**The role of environmental filtering on desert ant community assembly**

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Keywords:

**Abstract** (<350 words @ Functional Ecology)

1. Purpose

2. Methods

3. Results

4. Discussion

**Introduction**

The extent to which community assembly mechanisms are deterministic processes i.e. niche based is a central topic in ecology. Focussing on traits instead of species identities has emerged as a major tool in understanding the mechanistic drivers of community assembly (Gotzenberger et al. 2012, Swenson 2014, de Bello et al. 2021). Functional traits reflect aspects of morphology, life history or physiology that enable an organism to be successful in an environment (Violle et al. 2007). Functional traits therefore provide a general way to relate organisms to their environments. The empirical research that supports trait-based community assembly theory has primarily been tested plant ecology (Funk et al. 2017), though there is a growing recognition of the utility of arthropod trait-based ecology (Brousseau et al. 2018, Wong et al. 2019). Ants are a model animal system to study assembly processes because ant communities are often strongly structured by abiotic environmental conditions (Retana and Cerdá 2000, Gibb et al. 2015) and competition (Camarota et al. 2016), though the latter is the subject of continuing debate (Andersen 2008, Tschinkel and King 2017). Ants are one of the most dominant insect groups in terrestrial ecosystems, and in deserts, many species are keystone taxa through their strong influence on most ecological processes (Whitford 2000). Arthropod trait-based ecology is important to generalizable, mechanistic explanations of the processes that generate and maintain biodiversity (Wong et al. 2019).

There are two major hypothesized deterministic processes that predict contrasting but non-exclusive patterns in the trait distributions of coexisting species. Environmental filtering structures communities by only allowing only organisms capable of surviving local conditions to persist within the local species pool (Keddy 1992, Vellend 2010). Environmental filtering can therefore lead to a convergence in traits among coexisting species. In contrast, the concept of limiting similarity suggests that dissimilarity in traits among ecologically similar species can promote coexistence through reducing competition and partitioning resources and the environment (Abrams 1983, Götzenberger et al. 2012). Limiting similarity can therefore lead to a divergence in traits among coexisting species. At broad spatial scales, environmental filtering is expected to be the dominant assembly mechanism, whereas at the finer spatial scales that species interactions actually occur at, mechanisms related to biotic interactions such as limiting similarity should prevail.

The relative importance of environmental and biotic filtering mechanisms can change along environmental stress gradients. Theory predicts that environmental filtering should be stronger in more stressful environments whereas competition is more important in relatively benign environments (Weiher and Keddy 1995). This stress-dominance hypothesis of community assembly is related to the stress gradient hypothesis of plant community ecology that proposes that competition decreases with increasing environmental stress (Grime 1977, Bertness and Callaway 1994). There is extensive empirical support for the stress gradient hypothesis in plant communities (Lortie and Callaway 2006, He et al. 2013), however, in animal communities, tests are relatively rare. Similarly, most research in community assembly along stress gradients have focussed on plant communities which hinders our ability to generalize community assembly. Due to the ecological importance and dominance of ants in arid ecosystems, understanding how their communities may change under increasing stress and along climatic gradients is important research to predicting the outcome of global change on these ecosystems.

In deserts, shrubs reduce environmental stress by reducing daytime heat and retaining warmth overnight, creating locally stable micro-climates (McIntire and Fajardo 2014). Shrub facilitation often increases the cover and biomass of annual plants (Holzapfel et al. 2006, Pugnaire et al. 2011), as well as arthropod species richness and abundance beneath the canopy (Liu et al. 2016, Braun and Lortie 2020, Braun et al. 2021). Surface complexity can act as a filter on ant traits, for example longer-legged ant species are more successful on rugose surfaces that short-legged species (Kaspari and Weiser 1999). Therefore, at fine scales, there is the capacity for foundation shrubs and ground-covering vegetation to alter taxonomic composition, trait distributions and coexistence patterns of the ant community.

Community assembly mechanisms are widely known to be scale-dependent. We approach the question of desert ant community assembly at two main scales. We used nine sites across the San Joaquin Desert of California, each sampled three times over the summer months. We used population-level trait measurements to study functional dispersion along the gradient with reference to a null model. We then created species distribution models for each species in this study from a curated database of ant occurrences (Guenard et al. 2017), calculate the niche overlap and asked how it relates to traits. It can therefore provide an estimate of the environmental niche overlap between species at the largest scales relevant to the overall distribution of the species across North America. We examined the hypothesis that desert ant communities are assembled by niche-based processes by testing the following predictions: 1) There will be evidence for environmental filtering on ant communities through the following responses to environmental gradients: a) alpha and beta diversity, b) trait convergence or divergence i.e. changes to functional dispersion, and c) specific trait by environment interactions (community weighted mean trait values will be correlated with environmental gradients); 2) Dissimilarity in climatic environmental niche between species will be correlated their dissimilarity in traits; 3) Effect size measure of the trait dispersion of co-occurring ants will decrease with stress (stress gradient).

These predictions will provide an assessment on the relative importance of environmental filtering and limiting similarity along stress gradients at regional scales. The larger scale analysis will answer if traits are related to the overall distribution overlap between species.

**Methods**

*Field collection*

Ant communities (Hymenoptera: Formicidae) were sampled using pitfall traps at nine sites in the San Joaquin Valley, California, USA that span a distance of ~200 km from north to south (Figure 1). Each site was sampled once per month between July and September of 2020 for a total of 27 sampling instances (Appendix Table 1). The shrub species *Ephedra californica* (Ephedraceae) and *Atriplex* sp. (Chenopodiaceae) are the dominant perennial species at six of the sites and the remaining three sites are relatively open with few shrubs. White plastic drink cups (12.4 cm tall, 9 cm diameter) were placed with the top of the cup flush with the ground. In order to prevent vertebrate bycatch, 0.5-inch hardware cloth was placed horizontally within the trap and a piece of aluminum flashing was elevated three cm above the trap to shelter the trap. The traps were filled to a depth of three cm with 100% propylene glycol. Propylene glycol is a biodegradable, non-toxic preservative that does not evaporate and preserves DNA (Nakamura et al. 2020). At shrub sites, traps were placed at 12 pairs of shrub/open microsites and pairs were located at least 10 m apart. Shrub microsites were located beneath the canopy of a foundation shrub at the center of a 0.5 m quadrat placed just inside the dripline of the shrub. Open microsites were located randomly at least 2 m away from shrub microsites. At sites without shrubs in collections areas (i.e. within 500 -1000 m of collections), pitfalls traps were deployed every 10 m in open areas along two transects located at least 10 m apart. At each site, 24 pitfall traps were deployed continuously for 72 hours per sampling event. Each sampling location was georeferenced using a handheld GPS unit. The traps were deployed in different locations within the study site each month to avoid repeated measures. Throughout the season, 648 traps were deployed totaling 46 656 trap-hours (24 traps per site \* 3 sampling instances \* 72 hours). Site-level vegetation characteristics were measured each month by placing 0.5 m quadrats every 4 m in ten 25 m transects distributed around the site and recording the percent cover of ground-covering vegetation, rocky cover, woody cover and bare ground within the quadrat. Vegetation height was measured at the center of the quadrat.

*Lab work*

Ants were first identified to genus using Fisher & Cover (2007), and to species using AntWiki keys (www.antwiki.org). Representative individuals of each species were also barcoded by the Canadian Centre for DNA Barcoding (CCD). The resulting COI? sequences were compared to BINs in BOLD systems (https://boldsystems.org/). Two singletons, *Solenopsis molesta* and *Solenopsis aurea* were excluded from analyses. We measured the following morphological trait data from the ant specimens: Weber’s length, which is the length of the longest diagonal on the thorax and a measure of overall worker body size (Brown 1953); femur length, which relates to foraging ability in complex environment and thermoregulation (Feener Jr et al. 1988); mandible length, and head length and width, which relate to diet; scape length, which relates to chemosensory abilities; and eye size which relates to foraging behaviours (Weiser and Kaspari 2006). The latter six traits were divided by Weber’s body length to remove the impact of body size.

We measured each of the seven traits in up to six individuals per species, per site (265 individual ants) to capture the intraspecific variation in traits between populations. The majority of functional trait studies use traits measured at the species-level (de Bello et al. 2021), however traits captured at the population-level can better reflect environmental filtering (Jung et al. 2010, Violle et al. 2012) and may represent local adaptation (Kawecki and Ebert 2004). We dissected each ant and affixed them to microscope slides using Elmer’s glue. We placed each ant mount slide on top of a stage micrometer slide and took focus-bracketed photographs using a Canon 60D DSLR camera with a 60 mm macro lens and Canon EF 25 II extension tube. Helicon Focus software was used to combine the focus stacks into single images. We imported each composite image into ImageJ software and used the micrometer divisions within the image to calibrate the measurement scale within the software and then measured each trait using the software.

*Analysis*

We extracted the mean annual precipitation, mean annual temperature and maximum annual temperature for each site from WorldClim (Fick and Hijmans 2017). We extracted NDVI (normalized difference vegetation index) from EVIIRS (USGS EROS Visible Infrared Imaging Radiometer Suite). EVIIRS has a 375 m spatial resolution, and 7 and 14 day temporal resolution (USGS, 2021). We used the NDVI measurement collected from the date closest to the field sampling date (Appendix Table 2). NDVI is often used as an estimate of plant productivity within animal ecology (Pettorelli et al. 2011). We additionally extracted two below-ground measures from a recently published dataset of global soil temperature: mean annual soil temperature and the annual range of soil temperatures, both at the 5cm to 15 cm depth (Lembrechts et al. 2022).

All analyses used R version 4.1.0 (R Core Team 2022). Ants forage socially and this leads to clustering of individuals from the same colony (Longino and Coddington 2002). We converted the ant data from abundance to occupancy i.e. the proportion of pitfall traps at site that each ant species was detected in. We calculated site-level vegetation cover and height by taking the mean value of the 40 quadrats. We calculated variation in vegetation cover by taking the standard deviation of cover within the quadrats.

We combined the environmental variables (mean annual precipitation, mean annual temperature and maximum annual temperature, NDVI, mean annual soil temperature, annual range of soil temperatures, mean percent vegetation cover, variation in vegetation cover and mean annual vegetation height) into a composite environmental gradient using PCA. Prior to the PCA all variables were standardized to a mean of zero and unit variance (decostand: vegan, Oksanen et al. 2010).

We calculated functional dispersion (FDisp) for each of the 27 sites using the population-level trait means using the dbFD functioning in the FD package (Laliberté et al. 2014). Fdisp is the weighted average distance of species to the centroid in multivariate trait space and a measure of multivariate dispersion (Laliberté et al. 2014).

In order to test if the observed communities were functionally clustered or dispersed, we compared the observed communities to a null model. We generated 1000 random communities using the RandomizeMatrix function in the picante package (Kembel et al. 2010). The null models were generated using the independent swap algorithm, which holds rows sums i.e. species richness and column sums i.e. occupancy/abundance of each population constant while randomizing. FDisp was calculated for each of these 1000 matrices. Standardized effect size (SES) was then calculated for each site using the following formula: (Obs – MeanRandom)/SD Random) (Swenson 2014). Positive values of SES indicate that a community is functionally dispersed, whereas negative values indicate functional trait clustering (de Bello et al. 2021). A one sample t-test was used to determine if the mean value of SES across all the populations was significantly different than zero i.e. clustered or dispersed (de Bello et al. 2021). To determine if environmental filtering impacts SES scores along the environmental gradient, we regressed the SES scores against the first axis of the PCA (PC1).

We used variance partitioning to quantify the relative contribution of environmental factors, pure space i.e. dispersal limitations and history, and spatially structured environmental factors on variation in SES functional dispersion. By controlling for spatial auto-correlation, variance partitioning is able to quantify the component of variation resulting solely from environmental factors (Smith and Lundholm 2010). We converted the WGS 1984 site coordinates to cartesian coordinates using the geoXY function in the SoDA package (Chambers 2020). We then created Moran’s eigenvector maps (MEMs) from the cartesian coordinates using the dbmem function in adespatial (Dray et al. 2018). We used the SES functional dispersion values as the response, and the standardized environmental variable matrix i.e. the same matrix as the PCA input and the MEM matrix as predictors (varpart: vegan, Oksanen et al. 2010).

We calculated the community-weighted mean (CWM) trait values for each trait using the dbFD function in the FD package (Laliberté et al. 2014). In order to test if the mean value of each trait is correlated with environmental gradient, we regressed the CWM for each trait against the PC1 axis.

To describe general taxonomic diversity patterns, we fit a poisson GLM with species richness as the response and the PC1 and PC2 axes. We also decomposed taxonomic beta diversity into occupancy weighted turnover and nestedness components (betapart package, Baselga and Orme 2012, Baselga 2013). To test if the components of beta-diversity are related to the environment, we calculated the Euclidean distance between sites using the standardized environmental matrix and used Mantel tests to test for correlations.

*Large scale environmental niche overlap*

We conducted an additional set of analyses to examine the relationship between overall climatic niche overlap and trait similarity. We extracted occurrence data from the Global Ant Biodiversity Informatics (GABI) database (Guenard et al. 2017) for each of the 11 ant species in our study. We excluded the Brazilian occurrence points for *Dorymyrmex insanus* because they were the only points south of Panama and they are likely *D. pyramicus* (Cuezzo and Guerrero 2012). For each species, occurrence points were thinned to one point per raster cell to reduce spatial bias. We generated pseudo-absences by randomly sampling 10000 points using the randompoints function from the dismo package (Hijmans et al. 2017). For each species, the background sampling area was determined by buffering the minimum convex hull of the occurrences by 100 km. This step was done to ensure that the background points were relevant to the range of each species. Mean annual temperature, maximum annual temperature and mean annual precipitation rasters from Worldclim, and mean and range of annual soil temperature rasters were used as input into species distribution models. The two soil rasters were resampled using bilinear interpolation to match the cells and extent of the climate rasters. The rasters were clipped to the following extent: -140, 7; -70, 50. Thus, the area used to generate pseudoabsences was unique for each species and the area used for prediction i.e. the extent of the rasters was identical for all species to allow for the comparison of model predictions. We used the package ENMeval (Muscarella et al. 2017) to create species distribution models for each of the ant species. This package implements the MaxEnt algorithm. The approach used by ENMeval runs a series of models in succession, using different combinations of tuning parameters to avoid overfitting while maximizing goodness of fit. We used regularization values between 1 and 5, as well as the following feature classes: linear, linear + quadratic, hinge, linear + quadratic + hinge, which correspond to settings described within the packages vignette (Muscarella et al. 2017). We used random k folds at a value of five to determine which partitions to hold back for model validation. We chose models from the range of candidate models by using the one with the lowest AIC value. We assessed the predictive performance of each model using the area under the receiver operating characteristic curve (AUC). For the resulting SDM prediction rasters, we calculated Schoener’s D i.e. climatic niche overlap for each pair of species using the function calc.niche.overlap (Muscarella et al. 2017). We converted Shoener’s D to a dissimilarity index by subtracting each value from one. We then computed Gower dissimilarity for each pair of species using the species level mean trait values. We used a Mantel test to test if the dissimilarity in traits is correlated with the dissimilarity in climatic niche overlap between species (Oksanen et al. 2010). Significance was assessed using 999 permutations.

**Results**

A total of 15519 individual ants from 11 species were collected and identified. All species are native to California. The most abundant species were *Solenopsis xyloni*, the native Southern fire ant, and *Pheidole hyatti*, the big-headed ant. Mean species richness per site was 4.1 +/- 1.42SD and ranged from a minimum of two species to a maximum of eight species.

The first PCA axis explained 50.01% of the environmental variation (Figure 2). Mean annual precipitation, maximum and mean annual temperature, and mean vegetation height were the largest environmental contributors to the PC1 axis. The composite environmental gradient was therefore cooler, wetter sites (negative PC1 values) to hotter, drier sites (positive PC1 values).

*Taxonomic diversity patterns*

Alpha diversity was not significantly predicted by PC1 (GLM: p = 0.187) or PC2 (GLM: p = 0.25). Taxonomic beta diversity was dominated by the turnover component (87.9%). Nestedness accounted for the remaining 12.1% of observed taxonomic beta diversity. The nestedness component of beta diversity was significantly correlated with environmental distance (Mantel r: 0.164, p = 0.028), however, the turnover component was not significantly correlated with the environment (Mantel r: 0.082, p = 0.135).

*Assembly patterns*

There was evidence for significant trait divergence as mean SES functional dispersion (0.58 ± 0.86 SD) was significantly greater than zero (t-test, t = 3.54, p = 0.002). Functional trait divergence SESfdisp significantly decreased as PC1 increased (R2adj = 0.165, coef = -0.507, p = 0.019) but not PC2 (coef = 0.17, p = 0.4) (Figure 2). SESfdisp was not significantly different between sites with large foundation shrubs and sites comprised of open areas (lm, coef: -0.06, p = 0.86).

*Variance partitioning*

Environmental predictors explained 19% of the variation in SESfdisp, spatially distributed environmental factors explained 32% of the variation and pure space contributed 0% (Appendix Figure 3). Variation that remained unexplained by environment and space i.e. residual was 51%.

*Community-weighted mean traits*

Weber’s body length (R2adj = 0.26, p = 0.004) and relative femur length (R2adj = 0.243, p = 0.005) were both significantly and negatively correlated with the PC1 gradient (Figure 4). The remaining traits were not significantly related to the PC1 gradient. The contribution of intraspecific variation to overall trait variation depended on the trait (Figure 5).

*Large scale analyses*

Dissimilarity in climatic niche overlap (complement of Shoener’s D) was significantly correlated with Gower dissimilarity in traits (Mantel r: 0.03776, p = 0.028). All SDMs had an AUC > 0.7 and odds < .15.

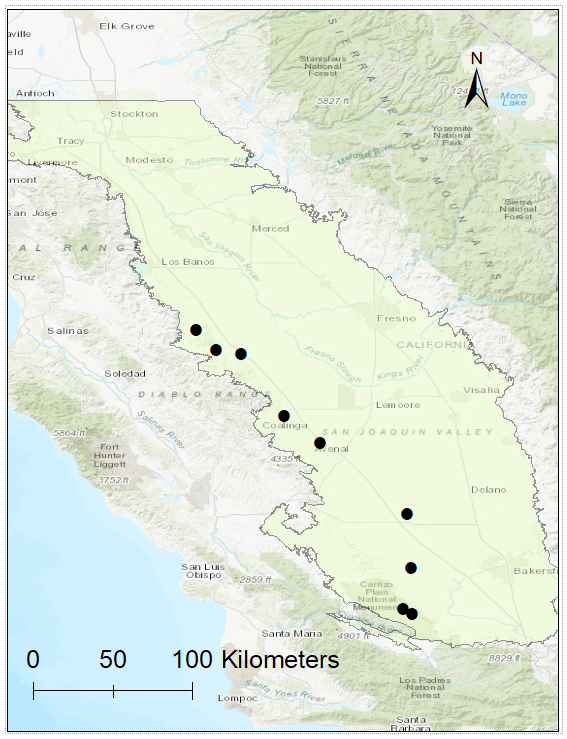


Figure 1: A map of the nine study areas. The San Joaquin Valley is the light green area.

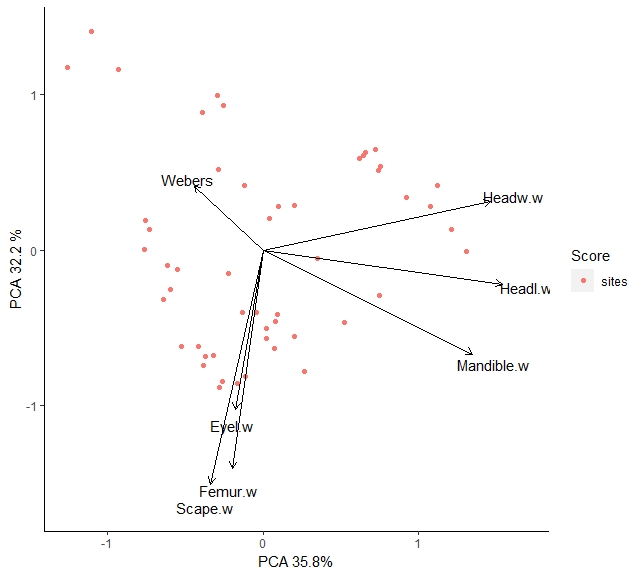
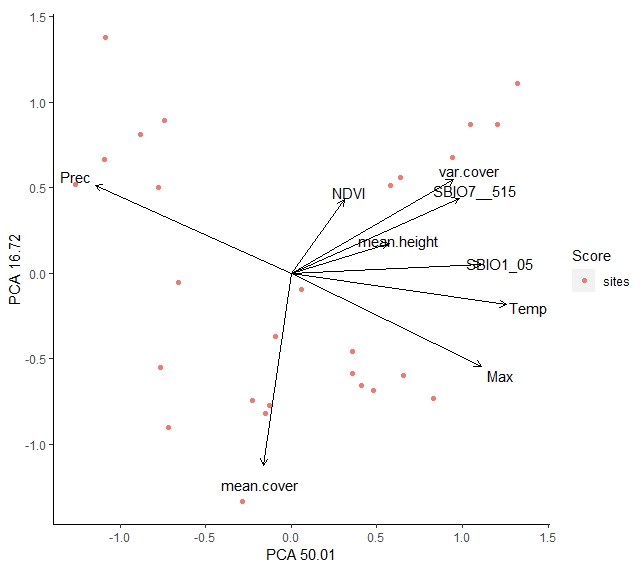


Figure 2: The relationship among environmental variables (A), and among traits (B). Principal components analysis was used to combine environmental variables into a compositive environmental gradient. The gradient ranges from relatively hot and dry to cooler and wetter.

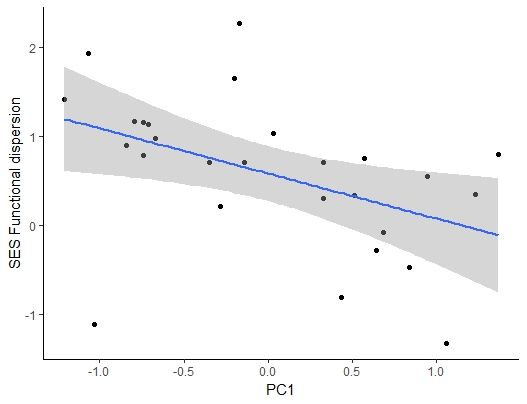


Figure 3: The relationship between the standardized effect size of functional dispersion and the composite environmental gradient (PC1). The shaded gray band represents the 95% confidence interval. The black points represent sampling instances.

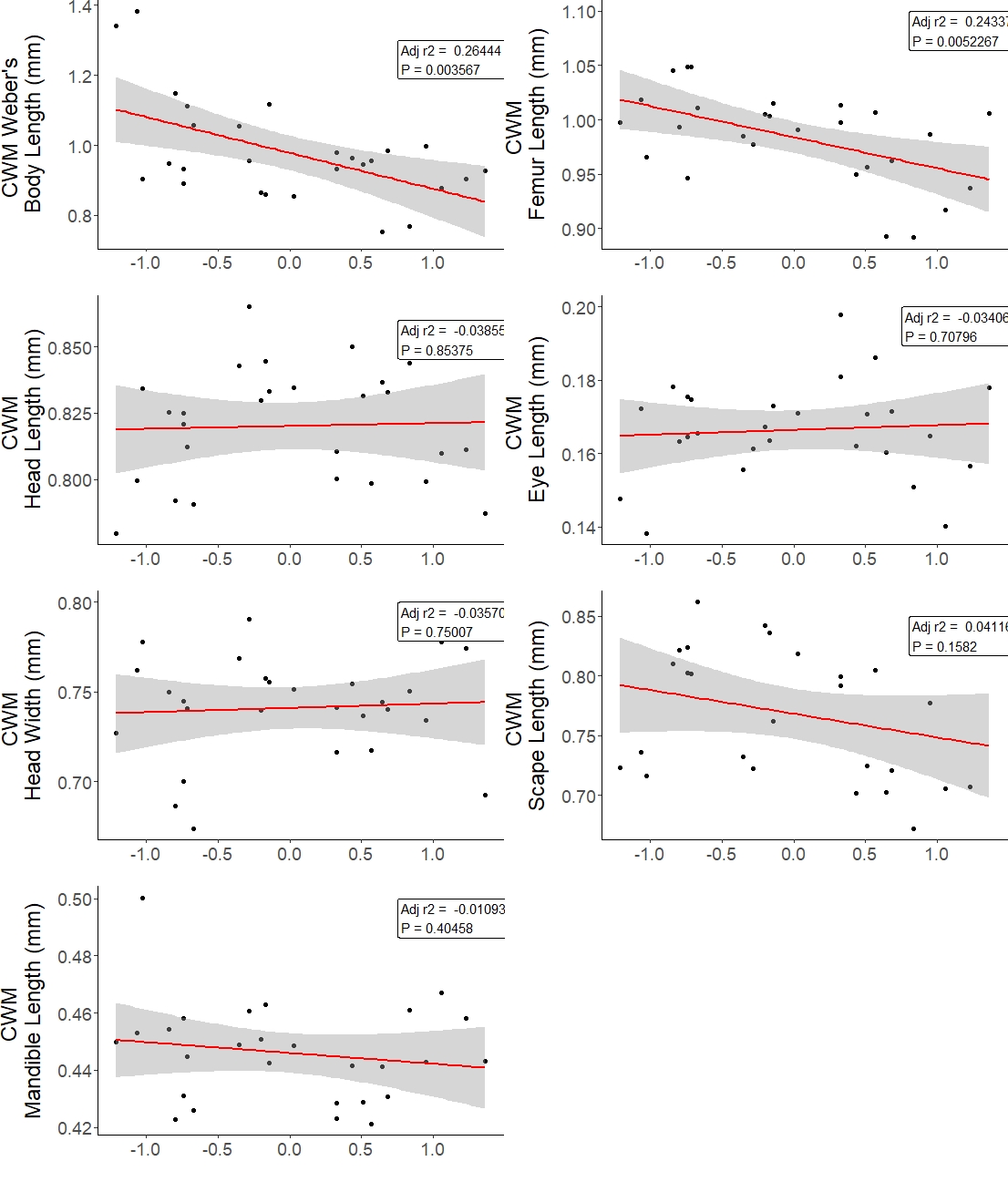


Figure 4: Linear regressions of community-weighted mean trait values and the composite environmental gradient (PC1). Sites with higher annual temperatures and lower annual precipitation are higher on the PC1 gradient. The shaded gray band represents the 95% confidence interval.

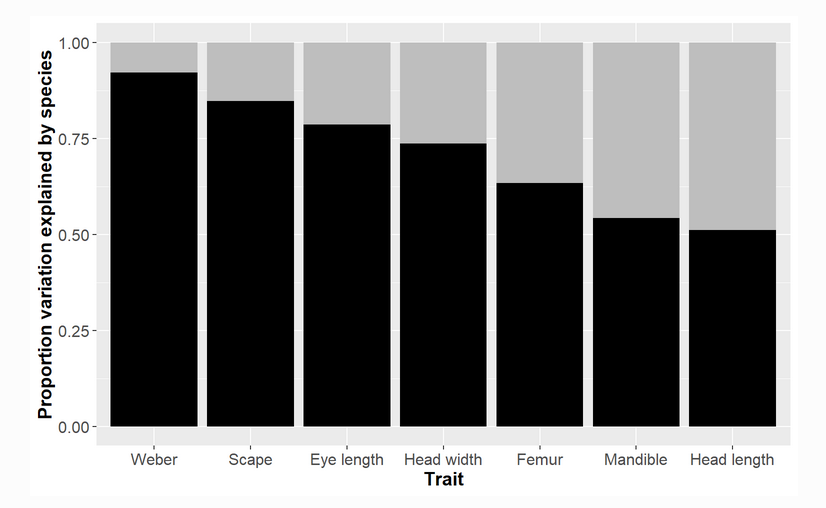
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Figure 5: ITV and traits

**Discussion**

P1: Hypothesis, predictions. Overall assembly conclusions. Environmental and biotic filtering acts jointly.

P2: Assembly processes are scale-dependent

P3: Contrast stress gradient predictions for ants vs plants

P4: Discussion on implications for body size and femur length CWM along gradient

**Appendix**

Table 1: Summary of sampling dates and locations.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Site Name | Pitfall Trap Sampling dates | Coordinate of site centroid | | |
|  | |  | | |
| CaS | July 10 - 13 | | 35.11995 | 119.6283 | |
| Aug 2 - 5 | | 35.12000 | 119.6280 | |
| Sept 18 - 21 | | 35.11600 | 119.6240 | |
| CaSl | July 9 - 12 | | 35.09 | -119.574 | |
| Aug 2 - 5 | | 35.089 | -119.576 | |
| Sept 18 - 21 | | 35.065 | -119.539 | |
| SemiT | July 15 - 18 | | 35.658 | -119.612 | |
| Aug 6 - 9 | | 35.658 | -119.612 | |
| Sept 24 – 27 | | 35.658 | -119.61 | |
| Lokern | July 14 - 17 | | 35.354 | -119.584 | |
| Aug 3 - 6 | | 35.354 | -119.584 | |
| Sept 23 - 26 | | 35.355 | -119.588 | |
| PaPl | July 23 - 27 | | 36.698 | -120.799 | |
| Aug 12 - 15 | | 36.696 | -120.795 | |
| Sept 10 -13 | | 36.7 | -120.801 | |
| Aven | July 21 - 24 | | 36.094 | -120.197 | |
| Aug 8 - 11 | | 36.088 | -120.19 | |
| Sept 6 - 9 | | 36.0878 | -120.1912 | |
| Mov | July 28 - 31 | | 36.563 | -120.547 | |
| Aug 13 - 16 | | 36.562 | -120.545 | |
| Sept 12 - 16 | | 36.561 | -120.548 | |
| SiCr | July 20 - 23 | | 36.586 | -120.687 | |
| Aug 12- 15 | | 36.586 | -120.686 | |
| Sept 12 - 16 | | 36.586 | -120.688 | |
| Coal | July 16 - 19 | | 36.213 | -120.305 | |
| Aug 8 - 11 | | 36.212 | -120.304 | |
| Sept 6 – 9 | | 36.213 | -120.303 | |

Table 2: Scene ID

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| eVIIRS NDVI | EVUSS20200630202007066 | EVIIRS NDVI 375M | 154.78 MiB | Complete |
| eVIIRS NDVI | EVUSS20200707202007136 | EVIIRS NDVI 375M | 155.12 MiB | Complete |
| eVIIRS NDVI | EVUSS20200714202007206 | EVIIRS NDVI 375M | 154.11 MiB | Available |
| eVIIRS NDVI | EVUSS20200714202007276 | EVIIRS NDVI 375M | 169.38 MiB | Complete |
| eVIIRS NDVI | EVUSS20200721202007276 | EVIIRS NDVI 375M | 154.01 MiB | Complete |
| eVIIRS NDVI | EVUSS20200728202008036 | EVIIRS NDVI 375M | 154.96 MiB | Available |
| eVIIRS NDVI | EVUSS20200728202008106 | EVIIRS NDVI 375M | 170.24 MiB | Complete |
| eVIIRS NDVI | EVUSS20200804202008106 | EVIIRS NDVI 375M | 155.96 MiB | Available |
| eVIIRS NDVI | EVUSS20200811202008176 | EVIIRS NDVI 375M | 155.71 MiB | Available |
| eVIIRS NDVI | EVUSS20200811202008246 | EVIIRS NDVI 375M | 168.62 MiB | Available |
| eVIIRS NDVI | EVUSS20200818202008246 | EVIIRS NDVI 375M | 153.81 MiB | Available |
| eVIIRS NDVI | EVUSS20200825202008316 | EVIIRS NDVI 375M | 153.74 MiB | Available |
| eVIIRS NDVI | EVUSS20200825202009076 | EVIIRS NDVI 375M | 167.25 MiB | Available |
| eVIIRS NDVI | EVUSS20200901202009076 | EVIIRS NDVI 375M | 152.77 MiB | Available |
| eVIIRS NDVI | EVUSS20200908202009146 | EVIIRS NDVI 375M | 147.03 MiB | Available |
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| eVIIRS NDVI | EVUSS20200915202009216 | EVIIRS NDVI 375M | 150.21 MiB | Available |
| eVIIRS NDVI | EVUSS20200922202010056 | EVIIRS NDVI 375M | 162.86 MiB | Available |

*From <*[*https://dds.cr.usgs.gov/queue/orderlist/BulkDownload/20220822\_104216/1*](https://dds.cr.usgs.gov/queue/orderlist/BulkDownload/20220822_104216/1)*>*

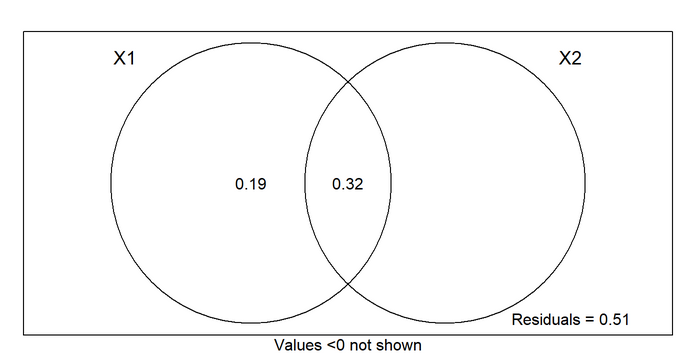


Figure 3: Variance partitioning

Supplemental Information

Table S1: Population level trait measurements

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