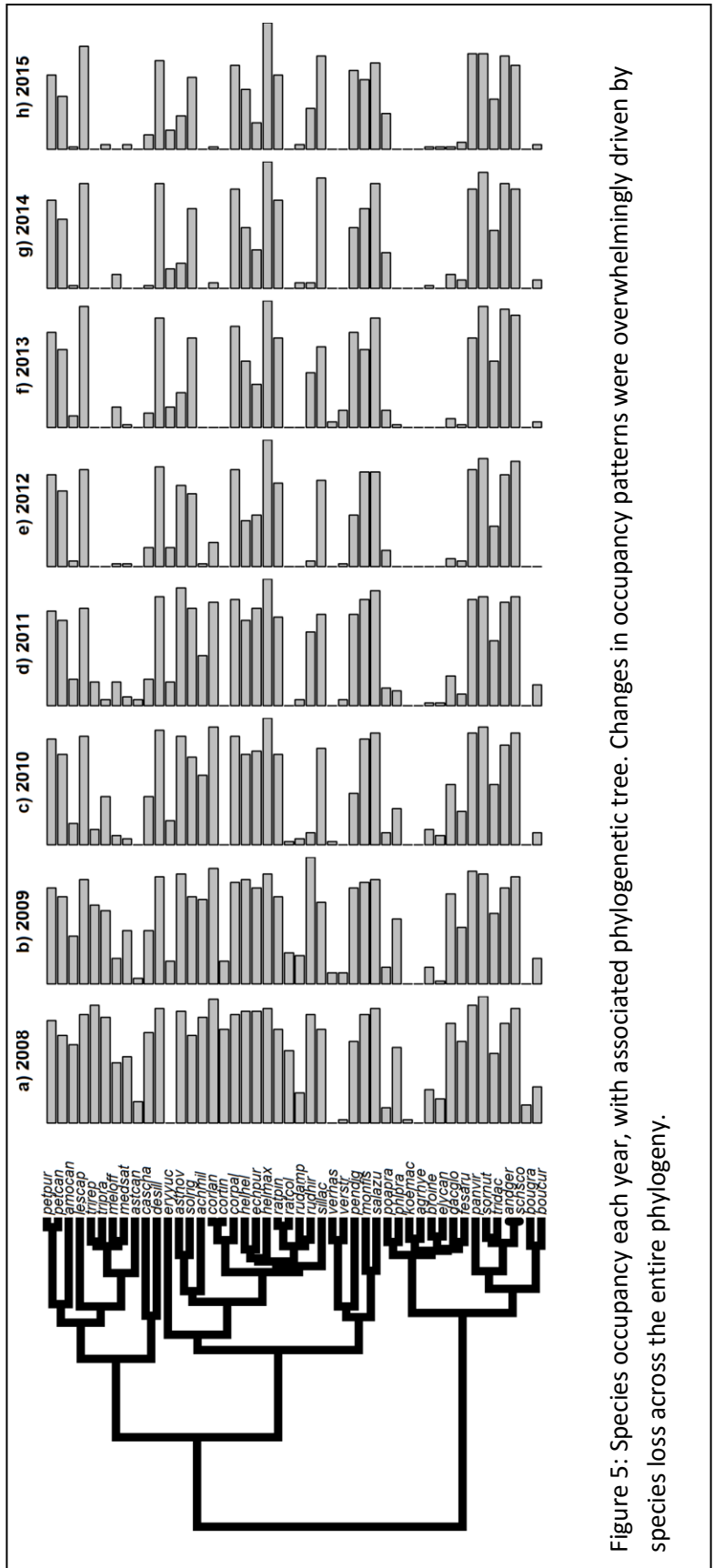


Figure 5: Species occupancy each year, with associated phylogenetic tree. Changes in occupancy patterns were overwhelmingly driven by species loss across the entire phylogeny.

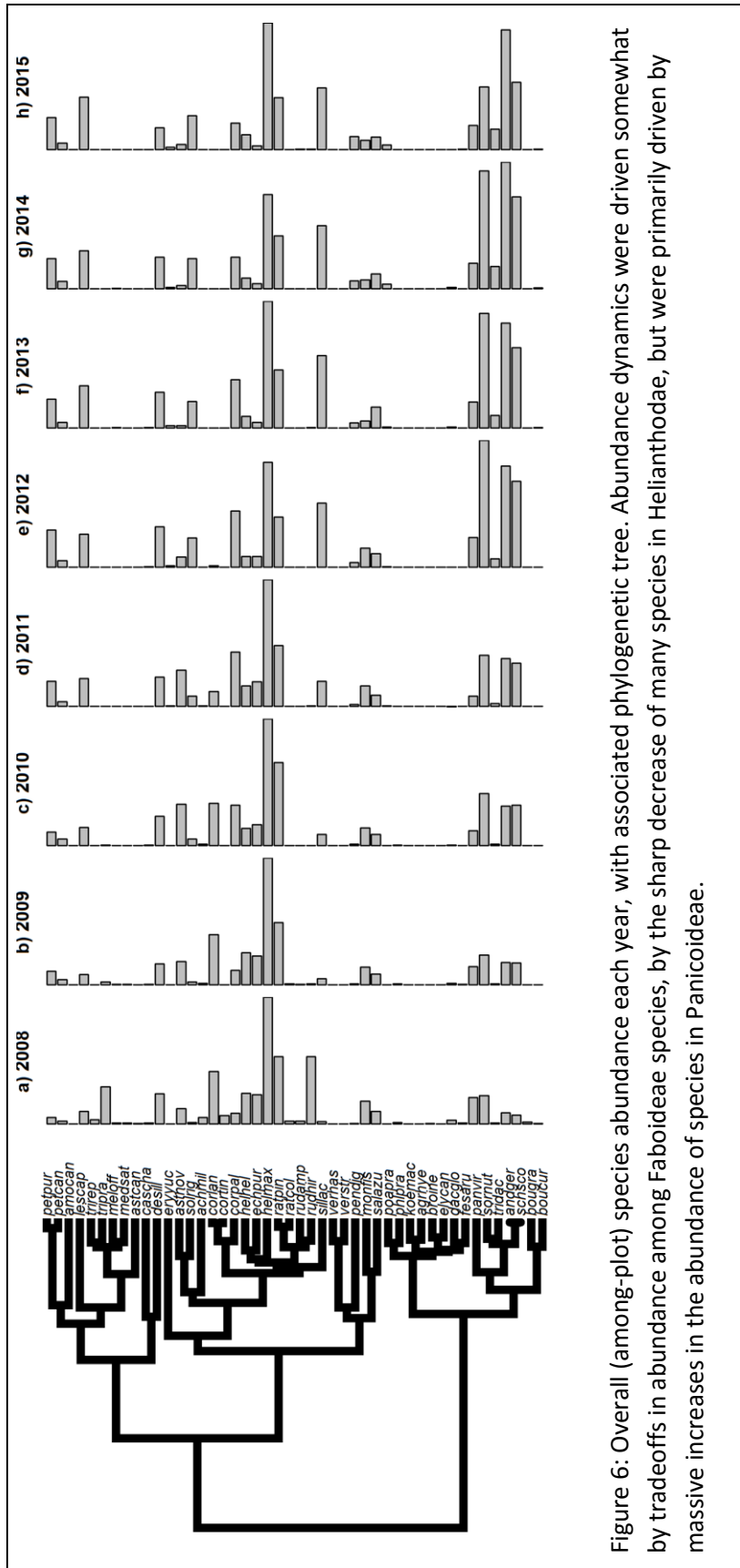
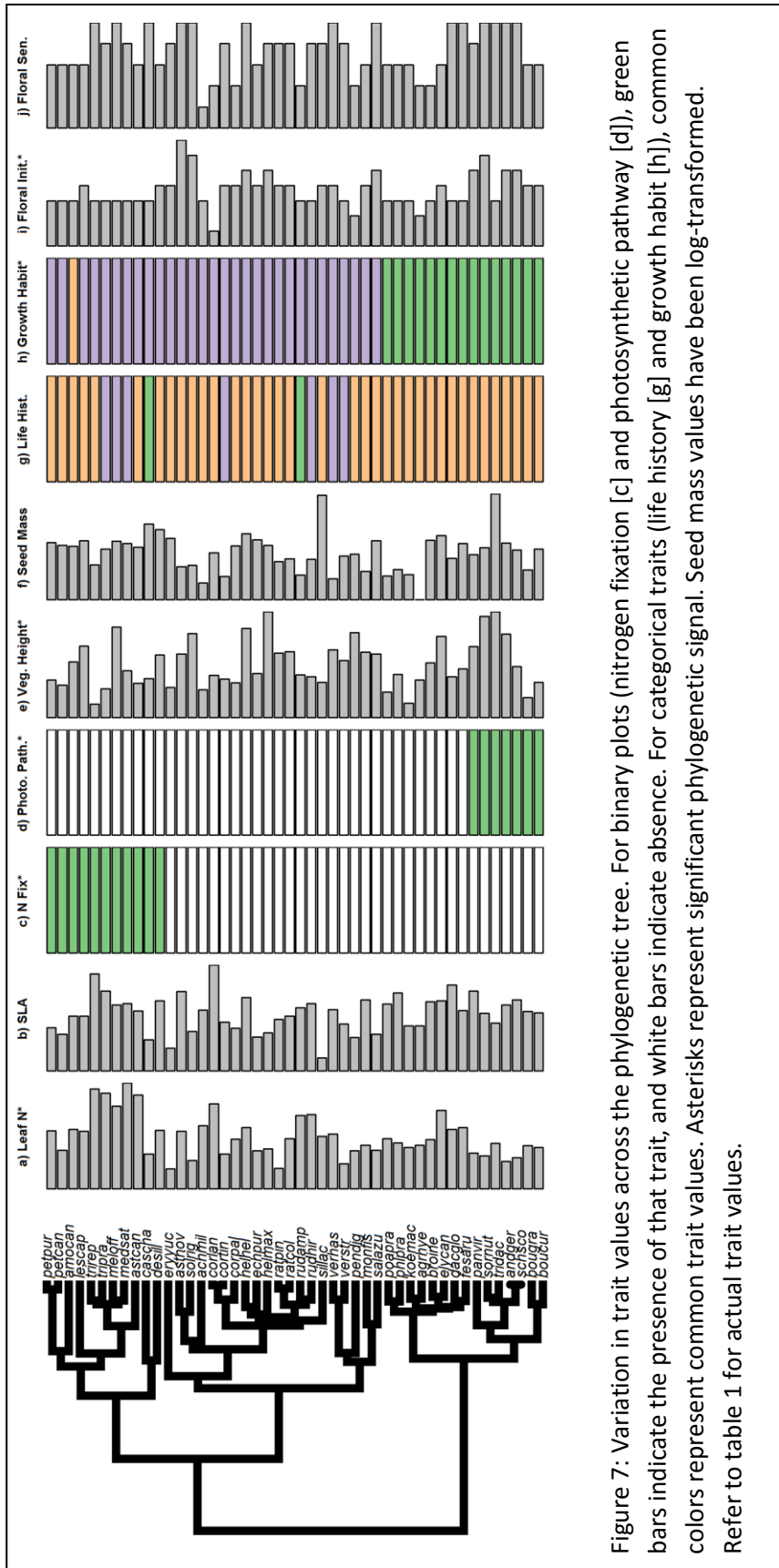


Figure 6: Overall (among-plot) species abundance each year, with associated phylogenetic tree. Abundance dynamics were driven somewhat by tradeoffs in abundance among Faboideae species, by the sharp decrease of many species in Helianthodae, but were primarily driven by massive increases in the abundance of species in Panicoideae.



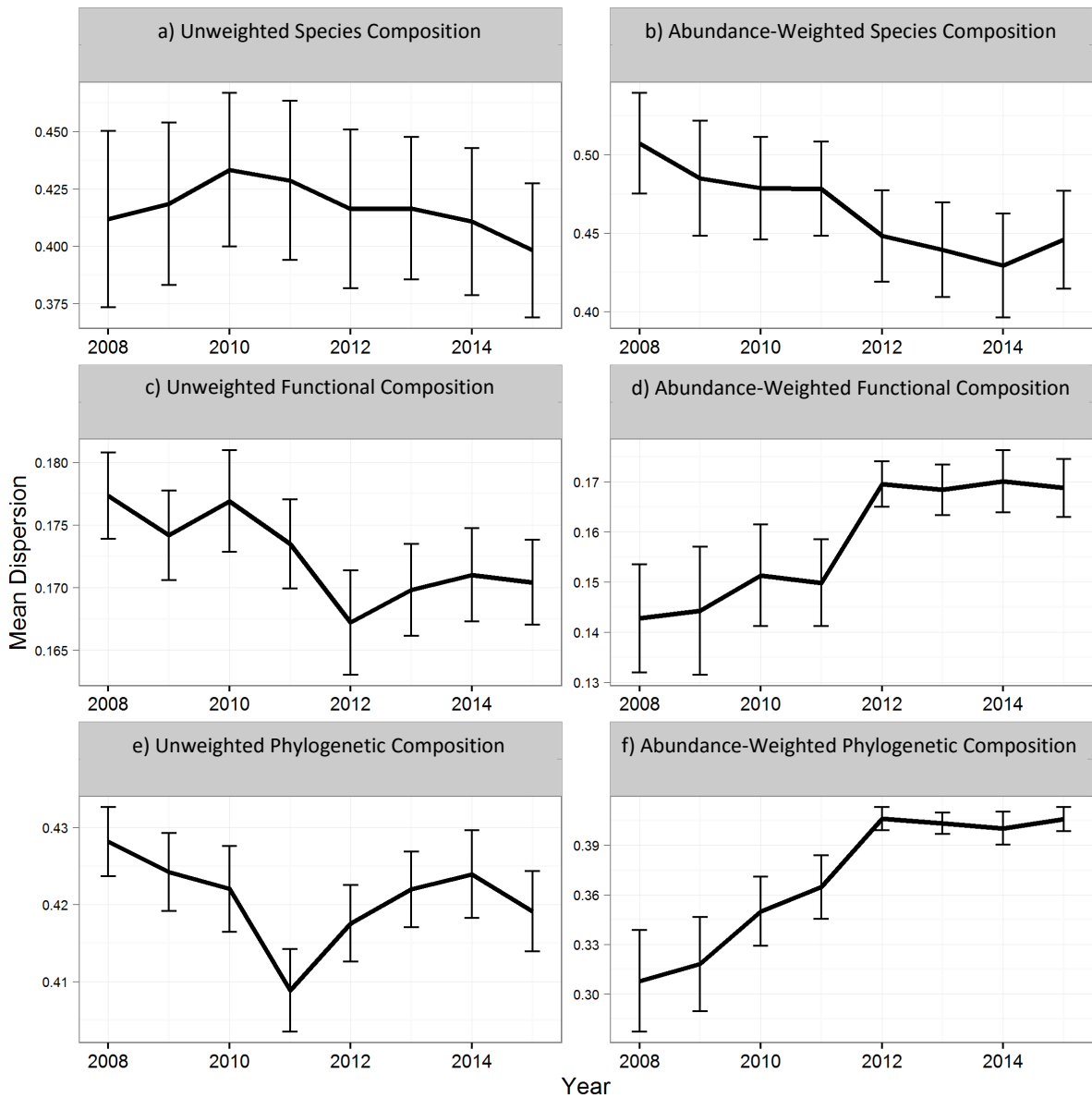
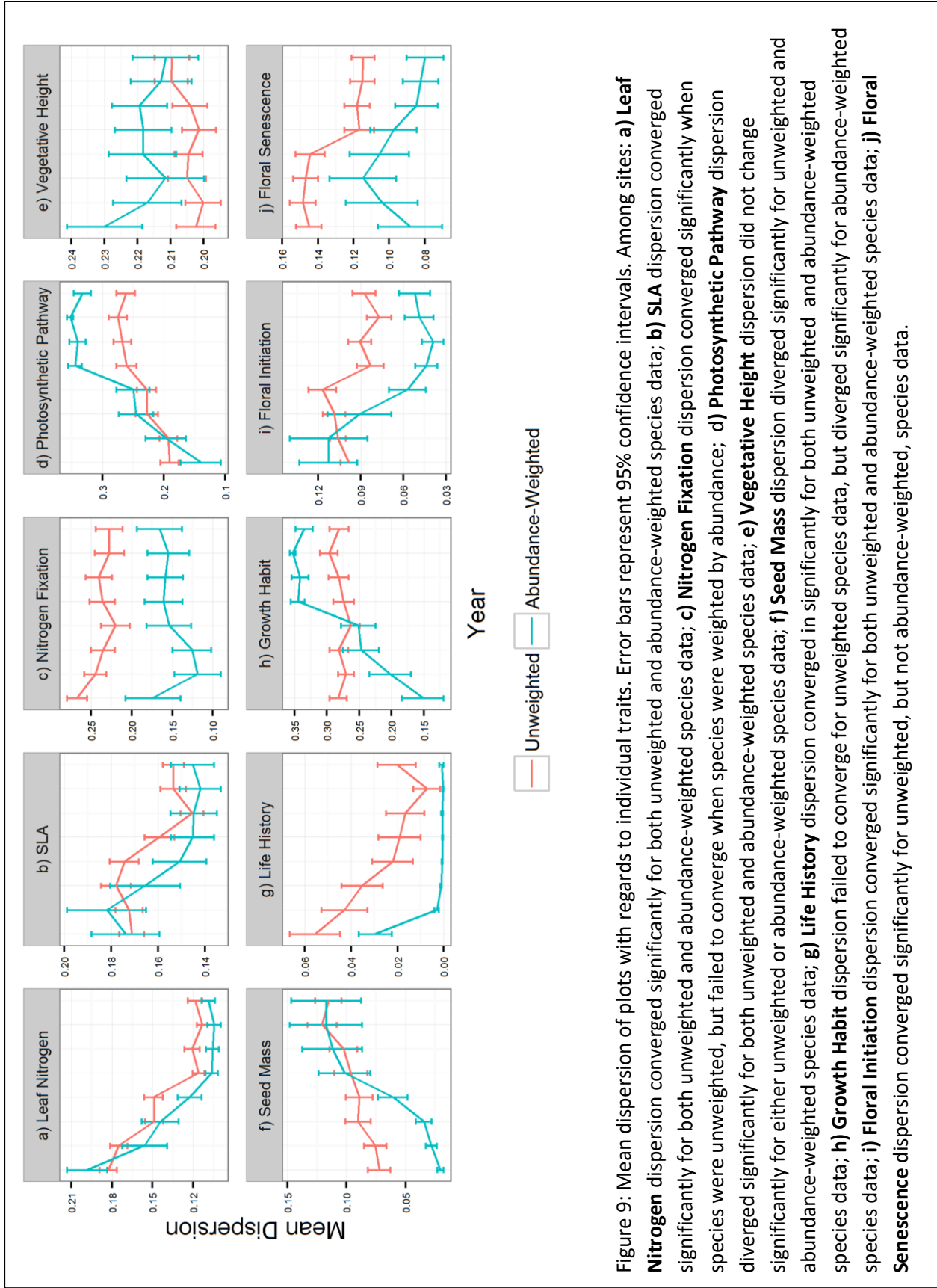


Figure 8: Mean dispersion from centroid among years: with respect to species composition, sites displayed a) no significant change in dispersion when species were not weighted by species abundance ($F = 0.4$, $p > 0.05$), and b) a significant decrease in dispersion when they were weighted by species abundance ($F = 2.76$, $p < 0.01$); with respect to functional composition, sites displayed c) a significant reduction in dispersion when species were unweighted ($F = 3.53$, $p < 0.005$), and d) a significant increase in dispersion when species were weighted by abundance ($F = 7.9$, $p < 0.001$); with respect to phylogenetic composition, sites displayed e) a significant change in dispersion over time ($F = 4.84$, $p < 0.001$), though this primarily reflects the substantial drop in 2011, and f) a significant increase over time when species were weighted by abundance ($F = 18.01$, $p < 0.001$).



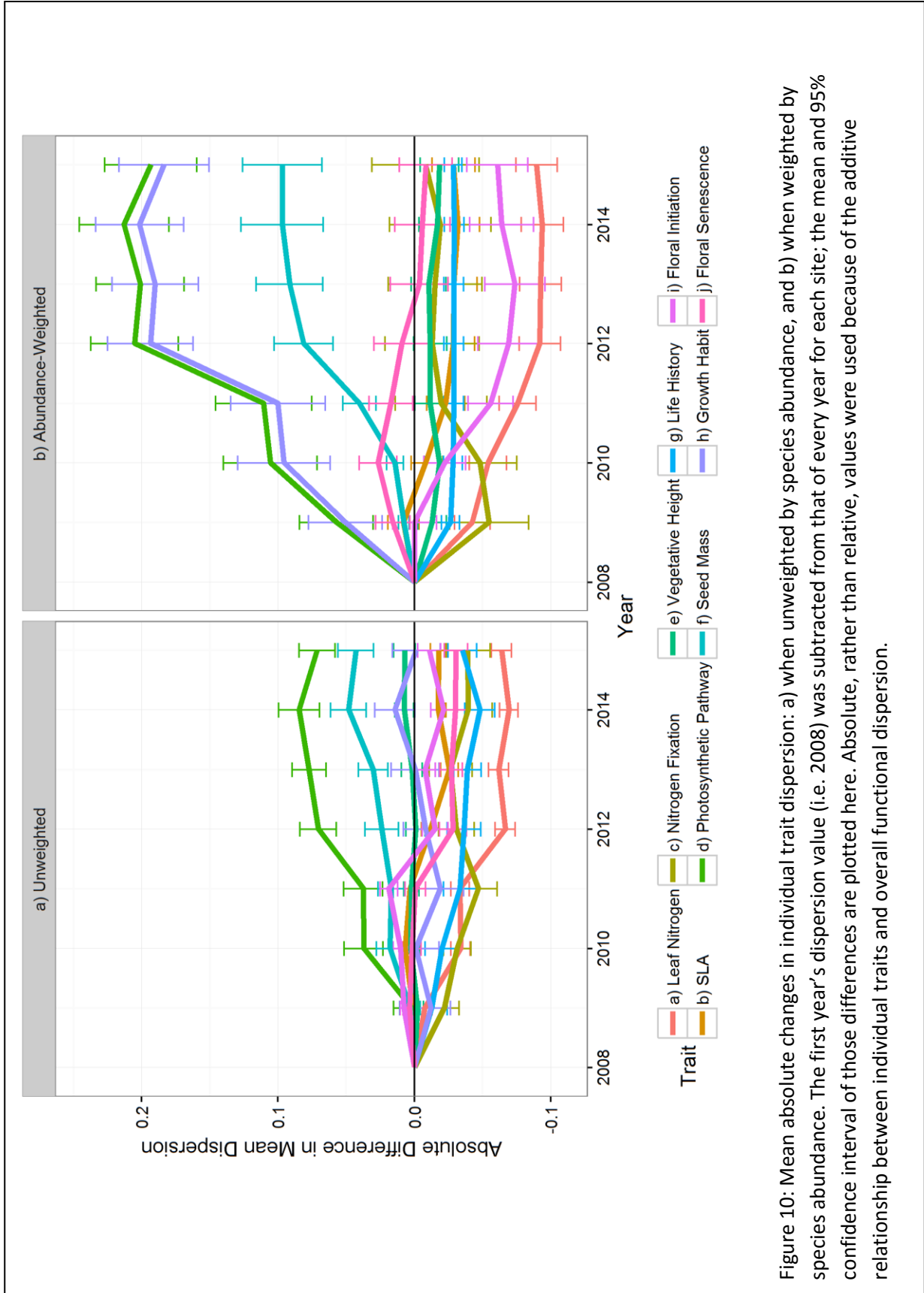


Figure 10: Mean absolute changes in individual trait dispersion: a) when unweighted by species abundance, and b) when weighted by species abundance. The first year's dispersion value (i.e. 2008) was subtracted from that of every year for each site; the mean and 95% confidence interval of those differences are plotted here. Absolute, rather than relative, values were used because of the additive relationship between individual traits and overall functional dispersion.

Trait	Weighting	β -Diversity	Trait Direction	CWM 2008	CWM 2015
Leaf Nitrogen	Unweighted	Converged	Decrease	22.14	18.28
	Abundance	Converged	Decrease	21.7	16.45
SLA	Unweighted	Converged	Decrease	17.5	15.31
	Abundance	Converged	Decrease	17.97	15.08
Nitrogen Fixation	Unweighted	Converged	Decrease	25.87%	20.76%
	Abundance	No Change	-	-	-
Photosynthetic Pathway	Unweighted	Diverged	-	-	-
	Abundance	Diverged	-	-	-
Vegetative Height	Unweighted	No Change	-	-	-
	Abundance	No Change	-	-	-
Seed Mass	Unweighted	Diverged	-	-	-
	Abundance	Diverged	-	-	-
Life History	Unweighted	Converged	Longer-lived	84% Perennial 13% Biennial 3% Annual	96% Perennial 3% Biennial 1% Annual
	Abundance	Converged	Longer-lived	82% Perennial 18% Biennial <1% Annual	100% Perennial <1% Biennial <1% Annual
Growth Habit	Unweighted	No Change	-	-	-
	Abundance	Diverged	-	-	-
Floral Initiation	Unweighted	Converged	Later	5.86	6.31
	Abundance	Converged	Later	6.04	6.62
Floral Senescence	Unweighted	Converged	Later	8.79	8.87
	Abundance	No Change	-	-	-

Table 2: Summary of individual trait dynamics among sites. The ' β -Diversity' column refers to the significant convergence, divergence, or insignificant change in dispersion among sites with respect to a given trait. 'Trait Direction' describes, when a given trait significantly converges, the trend in trait values over time (e.g. if sites are converging on a smaller or larger SLA). 'CWM 2008' and 'CWM 2015' list the community-weighted mean values of significantly-converging trait values for comparison (see table 1 for trait units).

LITERATURE CITED

- Abouheif, E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. *Evolutionary Ecology Research* 1:895-909.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245-253.
- Anderson, M. J., Ellingsen, K. E., and McArdle, B. H. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683-693.
- Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Steegen, J. C., and Swenson, N. G. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19-28.
- The Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, 161:105–121.
- Baraloto, C., Hardy, O. J., Paine, C. E. T., Dexter, K. G., Cruaud, C., Dunning, L. T., Gonzalez, M., Molino, J., Sabatier, D., Savolainen, V., and Chave, J. 2012. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology* 100:690-701.
- Beisner, B. E., Haydon, D. T., and Cuddington K. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376-382.

- Belyea, L. R. and Lancaster, J. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402-416.
- Benson, D. A., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J., and Sayers, E. W. 2009. GenBank. *Nucleic Acids Research* 37:D26-D31.
- Bertness, M. and Callaway, R.M. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Blomberg, S. P., Garland, T., and Ives, A. R. 2002. Testing for phylogenetic signal in comparable data: behavioral traits are more labile. *Evolution* 57:717-745.
- Bruneau, A., Mercure, M., Lewis, G. P., and Herendeen, P. S. 2008. Phylogenetic patterns and diversification in the caesalpinoid legumes. *Botany* 86: 697–718
- Cadotte, M., Albert, C. H., and Walker, S. C. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters* 16:1234-1244.
- Cardoso, D., Pennington, R. T., de Queiroz, L. P., Boatwright, J. S., Van Wykd, B-E., Wojciechowskie, M. F, and Lavin, M. 2013. Reconstructing the deep-branching relationships of the papilionoid legumes. *South African Journal of Botany* 89:58–75
- Caruso, T., Chan, Y., Lacap, D. C., Lau, M. C. Y., McKay, C. P., and Pointing, S. B. 2011. Stochastic and deterministic processes interact in the assembly of desert microbial communities on a global scale. *ISME* 5:1406-1413.
- Cavender-Bares, J., Ackerly, D.D., Baum, D. A., and Bazzaz, F. A. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163:823-843.
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., and Kembel, S. W. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12:693-715.

- Chase, J. M. 2003. Community assembly: when should history matter? *Oecologia* 136:289-298.
- Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328:1388-1391.
- Clements, F. E. 1916. *Plant Succession: Analysis of the Development of Vegetation*. Publication no. 242. Carnegie Institution of Washington, Washington, DC.
- Cooper, N. and Purvis, A. 2010. Body size evolution in mammals: complexity in tempo and mode. *American Naturalist* 175:727-738.
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchman, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., and Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335-380.
- D'Antonio, C. M. and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray, pp 169.
- Diamond, J. M. 1975. Assembly of species communities. In: *Ecology and Evolution of Communities*, eds Cody, M. L. & Diamond, J. M. Harvard University Press, Cambridge, MA 342-444.
- Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny,

- L. Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M. R. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15:295-304.
- Drake, J. A. 1990. The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147:213-233.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137:1-26.
- Drummond A. J., Suchard M. A., Xie D and Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7 *Molecular Biology And Evolution* 29: 1969-1973.
- Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32:1792-1797.
- Fox, B. J. 1987. Species assembly and the evolution of community structure. *Evolutionary Ecology* 1:201-213.
- Fukami, T. 2010. Community assembly dynamics in space. In: *Community Ecology: Processes, Models, and Applications*. (eds Verhoef, H. A. & Morin, P. J.). Oxford University Press, Oxford, pp. 45-54.
- Fukami, T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1-23.
- Fukami, T. and Nakajima, M. 2011. Community assembly: alternative stable states or alternative transient states? *Ecology Letters* 14:973-984

- Fukami, T. and Nakajima, M. 2013. Complex plant-soil interactions enhance plant species diversity by delaying community convergence. *Ecology* 101:316-324.
- Fukami, T., Bezemer, T. M., Mortimer, S. R., and van der Putten, W. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8:1283-1290.
- Gleason, H. A. 1927. Further views on the succession-concept. *Ecology* 8:299-326.
- Gower, J. C. 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27:857-871.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Journal of Ecology* 61:344-347.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Ecology* 79:902-910.
- Grime, J.P. 2007. Plant strategy theories: a comment on Craine (2005). *Ecology* 88:227-230.
- Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, G. A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. L., Davison, A. W., Gupta, P. L., Hall, W., Hand, D. W., Hannah, M. A., Hillier, S. H., Hodgkinson, D. J., Jalili, A., Liu, Z., Mackey, J. M. L., Matthews, N., Mowforth, M. A., Neal, A. M., Reader, R. J., Reiling, K., Ross-Fraser, W., Spencer, R. E., Sutton, F., Tasker, D. E., Thorpe, P. C., and Whitehouse, J. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79:259-281.
- Guo, H., Więski, K., Lan, Z., and Pennings, S. C. 2013. Relative influence of deterministic processes on structuring march plant communities varies across an abiotic gradient. *Oikos* 123:173-178.
- Harmon, L. J., Losos, J. B., Davies, T. J., Gillespie, R. G., Gittleman, J. L., Jennings, W. B., Kozak, K. H., McPeck, M. A., Moreno-Roark, F., Near, T. J., Purvis, A., Ricklefs, R. E., Schluter, D., Schulte II, J. A.,

- Seehausen, O., Sidlauskas, B. L., Torres-Carvajal, O., Weir, J. T., and Mooers, A. Ø. 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64:2385-2396.
- Helsen, K., Hermy, M., and Honnay, O. 2012. Trait but not species convergence during plant community assembly in restored semi-natural grasslands. *Oikos* 121:2121-2130.
- Holt, R. D. and Polis, G. A. 1997. A theoretical framework for intraguild predation. *The American Naturalist* 149:745-764.
- Hsiao, C., Chatterton, N. J., Asay, K. H., and Jensen, K. B. 1995. Phylogenetic relationships of the monogenomic species of the wheat tribe, Triticeae (Poaceae), inferred from nuclear rDNA (internal transcribed spacer) sequences. *Genome* 38:211-223.
- Hubbell, S. P. 2001. *The Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ, USA.
- Hurt, G. C. and Pacala, S. W. 1995. The consequences of recruitment limitation: reconciling chance, history, and competitive differences between plants. *Journal of Theoretical Biology* 176:1-12.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415-427.
- Jombart, J. and Dray, S. 2008. adephylo : exploratory analyses for the phylogenetic comparative method.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology*, 88:2427-2439.
- Kadereit, J.W. and Jeffrey, C. 2007. *The Families and Genera of Vascular Plants, Flowering Plants, Eudicots, Asterales*, vol. 8, Springer, Berlin.

Kardol, P., Van der Wal, A., Bezemer, T. M., de Boer, W., Duyts, H., Holtkamp, R., and Van der Putten, W. H. 2008. Restoration of species-rich grasslands on ex-arable land: seed addition outweighs soil fertility reduction. *Biological Conservation* 141: 2208-2217.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., v. Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C., Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., Chapin, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R. V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C., Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B., Messier, J., Moles, A. T., Müller, S. C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W. A., Patiño, S., Paula, S., Pausas, J. G., Peñuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E., Wirth, C.. 2011. TRY – a global database of plant traits. *Global Change Biology*, 17:2905–2935.

- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., and Webb, C. O. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463-1464.
- Kingman, J. F. C. 1982. The coalescent. *Stochastic Processes and their Applications* 13:235-248.
- Knowlton, N. 2004. Multiple "stable" states and the conservation of marine ecosystems. *Progress in Oceanography* 60:387-396.
- Kraft, N. J. B., Valencia, R., & Ackerly, D. D. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580-582.
- Laliberté, E. & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305.
- Law, R. 1999. Theoretical aspects of community assembly. In: *Advanced Ecological Theory*, ed McGlade, J. Blackwell, Oxford 143-171.
- Law, R. & Morton, R. D. 1993. Alternative permanent states of ecological communities. *Ecology* 74:1347-1361.
- Lewontin, R. C. 1969. The meaning of stability. *Brookhaven Symposia in Biology* 22:13-24.
- Lord, J., Westoby, M. and Leishman, M. 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. *American Naturalist* 146:349-364.
- Luh, H. -K. & Pimm, S. L. 1993. The assembly of ecological communities: a minimalist approach. *Journal of Animal Ecology* 62:749-765.

- MacArthur, R. & Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101:377-385.
- McCordle, B. H. and Anderson, M. J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290-297.
- Morin, P. J. 1999. *Community Ecology*. Blackwell Science, Malden, Massachusetts, USA.
- Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffrers, K., and Thuiller, W. 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* 3:743-756.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. 2015. *Vegan: Community Ecology Package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>.
- Paradis E., Claude J. & Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289-290.
- Pavoine, S., Gasc, A., Bosnall, M. B., and Mason, N. W. H. 2013. Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? *Journal of Vegetative Science* 24:781-793.
- Perry, L. G., Neuhauser, C., & Galatowitsch S. M. 2003. Founder control and coexistence in a simple model of asymmetric competition for light. *Journal of Theoretical Biology* 222:425-436.
- Peterson, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *American Naturalist* 124:127-133.
- Podani, J. 1999. Extending Gower's general coefficient of similarity to ordinal characters. *Taxon* 48:331-340.

- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Robinson, H. 2004. New supertribes Helianthodae and Senecionodae, for the subfamily Asteroideae (Asteraceae). *Phytologia* 86: 116-120.
- Samuels, C. L. & Drake, J. A. 1997. Divergent perspectives on community convergence. *TREE* 12:427-432.
- Sokal, R. R. & Rolf, F. J. 1962. The comparison of dendrograms by objective methods. *Taxon*, 11:33-40
- Soltis, D. E., Soltis, P. S., Endress, P. K., Chase, M. W. 2005. *Phylogeny and Evolution of Angiosperms*. Sinauer, Sunderland, MA.
- Sommer, U. 1991. Convergent succession of phytoplankton in microcosms with different inoculum species composition. *Oecologia* 87:171-179.
- Sonnier, G., Navas, M., Fayolle, A., & Shipley, B. 2012. Quantifying trait selection driving community assembly: a test in herbaceous plant communities under contrasted land use regimes. *Oikos* 121:1103-1111.
- Soreng, R. J., Peterson, P. M., Romaschenko, K., Davidse, G., Zuloaga, F. O., Judziewicz, E. J., Filgueiras, T. S., Davis, J. I., and Morrone, O. 2015. A worldwide phylogenetic classification of the Poaceae - (Gramineae). *Journal of Systematics and Evolution* 53:177-137.
- Stevens, P. F. 2001. Angiosperm Phylogeny Website. Version 12, July 2012. Accessed April 2016.
- Temperton, V. M., Hobbs, R. J., Nuttle, T., & Halle, S. 2004. *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice*. Island Press, Washington D.C., USA.

- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist* 125:827–852.
- Tilman, D., Kiesling, R., Sterner, R., Kilham, S., and Johnson, F. A. 1986. Green, bluegreen, and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon, and nitrogen. *Archiv für Hydrobiologie* 106:473-485.
- Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry, part 1: Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33:2-22.
- Vannette, R. L. & Fukami, T. 2014. Historical contingency in species interactions: towards niche-based predictions. *Ecology Letters* 17:115-124.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. 2002. Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics* 33:475-505.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10:609-620.
- Wen, J. & Zimmer, E. A. 1996. Phylogeny of *Panax* L. (the ginseng genus, Araliaceae): inferences from ITS sequences of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution* 6:167-179.
- Whitaker, R. H. 1960. Vegetation of Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.
- Whitaker, R. H. 1972. Evolution and Measurement of Species Diversity. *Taxon* 21:213-251.
- Wickham, H. *ggplot2: elegant graphics for data analysis*. Springer New York, 2009.

Wilson, J. B. and Stubbs, W. J. 2012. Evidence for assembly rules: limiting similarity within a saltmarsh.
Ecology 100:210-221.