Title

Rove beetle diversity, distribution, and ecology in the sonoran desert necrotic cactus niche

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Rove Beetle (Coleoptera: Staphylinidae) Diversity, Distribution, and Ecology in the Sonoran Desert Necrotic Cactus Niche

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Biology

by

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The Thesis of Dionné Mejía is approved and it is acceptable in quality and form for publication on microfilm:

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2016

DEDICATION

This thesis is dedicated to my parents José Luis Mejía and Mariana León Mejía for always supporting me and encouraging me to pursue higher education.

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ABSTRACT OF THE THESIS

Rove Beetle (Coleoptera: Staphylinidae) Diversity, Distribution, and Ecology in the Sonoran Desert Necrotic Cactus Niche

by

Dionné Mejía

Master of Science in Biology

University of California, San Diego, 2016

Professor Therese Ann Markow, Chair

The "necrotic cactus niche" contains a high diversity of desert arthropods, yet few studies of this niche have been conducted. Rove beetles (family Staphylinidae) have the highest species richness in this system, yet little is known about their distribution, ecology, specificity, or life history. For this study, over 5,000 rove beetles were collected from four species of rotting cactus. Three species—cardón (*Pachycereus pringlei*), senita (*Lophocereus schottii),* and organ pipe (*Stenocereus* *thurberi*)—were collected from Baja California Sur, Mexico and one species—California barrel cactus (*Ferocactus cylindraceus*)—was collected from Anza Borrego Desert State Park in southern California. Altogether, 21 morphospecies of rove beetles from six subfamilies were identified. The subfamilies Scaphidiinae and Osoriinae were found exclusively in cardón cactus. This study also assessed phylogeographic relationships and genetic diversity within the genus *Belonuchus* using sequence data from the barcoding locus of the mitochondrial cytochrome oxidase 1 gene. Morphological and genetic data support the presence of at least one undescribed *Belonnuchus* n.sp. with apparent host specificity to senita cactus. The ecological portion of this thesis consisted of a three-week study of rotting California barrel cactus in Anza Borrego Desert State Park and provided evidence that these rove beetles are specific to the rotting cactus niche and that they are primarily diurnal. This study adds to our understanding of rove beetles in the necrotic cactus niche and provide a baseline for future studies of necrotic cactus arthropods.

INTRODUCTION

Sonoran Desert Diversity

The deserts of North America are broken up into four regions based on vegetation characteristics: the Great Basin, Mojave, Sonoran, and Chihuahuan deserts. Of these, the Sonoran Desert has the densest vegetation and largest variety of plants adapted to heat and drought conditions (Shreve and Wiggins, 1964; Nabhan, 1999). The Sonoran Desert encompasses 310,000 square kilometers and includes southern California and Arizona in the United States, and Sonora and Baja California in Mexico (Center for Biological Diversity, 2011). Included in the Sonoran desert is the Colorado Desert in southern California, distinguished by its high summer temperatures, low elevation, and sparse vegetation. (Arizona-Sonora Desert Museum, 2015). The Sonoran Desert is characterized by the abundance of legume trees and columnar cacti, and includes 350 bird, 100 reptile, and 60 mammal species (Dimmitt, 2015; Shreve and Wiggins, 1964; Center for Biological Diversity, 2011). There are three hundred cactus species are endemic to the region and some can live for hundreds of years (Dimmitt, 2015). They support many desert organisms, attracting insect, bird, and bat pollinators with their flowers, as well larger animals—iguanas, foxes, and bighorn sheep—with their fruits and moisture-filled pulp (Chadwick, 2006). Despite its diversity, the Sonoran Desert has suffered from the introduction of invasive species, and, more importantly, from habitat fragmentation caused by human development (Nabhan, 1999).

Cactophilic Arthropods

An initial step in preserving the Sonoran Desert and its biodiversity is to document the current faunal diversity. Arthropods are a component of this diversity, acting as pollinators, detritivores, and prey items for vertebrates. Rotting cacti have been shown to contain a high diversity and abundance of arthropods relative to other desert regions, yet their arthropod communities remain largely understudied (Ferro et al., 2013). Cacti begin to rot as a result of physical injury or stress; the cactus tissue is first invaded by microbial decomposers such as yeast and bacteria, and secondarily by arthropod detritivores, predators, and parasites (Castrezana and Markow, 2001). The necrotic cactus niche is an ephemeral desert resource that can persist from several months to a year depending on the size and species of cactus (Breitmeyer and Markow, 1998). Eventually, the arthropods leave the cactus tissue and the cacti dry out and return their nutrients to the desert soil. Cactophilic arthropods are essential to the decomposition and recycling of nutrients in this niche, and ultimately for the desert ecosystem (Triplehorn and Johnson, 2005).

Despite their potential importance in the desert ecosystem, only four studies of arthropods communities associated with decaying cactus have been conducted. In 1899, H.G. Hubbard first wrote about the hidden diversity of arthropods in the giant rotting saguaro cactus (*Carnigea gigantea*). In 1916, while describing the natural history of southern Arizona, Charles Dury found a rotting fishhook barrel cactus (*Ferocactus wislizeni*) and reported that “one cannot see any insect life from the outside but cut or break open [the cactus] and the interior will be swarming with insects, mostly beetles, of many species.” Almost a century later, Castrezana and Markow (2001) sampled arthropods from three additional cactus species in the Sonoran desert: cardón (*Pachycereus pringlei*), organ pipe (*Stenocereus thurberi*), and senita (L*ophocereus schottii*) cactus. They found 34 species representing 10 orders of arthropods and evidence that cactus arthropod communities differed among cactus species. In 2013, Ferro et al. collected beetles (Coleoptera) from decaying fishhook barrel cacti (*Ferocactus wislizeni*) in Arizona and found beetles from 11 families and 35 species.

As part of the Cactus Arthropod Project, funded by that National Geographic Society, the Markow lab, myself included, collected arthropods from 14 rotting cacti in Baja California Sur and southern California, two regions in the Sonoran Desert. To expand the scope of our research, we replicated the study by Castrezana and Markow (2001) but collected from Baja California Sur, rather than Sonora. We also collected from the local California barrel cactus (*Ferocactus cylindraceus*) in Anza Borrego, California, located in the Colorado Desert subdivision of the Sonoran Desert. Through morphological identification, we identified 10 arthropod groups including beetles (Coleoptera), flies (Diptera), mites (Acari), earwigs (Dermaptera), spiders (Arachnida), pseudoscorpions (Pseudoscorpiones), true bugs (Hemiptera), springtails (Collembola), ants (Hymenoptera), a wasp (Hymenoptera), and a scorpion (Scorpiones). Like in previous studies, beetles had the highest species richness (Hubbard, 1899; Dury, 1916), followed by flies.

Flies in the genus *Drosophila* are the most well-studied taxon in the necrotic cactus niche. Several species of *Drosophila* are thought to exhibit 1:1 cactus host specificity as a result of the evolution of unique enzymes that can detoxify allelochemicals found in rotting cactus (Kircher, 1969; Frank and Fogleman, 1992). One species, *Drosophila pachea*, has evolved to be nutritionally dependent upon senita cactus (L*ophocereus schottii*) and cannot tolerate other cactus species (Lang et al., 2012). Another pattern observed in rotting cactus specialists, such as *Drosophila* *nigrospiracula,* is an increased dispersal rate compared to generalist species, such as *D. melanogaster*. This increase is likely due to the food stress and unpredictability of the necrotic cactus niche (Johnson and Heed, 1976).

Cactus beetles, however, are poorly understood in comparison. While we know that certain beetle families—Staphylinidae, Histeridae, Hydrophilidae, and Tenebrionidae—occur with relatively high density and diversity in rotting cactus (Hubbard, 1899; Castrezana and Markow, 2001; Ferro et al., 2013), their distribution, behavior, evolutionary history, and ecology remain obscure.

Family Staphylinidae

Several studies have found that rove beetles (Staphylinidae) represent the highest species richness among cactophilic arthropods and beetles (Hubbard, 1899; Ferro, 2013). My thesis aims to understand the diversity, distribution, ecology, and specificity of cactophilic rove beetles in the Sonoran Desert. Since rotting cacti are an understudied ecological niche, some of the rove beetle species in my study may be undescribed.

Staphylinidae is the most speciose beetle family known, with over 54,000 described species, 4,153 of which are found in North America (Triplehorn and Johnson, 2005). Staphylinids are elongated beetles characterized by their short elytra, or hardened forewings, that typically cover the entire abdomen in other beetles (Frank and Thomas, 1999; Fig.1). Despite their small size (1 to 40 mm) most adult and larval rove beetles are insect predators (Frank and Thomas, 1999). They are also fast runners and good fliers, and thus probably good dispersers (Borror and White, 1970).

Though they are found worldwide in most habitats, rove beetles are often associated with decomposing environments, living in fungi, carrion, and rotting plant material (Borror and White, 1970). Surveys of necrophagous, or carrion-loving, rove beetles have been conducted in various ecosystems including deserts, many of which report rove beetles with the highest species richness. For example, Jiménez-Sánchez et al. (2013) collected necrophagous beetles in semiarid regions, including areas with columnar cacti, in Puebla, Mexico, using squid-baited traps; they found 9 staphylinid species from 7 genera, accounting for 50% of the necrophagous beetle species richness and the highest abundance (74.2%) in their study.

Variables affecting staphylinid diversity

Staphylinid diversity and composition in the necrotic niche may be influenced by variables such as cactus species, cactus chemistry, season, and stage of necrosis. Previous studies have found that large cactus species, such as the giant cardón cactus (*Pachycereus pringlei)* harbor the most diversity (Castrezana and Markow, 2001; Richmond et al., in prog.) likely because larger cactus rots can support more prey organisms on which staphylinids can feed. Differences in cactus chemistry may also influence host suitability, and seasonal changes may affect species composition and diversity. Castrezana and Markow (2001) found that beetle species diversity declined from spring to summer, possibly due to increased temperatures. Rove beetle species composition has also been shown to differ throughout the progression of necrosis (Ferro et al., 2013; Dekeirsschieter et al., 2013). Ferro et al. (2013) found that predatory beetles, like staphylinids, were most abundant in late succession necroses. This is likely because they depend on the presence of established prey arthropod populations, which require time to proliferate (Ferro et al., 2013). The relationship between staphylinid composition and stage of necrosis implies that rove beetles must be sampled from multiple cactus species in varying stages of succession to obtain accurate measures of diversity.

Genus *Belonuchus*—Case study

Rove beetles in the *genus Belonuchus* (Staphylininae; Staphylinini) are of particular interest for studies of genetic diversity and host specificity since they are known from many cactus species. Though *Belonuchus* occur in various environments, they are commonly associated with decomposing matter (Frank and Barrera, 1990). *Belonuchus ephippiatus* is known from *Ferocactus, Cereus, Opuntia,* and *Agave* (Smetana, 1995; Ferro et al., 2013). Pfeiler et al. (2013) found an unknown *Belonuchus* n.sp. exclusively on senita cactus (*Lophocereus schottii*) in Baja California. During my preliminary work on the Cactus Arthropod Project, I also found staphylinids that I identified as *Belonuchus* in cardón (*Pachycereus pringlei*), organ pipe (*Stenocereus thurberi*), senita (Lophocereus schottii), and barrel (*Ferocactus cylindraceus*) cactus. These specimens showed large size variation and were consequently difficult to classify into morphospecies. Studying the diversity of *Belonuchus* using molecular markers allowed me to determine the presence or absence of cryptic species, host-specificity, and geographic clustering.

The diversity, distribution, and ecology of cactophilic staphylinids

Studies of rove beetles in the necrotic cactus niche have thus far been limited to broad diversity surveys, yet virtually nothing is known about rove beetle ecology, behavior, host specificity, or life histories. My thesis consisted of two components; first

I investigated the diversity and distribution of staphylinids in four species of rotting cactus and second I investigated their behavioral and ecological adaptations to this niche. In order to understand the diversity and distribution of staphylinids in the rotting cactus ecological niche I investigated 1) how many morphospecies, genera, and subfamilies of staphylinids are present in the niche, 2) which variables are associated with staphylinid diversity in rotting cactus and 2) the genetic diversity in the genus *Belonuchus*. In order to understand more about the behavioral and ecological adaptations staphylinids have evolved in order to survive in the desert I investigated 1) how the internal conditions of cactus rots change throughout the course of decay, 2) whether cactophilic rove beetles are specific to the rotting cactus niche, and 3) how rove beetle behavior and lifecycle are adapted to the necrotic cactus niche.

To investigate these questions I compared staphylinid diversity among three cactus species—cardón, organ pipe, and senita—from Baja California Sur, Mexico and one species—California barrel cactus—from Anza Borrego Desert State Park in California. I also tested whether rove beetle diversity was associated with variables including cactus species, season, and stage of cactus necrosis. I also sequenced the barcoding gene from a subset of *Belonuchus* specimens in order to determine their genetic diversity and phylogeographic relationships. Finally, I conducted a multi-week ecological study of necroses of the California barrel cactus (*Ferrocactus cylindraceus*) and of their staphylinid communities to better understand the evolution of behavioral and ecological adaptations. Together, this study serves to better our understanding of rove beetles, the most prominent group in the necrotic cactus niche, and serves as a baseline for future studies of arthropods in the necrotic cactus niche.

MATERIALS AND METHODS

Specimen collection

As part of the Cactus Arthropod Project, the Markow lab, myself included, collected arthropods from rotting cacti in Baja California Sur, Mexico and Anza Borrego Desert State Park in Southern California. We collected samples from 14 rotting cacti, including six cardón (*Pachycereus pringlei*), three organ pipe (*Stenocereus thurberi*), two senita (L*ophocereus schottii*), and four barrel (*Ferocactus cylindraceus*) cacti. The cardón, organ pipe, and senita cactus samples were collected from various locations near La Paz, Baja California Sur, Mexico, while the barrel cactus samples were collected from Anza Borrego Desert State Park, California, USA (Fig. 1). Baja samples were collected in December 2012 and June 2013; Anza Borrego samples were collected in March 2013 and April 2014. All staphylinid specimens were manually extracted from the necrotic tissue and preserved in 95% ethanol. Small specimens (<2mm) were collected using a Berlese funnel with an ethanol-filled collection jar. Necrotic tissue from one Anza Borrego sample (barrel 1) was placed into buckets and covered with cheesecloth and re-sampled after three weeks to determine if arthropods were pupating in the cactus tissue.

Specimen identification

Staphylinid specimens were sorted using external morphological features and assigned to morphospecies. I then identified all specimens to subfamily, and to genus when possible, using the following keys: American Beetles: Staphylinidae Latrielle, 1802 (Newton et al., 2000), Key to North American Staphylinidae Subfamilies (Ferro et al., 2015), and Staphylinidae of Canada and Adjacent United States (Brunke et al., 2011). I also used additional keys to identify specimens in the tribe Paederini (Frania, 1986) and subtribe Philonthina (Chani-Posse, 2014). I used images on bugguide.net to help confirm my designations.

Diversity data analysis

After I assigned specimens to morphospecies, I used the program EstimateS V. 9.1.0 (Colwell et al., 2012) to measure species richness by cactus species and cactus specimen (Colwell et al., 2004; Colwell et al., 2012). Because sampling was unequal among cactus species, I also used EstimateS to extrapolate rove beetle species richness to two samples past the cactus species with the highest sampling. I calculated the Shannon (Magurran, 2004) and Fisher's alpha (Magurran, 2004, Hayek and Buzas, 1996) diversity indices and compared compositional differences among cactus species using both the Chao-Sorensen abundance-based similarity index corrected for unseen species and the uncorrected Chao-Sorenson similarity index (Chao et al., 2005).

For the cardón samples, I used the Chao-Sorensen abundance-based similarity index to compare rove beetle composition (Chao et al., 2005). I assessed the differences between summer and winter cardón cactus samples and among samples determined to be at different stages of necrosis, based on descriptions in our field notes. I excluded the other cactus species from this analysis mainly to control for the effect of cactus species on staphylinid composition and diversity, but also because cardón was the most well-sampled species.

Genetics: *Belonuchus* case study

After sorting specimens to morphospecies I determined that there were multiple morphospecies in the genus *Belonuchus* from several cactus samples from Baja

California Sur and Anza Borrego. To assess the species-level diversity, taxonomist Dr. Stylianos Chatzimanolis (University of Tennessee Chatanooga) identified my *Belonuchus* specimens to species. For a subset of specimens (31 specimens) from Anza Borrego and Baja California Sur identified as *Belonuchus*, I also extracted genomic DNA from the thorax using the Quiagen DNeasy Blood and Tissue Kit (QIAGEN Inc, Valencia, CA) and used the polymerase chain reaction (PCR) to amplify the barcoding locus of the mitochondrial gene *cytochrome oxidase* subunit I (CO1) gene with the HCO and LCO primers (Folmer et al., 1994). I cleaned the PCRs using Thermo Scientific's Exonuclease I (Exo I) and Thermosensitive Alkaline Phosphate (FastAP) and sent them to GENEWIZ (La Jolla, CA) for sequencing. I used the program Sequencher v 4.8 (Gene Codes Corp., AnnArbor, Michigan) to edit the sequences and Se-Al v 2.0 (Ashworth Laboratories, Edinburgh, Scotland) to align them. I used jModelTest v 0.1.1 (Posada, 2008) to find the best-fit model of molecular evolution for the genetic data and ran the sequences in MrBayes v 3.2.2 (Huelsenbeck and Ronquist, 2001) using this model. I constructed a *Belonuchus* phylogeny using my sequences combined with sequences collected by the Markow lab at LANGEBIO (Irapuato, Mexico) from specimens in *Myrtillocactus* in San Miguel de Allende (Guanajuato, Mexico), and with published sequences from Pfeiler et al. (2013) from specimens collected in senita cactus (Baja Peninsula, Mexico).

Ecology

I conducted a multi-week observational study of rotting cactus in Anza Borrego State Park in southern California to further understand the ecology of cactophilic staphylinids. I traveled to Anza Borrego from March 19, 2016 to April 8, 2016 and located six cactus rots at different stages of succession. For each three-day interval I visited two cactus rots a day at dawn and 3 pm, measured the internal pH and temperature using the FieldScout SoilStick, and recorded the moisture level using a qualitative method (Ferro et al., 2013). During each visit, I observed the rot for one hour for signs of staphylinid activity and cactus colonization.

To determine the host-specificity of cactophilic staphylinids, I set up 6 chicken-based meat-baited and 6 unbaited pit-fall traps that were separated by at least 20 meters from one another and by at least 50 meters from known cactus rots. I also set up 6 unbaited traps directly next to known rotting cacti. I constructed pit-fall traps using 1 liter yogurt containers covered with mesh wire. The baits were placed in cheesecloth and hung from the mesh wire using paperclips. To test for diurnal and nocturnal activity, I set up day-only (6am to 7pm) and night-only (7pm to 6am) pit-fall traps by covering the yogurt containers with lids. Five cactus-baited traps were designated as day traps and five as night traps. I collected each pit-fall trap after 3 days.

I set up a flight-interception trap (FIT) to test for diurnal and nocturnal activity (Chatzimanolis et al., 2004; Peck and Davies, 1980) for 10 days and collected staphylinids at 6am and 7pm. I constructed my FIT by attaching a vinyl plastic sheet (90 cm tall by 120 cm wide) to two 1.2 m tall fence posts using rope and duct tape. I placed four plastic containers (15 cm by 30 cm) filled with soapy water directly underneath the plastic sheet to collect flying staphylinids. I also used a blacklight and a white sheet tied between two trees to test for nocturnal activity. I collected any rove beetles attracted to the blacklight both on the sheet and on the ground underneath the sheet.

On April 8, 2016 I collected both adult and larval staphylinids and necrotic tissue from barrel cactus #4. I separated the adult and larval rove beetles by morphospecies and placed them into glass jars filled with moist vermiculite and covered them with tissues and rubberbands to maintain airflow. I also placed a wet sponge into each jar to maintain moisture levels. The staphylinids were fed a diet of *Drosophila melanogaster* larvae, since they are known to feed on fly larvae (Frank and Thomas, 1999). The purpose of this experiment was to observe staphylinid behavior and life cycle in the laboratory.

RESULTS

Diversity

A total of 5079 staphylinid specimens were collected from 14 necrotic cactus samples. These specimens represented 21 morphospecies in 6 subfamilies. The subfamily Aleocharinae had the highest species richness with nine morphospecies, followed by Staphylininae with five species, then Paederinae, Osoriinae, and Tachyporinae, each with two species, and finally Scaphidiinae, with one species (Fig. 2, Fig 3). Most specimens were identified to tribe or genus with the exception of some Aleocharinae, which are notoriously difficult to distinguish morphologically due to their small size and the limited literature of this group (Newton et al., 2000; Table 1).

Comparison of species richness among cactus species showed that cardón had the most species with 18 morphospecies, nine of which were unique to cardón; barrel cactus had 11 species including two uniques, senita had four species including one unique, and organ pipe had four species and no uniques (Table 1). Cardon cacti also had two unique subfamilies—Osoriinae and Scaphidiinae. The Shannon diversity was highest for barrel cactus (H = 1.25), while the Fisher's alpha diversity was highest (α = 2.67) for cardón cactus (Table 2). The species accumulation curves for the four cactus species extrapolated out to eight samples indicated that cardón would likely have the highest species richness, followed by barrel, senita, and organ pipe (Fig. 4). Organ pipe showed the only plateau in species richness, while the other three cactus species continued to accumulate species after 8 samples. Using the Chao Sorenson abundance-based similarity index, I measured the similarity among cactus species (Chao et al., 2005). Pairwise comparisons showed that organ pipe, cardón, and barrel cacti ere more similar to one another (>0.799) than they were to senita cacti (<0.33) (Table 3).

Rove beetle morphospecies abundance varied greatly, both among and within cactus rot species. A single species of Aleocharinae (Aleocharinae 1) accounted for 67.8% of all specimens, with over 1000 individuals in both cardón 12 and barrel 3. Conversely, 8 morphospecies of Staphylinidae (40% of all morphospecies) had 4 individuals or less (Table 1).

Cardón comparisons by stage of necrosis and season

Comparisons among the six cardón samples revealed that rove beetle species richness and composition also varied within cactus species. Species richness ranged from 5 species (cardón 19) to 14 species (cardón 12) (Table 4). I calculated the Chao-Sorenson abundance-based similarity index (Chao et al., 2005) between pairwise cardón samples (Table 4). Most cardón samples had high species composition similarity, with values ranging from 0.89-1. Cardón sample 2, however, had the least similar species composition, with similarity values ranging from 0.495-0.831. Based on our field notes, it is possible that cardón samples were at different stages of necrosis when collected; cardón 2 was the driest and oldest cardón sample while cardón 7 and 12 were very wet. The other cactus samples (cardón 10, cardón 13, cardón 19) were contained cactus tissue of varying ages and were difficult to categorize. The “wet” samples had the highest staphylinid abundance, while the “dry” sample had the lowest (Table 5). Interestingly, the dry cardón 2 also had two unique species from the subfamilies Scaphidiinae (*Baeocera* sp.) and Osoriinae (*Lispinus* sp.)

Comparison between summer (June) and winter (December) cardón samples did not show a strong association between season and species composition. Of the 18 staphylinid species found in cardón cactus, 12 were found from both seasons. Four species occurred only in December and two occurred only in June (Table 6). Cactus samples from the same season were no more similar to one another than to those of the opposite season (t=-0.197; p=0.577).

Genetics: ***Belonuchus*** case study

A phylogeny of necrotic cactus *Belonuchus* specimens was constructed using CO1 sequences of 55 specimens collected from cardón, organ pipe, senita, and *Myrtillocactus.* The mtDNA COI gene tree (Fig. 5) of *Belonuchus* specimens was well supported (>0.9 posterior probability at major nodes) with clades grouping by locality forming distinct groups from Anza Borrego, CA, USA Baja California Sur, MX, and Guanajuato, MX. In addition, one group consisted exclusively of specimens associated with senita cactus (*Lophocereus schottii)* in the Baja Peninsula. The Anza Borrego and Baja California Sur group specimens were morphologically identified as *Belonuchus ephippiatus*. The Guanajuato specimens collected from *Myrtillocactus* by the Markow lab at LANGEBIO also appeared morphologically identical to *Belonuchus ephippiatus*. The specimens from senita cactus in the Baja Peninsula did not key correctly to species using existing keys, and may be an undescribed species. *Belonuchus* n.sp. was found exclusively on senita cactus, while *Belonuchus ephippiatus* was found in all cactus species—organ pipe, cardón, barrel, and *Myrillocactus*—except senita.

Ecology

I measured the temperature and pH of six barrel cactus rots over the course of 10 days and found that the internal temperature of the cactus was significantly cooler than the ground temperature when measured at 3:00pm. the hottest time of day ($t = -3.07$; $p = 0.034$; Fig. 6). The maximum ground temperature was 47.8˚C, the maximum ambient temperature was 46.4˚C, and the maximum internal cactus temperature was 45.7˚C. The difference between internal cactus temperature and the ambient temperature was less pronounced, and the differences between all three measurements were reduced during very windy days (Fig. 6). Ground, ambient, and internal cactus temperatures were approximately equal in the early morning (7:00am). The pH of rotting cactus samples ranged from 7.09 to 9.07, with an average of 8.36, over the course of 10 days. I dissected one cactus (barrel 6) which contained necrotic tissue of varying ages, including live tissue and decomposed "soil-like" tissue. The cactus tissue changed in color with the progression of necrosis, where live tissue was white, followed by orange, orange-brown, and dark-brown tissue. The pH of the live tissue was as low as 5.39 and the decomposed, soil-like tissue had a pH as high as 8.59. There were also portions of rotting tissue that were bright red and did not appear to be undergoing typical successional stages, yet had intermediate pH readings (6.04-7.06).

Staphylinids collected from pit-fall traps showed a high degree of host-specificity for rotting cactus ($F = 13.8$, $p < 0.0001$). The initial meat-baited and unbaited traps did not collect any rove beetles. After six days without collecting rove beetles, I decided to dissect a rotting barrel cactus (barrel #6) and used the pulp to create cactus-baited pit-fall traps. I removed all arthropods and larvae from the pulp to remove the possibility of false positive data. Altogether I collected a single rove beetle from a meat-baited trap, and collected 10 individuals from cactus-baited traps (Fig. 7). No individuals were collected from unbaited traps or from unbaited traps placed next to rotting cacti. Staphylinids were also mostly active during the day, with a total of 25 individuals collected in day traps and one individual collected from a night trap (Fig. 8). Of these, 10 were collected from cactus-baited day traps and none from cactus-baited night traps ($t=-3.65$, $p=0.011$). In addition, 15 individuals were collected from flight-interception day traps and one from a flight interception night trap ($t=-2.38$, $p=0.017$).

During my field observations in Anza Borrego, I collected both adult and larval staphylinids from rotting cacti, indicating that staphylinids complete their lifecycles within the cactus. To learn more about their behavior and lifecycles, I collected staphylinid adults and larvae from barrel cactus #6 and raised them in the laboratory. Both the *Maseochara* sp. (one individual) and *Belonuchus ephippiatus* (2 individuals) adults were observed to eat as many as five *Drosophila melanogaster* larvae at a time. Larval staphylinids were reared in separate containers, as they displayed aggression towards one another when placed in the same container. Adult staphylinids were separated into containers by species, and did not display aggression. Both the adults and larvae were very mobile and the larvae used the cactus tissue to construct a nest before pupating. All staphylinids preferred to burrow deep within the cactus tissue and became aggravated when disturbed. Both *Maseochara* sp. and *Belonuchus ephippiatus* displayed the raised abdomen behavior typical of many staphylinids when disturbed. Adults of both species continued to live after a month. Both larvae pupated after 9 days but had not eclosed 3 weeks later. This study of rove beetle lifecycle currently ongoing.

DISCUSSION

This study found over 5,000 staphylinids representing 21 morphospecies from six subfamilies. Cardón had the most staphylinid species, followed by barrel, and organ pipe and senita had the fewest. Cardón also had two unique staphylinid subfamilies: Osoriinae and Scaphidiinae. Species accumulation curves indicated that all cactus species except organ pipe would likely continue to accumulate rove beetle species with additional sampling. The comparisons among cardón samples showed that stage of necrosis may be associated with rove beetle diversity and composition, but season showed no association. Two species of *Belonuchus* were identified with apparent host specificity (*Belonuchus* n. sp. and *Belonuchus ephippiatus*) and the gene tree showed specimens grouping by locality. The ecological study showed that cactus temperatures stay cooler than ground temperature and that rotting cactus tissue becomes more basic with the progression of decay. Finally, rove beetles collected from cactus were found to prefer rotting cactus baits over meat baits, were primarily diurnal, and adult rove beetles lived for at least 30 days in the laboratory.

Diversity

Cardón comparisons by stage of necrosis and season

Comparison among cardón samples showed that cardón sample 2 was the most dissimilar sample, according to the Chao-Sorenson similarity index. Observations in the field indicated that cardón sample 2 was very dry compared to other cardón samples, implying that it was in the later stages of succession. The cardón samples that were categorized as being earlier in succession (cardón 7 and cardón 12) had higher species richness and abundance, as well as three unique Aleocharine species. The dry cardón 2 sample had two morphospecies—*Baeocera* sp. and *Lispinus* sp.—that were not found in any other cactus species. Although *Lispinus* has been previously reported from rotting cacti, *Baeocera* is generally considered a fungus-feeder and was not previously reported from rotting cactus (Newton et al., 2000). However, rotting cacti occasionally become moldy, especially the older and drier rots (personal observation). These observations are consistent with Ferro et al. (2013), which found that beetle species composition varied between the stages of cactus necrosis. However, my study was limited by a small sample size and the results should be interpreted with caution. There were unique rove beetle species in both "wet" and "dry" cardón samples, indicating that more sampling of necrotic cactus of different successional stages is needed to accurately assess rove beetle diversity and life history.

Comparison among cardón samples did not show an association between season and diversity. More staphylinid species were unique to samples collected in December than to those collected in June; however, the majority of species were generalists occurring in samples from both seasons. Castrezana and Markow (2001) also observed fewer arthropod species in summer than in spring, and observed that there were fewer species with higher abundances in the summer. However, these results must also be interpreted with caution since variation among cactus samples was high in my study due to the difficulty of sampling rots of the same relative size and stage of necrosis.

Cactus chemistry and senita cactus

Cactus chemistry may also contribute to differences in species composition. Previous studies have examined how differing toxicity levels of cactus tissue affect insect host-specificity. These studies have found that cardón cactus is less toxic with regards to its allelochemistry than either organ pipe or senita cactus (Fogleman and Danielson, 2001). Organ pipe cacti have high levels of triterpene glycosides (20-30% dry weight) as well as unusual fatty acids; and both organ pipe and senita cactus have unusual sterols (Kircher and Bird, 1982; Campbell and Kircher, 1980). The allelochemistry of barrel cactus is not known. These differences in cactus chemistry may help to explain the low diversity of rove beetles in organ pipe and senita cactus, which are more toxic than either saguaro or cardón.

Differences in cactus chemistry can also lead to host specialization and niche partitioning in rotting cactus. Results from this study and from Pfeiler et al. (2013) indicate that *Belonuchus* n. sp. is a specialist on rotting senita cactus. Senita specialization has only ever been shown in one other arthropod, *Drosophila pachea*, which evolved nutritional dependence on lathosterol in order to produce 7-dehydrocholesterol (7DHC), a precursor for the steroid hormone ecdysone, which is critical for insect development (Heed and Kircher 1965). It is hypothesized that *D. pachea* first evolved the ability to detoxify senita compounds and later became nutritionally dependent on senita cactus, which is the only plant in the Sonoran Desert containing Δ7-sterols like lathosterol (Lang et al., 2012; Campbell and Kircher, 1980). One possible explanation for the apparent host-specialization of *Belonnuchus* n.sp. is that it may also depend on chemicals found only in senita cactus. *Belonnuchus* n.sp., may have evolved the ability to detoxify senita cactus and may specialize on senita because competitors, like *Belonuchus ephippiatus*, are unable to utilize it. Potential niche partitioning in rotting cactus would be interesting to explore further. This specialization is also interesting because *Belonuchus* do not feed directly on the cactus tissue, but are instead predators of fly larvae, which feed on the tissue.

In addition to hosting a unique species, senita cactus also had the most dissimilar species composition compared to the other cactus species. The Shannon diversity index yielded a higher diversity value for senita cactus than for cardón cactus and senita diversity fell within the margin of error of barrel diversity, when extrapolated to eight samples (Fig. 3). These results suggest that senita cactus, which had only four different species of staphylinid, may have higher diversity than what was captured in this study. In our surveys, senita cacti were less abundant compared to organ pipe and cardón in Baja California Sur, and also likely have the shortest length of necrosis due to their thin branches, making them difficult to sample (Breitmeyer and Markow, 1998). The senita cacti that we collected were in early stages of necrosis, with only small patches of rotting tissue. Future efforts should focus on collecting more senita samples for a more accurate measure of diversity.

Comparison among previous studies

Few studies have examined arthropod diversity, including rove beetle diversity, in the necrotic cactus niche. Ferro et al. (2013) summarized four major studies in a table which I modified to include my data and to compare rove beetle diversity among six species of rotting cactus (Hubbard, 1899; Dury, 1916; Castrezana and Markow, 2001). Hubbard (1899) first studied this niche in the giant saguaro in Arizona, which are similar in size, shape, and chemistry to the cardón cactus (Fogleman and Danielson, 2001). Like cardón, saguaro had high species richness (18 species) and also had rove beetle subfamilies that were not found in other cactus species including Pselaphinae, Omaliinae, and Scydemaeninae (Table 8). California barrel and fishhook barrel cactus had comparable species richness to one another (12 and 11 species) and fishhook barrel also had one unique subfamily called Oxyteliinae. Senita and organ pipe cactus had the fewest species (5 and 6 speciees).

These data suggest that cactus size and chemistry is correlated with rove beetle diversity. While saguaro and cardón are the largest cacti, barrel cacti are of intermediate size and consist of a single wide column, and organ pipe and senita cactus have the thinnest branches (Breitmeyer and Markow, 1998). Branch width is likely associated with length of necrosis and therefore wider branches allow more time for rove beetle species to colonize and reproduce within the necrotic tissue. Additionally, as mentioned previously, cardón and saguaro cactus have relatively low toxicity with regards to their allelochemistry compared to organ pipe and senita cactus, which may affect their host-suitability (Fogleman and Danielson, 2001).

Future studies should continue to address the variables that affect rove beetle diversity in the necrotic cactus niche. Isolating the effects of season, cactus size, cactus chemistry, and stage of necrosis on staphylinid diversity will be an important step. Sampling of different cactus species will also allow for further comparison of species composition. For example, sampling of agria cactus (*Steocereus gummosus*) would be useful for comparison, since the alleochemistry is known (Kircher and Bird, 1982). There are also several species of barrel cactus in the Sonoran Desert that have not been studied, including the Sonora Barrel (*Ferocactus echidne*) and the local coast barrel cactus (*Ferocactus viridescens*) in San Diego County. Necrotic cacti in other American deserts, including the Mojave, Great Baisin, and Chihuahuan, should also be studied.

Natural History of Rove Beetle Taxa

Aleocharinae was the rove beetle subfamily with the highest diversity in this study. At least nine morphospecies were identified from the subfamily Aleocharinae, but further taxonomic identification proved difficult. Aleocharinae are the most diverse subfamily of the staphylinids, with over 12,000 described species worldwide in 51 tribes. Most specimens are less than 3 mm in size (Newton et al., 2002). In my study, one small (1.5 mm) aleocharine morphospecies (Aleocharinae 1) represented over 1000 individuals in both cardón 12 and barrel 3 (Fig. 3a). Both cactus samples were large and "wet," indicating that they may have been rotting for multiple months, which may in part explain why these abundances were so high. Three morphospecies in the subgenus *Maseochara* (genus *Aleochara*) were identified (Fig. 3b, c, g). *Maseochara* are known from decaying cacti including saguaro, *Ferocactus*, and *Opuntia*, as well as from sotol (*Dasylirion wheeleri*) and carrion (Klimaszewski 1984, LeConte 1858, Ferro et al 2013). Adult *Maseochara* are known to feed on dipteran eggs and larvae, especially Syrphidae, and the larvae are ectoparasites of fly pupae (Klimaszewski 1984).

Five morphospecies in the subfamily Staphylininae were identified in this study. A total of three species were found from the subtribe Philonthina, including the two *Belounuchus spp.* from the genetic analysis (Fig. 3j-k), and one *Gabrius sp* (Fig. 3l). *Belonuchus* is known from rotting cacti and other decaying organic matter, while *Gabrius* is known from dead trees. I also collected two species in the tribe Xantholinini (Fig. 3m-n), which are known from rotting environments including cacti. Hubbard (1899) and Dury (1916) also reported an additional rare species that was not collected in this study, *Xanthopygus cacti* Horn, from saguaro and fishhook barrel cacti (*Ferocactus wislizeni*).

I also identified two morphospecies in the subfamily Paederinae, *Deroderus* sp. (Fig. 3o) and *Lithocharis* sp. (Fig. 3p). The genus *Deroderus* was collected from all cactus species in this study and has been previously collected from saguaro (Hubbard, 1899) and from fishhook barrel cactus (Ferro et al., 2013; Fig. 8).

I collected two Tachyporinae species from the genus *Tachinus* (Fig. 3q-r). Tachyporines are known from other rotting cacti, including fishhook barrel cactus and saguaro (Ferro et al, 2013; Hubbard, 1899). Unlike most staphylinids, which are predators, tachyporines in this niche are cactus scavengers (Hunter et al., 1912).

Two morphospecies were identified from the subfamily Osoriinae (*Lispinus* sp. and *Eleuisis* sp.*;* Fig. 3s-t), also known as the unmargined rove beetles. Like the tachyporines, osoriines are not predatory. Osoriinae are typically either sacrophages, feeding on decaying organic matter, or mycophages, feeding on fungus (Newton et al., 2000). Most Osoriinae are known from tree bark, and many are dorso-ventrally flattened as an adaptation to this environment (Irmler, 2010). The genus *Lispinus* is known from rotting cacti (Irmler, 2010), and this study found one *Lispinus* sp. individual from a single cactus sample (cardón 2). I also found 14 *Eleusis* sp. individuals*,* which were not previously known from cactus, in multiple cardón cactus samples (cardón 7, 10, 12).

One morphospecies with only two individuals was identified from the subfamily Scaphidiinae in the genus *Baeocera.* Scaphidiinae is a morphologically distinct subfamily formerly regarded as a separate family (Newton et al., 2000). Also known as the shining fungus beetles, schaphidiids are known to feed on slime molds (Newton et al., 2000). They occur in fungi, rotting wood and logs, leaf litter, and compost and have not been previously reported from rotting cacti (Newton, 1984).

Genetics: *Belonuchus* case study

Molecular data and morphological identification suggest that *Belonuchus* n .sp. is a new species, but comparison among specimens in existing collections will be needed to confirm this assertion. Since this study focused primarily on staphylinid beetles from Baja and Southern California, my samples were limited to these areas. However, Pfeiler et al (2013) sampled senita cactus in both peninsular and mainland Mexico and did not find any *Belonuchus* n. sp. specimens in mainland samples. Together, these studies suggest that *Belonuchus* n. sp. is limited to senita cactus in the Baja peninsula.

The phylogeny also suggests that specimens identified as *Belonuchus ephippiatus* may actually represent multiple species. Based on the COI gene tree, *Belonuchus* populations grouped by geographic region, and *B. ephippiatus* did not form a monophyletic group. The genetic differences among *B. ephippiatus* populations ranged from 11.8%- 14.5% and were comparable to ranges for interspecific divergences, suggesting that specimens identified as *B. ephippiatu*s may actually represent multiple species (Sbordoni, 2010). *B. ephippiatus* also showed a generalist distribution, occurring in every sampled cactus species, except senita, and from all three localities. This is consistent with current identification of *B. ephippiatus* as a generalist species, occurring in multiple genera of cactus and even non-cactus groups, like agave (Smetana, 1995).

The necrotic cactus *Belonuchus* phylogeny is currently incomplete, with more sampling and sequence data needed to reveal missing links. For example, more sampling for *Belonuchus* n. sp. in mainland Mexico will be needed to confirm its geographic restriction. There may also be additional *Belonuchus* species in the rotting cactus niche that were not observed in this study. My phylogeny is also limited because I only sequenced a single gene, the mtDNA CO1 gene, and only included 55 specimens in the gene tree.

Ecology

My temperature measurements of six rotting barrel cacti showed that rotting cactus tissue stays significantly cooler compared to ground temperatures during the hottest time of the day. This suggests that rotting cacti act as semi-closed, moist environments that shield arthropods from the desert heat.

My study also found that cactus tissue becomes more basic with the progression of necrosis, ranging from 5.39 in live tissue to 9.07 in decomposed tissue. My pH readings of six rotting barrel cacti did not change significantly over the course of 10 days, indicating that the complete decomposition of a barrel cactus is a longer process. Dissection of rotting barrel cacti also showed that the process of necrosis is complex, with some cacti containing both live and decomposed portions, with some rotting from top-to-bottom, bottom-to-top, or inside-out. Many barrel cacti in the field also appeared to have sealed themselves off from necrosis, or to only be rotting in certain areas. One cactus—barrel #6—also contained bright red portions of rotting tissue, which may have been caused by a unique bacterial community.

I tested the specificity of these rove beetles using meat baited and cactus baited pit-fall traps, and found strong evidence that rove beetles sampled from rotting cactus preferred rotting cactus over meat baits (Fig. 3). Rove beetles were almost exclusively attracted to rotting cactus traps, with only one individual (Aleocharinae 12) collected from a meat-baited trap. Rove beetles were also primarily diurnal, with only one individual (Aleocharinae 12) collected from a night flight-interception trap. My study is the first study of cactus specificity in any necrotic cactus beetle. Further experiments could test whether or not rove beetles prefer rotting cactus over similar baits including rotting agave and other rotting succulents, in order to determine whether these beetles are specific to rotting cactus.

Four species of rove beetles were also collected in flight interception traps that were not sampled from barrel cactus. These rove beetles may occupy a variety of desert niches other than rotting cactus in Anza Borrego, California. However, additional rove beetle species not captured by my study may also occur in cactus species such as prickly pear (*Opuntia*) and cholla cactus (*Cylindropuntia*), which are common in Anza Borrego. Though these cacti are not as massive as the barrel, rove beetles have been documented in prickly pear cactus (Hubbard, 1899).

Based on results from this study, cactophilic rove beetles may live for at least 2 months. Adult rove beetles collected in Anza Borrego continued to live for over one month in the laboratory and third instar larvae pupated after 9 days and had not eclosed 3 weeks later. Quezada et al. (1969) studied a rove beetle (*Xanthopygus cognatus*) occupying rotting, insect-infested coconut and papaya trees. Rotting coconut and papaya trees, like rotting cacti, are ephemeral resources with a finite duration. Like the beetles in my study, *Xanthopygus cognathus* is also a predatory rove beetle. However, the entire *X. cognathus* lifecycle, from egg to adult, was completed in only 20 days, while the beetles in this study (*Maseochara* sp. and *Belonuchus ephippiatus*) lived for over a month (Quezada et al., 1969). These differences may be related to duration of necrosis; palm tree stems and crowns are less massive than barrel cacti, and likely shorter lived. Based on field observations it is likely that rotting barrel cacti can persist for several months (Ferro et al., 2013). This supports the hypothesis that rove beetle lifecycle is adapted to the ephemerality of their habitat.

When observing rove beetle behavior in the field and laboratory I noted that they would often burrow into the tissue or soil. This is consistent with Quezada et al. (1969), which found that rove beetles were reluctant to spend time in brightly lit areas. In both studies, rove beetles preferred to eat their prey in sheltered areas. This may be a behavioral adaptation for avoiding predators and for escaping from the desert heat. This may also explain why adult staphylinids occurred with such high density in rotting cactus compared to in traps.

This study of rove beetles adds to the standing knowledge of their diversity in rotting cacti and explores the variables that affect their diversity. It provides novel findings about rove beetle behavior, specificity, and lifecycle in this niche. More work will be needed to better isolate the variables that affect rove beetle diversity and to continue to explore staphylinid diversity in other cactus species. Trends observed in this study will also be useful for future studies of necrotic cactus taxa, which will continue to expand our knowledge of the fascinating and complex necrotic cactus niche.

FIGURES AND TABLES

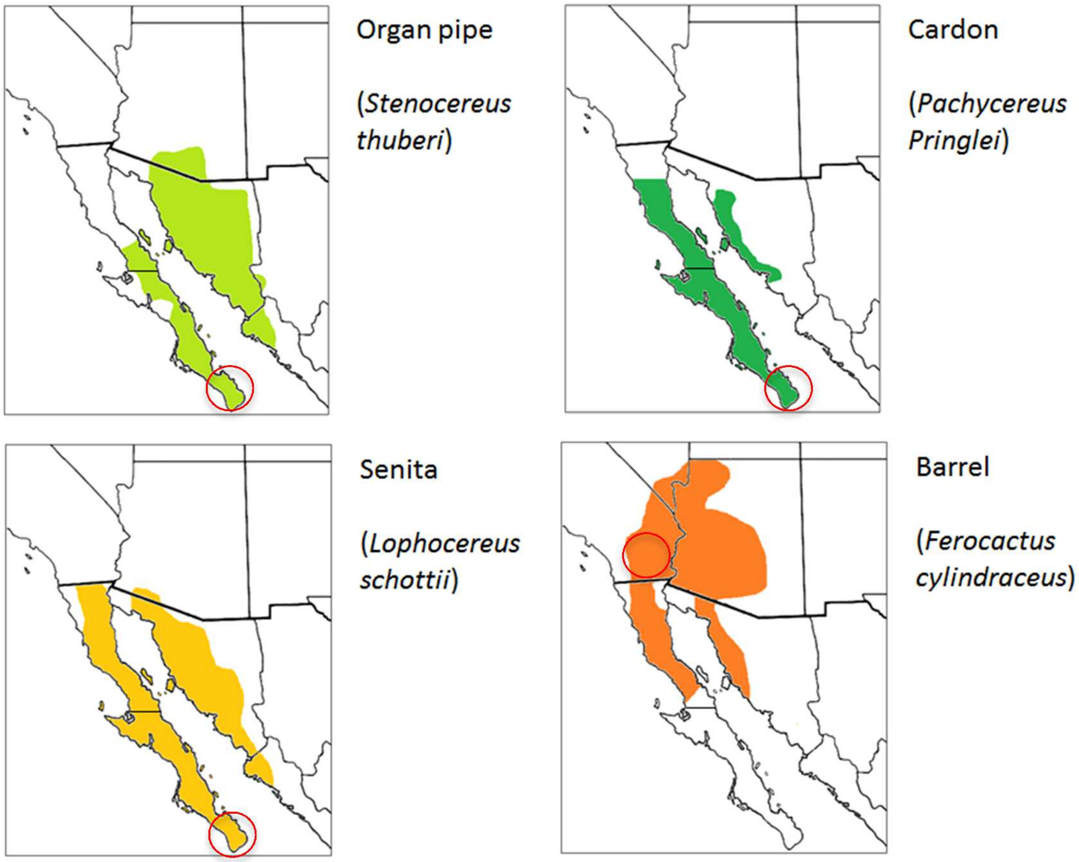

Figure 1. Distribution maps of four Sonoran Desert cactus species, following "Sonoran Desert Plants" by Turner, Bowers, and Burgess (1995). Collection sites for this study are circled.

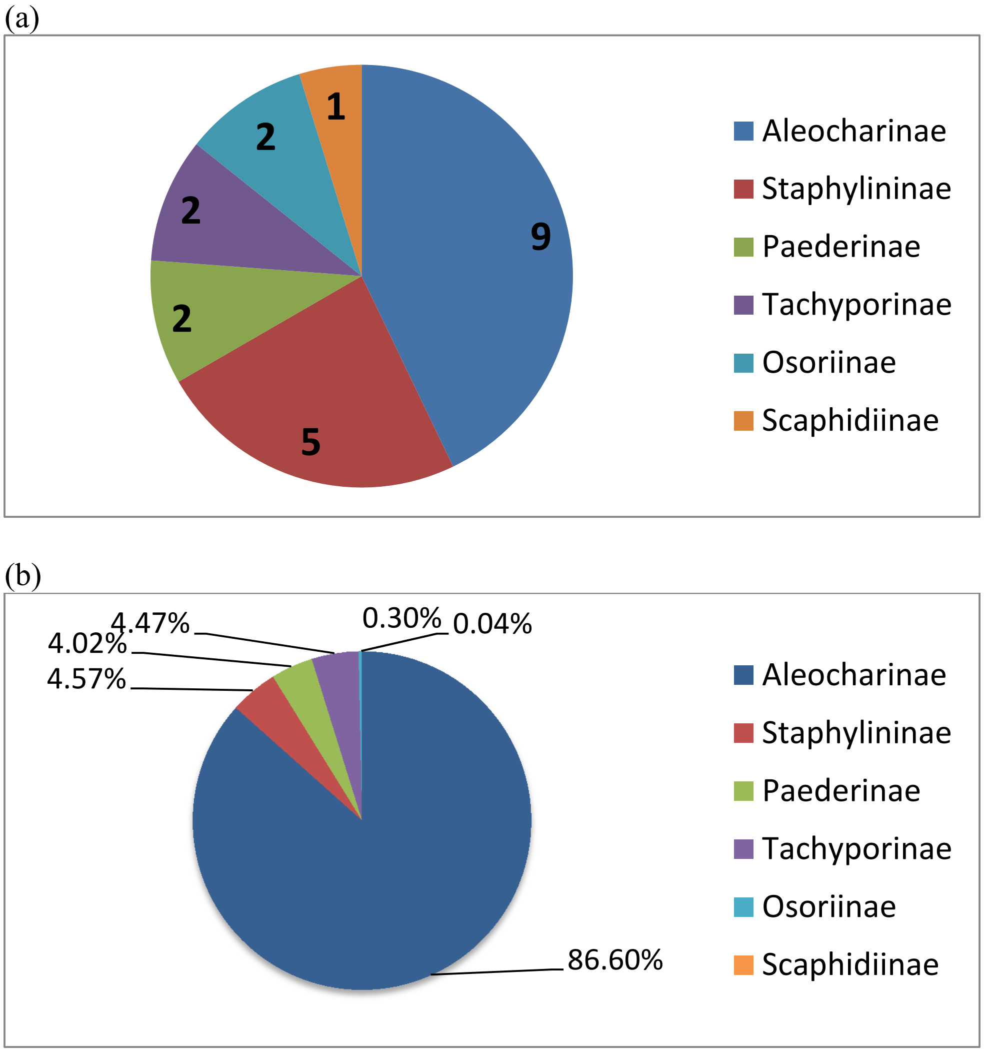

Figure 2. (a) Staphylinid species richness by subfamily and (b) staphylinid abundance by subfamily

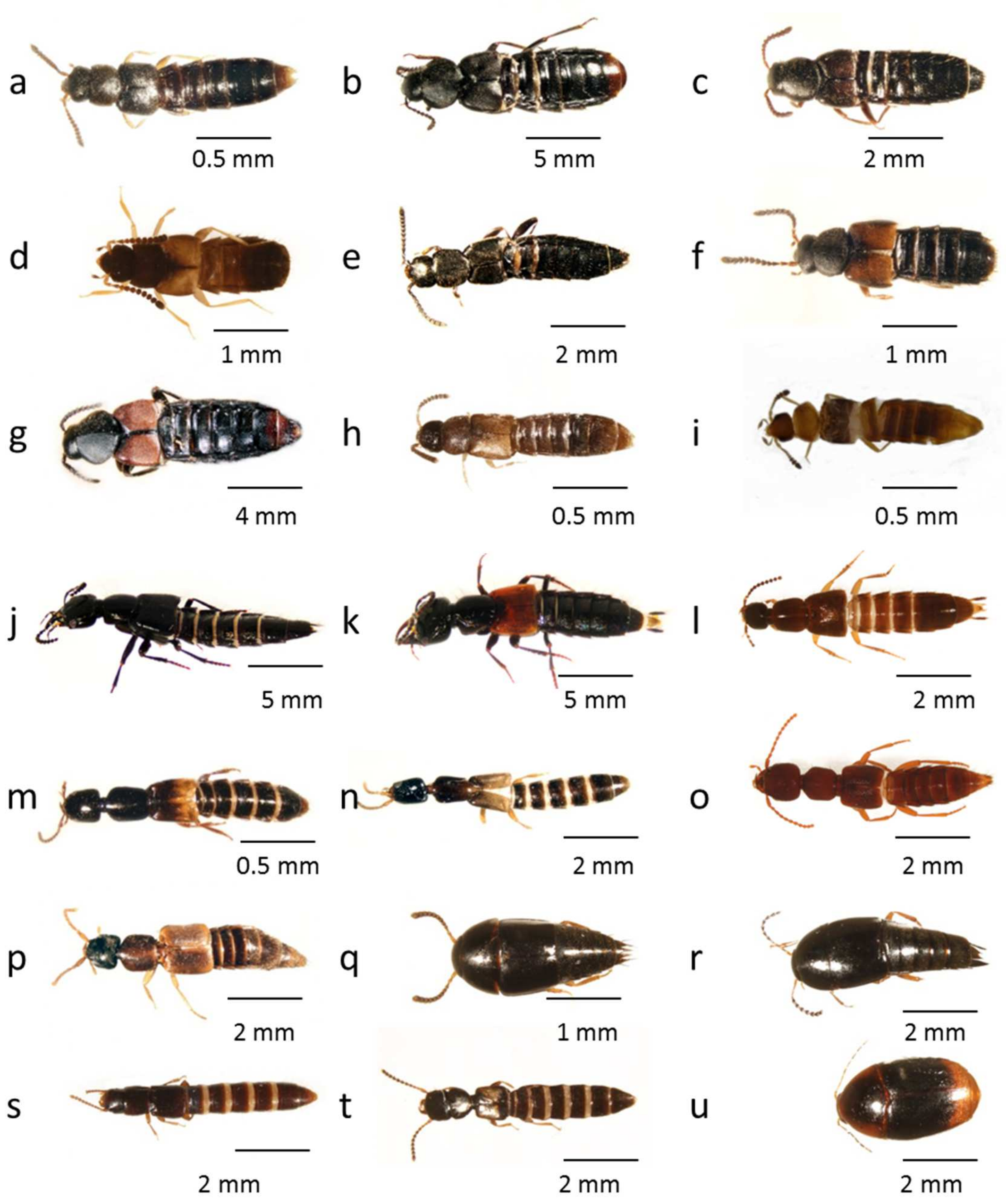

Figure 3. Images of rove beetle morphospecies (a) Aleocharinae sp. (b) *Aleochara (Maseochara*) sp. (c) *Aleochara (Maseochara)* sp. (d) Aleocharinae sp. (e) Aleocharinae sp. (f) Aleocharinae sp. (g) *Aleochara (Maseochara)* sp. (h) Aleocharinae sp. (i) Aleocharinae sp. (j) *Belonuchus* sp. (k) *Belonuchus ephippiatus* (l) *Gabrius* sp. (m) Xantholini sp. (n) Xantholini sp. (o) *Deroderus* sp. (p) *Lithocharis* sp. (q) *Tachinus* sp. (r) *Tachinus* sp. (s) *Lispinus* sp. (t) *Eleusis* sp. (u) *Baeocera* sp.

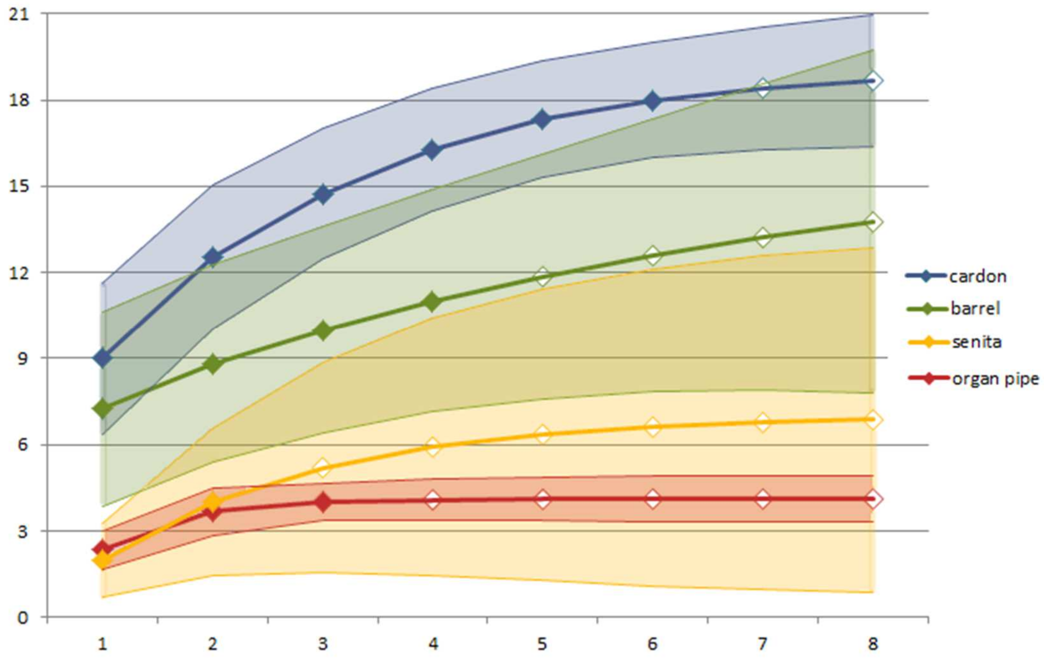

Figure 4. Staphylinid species accumulation curves in four species of necrotic cacti. Shaded points indicate samples from this study and unshaded points indicate samples extrapolated using EstimateS. Shaded regions indicate the 95% confidence intervals.

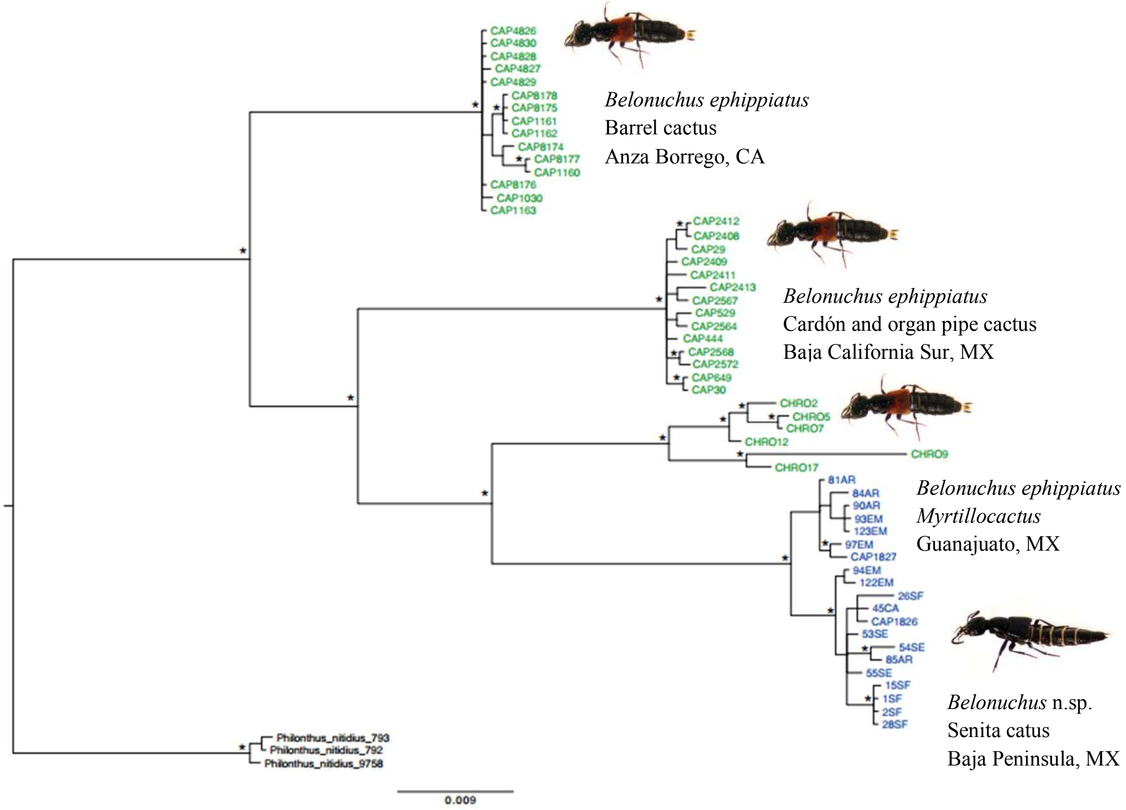

Figure 5. Phylogeny of genus *Belonuchus* collected from rotting cacti in the Sonoran Desert, constructed using cytochrome oxidase 1 sequence data.

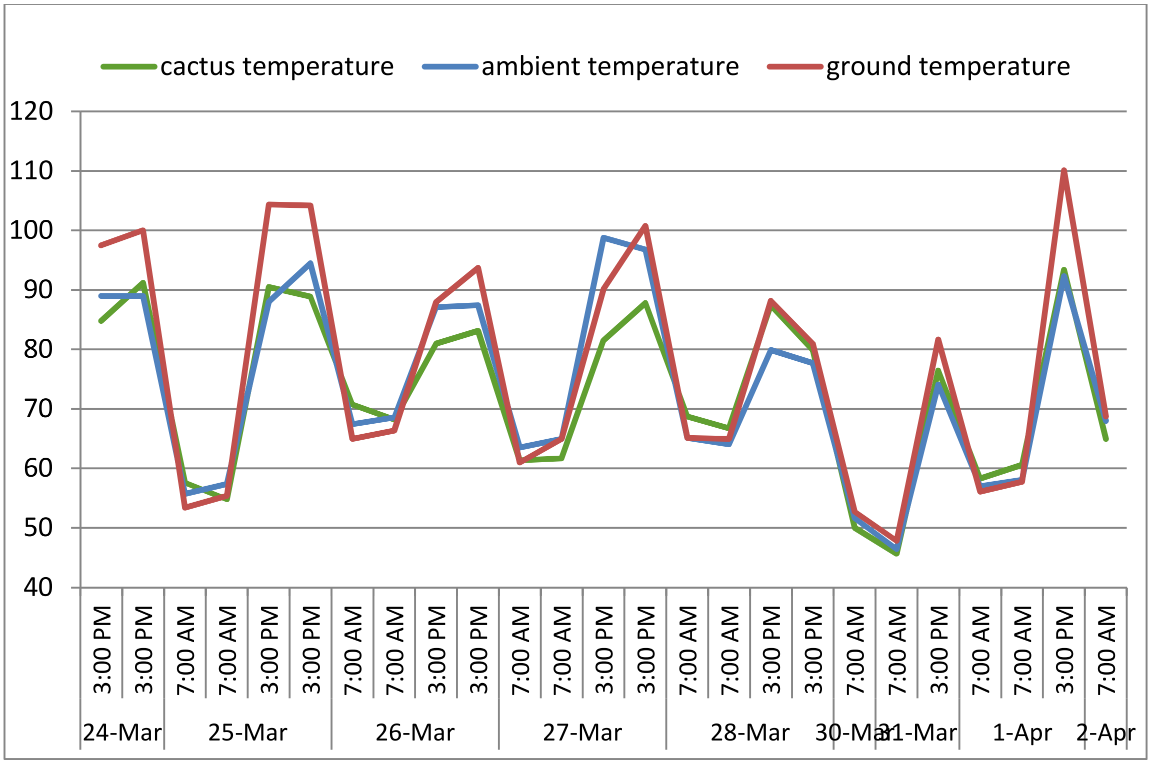

Figure 6. Internal rotting cactus temperature, ambient temperature, and ground temperature at sunrise and hottest time of day in Anza Borrego, California from March 24th to April 2nd, 2016

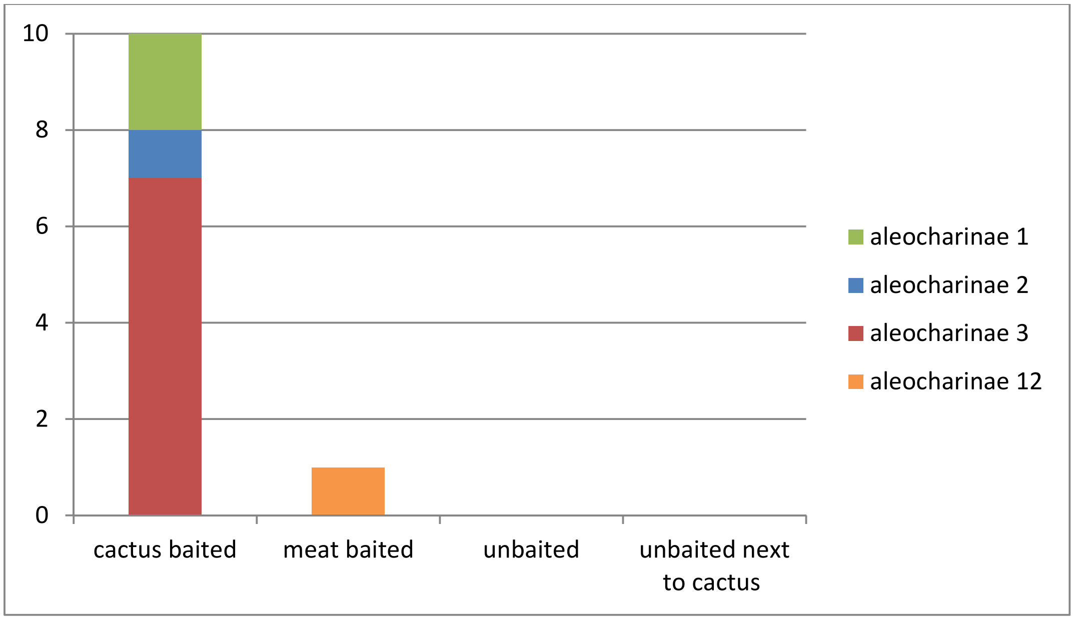

Figure 7. Host specificity of rove beetles in Anza Borrego Desert State Park.

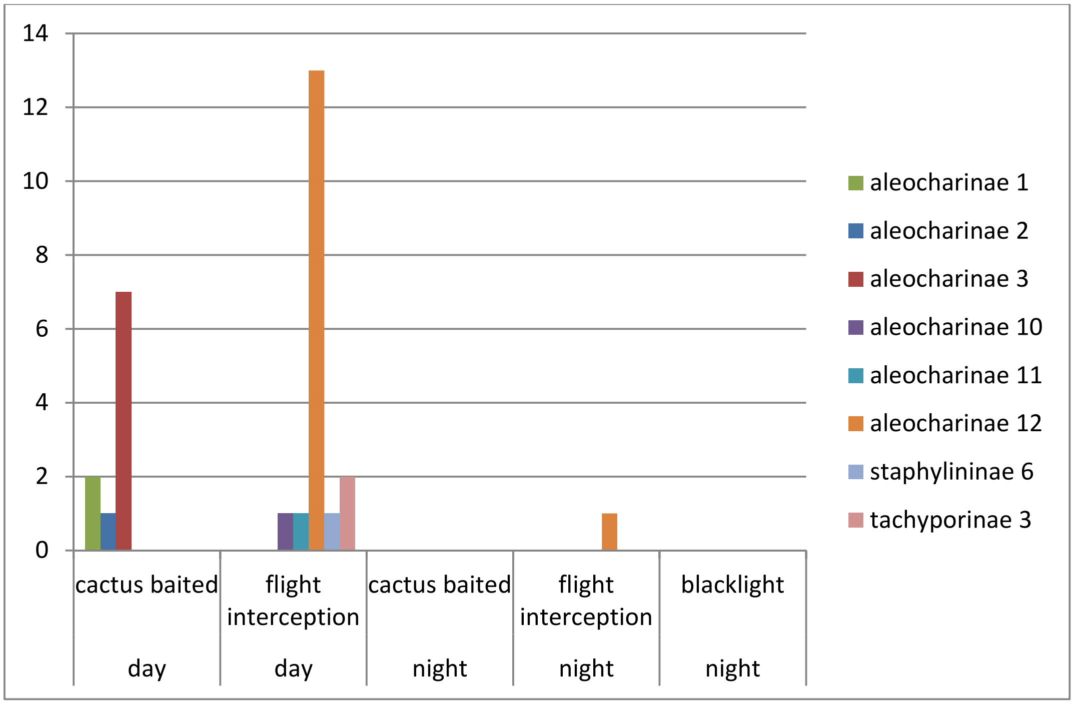

Figure 8. Diurnal and nocturnal activity of cactophilic staphylinids collected in flight interception traps, cactus baited pit-fall traps, and blacklights in Anza Borrego Desert State Park.

Table 1. Staphylinid species composition and abundances in 4 species of necrotic cactus. Staphylinid species unique to each cactus species indicated in red.

	Tribe/genus	Cardón	Barrel	Senita	Organ pipe	Total
Aleocharinae 1	unknown	1752	1612	0	51	3415
Aleocharinae 2	*Aleochara (Maseochara)* sp.	12	246	0	0	258
Aleocharinae 3	*Aleochara (Maseochara)* sp.	45	96	15	0	156
Aleocharinae 4	unknown	0	3	0	0	3
Aleocharinae 5	unknown	2	0	0	0	2
Aleocharinae 6	unknown	4	528	0	0	532
Aleocharinae 7	*Aleochara (Maseochara)* sp.	3	0	0	0	3
Aleocharinae 8	unknown	34	0	0	0	34
Aleocharinae 9	unknown	2	0	0	0	2
Staphylininae 1	*Belonuchus* sp.	0	0	2	0	2
Staphylininae 2	*Belonuchus ephippiatus*	45	143	0	4	192
Staphylininae 3	Xantholini sp.	28	0	0	0	28
Staphylininae 4	Xantholini sp.	4	0	0	0	4
Staphylininae 5	*Gabrius* sp.	4	1	0	0	5
Paederinae 1	*Deroderus* sp.	174	4	1	21	200
Paederinae 2	*Lithocharis* sp.	0	3	0	0	3
Tachyporinae 1	*Tachinus* sp.	138	32	0	0	180
Tachyporinae 2	*Tachinus* sp.	4	41	0	1	46
Osoriinae 1	*Lispinus* sp.	1	0	0	0	1
Osoriinae 2	*Eleusis* sp.	14	0	0	0	14
Scaphidiinae 1	uknown	2	0	0	0	2
Total		2240	2708	2	77	5079

Table 2. Staphylinid diversity by cactus species.

Cactus species	Cardón	Barrel	Senita	Organ pipe
Observed species richness	18	11	4	4
Observed singletons	1	1	1	1
Observed uniques	9	2	1	0
Shannon diversity index	0.93	1.25	1.01	0.84
Fisher's alpha diversity Index	2.67	1.31	1.28	0.9

Table 3. Pair-wise similarity indices for cardón, barrel, senita, and organ pipe cactus samples. Top: Chao's Sorenson abundance-based similarity index (corrected for unseen species), Bottom: Chao's Sorenson abundance-based similarity index (uncorrected)

	Cardón	Barrel	Senita	Organ Pipe
Cardón		0.986	0.325	0.938
Barrel	0.937		0.094	0.804
Senita	0.272	0.093		0.066
Organ pipe	0.985	0.799	0.093	

Table 4. Pair-wise similarity indices for cardón cactus samples. Top: Chao's Sorenson abundance-based similarity index (corrected for unseen species), Bottom: Chao's Sorenson abundance-based similarity index (uncorrected)

	cardón 2	cardón 7	cardón 10	cardón 12	cardón 13	cardón 19
cardón 2		0.634	0.831	0.857	0.526	0.725
cardón 7	0.574		0.997	0.988	0.963	0.988
cardón 10	0.585	0.975		1	0.977	1
cardón 12	0.812	0.987	0.994		0.998	1
cardón 13	0.495	0.952	0.964	0.995		0.994
cardón 19	0.596	0.925	0.967	0.975	0.89	

Table 5. Staphylinid abundance by morphospecies categorized by stage of cactus necrosis based on field notes of cardón cactus samples. Species unique to “wet/saturated” samples highlighted in green. Species unique to the “dry/older” sample highlighted in red.

Staphylinid morphospecies	wet/saturated		dry/older	unable to categorize		
	cardon 7	cardon 12	cardon 2	cardon 10	cardon 13	cardon 19
Aleocharinae 1	113	1535	1	67	35	1
Aleocharinae 2		10			2	
Aleocharinae 3	1	40		1	3	
Aleocharinae 4						
Aleocharinae 5	2					
Aleocharinae 6	2	2				
Aleocharinae 7		3				
Aleocharinae 8		4	2			
Aleocharinae 9	1		1			
Staphylininae 1						
Staphylininae 2	8	23		1	13	
Staphylininae 3	3	22		1	1	1
Staphylininae 4		1	1	1		1
Staphylininae 5		1	1			
Paederinae 1	48	80	3	1	36	6
Paederinae 2						
Tachyporinae 1	2	89	1	3	9	34
Tachyporinae 2	2	2				
Osoriinae 1			1			
Osoriinae 2	7	4		3		
Scaphidiinae 1			2			
Total	189	1816	13	78	99	43

Table 6. Staphylinid abundances by morphospecies of cardón cactus samples separated by season. Red indicated June samples and blue indicated Decemeber samples.

Species	cardón 2	cardón 7	cardón 10	cardón 12	cardón 13	cardón 19
Aleocharinae 1	1	113	67	1535	35	1
Tachyporinae 1	1	2	3	89	9	34
Paederinae 1	3	48	1	80	36	6
Staphylininae 3		3	1	22	1	1
Staphylininae 2		8	1	23	13	
Osoriinae 2		7	3	4		
Aleocharinae 3		1	1	40	3	
Staphylininae 4	1		1	1		1
Aleocharinae 6		2		2		
Tachyporinae 2		2		2		
Aleocharinae 8	2			4		
Staphylininae 5	2			2		
Scaphidiinae 1	2					
Osoriinae 1	1					
Aleocharinae 9	1	1				
Aleocharinae 5		2				
Aleocharinae 2				10	2	
Aleocharinae 7				3		
Aleocharinae 4						
Staphylininae 1						
Paederinae 2						

Table 7. Number of staphylinid morphospecies by subfamily collected from six species of rotting cactus by this study, Ferro et al (2013), Castrezana and Markow (2001), Dury (1916), and Hubbard (1899).

Subfamily	Cardon *Pachycereus pringlei*		Saguaro *Carnegiea gigantea*	Organ pipe *Stenocereus thurberi*		Senita *Lophocereus schottii*		California Barrel *Ferocactus cylindraceus*	Fishhook Barrel *Ferocactus wislizeni*	
	This study	Markow (2001)	Hubbard (1899)	This study	Markow (2001)	This study	Markow (2001)	This study	Ferro et al. (2013)	Dury (1916)
Aleocharinae	9		7	1		1		5	5	1
Staphylininae	5	1	3	1	1	1	1	2	1	2
Tachyporinae	2	1	3	1	1	1		2	2	
Paederinae	2		1	1		1		2	1	
Oxyteliinae									2	
Pselaphinae			1							
Omaliinae			1							
Scydmaeninae			1							
Osoriinae	2									
Scaphidiinae	1									

Table 8. Comparison of staphylinid taxa by species richness collected by this study, Ferro et al (2013), Castrezana and Markow (2001), Dury (1916), and Hubbard (1899).

subfamily	tribe/genus/species	Cardon		Saguaro	Organ pipe		Senita		California Barrel	Fishhook Barrel	
		This study	Castrezana and Markow (2001)	Hubbard (1899)	This study	Castrezana and Markow (2001)	This study	Castrezana and Markow (2001)	This study	Ferro et al. (2013)	Dury (1916)
Aleocharinae	*Aleochara (Maseochara)* sp.	3		3			1		2	2	1
	Apheloglossa rufipennis			1							
	Diestota sp.									2	
	Oligota sp.			1							
	Placusa vaga									1	
	Unknown	6		2	1				3		
Staphylininae	*Belonuchus ephippiatus*	1		1	1				1	1	1
	Belonuchus n.sp.						1				
	Platydracus phoenicurus		1			1		1			
	Xantholini *sp.*	2									
	Gabrius sp.	1							1		
	Xanthopygus cacti			1							1
	Neohypnus dimidiatus			1							
Tachyporinae	*Tachyporus* sp.		1			1					
	Coproporus hepaticus			1							
	Coproporus laevis			1							
	Tachinomorphus grandis									1	
	Tachinomorphus grossulus			1						1	
	Tachinus sp.	2			1		1		2		
Paederinae	*Lithocharis* sp.								1		
	Deroderus sp.	1			1		1		1	1	
	Deroderus tabacinus			1							
Oxyteliinae	*Carpelimus* sp.									1	
	Platystethus spicules									1	
Pselaphinae	*Hamotus elongates*			1							
Omaliini	*Hapalaraea cacti*			1							
Scydmaeninae	*Eumicrus lucanus*			1							
Osoriinae	*Eleusis* sp.	1									
	Lispinus sp.	1									
Scaphidiinae		1									

APPENDIX

Table S1. Details of *Belonuchus* specimens used to construct gene tree

Specimen	Species ID	Cactus species	Locality
CAP 1030	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 1160	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 1161	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 1162	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 1163	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 4826	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 4827	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 4828	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 4829	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 4830	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 8174	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 8175	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 8176	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 8177	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 8178	*Belonuchus ephippiatus*	Barrel (*Ferocactus cylindraceus*)	Anza Borrego, California, USA
CAP 2408	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 2409	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 2411	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico

Table S1. Details of *Belonuchus* specimens used to construct gene tree, continued

CAP 2412	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 2413	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 2564	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 2567	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 2568	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 2572	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 29	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 30	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 444	*Belonuchus ephippiatus*	Cardón (*Pachycereus pringlei*)	La Paz, Baja California Sur, Mexico
CAP 529	*Belonuchus ephippiatus*	Organ pipe (*Stenocereus thurberi*)	La Paz, Baja California Sur, Mexico
CAP 649	*Belonuchus ephippiatus*	Organ pipe (*Stenocereus thurberi*)	La Paz, Baja California Sur, Mexico
CHRO 12	*Belonuchus ephippiatus*	*Myrtillocactus*	San Miguel de Allende, Guanajuato, Mexico
CHRO 17	*Belonuchus ephippiatus*	*Myrtillocactus*	San Miguel de Allende, Guanajuato, Mexico
CHRO 2	*Belonuchus ephippiatus*	*Myrtillocactus*	San Miguel de Allende, Guanajuato, Mexico
CHRO 5	*Belonuchus ephippiatus*	*Myrtillocactus*	San Miguel de Allende, Guanajuato, Mexico
CHRO 7	*Belonuchus ephippiatus*	*Myrtillocactus*	San Miguel de Allende, Guanajuato, Mexico
CHRO 9	*Belonuchus ephippiatus*	*Myrtillocactus*	San Miguel de Allende, Guanajuato, Mexico
CAP1826	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	La Paz, Baja California Sur, Mexico
CAP1827	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	La Paz, Baja California Sur, Mexico
81AR	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Armenta, Baja California Sur, Mexico

Table S1. Details of *Belonuchus* specimens used to construct gene tree, continued

84AR	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Armenta, Baja California Sur, Mexico
85AR	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Armenta, Baja California Sur, Mexico
90AR	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Armenta, Baja California Sur, Mexico
45CA	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Catavina, Baja California, Mexico
122EM	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Ensenada de los Muertos, Baja California Sur, Mexico
123EM	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Ensenada de los Muertos, Baja California Sur, Mexico
93EM	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Ensenada de los Muertos, Baja California Sur, Mexico
94EM	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Ensenada de los Muertos, Baja California Sur, Mexico
97EM	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	Ensenada de los Muertos, Baja California Sur, Mexico
53SE	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	La Sepultura, Baja California, Mexico
54SE	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	La Sepultura, Baja California, Mexico
55SE	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	La Sepultura, Baja California, Mexico
15SF	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	San Felipe, Baja California, Mexico
1SF	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	San Felipe, Baja California, Mexico
26SF	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	San Felipe, Baja California, Mexico
28SF	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	San Felipe, Baja California, Mexico
2SF	*Belonuchus* n.sp.	Senita (*Lophocereus schottii*)	San Felipe, Baja California, Mexico

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