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Biodiversity of cactophilic microorganisms in western Argentina: community structure and species composition in the necroses of two sympatric cactus hosts

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ABSTRACT

The cactus-yeast-*Drosophila* system is a model system in evolutionary biology, and the participating saprotrophic microorganisms represent one of the most thoroughly studied microbial communities. However, much of the cactus-dominated regions of South America, home to endemic versions of this classical system, remain understudied. A combined morpho-physiological and molecular approach was employed to identify the fungal members of the cactus-yeast-*Drosophila* system in western Argentina. We identified twenty one species of saprotrophic organisms in the necroses of *Opuntia sulphurea* and *Trichocereus terscheckii* in a region of sympatry, where both cacti are exploited by cactophilic *Drosophila*. After excluding opportunistic isolates, we determined that the saprobe community of *O. sulphurea* was composed of eight species (including the first consideration of filamentous fungi as community members), whereas the community of *T. terscheckii* represented a subgroup of the former. We explain this nested pattern by considering the physiological and ecological attributes of both hosts and vectors involved.

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Introduction

Cacti are a central physiognomic element of most arid and semi-arid regions of the New World, dominating the plant communities of desert environments (Anderson, 2001). Their large population sizes, along with their capacity to store massive amounts of water and maintain high energy production efficiencies in arid climates (Ehleringer and Monson, 1993) has led to their establishment as key players in the ecological dynamics of neotropical and nearctic deserts (Fleming and Valiente-Banuet, 2002; Wolf & Martínez del Rio, 2003). In particular, cactus necroses represent extremely rich microhabitats in an otherwise hostile environment, hosting outstandingly diverse arthropod (Olson, 2000; Castrezana and Markov, 2001) and microbial communities (Foster and Fogleman, 1993; Lachance et al., 1988). Among this biodiversity that depends on the exploitation of decaying cactus tissues, rests the cactus-yeast-*Drosophila* system, a model for studies in evolutionary biology (Barker and Starmer, 1982), microbial ecology (Ganter, 2011) and chemical ecology (Fogleman and Danielson, 2001).

The system relies on three major interactors: (a) members of the family Cactaceae, both prickly pears (*Opuntia* spp.) and columnar cacti, whose necrotic cladodes and stems are used as substrata (and are therefore referred to as hosts); (b) the community of saprotrophic microorganisms that initiate and participate in the decomposing process; and (c) a guild of cactophilic species of the genus *Drosophila*, whose adult and larval stages feed on the decaying cactus tissues, also known as “rots”, and the microorganisms present (Barker and Starmer, 1982; Starmer et al., 1991). The process is initiated when cacti are damaged or senescent, leading to the initial stages of decomposition which are thought to be dominated by bacteria (Lachance et al., 1988; Fogleman and Foster, 1989). The volatile compounds produced during the bacterial fermentation of the tissues attract certain species of arthropods, among which are cactophilic *Drosophila*. These feed and lay their eggs on the necrosis, inoculating in the process certain species of fungi (especially yeasts). These yeasts grow vigorously, chemically and physically modifying the substratum and serving as food for larvae while producing host specific volatile profiles which in turn are used by the flies as cues for suitable environments (Fogleman and Foster, 1989; Barker and Starmer, 1999; Fogleman and Danielson, 2001). The interaction between cactophilic *Drosophila* and yeasts has been described as a diffuse mutualism (Starmer et al., 1991), with yeasts benefiting through their use of flies as vectors that transport them to temporally bounded and spatially dispersed resources (Ganter, 2011).

The study of the cactophilic yeast community was pivotal in the early steps of microbial ecology as a discipline (Lachance and Starmer, 1998), and is therefore one of the most thoroughly studied microbial communities. The diversity of yeasts found in cactus necroses is quite limited, with relatively few endemic species dominating the habitat (Ganter, 2011). These species are nutritionally specialized (Lachance et al., 1988), and make up a community that is temporally persistent (Latham, 1998) and different from other sympatric yeast communities (Ganter et al., 1986; Ganter, 2011), supporting the existence of the cactophilic niche. Within this community, some yeasts are considered to be generalists and are widely distributed, others are restricted to certain host species or geographic regions (Starmer et al., 1991). Both community structure and species composition are qualities that depend on a myriad of factors, of which vector ecology and host chemistry are likely to be the most important (Ganter et al., 1986; Heed et al., 1976; Starmer et al., 1991). It is, therefore, expected that the biological attributes of both vectors and hosts have an impact on the structure of the cactophilic microbial community at a local scale, raising the value of research aiming at the characterization of regional versions of the classical cactus-yeast-*Drosophila* system.

One of the most successful clades of the genus *Drosophila* is the *repleta* species group (Throckmorton, 1975), which diversified in the arid and semi-arid regions of the New World due to their ability to colonize cactus necroses (Durando et al., 2000; Oliveira et al., 2012). Within this group, the *buzzatii* cluster is a monophyletic group of seven species found mainly in open, xerophytic regions of South America’s “diagonal of dry formations” (Manfrin and Sene, 2006). Two of these species, *Drosophila buzzatii* and *D. koepferae*, occur in the Andean regions of western Argentina (Fontdevila et al., 1988; Ruiz and Wasserman, 1993). *D. buzzatii* uses necrotic cladodes of *Opuntia* spp. as primary hosts, whereas *D. koepferae* mainly exploits columnar cacti of the genera *Cereus* and *Trichocereus* (Fanara et al., 1999; Hasson et al., 2009; Soto et al., 2012). Nonetheless, a certain degree of overlap in host exploitation occurs in the vast areas where both species live in sympatry, with the two species emerging from both resources, despite maintaining their preference for their respective primary host (Hasson et al., 1992, 2009). In some of these regions of sympatry, two dominant species, the prickly pear *Opuntia sulphurea* and the columnar cactus *Trichocereus terscheckii* (cardón) are used as feeding and breeding substrata by both fly species (Soto et al., 2012). Although this oligophagous habit is not uncommon in the *D. repleta* group (Oliveira et al., 2012), most *Drosophila* species only exploit a single host at a given locality, as occurs for example in the cactus-yeast-*Drosophila* system of the Sonoran desert (Fogleman and Abril, 1990; Fogleman and Danielson, 2001). Since cactophilic yeasts disperse exclusively through the use of flies as vectors, both their biogeography and their realized niche are dependent on the ecology of their vectors (Ganter, 2011). Consequently, systems with highly specialized *Drosophila* species, that feed and breed on a single cactus host, develop differentiated cactus-specific yeast communities even in sympatry (Starmer and Fogleman, 1986; Ganter, 1988, 2011). Whether or not this pattern of isolated communities will develop in systems where there is a constant flow of vectors between different cactus species is still an open question.

Once the requisite of dispersion has been fulfilled, the second factor affecting yeast community structure is the presence of toxic host chemicals (Starmer et al., 1991). Columnar cacti are known to present more complex chemistries than prickly pears, being rich in allelochemicals such as triterpene glycosides, medium-chain fatty acids, alkaloids and sterol diols (Fogleman and Danielson, 2001). Several cases in which the cactus chemistry affects host use by both flies and