

Plant Biotic Interactions in the Sonoran Desert

Conservation Challenges and Future Directions

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INTRODUCTION

Biotic interactions are vital to ecosystem functioning. Interactions among individuals lie at the core of population and community dynamics, and therefore play a central role in the existence and persistence of species. Plants form the food base of most terrestrial ecosystems and are therefore not surprisingly involved in a substantial portion of biotic interactions. Plants, animals, and microbes face great challenges to survival in the desert environment, and these interactions play a critical role in the survival of many species.

The Sonoran Desert flora is well documented and certain of its iconic interactions are well understood. For example, saguaros and the bats that pollinate them and disperse their fruits have become textbook examples of mutualisms (e.g., Shreve and Wiggins 1964; Turner et al. 2005). However, what do we know about plant-animal, plant-plant, and plant-microbe interactions in the Sonoran Desert more generally? What role do such interactions play in the ecology and evolution of the Sonoran Desert ecosystem? How are these interactions affected by global changes, and how can we conserve interactions? These questions inspired a discussion session convened at the Next Generation Sonoran Desert Researchers (NGSDR) 2012 Summit. Ultimately, participants identified the following five critical needs regarding research and conservation. We need to (1) improve our knowledge of the natural history (diversity, ecology, evolution) of interactions, both as individual entities and as

players in the broader ecological community; (2) monitor interactions on broad spatio-temporal scales to be able to identify the consequences of climate change, especially for seasonal interactions involving migratory species; (3) identify the human activities with the greatest impacts on interactions; (4) develop criteria to compile a “priority interaction list” to improve and strengthen our ecosystem conservation efforts; and, finally, (5) use interactions to restore disrupted habitats and ecosystems.

Here we provide a comprehensive yet concise overview of biotic interactions involving the flora, fauna, and microbiota of the Sonoran Desert, summarizing and expanding results of the NGSDR 2012 Summit discussion. We briefly present the broad categories of interspecific interactions involving Sonoran Desert plants, identify and describe threats known to negatively affect them as well as positive links with human activities, and present ongoing conservation needs and restoration efforts. We conclude by suggesting future research directions and recommendations required for urgent conservation and restoration efforts.

DIVERSITY OF BIOTIC INTERACTIONS

All living organisms on Earth are involved in interactions with other organisms. Interactions are “mutualistic” when both organisms benefit and “antagonistic” when only one benefits at the expense of the other. They are “facultative” when participants do not strictly depend on one another and interact with several other species; they are “obligate” when at least one species relies on the other and rarely interacts with other species, making the interaction a matter of life and death in some cases. Although obligate interactions represent only a minor fraction of the immense web of biotic interactions, their more constant association and higher specificity make them easier to study (Davidson and McKey 1993; Futuyma and Agrawal 2009). In contrast, facultative interactions are both more common and complicated, since species interact with many partners and the associations can fluctuate between mutualistic and antagonistic (e.g., Bentley 1977; Ness 2006).

Here, we focus on interspecific interactions in which Sonoran Desert plants regularly engage. We group them based on the harm or benefits animals and microbes confer. This includes two forms of antagonism, herbivory and parasitism, and five forms of mutualism, pollination, seed dispersal, biotic protection, facilitation, and microbe-mediated nutrition. These are detailed below. An extensive bibliography is provided in appendix 1.

(i) Plant-Herbivore Interactions

Plants are the most common terrestrial food resource for animals. Most plant-consuming animals are insects; among vertebrates, most are mammals (Herrera and Pellmyr 2002). Plants in desert habitats are particularly important for animal consumers, because they represent a critical source not only of nutrients but also water. Effects of herbivores on plant fitness differ depending on the plant parts consumed. For example, the loss of reproductive parts, such as flower buds, is worse for the plant than having some leaves eaten. In the Sonoran Desert, herbivory studies have focused on mammal consumption of woody legumes and cacti, insect herbivory in general and by leaf cutter ants in particular, florivory (flower consumption) experienced by cacti, pollen plundering, nectar robbing, frugivory (fruit consumption), and seed consumption by various animals including rodents, ants, and beetles.

(ii) Plant Host-Parasite Interactions

Host plants can be attacked by animals in a way that resembles parasitism more than herbivory as it is traditionally imagined. Notable among these plant parasites are galling insects, especially wasps. Galls are plant tissue produced by the plant in response to the insect infestation. These tissues nourish the developing larvae. In the Sonoran Desert, galling insects have been studied extensively on creosote (*Larrea tridentata*) and willow (*Salix* spp.). Plants can also be parasitized by other plants. Some of these are holoparasites (which do not photosynthesize), including root-parasitic boomrape (*Orobanche ludoviciana*) and sandfood (*Pholisma sonorae*), and hemiparasites (which photosynthesize on their own to some extent), including desert mistletoe (*Phoradendron californicum*).

(iii) Plant-Pollinator Mutualisms

Plant-pollinator interactions are by far the best-studied mutualisms (Bronstein et al. 2006). In the Sonoran Desert, hummingbirds, bats, bees, moths, and wasps are well known for their pollinator services, i.e., their ability to transfer pollen between plants (see Chambers et al. 2004). Several Sonoran Desert pollination systems are particularly well investigated, including those involving columnar cacti, which (depending on the species) are pollinated by bats, hawkmoths, moths, hummingbirds, and other birds.

(iv) Plant-Seed Disperser Mutualisms

Seed dispersal by animals offers several notable benefits to desert plants (Howe and Miriti 2004): Seeds move away from the parent, thus reducing intraspecific competition (with siblings and the parent plant) as well as enemy attack (from species-specific predators, parasites, and pathogens) (Janzen 1970; Connell 1971; Howe and Smallwood 1982; Howe 1986). Deposition sites are likely to be richer in nutrients and moisture—for example, beneath bird perch trees or in ant refuse piles (Wenny 2001; Purves et al. 2008). Furthermore, seeds passing through the vertebrate gut may be scarified and germinate more readily (e.g., Traveset and Verdú 2002). The best known dispersers of Sonoran Desert plants are bats, rodents, and other mammals, but other animals, such as birds, lizards, and ants, also disperse desert seeds.

(v) Plant Protection Mutualisms

Not only are ants efficient seed dispersers, they also often protect plants. Plants in over 100 families (including some ferns) use ants to defend them against (insect) herbivores (Rico-Gray and Oliveira 2007; Chamberlain and Holland 2009; Weber and Keeler 2013). To attract ants, plants offer nectar, a carbohydrate-rich liquid reward secreted by extrafloral nectaries (EFNs) located on developing leaves, inflorescences, floral buds, and young fruits (see Koptur 1992). In the Sonoran Desert, barrel cacti, chollas, and senita cactus, as well as desert cotton, all bear EFNs and use ants as bodyguards. Several other Sonoran Desert plants bear EFNs, but it is not clear if the visiting ants provide any protection. Paper wasps (*Polistes* spp.) visit EFNs of cultivated desert willows (*Chilopsis linearis*; Marazzi B., personal observation), but the wasps' protective service is known only from a tropical EFN-bearing plant (Cuautele and Rico-Gray 2003).

(vi) Plant-Plant Interactions

Plants form positive interactions not only with animals, but also with other plants. One of the most prominent is the nurse plant-seedling interaction, which is an association of establishing seedlings with adult plants. Nurse plants are usually perennial plants that create, within the

reach of their roots and branches, micro-environments termed “resource islands” (Halvorson et al. 1994), benefiting seedlings that grow beneath them. It is generally assumed that the nurse plants are neither benefited nor harmed by this. Nurse plants occur in 40 angiosperm families and tend to be distributed in arid and semiarid environments (Flores and Jurado 2003). Notable Sonoran Desert nurse-seedling interactions include ironwood and some woody legumes as nurse species for young saguaros (*Carnegiea gigantea*) and other large cacti such as the giant cardon (*Pachycereus pringlei*), the senita cactus (*Lophocereus* [= syn. *Pachycereus*] *schottii*), and the Sonoran night-blooming cereus (*Peniocereus striatus*).

(vii) Plant-Microbe Interactions

There is an entire world of cryptic interactions belowground. Plants interact with microorganisms that inhabit the soil, as well as with those that reside naturally on plant surfaces and that live within plant tissues. An explosion of knowledge over the past decade has revealed that plants interact far more frequently with beneficial microbes than was previously recognized (Partida-Martínez and Heil 2011). These interactions play key roles in enabling plants to survive in stressful environments (Rodríguez et al. 2004; Philippot et al. 2013). Five categories of beneficial microbes have been studied in the Sonoran Desert (see appendix 1, section vii). First, endo- and ectomycorrhizal and dark septate fungi live in symbiotic relationships with plant roots. They appear to be abundant in stressed environments and are nearly ubiquitous in the dominant plants of arid rangelands in the Southwest (Barrow and Aaltonen 2001; Mandyam and Jumpponen 2005), suggesting that they may be important in allowing these plants to colonize these stressful environments. Second, *Rhizobium* bacteria live in symbiotic relationships with legume plant roots (e.g., Sprent 2009), forming nodules within which they reduce atmospheric N₂ to a form usable by plants (Long 2001; Bainbridge 2007; Fujita et al. 2014). These associations effectively act as “fertilizers,” since they represent a primary mechanism releasing nitrogen into arid land soils, which are typically low in nitrogen (Jenkins et al. 1987). Endophytic bacteria and fungi that live entirely within plant tissues for at least some part of their life cycle form the third category of microbes interacting with plants. They help plants to tolerate high-stress environments, enabling them to survive where otherwise they could not (Rodríguez et

al. 2004, 2009; Rodriguez and Redman 2008; Puente et al. 2009a, 2009b). Fourth, other beneficial rhizosphere microorganisms such as archaea, bacteria, and fungi are associated with plants. They confer many of the same benefits as the previous interactions, such as improved plant nutrition, increased drought and salinity tolerance, reduced susceptibility to disease, and increased resistance to insect herbivores (Yang et al. 2009; Pineda et al. 2010; Philippot et al. 2013). Furthermore, the microbial inhabitants of the rhizosphere can interact with each other to produce synergistic effects promoting plant growth (Artursson et al. 2006). Finally, biological soil crusts are associations of cyanobacteria, green algae, heterotrophic bacteria, fungi, lichens, and mosses that live within and on the surface of the uppermost layer of soil. As drivers of many biogeological processes, they have significant indirect effects on plant communities (Pointing and Belnap 2012), but also interact with vascular plants directly through a variety of effects on their germination, survival, and growth (Belnap 2003b; Belnap et al. 2003; Godínez-Alvarez et al. 2012).

Although we have presented these classes of biotic interactions as separate phenomena, it is critical to recognize that these interactions do not occur individually and isolated in time. Nor are they independent from one another. Plants benefit (and suffer) from multiple simultaneous positive (and negative) interactions, which are as diverse aboveground as they are belowground, forming a complex mosaic of interaction webs. This mosaic shapes the very existence of individuals and communities. Humans have been part of these webs for most of their history. Although there are still positive relationships among humans, plants, and other organisms, these positive interactions have been overwhelmed by a myriad of anthropogenic threats to biotic interactions, largely a result of rapid population growth and the associated growth in demand for natural resources as well as the erosion of indigenous cultures with strong ethics of caring for biodiversity.

POSITIVE RELATIONS BETWEEN HUMANS AND PLANTS

The interactions between indigenous peoples and the plants they depend upon have resulted in significant benefits to plants that include range expansions and increased genetic and species diversity. The present-day ranges of many Sonoran Desert species and the distributions of populations across species ranges reflect the influence of cultural dispersal

by indigenous groups, which enabled species to establish in areas they would have been otherwise unlikely to reach. For example, many columnar cacti and prickly pear species (*Opuntia* spp.) exhibit disjunct populations on the mainland and the midriff islands in the Sea of Cortés. Their presence on certain midriff islands may be in part the result of intentional dispersal by the Seri, who commemorated the birth of a child by marking the birth site with a living succulent (Nabhan 2002).

The distribution and species diversity of agaves, which were important sources of food and fiber for pre-Columbian peoples, have been heavily influenced by cultural dispersal (Hodgson 2001). For example, Minnis and Plog (1976) surmised that the western portion of the range of *Agave parryi* in southern Arizona reflected anthropogenic range expansion. Other species, such as *Agave murpheyi*, are domesticated species that represent the legacies of pre-Columbian cultivation practices and that today can be found only in association with archaeological sites (Parker et al. 2007).

Bringing a species into cultivation is assumed to result in reduced genetic diversity in the cultivated population as compared to the wild populations (Tanksley and McCouch, 1997), but in some instances, management and cultivation practices can have the opposite effect. For example, Casas et al. (2005) show that genetic diversity of the columnar cactus *Stenocereus stellatus*, a species endemic to central Mexico, is greater in both cultivated home garden populations and managed *in situ* populations than in wild populations, due at least partially to the continual introduction of new plant material with desired attributes into these populations. This example suggests that traditional management and cultivation practices may play an important role in the conservation of genetic diversity for many plant species.

In addition to having positive impacts on the distribution and genetic diversity of individual species, indigenous people in the Sonoran Desert have modified the environment in ways that promote plant species diversity. These modifications may have taken place thousands of years in the past or may be part of current land use practices. For example, in Baja California the weathering of ancient shell middens has altered soil properties within the vicinity of the middens, creating habitat islands that harbor a suite of plant species that differs substantially from the flora of the surrounding matrix, thereby enhancing the floristic diversity of the landscape (Vanderplank et al. 2014). The development and maintenance of desert oases provides another example of a positive human

impact on plant diversity. A striking example comes from the comparison of two desert oases, Quitovac, Sonora, and Quitobaquito, Arizona, less than 100 kilometers apart (Nabhan et al. 1982). At the time of the comparison, Quitovac was an actively managed agricultural site, while cultivation of domesticated plants had not occurred at Quitobaquito in more than 25 years. The diversity of Quitovac (122 plant species, excluding the domesticated ones) significantly exceeded that of Quitobaquito (78 plant species) with one of the most significant drivers of the greater diversity of the former being the cultivation of domesticated trees that created habitat for many native desert species.

CURRENT THREATS TO INTERACTIONS AND CASE STUDIES

The Identity of Threats

In this section, we focus on threats derived from human activities that are directly or indirectly affecting species and their interactions in the Sonoran Desert. Because it is impossible for us to review all threats in detail, we provide an overview for the most relevant ones: the most widespread threats, including (a) habitat fragmentation and loss, (b) altered water availability, (c) livestock grazing, and (d) invasive exotic species; (e) more minor threats, such as tree cutting and exploitation, rare species collecting, and off-road vehicles; and, finally, (f) global climate change, representing the most pervasive threat to species interactions.

Although illustrated here separately, threats are not isolated phenomena, but interact with one another. However, we are only at the beginning of understanding these interactions. For example, only recently have scientists begun to quantify and test for interacting effects between current climate, climatic change, and habitat loss on biodiversity, showing that current climate and climate change are important factors determining the negative effects of habitat loss on species density and/or diversity (e.g., Mantyka-Pringle et al. 2012). Furthermore, a recent study shows that disturbance of desert soil ecosystems can contribute to massive destabilization and to mobilization of dust, resulting in large-scale dust storms that have profound negative impacts across intercontinental distances (Pointing and Belnap 2014).

(a) Habitat Fragmentation and Habitat Loss

Over 50% of Earth's land surface has been modified in some way by humans (Hooke et al. 2012). Habitat fragmentation and habitat loss are the most apparent forms of habitat degradation and are the greatest threats to terrestrial ecosystems and biodiversity (Fahrig 2003; Mantyka-Pringle et al. 2012). The negative effects of habitat fragmentation and loss are extensive and difficult to estimate, as they apply to both measures of biodiversity, such as species richness, population size and distribution, genetic diversity, population growth rate, breeding and dispersal success, predation rate, foraging success, and characteristics of ecological networks (see review by Fahrig 2003; Gonzalez et al. 2011; and literature cited therein). Many studies have focused on effects of habitat fragmentation and loss on plant-pollinator interactions (e.g., Rathcke and Jules 1993; Steffan-Dewenter and Tschardt 1999; Aguilar et al. 2006; review by Burkle et al. 2013), and to a lesser extent on interactions between plants and seed dispersers (e.g., Levey et al. 2005; Cramer et al. 2007). Few studies have looked at more complex ecological networks (Gonzalez et al. 2011).

In the Sonoran Desert, drivers of habitat fragmentation and loss include agricultural development (including the abandonment of agricultural lands), mining, urbanization, and construction of roads (especially highways), fences, the wall along the U.S.-Mexico border, utility corridors (such as powerlines, pipelines, canals, and railway lines), and utility-scale solar energy developments. Very few studies document effects of fragmentation and habitat loss in the Sonoran Desert, however. Most of them focus on the effects on animal species or communities, rather than on species interactions. For example, Green and Baker (2003) demonstrated that urbanization strongly affects bird communities. In 21 upland sites and 21 riparian sites in metropolitan Phoenix, Arizona, they found significant negative correlations between housing density and road density and native bird species richness. The interactions in which those birds may be involved can be inferred to have changed, but this has not been documented. In another case, habitat fragmentation in the Sonoran Desert of the southern Baja Peninsula caused the local extinction of a lizard, *Urosaurus nigricaudus*, in isolated patches (Munguia-Vega et al. 2013). However, the effect on interactions that species may have had with plants remains unknown.

The effects of habitat fragmentation on plant-pollinator interactions

were addressed by Cane et al. (2006), who found that pollinator diversity was relatively well retained in desertscrub fragments resulting from urbanization within the Tucson Basin of Arizona over the past 50 years. The fragments were dominated by creosote bush, *Larrea tridentata*, which is visited by over 120 native bee species. Although ground-nesting specialist bees were missing from the smallest fragments, the bee fauna within these habitat fragments was nearly as diverse as in the surrounding desert. The authors suggest that floral resources provided by creosote bush may be insufficient to support specialist bee populations within the smallest fragments. As creosote bush is one of the most abundant and reliable floral resources within the Sonoran Desert, the results of this study may not generalize to other plant species and their pollinators (Cane et al. 2006).

(b) Altered Water Availability

Anthropogenic changes in the availability of water in arid ecosystems stem from both aggressive water development (Merritt and Bateman 2012) and climate change (Overpeck et al. 2012). Water development results not only in decreases in groundwater and annual flow volumes, but also altered stream flow and disturbance regimes, with great impacts on aquatic and riparian communities (Merritt and Bateman 2012). In the Sonoran Desert, this can result in the conversion of riparian forests to shrublands (Merritt and Bateman 2012). The effects of the loss and degradation of riparian habitat on plant biotic interactions in the Sonoran Desert have been poorly studied. Altered water availability also comes in the form of altered precipitation regimes and changes in mean annual rainfall totals associated with global climate change. Below, under “The Identity of Threats,” we summarize research from both the Sonoran Desert and elsewhere on how changes in water availability affect plant-plant and plant-herbivore interactions. The effects of drought on plant-microbe interactions are also discussed.

Changes in water availability can cause plant-plant interactions to shift along a continuum from competition to facilitation (Greenlee and Callaway 1996; Tielborger and Kadmon 2000). Movement along this continuum is highly context dependent, with competition expected under very high or low levels of stress and facilitation expected under intermediate stress levels (McCluney et al. 2012). However, predicting how changes in water availability will affect plant-plant interactions is

complicated, because interactions depend not only on current and future levels of water availability, but on other characteristics of water availability such as intra- and inter-annual variation in precipitation (Butterfield et al. 2010).

Similarly, the outcome of plant-herbivore interactions varies from mutualistic to antagonistic depending on water availability. The influence of water availability on the dietary preferences of herbivores such as many rodent and insect species may have significant consequences for the plants they consume. Bird and mammal species that depend largely or entirely on plants to meet their moisture requirements, such as some hummingbirds and migratory bats, may be vulnerable to the effects of prolonged drought on nectar and fruit production of their host plants. For example, under normal levels of rainfall white-throated wood rats (*Neotoma albigula*) eat the fruits and act as seed dispersers of saguaros, but when moisture levels are low, they will feed on cactus stems with negative effects on the plant (McCluney et al. 2012).

(c) Livestock Grazing

In both the U.S. and Mexico, livestock grazing has been widespread across the landscape for at least 150 years (Fleischner 1994). Livestock grazing has had somewhat different impacts in the U.S. and Mexico because rangeland management practices differ. Most importantly, grazing in northern Mexico often involves the development of non-native grass pastures, in which native trees, shrubs, and succulents are removed and non-native forage species are planted (Brenner 2011). The most widely planted species in northwestern Mexico is non-native buffelgrass, *Pennisetum ciliare*. Effects of this landscape transformation are discussed below. Here we focus on the physical presence of the livestock.

Urban areas and steep mountains are the only areas really free from grazing, at least in the U.S., making comparisons to a truly ungrazed ecological baseline difficult to obtain (Turner 1990; Fleischner 1994). Long recovery times following cessation of grazing (Blydenstein et al. 1957; Guo 2004; Lawley et al. 2013) or even irreversible changes from threshold effects (Browning and Archer 2011) further complicate experimental manipulations, but we have gained some understanding of the ways in which grazing affects interactions in the Sonoran Desert. Grazing livestock trample and consume vegetation, disturb the soil surface, and alter nutrient dynamics, water availability, and water quality

(Fleischner 1994). The resulting ecological changes include shifts in the structure and composition of vegetation (Waser and Price 1981; Fleischner 1994; Brooks et al. 2006; Beschta et al. 2013), leading to changes in the rates (Liao and Boutton 2008) and spatial patterns (Allington and Valone 2014) of nutrient cycles. In addition, the degradation of biological soil crusts leads to greater erosion (Belnap 2003a) and to lower water availability and quality (Fleischner 1994; Beschta et al. 2013).

These changes have had large impacts on soil-based plant-microbe interactions in the Sonoran Desert, as evidenced by damaged and reduced soil crusts (Belnap and Lange 2001), as well as changes to root branching structures of grasses (Blydenstein 1966) and soil nutrient concentration under woody shrubs (Allington and Valone 2014). An increase in the density of woody shrubs has been widely considered to be tied to grazing rates, as livestock remove grass from the landscape, alleviating both competition and widespread fires (Van Auken 2000). Microbial activity under these woody shrubs is considerably different than in grasslands (Liao and Boutton 2008), which could affect the rhizosphere and hence competitive abilities of plants, even leading to lasting or cascading effects after initial removal of grass (Browning and Archer 2011).

Grazing has affected rates of both herbivory and granivory. Cattle, sheep, and goats are all herbivores that reduce the total density of grasses (Pol et al. 2014) and annuals in particular (Waser and Price 1981). This certainly has an effect on interactions between native herbivores such as desert tortoises and the remaining vegetation (Grandmaison et al. 2010). Where succulent establishment is limited by livestock trampling or herbivory (Bowers 1997; Morales-Romero et al. 2012), it may intensify effects of native herbivores like woodrats (Hayes et al. 2013) on remaining cactus. Livestock reduce the availability of grass seed on the landscape, which leads to cascading effects for granivorous small mammals and ants (Pol et al. 2014). However, reduced cover of grasses may allow higher densities of woody leguminous shrubs (Van Auken 2000), whose seeds are preferred by a different group of granivores, leading to a shift in granivore interactions.

Interactions with mutualists such as pollinators have likely been altered by grazing at scales larger than studies using small grazing exclosures can reveal. Regional changes in vegetation density that results from grazing (Turner 1990) may have effects not only on the pollinators of plants whose density is directly affected by grazing, but also on the pollinators of other plants. For example, the loss of succulents that can

result from the loss of nurse plants under heavy grazing (Turner et al. 1966; Bowers 1997) may result in a change of floral resources available to the pollinator community, eventually leading to changes in the composition of pollinator communities. Changes in the pollinator community may have significant consequences for the plant community. For example, in the Monte Desert of Argentina, Aschero and Vázquez (2009) found that pollinator visitation and seed set of the native leguminous tree *Prosopis flexuosa* was greater where cattle had been excluded for over 35 years.

(d) Introduced Exotic Species

Invasion by exotic animal and plant species can result in the loss of native mutualists or their replacement or displacement by non-native species and can alter the shape of trade-offs among reproduction, plant defense, and dispersal. Little research has been done on the ecological consequences of the introduction of exotic plant species on native Sonoran Desert and dryland communities (Schlesinger et al. 1990; Burgess et al. 1991; Van Devender et al. 1997). Several plant species are known to have become invasive in the Sonoran Desert (62 according to Tellman 2002). Most have localized ranges or habitats, but a few like buffelgrass, desert mustard (*Brassica tournefortii*), and ice plants (*Mesembryanthemum crystallinum*) cover extensive areas. Although Tellman (2002) reports 350 and 230 introduced exotic plant and animal species, respectively, in the Sonoran Desert, not all of these pose serious threats. Among those that do is buffelgrass, which we discuss below because buffelgrass is widely believed to pose a greater risk to the ecological integrity of the Sonoran Desert than any other threat. It has the potential to transform much of this region from a desert dominated by iconic cacti to one that more closely resembles a savanna, with far-reaching consequences for both species interactions and ecosystem functioning that we have barely begun to understand.

The case of buffelgrass invasion and transformation of the Sonoran Desert by the introduction of the fire-grass cycle is particularly severe. This C4 savanna grass native to East Africa and the Middle East has been planted in arid regions worldwide, including in Arizona since the late 1940s and in Sonora since the 1970s (Cox et al. 1988; Marshall et al. 2012). Due to its deliberate cultivation in northwestern Mexico and its spread beyond pasture boundaries, it is now a dominant species in central

Sonora, mainly in the Plains of Sonora Subdivision of the Sonoran Desert (figure 1). In Sonora, ranchers continue to bulldoze or burn native vegetation to plant buffelgrass in a process known as *desmonte* (Burquez-Montijo et al. 2002; Franklin et al. 2006; Brenner et al. 2012). Throughout the Sonoran Desert, buffelgrass has spread from planted pastures to disturbed roadsides, and then to washes and undisturbed hillsides (Olsson et al. 2012a; Brenner and Kanda 2013). Where buffelgrass colonizes outside pastures, its propensity to burn hotter and spread fire transforms the landscape (McDonald and McPherson 2011, 2013), as have grass invasions elsewhere (D'Antonio and Vitousek 1992), by reducing densities of native perennials unaccustomed to wildfire (McLaughlin and Bowers 1982). Even in the absence of fire, buffelgrass reduces plant diversity (Olsson et al. 2012b), a process that is largely driven by buffelgrass suppressing seedling establishment (Morales-Romero et al. 2012; P. Sommers, unpublished data). The effects of buffelgrass pasture development and invasion have not been well studied (Marshall et al. 2012), but pasture development is likely to have significant effects on key interactions in the Sonoran Desert.

The disruption of pollination and seed dispersal interactions by land transformation has likely occurred as key desertscrub and thornscrub plant species have been greatly reduced in abundance as a result of the clearing of native vegetation during the development of buffelgrass pastures. Some of these plant species (e.g., *Fouquieria splendens*, *F. macdougalii*, *Ipomoea arborescens*, *Justicia californica*) are associated with the migration of vertebrate pollinators like perching birds and hummingbirds (figure 2). Extensive land transformation in central Sonora has most likely affected the migration corridors of bats and hummingbirds (figure 3). In addition to the development of extensive tracts of buffelgrass grasslands, the presence of large irrigation districts associated with the major Sonoran rivers (from north to south: Colorado, Concepción, Sonora, Yaqui, Mayo, and Fuerte Rivers) and the large-scale shrimp farms along the coast have eradicated large tracts of Sonoran Desert that harbored key species (e.g., *Agave* spp., columnar cacti, kapok trees [*Ceiba aesculifolia*]) for the migration of bats and hummingbirds.

Buffelgrass might also alter pollination rates for plants primarily pollinated by insects. Patches of dense grass create a buffered microclimate underneath the plants that appears to benefit winter annuals' growth (P. Sommers, personal observation). However, both the development of buffelgrass pastures and buffelgrass invasion reduce plant diversity and the cover of shrubs, forbs, grasses, and succulents (Franklin and Molina-Freaner 2010; Olsson et al. 2012b). These changes to the diversity and

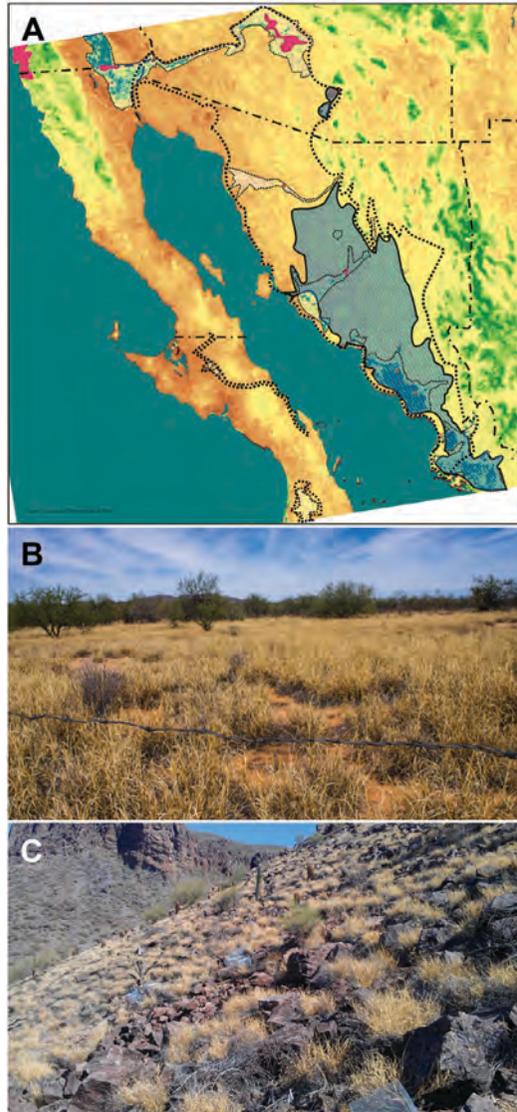


Figure 1: Buffelgrass invasion and pasture. A. Extent of buffelgrass invasion in the Sonoran Desert (dotted line), intentional transformation of the desert into grasslands of buffelgrass (blue shading; other shadings not relevant for this paper). From Burquez-Montijo et al. (2002). NDVI image from the Arizona Regional Image Archive. B and C are examples of buffelgrass in the Sonoran Desert. B, land converted into a buffelgrass pasture in Carbo, north of Hermosillo, Sonora; C, natural lands invaded by buffelgrass in the Tucson Mountains, Arizona, south slope of Panther Peak, Arizona.

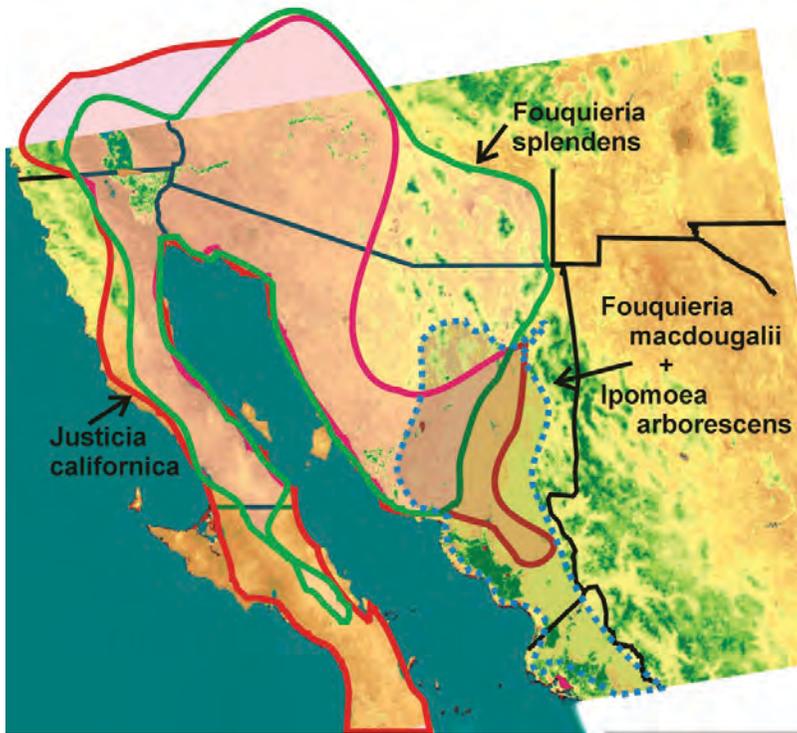


Figure 2: Major staple nectar plants for hummingbirds during the spring migration. Red: *Justicia californica*; green: *Fouquieria splendens*; blue: *Ipomoea arborescens* and *Fouquieria macdougalii*. NDVI image from the Arizona Regional Image Archive.

structure of vegetation likely alter floral and nesting resources available to the native bee fauna. In addition, patches of dense buffelgrass may interrupt the direct line of sight to floral resources for insect pollinators and could potentially reduce wind speeds, affecting wind-pollinated species.

Plant-plant interactions as well as plant-host parasite interactions are dramatically altered by both buffelgrass pasture development and buffelgrass invasion. The development of buffelgrass pastures involves the removal of large trees and shrubs, many of which function as nurse plants, which are important for the recruitment of many desert species. Soil fertility and the diversity of plant and animal life are much higher under the canopy of trees than outside their shade (e.g., García-Moya and McKell 1970; Vetaas 1992; Burquez and Quintana 1994; Schlesinger and Pilmanis 1998). Once the trees are removed, a large guild of

endangered cactus ferruginous pygmy owl (*Glaucidium brasilianum cactorum*), build nests in saguaro cavities, and their densities are closely related to saguaro density (Flesch and Steidl 2010). Buffelgrass cover itself also increases the activity of pocket mice (P. Sommers, unpublished data) that prefer to forage under plant cover as a refuge from owl attacks (Brown and Kotler 2004). Even when densities of other granivores, such as ants, are unchanged (Franklin 2012), those granivores may prefer native seeds to buffelgrass seed, which may effectively increase the intensity of granivory for remaining native plants. Smaller terrestrial animals, including desert tortoises, lizards, and small mammals, are also common victims of buffelgrass fires. They are either lost during the fire or afterwards, due to lack of resources or thermal refuge following the removal of standing biomass (Esque et al. 2003). Few native species may be able to consume the grass itself, or may be poorly adapted to rely on it for sufficient nutrition, which might increase the intensity of herbivory on remaining native plants. Several studies outside of the Sonoran Desert have shown that buffelgrass reduces insect diversity (Binks et al. 2005) and bird diversity (Flanders et al. 2006; Smyth et al. 2009).

Changes in the thermal environment may lead to shifts in insect community structure with cascading effects. For example, changes in ant diversity and community structure could shift the degree of herbivory experienced by fishhook barrel cactus (*Ferocactus wislizeni*) or other plants that rely on these mutualists for defense from other insect herbivores.

Very little is known about plant-microbe interactions with buffelgrass and its competitors in the Sonoran Desert. Buffelgrass has been found to reduce the growth rate of other species watered with its leachate, though the mechanism remains unknown (Hussain et al. 2008). Since soil and seed bank characteristics across sites with buffelgrass, native vegetation, and treated buffelgrass appear otherwise similar (Abella et al. 2013), this may be because buffelgrass negatively affects native species' microbial affiliations.

(e) Other Minor Threats

The most extensive minor threat in the Sonoran Desert may be off-road vehicle (ORV) recreation. ORV recreation affects ecological interactions primarily through crushing soils and vegetation. Most of the research on effects of ORVs has been done in the Mojave Desert, with one published study from the Sonoran Desert conducted in the Organ Pipe National Monument in Arizona (Webb et al. 2013). However,

our experience is that ORVs are common throughout the Sonoran Desert, and many of the impacts to soils are similar.

Off-road vehicles alter plant-microbe interactions by crushing plants, destroying biological soil crusts, compacting soil, and increasing erosion. The cyanobacteria and lichens in crusts are a major source of nitrogen fixation for plants in desert ecosystems (Belnap and Lange 2001), and nitrogenase activity frequently declines markedly following ORV disturbance (Belnap 2002). Vehicular traffic reduces infiltration of the soils and increases runoff, which reduces availability of water and nutrients to microbes and to plants (Eckert et al. 1979; Iverson et al. 1981). These effects to the soil take on the order of many decades to several centuries to reverse (Iverson et al. 1981; Webb et al. 2013).

ORVs drive changes in animal communities through their effects on vegetation and its interactions with animals. ORV use in the Arizona Uplands Sonoran Desert reduces the abundance of some small mammals (*Neotoma albigula* and *Peromyscus eremicus*) but not others (*Chaetodipus baileyi* and *Dipodomys merriami*), primarily by altering the vegetation community (Reid 2012). Similarly, ORV use in the Mojave Desert negatively affects lizard densities, with differing magnitude of effects on different lizard species, leading the authors to reason that changes in plant community from ORV use were driving the changes in lizard populations (Busack and Bury 1974). Changes in the abundance of animal species that rely on different plant types for food, water, and shelter reflect the importance of their consumptive interactions.

Collection and exploitation of plants and animals may further reduce their densities on the landscape, affecting interactions. Desert tortoises continue to be illegally collected (Grandmaison and Frary 2012), presumably for the pet trade. Ironwood trees are frequently cut for making artisan crafts and charcoal (Suzan et al. 1999), leading to a lack of recruitment in populations in Sonora and Baja California (Suzan et al. 1997). Ironwood trees function as nurse plants (Suzan et al. 1996) and support rich animal and plant assemblages under their canopies (Bestelmeyer and Schooley 1999; Butterfield et al. 2010).

(f) Global climate change

The Sonoran Desert is getting warmer and drier (Weiss and Overpeck 2005). Warming has been and will continue to be concentrated in summer and fall, with hotter and longer heat waves and more frequent and severe droughts (Seager and Vecchi 2010; Overpeck et al. 2012). In addition,

the frequency of freezing events is decreasing (Weiss and Overpeck 2005). How will these changes affect desert vegetation and what will the Sonoran Desert look like 50 years from now? In some cases, the answers to these questions might seem straightforward. For example, Brusca et al. (2013) showed significant overall upward movement of the lower elevation boundaries of 27 plant species sampled in the Santa Catalina Mountains in southern Arizona. In other cases, the answers to these questions are counterintuitive. Kimball et al. (2010) showed that in winter annual communities in the Sonoran Desert, recent warming and drying has led to increased dominance of cold-adapted species.

A great deal of research has now investigated the consequences of global climate change on individual organisms (Chen et al. 2011; Buckley and Kingsolver 2012; Kingsolver et al. 2013). Most of the research focus has been on charismatic, highly threatened species in polar regions such as the polar bear, and on familiar and iconic temperate-zone organisms. Currently, we know considerably less about how rising temperatures will affect desert organisms, either ecologically or physiologically. It would be easy to assume that, as Sonoran Desert plants and animals are well adapted to high temperatures, they could tolerate a warmer world more easily than other organisms. It is quite possible, however, that they are already at or near their maximum thermal tolerance. Determining whether this is the case before we are unpleasantly confronted with it as a reality will require carefully controlled studies in thermal physiology (Angilletta 2009). It has been recently pointed out that certain mobile organisms common in desert habitats, particularly reptiles, exhibit behaviors that allow them to escape locations where temperatures are close to exceeding their maximum tolerances (Sunday et al. 2014). How widespread these behaviors are, as well as whether desert plants too have thermal adaptations that only emerge at very high temperatures, is a critical question for the future.

The fates of organisms depend in many ways on their interactions with other species, and interactions too are sensitive to climate (Tylianakis et al. 2008; Gilman et al. 2010). The clearest documentation of temperature-sensitive interactions to date involves ants, organisms that by their biomass and diverse ecological roles play dominant roles in the Sonoran Desert. Recent studies have made clear that different ant species occupy different thermal niches. Scaling up to the community level, ant communities are structured according to varying temperature sensitivity of their many component species: Competitively dominant ant species tend to have lower thermal tolerances than species lower down in the competitive hierarchy (Cerdeña et al. 1998; Dunn et al. 2007). The implication is that, in a warming

world, ant community structure is likely to shift, with aggressive dominants lost and less competitive ants becoming more common.

A community-level pattern such as this can be predicted to have significant consequences for other trophic levels. It is perhaps clearest how mutualisms might be affected if this were to take place. Aggressive ants can be more effective mutualists, as their aggression is directed not only toward conspecifics but at the enemies of partners they protect as well (see section v in appendix 1). Unaggressive ants, in contrast, often run from danger, assuring that they will be relatively ineffective mutualists. If unaggressive ants were to increase in abundance in a warmer world, as postulated above, this would not be good news for species that rely upon biotic defense. Fitzpatrick et al. (2013, 2014) have explored such a scenario in the fishhook barrel cactus (*Ferocactus wislizeni*) and a community of ants that feed at its extrafloral nectaries and that guard it from herbivores (Ness et al. 2006, 2009). Field and laboratory experiments show that the most thermally tolerant ant associate at the Desert Laboratory in Tucson, *Forelius pruinosus*, is also an exceptionally poor defender of this cactus (Ness et al. 2006; Fitzpatrick et al. 2014). This would not be a major concern if the plant's enemies could not persist at the temperatures at which the ant community is likely to turn over. In fact, however, the dominant herbivore at the study site, a plant-sucking bug (*Narnia pallidicornis*), has a thermal tolerance higher than any of the ants (Fitzpatrick et al. 2013). Thus, if barrel cacti were able to withstand considerably warmer temperatures—still an open question—it could well be confronted with the same herbivore but have as its only defender only a very poor mutualist.

Results of long-term studies in the Sonoran Desert suggest that a mechanistic understanding of changes in plant-plant interactions will be necessary to forecast community response to current climate change (Huxman et al. 2013). Traits of seeds and seedlings have proven critical in determining the response of both annual and perennial plants to climate change in the Southwest. In winter annual communities on Tumamoc Hill, recent warming and drying has led to increased dominance of cold-adapted species that exhibit less inter-annual demographic variation. Germination-triggering rains have been occurring later in the year during the cooler months, leading to increased abundance of cold-adapted species (Kimball et al. 2010). Another example comes from the study of woody plant encroachment in the grasslands of the Southwest. Mesquite (*Prosopis velutina*) has dramatically increased in abundance, but other species, such as *Acacia* (*Senegalia*) *greggii*, that share the same

habitat and that are similar with respect to growth form and life history have changed little in abundance. The ability of *P. velutina* to take advantage of small, pulsed rainfall events through earlier emergence and faster growth rates, especially in the taproots, may largely explain why *P. velutina* has been favored over *A. greggii*, despite great similarity in adult plants (Woods et al. 2014).

Climate envelope models represent perhaps the simplest attempts to predict the effects of climate change on individual species. However, recent research suggests that models that ignore species interactions will often fail to provide a realistic picture. In a review of 146 studies of changes in species distributions and abundance in response to climate change, Ockendon et al. (2014) show that in a majority of cases, the proximate mechanism of population change was biotic rather than abiotic; population changes were most often mediated via the effects of interactions rather than via the direct effects of climate. For example, decreasing frequency of freezing events in the Sonoran Desert may result in the northward expansion of woody legume and cactus species that are limited by freezing temperatures, but predictions are complicated by the spread of invasive plant species, particularly grasses that alter the natural fire regime of the Sonoran Desert (Weiss and Overpeck 2005) and reduce plant community diversity even in the absence of fire (Olsson et al. 2012b). Long-term studies of saguaros in the northern Sonoran Desert suggest that although climate can have strong effects on population demographics, characteristics of the local environment are important for understanding recruitment, growth, mortality, and abundance, as evidenced by the lack of synchrony among populations throughout the region (Pierson et al. 2013).

CURRENT CONSERVATION NEEDS AND RESTORATION EFFORTS

Attention to the conservation of interactions worldwide has been almost exclusively focused on pollination (Kearns et al. 1998; Potts et al. 2010). Concern about other interactions most often arises during extinction risk assessments of endangered key species and habitats. Here we provide representative examples of conservation efforts in the Sonoran Desert that benefit interactions, counteracting the impacts of threats presented in the section. We also provide insights on promising restoration efforts in which interactions feature at the forefront.

The Need for Protected Areas and Dispersal Corridors

As the leading causes of species extinctions, habitat loss and fragmentation are major contributors to the erosion of species interactions. Therefore, developing networks of protected areas is essential to the conservation of both species and their interactions. Such networks will become increasingly important as climate change forces species to shift their ranges. The development of northwestern Mexico has relied on extensive rather than intensive use of the land. Cattle ranching activities have extirpated large areas of natural vegetation, mainly through the introduction of exotic grass species that are now fully naturalized. New ecosystem dynamics, mainly the fire-grass cycle, in some areas have deeply altered the environment of biotic interactions. There has been little effort to establish large nature reserves. The few that currently exist are concentrated in Baja California and extreme northwestern Sonora. Little is protected along the coast and the Sierran foothills (Burquez and Martinez-Yrizar 2006). A much more comprehensive reserve system is present in Arizona, where different management practices and a more homogeneous and extensive network of protected areas provide wildlife corridors still absent in northwestern Mexico.

Management of Invasive Buffelgrass

Management of buffelgrass has primarily focused on its removal rather than on conservation of native species' interactions in its presence. Buffelgrass has been listed as a prohibited noxious weed in Arizona since 2005 (Arizona Administrative Register 2005), although no enforcement or management has resulted from that designation (Travis Bean, personal communication). Since its seeds remain viable for many years in the soil (Winkworth 1971), continued coordinated and sustained removal efforts are required for successful control. Natural resource managers have concluded that eradicating buffelgrass in southern Arizona is not feasible, and instead focus efforts on reducing density in the most accessible areas (Frid et al. 2010, 2013). These cross-jurisdictional efforts are organized by the Southern Arizona Buffelgrass Coordination Center (www.buffelgrass.org). It can be manually removed year-round, which is primarily done by volunteer crews, but the most economically efficient treatment method for agencies has typically been to spray glyphosate. Grass must be green for this herbicide to be effective, which usually

restricts its use to the monsoon season (July to September). Recent research suggests that another herbicide, imazapyr, is an effective pre-emergent that can be applied year-round (Travis Bean, personal communication). Many of the invasions of greatest concern on public land, however, are in remote areas with rugged terrain that make it unsafe and uneconomical for activities of field crews. In spring 2014 Saguaro National Park completed a Restoration Plan and Environmental Assessment that evaluates the environmental impacts of helicopter application of herbicides for buffelgrass control (Dana Backer, personal communication).

In Sonora, the level of clearing via desmonte has varied from chaining, which removes virtually all succulents, shrubs, and trees, to more selective partial clearing (PATROCIPES 1995) to leave shade for cattle (Morales-Romero and Molina-Freaner 2008). In the 1990s the most environmentally damaging clearing methods, such as chain dragging, were prohibited, but land conversion continues and little funding is available for inspections or enforcement (Brenner 2011; Brenner and Kanda 2013). Even in pastures that experience a lower intensity of clearing, negative impacts on the future populations of remaining native perennials are likely (Morales-Romero et al. 2012), and grass continues to spread from pastures along roadsides and up the foothills (Burquez-Montijo et al. 2002, Franklin et al. 2006; Brenner et al. 2012). Roadside invasions are typically treated by burning, which only induces a return of the population (A. Burquez, personal communication), and no organized or official efforts to manage populations on the hillsides surrounding pastures are currently under way.

Given the low likelihood of eradicating buffelgrass from the Sonoran Desert, attention to defensible areas should consider not only sensitive species, but sensitive interactions.

Restoration Using Plant-Microbe Interactions

Recent research on plant-microbe interactions has provided evidence of their important role in generation and maintaining the productivity and diversity of terrestrial ecosystems (Reynolds et al. 2003). A growing body of research has demonstrated that restoration of degraded habitats often requires restoration of soil microbial food webs. However, restoration strategies often do not consider the microbial component of the ecosystem. In the Sonoran Desert, restoration of native plant

communities has been only marginally effective, with revegetation usually involving intensive irrigation and fertilization (Bean et al. 2004; Banerjee et al. 2006). The main challenge for revegetation of degraded soils is to establish plants in substrates that have lost their beneficial plant-associated microorganisms, and therefore much of their fertility and potential to support vegetation (Bashan et al. 2012). Innovative approaches that combine principles of microbiology and plant ecology suggest that plant-microbe interactions can be used as a tool for restoring degraded desert soils by improving soil properties and biological interactions in the plant-soil interface (Requena et al. 2001; Bashan et al. 2012).

On the Baja California Peninsula, native desert plants, such as giant cardon, organ pipe cactus (*Stenocereus thurberi*), chollas, *Mammillaria fraileana*, *Pachycormus discolor*, *Ficus palmeri*, and boojum tree (*Fouquieria columnaris*), have been screened for culturable plant growth-promoting bacteria (PGPB) and arbuscular mycorrhizal (AM) fungi (Puente et al. 2004a; Bashan et al. 2007; Lopez et al. 2011). Inoculation of plants with nitrogen-fixing bacteria and phosphate-solubilizing bacteria, which colonize the interior of plants and the rhizoplane, can improve the performance of cacti growing on rocky substrates. Over time, establishment of plants and their associated bacteria contributes to soil development (Puente et al. 2004b; Lopez et al. 2011). A more complex approach takes advantage of nurse tree associations. Revegetation of highly eroded desert lands in the southern part of the Baja Peninsula was attempted with combinations of legume shrubs and cardon cacti that were inoculated with combinations of PGPB and AM fungi and provided with small amounts of compost and limited water, not exceeding natural rainfall levels (Bashan et al. 2009, 2012). After three years, the most successful treatment in terms of plant survival was the combination of cardon and mesquite amargo (*Prosopis articulata*), where certain combinations of amendments (native PGPB, native fungi, and compost) were applied. Through the use of nurse plant relationships in combination with applications of native soil microbiota, stabilization and revegetation were achieved quickly (Bashan et al. 2012). Long-term revegetation using native plant associations and their microorganisms is advised to restore plant succession of abandoned lands and disturbed desert areas filled with exotic plants (Carrillo-Garcia et al. 2000; Bashan et al. 2009). Research is now being conducted to understand the interrelations among nurse plants, soil microbial communities, and properties of soils in natural and induced resource islands.

PERSPECTIVES AND FUTURE DIRECTIONS

We concur with the conclusions of the Next Generation Sonoran Desert Researchers 2012 Summit session on plant-animal and plant-microbe interactions: We need to identify the human activities with the greatest impacts on interactions, develop criteria to compile a “priority interaction list” to improve and strengthen ecosystem conservation efforts, and use interactions to restore disrupted ecosystems. In other words, we urgently need to increase fundamental research aimed at understanding and predicting the effects of human impacts on interactions. These efforts are critical to move successfully from research to (i) concrete recommendations and policy implementation, (ii) protocols for extinction risk assessments of species interactions, and (iii) implementation of interactions in ecosystem restorations.

Research Efforts on Human Impacts on Interactions

Habitat degradation and anthropogenic climate change pose massive threats to species interactions in the Sonoran Desert, but effects of such human impacts are still sparsely documented. As trivial as it might sound, to limit the extent and intensity of any human impact as much as possible is the best management option in arid lands (Lovich and Bainbridge 1999). An important component of limiting impacts is to counteract their effects. In this sense, we urge Sonoran Desert researchers to identify “pristine” patches within the degraded and fragmented landscape and document their interaction networks in as much detail as possible. These data are critical for reconstructing regional networks of species interactions and elucidating possible outcomes of the effects of anthropogenic change on such networks and therefore on biodiversity and ecosystem functioning (Fortuna et al. 2013).

With respect to climate change, we urge following the steps recommended by the conference Climate Change and Species Interactions: Ways Forward (see the special issue of the *Annals of the New York Academy of Sciences*, vol. 1297, September 2013). Its goal was to provide new concepts, models, empirical approaches, and statistical tools to enable biologists to predict where individual species will move, and how communities will assemble, disassemble, and change in structure and function as the climate continues to change. Three main priorities were identified (Angert et al. 2013): (1) Utilize tractable study systems as case

studies to illustrate possible outcomes, test processes highlighted by theory, and feed back into modeling efforts; (2) develop a robust analytical framework that allows for better cross-scale linkages; and (3) determine over what time scales and for which systems prediction of biological responses to climate change is a useful and feasible goal. It also identified several research questions for future research directions on climate change and species interactions (see appendix 2).

From Research to Concrete Recommendations and Policy Implementation

It is an absolute priority to convene panels of experts to assess the human activities that directly or indirectly disrupt species interactions in the Sonoran Desert and to provide concrete recommendations and measures for public and private authorities. Such an initiative has recently been achieved by the Conservation Biology Institute for the California Desert Renewable Energy Conservation Plan (CBI 2010). Many examples exist at a global scale, notably the very recent and inspirational *Scientific Consensus on Maintaining Humanity's Life Support Systems in the 21st Century* (see Barnosky et al. 2014). These should serve as examples for regional initiatives.

The chain from basic research to policy implementation is rarely simple or short. Long-term study has now resulted in a National Academy of Sciences report (National Research Council 2007) demonstrating significant declines in pollinator populations and offering specific recommendations to the government. The North American Pollinator Protection Campaign (NAPPC) has been engaging the U.S. government on pollinator conservation and signing agreements with agencies such as the U.S. Fish and Wildlife Service, the U.S. Department of Agriculture, the National Park Service, and others (www.nappc.org). Much remains to be done, but the level of the debate and of awareness of biodiversity loss is increasing. A next step might be to characterize interactions by the degree of endangerment they face. The first protocol to prioritize biological entities for conservation was the IUCN Red List, and a few years ago a new effort to classify and enlist endangered ecosystems was initiated (Keith et al. 2013; Rodriguez et al. 2007, 2011, 2012). Because interactions are a crucial component of biodiversity and connect individuals and communities within ecosystems, the obvious next step is to characterize interactions and compile a protocol to determine interaction endangerment.

From Research to a "Priority Interaction List"

When developing a protocol to assess the extinction risk of terrestrial interactions, the characteristics of the interaction are the first aspect to consider—such as the nature of the interaction, species specificity of the interacting partners, their trophic level, geographic and temporal distribution, and patterns of interactions in communities. For example, the obligate, species-specific Sonoran Desert pollination mutualism between figs and fig wasps would be expected to have the highest extinction risk among pollination interactions. Another aspect to consider includes the tools for identification of interactions. For example, networks of interactions and interacting species could allow us to identify levels of specialization and redundancies in the network. Finally, the protocols should also include anthropogenic factors, such as the relevance of the interaction for humans, the (positive or negative) influence of humans on the interaction, the degree of ecosystem disturbance within the distribution of the interaction, the conservation status of interacting species, and the extinction risk of the species involved in the interaction. It will be necessary to use information from Sonoran Desert species (and ecosystem) Red Lists and other published data, such as studies demonstrating the effects of keystone species in the Sonoran Desert. Compiling a priority list of Sonoran Desert interactions would prompt implementation of more accurate ecosystem management strategies, and would most likely trigger the inclusion of species interactions in habitat restoration plans.

From Research to Restoration

Habitat restoration and ecosystem restoration have become priorities at a global scale (Aronson and Alexander 2013). They are now important components of “biodiversity offsets,” i.e., “conservation actions intended to compensate for the residual, unavoidable harm to biodiversity caused by development projects, so as to ensure no net loss of biodiversity” (ten Kate et al. 2004). Although biodiversity offsets are generally considered a useful policy instrument (Gibbons and Lindenmayer 2007), their poor definition and assessment of biodiversity is an issue (Burgin 2008). Even though species interactions are fundamental components of biodiversity, they are mentioned as one of several “species characteristics” in the key considerations that guide goals setting for habitat restoration projects

(Miller and Hobbs 2007; Galatowitsch 2012). Yet, it is reassuring to know that evaluations of large-scale restoration projects following important natural disasters, such as the oil spill in the Gulf of Mexico, do consider the importance of species interactions in designing restoration efforts (e.g., Peterson et al. 2011). As we have shown, there are increasing efforts to use microbe-plant interactions to restore degraded Sonoran Desert habitats. We recommend that researchers focusing on Sonoran Desert species, interactions, and communities, as well as policy makers, demand formal inclusion of these (and other) species interactions in restoration projects, especially of biodiversity offsets.

The survival of the unique Sonoran Desert biota depends upon an intricate and complex web of species interactions, which we are just beginning to understand. We must now increase our efforts to identify and understand the threats to interactions and we must now call for effective measures that include interactions to counteract any of the threats' negative impacts. We need to act now if we want the next generations to witness the incredible biodiversity of the Sonoran Desert and to live as part of its unique biota. ❖

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