

# Predicting plant trait similarity along environmental gradients

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**Abstract** Plant traits affect the success or failure of plants to establish, grow, and reproduce. Although we have an increased understanding of certain individual plant traits and their relative effects on performance and fitness, it is a challenge to predict relative similarity of traits between neighbouring plants. Assembly rules suggest that abiotic filters will restrict the range of viable strategies, thus creating a community of plants that share a similar suite of traits. In contrast, limiting similarity predicts that segregation of species' resource use will lead to character displacement. What is the relative strength of these two processes and do they differ depending on site condition? We know that trait similarity of plants can vary with site productivity and disturbance. In this study, we investigate the interaction of these two ecological factors and how they affect plant trait similarity. We find support for the hypothesis that trait convergence occurs at low productivity/high disturbance and high productivity/low disturbance, and trait

dispersion is most likely at intermediate levels of disturbance and productivity. The relationships among evolution, plant traits, and ecology are multivariate, hierarchical, and complex making plant traits at the ecosystem level an exciting and challenging agenda for the future.

**Keywords** Plant traits · Community assembly · Vegetation · Limiting similarity

## Niche differentiation and coexistence

Ever since Darwin (1859) proposed that coexistence between species is necessitated by variation in species traits there has been a focus on competition and niche differentiation to explain plant community patterns (MacArthur and Levins 1967; Diamond 1979; Goldberg and Barton 1992; Pacala and Tilman 1994). Coexistence facilitated by the divergence of species traits is supported by strong experimental evidence and mathematical models (Tilman 1982; Rees et al. 2001; Uriarte and Reeve 2003; Stubbs and Wilson 2004; Schwilk and Ackerly 2005). However, empirical studies in natural plant communities show mixed results (Grime 2006; Jiang et al. 2010; Violle et al. 2011; Bennett et al. 2013; Best et al. 2013; Narwani et al. 2013; Park and Potter 2013). A review by Cahill et al. (2008) of 142 species from five multispecies experiments showed that the relationship between

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competition intensity and relatedness was weak, which led the authors to conclude that Darwin's assertion that competition will be strongest among closely related species is not supported by empirical data.

Recent studies have demonstrated a narrower range of trait values within communities than expected from a random sampling, and evidence to support the simultaneous forces of habitat filtering leading to sharing of trait values and niche partitioning that limits the similarity of coexisting species (Diaz et al. 2004; Fukami et al. 2005; Cornwell and Ackerly 2009; Mayfield and Levine 2010; Adler et al. 2013; Godoy et al. 2014; Kraft et al. 2015a; Butterfield 2015). Assuming there are mechanisms responsible for trait divergence and trait convergence in plants and if it is possible to determine environmental site conditions that predicate trait similarity it is possible to develop trait-based models of plant community assemblages and ecosystem function (Adler et al. 2013; Coyle et al. 2014; Kraft et al. 2015a, b).

### Divergence and convergence in plant traits

A multitude of factors influence the structure of plant communities; therefore, attempts to explain species assemblage have led to a range of partially overlapping hypotheses (Table 1). Hypotheses explaining the divergence of plant traits are based upon ways in which plants have diversified their niche requirements: competition past (Connell 1980) or present (Chesson 2000), resource acquisition (Tilman 1982), limiting similarity (MacArthur and Levins 1967), and coevolution (Turkington 1989). Hypotheses explaining trait convergence have relied on robust trait–environment linkages: plant strategy theory (Grime 1977), growth-rate hypothesis (Coley et al. 1985), and centrifugal organization (Keddy 1990). For example, high-productivity freshwater marshes that experience little disturbance have been shown to be dominated by tall-statured, fast-growing, clonal dominants, thus sharing similar traits (Keddy 1990). Recent work has emphasized the coexistence of mechanisms that involve resource partitioning and spatial or temporal environmental heterogeneity (Adler et al. 2013; Coyle et al. 2014; Kraft et al. 2015a, b).

Advances in the development of large databases of plant traits and field studies have helped to clarify some

community patterns (Grime et al. 1997; Diaz et al. 2004; Fukami et al. 2005; Reich et al. 2007; Fraser et al. 2015; Kunstler et al. 2016). Of primary interest are two mechanisms responsible for trait convergence and divergence in plants: productivity and disturbance (Grime 2006). Productivity has been proposed to cause convergence in trait similarity, while disturbance has been related to divergence in species traits (Grime 2006). However, Grime (2006) postulates that productivity is a relatively stable factor across space and time within a plant community, and therefore variation in evolutionary response to changes in productivity is thought to be little. Following this argument, Grime (2006) stressed the importance of disturbance as the major factor in determining divergence and the relative similarity in traits in plant communities.

There is a great variation in terrestrial primary productivity, from the micro to macro scale. At the macro scale, productivity can be correlated to general climatic factors including photoperiod, light intensity, moisture, and humidity (Rosenzweig 1968; Sala et al. 1988). At the micro scale, environmental and biological properties can lead to a greater variation in productivity; for example, nutrient pulses and zones of depletion caused by root foraging in the soil can occur rapidly (Bilbrough and Caldwell 1997). This variation in primary productivity has been related to many factors, including plant and animal composition, diversity, competition, trophic interactions, and priority effects (Hairston and Hairston 1993; Bilbrough and Caldwell 1997; Hutchings et al. 2003; Körner et al. 2008). While plants adapted to low- and mid-productivity sites can express variation in trait characteristics, at high-productivity plants often express trait convergence (Grime et al. 1997; Diaz et al. 2004). Plants adapted to high-resource sites generally invest relatively little in plant–herbivore defences (Coley et al. 1985) and have high leaf nutrient concentrations (Wright et al. 2004). Keddy (1990) has argued that environmental site characteristics at high productivity are limited, whereas there is the potential for many different types of low-productivity sites. High-productivity site requires high resource availability of nutrients, water, and light. Plant species that have adapted to these conditions are generally tall-statured, with high leaf area index and high relative growth rates (Keddy 1990; Grime et al. 1997). At the other extreme end of site productivity, low productivity might be caused by many different factors which would

**Table 1** Hypotheses for trait divergence and trait convergence

## Trait divergent niche-based theories

*Limiting similarity*—MacArthur and Levins (1967). The smallest difference between competitors that allows their coexistence. Larger differences between competing species will lead to greater stability

*The ghost of competition past*—Connell (1978). The asserted effect of competition is to eliminate itself by causing niche divergence in competing species, and as a consequence, it is difficult to prove or disprove that competition is responsible for the divergence

*R\* theory*—Tilman (1982). Based on logistic-competition theory, the regulation of population size is modelled on resource dynamics, i.e. supply and consumption of resources. Coexistence is only possible through ecological segregation of resource use

## Trait convergent trait–environment-based theories

*Plant strategy theory*—Grime (1973b). Two external factors control plant performance and fitness: stress (S) and disturbance (D). The interaction of these two factors results in three primary plant strategies: ‘competitors’ that occupy low S/low D sites, ‘stress-tolerators’ that occupy high S/low D sites, and ‘ruderals’ that occupy low S/high D sites

*Growth-rate hypothesis*—Coley et al. (1985). Plant species are adapted to habitats based on resource limitation. Plants with intrinsically fast growth rates must allocate more carbon to growth and less carbon to chemical defences, thereby making a small investment in broadly effective plant defences compared to plants with intrinsically slow growth rates

*Centrifugal organization*—Keddy (1990). A combination of important ecological gradients, both biotic and abiotic, that describes patterns of vegetation and plant traits. Biomass is the predominant gradient, with other varying gradients radiating out of a central habitat type of low site variation

## Trait-based coexistence mechanisms

*Coexistence mechanisms*—Adler et al. (2013). Mechanisms that control trait similarity include spatial and temporal heterogeneity, natural enemies, and resource partitioning, and these mechanisms operate simultaneously. Therefore, coexistence likely results from trade-offs among many axes of trait variation

therefore require different trait adaptations. A plant adapted to an environment with limited water availability must have plant traits to tolerate drought, such as waxy cuticle, high stomatal density, and leaf hairiness, to survive and grow (Wright et al. 2004). Plant survival in high saline soils is determined by the ability to exude salts or store them in specialized cell vacuoles (Cheeseman 1988). Both of these low-productivity environments require different plant trait strategies, but it is more likely to find trait convergence by site according to the cause of low productivity. Therefore, we suggest that plant trait convergence is most likely to occur at the extreme ends of the site productivity gradient, but that trait convergence at high productivity is comparable across sites and trait convergence at low productivity is dependent on site and may include a wider variety of different trait characteristics for survival and growth under their particular site condition.

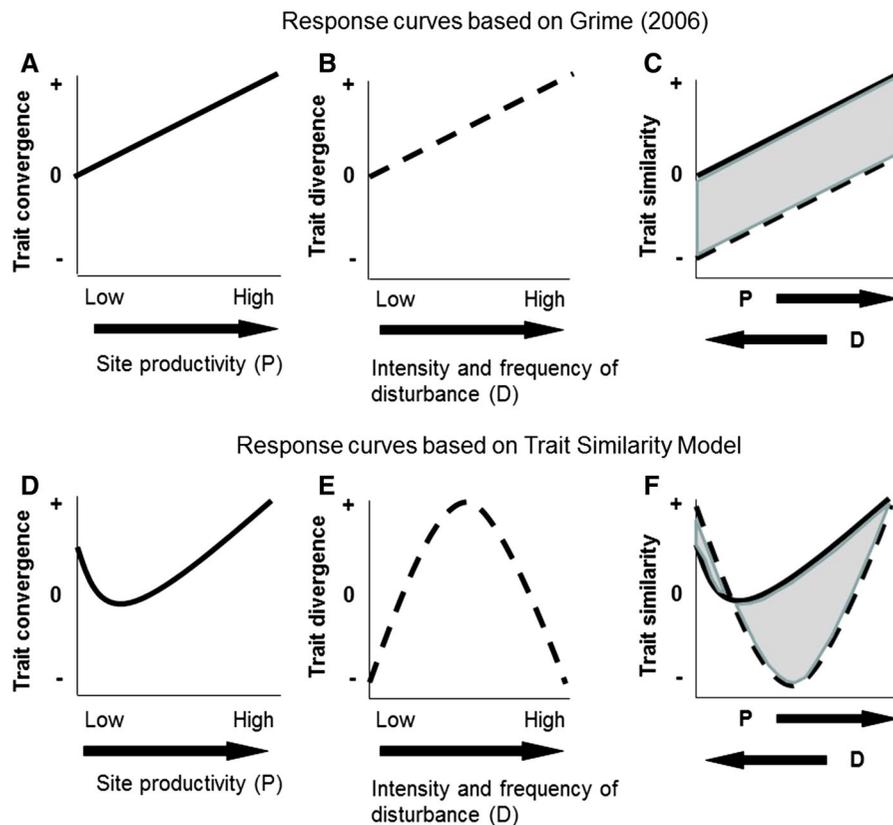
The role of disturbance in controlling diversity in plant communities is well established (Grubb 1977; Connell 1978; Pickett and White 1985) and intermediate levels of disturbance have been associated with maximum diversity (Grime 1973a; Connell 1978). Disturbance can allow coexistence between potential

dominants and smaller subordinates (Fraser and Grime 1999; Fine et al. 2004), and provides opportunities for species with different regenerative life-history traits to coexist (Grubb 1977; Thompson et al. 1996). A few traits, such as short life span and high seed dispersal, have a general association with responses to disturbance, but further detailed studies show that plant traits are specific to the type of disturbance (Grime 1977), respond to disturbance characteristics (e.g. severity, spatial scale, and frequency) (Denslow 1980), and display more than one strategy for survival under any given condition (Cunningham et al. 1999; Westoby et al. 2002; Pierce et al. 2007). The different characteristics of disturbance and the many ways plants have evolved to respond to disturbance have therefore likely led to trait divergence (Grime 2006). However, frequent (i.e. predictable) and intense disturbances are often associated with plants with similar suites of traits, e.g. arable weeds and fire-adapted plants (McIntyre et al. 1999), suggesting the potential for trait convergence when disturbance is frequent and intense. A site with minimal disturbance is also predictable and therefore also potentially associated with trait convergent forces.

## Trait similarity of plant traits

We predict that the coexistence of mechanisms (Adler et al. 2013; Kraft et al. 2015a, b), specifically the interaction between productivity and disturbance, can influence trait similarity in the assemblage of plant communities (Fig. 1). In Figs. 1a–c, we illustrate the ideas associated with Grime’s hypothesis (Grime 2006). Plant species adapted to the high end of the productivity gradient will experience trait convergence (Fig. 1a). In contrast, disturbance promotes trait

divergence (Fig. 1b). However, productivity and disturbance as mechanisms of trait convergence and trait divergence, respectively, are interacting properties in plant communities and therefore may be used to construct a general model of species trait adaptation. Figure 1c shows the interaction of two processes depicted in Fig. 1a and b, and can be used to make three predictions: (1) trait convergence between species is likely greatest at high productivity and low disturbance; (2) trait divergence between species is likely to be greatest at low productivity and high



**Fig. 1** Productivity and disturbance may interact to affect trait similarity. **a–c** According to Grime (2006), the convergence of plant traits occurs at low productivity and is amplified by high productivity (**a**), and trait divergence between plant species is caused by disturbance (**b**). Therefore, interaction of these two processes in a community suggests that trait similarity is most likely at high productivity/low disturbance sites and trait dissimilarity is most likely at low productivity/high disturbance sites (**c**). **d–f** A modified model based on empirical evidence suggests that trait convergence will occur at low and high productivity (**d**), and trait divergence occurs at intermediate disturbance, with trait convergence at low and high disturbance (**e**). In this scenario, the interaction of productivity and

disturbance would suggest that trait similarity occurs at low productivity/high disturbance and high productivity/low disturbance. Trait dissimilarity is most likely at intermediate levels of disturbance and productivity. In the figure, the effect of productivity on trait similarity is identified as a *solid line* while disturbance is a *dashed line*. The *shaded area* indicates potential for trait similarity between individual plants. The value of ‘0’ on the y-axis indicates the null response when there is no measurable effect on plant traits with respect to either productivity or disturbance, whereas ‘+’ and ‘–’ represent variations from the null; such that ‘–’ trait similarity indicates divergence from the null, and ‘+’ is convergence

disturbance; and (3) the potential for variation in trait similarity and dissimilarity between species remains similar across the productivity/disturbance gradient.

In Figs. 1d–f, we propose a modified model based on empirical evidence presented above. Plants adapted to high and low ends of the productivity gradient will display trait convergence (Fig. 1d); however, trait convergence will be greatest at high productivity because of the limited successful plant traits associated with resource capture when resource availability is high. Disturbance can cause trait divergence (Fig. 1e) but only at intermediate levels. At low and high frequency and intensity of disturbance, plants have adapted to predictable scenarios and display trait convergence. The predictions based on the interaction of Fig. 1d and e are as follows: (1) trait convergence between species is greatest at high productivity/low disturbance and low productivity/high disturbance; (2) trait divergence is likely to be greatest at intermediate levels of productivity and disturbance; and (3) variation in trait similarity is at a maximum at intermediate levels of productivity and disturbance because of opposing divergent and convergent adaptive processes. That is, the likelihood of finding two species with similar or dissimilar plant traits is least predictable at intermediate productivity and disturbance.

While this trait similarity model is not directly related to coexistence, we can infer that the potential for coexistence is highest where there is greatest potential variation in traits between species, which occurs at intermediate productivity and disturbance. This pattern corresponds with Grime's hump-backed model of species richness (Grime 1973a), which is an empirically well-supported relationship in the literature (Rajaniemi 2003; Fraser et al. 2015; but see Adler et al. 2011). An increase in trait variation within a community will logically increase functional diversity.

Fukami et al. (2005) illustrates the importance in measuring plant traits and species composition with respect to convergent and divergent processes. In their paper, initial plant composition was manipulated on abandoned arable land. Although species identity remained divergent over a nine-year period, there was a convergence in species traits. Cornwell and Ackerly (2009) showed evidence of both habitat filtering and trait similarity in a test of shifts in plant trait distributions across a soil moisture environmental gradient. In their study, the range of specific leaf area measurements were more restricted than a null model

would predict for plants growing at the dry end of the gradient, suggesting trait filtering. However, they found a non-random, even spacing of trait values relative to the null model, suggesting limiting similarity. Accordingly, Adler et al. (2013) present an argument that trait differences are a result of coexistence mechanisms, including habitat heterogeneity, natural enemies, and resource partitioning. Recent studies demonstrate the importance of multiple factors on trait dispersion (Coyle et al. 2014; Kraft et al. 2015b; Butterfield 2015). In this discussion, we have referred to variation in traits between species. Significant trait variation can also occur within species (Turkington 1989; Booth and Grime 2003; Cahill et al. 2005), and the trait similarity model can equally be applied to intraspecific trait variation. For example, the trait similarity model predicts that genotypes of species established in high-productivity environments would have higher trait similarity and smaller variance in traits than genotypes of the same species established in mid-productivity environments.

### Testing the model

Table 2 is a list of suggested plant traits for measurement to test trait similarity in habitats that vary in productivity and disturbance (Grime et al. 1997; Weiher et al. 1999; Wright et al. 2004; Diaz et al. 2004). Although studies have attempted to classify specific disturbance response traits (McIntyre et al. 1999) and productivity response traits (Cunningham et al. 1999) there is overlap and therefore we have listed the most likely traits to be related to one or both of these two factors. Information at the plant trait level, when measured, has generally been used as a predictive tool to determine environmental site condition, or to predict relative species abundance and performance across environmental gradients. To increase the understanding of plant communities and to test the trait similarity model, it is necessary to incorporate plant–plant interactions at the level of plant traits. Multivariate information on plant traits can be analysed using similar statistical procedures traditionally applied to plant communities. For example, Sorensen's similarity coefficient (Sørensen 1948) may be used to determine the similarity of one individual plant between that of its neighbour based on data from a suite of plant traits. The mean and

**Table 2** Plant traits for field measurement

| Function             | Trait                           |
|----------------------|---------------------------------|
| Dispersal            | Seed mass                       |
|                      | Seed shape                      |
|                      | Onset of flowering <sup>†</sup> |
|                      | Number of flowers               |
| Persistence          | Specific leaf area <sup>†</sup> |
|                      | Leaf water content <sup>†</sup> |
|                      | Leaf C:N ratio                  |
|                      | Stomatal density                |
|                      | Aboveground biomass             |
|                      | Height <sup>†</sup>             |
|                      | Vegetative spread <sup>†</sup>  |
|                      | Resprouting ability             |
|                      | Palatability                    |
|                      | Specific stem density           |
| Specific root length |                                 |
| Root tissue density  |                                 |

Derivatives of traits with an (†) were used in the preliminary analysis reported here

variation of Sorensen's similarity coefficients could then be used to determine trait similarity within a community that can then be compared to communities under different environmental site conditions. A similar method using partial correlations on plant functional types or species as community components has been used by Pillar et al. (2009) to define convergent and divergent trait patterns.

Alternatively, plot-level functional trait data can be condensed into multivariate dissimilarity matrices using ordination such as non-metric multidimensional scaling (NMDS). Trait variability can be determined at the plot level as mean deflections in dissimilarity coefficients (i.e. Bray–Curtis dice or Gower distance) from the centroid within an NMDS ordination plot, and these variability estimates can then be compared via permutation tests of multivariate dispersion (Anderson 2004). Villeger et al. (2008) provides a comprehensive discussion of methods for estimating functional composition of plant communities.

While the trait similarity model can be applied to both inter- and intraspecific plant interactions, the calculations for inter- and intraspecific interactions must be analysed separately. Otherwise, the mean community similarity coefficient values may be biased

towards high similarity in monoculture communities compared to mixed species communities.

The challenge in testing the trait similarity model is to select and measure the appropriate traits to best represent the growth performance and fitness of plants. It is important to identify which traits are linked to specific disturbance regimes and productivity gradients and which of these attributes are functionally significant. Future research should be based on standardized field measurements where different traits linked with particular combinations of productivity and disturbance at the community level. A common list of traits should be adopted and a standardized methodology of recording traits should be followed in different systems in the world.

### A preliminary test of the trait similarity model

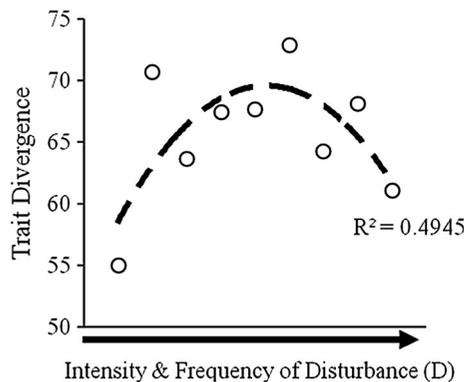
A fully factorial experiment was conducted by Carlyle et al. (2011) from 2005 to 2007 in Lac du Bois Provincial Park, consisting of semi-arid grasslands characteristic of central British Columbia, Canada (UTM 10 E 0680737 N5625980; elevation 731 m a.s.l.). Interactions among factors known to drive plant productivity were manipulated within a regularized grid (elevated temperature via open top chambers, drought via rainout shelters, increased water availability via watering, and restriction of grazing). For a complete description of the experimental design and methods see Carlyle et al. (2011). A subset of the recommended focal plant traits were recorded for the dominant species within each 1 m<sup>2</sup> survey plot, and peak biomass was collected following 2 years of manipulation. This experiment presents two potential avenues of investigation. First, the experimental treatments represent modulations of constraints on productivity (i.e. disturbance), and may be used to evaluate the general relationship shown in Fig. 1d. Second, as productivity was estimated in 2008, the relationship presented in Fig. 1c may also be evaluated.

As manipulations have been established that place limits on productivity, a simple scheme describing the 'degree of limits placed on productivity' in a multi-factorial experiment within an assumed homogeneous landscape could approximate the following: combinatorial treatments are scored in terms of the severity of their contribution to placing limits on production.

Plots with multiple restrictions (e.g. Grazing + reductions in rainfall) are assumed to have greater limits placed on productivity. Treatments that add resources (watering) are considered to increase productivity. According to the trait similarity model, those communities with intermediate restrictions on plant productivity will express the greatest degree of trait dissimilarity that exceeds both highly restricted communities and those that have recently experienced a release from resource restrictions.

### Disturbance similarity association

Figure 2 represents the results of a Permutation Analysis of Multivariate Dispersion or ‘PERMDISP’ (Anderson 2004) for treatments classified by disturbance class (rankings) for interspecific trait dissimilarities. PERMDISP is a multivariate equivalent to the Levene’s test (Levene 1960). Differences in trait dispersion are derived from distances between points in multivariate space to their centroid and significance is determined through permutation of these observations. The test is flexible enough to accommodate any number of distance coefficients and is therefore useful in assigning significance to differences in multivariate trait dispersion where data properties require non-euclidean distance coefficients (in this case, Bray–

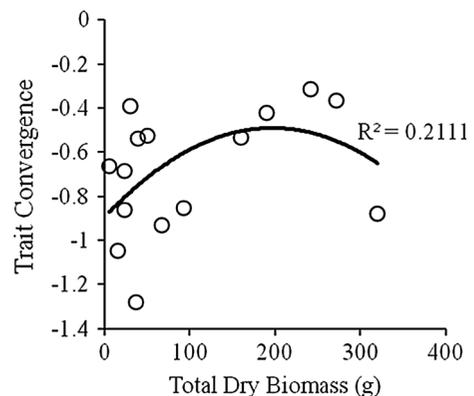


**Fig. 2** Treatment effects on multivariate dispersion. Points represent mean within-group dissimilarity (aggregated to species, using the Bray–Curtis dissimilarity coefficient). The dashed line presents a first-order polynomial fit to the dataset ( $R^2 = 0.4945$ ). As average similarity/dissimilarity calculated via the PERMDISP program represents residuals from centroids in clusters generated via NMDS, the scale of the y-axis is unitless

Curtis). The analysis indicated significant differences in community dissimilarity based on the Bray–Curtis dissimilarity coefficient ( $F_{1,9} = 2.29$ ,  $P = 0.022$ ), and the shape of the relationship was best approximated by a first-order polynomial ( $R^2 = 0.49$ ) reflective of the expected unimodal relationship depicted in Fig. 1d. These preliminary results suggest that interspecific trait dissimilarity peaks at intermediate levels of disturbance and traits appear to converge at low and high levels as predicted by the trait similarity model.

### Biomass similarity association

The same ANOVA-type analysis performed above can be applied to groups of plots sharing similar total biomass to test whether plots expressing high and low productivities express trait convergence as depicted in Fig. 1c. The dataset was divided into 15 bins ( $n = 14$  plots per bin) and a distance matrix generated using the Gower similarity coefficient. The resulting PERMDISP analysis revealed significant interbin differences among groups ( $F = 1.74$ ,  $P = 0.047$ ) (Fig. 3), while polynomial regression indicated a weak unimodal downward relationship ( $R^2 = 0.211$ ). As there are striking differences among sites in terms of productivity (the upper elevation site was over 6 times more productive than the remaining sites), there is a need for additional data and a greater coverage of sites to test this relationship.



**Fig. 3** Biomass association with multivariate dispersion. Points represent mean within-group similarity (aggregated to species, using the Gower Similarity Coefficient). Values represent 1-within-group dissimilarity. The solid line presents a first order polynomial fit to the dataset ( $R^2 = 0.211$ )

These results specifically address local-scale variations in plant trait similarity resulting from experimentally manipulated micro-environments. Inferences made from these data are inherently local, and trait variation is constrained by the potential range of trait values afforded by the regional species pool. A complete understanding of the scale-specific drivers of plant trait variation will require performing similar manipulations over a range of habitat types and simultaneously addressing drivers of trait variation within the local community and the regional species pool.

### Concluding remarks

Explaining trait similarity is likely to involve multiple mechanisms (Adler et al. 2013; Kraft et al. 2015a, b). Here, we test trait similarity for two of the principal mechanisms: productivity and disturbance. This approach reconciles two conflicting views, trait divergence through niche differentiation and competition and trait convergence through assembly rules and shared functional groups adapted to specific abiotic and biotic filtering, in understanding species assemblages, and in turn suggests how to predict functional similarity in plant communities. Ecosystem processes linked to plant traits may also be better understood through the prediction of plant trait similarity according to site environmental condition.

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