The relative importance of habitat filtering and biotic interactions on desert ant community assembly

**Abstract**

**Introduction**

P1: The extent to which community assembly mechanisms are deterministic processes i.e. niche based is a central topic in ecology. Ants are a model system to study deterministic community assembly processes because ant communities are often strongly structured by environmental conditions ([Retana and Cerdá 2000](#_ENREF_38), [Gibb et al. 2015a](#_ENREF_14)) and competition ([Camarota et al. 2016](#_ENREF_9)), though the latter is the subject of continuing debate ([Andersen 2008](#_ENREF_2), [Tschinkel and King 2017](#_ENREF_41)). There are two major hypothesized processes that predict contrasting but non-exclusive patterns in the trait and spatial distributions of coexisting species. Habitat filtering structures communities by only allowing only organisms capable of surviving local conditions to persist within the local species pool ([Vellend 2010](#_ENREF_42)). This mechanism can lead to a convergence in ecological attributes or traits among species in that area. In deserts, traits that allow organisms 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](#_ENREF_1)). 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.

P2: Functional traits reflect aspects of morphology, life history or physiology that enable an organism to be successful in an environment. Plant ecologists have relatively recently incorporated the role of facilitation by foundation plants into trait-based community assembly theory ([Schöb et al. 2012](#_ENREF_39)). In deserts, shrubs reduce environmental stress by reducing daytime heat and retaining warmth overnight, creating locally stable micro-climates ([McIntire and Fajardo 2014](#_ENREF_29)). Shrub facilitation often increases the cover and density of annual plants growing beneath the canopy ([Holzapfel et al. 2006](#_ENREF_19), [Pugnaire et al. 2011](#_ENREF_37)). 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](#_ENREF_21)). Therefore, at fine scales, foundation shrubs may alter trait distributions, taxonomic composition and coexistence patterns of the ant community directly through canopy facilitation and indirectly through facilitation of the annual understory. There is also the capacity for the relative importance of these interactions to change along environmental gradients. The stress gradient hypothesis proposes that competitive interactions decrease as environmental stress increases ([Bertness and Callaway 1994](#_ENREF_5)). 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. Due to the ecological important 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.

P3:

P4: Ant community assembly is structured by deterministic rather than neutral processes.

1) The trait distribution of co-occurring ant species will be clustered at large scales and dispersed at small scales

2) Shrub canopy influences ant assembly directly through amelioration and indirectly through the annual community

**Methods**

*Field collection methods*

A total of nine sites spanning a distance of approximate 135 miles of the San Joaquin Valley, California were surveyed over three summer months in 2020 (Table 1, Appendix Table 1). The shrub species *Ephedra californica* (Ephedraceae) or Atriplex is the dominant perennial species at six of the sites and the remaining three sites are relatively open with few shrubs. The vegetation and other ground cover characteristics were estimated each month at collection. A total of ten 25 m length transects were deployed at each study site. Every four meters along the transects, 0.5 m quadrats were placed and the percent cover of dried, ground-covering vegetation, rocky cover, woody cover, and bare ground were recorded (n = 60 per site). Vegetation height was measured at the center of the quadrat and the dominant vegetation type was recorded.

We used pitfall traps to measure the ground-active arthropod communities. 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, we also estimated microsite-level vegetation characteristics. 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). Each sampling location was georeferenced using a handheld GPS unit.

Ant communities were sampled using pitfall traps. Each trap was deployed once per month between July and September, 2020 (three times per site) for 72 hours per sampling instance. The traps were filled with propylene glycol and covered with 0.5 inch steel mesh with an aluminum flashing roof to prevent vertebrate bycatch. A total of 24 traps were deployed per site. At shrubbed sites, 12 traps were placed beneath the canopy of a shrub and 12 were placed at least 2 m away in an open area. At the unshrubbed sites, traps were deployed every 10 m along two transects 10 m apart. Different sampling locations within the site were used each month. Percent cover of ground vegetation, bare ground, woody debris and rocks were recorded, as well as the vegetation height in the centre of a 0.5 m by 0.5 m quadrat placed at the trapping site. The main vegetation type was recorded (typically grass or forb). The width and height of the shrub were recorded. IR sensors were used to record the ground surface temperature at each site.

*Lab methods*

Ant individuals were identified to genus using Fisher and Cover (2007), and to species using AntWiki keys ([www.antwiki.org](http://www.antwiki.org)).

I measured the traits in six individuals per species, per site for a total of x individual ants. I dissected each ant and affixed them to a slide using glue. I placed the slide on top of a stage micrometer slide, and took stacks of focus bracketed photographs using a Canon 60D DSLR with a 60 mm macro lens and x extension tube. The software Helicon focus was used to make the stacks and convert into slide photos. I imported each photo into ImageJ, setting the measurement scale to the micrometer divisions and then measured each trait in the software.

*Analytical methods*

We extracted climate data including mean annual temperature (MAT), mean annual precipitation (MAP) and maximum temperature from Worldclim (Fick & Hijmans, 2017) using the point location of the centroid of the study site (Appendix Table 1). We calculated deMartonne’s aridity using the following equation: aridity = P/(T + 10) where P = annual precipitation and T = mean annual temperature. We calculated the mean cover of each ground-cover vegetation type at each study site from the quadrats. We extracted ESI…. I will also extract 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](#_ENREF_30)) data for each site and study period. This 70 m resolution satellite data provides the evaporative stress indicator, a measure of plant water-stress based on temperature and evapotranspiration.

Fourth corner

Trait distributions

Trait SES vs env SES or something

**Results**

We collected a total of ~15000 ants from 13 species. The most abundant species are *Solenopsis xyloni*, a native fire ant, and *Pheidole*, the big-headed ant. These species are both considered ecologically dominant in deserts. There is no evidence of *S. invicta*, or the argentine ant *Linepithema humile*, both major invaders across North America.

* Different traits varied in intraspecific variation