Trait and phylogenetic patterns reveal deterministic community assembly mechanisms on Mount St. Helens

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Abstract Primary plant succession provides an excellent natural experiment to test ecological questions about community assembly following major disturbances. Temporal phylogenetic and functional trait dispersion patterns can give insight into the relative importance of stochastic and deterministic processes, as well as the potential identity of deterministic (biotic vs. abiotic) drivers (e.g. dispersal, growth, nutrient acquisition, and herbivore resistance ability). We used 28 years of plant composition data across four primary succession sites at Mount St. Helens (collected since the 1980 volcanic eruption) to examine phylogenetic dispersion and trait patterns over time. We expected to find more evidence of clustering or random phylogenetic patterns early in succession (where environmental filtering and stochasticity are thought to dominate), with a switch to overdispersion via processes such as niche differentiation later in succession. Contrary to expectations, phylogenetic relatedness and trait dispersion patterns were idiosyncratic. We found evidence of deterministic community assembly even early in succession, suggesting that both local-scale abiotic filtering and biotic interactions start playing a role shortly after the initiating disturbance. Traits were less predictive of successional patterns, with few consistent changes in trait distribution across all sites, even though the traits we examined are linked to the processes thought to be important during succession. Together, these results suggest that the drivers of community assembly during succession may be less generalizable and more complex than previously thought. We suggest that combining experiments and these analytical tools with long-term monitoring could be a useful step forward.

Keywords Competition · Environmental filtering · Facilitation · Herbivory · Plant succession · Plant functional trait · Primary succession · Sub-alpine

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Introduction

Understanding how species assemble following disturbance events persists as a central question in ecology (Diamond 1975; Weiher and Keddy 1995). Species traits, environmental factors, and stochastic events are all assumed to interact and influence successional trajectories (Ackerly and Cornwell 2007; Connell and Slatyer 1977). For example,

Table 1 Hypothesized functional trait dispersion patterns during succession (see Fig. 1 for hypothetical examples) and actual patterns documented at all four sites

	Trait	Hypothesis	Abraham plains	Studebaker ridge	Pumice plain	Lahar
Dispersal	Seed weight	Clustered	*Clustered*	*Clustered*	Clustered to overdispersed	*Overdispersed*
Stress tolerance and competitive ability	Height	Clustered	More clustered	*Clustered*	Less clustered	More clustered
	SLA	Clustered	*Overdispersed*	*Clustered*	*Clustered*	More clustered
Nutrient acquisition	Leaf % N	Overdispersed	*Clustered*	More clustered	Less clustered	*Clustered*
	Leaf % P	Overdispersed	*Overdispersed*	Overdispersed to clustered	Overdispersed to clustered	*Overdispersed*
	N:P	Overdispersed	*Clustered*	Overdispersed to clustered	*Clustered*	*Overdispersed*
Herbivore resistance	Leaf thickness	Overdispersed	*Overdispersed*	Clustered to overdispersed	Clustered	*Overdispersed*
	C:N	Overdispersed	*Overdispersed*	*Clustered*	*Overdispersed*	*Overdispersed*
	C:P	Overdispersed	More overdispersed	*Clustered*	*Overdispersed*	*Overdispersed*

Italicized indicates non-significant relationship through time ($p > 0.05$)

communities are thought to be strongly structured by dispersal limitation and stochastic processes (e.g. priority effects) early in succession, when seed limitation and chance events dominate recolonization processes. Harsh abiotic conditions may additionally result in strong environmental filtering effects early in succession (Connell and Slatyer 1977; Walker and del Moral 2003), with traits associated with stress tolerance determining species composition (Liancourt et al. 2005). However, these harsh abiotic conditions can also sometimes be ameliorated by facilitation (Brooker et al. 2008; Chapin et al. 1994; Walker and del Moral 2003). By contrast, biotic interactions such as competition and herbivory are thought to become increasingly important as succession progresses, abiotic conditions become less limiting, and communities increase in diversity (Connell and Slatyer 1977).

Modern analytical tools utilizing the phylogenetic and functional traits of species co-occurring in communities have provided a new opportunity to gain insight into potential drivers of community assembly (Cavender-Bares et al. 2009; Coyle et al. 2014; Douma et al. 2012; Fukami et al. 2005; Götzenberger et al. 2012; HilleRisLambers et al. 2012; Spasojevic and Suding 2012), and in particular, provide new synthesis on the multiple mechanisms that drive succession

(Meiners et al. 2014). In these analytical frameworks, phylogenetic relatedness can act as an integrated index of similarity in ecological strategies assuming there is phylogenetic trait conservatism (Cadotte et al. 2013; Kraft et al. 2007; Webb et al. 2002; but see Prinzing et al. 2008), and distributions of specific functional traits (mean distance in multidimensional trait space, sensu Laliberte and Legendre 2010) can reflect the environmental and biotic constraints operating during community assembly (Cadotte et al. 2009; Violle et al. 2007). For example, the harsh, dry, and stressful environments found early in succession can impose a strong environmental filter, resulting in clustered phylogenetic and/or trait distributions (Webb et al. 2002; Weiher and Keddy 1995). If these environmental filters are associated with high wind, cold temperatures and low resources (Walker and del Moral 2003), functional trait diversity in height may decline (Douma et al. 2012; Purschke et al. 2013; Spasojevic and Suding 2012). Biotic interactions are also thought to leave their imprint on phylogenetic and trait distributions, but primarily later in succession (Måren et al. 2018). For example, phylogenetic overdispersion has been linked to facilitation (Butterfield et al. 2013), as well as competition for light and nutrients (e.g. Purschke et al. 2013). The latter is accompanied by a
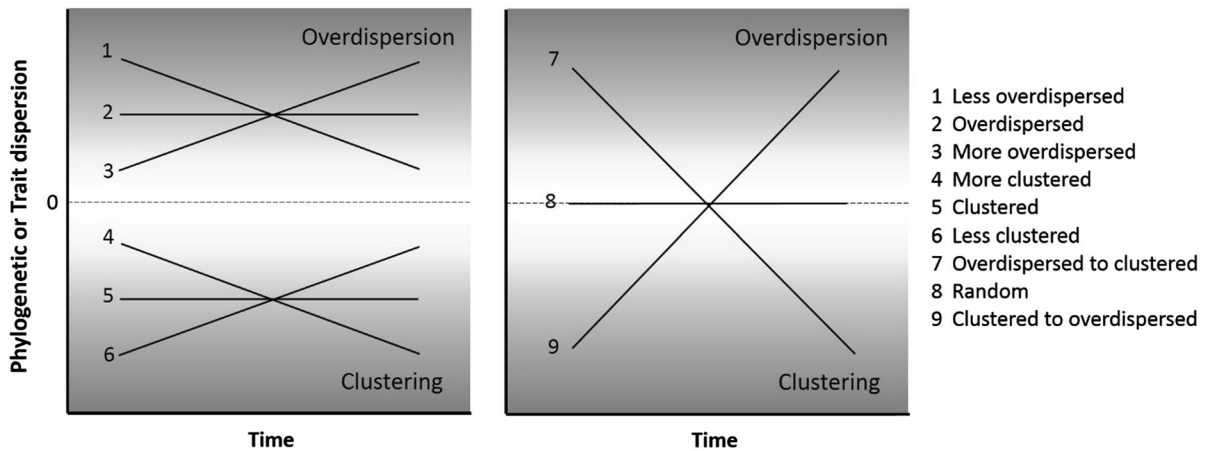
Fig. 1 Conceptualized phylogenetic and trait dispersion patterns through time. Phylogenetic and trait diversity can be overdispersed, random, or clustered compared to null communities. These variations in patterns through time lead to 4 main patterns and hypotheses: (H0) Phylogenetic or trait pattern is *random* (line 8). Neutral forces dictate community assembly patterns. Alternatively, traits important to successional processes may have differing patterns, leading to random patterns. (H1) Phylogenetic or trait pattern is *overdispersed* and *increases* or *decreases* through time (line 1, 2, 3). Biotic interactions such competition, facilitation, or herbivore interactions could play a role. Here, we expect dispersal and stress tolerance/competitive ability traits to be overdispersed during succession (Table 1). (H2) Phylogenetic or trait pattern is *clustered* and *increases* or *decreases* through time (line 4, 5, 6). Environmental filtering or competitive hierarchy leading to greater similarity causes patterns of clustering. Here, we expect nutrient acquisition and herbivore resistance traits to be clustered during succession (Table 1). (H3) Phylogenetic or trait pattern goes from *overdispersed* to *clustered* through time (line 7). Early in succession, there is biotic interactions (e.g. competition, facilitation, herbivory) caused limiting similarity, but over the course of succession, environmental conditions allow only similar species to co-exist. (H4) Phylogenetic or trait pattern goes from *clustered* to *overdispersed* through time (line 9). Plant succession theories suggest this pattern to true where environmental filtering plays a larger role in structuring communities early in succession, but a switch to overdispersion later in succession (Connell and Connell and Slatyer 1977)

wider distribution of nutrient acquisition trait values (Ackerly and Cornwell 2007; Webb et al. 2002) due to niche partitioning and subsequent limiting similarity among species (Cavender-Bares et al. 2004; Macarthur and Levins 1967; Stubbs and Bastow Wilson 2004; Weiher and Keddy 1995). Competitive interactions can also lead to phylogenetic and trait clustering, where only species with similar competitive abilities are able to persist in a given environment (Mayfield and Levine 2010). Random phylogenetic relatedness and trait distribution patterns (e.g. neither clustered nor overdispersed) may be indicative of stochastic controls over successional community composition, or multiple deterministic processes (both overdispersion and clustering mechanisms) that together cancel each other out to produce stochastic patterns (Cadotte et al. 2009; Kraft et al. 2007).

Looking at phylogenetic and trait dispersion patterns together (Fig. 1) can provide unique insight into mechanisms that promote species coexistence (Cadotte et al. 2013; Kraft et al. 2007). If phylogenetic and trait patterns are matched (e.g. phylogenetic overdispersion increasing through time paired with overdispersion of specific leaf area, SLA), it suggests that phylogenetic history influences species ecological function (Webb et al. 2002) and additional tests of phylogenetic conservatism would confirm this relationship (Blomberg et al. 2003). Differences in dispersion patterns suggest that functional diversity may change irrespective of past evolutionary interactions between lineages (Prinzing et al. 2008). Alternatively, if the patterns are mismatched, then either unmeasured underlying traits are phylogenetically conserved and driving dispersion patterns, traits important to community assembly are not phylogenetically conserved (Pavoine et al. 2013), or trade-offs between simultaneously operating traits obscure phylogenetic and multivariate trait patterns (Best et al. 2012; Buckley and Kingsolver 2012; Spasojevic and Suding 2012; Swenson and Enquist 2009).

Understanding the drivers of succession has been complicated both by our general lack of long

Table 2 Summary of patterns of community-weighted means (mean trait weighted by relative abundance of each species) through time as hypothesized and found across all four sites (see Fig. 3, Appendix E, F, G, H, I, J, K, L for non-linear trends through time)

	Trait	Hypothesis	Abraham plains	Studebaker ridge	Pumice plain	Lahar
Dispersal	Seed weight	Increase[1,3,5,6]	Same	Same	Same	Same
Stress tolerance and competitive ability	Height	Increase[1,2,5]	Same	Same	Same	Same
	SLA	Increase[2,4]	Decrease	Same	Decrease	Same
Nutrient acquisition	Leaf % N	Increase[3,4]	Same	Same	Increase	Decrease
	Leaf % P	Decrease[3,4]	Decrease	Same	Decrease	Same
	N:P	Increase[3,4]	Increase	Same	Increase	Decrease
Herbivore resistance	Leaf thickness	Increase[7]	Increase	Same	Same	Same
	C:N	Increase[3,4]	Increase	Increase	Decrease	Increase
	C:P	Increase[3,4]	Increase	Decrease	Increase	Same

List of relevant papers: 1: (Prach et al. 1997) 2: (Kahmen and Poschlod 2004) 3: (Huston and Smith 1987) 4: (Bazzaz 1979) 5: (Walker and del Moral 2003) 6: (Tsuyuzaki and del Moral 1995) 7: (Davidson 1993)

successional time series of species abundances following disturbance, and, until recently, the sophisticated statistical tools necessary to identify the important mechanisms and provide an integrative understanding of the multiple drivers of succession (Meiners et al. 2014). We address these issues by applying phylogenetic and functional trait statistical tools to a 28-year dataset collected from four primary succession sites at Mount St. Helens (MSH, Washington, USA) to infer community assembly mechanisms. We use these tools to explore the relative importance of stochastic versus deterministic processes on primary succession, and then relate phylogenetic history to traits thought to be critical to successional dynamics (e.g. species dispersal, growth, nutrient acquisition, and herbivore resistance) to infer mechanism. While drawbacks to these phenomenological analyses exist (Adler et al. 2013), the large disturbance provided by the eruption of Mount St. Helens, paired with long-term abundance data and extensive trait data, provides a unique opportunity to uncover potential drivers of succession. Our objectives are to determine (1) how phylogenetic and trait diversity patterns change over the course of primary succession, (2) whether functional trait diversity patterns indicate specific successional mechanisms through time, and (3) whether generalities exist in successional patterns among sites.

We expected to find more evidence of clustering or random phylogenetic patterns early in succession (where environmental filtering and stochasticity are thought to dominate), with a switch to overdispersion via processes such as niche differentiation later in succession (Connell and Slatyer 1977, Fig. 1, line 9). To account for potentially interacting processes, we relied on patterns in specific functional trait distributions to aid in uncovering potential mechanisms responsible. For example, if dispersal is a critical process driving successional trends, we expected to find that seed weight is clustered throughout succession (Fig. 1, line 1–3, Table 1), but that lighter seeds are abundant early in succession and species with heavier seeds become abundant as succession progresses (Table 2). We expected that environmental filtering (from harsh alpine winds) would lead to clustering in plant height early in succession, switching to overdispersion over successional time as a complex forest structure develops (Tables 1, 2). Because specific leaf area (SLA) represents a continuum from stress tolerant to resource acquisitive strategies, we expected SLA to be clustered throughout succession, with low SLA species dominating early in succession (when drought stress is high) and high SLA species dominating later in succession (when competitive interactions dominate—Table 2). We expected that traits reflecting nutrient acquisition and herbivore resistance ability traits would become increasingly overdispersed during succession (indicating limiting similarity), as biotic interactions intensify due to the importance of plant–herbivore–

interactions in this system (Apple et al. 2009; Bishop 2002; Fig. 1, line 3, Table 1). Finally, we expected integrated measures of phylogenetic and trait patterns, as well as single trait patterns, to be similar across sites due to the fact that the same major disturbance reset plant communities at all sites to a blank slate.

Methods

Study site and plant community composition data

Our study utilizes long-term data (collected by Roger del Moral) from four primary succession sites in Mount St. Helens, Washington, created after the May 1980 volcanic eruption (del Moral 2010; del Moral and Wood 2012 for site specifics and exact plot locations; see Fuller and del Moral 2003). Abraham Plains is the most isolated site, located on the east side of the mountain and the disturbance reflects damage from the direct blast, mudflows, and secondary pumice deposits. Studebaker Ridge is the second-most isolated site on the northwest side of the mountain, and the disturbance was caused by a searing and soil removal from the initial blast. Pumice Plain is located on the north side of the mountain and represents a blast created disturbance with extensive pumice depositions. Lahar is located on the south side of the mountain and disturbance was created by scouring mudflows. Of all four sites, this site is the least isolated and in closest proximity to intact vegetation (*Abies-Pinus* forest) and seed sources. Sites were sampled at the end of the growing season yearly from 1982 to 2010 (with a few exceptions, see del Moral 2010; del Moral and Wood 2012) and plant species percent abundance was measured for each plot. For each site, we use two datasets (except Studebaker Ridge, which only has the dataset using circular plots). The first dataset is composed of 400 plots (each 1 m^2) in a contiguous area. The second dataset is composed of 24 circular plots (250 m^2 each) sampled using ¼ m^2 quadrats that were arrayed along transects at 50 m intervals (del Moral 2010). To ensure that differences in plot size between the two datasets did not affect analyses, we examined patterns for each type of dataset separately as well as together and found that qualitative results were similar, thus, we present results from analyses of both datasets.

Species richness over time (originally reported in del Moral 1999, 2010; del Moral and Chang 2015; del Moral et al. 2010, 2012; del Moral and Wood 2012; Wood and Del Moral 1987) increases over time across all sites (Appendix A). Average species richness across the sites were Abraham Plains = 9.323, Lahar = 13.888, Pumice Plain = 14.397, Studebaker Ridge = 13.686. Herbaceous plants and mosses dominate across all sites, with a slow increase in woody species over time (del Moral 1999, 2009; del Moral et al. 2010, 2012; Wood and del Moral 1988; Wood and Del Moral 1987).

Phylogenetic analyses

To examine phylogenetic patterns across time, we generated a regional phylogenetic tree separately for each site, comprised of all species (including vascular plants, mosses, and ferns) ever found at the site over the study, using Phylomatic (Webb and Donoghue 2005). Branch lengths were assigned using the BladJ function of the Phylocom software (Wikström et al. 2001). We used separate regional species pool for each site due to large differences in environment, disturbance history, and degree of isolation (see above). Furthermore, these sites are located on different sides of the mountain (northeast, northwest, and south), with different seed sources available for colonization and, therefore, with some but not completely overlapping species composition. Thus, phylogenetic analyses that use separate regional species pool allow us to account for dispersal limitation. However, to verify species pool size did not influence our conclusions (Cavender-Bares et al. 2006; Lessard et al. 2012a, b), we also performed phylogenetic analyses using a single regional tree comprised of all four sites together, representing the entire known species pool for the blast zone on MSH (Appendix B).

We calculated phylogenetic relatedness values in R (R Development Core Team) using the 'Picante' package (Kembel et al. 2009). Each year for every plot, we calculated mean pairwise dissimilarity (MPD) which is a measure of relatedness between species in a given community. We compared MPD values to null MPD values, which were calculated by randomizing the tips of the tree 999 times while preserving species richness and occurrence frequencies. We then calculated SES = (observed MPD − randomized MPD)/SD (randomized MPD) following Gurevitch et al. (1992)

and Spasojevic and Suding (2012). These SES values parallel functional dispersion analysis values (FDis, see below) in whether they indicate overdispersion or clustering patterns. Thus, a positive SES indicates phylogenetic overdispersion where individuals are less closely related than expected at random, a negative SES indicate phylogenetic clustering where individuals are more closely related than expected at random, and an SES of zero indicates no difference between null and expected values. Significant SES values (statistically significant deviation from null) had a $p < 0.05$ (Kembel et al. 2009).

Trait data

To understand patterns of plant functional trait diversity during succession, we collected trait data for the 22 most common species across all sites. These 22 species represent 84.4–86.6% (Pumice Plain), 71.4–80.5% (Studebaker Ridge), 60.1–64.6% (Lahar), and 45–58.5% (Abraham Plains) of total species abundance (percent cover) from 1982 to 2010. The remaining unrepresented species are predominantly comprised of mosses, for which accompanying plant trait data is less comparable to vascular plants (e.g. SLA and seed weight) and thus unable to be measured. Plant traits were collected from Mount St. Helens, near the Pumice Plain site in the summer of 2012. All trait measurements were measured on ten individuals for each species, or samples (e.g. leaves, seeds) were collected from ten individuals and traits measured back in the lab after storing and transporting samples in paper or plastic ziplock bags. Measured traits are meant to be the best available representation of species at MSH. However, we cannot discount the possibility that plasticity may have changed plant traits over the course of succession and acknowledge that importance of intraspecific trait variation cannot be addressed with our sampling (Pakeman and Quested 2007).

We measured a variety of traits related to processes assumed to be important during succession. First, we measured seed weight (individual seed weight) as an indicator of dispersal ability. For species where seeds were extremely light, 100 seeds were counted out and weighed to determine weight per seed. For species we could not field-collect (*Achilea millifolium, Alnus viridis, Anaphalis margaritacea, Cistanthe umbellate, Epilobium anagallidifolium, Luetkea pectinata*), we used values from the Kew Garden dataset (Royal Botanic Gardens Kew Seed Information Database 2008). To assess growth, competitive, and stress-tolerance abilities, we measured plant height, specific leaf area, and leaf thickness on each of the ten individuals per species (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). Height was measured from the base of the plant to the highest point of photosynthetically active tissue at the end of the growing season, and is a measure of light acquisition ability as well as a correlate to overall plant biomass (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). Specific leaf area (SLA; leaf area per unit leaf dry mass) is a measure of photosynthetic capacity as well as leaf longevity (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). We measured SLA by collecting 10 (less if the plant has fewer than 10) fully formed, undamaged leaves and immediately placed them into sealed plastic bag wrapped in a moist paper towel. Leaves were scanned within 5 h of collection and then dried at 55 °C for 48 h before weighing to determine dry leaf weight. Mean SLA was calculated for each individual. Leaf thickness was measured for each collected leaf using digital calipers at the widest part of the leaf, not including the mid-vein. To assess plant tissue nutrient content (correlated with nutrient acquisition ability), we measured total carbon, nitrogen, and phosphorus as well as calculated C:N, C:P, and N:P ratios in collected plant leaf tissue (note: nutrient values for *Alnus viridis, Carex microptera, Castilleja miniata, Eriogonum pyrolifolium* were not measured due to insufficient tissue amount). Collected leaf tissue was dried at 55 °C for 48 h and sent to the Smithsonian Tropical Research Institute Soils laboratory (Panama) for plant tissue nutrient analyses.

Linking phylogeny to traits

To assess whether measured traits are phylogenetically conserved, we calculated Blomberg's *K* statistic (Blomberg et al. 2003) using the R package 'phytools' (Revell 2011). *K* values close to zero indicate closely related species are less similar in trait values than expected. Significance of the signal was access by comparing observed *K* values with null distribution of *K* by shuffling the tips (999 runs).

Functional trait analyses

We calculated community-weighted means (CWM) for all traits, for each plot per year at each of the four sites. CWM is the sum of all trait values in the community (plot) weighted by their relative abundance (Garnier et al. 2004) and represents Grime's biomass ratio hypothesis (the relative contribution of each species to ecosystem properties should be proportional to its contribution to total primary productivity, Grime 1998). To examine functional trait diversity patterns through time, we calculated functional trait dispersion in R (R Development Core Team 2010) using the R package 'FD' (Laliberte and Legendre 2010). Functional trait dispersion (FDis) is a measure of trait diversity that calculates the mean distance of each species to the centroid of all species in the community where species are weighted by relative abundance (Laliberte and Legendre 2010). We calculate FDis for each trait separately as well as all traits in combination (multivariate FDis). We calculated null FDis for each plot where trait data (i.e. species identity) was randomly shuffled, and species relative abundance and richness was kept constant (Laliberte and Legendre 2010; Spasojevic and Suding 2012). 95% confidence intervals (CI) were determined over 999 iterations. Functional diversity was the difference between observed FDis and null FDis, where positive values indicated trait overdispersion and negative values indicated trait clustering (Laliberte and Legendre 2010).

Statistical analysis

To evaluate both phylogenetic (SES) and functional trait dispersion (FDis) trends over time, we ran a linear mixed-effects model using the 'nlme' package in R (Pinheiro et al. 2013). Our model included "plot" as a random effect. To calculate r^2 for mixed-effects models, we used the r2glmm package in R (Jaeger 2016). To account for temporal autocorrelation, we used corAR1 correlation class (autocorrelation structure of order 1), which adds a variance–covariance matrix to account for the exponential decay of correlation with temporal distance (Pinheiro et al. 2013). To examine patterns of community-weighted trait means, we used non-linear generalized additive models (GAMs) using the 'mgcv' package in R (Wood 2006).

Results

Phylogenetic diversity patterns over time

Phylogenetic diversity patterns show greater overdispersion through time across three of the four primary succession sites, however whether communities started off random, overdispersed, or clustered
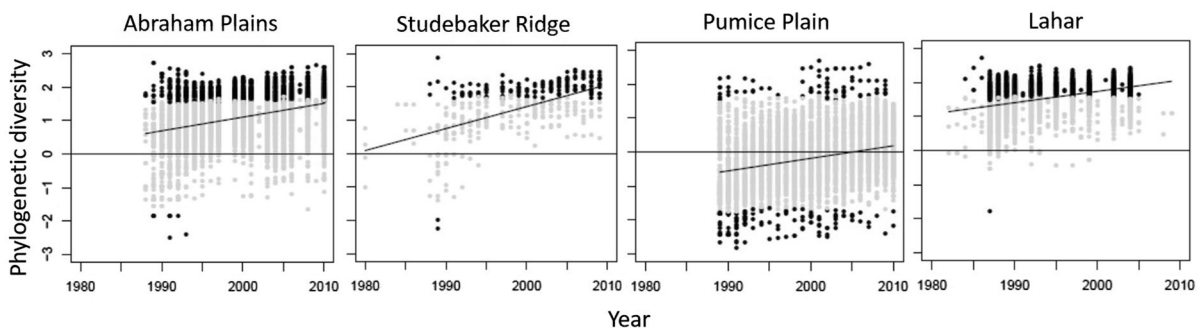

Fig. 2 Phylogenetic diversity patterns for plots through time across 4 primary succession sites on Mount St. Helens. Phylogenetic diversity increases through time for all sites except for Pumice Plain (Abraham Plains: t value = − 100.894, slope = 0.050, r^2 = 0.189, $p < 0.001$; Lahar: t value = − 35.090, slope = 0.017, r^2 = 0.189, $p < 0.001$; Pumice Plain: t value = 0.101, slope = − 0.001, r^2 = 0, $p = 0.981$; Studebaker Ridge: t value = − 130.719, slope = 0.066, r^2 = 0.492, $p < 0.001$). Phylogenetic diversity SES > 0

indicates overdispersion or greater phylogenetic diversity than null expectations, SES < 0 indicates clustering or less phylogenetic diversity than null expectations, black points indicate plots where SES significantly differed from null models ($p < 0.05$). Sites Lahar and Studebaker Ridge are significantly overdispersed through time, Abraham Plains is predominately clustered early in succession and becomes overdispersed later in succession, and Pumice Plain is predominately clustered through time

differed across sites over time (Fig. 2). For all sites except Pumice Plain, mixed-effects models indicated significantly increasing phylogenetic diversity (trending towards overdispersion) during succession (Fig. 2). Phylogenetic diversity (SES) values indicate significant phylogenetic overdispersion (i.e. greater than 0) compared to null models for almost all plots in Lahar and Studebaker Ridge sites (Fig. 2). In Abraham Plains, however, SES values indicate plots are predominately phylogenetic clustered early in succession (before 2000) but switch to becoming predominately overdispersed later in succession (Fig. 2). Finally, Pumice Plain SES values indicate that plots are predominately phylogenetically clustered over the all 30 years of succession. To verify species pool size did not influence our conclusions (Cavender-Bares et al. 2006; Lessard et al. 2012a, b), we also performed phylogenetic analyses using a single regional tree representing the entire known species pool for the blast zone on MSH (Appendix B). The main

differences found were that two sites (Abraham Plains and Pumice Plains) showed stronger overdispersion patterns over the course of succession (Fig. 2, Appendix B). Broader species pools tend to find communities that are more related (phylogenetic clustering) than expected compared to narrower species pools (Cavender-Bares et al. 2006), thus the fact that we found stronger overdispersion with a larger species pool indicates regional filtering effects (dispersal and/or environmental) play less of a role than site-level effects.

Linking phylogeny to traits important to succession

Across all 22 species examined, all traits had K values between 0.298 and 0.443. However, none of these values are significant, indicating low phylogenetic signal in our measured traits (Table 1). Furthermore, trait values were not strongly clustered across the
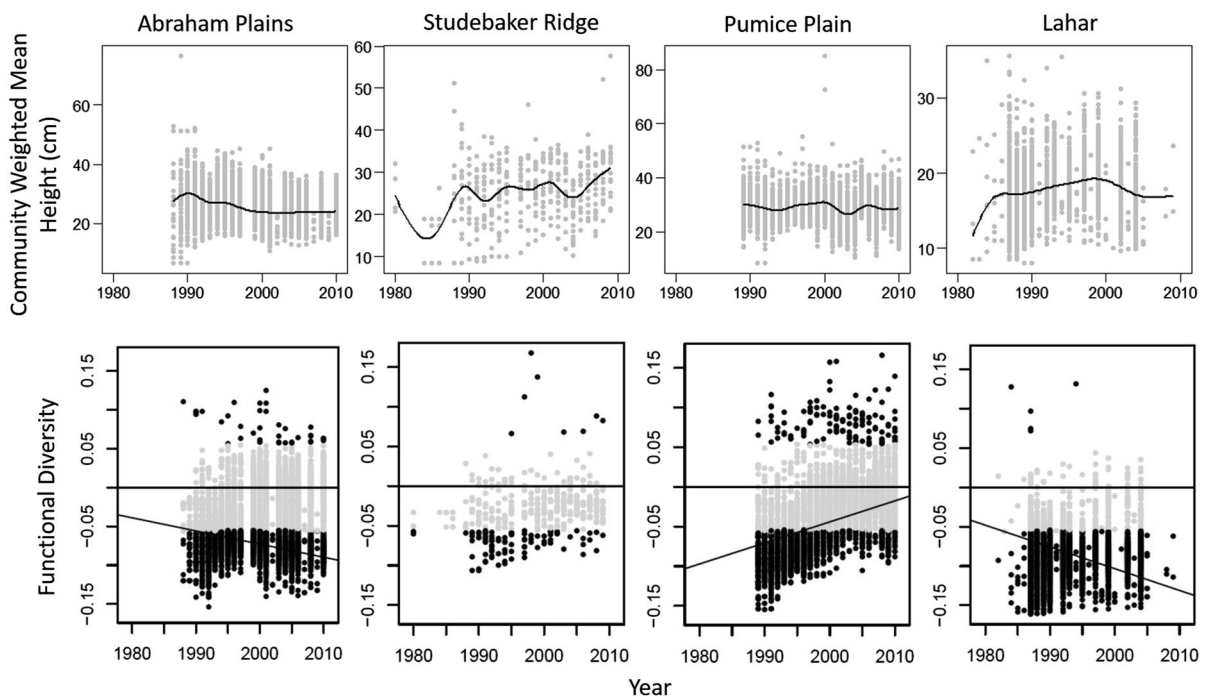

Fig. 3 Community-weighted mean (top) for height over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0.158$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.137$, $p < 0.001$; Pumice Plain: $r^2 = 0.0311$, $p < 0.001$; Lahar: $r^2 = 0.0516$, $p < 0.001$). Functional trait diversity (bottom) for height over time across all 4 sites (Abraham Plains:

t value $= -2.514$, slope $= -0.002$, $p = 0.013$; Studebaker Ridge: t value $= 1.632$, slope $= 0.0003$, $p = 0.103$; Pumice Plain: t value $= 4.442$, slope $= 0.003$, $p < 0.0001$; Lahar: t value $= -4.123$, slope $= -0.003$, $p < 0.0001$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null

phylogenetic tree for any of the measured trait (e.g. species with high SLA are not all from particular families; Appendix C). The fact that our measured traits are not phylogenetically conserved is one likely reason why our multivariate functional trait diversity (Appendix D) and phylogenetic patterns do not match (Fig. 2). Thus, we focus on trait dispersion for each individual trait to understand specific processes important to succession.

Functional trait diversity patterns over time

Dispersal ability

Trends for community-weighted seed weight are relatively unchanged over time across all sites (Table 2, Appendix E). Functional dispersion patterns for seed weight over time are inconsistent across the four sites, with seed weight distributions at two sites more clustered (Abraham Plains, Studebaker Ridge) though no trend over time (Table 1, Appendix E). Conversely, seed weight distributions transition from clustered to overdispersed at Pumice Plain, and remain more overdispersed through time at Lahar (Table 1, Appendix E).

Stress tolerance and competitive ability

Trends for community-weighted height and specific leaf area are relatively unchanged over time across all sites, with a small decrease in SLA over time at two sites (Table 2, Fig. 3, Appendix F). Height dispersion was generally clustered over the course of succession, with two sites showing increased clustering over time (Abraham Plains and Lahar) and one site becoming less clustered over time (Pumice Plain) Table 1, Fig. 3). SLA dispersion patterns are also generally clustered, with the exception of Abraham Plains which is overdispersed (Table 1, Appendix F).

Nutrient acquisition

Overall, nutrient acquisition traits did not show consistent patterns over time across the four sites (e.g. leaf nitrogen and N:P ratio), although leaf phosphorus noticeably decreased over time in two sites (Abraham Plains, Pumice Plains, Table 2, Appendix G, H, I). Leaf nitrogen dispersion patterns are generally clustered, though sites differed in whether they became more or less clustered through time (Table 1, Appendix G). There were no consistent dispersion patterns in leaf phosphorus, with two sites overdispersed (Abraham Plains, Lahar) and two sites going from overdispersed to clustered (Studebaker Ridge, Pumice Plain, Table 1, Appendix H). However, N:P ratio dispersion patterns are generally clustered, except for Lahar which is overdispersed (Table 1, Appendix I).

Herbivore resistance

In general, community-weighted trait values for herbivore resistance (leaf thickness, C:N, C:P ratios) showed a shift in traits towards same or greater herbivore defense during succession, although these patterns were not consistent among the four sites. For example, leaf thickness, C:N, and C:P ratios increased over time for many sites, though Pumice Plain and Studebaker Ridge are an exception to this pattern for leaf C:N and C:P ratio respectively (Table 2, Appendices J, K, L). We also saw trait overdispersion in herbivore-resistance traits, particularly later in succession (Table 1, Appendices J, K, L). The few exceptions are Studebaker Ridge (C:N, C:P) and Pumice Plain (leaf thickness), which have clustered trait dispersion patterns (Table 1, Appendices J, K, L).

Discussion

Using 28 years of community composition data, we find evidence of deterministic community assembly that suggests both environmental filtering effects (Coyle et al. 2014; e.g. Laliberté et al. 2014; Spasojevic and Suding 2012), as well as biotic interactions such as competition (e.g. Bennett et al. 2013; Violle et al. 2011), facilitation (e.g. Butterfield et al. 2013; Valiente-Banuet and Verdú 2007), and herbivory (e.g. Fine et al. 2006) are important. These results are surprising because stochastic events such as chance colonization events generally assumed to dominate in isolated, barren environmental conditions like post-eruption Mount St. Helens' should result in few significant phylogenetic or trait-based patterns, particularly early in succession (Måren et al. 2018). Across our sites, we did not find support for our hypotheses of greater clustering or random phylogenetic patterns early in succession (Fig. 1, line 9).

Instead, clustered stress tolerance and nutrient acquisition trait dispersion patterns suggest a role for abiotic environmental filtering, while generally increasing overdispersion in phylogenetic relatedness and herbivore resistance traits imply biotic interactions such as facilitation, herbivory, and competitive interactions are important. Overall, the site-specific differences in functional trait patterns implies that successional processes are complex, variable, and less generalizable than previously thought. Differences between sites such as distance to seed source (Titus and Bishop 2014; Turley et al. 2017; Wood and del Moral 2000), disturbance legacy effects (Franklin 1990; van de Voorde et al. 2011), and priority effects (Fukami et al. 2005) likely explain divergent assembly patterns. The idiosyncratic nature of these succession patterns and lack of convergence follow secondary succession patterns in tropical forest systems (Norden et al. 2015, 2017; Vandermeer et al. 2004). Despite this complexity, patterns in specific trait means and dispersion over time did afford us several insights about succession processes.

The phylogenetic patterns we found differed from occasionally strong and site-specific trait dispersion patterns are consistent with other findings (Bernard-Verdier et al. 2013; Mason and Pavoine 2013; Pavoine et al. 2013; Swenson and Enquist 2009). A lack of phylogenetic conservatism for our measured traits (Appendix C) provides one explanation for the mismatch between phylogenetic and trait patterns (Bernard-Verdier et al. 2013; Cadotte et al. 2013; Pavoine et al. 2013; Swenson and Enquist 2009). It also suggests that additional studies are needed to specifically determine the relative importance of different mechanisms (e.g. competition, facilitation, abiotic filtering), the potential importance of intraspecific trait variability (Siefert et al. 2015; Violle et al. 2012), and choice of traits examined on understanding succession trajectories (Bernard-Verdier et al. 2012). Patterns in means and dispersion of the functional traits we measured presumably also reflect processes important during succession (but not the same processes driving phylogenetic patterns). Site-specific trait-dispersion patterns imply these processes are not consistently important in all four primary successional sites. For example, seed weight was overdispersed at some, but not all sites, potentially implying greater competition within seed size classes but only in less isolated sites that presumably

experience greater seed rain (Appendix E). Site-specific variation in other trait and trait-dispersion patterns could reflect site-specific differences in climate, substrate, or biotic interactions—although we were unable to find such patterns with existing environmental data. In addition, inconsistencies in patterns across the four sites may also suggest that deterministic versus stochastic processes are scale dependent. While we found evidence for deterministic progressions in phylogenetic and trait patterns at the local plot scale, different deterministic progressions (e.g. clustered vs. overdispersed patterns) through time across all sites could also suggest that regional successional progressions are more stochastic.

We hypothesize that harsh winds and drought conditions act as a strong environmental filter in these sub-alpine environments, resulting in a narrow range of height and SLA values (i.e. clustering) at three sites. This is consistent with findings at other low resource, alpine sites (Spasojevic and Suding 2012; Yang et al. 2012). Mean community SLA decreased during succession in two of the driest, greatest intensity blast site on the north side of the mountain (Abraham Plains, Pumice Plains), Fig. 3, Appendix F), consistent with a plant species with longer lived leaves dominating under harsh, dry conditions. However, height and SLA results were not consistent with environmental filtering at all four sites. Increased herbivory pressure from insect and mammal populations could be driving some of these differences in the height and leaf trait patterns across sites. Herbivory has been found to be a main driver of plant community dynamics on Mount St. Helens (Bishop 2002; Yang et al. 2011), however further research is necessary to quantify differences in herbivore dynamics across the landscape.

Abiotic and biotic environmental filtering effects due to strong nutrient limitation, as well as competitive interactions for limiting nutrients, play a role during succession at our sites, based on the inconsistent patterns between leaf nutrient trait dispersion patterns. Plant species that are better at acquiring nitrogen and phosphorus should benefit from more growth and greater overall competitive ability, since leaf nutrient content for both nitrogen and phosphorus is strongly correlated to photosynthetic capacity in early successional species (Reich et al. 1995). Additionally, obtaining adequate nutrients is often difficult in nutrient poor environments like post-eruption Mount St. Helens (Gill et al. 2006). That we found

clustered leaf nitrogen and N:P ratios across most sites (Table 1, Appendix G and I) implies that nitrogen limitation (Gill et al. 2006; Marleau et al. 2011) had an environmental filtering effect. By contrast, we found that leaf phosphorus content was dissimilar within plant communities across all sites, an indication of competitive interactions allowing certain plant species greater acquisition of phosphorus (Table 1, Appendix F). However, this was not consistent across sites, with plant communities at two sites transitioning to clustered leaf phosphorus during succession, indicating that phosphorus limitation later in succession had an environmental filtering effect (Studebaker Ridge and Pumice Plain, Table 1, Appendix F). Phosphorus availability often declines over time in volcanic soils (Walker and Syers 1976), which may exert a strong environmental filtering effect as succession progresses (Table 2, Appendix H). Overall, the inconsistent patterns across sites for all nutrient acquisition traits suggest that complex processes dictate plant growth and competitive performance over succession. In addition to limitations placed by soil nutrient availability, there is a tradeoff between nutrient retention within plant tissue and herbivore resistance for plants (Fine et al. 2006). Differences in herbivory rates across Mount St. Helens (J. Bishop unpublished data) could also help explain the complex patterns as strong herbivore pressure is known to shape plant community structure on Mount St. Helens (Apple et al. 2009; Bishop 2002).

Plant herbivory is also influenced by leaf traits (including leaf nutrient content and leaf thickness), and thus likely to influence trait patterns in our data set. We therefore expected to find overdispersion (i.e. dissimilarity among species in their herbivore defense strategies) over the course of succession, and did find evidence of biotic interactions driving the dissimilarity patterns in leaf thickness, leaf C:N and C:P ratios across most, but not all, sites during succession (Table 1). Overall, this suggests that over the course of succession on Mount St. Helens, plants have different strategies for dealing with the tradeoff between fulfilling metabolic needs with enough nutrient storage in tissues and defending against herbivory by being less palatable and investing more resources in leaf toughness (Kurokawa et al. 2009; Mattson 1980). Together, these results support the idea that strong biotic forces shape community assembly processes at Mount St. Helens.

Conclusions

Overall, we draw two novel and somewhat surprising main conclusions from this study. First, strong deterministic factors (both abiotic and biotic) shape the plant community of Mount St. Helens early in primary succession, even in the face of isolation and potential for stochastic processes to dominate. Future research should examine the roles of specific biotic interactions such as competition, facilitation, and herbivory, as well as their interactions. Second, our study suggests that successional processes are less generalizable than previously thought, and that complex and variable processes such as legacy effects and local-scale environmental differences due to habitat heterogeneity ultimately determine community assembly. Our findings highlight the possibility that smaller scale studies may miss the importance of larger scale heterogeneity across sites. A lack of generality across sites, as well as a lack of concordance between phylogenetic and key traits presumed to be important to succession, suggests that these phenomenological quantitative methods are only the first step to describing community assembly patterns (Adler et al. 2013). Interactions between trait variation and environmental heterogeneity across successional sites could provide additional mechanistic understanding of abundance patterns and interaction of species over the course of succession (Adler et al. 2013), but we expect that experimental studies will be needed to disentangle the mechanisms that drive community assembly during primary succession.
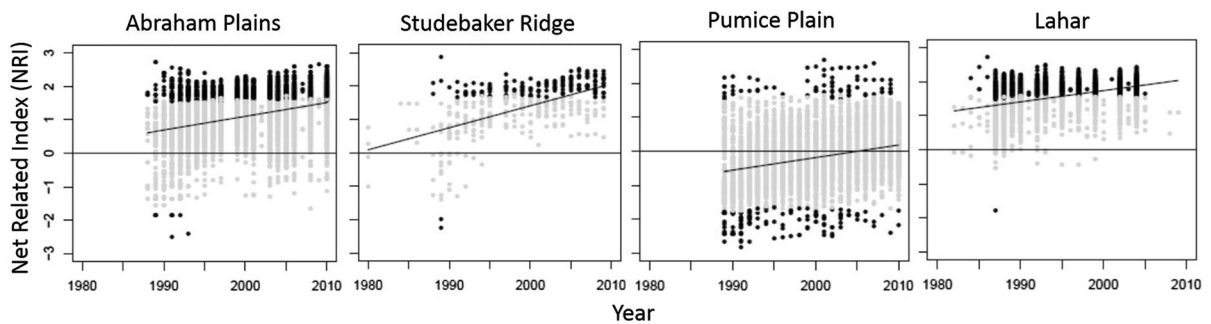
Appendix A

Species richness across 4 sites on Mount St. Helens (del Moral 2010; del Moral et al. 2012), further analyses originally reported in (del Moral and Chang 2015; del Moral et al. 2010, 2012; Wood and Del Moral 1987).
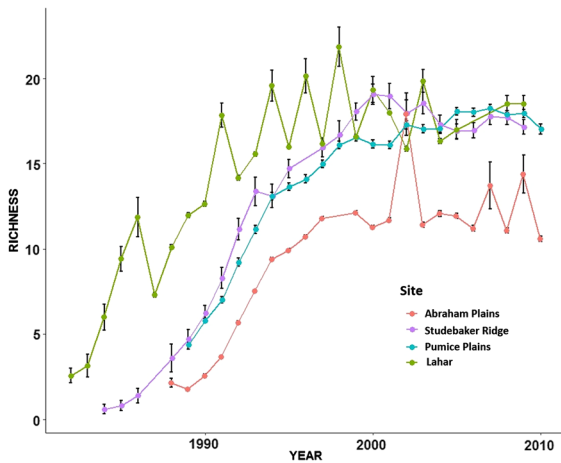
Appendix B

Phylogenetic diversity patterns for plots through time across 4 primary succession sites on Mount St. Helens recalculated using larger species pool (includes species from all 4 sites for each analysis) compared to Fig. 2. Phylogenetic diversity increases through time for all sites (Abraham Plains: t value = $-$ 28.885, slope = 0.0504, r^2 = 0.167, $p < 0.001$; Studebaker Ridge: t value = $-$ 7.994, slope = 0.0661, r^2 = 0.437, $p < 0.001$; Pumice Plain: t value = $-$ 0.2613, slope = 0.101, r^2 = 0.01, $p < 0.001$; Lahar: t value = $-$ 4.909, slope = 0.0179, r^2 = 0.02, $p < 0.001$). Net related index (NRI) > 0 indicates overdispersion or greater phylogenetic diversity than null expectations, NRI < 0 indicates clustering or less phylogenetic diversity than null expectations, black points indicate plots where NRI significantly differed from null models ($p < 0.05$).
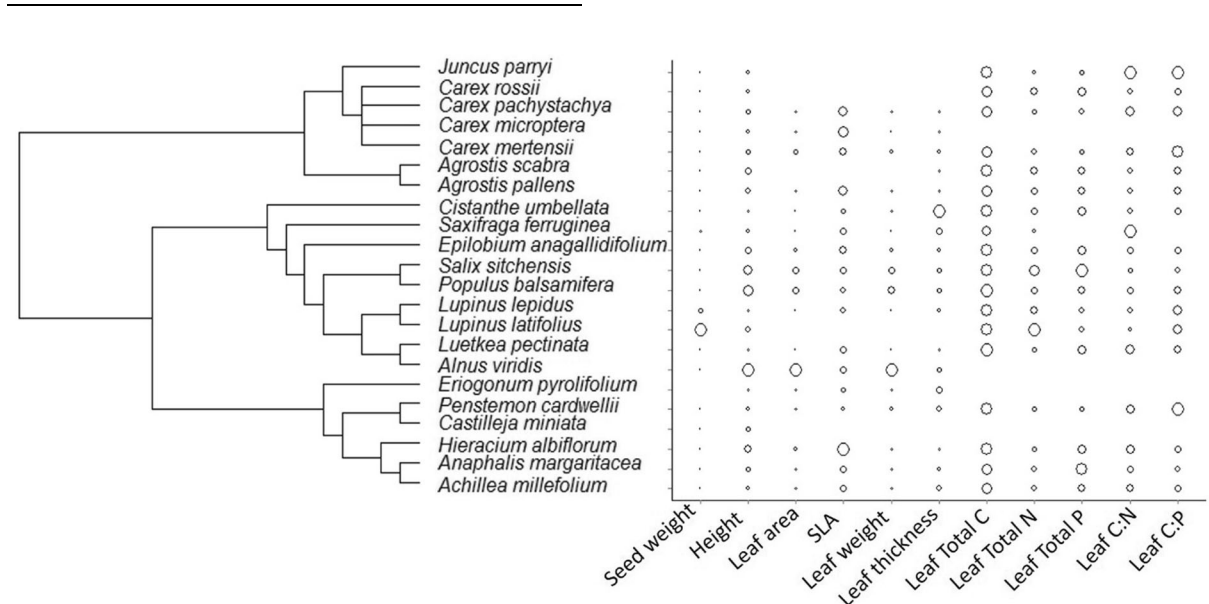
Appendix C

Phylogenetic signal in measured traits for 22 most common species across all 4 primary succession sites. Blomberg's K value, close to zero indicates strong phylogenetic signal, significant p value indicates

|	Trait	K	p value
Dispersal	Seed weight	0.44336	0.195
Stress tolerance and competitive ability	Height	0.37459	0.416
	SLA	0.29877	0.846
Nutrient acquisition	Leaf total N	0.40747	0.344
	Leaf total P	0.32844	0.829
	N:P	0.42241	0.385
Herbivore resistance	Leaf thickness	0.33616	0.68
	C:N	0.32984	0.698
	C:P	0.30517	0.921

Appendix D

Phylogenetic tree of the 22 common species found across primary succession sites with a graph depicting their relative dispersal (seed weight), growth (height, leaf area, SLA, leaf weight, leaf thickness), and nutrient content traits (leaf total C, leaf total N, leaf total P, leaf C:N ratio, leaf C:P ratio). Points are relativized by the maximum trait value for each trait.

Appendix E

Community-weighted mean (top) for seed weight over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0.00806$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.162$, $p < 0.001$; Pumice Plain: $r^2 = 0.182$, $p < 0.001$; Lahar: $r^2 = 0.17$, $p < 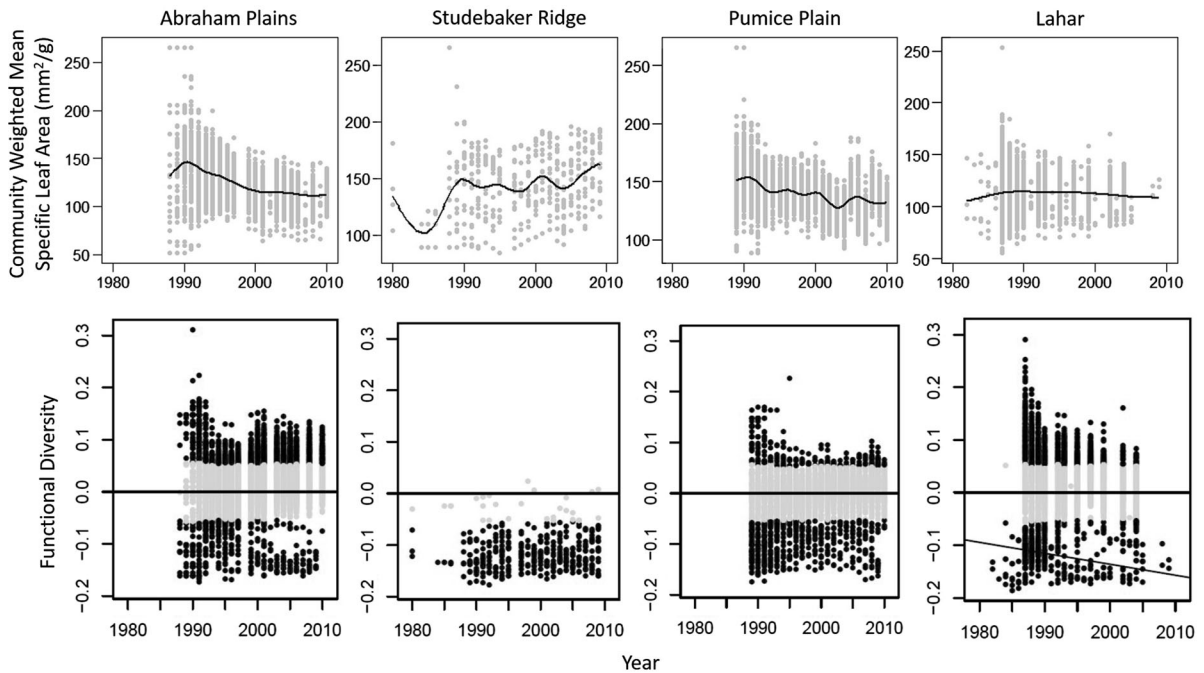0.001$). Functional trait diversity (bottom) for seed weight over time across all 4 sites, (Abraham Plains: t value = 0.882, slope = 0.0001, $p = 0.379$; Studebaker Ridge: t value = − 1.660, slope = − 0.0008, $p = 0.098$; Pumice Plain: t value = 5.399, slope = 0.003, $p < 0.0001$; Lahar: t value = 0.675, slope = 0.000753, $p = 0.501$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.
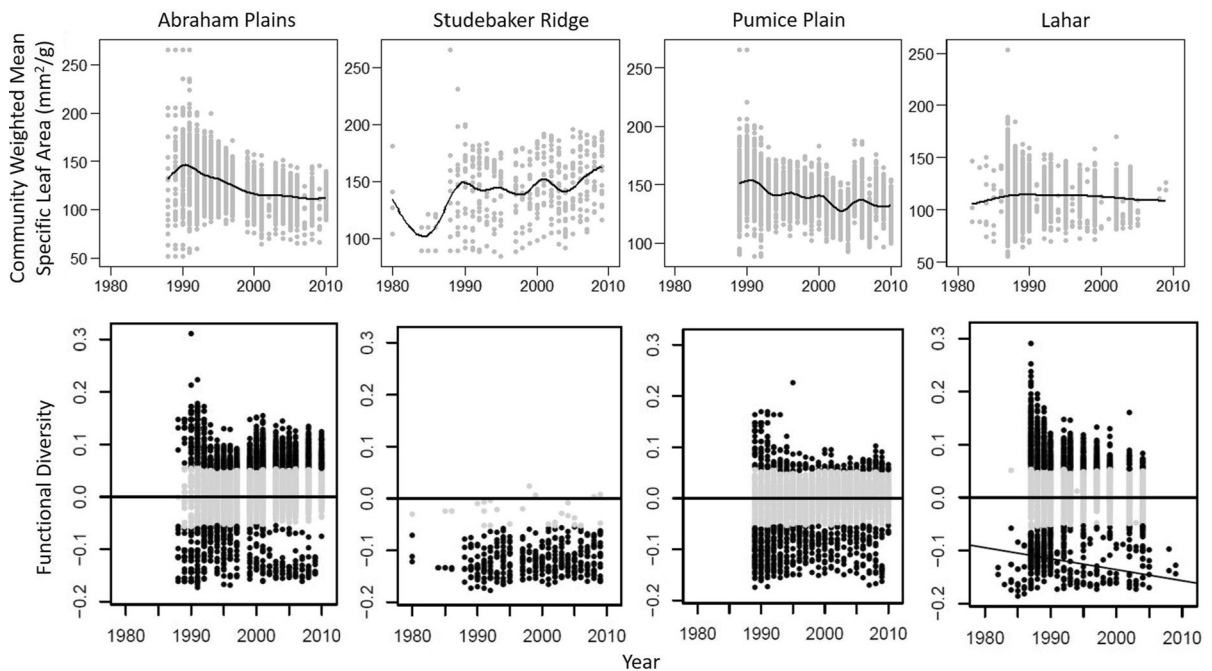
Appendix F

Community-weighted mean (top) for specific leaf area over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0.307$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.114$, $p < 0.001$; Pumice Plain: $r^2 = 0.194$, $p < 0.001$; Lahar: $r^2 = 0.00754$, $p < 0.001$). Functional trait diversity (bottom) for specifi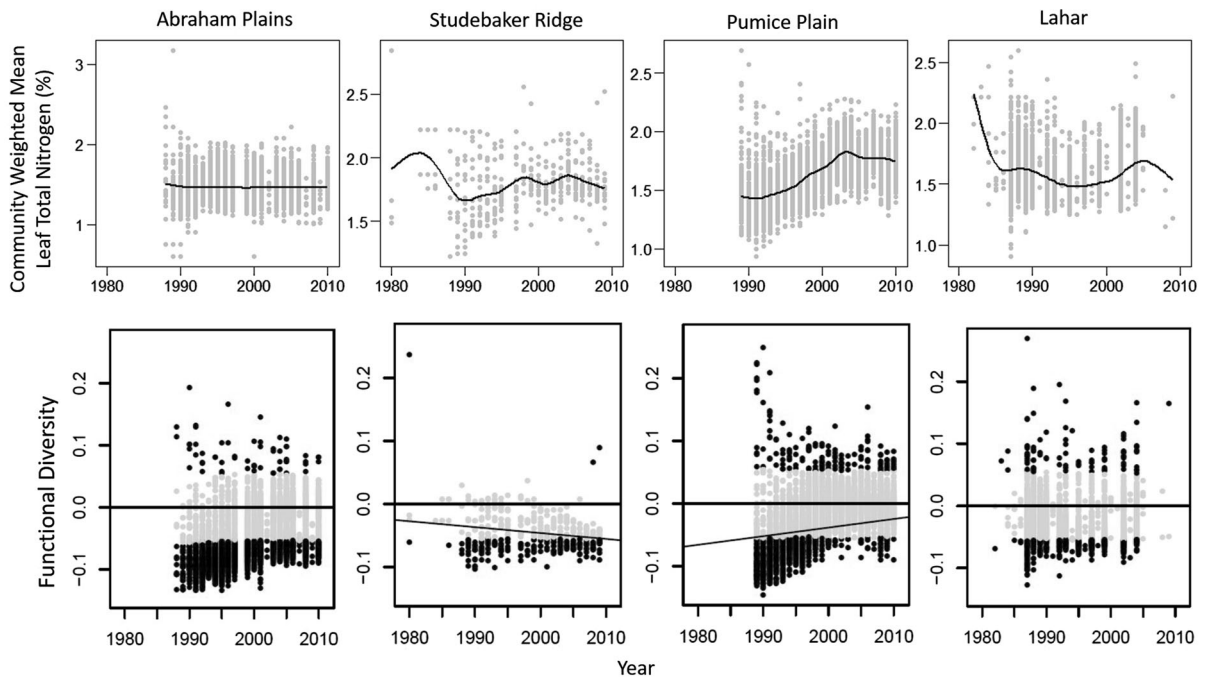c leaf area over time across all 4 sites, (Abraham Plains: t value $= -1.603$, slope $= -0.0007$, $p = 0.111$; Studebaker Ridge: t value $= -1.747$, slope $= -0.001$, $p = 0.081$; Pumice Plain: t value $= 1.430$, slope $= 0.0008$, $p = 0.154$ Lahar: t value $= -2.579$, slope $= -0.002$, $p = 0.011$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.

Appendix G

Communityweighted mean (top) for total leaf percent nitrogen over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0027$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.11$, $p < 0.001$; Pumice Plain: $r^2 = 0.439$, $p < 0.001$; Lahar: $r^2 = 0.145$, $p < 0.001$). Functional trait diversity (bottom) for total leaf percent nitrogen over time across all 4 sites, (Abraham Plains: t value = 1.112, slope = 0.0006, $p = 0.268$; Studebaker Ridge: t value = -2.666, slope = -0.0009, $p = 0.008$; Pumice Plain: t value = 2.786, slope = 0.001, $p = 0.006$; Lahar: t value = 0.962, slope = 0.0007, $p = 0.337$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.

Appendix H

Community-weighted mean (top) for total leaf percent phosphorus over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0.555$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.161$, $p < 0.001$; Pumice Plain: $r^2 = 0.314$, $p < 0.001$; Lahar: $r^2 = 0.0507$, $p < 0.001$). Functional trait diversity (bottom) for total leaf percent phosphorus over time across all 4 sites, (Abraham Plains: t value $= -1.593$, slope $= -0.002$, $p = 0.114$; Studebaker Ridge: t value $= -4.981$, slope $= -0.003$, $p < 0.0001$; Pumice Plain: t value $= -4.647$, slope $= -0.003$, $p < 0.0001$; Lahar: t value $= -1.568$, slope $= -0.001$, $p = 0.119$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.
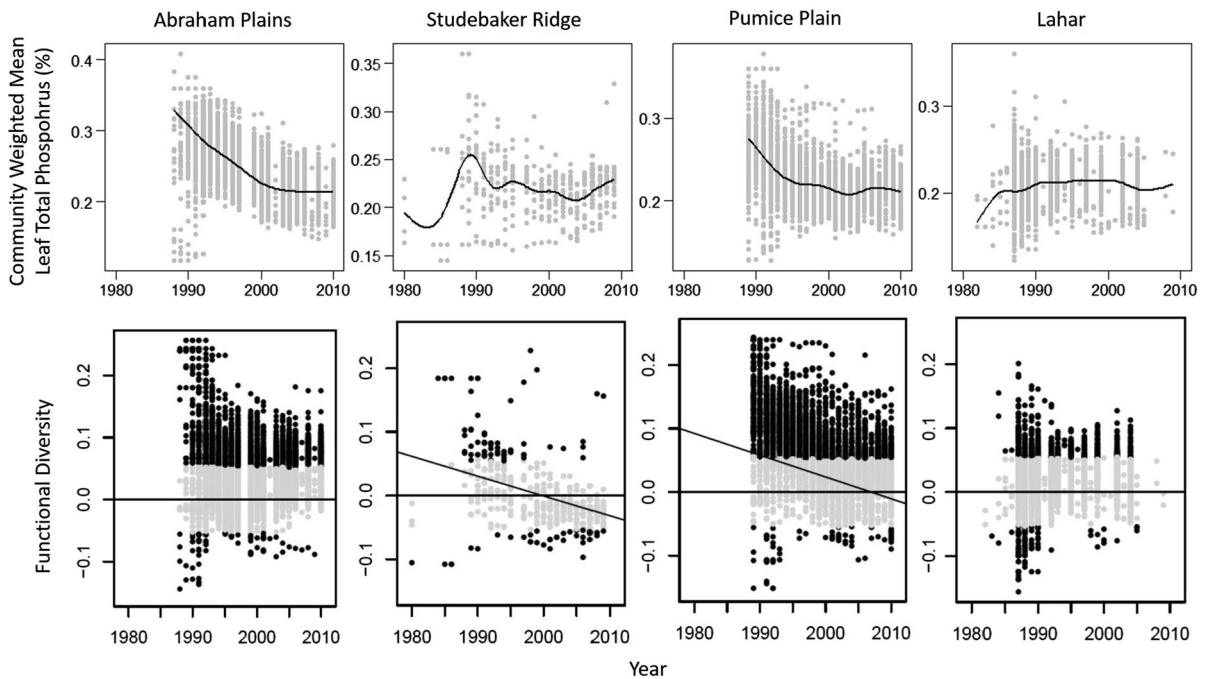
Appendix I

Community-weighted mean (top) for leaf nitrogen:phosphorus (N:P) ratio over time across all 4 sites. Each gray point represents a plot, curve is nonlinear generalized additive model of best fit (Abraham Plains: $r^2 = 0.60961$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.15$, $p < 0.001$; Pumice Plain: $r^2 = 0.379$, $p < 0.001$; Lahar: $r^2 = 0.168$, $p < 0.001$). Functional trait diversity (bottom) for leaf nitrogen:phosphorus
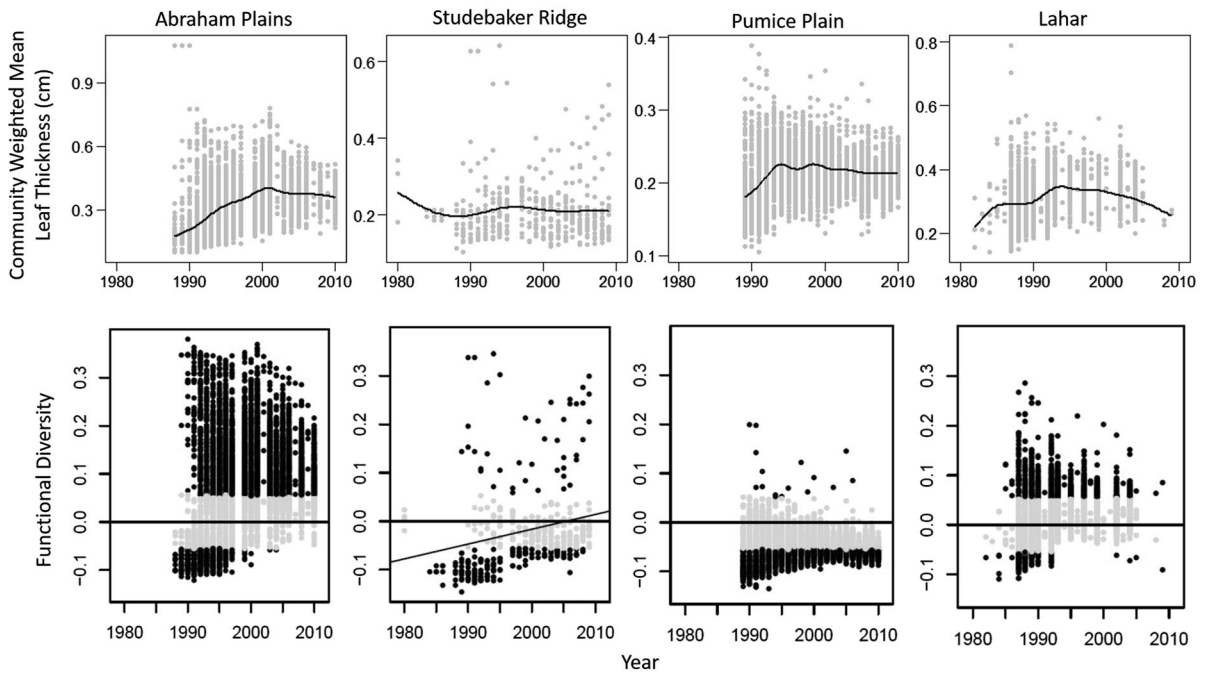
(N:P) ratio over time across all 4 sites, (Abraham Plains: t value = − 1.029, slope = − 0.0004, $p = 0.305$; Studebaker Ridge: t value = − 4.976, slope = − 0.002, $p < 0.0001$; Pumice Plain: t value = 0.318, slope = 0.0001, $p = 0.723$; Lahar: t value = 0.272, slope = 0.0002, $p = 0.786$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.
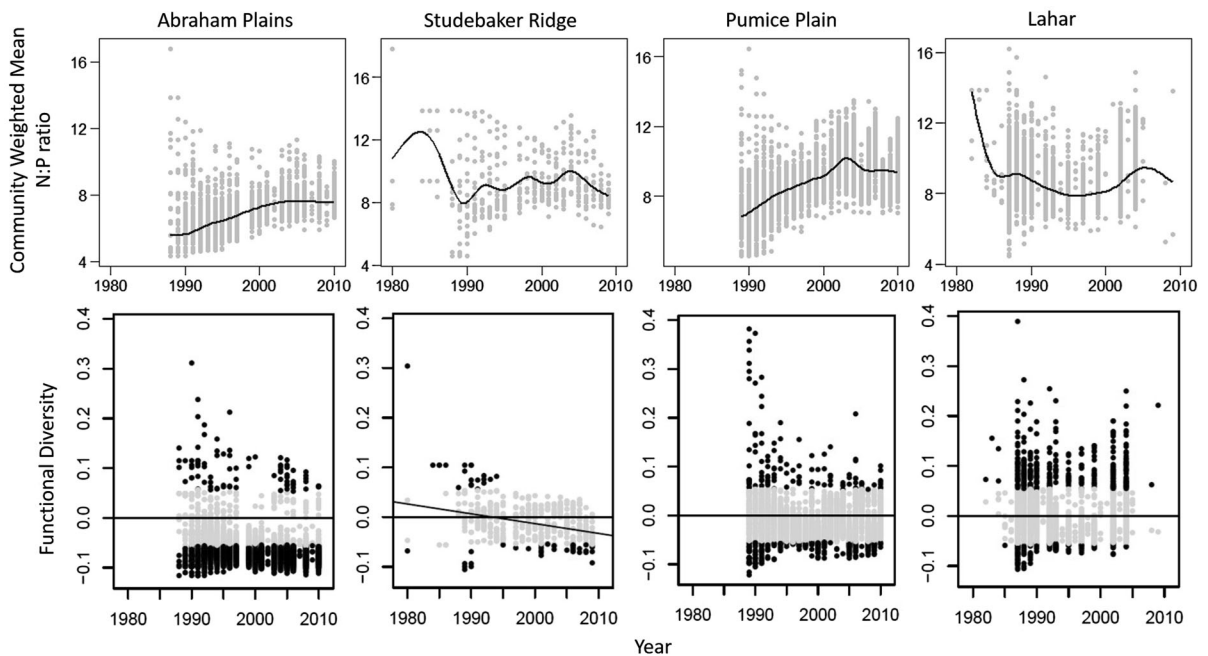
Appendix J

Community-weighted mean (top) for leaf thickness over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0.353$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.0112$, $p < 0.001$; Pumice Plain: $r^2 = 0.124$, $p < 0.001$; Lahar: $r^2 = 0.127$, $p < 0.001$). Functional trait diversity (bottom) for leaf thickne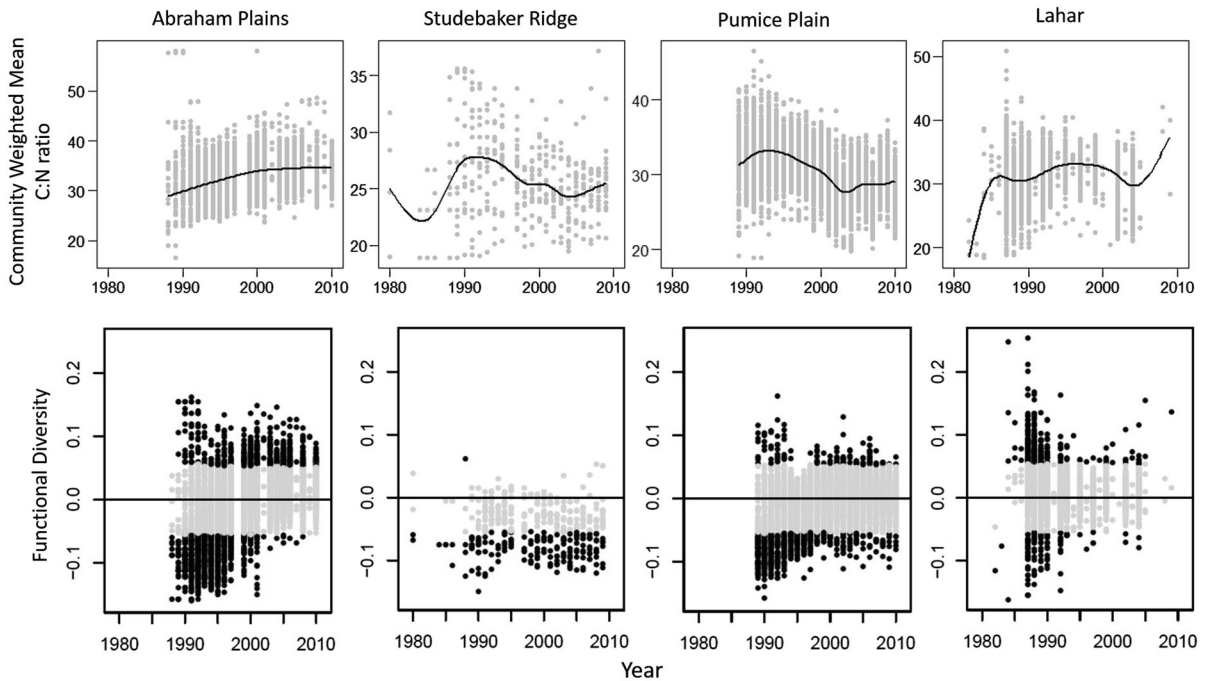ss over time across all 4 sites, (Abraham Plains: t value = 1.234, slope = 0.003, $p = 0.219$; Studebaker Ridge: t value = 2.947, slope = 0.003, $p = 0.003$; Pumice Plain: t value = 0.355, slope = 0.0002, $p = 0.722$; Lahar: t value = 1.301, slope = 0.001, $p = 0.195$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.

Appendix K

Community-weighted mean (top) for leaf carbon:nitrogen (C:N) ratio over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0.216$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.14$, $p < 0.001$; Pumice Plain: $r^2 = 0.259$, $p < 0.001$; Lahar: $r^2 = 0.131$, $p < 0.001$). Functional trait diversity (bottom) for leaf C:N ratio over time across all 4 sites, (Abraham Plains: t value = 1.579, slope = 0.002, $p = 0.117$; Studebaker Ridge: t value = − 1.793, slope = − 0.0007, $p = 0.074$; Pumice Plain: t value = 0.425, slope = 0.0003, $p = 0.671$; Lahar: t value = 1.151, slope = 0.0009, $p = 0.251$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.

Appendix L

Community-weighted mean (top) for leaf carbon:phosphorus (C:P) ratio over time across all 4 sites. Each gray point represents a plot, curve is non-linear generalized additive model of best fit (Abraham Plains: $r^2 = 0.544$, $p < 0.001$; Studebaker Ridge: $r^2 = 0.121$, $p < 0.001$; Pumice Plain: $r^2 = 0.288$, $p < 0.001$; Lahar: $r^2 = 0.544$, $p < 0.001$). Functional trait diversity (bottom) for leaf carbon:phosphorus (C:P) ratio over time across all 4 sites, (Abraham Plains: t value = 2.536, slope = 0.005, $p = 0.012$; Studebaker Ridge: t value = $-$ 0.908, slope = $-$ 0.0004, $p = 0.364$; Pumice Plain: t value = 1.363, slope = 0.001, $p = 0.174$; Lahar: t value = 0.761, slope = 0.0007, $p = 0.448$), each point represents a plot. Black indicates significantly different from null (999 runs), gray indicates not significantly different from null.
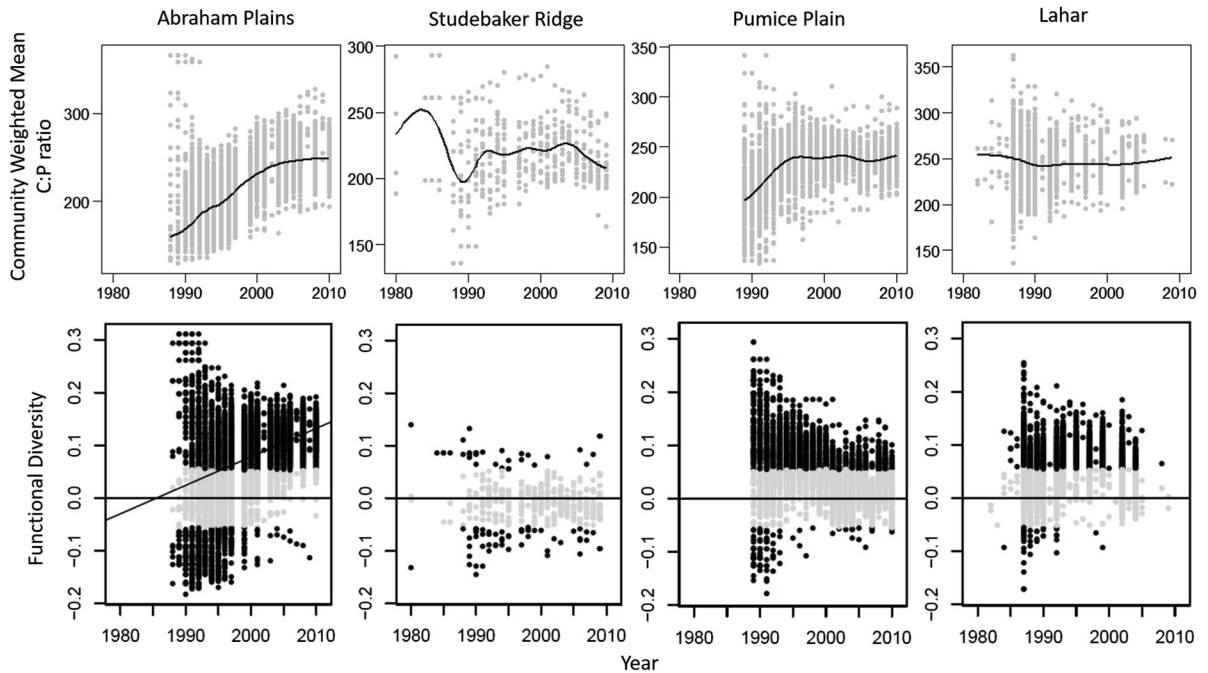
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