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Travel, Sex, and Food: What's Speciation Got to Do with It?

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Abstract

We discuss the potential interactions among travel (dispersal and gene flow), bacterial “sex” (mainly as horizontal gene transfer), and food (metabolic plasticity and responses to nutrient availability) in shaping microbial communities. With regard to our work at a unique desert oasis, the Cuatro Ciénegas Basin in Coahuila, Mexico, we propose that diversification and low phosphorus availability, in combination with mechanisms for nutrient recycling and community cohesion, result in enhanced speciation through reproductive as well as geographic isolation. We also discuss these mechanisms in the broader sense of ecology and evolution. Of special relevance to astrobiology and central to evolutionary biology, we ask why there are so many species on Earth and provide a working hypothesis and a conceptual framework within which to consider the question. Key Words: Microbial ecology—Microbial mats—Evolution—Horizontal gene transfer—Metabolism. *Astrobiology* 12, 634–640.

1. Introduction

WE NOW KNOW that microbes interact with their environment in ways that can be described in terms of biogeographic regions (Hanson *et al.*, 2012) that can house not only cosmopolitan species but also microorganisms that are endemic and/or specific to a particular ecology. It is the individuality of this latter group that largely characterizes a specific biogeographic region or regions. This characterization provides an empirical and theoretical framework in which to consider the processes and mechanisms of a microbial population adapting to its local environment independently of its taxonomical status. The ability to describe biogeographic regions is completely tied to our increased technical proficiency in sequencing target nucleic acids at a large scale in environmental samples, which allows us to move from considering microbial ecology in single, pure, environmentally derived culture analysis to studies of whole communities across geographic distance. This is precisely what microbial population geneticists needed to begin to consider the population dynamics of microbes. Indeed, the call is to bear in mind classic evolutionary processes—selection, drift, dispersal, and mutation—as the mechanisms that maintain microbial biogeographic patterns (Hanson *et al.*, 2012).

However, our ability to assess biogeographic regions provides another opportunity for exploration to discover the

actual processes that serve to populate a biogeographic region with its species. In other words, which mechanisms create, maintain, or diminish diversity in a biogeographic region? This specific question is part of a larger scientific quest: understanding the maintenance of global diversity. Certainly it is this diversity that fuels the fundamental, underlying processes that maintain the Earth system in terms of elemental recycling, as well as life's dynamic and tenacious ability to colonize an astonishing array of habitats. It even fuels our intelligent speculation for extraterrestrial life.

The Cuatro Ciénegas Basin (CCB) is a unique, well-studied biogeographic region, an oasis in the Chihuahuan Desert with very little nutrients (ultraoligotrophic) and a high biodiversity (Souza *et al.*, 2006, 2008). The widespread oligotrophy and geochemical conditions that impact the concentrations and relative ratios of limiting nutrient supplies (Elser *et al.*, 2005) have resulted in utilization of the CCB as a research proxy for early Earth, when nutrients were extremely scarce (Anbar *et al.*, 2007; Papineau, 2010), and as an analogue of Gale Crater on Mars, the current target of choice for exploration for NASA's Mars Science Laboratory.

Evidence from comparative genomics and molecular clock assessments from the CCB indicate that roughly 50% of the microbial taxa appear to be most closely related to other marine biogeographic regions rather than to microbes from inland waters. The most plausible explanation for this

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apparent genetic relict of a marine life is the geographic evidence for previous ancient oceans that entered the region 200 million years ago (Alcaraz *et al.*, 2008, 2010; Desnues *et al.*, 2008; Moreno-Letelier *et al.*, 2011, 2012 in this issue; Peimbert *et al.*, 2012 in this issue). However, molecular clock estimation places some of the constituents of the CCB to a divergence event in the Precambrian 800 million years ago (Domínguez-Escobar *et al.*, 2011; Moreno-Letelier *et al.*, 2011) with subsequent colonization in the area as well as with a consistent and ongoing local speciation and diversification in the microbial community, including viruses (Desnues *et al.*, 2008), bacteria (Escalante *et al.*, 2008, 2009; Cerritos *et al.*, 2011; Rebollar *et al.*, 2012), and diatoms (Winsborough *et al.*, 2009). Thus, a significant portion of the CCB microbiota appears to have evolved from these relict ancestral marine taxa to form the extant and continuously diversifying local biota that defines a highly endemic CCB biogeographic region.

Here, we consider several factors that may have led to this apparent wealth of microbial diversity, with particular attention to the roles of travel (dispersal and gene flow), bacterial “sex” [both recombination within species and horizontal gene transfer (HGT) among lineages, as mediated by nutrient deficiency], and food (metabolic plasticity and responses to nutrient availability) in shaping microbial communities. Our motivation is to offer an additional conceptual framework for population microbiologists that can help progress our understanding of *how* diversity might be achieved and maintained in a biogeographic region. We do so in the context of the CCB, where genetic and geographic isolation of microorganisms has been observed under the constant pressure of an insufficient “food source.” Our working hypothesis (Souza *et al.*, 2008) is that the extreme long-term oligotrophy has impacted the biogeographic region in such a way that populations have been isolated in their potential to access genetic resources through sex (HGT), which has promoted localized diversification with accompanying unusual rates of speciation.

2. Travel

The aquatic ecosystems of the CCB are located *ca.* 720 m above sea level and are separated from the closest shoreline by >800 km of mountainous and arid terrain. Although this effectively “isolates” these aquatic ecosystems from the closest marine environment, the possibility of long-range dispersal as a means of “seeding” these remote habitats must be excluded. As mentioned above, the idea of biogeographic regions in the microbial realm has been established recently. In contrast to macroorganisms, where it has been known for some time that distinct biogeographic patterns are the rule (Rosenzweig, 1995), the hypothesis that “everything is everywhere, but the environment selects” (EEBES, Baas Becking, 1934; de Wit and Bouvier 2006) has been the working rule of thumb for the microbial realm. Historically, the logic suggested that the combined effects of small body size, rapid asexual reproduction, and high population densities should facilitate broad, unlimited dispersal, which would prevent the formation of distinct microbial communities by distance and elimination of “detectable” biogeographic patterns (reviewed in Fenchel *et al.*, 1997; Finlay and Clarke, 1999; Finlay, 2002; A.C. Martiny *et al.*, 2006; Fierer, 2008; Cermeno and Falkowski, 2009; Shurin *et al.*, 2009). Assessing EEBES

has been difficult because less than 1% of the microbes can be cultured (Amann *et al.*, 1995), and previous work may have overemphasized cosmopolitan generalists that are easy to culture. However, microbial ecologists are now deploying “cultivation independent” techniques, such as small-subunit 16S (ribosomal) rRNA gene analysis, to identify uncultivable microorganisms (Stackebrandt and Ebers, 2006), which allows for comprehensive assessment of EEBES for the first time.

Several methodologies have been employed to assess the diversification and species content of a biogeographic region with use of the 16S as a taxonomical marker, including phylogenetic reconstructions within individual species (Achtman *et al.*, 1999; Helgason, *et al.*, 2004) and community-level dynamics (Horner-Devine *et al.*, 2004). Rarefaction curves (taxa-accumulation curves), whereby the number of operational taxonomic units (OTUs) are plotted as a function of sampling effort, rarely reach an asymptote (Curtis *et al.*, 2002; Curtis and Sloan, 2005), even if hundreds of thousands of sequences are analyzed with next-generation methods such as 454 pyrosequencing tags (Sogin *et al.*, 2006; Roesch *et al.*, 2007; Fierer, 2008). At present, capturing the “full” genetic diversity within any given environmental sample appears to be extremely unlikely (Hughes *et al.*, 2001; Curtis and Sloan, 2005), and this has led to the idea of chronic subsampling of the environment. If this is the case, we could easily imagine that each sampling site will have all the known taxa, and as a result we would expect little variation in the general microbial diversity as a function of distance, since each similar site would contain an equivalent list of taxa (Finlay, 2002). However, an increasing number of studies clearly indicate a positive power-law relationship between the number of species and the size of the area, which suggests both geographic structure and a particular accompanying community structure (Finlay, 2002; Torsvik *et al.*, 2002; Papke *et al.*, 2003; Whitaker *et al.*, 2003; Horner-Devine *et al.*, 2004; Gans *et al.*, 2005; Noguez *et al.*, 2005; Tringe *et al.*, 2005; Silva *et al.*, 2005; Hong *et al.*, 2006; J.B.H. Martiny *et al.*, 2006; Cadillo-Quiroz *et al.*, 2012; Hanson *et al.*, 2012).

Even if we can never be sure that our lack of sampling is missing a relevant part of the local diversity, common sense dictates that limits to global dispersal are numerous. Certainly, anaerobes would be a classic example of physiological limits on dispersal (Maron *et al.*, 2005; Litchman, 2010). Even in the case of spore-forming generalists that can migrate effectively, such as *Bacillus*, some species within this genus exhibit considerable local differentiation and diversification (Stach *et al.*, 2003; Alcaraz *et al.*, 2008; Hubert *et al.*, 2009; Jungblut *et al.*, 2010; Oakley *et al.*, 2010), which suggests limits to migration. A particular, good context within which to consider EEBES would be globally distributed but environmentally stringent environments. Recognizing that if EEBES is the mechanism most at play, such environments would select from the global pool; thus similar environments around the world should harbor the same organisms. Evidence suggests that this is at least partially true but only at relatively high taxonomic levels. For example, the genus *Sulfolobus* is located almost wherever there is volcanic activity, and *S. solfataricus* has been found in areas including Yellowstone National Park, Mount St. Helens, Iceland, Italy, and Russia (Brock *et al.*, 1972). Nevertheless, population genetics has shown that geographic structure and differentiation of genotypes between sites are commonplace in

Sulfolobus (Papke *et al.*, 2003; Whitaker *et al.*, 2003; Whitaker, 2006). Furthermore, a recent study in which high-throughput sequencing and comparative genomic tools were used shows clear patterns of differentiation between sites, while gene flow between coexisting isolates within a site ensures species cohesion at the local level (Cadillo-Quiroz *et al.*, 2012). Greater efficiency in sampling techniques elsewhere provides similar results; geographic structure has been demonstrated in *Desulfolobus* (Oakley *et al.*, 2010), deep-sea methanogens (Tavormina *et al.*, 2010), Antarctic cyanobacteria (Pointing *et al.*, 2009), and the marine Cyanobacteria *Prochlorococcus* (A.C. Martiny *et al.*, 2006). This implies that even large-scale and intensive mixing via ocean currents does not obscure biogeographic patterns, even among microorganisms that were previously assumed to be cosmopolitan (Shapiro *et al.*, 2012).

We see clear patterns of biogeographic regions with respect to the CCB. The geographic isolation occurs at small scales and, as a result and despite higher-level similarities (*i.e.*, similar marine-related taxa), each site is different at increasing resolution from the other sampled sites (Desnues *et al.*, 2008; Breitbart *et al.*, 2009; Escalante *et al.*, 2009; Bonilla-Rosso *et al.*, 2012 in this issue; Rebollar *et al.*, 2012). In fact, in the CCB we observe an increase in both gamma and beta diversity (the slope in the taxa-area power function) as we increase the sampling area. In contrast, a strong dominance of just a few taxa over large areas has been observed in other desert environments by researchers working with different methods at various sites (Kuske *et al.*, 1997; Dunbar *et al.*, 1999; Gundlapally and Garcia-Pichel, 2006).

In addition to evidence of geographic structure within the CCB, our findings suggest high local diversity, which appears to be independent of the sampling method (Souza *et al.*, 2006; Escalante *et al.*, 2008). Early studies revealed a higher number of OTUs of *Bacillus* than would generally be expected in an oligotrophic aquatic ecosystem. This included surveys of cultivated strains with the use of BOX-PCR and 16S rDNA gene sequences (Cerritos *et al.*, 2011; G. Olmedo, personal communication). These studies revealed the presence of several new *Bacillus* species (Cerritos *et al.*, 2008; M. Avitia and R. Cerritos, personal communication) with highly distinct genomes (Alcaraz *et al.*, 2008, 2010).

These early hints have been borne out with more intensive work with next-generation genomics techniques. Recently, high-throughput sequencing of microbialites within the CCB, with 454 pyrosequencing and detailed metagenomic analysis, allowed for identification of 1200 unique OTUs in a single microbial mat, with very little overlap to other studied metagenomes from the CCB (Bonilla-Rosso *et al.*, 2012 in this issue). Furthermore, with 454 pyrosequencing of 16S rDNA gene tags, 56,000 new OTUs were estimated in a single soil sample of the CCB, most of them different from another soil sample 1 km away (López-Lozano *et al.*, personal communication). Considering that, with the same technique and the same primer, Sogin and co-authors (2006) found between 2000 and 3000 different OTUs in several marine sediment samples and remarked about the high diversity of this “rare biosphere,” Cuatro Ciénegas appears to be 10-fold more diverse. Paradoxically, this diversity is comparable with studies in fertile temperate soils, where the availability of organic matter is abundant and conditions are extremely humid (Curtis and Sloan, 2005; Fierer and Jackson, 2006;

Roesch *et al.*, 2007). However, the ample availability of resources, in community theory, can easily sustain a diverse community; it is the case of CCB biodiversity in extreme oligotrophy that is hard to explain. The fact that each sampling site is different from the next site suggests that either migration is rare or each community is adapted to very specific local conditions.

3. Sex

Prokaryotes reproduce by binary fission, which forms clonal lineages that diversify by mutations that slowly accumulate by vertical descent. This eventually gives rise to diversifying lineages, as new mutations steadily increase and new niches become available. Nevertheless, novel genetic variation is occasionally introduced by HGT, a form of bacterial sex. (In the microbial context, “sex” is considered the exchange of exogenous genetic material.) This input of new genes can arrive by plasmid acquisition (Anderson and Hughes, 2010) via double-stranded recombination, which is essentially mediated by proteins responsible for DNA repair. This is considered the main physical process by which genes are transferred between microbial donors and receptors in transduction (virus infection), transformation (DNA uptake by competent bacteria), or conjugation (plasmid dynamics) (Kuzminov, 1995; Seigneur *et al.*, 1998; Cox, 2000; Redfield, 2001). A legacy of HGT is the potential for trait-based evolutionary innovations (Redfield, 2001). Depending on the genes that are mobilized and the ecological context of the receiver, HGT can have a strong adaptive value if it allows the acquiring cell to use new resources and occupy new niches (Bolhuis *et al.*, 2010). For example, this is apparent with respect to the small, photosynthetic cyanobacterium *Prochlorococcus*, where each strain seems to possess a different strategy for scavenging P in the oligotrophic ocean gyres (A.C. Martiny *et al.*, 2006). The patchwork pattern of their P acquisition genes, and evidence of viral components in their genomes, suggests that transduction by viruses is the mechanism for frequent HGT in these ocean dwellers (A.C. Martiny *et al.*, 2006).

The notion of bacterial “sex” as a promiscuous senseless exchange of genes between different phyla was elegantly argued in the work of Ford Doolittle (Baptiste *et al.*, 2008) and Howard Ochman (van Passel *et al.*, 2008). This has led some researchers to claim that there are no bacterial species but merely the existence of a diverse pool of disposable genes (Lawrence and Retchless, 2010). This view is extreme, but it occurs in the context of a large effective population size where even rare migration of genes can have a large homogenizing effect (*i.e.*, enteric bacteria) (Charlesworth and Charlesworth, 2010). If extensive bacterial sex is combined with the potential for limitless dispersal (via vectors such as plants and animals or atmospheric or ocean currents), the migration of genes, as well as cell-cell contact between individuals, could mix different populations. Consequently, this would result in the maintenance of a single cohesive gene pool and therefore reduce the probability of local differentiation. In the extreme version of this view of life, we cannot explain microbial diversity.

Despite the theoretical possibility of unlimited HGT, it has been argued that the effects of bacterial “sex” are, in fact, exaggerated. For example, a reduced role for HGT may

reflect inherent differences in overall cell organization between lineages, which would significantly lower the success of recombinants resulting from lateral gene exchange (see review by Thomas and Nielsen, 2005). Furthermore, lateral gene exchange occurs rarely between different lineages, even if it may have important consequences for population structure within species (e.g., Souza *et al.*, 1992, 1997; Silva *et al.*, 2003, 2005; Castillo *et al.*, 2005). For example, we believe that the case of antibiotic resistance moving rampantly between microbes in hospitals represents an extreme case of positive selection between extremely stressed pathogens. Such pathogens may exchange plasmids with integrons but nevertheless maintain an intact genetic core (see review by Anderson and Hughes, 2010). Consequently, this effectively dispels the notion of a large pool of available genes; therefore, it is possible to identify lineages and, hence, species.

The CCB is a remarkable case of microbial endemism that is the product of verifiable events of HGT, as demonstrated by the genome of *Bacillus coahuilensis* (Alcaraz *et al.*, 2008). In general, members of the genus *Bacillus* are understood to be cosmopolitan travelers that are capable of broad dispersal owing to their ability to form spores; therefore, they have the capacity to endure periods of environmental instability (Porwal *et al.*, 2009). The genome of *B. coahuilensis*, however, suggests the evolution of unique adaptations to a chronically low P environment, including the remarkable ability to produce sulfolipids in place of P-rich phospholipids and significant reductions in genome size (Alcaraz *et al.*, 2008). Both of these adaptations may be interpreted as P-sparing mechanisms that reduce the overall cell demand for phosphate (Lewis, 1985; Alcaraz *et al.*, 2008; Souza *et al.*, 2008). Such specialization could also suggest that this particular species is a long-term resident of the CCB and does not travel well; it carries few of the spore-forming genes known for *B. subtilis*, and interestingly, the same occurs with other species of *Bacillus* within the CCB (Alcaraz *et al.*, 2010). Furthermore, *Bacillus* from the CCB seems to sporulate at low frequency (G. Olmedo, personal communication). If such evolutionary “fine-tuning” is required by the majority of microorganisms that inhabit the CCB, then colonization by invading bacteria is unlikely not only because any new arrival will fail to outcompete the established cohesive microbial community (Litchman, 2010) but also these newcomers may become a likely source of nutrients for local scavengers that present mechanisms for bursting nonresistant cells (Peimbert *et al.*, 2012).

4. Food

As mentioned before, CCB communities are severely limited by phosphorus, and this has effects on trophic interactions (Elser *et al.*, 2005, 2006). CCB waters have low levels of available phosphorus together with a strong stoichiometric imbalance relative to N. In this case, it appears that species diversity is maintained in the face of fierce competition for dwindling resources, which places a premium on the ability to scavenge for phosphorus. Metagenomic analysis of an oncolite within a ultraoligotrophic river in the CCB [Río Mesquites (C:N:P of 900:150:1; Breitbart *et al.*, 2009)] implied that even though the microbial community was dominated by Cyanobacteria, there was a high number of ribotypes (261 ribotypes) within this phylum. As expected,

high-affinity phosphorus acquisition genes from the *pho* and *pst* gene families were overrepresented in this metagenome (Breitbart *et al.*, 2009), which supports the concept of specialization to an extremely P-limited environment. Conditions experienced by the microbes in these Río Mesquites oncolites, which move with the oxygen-rich river flow, are totally different from those experienced in the Pozas Rojas in the CCB, where stationary hypersaline microbial mats experience highly variable temperature (seasonal temperature 4–75°C) and the probabilities of colonization of new niches are reduced. While oligotrophy and extreme stoichiometric imbalance is a shared condition for these two sites (N:P ratios at Pozas Rojas are potentially as imbalanced as 157:1), a metagenome of Poza Roja points toward alternative strategies, as genes affiliated with phosphorus metabolism are not overrepresented in this community. Here, gene composition suggests that an alternative strategy of partitioning or “micro-splitting” the niche by extreme specialization in degradation of an ample and complex array of metabolic by-products (Peimbert *et al.*, 2012 in this issue). As a result of this fierce competition, in this community we observed 355 different ribotypes of novel *Pseudomonas* in addition to 20 more phyla, including Cyanobacteria, *Chlorobium*, and Chloroflexi as primary producers (Bonilla-Rosso *et al.*, 2012 in this issue). Concomitantly, the presence of several genes for antibiotic production and resistance implies that the *Pseudomonas* in Pozas Rojas may be evolving in order to escape antagonistic and competitive interactions. This is in line with a “Red Queen” model (Venditti *et al.*, 2010; Wilson and Sherman, 2010), whereby species constantly arise by reproductive isolation and rare stochastic events.

We suggest that the microbial diversity of the CCB is maintained by the mechanisms that include lack of food (metabolic plasticity in response to nutrient availability), HGT (relevant but infrequent), and ineffective travel (isolation) due to both the low genetic diversity in the local clones and the fierce competition for scarce nutrients. The combination of diversification and low-P conditions, together with mechanisms for phosphorous acquisition in extant CCB bacteria, were the impetus for our working hypothesis. More explicitly, the lack of P results in reduced HGT because of reduced cell-to-cell contact under oligotrophy, high rates of degradation of free DNA in the environment, and muted viral reproduction (Souza *et al.*, 2008). Stated simply, low P enhances speciation by promoting both geographic and reproductive isolation. However, beyond the specific case of the CCB, we suggest that, to study the occurrence and origin of endemic communities comprehensively, not only must diversity be addressed but the mechanisms that generate and maintain it must be assessed as well. In general, we strongly suggest that those studies should be accompanied with detailed studies of the ecological conditions of the site as well as their geological history.

5. Conclusions and Future Work

Relative to “complex” eukaryotic life, prokaryotes collectively possess an enormous metabolic diversity due to their deep evolutionary roots and remarkable capacity to adapt and ultimately thrive even under some of the most inhospitable conditions on Earth. When we consider the evolutionary causes that have facilitated Earth’s biogeochemical

stability and enormous diversity, the role of “travel, sex, and food” appears to be crucial. To assess this, not only do we need to explore other analogues of early Earth where food is scarce but we should also experimentally manipulate nutrient availability in microbial communities at places like the CCB and monitor how microbial diversity responds to shifts in nutrients, either via studies of well-studied focal taxa such as Pseudomonads or Bacilli or via inference by using metagenomics and transcriptomics. Such experiments are already underway at the CCB, where we are also embarking on studies in which open-air mesocosms within pools of different sizes are being used and targeting a diverse array of species to see, with the use of clone libraries, how migrants are accepted, or not, into microbial communities. With such studies in this “desert Galapagos,” we hope to further illuminate the enduring puzzle of Earth’s remarkable microbial diversity.

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Abbreviations

CCB, Cuatro Ciénegas Basin; EEBES, “everything is everywhere, but the environment selects”; HGT, horizontal gene transfer; OTUs, operational taxonomic units.

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