

**Assessing Plant Community Assembly Along an Elevational Gradient: A Functional Niche  
Hypervolume Approach**

Student: Kenji T. Hayashi

Mentors: Brian J. Enquist, Lorah B. Patterson

Full Time Independent Research  
Summer 2017

## Abstract

Niche-based processes, such as environmental filtering and niche differentiation, have been proposed to contribute to the assembly of ecological communities. While functional traits can be useful for testing hypotheses regarding niche-based community assembly, most studies utilizing functional traits to examine such hypotheses have focused on patterns of individual traits or of mean trait values. We tested for signatures of environmental filtering and niche differentiation on the assembly of subalpine meadow communities in the Rocky Mountains, Colorado, USA by constructing site-level and species-level trait space hypervolumes from field-collected functional trait data (foliage height, SLA, LDMC). We found a trend of increasing community trait space volume and decreasing community trait space density (species/volume) with increasing elevation. Species-level trait space, however, exhibited no relationship with elevation. Additionally, we found that pair-wise distances of species-level trait space hypervolume increases with elevation. Overall, contrary to conventional hypotheses regarding niche-based community assembly, our results support a pattern of larger community trait space at higher elevations and more “packed” trait space at lower elevations. Incorporation of additional communities, sites, and trait combinations into our study should yield further insights into the patterns observed here.

## Introduction

Understanding the processes, or “rules,” that govern the assembly of ecological communities is a central goal in community ecology (Diamond, 1975; Keddy, 1992; Weiher et al., 1998). Niche theory proposes that community assembly is dictated by differences or similarities in ecological strategies (i.e. niches *sensu* Elton, 1927) among co-occurring species, and by the relationship of abiotic conditions with those strategies (Weiher & Keddy, 1999; Wright, 2002; Silvertown, 2004). Conversely, neutral theory proposes that community assembly is a product of stochastic dispersal and demographic processes, where all species are considered ecologically and competitively equivalent (Hubbell 2001). While these theories are not necessarily mutually exclusive (Adler et al., 2007), the concept of the niche and its importance in community ecology has long received more attention (e.g. Grinnell 1917, Elton 1927, Hutchinson 1957, Hutchinson 1978).

The primary niche-based processes proposed to be involved in community assembly are environmental filtering and niche differentiation (Cornwell et al., 2006; Kraft et al., 2008). Environmental filtering is the process by which the abiotic environment serves as a filter that favors the establishment or survival of species possessing certain ecological strategies (Keddy, 1992; Weiher & Keddy, 1999). Environmental filtering should result in a decrease in the variety of ecological strategies observed within a community (Weiher & Keddy, 1995; Ackerly & Cornwell, 2007). Niche differentiation, stemming from the notion that species with highly similar ecological strategies cannot stably coexist (Gause, 1934; MacArthur & Levins, 1967; Abrams, 1983), is the phenomenon in which co-occurring species exhibit diverging ecological strategies (Janzen, 1970; Weiher & Keddy, 1995; Chesson, 2000; Silvertown, 2004; Stubbs & Wilson, 2004). These two non-random, niche-based processes of community assembly are not

mutually exclusive, but rather could operate simultaneously (Weiher et al., 1998; Kraft et al., 2008; Cornwell & Ackerly, 2009; Jung et al., 2010; Spasojevic & Suding, 2012).

Species' morphological and functional traits have been proposed to reflect ecological strategies (Ricklefs & Travis, 1980; Hopf & Brown, 1986; Moulton & Pimm, 1987; Ricklefs, 1990). This has led to the development of trait-based approaches to studies of community assembly (Stubbs & Wilson, 2004; McGill et al., 2006; Westoby & Wright, 2006; Ackerly & Cornwell, 2007; Cingolani et al., 2007; Schamp et al., 2008; Webb et al., 2010; Violle et al., 2014). Indeed, several studies provide support for a strong correlation between morphological or functional space and ecological space (e.g. Hespénheide, 1973; Cody & Mooney, 1978), suggesting that major traits that differentiate co-occurring species may be closely related to ecological strategies of resource partitioning and coexistence (Ackerly, 2004). The functional niche, defined as an  $n$ -dimensional hypervolume in functional space where axes are associated with functional attributes (Rosenfeld, 2002), may thus reflect ecologically relevant characteristics of organisms (Violle & Jiang, 2009; Devictor et al., 2010; Violle et al., 2012). Recent advances in techniques for estimating niche or trait space from observational data may enable hypotheses regarding niche-based community assembly to be tested directly using functional trait hypervolumes (Mouillot et al., 2005; Cornwell et al., 2006; Blonder et al., 2014, 2017). This multi-dimensional approach possesses significance over single-trait approaches because community assembly has been proposed to be driven by integrated phenotypes rather than by single traits (Bonser, 2006).

Here we employ a functional trait hypervolume approach to directly assess trait space dynamics of vascular plant communities along an elevational gradient in the Rocky Mountains of Colorado, USA. We address the following questions: (1) How do plant communities differ in functional trait composition and (2) how does the volume, overlap, and packing of trait space within plant communities shift along an elevational gradient? (3) How do the observed patterns of trait space dynamics compare to predictions of niche-based community assembly theory? While prior studies have found evidence for niche-based mechanisms of community assembly along elevational gradients (e.g. Stubbs & Wilson, 2004; Kraft et al., 2008; Schamp et al., 2008; Kluge & Kessler, 2011; Hoiss et al., 2012), these studies have mainly employed individual traits or mean trait values to assess trait-based community assembly. Our approach is unique in that we simultaneously utilize multiple trait axes and can account for intraspecific trait variation both within and among communities to examine holistic multi-dimensional trait space. Finding evidence for niche-based processes in community assembly is important, as niche dynamics are thought to play a central role in stable coexistence of species (Chesson, 1991, 2000; Leibold, 1995). Furthermore, this trait based approach is relevant to studies of biodiversity and ecosystem functioning since the functional significance of biodiversity is thought to arise largely from functional trait diversity (Hooper et al., 2005).

We tested the following niche-based hypotheses of plant community assembly: (1) ecologically relevant functional traits under the influence of environmental factors should display directional shifts in trait values along an elevational gradient. (2) The volume of total community-level trait space should be larger at lower elevations (i.e. at more benign conditions along an environmental gradient) than at higher elevations due to increased niche differentiation (Tilman et al., 1997), whereas the volume of total community-level trait space should be smaller

at higher elevations (i.e. at harsher conditions along an environmental gradient) as a result of the presence of inviable trait combinations due to environmental filtering (Lamanna et al., 2014). (3) At lower elevations (i.e. at more benign conditions along an environmental gradient), trait space hypervolumes for each species within a community should overlap less or should be more evenly distributed in  $n$ -dimensional hyperspace than at higher elevations (i.e. at harsher conditions along an environmental gradient) (Roughgarden, 1972; Brown, 1975). To test these hypotheses, we constructed trait space hypervolumes from locally observed plant functional traits at four sites along a gradient of increasing elevation and examined the relationship between elevation and the volume, density, and packing of trait space hypervolumes within communities.

## Methods

### *Study Sites*

We selected four study sites along an elevational gradient in Washington Gulch (Rocky Mountains, Colorado, USA) ranging from approximately 2710 to 3370 m in elevation (Figure 1). These study sites were located within subalpine meadows dominated by perennial herbaceous forbs and graminoids as well as some small shrubs. Species composition, species abundance, and vegetation cover for each site were assessed during the summer of 2016 at peak biomass, defined as approximately eight weeks after snowmelt, using five equally spaced 1.2 m  $\times$  1.2 m plots at each site. Species abundance was assessed by counting the number of individuals of every species present within each plot, and vegetation cover was estimated by documenting the species with the greatest percent ground cover in 169 subplots within each plot. These four sites exhibit high degrees of species turnover between one another, as is illustrated by high Jaccard pair-wise dissimilarity indices (Table 1), calculated with the R package *betapart* version 1.4-1 (Baselga, 2010, 2012; R Development Core Team, 2017).

### *Trait Data*

We measured vascular plant functional traits during June through August of 2017, at around peak biomass for each site. For each species, we obtained functional trait data for a minimum of five randomly selected individuals, with few exceptions (Table 2). To effectively characterize community functional trait space, trait axes with ecological significance must be selected (Silvertown, 2004). We selected to examine three plant functional traits proposed to be associated with ecologically relevant plant strategy axes: foliage height, specific leaf area (SLA), and leaf dry matter content (LDMC) (Westoby, 1998; Westoby et al., 2002; Garnier, 2004; Jung et al., 2010). Foliage height (cm), the height from the base of the plant to the tip of the highest leaf, is involved in competition for light (Thomson et al., 2011). For graminoids, we defined foliage height as the higher of either the base of the lowest floret or the tip of the highest leaf in order to better characterize their growth forms and general canopy heights (Pérez-Harguindeguy et al., 2013). This resulted in the tip of the highest leaf being measured for most graminoids observed. SLA (cm<sup>2</sup>/g), the ratio of fresh leaf area to its oven-dried leaf mass, represents the light-intercepting area of a leaf per unit dry mass and is related to leaf longevity and maximum

photosynthetic rates (Reich et al., 1992, 1997, 1999; Wright et al., 2004). LDMC (mg/g), the ratio of oven-dried leaf mass to fresh leaf mass, approximates leaf tissue density and is related to nutrient retention, potential relative growth rate, and leaf lifespan (Poorter & Ganier, 1999; Ryser & Urbas, 2000; Hodgson et al., 2011; Pérez-Harguindeguy et al., 2013 and references therein).

For every individual sampled, we measured foliage height and collected a single leaf, including the pedicle, that best met the following criteria: (1) approximately the third leaf from the apical meristem, (2) a well-developed, sun-exposed, healthy leaf with no herbivory, (3) a leaf representative of the entire plant. We stored the collected leaves in paper envelopes inside a cooler bag with ice packs and measured leaf area and fresh leaf mass no more than seven hours after collection of the leaf. We determined leaf area by analyzing digital scans of individual leaves using an ImageJ program <[www.github.com/bblonder/leafarea/](https://www.github.com/bblonder/leafarea/)>. We then dried leaves in an oven at 60 to 65 °C for a minimum of 72 hours and measured their oven-dried masses. We used these measurements to calculate SLA and LDMC.

### *Hypervolume Construction*

We constructed site-level and species-level functional trait hypervolumes with three trait axes (foliage height, SLA, LDMC) using the *hypervolume* R package version 2.0.6.7 (Blonder et al., 2014, 2017; R Development Core Team, 2017). In order to construct hypervolumes, trait data were log-transformed so as to make axes comparable to one another. Site-level hypervolumes were constructed by pooling all observations for each site, using both the Gaussian kernel density estimate (KDE) (parameters: bandwidth estimated using a Silverman bandwidth estimator (Silverman 1992) implemented with the `estimate_bandwidth` function, threshold = 0.95) and the one-class support vector machine (SVM) methods (parameters:  $\nu = 0.01$ ,  $\gamma = 0.5$ ) (Figures 2-3, [Movies S1-S8](#)). Species-level hypervolumes were constructed for each species at each site using the Gaussian KDE method (parameters: bandwidth estimated using a Silverman bandwidth estimator (Silverman 1992) implemented with the `estimate_bandwidth` function, threshold = 0.95) (Figure 4, [Movies S5-S8](#)). The Gaussian KDE method creates padding around observational data and estimates hypervolumes as specified by a chosen probability threshold. For species with small sample size (e.g.  $n = 5$  individuals sampled), this method should be more appropriate than the SVM method which is trained on and wraps tightly around the observational data, as it is unlikely that the full extent of trait space has been sampled with just the observational data. Upon the construction of hypervolumes, we weighted all observational data by species abundance. We duplicated observations for each species such that the number of observations used to construct the hypervolumes were proportional to the abundance of each species at that site.

### *Data Analysis*

We assessed the relationships between community functional traits and elevation by regressing all mean trait values (foliage height, SLA, LDMC) for each species at each site with elevation. We obtained volumes of site-level and species-level trait space hypervolumes, and calculated pair-wise overlap statistics (intersection, Jaccard similarity index, Sorensen overlap;

see Table 3 for definitions) and pair-wise centroid distances using built-in functions of the *hypervolume* R package. We computed pair-wise intersection, Jaccard similarity index, and Sorensen overlap values as the mean of two iterations of the same pair-wise function but with the input order of the two focal hypervolumes switched, because these operations yielded slightly different values. We calculated hypervolume density (species/volume) for each site as the ratio of the number of species sampled and the volume of the site-level hypervolume. We assessed the behavior of the site-level hypervolumes by regressing the volume and density of the hypervolumes against elevation. We also examined the behavior of the volumes, overlap (intersection, Jaccard similarity index, Sorensen overlap), and distances of species-level hypervolume by regressing all pair-wise values at each site with elevation. We further tested for pair-wise differences in the mean volumes of the species-level hypervolumes at each site with two-sample t-tests. We completed all analyses in the R environment (R Development Core Team, 2017).

## Results

### *Community Trait Values*

For each site, we collected trait data for species such that species that collectively represent at least 75 % of the abundance and 80 % of the vegetation cover at each site were sampled and represented in our analyses (Table 2). Community foliage height and SLA both exhibited significant increases with elevation (foliage height:  $R^2 = 0.044$ ,  $F_{1,92} = 4.201$ ,  $P = 0.0432$ ; SLA:  $R^2 = 0.31$ ,  $F_{1,92} = 42.29$ ,  $P = 4.02 \times 10^{-9}$ ) (Figure 5A & B). Community LDMC exhibited a significant decrease with elevation ( $R^2 = 0.21$ ,  $F_{1,92} = 25.05$ ,  $P = 2.67 \times 10^{-6}$ ) (Figure 5C).

### *Volume and Density of Hypervolumes*

Site-level hypervolumes displayed a non-significant trend of increasing volume with increasing elevation (SVM:  $R^2 = 0.44$ ,  $F_{1,2} = 0.3367$ ,  $P = 0.337$ ; Gaussian KDE:  $R^2 = 0.74$ ,  $F_{1,2} = 5.565$ ,  $P = 0.142$ ) (Figure 6A & B). In contrast, site-level hypervolumes displayed a trend of decreasing density with increasing elevation (SVM:  $R^2 = 0.21$ ,  $F_{1,2} = 0.5257$ ,  $P = 0.544$ ; Gaussian KDE:  $R^2 = 0.97$ ,  $F_{1,2} = 57.75$ ,  $P = 0.0167$ ) (Figure 6C & D). These results are robust to the method employed to construct the site-level hypervolumes. Species-level hypervolumes exhibited a non-significant increase in volume with increasing elevation ( $R^2 = 0.037$ ,  $F_{1,92} = 3.503$ ,  $P = 0.0644$ ), and results of pair-wise two sample t-tests comparing mean volumes of species-level hypervolumes by site indicate that there are few to no significant differences in the volumes of species-level hypervolumes by elevation (Figure 7, Table 4).

### *Overlap and Distance of Hypervolumes*

Pair-wise intersections and Jaccard similarity index of species level hypervolumes exhibited weak significant positive relationships with elevation (intersection:  $R^2 = 0.0064$ ,  $F_{1,1090}$

= 6.987,  $P = 0.00833$ ; Jaccard similarity index:  $R^2 = 0.0060$ ,  $F_{1,1090} = 6.619$ ,  $P = 0.0102$ ) (Figure 8A & B). Pair-wise Sorensen overlap of species-level hypervolumes, however, did not display any significant relationship with elevation ( $R^2 = 1.09 \times 10^{-7}$ ,  $F_{1,1090} = 0.0001185$ ,  $P = 0.991$ ) (Figure 8C). Pair-wise centroid distances of species-level hypervolumes exhibited a significant positive trend with increasing elevation ( $R^2 = 0.065$ ,  $F_{1,1090} = 75.79$ ,  $P < 2.2 \times 10^{-16}$ ) (Figure 8D).

## Discussion

Here we illustrate that individual vascular plant functional traits exhibit directional shifts along an environmental gradient of increasing elevation. The observed increase in community SLA with increasing elevation is consistent with results from prior studies (e.g. Gonzalo-Turpin & Hazard, 2009; Sides et al., 2014) (Figure 5B). Higher SLA (i.e. thinner leaves) is thought to maximize resource use and acquisition at higher elevations where the growing season is shorter (Hirose & Werger, 1995; Kudo, 1996; Gonzalo-Turpin & Hazard, 2009; Sides et al., 2014). The observed decrease in community LDMC is consistent with prior findings for individual species (Schöb et al., 2013), but appears to contradict the theory that community leaves should exhibit more conservative strategies, such as higher LDMC, at higher elevations (Dubuis et al., 2013) (Figure 5C). The observed pattern of increasing foliage height with increasing elevation is also inconsistent with prior findings (e.g. Gonzalo-Turpin & Hazard, 2009; Kichenin et al., 2013) (Figure 5A). These patterns of decreasing LDMC and increasing foliage height with increasing elevation may be related to the need for high-elevation, short-growing-season species to effectively utilize resources to obtain a net positive carbon gain during the growing season and to out-compete surroundings species (Sides et al., 2014). Together, these results suggest that these three plant functional traits are significantly linked with environmental factors. Therefore, these functional traits may be considered ecologically relevant trait axes along which plant species can be functionally differentiated.

Niche-based community assembly theory suggests that community functional trait space should decrease with increasing elevation due to higher degrees of niche differentiation at lower elevations and more environmental pressure associated with lower temperatures and a shorter growing season due to environmental filtering at higher elevations (Tilman et al., 1997; Lamanna et al., 2014). Contrary to these predictions, site-level trait space hypervolumes tended to increase in volume with increasing elevation (Figure 6A & B). Moreover, we predict that higher levels of niche differentiation at lower elevations and less trait variation at higher elevations, as a result of environmental filtering, should lead to a higher density (species/volume) of trait space hypervolumes at higher elevations than at lower elevations. Contrary to this prediction, site-level hypervolumes exhibited a decrease in density with increasing elevation (Figure 6C & D). Thus, our results fail to support predictions of niche-based community assembly theory. These results indicate that there is tighter trait-base “packing” of species into a community at lower elevations than at higher elevations. An increase in the volume and a decrease in the density of site-level trait space hypervolumes with increasing elevations might suggest that, at least in the subalpine meadows of the Rocky Mountains, the volumes of species-level hypervolumes are, on average, relatively constant across elevation. Our results that the volumes of species-level hypervolumes

display no significant directional trend with increasing elevation are consistent with this observation (Figure 7, Table 4).

We observed the pair-wise intersections and Jaccard similarity indices of species-level hypervolumes within communities displaying a weak positive relationship with elevation (Figure 8A & B). While these relationships are significant, the slopes of these relationships are such that elevation has little effect on the pair-wise intersections of Jaccard similarity indices of species-level hypervolumes (slopes:  $9.286 \times 10^{-16}$ ,  $1.136 \times 10^{-5}$  respectively). Pair-wise Sorensen overlap did not exhibit a significant relationship with elevation (Figure 8C). Under the niche-based processes of niche differentiation and environmental filtering, we might expect to observe an increase in pair-wise overlap of species-level hypervolumes with increasing elevation (Tilman et al., 1997; Lamanna et al., 2014). Our results are inconsistent with this prediction. Notably, pair-wise centroid distances of hypervolumes exhibited a significant positive trend with increasing elevation (Figure 8D). This observation is consistent with the observed pattern of tighter species “packing” at lower elevations than at higher elevations.

By employing a functional trait hypervolume approach using three ecologically relevant trait axes (foliage height, SLA, LDMC), we were able to directly test conventional hypotheses regarding niche-based community assembly. Our results fail to support the presence of mechanisms such as niche differentiation or environmental filtering in plant community assembly along our elevational gradient. Rather, we show that community-level trait space exhibits an increase in volume and decrease in density with increasing elevation. A corollary of this observed pattern is that, on average, elevation has little to no effect on the volumes of the trait space of individual species. Consistent with these observations, we found pair-wise distances of species-level trait space hypervolumes to be significantly and positively related to elevation. Collectively, these results suggest that subalpine meadow plant communities in the Rocky Mountains are more “packed” in terms of key functional traits at lower elevations than at higher elevations.

It should be noted that processes other than environmental filtering can give rise to signals of filtering (Scheffer & Nes, 2006; Mayfield & Levine, 2010; Vellend et al., 2014; Kraft et al., 2015; Cadotte & Tucker, 2017). Moreover, while we failed to detect signatures of niche-based community assembly, more rigorous tests using null models may yield further insights into the trait-space dynamics along our elevational gradient (Gotelli & Graves 1996). Incorporation of additional functional traits (e.g. seed mass; Westoby, 1998) and different combinations of trait axes into our analyses, as well as the utilization of null models to test our hypotheses, should be the next steps in further elucidating the role of niche-based plant community assembly mechanisms along this elevational gradient.

## References

- Abrams, P. (1983) The theory of limiting similarity. *Annual Review of Ecology and Systematics*, **14**, 359–376.
- Ackerly, D.D. (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, **74**, 25–44.
- Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly:

- Partitioning of species trait values into within- and among-community components. *Ecology Letters*, **10**, 135–145.
- Adler, P.B., HilleRisLambers, J., & Levine, J.M. (2007) A niche for neutrality. *Ecology Letters*, **10**, 95–104.
- Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.
- Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.
- Blonder, B., Babich Morrow, C., Maitner, B., Harris, D.J., Lamanna, C., Violle, C., Enquist, B.J., & Kerkhoff, A.J. (2017) New approaches for delineating n-dimensional hypervolumes. *Methods in Ecology and Evolution*, **38**, .
- Blonder, B., Lamanna, C., Violle, C., & Enquist, B.J. (2014) The n-dimensional hypervolume. *Global Ecology and Biogeography*, **23**, 595–609.
- Bonser, S.P. (2006) Form defining function: interpreting leaf functional variability in integrated plant phenotypes. *Oikos*, **114**, 187–190.
- Brown, J.H. (1975) Geographical ecology of desert rodents. In M.L. Cody & J. Diamond (Eds.), *Ecology and evolution of communities* (pp. 315–341). Cambridge, MA: Harvard University Press.
- Cadotte, M.W. & Tucker, C.M. (2017) Should environmental filtering be abandoned? *Trends in Ecology and Evolution*, **32**, 429–437.
- Chesson, P. (1991) A need for niches? *Trends in Ecology and Evolution*, **6**, 26–28.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.
- Cingolani, A.M., Cabido, M., Gurvich, D.E., Renison, D., Díaz, S. (2007) Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits? *Journal of Vegetation Science*, **18**, 911–920.
- Cody, M.L. & Mooney, H.A. (1978) Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics*, **9**, 265–321.
- Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.
- Cornwell, W.K., Schilke, D.W., & Ackerly, D.D. (2006) A trait-based test for habitat filtering: Convex hull volume. *Ecology*, **87**, 1465–1471.
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., & Mouquet, N. (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology*, **47**, 15–25.
- Diamond, J. (1975) Assembly of species communities. In M.L. Cody & J. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342–344). Cambridge, MA: Harvard University Press.
- Dubuis, A., Rossier, L., Pottier, J., Pellissier, L., Vittoz, P., & Guisan, A. (2013) Predicting current and future spatial community patterns of plant functional traits. *Ecography*, **36**, 1158–1168.
- Elton, C.S. (1927) *Animal ecology*. New York, NY: MacMillan Co.

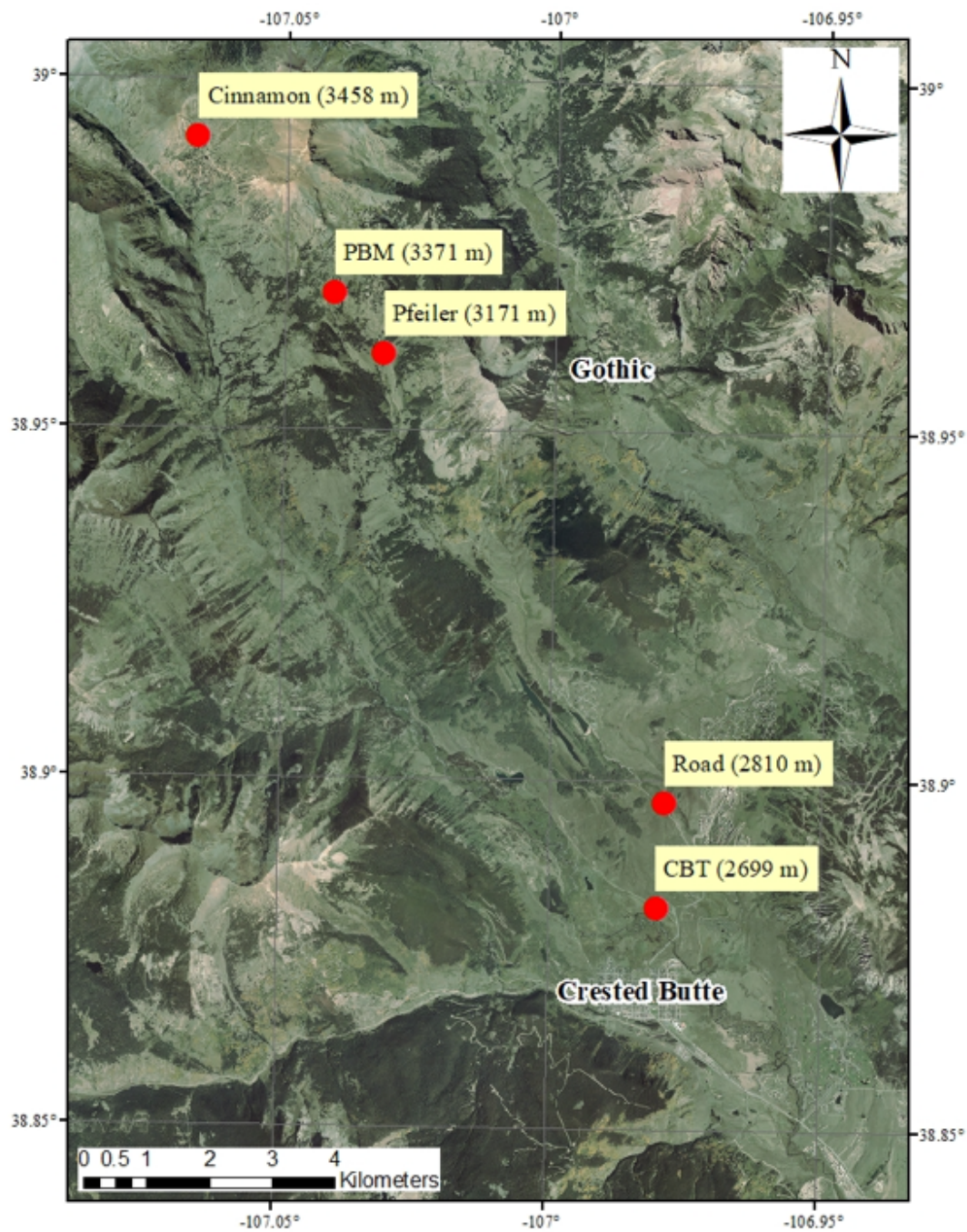
- Garnier, E. et al. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.
- Gause, F. (1934) *The struggle for existence*.
- Gonzalo-Turpin, H. & Hazard, L. (2009) Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology*, **97**, 742–751.
- Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology*. Washington, DC, USA: Smithsonian Institution Press.
- Grinnell, J. (1917) The niche-relationships of the California Thrasher. *The Auk*, **34**, 427–433.
- Hespenheide, H.A. (1973) Ecological inferences from morphological data. *Annual Review of Ecology and Systematics*, **4**, 213–229.
- Hirose, T. & Werger, M.J.A. (1995) Canopy structure and photon flux partitioning among species in a herbaceous plant community. *Ecology*, **76**, 466–474.
- Hodgson, J.G., Montserrat-Martí, G., Charles, M., Jones, G., Wilson, P., Shipley, B., Sharafi, M., Cerabolini, B.E.L., Cornelissen, J.H.C., Band, S.R., Bogard, A., Castro-Díez, P., Guerrero-Campo, J., Palmer, C., Pérez-Rontomé, M.C., Carter, G., Hynd, A., Romo-Díez, A., De Torres Espuny, L., & Royo Pla, F. (2011) Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Annals of Botany*, **108**, 1337–1345.
- Hoiss, B., Krauss, J., Potts, S.G., Roberts, S., & Steffan-Dewenter, I. (2012) Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4447–4456.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hopf, F.A. & Brown, J.H. (1986) The bull's-eye method for testing randomness in ecological communities. *Ecology*, **67**, 1139–1155.
- Hubbell, S.P. (2001) *The unified neutral theory of species abundance and diversity*. Princeton, NJ: Princeton University Press.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold spring harbor symposium on quantitative biology* **22**, 415–427.
- Hutchinson, G.E. (1978) *An introduction to population ecology*. New Haven, CT: Yale University Press.
- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist*, **104**, 501–528.
- Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. (2010) Intraspecific variability and trait-based community assembly. *Journal of Ecology*, **98**, 1134–1140.
- Keddy, P.A. (1992) Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157–164.
- Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W., & Freschet, G.T. (2013) Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, **27**, 1254–1261.
- Kluge, J. & Kessler, M. (2011) Phylogenetic diversity, trait diversity and niches: Species

- assembly of ferns along a tropical elevational gradient. *Journal of Biogeography*, **38**, 394–405.
- Kraft, N.J.B., Godoy, O., & Levine, J.M. (2015) Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences*, **112**, 797–802.
- 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.
- Kudo, G. (1996) Intraspecific variation of leaf traits in several deciduous species in relation to length of growing season. *Ecoscience*, **3**, 483–489.
- Lamanna, C., Blonder, B., Violle, C., Kraft, N.J.B., Sandel, B., Símová, I., Donoghue, J.C., Svenning, J.-C., McGill, B.J., Boyle, B., Buzzard, V., Dolins, S., Jorgensen, P.M., Marcuse-Kubitza, A., Morueta-Holme, N., Peet, R.K., Piel, W.H., Regetz, J., Schildhauer, M., Spencer, N., Thiers, B., Wiser, S.K., & Enquist, B.J. (2014) Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences*, **111**, 13745–13750.
- Leibold, M.A. (1995) The niche concept revisited: Mechanistic models and community context. *Ecology*, **76**, 1371–1382.
- MacArthur, R.H. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, **101**, 377–385.
- Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.
- McGill, B.J., Enquist, B.J., Weiher, E., & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- Mouillot, D., Stubbs, W.J., Faure, M., Dumay, O., Tomasini, J.A., Wilson, J.B., & Chi, T.D. (2005) Niche overlap estimates based on quantitative functional traits: A new family of non-parametric indices. *Oecologia*, **145**, 345–353.
- Moulton, M.P. & Pimm, S.L. (1987) Morphological assortment in introduced Hawaiian passerines. *Evolutionary Ecology*, **1**, 113–124.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A.C., Aquino, S., & Cornelissen, J.H.C. (2013) New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167–234.
- Poorter, H. & Garnier, E. (1999) Ecological significance of inherent variation in relative growth rate and its components. In F. Pugnaire & F. Valladares (Eds.), *Handbook of functional plant ecology* (pp. 81–120). Boca Raton, FL: CRC Press.
- R Development Core Team (2017). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org>.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, C., Bowman, W.D., & Sep, N. (1999) Generality of Leaf Trait Relationships : A Test across Six Biomes. **80**,

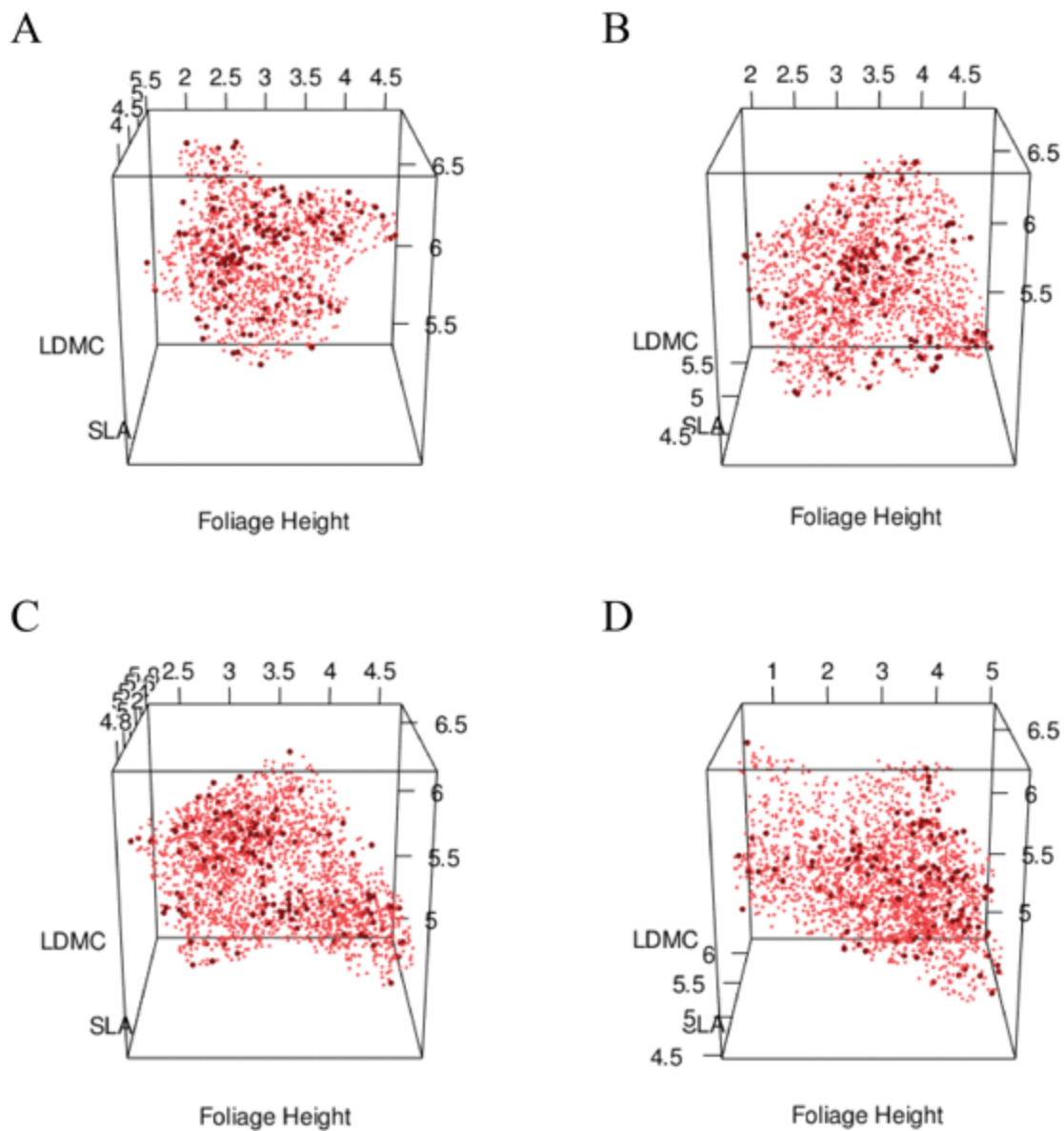
1955–1969.

- Reich, P.B., Walters, M.B., & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristic among diverse ecosystem. *Ecological Monographs*, **62**, 365–392.
- Reich, P.B., Walters, M.B., & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in plant functioning. *Ecology*, **94**, 13730–13734.
- Ricklefs, R.E. (1990) *Ecology*. New York, NY: W. H. Freeman.
- Ricklefs, R.E. & Travis, J. (1980) A morphological approach to the study of avian community organization. *The Auk*, **97**, 321–338.
- Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**, 156–162.
- Roughgarden, J. (1972) Evolution of niche width. *The American Naturalist*, **106**, 683–718.
- Ryser, P. & Urbas, P. (2000) Ecological significance of leaf life span among Central European grass species. *Oikos*, **91**, 41–50.
- Schamp, B.S., Chau, J., & Aarssen, L.W. (2008) Dispersion of traits related to competitive ability in an old-field plant community. *Journal of Ecology*, **96**, 204–212.
- Scheffer, M. & van Nes, E.H. (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences*, **103**, .
- Schöb, C., Armas, C., Guler, M., Prieto, I., & Pugnaire, F.I. (2013) Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology*, **101**, 753–762.
- Sides, C.B., Enquist, B.J., Ebersole, J.J., Smith, M.N., Henderson, A.N., & Sloat, L.L. (2014) Revisiting darwins hypothesis: Does greater intraspecific variability increase species ecological breadth? *American Journal of Botany*, **101**, 56–62.
- Silverman, B.W. (1992) *Density estimation for statistics and data analysis*. Chapman & Hall, London.
- Silvertown, J. (2004) Plant coexistence and the niche. *Trends in Ecology and Evolution*, **19**, 605–611.
- Spasojevic, M.J. & Suding, K.N. (2012) Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, **100**, 652–661.
- Stubbs, W.J. & Wilson, J.B. (2004) Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, **92**, 557–567.
- Thomson, F.J., Moles, A.T., Auld, T.D., & Kingsford, R.T. (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, **99**, 1299–1307.
- Tilman, D., Knops, J., Wedin, D., Reich, P.B., Ritchie, M., & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.
- Vellend, M., Srivastava, D.S., Anderson, K.M., Brown, C.D., Jankowski, J.E., Kleyhans, E.J., Kraft, N.J.B., Letaw, A.D., Macdonald, A.A.M., Maclean, J.E., Myers-Smith, I.H., Norris, A.R., & Xue, X. (2014) Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos*, **123**, 1420–1430.
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C.M., Jung, V., & Messier, J. (2012) The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology and Evolution*, **27**, 244–252.

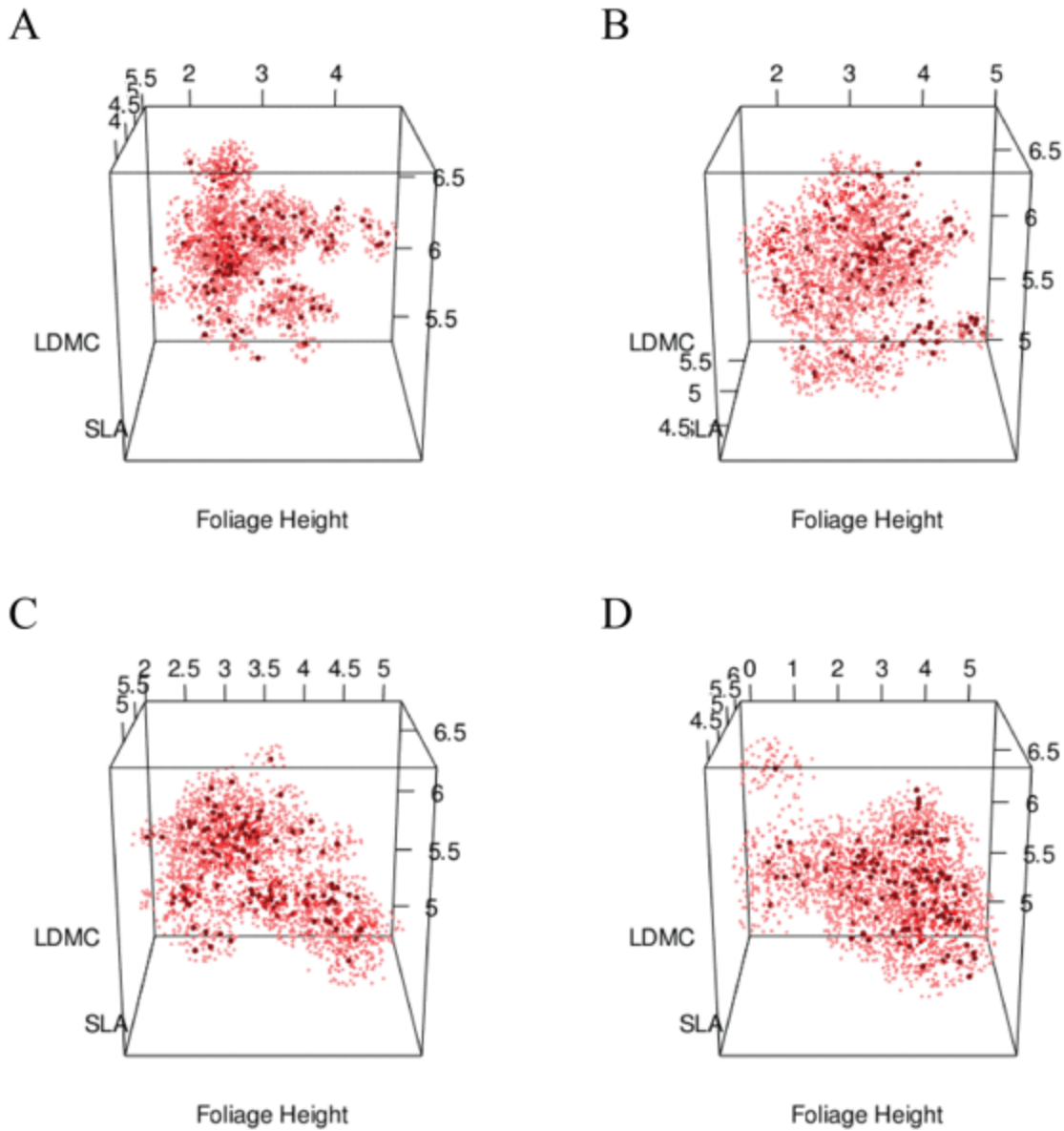
- Violle, C. & Jiang, L. (2009) Towards a trait-based quantification of species niche. *Journal of Plant Ecology*, **2**, 87–93.
- Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., & Kattge, J. (2014) The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences*, **111**, 13690–13696.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., & LeRoy Poff, N. (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, **13**, 267–283.
- Weiher, E. & Keddy, P.A. (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, **74**, 159–164.
- Weiher, E., Clarke, G.D.P., & Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, **81**, 309–322.
- Weiher, E. & Keddy, P.A. (1999) *Ecological assembly rules: Perspectives, advances, retreats*.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby, M., Falster, D.S., Moles A.T., Vesk P.A., & Wright I.J. (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklass, E.J., & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright, J.S. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.



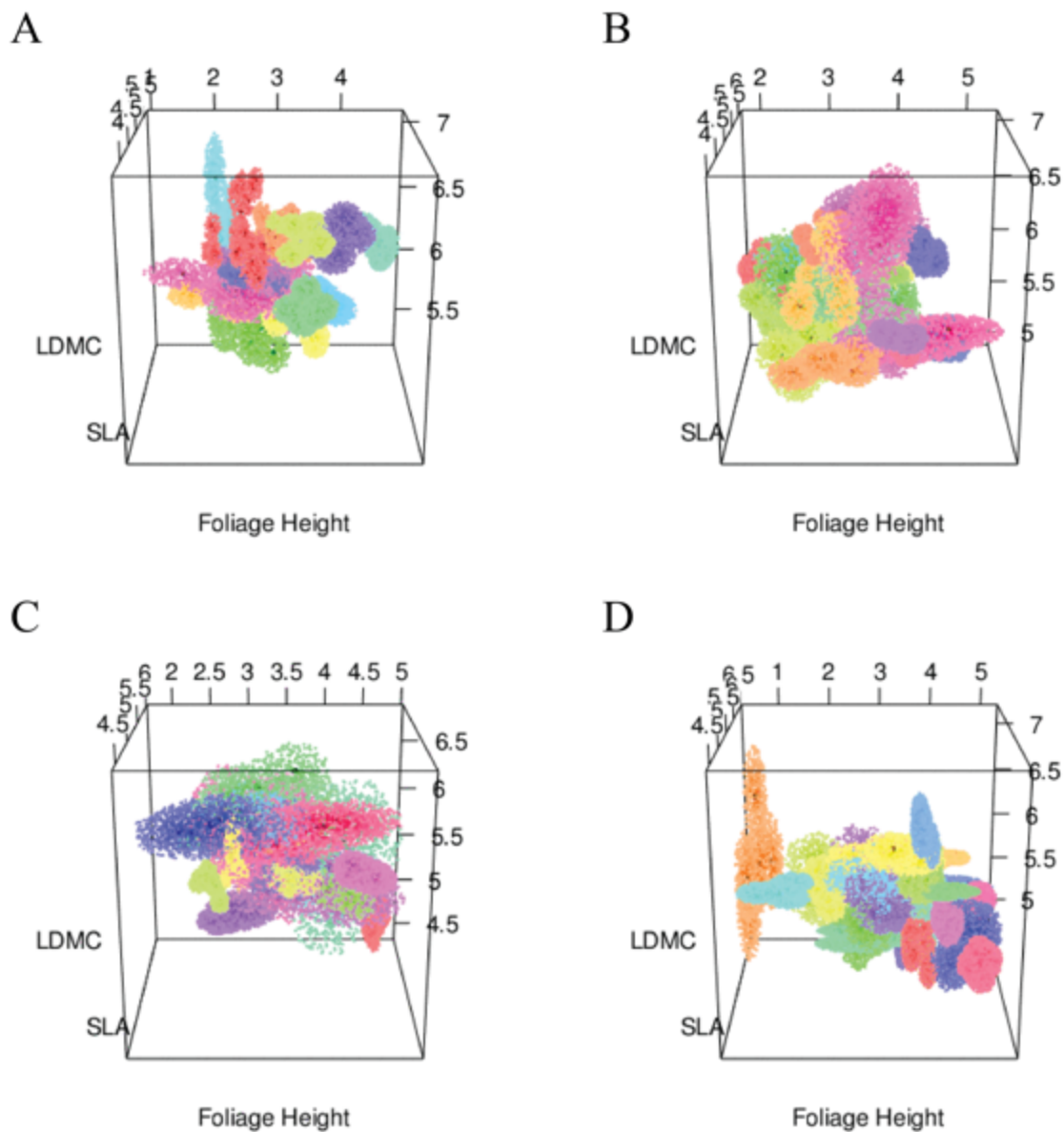
**Figure 1.** Map of study sites: CBT (Crested Butte Landtrust; 38.8819, -106.9803), Road (38.8969, -106.9786), Pfeiler (38.9609, -107.0314), PBM (Painter Boy Mine; 38.9695, -107.0409), Cinnamon (38.9916, -107.0664).



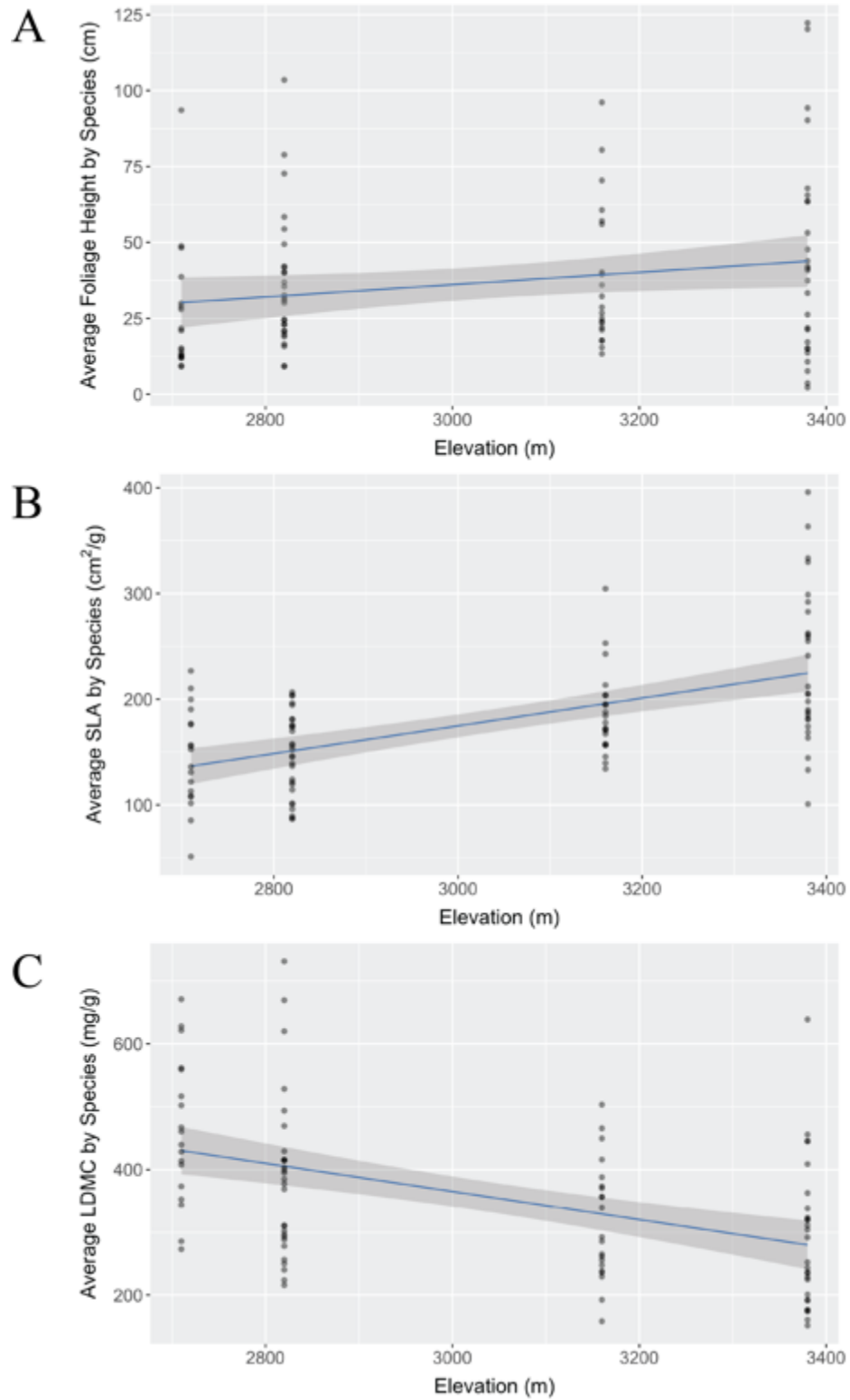
**Figure 2.** Site-level hypervolumes constructed with the One-Class Support Vector Machine method. (A) CBT, (B) Road, (C) Pfeiler, (D) PBM. These images are animated in Movies S1, S3, S5, S7.



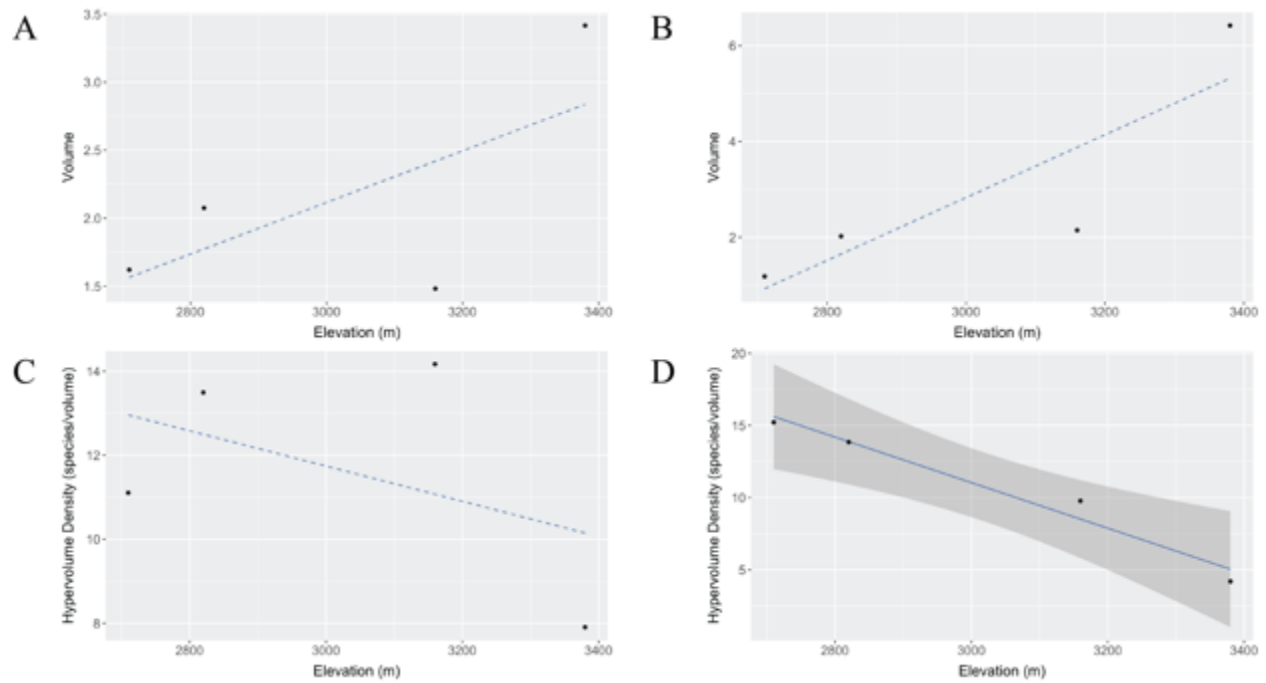
**Figure 3.** Site-level hypervolumes constructed with the Gaussian Kernel Density Estimate method. (A) CBT, (B) Road, (C) Pfeiler, (D) PBM. These images are animated in Movies S2, S4, S6, S8.



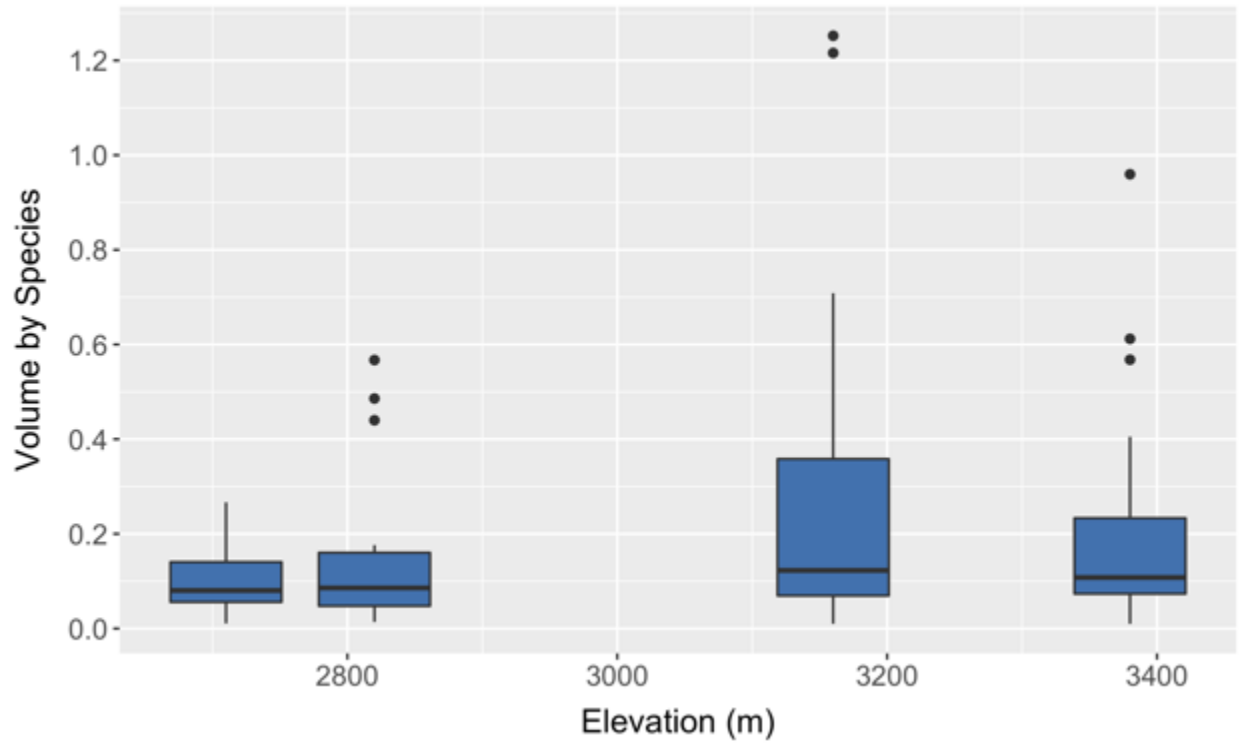
**Figure 4.** Species-level hypervolumes constructed with the Gaussian Kernel Density Estimate method. (A) CBT, (B) Road, (C) Pfeiler, (D) PBM. These images are animated in Movies S9-S12.



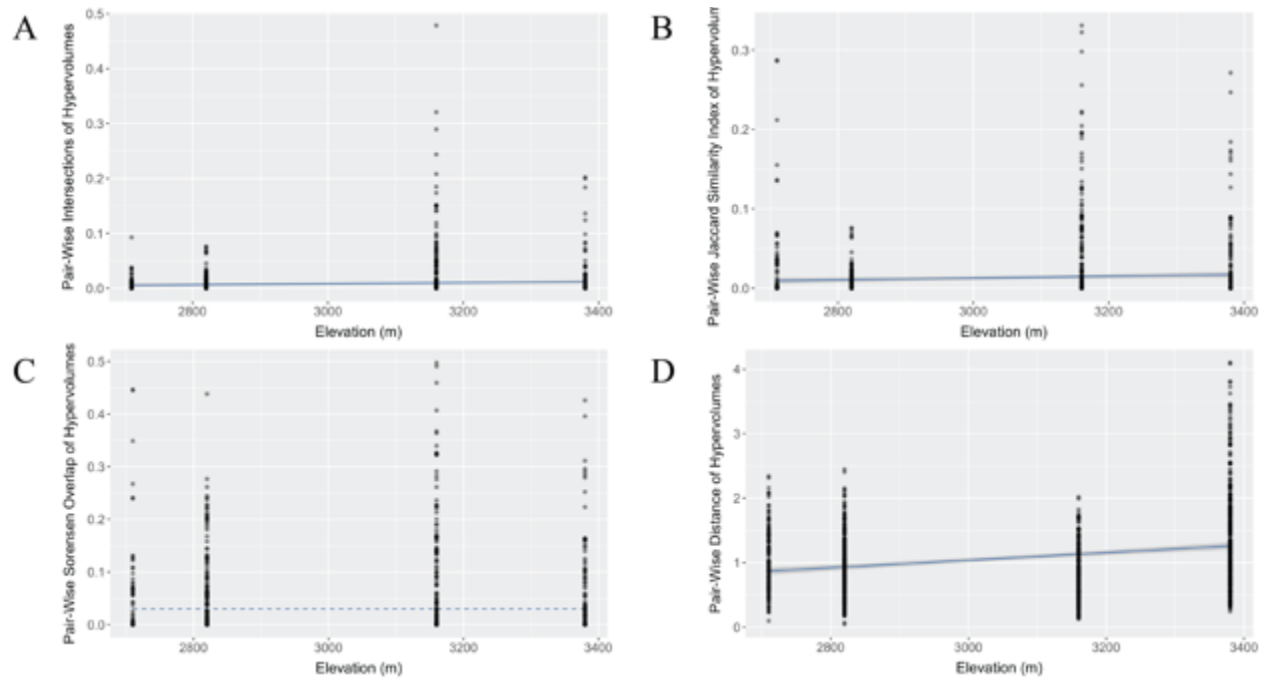
**Figure 5.** The relationship between mean trait values for each species and elevation. Each point represents the mean trait value for a single species. (A) Foliage height, (B) specific leaf area, (C) leaf dry matter content. The shaded areas represent the 95 % confidence interval.



**Figure 6.** The relationship between the volumes of site-level hypervolumes and elevation, calculated with the (A) One-Class Support Vector Machine method and (B) Gaussian Kernel Density Estimate method. The relationship between the densities of site-level hypervolumes and elevation, calculated with the (C) One-Class Support Vector Machine method and (D) Gaussian Kernel Density Estimate method. The solid lines represent significant relationships, with 95 % confidence interval shown as shaded areas. The dotted lines represent non-significant relationships.



**Figure 7.** The relationship between the volumes of species-level hypervolumes and elevation.



**Figure 8.** The relationships between elevation and (A) pair-wise intersections, (B) pair-wise Jaccard similarity indices, (C) pair-wise Sorensen overlap, (D) pair-wise distances of species-level hypervolumes. Each point represents a single pair-wise value. The solid lines represent significant relationships, with 95 % confidence interval shown as shaded areas. The dotted lines represent non-significant relationships.

**Table 1.** Jaccard pair-wise dissimilarity\* of site species composition.

|         | CBT | Road   | Pfeiler | PBM    |
|---------|-----|--------|---------|--------|
| CBT     |     | 0.7895 | 0.9167  | 0.9535 |
| Road    |     |        | 0.8605  | 0.9000 |
| Pfeiler |     |        |         | 0.8293 |
| PBM     |     |        |         |        |

\* Jaccard dissimilarity =  $(b + c)/(a + b + c)$ , where  $a$  is the number of species present in both sites,  $b$  is the number of species unique to the first site and, and  $c$  is the number of species unique to the second site (Baselga 2012).

**Table 2.** Functional trait data sampling effort by site in terms of species richness, abundance, and vegetation cover (%) sampled.

| Site    | Elevation (m) | Species Richness | Species Sampled | Richness Sampled (%) | Abundance Sampled (%) | Vegetation Cover Sampled (%) |
|---------|---------------|------------------|-----------------|----------------------|-----------------------|------------------------------|
| CBT     | 2710          | 22               | 18              | 81.8                 | 98.4                  | 99.7                         |
| Road    | 2820          | 41               | 28              | 68.3                 | 77.0                  | 83.1                         |
| Pfeiler | 3160          | 26               | 21              | 80.8                 | 93.3                  | 91.0                         |
| PBM     | 3380          | 36               | 27              | 75.0                 | 85.6                  | 99.0                         |

**Table 3.** Pair-wise hypervolume overlap statistics.

| Overlap Statistic        | Definition                                                                                   |
|--------------------------|----------------------------------------------------------------------------------------------|
| Intersection             | The intersection (i.e. overlapping volume) of hv1 and hv2.                                   |
| Jaccard Similarity Index | Volume of intersection of hv1 and hv2 divided by volume of union of hv1 and hv2.             |
| Sorensen Overlap         | Twice the volume of intersection of hv1 and hv2 divided by volume of hv1 plus volume of hv2. |

**Table 4.** Results of pair-wise two-sample t-tests for mean volumes of species-level hypervolumes by site.

|         | CBT | Road                      | Pfeiler                      | PBM                          |
|---------|-----|---------------------------|------------------------------|------------------------------|
| CBT     |     | t = -0.6278<br>P = 0.5334 | t = -2.1491<br>P = 0.04285 * | t = -1.8114<br>P = 0.07866 . |
| Road    |     |                           | t = -1.8553<br>P = 0.0757 .  | t = -1.2634<br>P = 0.2131    |
| Pfeiler |     |                           |                              | t = 1.0434<br>P = 0.305      |
| PBM     |     |                           |                              |                              |

Significance codes: '\*' = 0.05, '.' = 0.1, ' ' = 1

## **Supporting Information**

Movies S1-S12. Animated gifs of three-dimensional renderings of constructed hypervolumes.

Access at: <https://drive.google.com/open?id=0B6jWs0ml9IQrUIN3RkU4dklHQTA>.