Abstract

Introduction

The extent to which community assembly mechanisms are deterministic processes i.e. niche based is a central topic in ecology. There are two major hypothesized processes that predict contrasting but non-exclusive patterns in the trait and spatial 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 (Vellend, 2010). This mechanism can lead to a convergence in ecological attributes or traits among species in that area. In deserts, traits that allow organisms to cope with environmental stressors such as water stress and temperature extremes are common. In contrast, limiting similarity predicts that competitive exclusion results among ecologically similar species (Abrams, 1983). This mechanism can lead to a divergence in traits among coexisting species. These processes work together but at differing scales, at large scales habitat filtering is expected to be stronger than biotic interactions, whereas at the fine scales that interactions actually occur at, biotic interactions prevail.

Functional traits reflect aspects of morphology, life history or physiology that enable an organism to be successful in an environment (Violle et al., 2007). Plant ecologists have incorporated the role of facilitation by foundation plants into trait-based community assembly theory (Schöb et al., 2012). In deserts, shrubs reduce environmental stress by reducing daytime heat and retaining warmth overnight, creating locally stable micro-climates (McIntire & 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 (Braun et al., 2021; Braun & Lortie, 2020; Liu et al., 2016). 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 & 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.

The relative importance of environmental and biotic filtering mechanisms to can change along environmental gradients. The stress gradient hypothesis proposes that competitive interactions decrease in importance as environmental stress increases (Bertness & Callaway, 1994). There is extensive empirical support for the stress gradient hypothesis in plant communities (He et al., 2013; Lortie & Callaway, 2006), however, in animal communities, tests are relatively rare. 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.

We studied desert ant community assembly. We hypothesized that desert ant communities are assembled through niche-based processes. We expect the following the 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 i.e. decreases in functional diversity and functional divergence, c) community trait composition (community weight mean trait values), and d) specific trait by environment interactions (fourth corner analysis). 2) The trait distributions of co-occurring ants will be more dispersed than expected (biotic filtering). 3) Effect size measure of the trait dispersion of co-occurring ants will decrease with stress (stress gradient).

**Methods**

*Field collection*

Ant communities 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. The shrub species *Ephedra californica* (Ephedraceae) and *Atriplex* sp. 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. The traps were deployed in different locations within the study site each sampling instance to avoid repeated measures. Throughout the season, 648 traps were deployed totaling 46 656 trap-hours (24 traps per site \* 3 sampling events \* 72 hours). During each sampling instance, microsite-level vegetation characteristics were estimated. At each pitfall trap location we measured the percent cover of ground-covering vegetation, rocky cover, woody cover and bare ground. Vegetation height was measured at the center of the quadrat and the dominant vegetation type was recorded. At shrub microsites, we measured the longest dimension of the shrub canopy axis, its perpendicular width, and the height of the focal shrub to the tip of the highest green tissue (Lortie et al., 2018). 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 repeating the microsite level measurements. Each sampling location was georeferenced using a handheld GPS unit.

*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 and compared to BINs in BOLD systems. I measured the following morphological trait data from the ant specimens: Weber’s length (W. L. Brown, 1953), which is the length of the longest diagonal on the thorax and a measure of overall worker body size. Femur length relates to foraging ability in complex environment and thermoregulation (Feener Jr et al., 1988), mandible length and head size with relate to diet, scape length relates to chemosensory abilities and eye size relates to forage behaviours (Weiser & Kaspari, 2006). The latter six traits were divided by Weber’s body length to remove the impact of body size.

I measured each of the seven traits in up to six individuals per species, per site (265 individual ants) to capture the intraspecific variation between populations. The majority of functional ecology papers 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 & Ebert, 2004). I dissected each ant and affixed them to microscope slides using Elmer’s glue. I 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. I imported each composite image into ImageJ software, used the micrometer divisions within the image to calibrate the measurement scale within the software and measured each trait using the software.

*Analysis*

I extracted local estimates of water stress during the sampling period from NASA's ECOsystem Spaceborne Thermal Radiometer Experiment on Space Station (EcoStress) (Meerdink et al., 2019) data for each site and study period. This 70 m resolution satellite data provides the evaporative stress indicator (ESI), a measure of plant water-stress based on temperature and evapotranspiration. I extracted climate data for each site from WorldClim, and calculated deMartonne’s aridity index (aridity = P/(T+10) where P = annual precipitation and T = mean annual precipitation (Fick & Hijmans, 2017). I converted the abundance-based data to incidence-based because ants forage socially and this leads to clustering of individuals from the same colony (Longino & Coddington, 2002). I calculated functional richness and divergence indices within the population-level trait means using the FD package (Laliberté et al., 2014). I used GLMM to model alpha, beta and functional diversity in response to the environmental variables using site as a random effect (glmmTMB, Brooks et al., 2017).

I calculated the community weighted mean (CWM) value for each trait at each pitfall trap. CWM using incidence-based data is the mean value of the trait among the species present. To relate environmental variables and CWM, I carried out a db-RDA with the CWM trait values as the response and environmental variables as predictors using the capscale function of the vegan package in R (Oksanen et al., 2010). I conditioned the model on Site, and also conducted the permutation tests within strata of sites to account for within site correlation structures when assessing significance.

Four corner analysis is a formal test for trait by environmental interactions. It relates species traits, species abundances and environmental conditions to determine the relation of species traits to the environment (Legendre et al., 1997). I used a GLM based approach to calculating the fourth corner (Brown et al., 2014), however, this method cannot incorporate intraspecific trait values.

**Results**

A total of 15519 individual ants from 11 species were collected and identified. All species are native to California. The most abundant species are *Solenopsis xyloni*, the native Southern fire ant, and *Pheidole hyatti*, the big-headed ant. These two species are both considered ecologically dominant in deserts. I have completed the trait measurements and I am currently working through the analyses. I used GLMM to model the drivers of ant species richness. Species richness decreases with increasing aridity (p = 0.0168) and differs between the study months (p = 0.0329). Beta-diversity is driven more strongly by the species turnover component than nestedness. Beta-diversity increases with increasing water stress (ESI, p = 0.004). The db-RDA on community weighted mean trait values showed that ESI significantly drives mean trait values (p = 0.001). A Mantel test between the Euclidean distance of ESI and gower dissimilarity in traits showed a significant correlation between traits and ESI (0.056, p = 0.01). Fourth corner analysis with species-level trait values included showed a significant trait \* env interaction (p = 0.04). These preliminary results suggest that water stress acts as an environmental filter on ant communities of the San Joaquin valley.

Supplemental Information

Table S1: Population level trait measurements