

PLANT BIOTIC INTERACTIONS IN THE SONORAN DESERT: CURRENT KNOWLEDGE AND FUTURE RESEARCH PERSPECTIVES

Kimberly A. Franklin,^{1,*} Pacifica N. Sommers,[†] Clare E. Aslan,^{2,*} Blanca R. López,[‡] Judith L. Bronstein,[†]
Enriquena Bustamante,[§] Alberto Búrquez,[§] Rodrigo A. Medellín,^{||} and Brigitte Marazzi^{1,#}

*Arizona-Sonora Desert Museum, 2021 North Kinney Road, Tucson, Arizona 85743, USA; †Department of Ecology and Evolutionary Biology, University of Arizona, 1041 East Lowell Street, Tucson, Arizona 85721, USA; ‡Centro de Investigaciones Biológicas del Noroeste, Environmental Microbiology Group, Calle IPN 195, La Paz, Baja California Sur 23096, Mexico; §Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM)–Unidad Hermosillo, Avenida (Av.) Luis Donaldo Colosio y Av. Sahuaripa s/n, 83250 Hermosillo, Sonora, Mexico; ||Instituto de Ecología, UNAM, Circuito Exterior s/n junto al Jardín Botánico Exterior, 04510 Ciudad Universitaria, Distrito Federal, Mexico; and #Instituto de Botánica del Nordeste–Universidad Nacional del Nordeste–Consejo Nacional de Investigaciones Científicas y Técnicas, Facultad de Ciencias Agrarias, Av. Sargento Cabral 2131, 3400 Corrientes, Argentina

Editor: Patrick S. Herendeen

Premise of research. Biotic interactions have long been considered to be of less importance in structuring desert systems than other ecosystem types, but biotic interactions often play a critical role in meeting the challenges posed by the extreme conditions of desert environments. The Sonoran Desert, in particular, is home to several textbook examples of mutualisms, such as the interactions between the iconic saguaro cactus and its bat pollinators. But what do we know about the diversity, ecology, and evolution of plant-animal, plant-plant, and plant-microbe interactions and their impacts on individual plants and plant species in the Sonoran Desert?

Methodology. To address this question, we review the published research on seven common kinds of plant biotic interactions by revisiting the respective literature, identifying gaps in our knowledge, and outlining future research directions.

Pivotal results. Numerous gaps in our knowledge of plant biotic interactions in the Sonoran Desert were identified. Studies of insect herbivory, bee pollination, and plant-microbe interactions are poorly represented in the Sonoran Desert literature. Across all categories of interaction, few have examined the impacts of interactions on plant fitness or context-dependent variation in the outcomes and strengths of interactions. For the most part, interactions have been studied at single locations and over short periods of time, resulting in an incomplete understanding of their diversity, ecology, and evolution.

Conclusions. Plant biotic interactions shape the habitats in which they occur and play an important role in the maintenance of species diversity. Therefore, we call for increased efforts to fill the gaps in our understanding of plant biotic interactions in the Sonoran Desert, with an emphasis on studies linking interactions to plant fitness and the context-dependent nature of interactions. Without this knowledge we have limited capacity to predict the outcomes of global change on species interactions and to develop measures to conserve the biodiversity of the Sonoran Desert region.

Keywords: arid lands, mutualism, antagonism, natural history, interspecific interactions, plant-plant interactions, symbiosis.

Introduction

No organism on Earth lives in complete isolation; all are involved in interactions with other organisms. Biotic interactions are fundamental components of biodiversity and play critical roles in ecosystem functioning. Biotic interactions have long been con-

sidered to be of less importance in structuring desert systems than in other ecosystem types (Noy-Meir 1973), but that view is changing. In addition to unique adaptations, interactions are a primary means by which many species meet the challenges of survival in harsh desert environments. Furthermore, the relative simplicity of desert systems has made them attractive for study and has allowed biologists to uncover the profound influence species interactions can have on the structure of biological communities (Ward 2009).

In comparison to that of other deserts, the flora of the Sonoran Desert is diverse, with approximately 2500 species (Dimmitt et al. 2015), and its characteristic elements are well understood (e.g., Shreve and Wiggins 1964; Turner et al. 2005). The large legumi-

¹ Authors for correspondence; e-mail: kfranklin@desertmuseum.org, marazzibrigitte@gmail.com.

² Current address: Northern Arizona University, Flagstaff, Arizona 86011, USA.

Manuscript received April 2015; revised manuscript received September 2015; electronically published March 4, 2016.

nous trees and columnar cacti that dominate its structurally diverse plant communities further distinguish the Sonoran Desert from other North American deserts. As a result, the Sonoran Desert has been the backdrop for many studies of plant biotic interactions, with an emphasis on the columnar cacti and their interactions with nurse plants and specialist pollinators. While these spectacular interactions have become textbook examples, the vast majority of plant biotic interactions are much less conspicuous, most involving insects and microbes rather than vertebrates and generalists rather than specialists.

Our current knowledge of plant biotic interactions in the Sonoran Desert is fragmentary. Here, we provide an overview of the state of our knowledge of plant biotic interactions in the Sonoran Desert. We summarize what is known of the impacts of plant biotic interactions from the perspective of plants, at both ecological and evolutionary timescales. We conclude by identifying gaps in the literature and providing suggestions for future work.

Diversity of Plant Biotic Interactions

Plant biotic interactions are diverse with regard to the taxonomy and trophic levels of the species involved, the effects they have on the fitness of the interacting individuals, and the degree to which the interacting species depend on each other for survival (e.g., Herrera and Pellmyr 2002; Schoonhoven et al. 2005). Interactions are commonly categorized on the basis of the outcomes for the interacting individuals and their degree of dependence on the interaction. Interactions in which both individuals benefit are “mutualistic”; when one individual benefits at no cost to the other, they are “commensalistic”; and when one benefits at the expense of the other, they are “antagonistic” (Bronstein et al. 2006; Bronstein 2015). Each of these interactions can be “facultative,” with none of the interacting species entirely dependent on the other but rather interacting with several other species (i.e., the interacting species are generalists), or “obligate,” with at least one species relying on the other and rarely interacting with other species (i.e., the interacting species are specialists). Furthermore, the outcomes of interactions can vary in space and time, shifting along a spectrum from mutualism to antagonism according to the broader abiotic and biotic context (e.g., Bentley 1977; Ness 2006) and adding complexity, especially to the study of facultative interactions (van Dam 2009). Obligate interactions represent only a minor fraction of the immense web of biotic interactions, and their relative simplicity makes them easier to study (Davidson and McKey 1993; Futuyma and Agrawal 2009). Hence, studies of obligate interactions have been more numerous and have produced well-known examples of specialization, especially in pollination biology, also in the Sonoran Desert (e.g., figs and fig wasps; see below).

Here, we categorize plant biotic interactions on the basis of the resulting cost (e.g., tissue damage, loss of nutrients, disruption of other interactions) or benefit (e.g., pollination, seed dispersal, nutrient acquisition) to the plant. In particular, we review studies on two forms of antagonism, plant-herbivore (A-I) and plant host-parasite (A-II) interactions; one form of commensalism, plant-plant (C-I) interactions; and four forms of mutualism: plant-pollinator (M-I), plant-seed disperser (M-II), plant-protective agent (M-III), and plant-microbe (M-IV) interactions (figs. 1–3). We reviewed the literature for each category of interaction, relying

on both comprehensive searches in the Web of Science and our collective experience and expertise. For certain categories of interactions, such as plant-pollinator interactions, our review is necessarily incomplete, and we present a selection of the most relevant studies and most thoroughly studied systems. To our knowledge, we are the first to attempt to synthesize the impact of species interactions on the vegetation of a specific biome.

Plant-Herbivore Interactions (A-I)

Herbivory, broadly defined, is the consumption of plant tissues and products, including leaves, flowers, seeds, fruits, roots, wood, sap, and nectar. Herbivory in terrestrial systems is common, as many animal species rely on plants to meet their energetic needs. In arid environments, plants may also represent a critical source of water for consumers. Thus, their availability can strongly influence the composition and dynamics of desert herbivore communities.

Mammals are the most common vertebrate herbivores, while insects represent the dominant group of invertebrate herbivores (Herrera and Pellmyr 2002). Microbes can also be considered herbivores, but the unique relationships between plants and microbes are reviewed separately. In addition to mammalian and insect herbivory, we distinguish among herbivory in a strict sense (consumption of leaves, shoots, and stems), florivory (consumption of flowers before seed coat formation), nectar robbing, and granivory, or seed predation (consumption of seeds). Because frugivory (consumption of fruits) is often associated with seed dispersal, it is treated in “M-II: Plant-seed disperser interactions” (but see Bronstein et al. 2007, for a review of desert fleshy fruits and frugivores; see also fig. 2).

Mammalian Herbivory

Many studies have focused on herbivory by mammals. While relationships between the desert environment and the diets of ungulates, such as the desert mule deer (*Odocoileus hemionus eremicus*; e.g., Anthony 1976; Krausman et al. 1997) and the bighorn sheep (*Ovis canadensis*; e.g., Brown et al. 1976; Holt et al. 1992), are particularly well studied, the impacts on the plants they consume have not been documented. In contrast, the impact of rodents on the distribution, cover, density, and reproductive success of key vegetation elements, such as woody legumes and cacti, has been the focus of much research.

Rodents and lagomorphs forage on the seedlings of many Sonoran Desert plants (Niering et al. 1963; Steenbergh and Lowe 1977; McAuliffe 1986), often causing significant mortality. For example, herbivory by cottontail rabbits (*Silvilagus audubonii*), jackrabbits (*Lepus alleni* and *Lepus californicus*), ground squirrels (*Spermophilus* spp.), and white-throated woodrats (*Neotoma albigula*) was found to limit the establishment of foothill palo verde (*Cercidium microphyllum*; McAuliffe 1986). Rodents also forage on juvenile cacti (Niering et al. 1963), because the plant tissue is not yet protected by spines and toxic oxalates. The white-throated woodrat is the only Sonoran Desert mammal able to digest these oxalates. Its diet consists primarily of *Opuntia* and *Cylindropuntia* cacti and secondarily of saguaro (*Carnegiea gigantea*), allowing its persistence in drier habitats (Brown et al. 1972; Steenbergh and Lowe 1977). In the absence of prickly pears and chollas, woodrats feed more heavily on saguaros,



Fig. 1 Examples of plant-animal and plant-plant interactions in the Sonoran Desert. *A, B*, Insect herbivory: *A*, leaf herbivory by a caterpillar of the Gulf fritillary butterfly (*Agraulis vanillae*); *B*, florivory by flower longhorn beetles (*Crossidius pulchellus*). *C*, Plant host–parasite interaction with desert mistletoes (*Phoradendron californicum*) on a legume tree (photo courtesy of Jonathan Knighton/Wisor). *D, E*, Pollination of Sonoran Desert cacti in the Plains of Sonora, southern Sonoran Desert: *D*, hawk moth (*Hyles lineata*) visiting flowers of queen of the night (*Peniocereus striatus*); *E*, the broad-billed hummingbird (*Cynathus latirostris*) visiting flowers of the octopus cactus (*Stenocereus alamosensis*). *F*, Protective interaction with *Crematogaster* ant visiting extrafloral nectaries of the fishhook barrel cactus (*Ferocactus wislizeni*; photo courtesy of Michele Lanan). *G*, Plant-plant interaction between young saguaros (*Carnegiea gigantea*) and nurse legume plants, including a palo verde (*Cercidium* sp.).

affecting their reproductive output (Hayes et al. 2013). Mature saguaros with conspicuous woodrat damage produce significantly fewer flowers and fruits than undamaged plants, suggesting that increasing woodrat herbivory could ultimately affect the episodic recruitment pulses that are vital to the persistence of saguaro populations (Hayes et al. 2013).

Insect Herbivory

Herbivorous insects include species that specialize on leaves, stems, roots, phloem, and sap. Although they are common in desert environments, they have been the focus of surprisingly little research (fig. 1*A, 1B*). In other systems, herbivorous in-

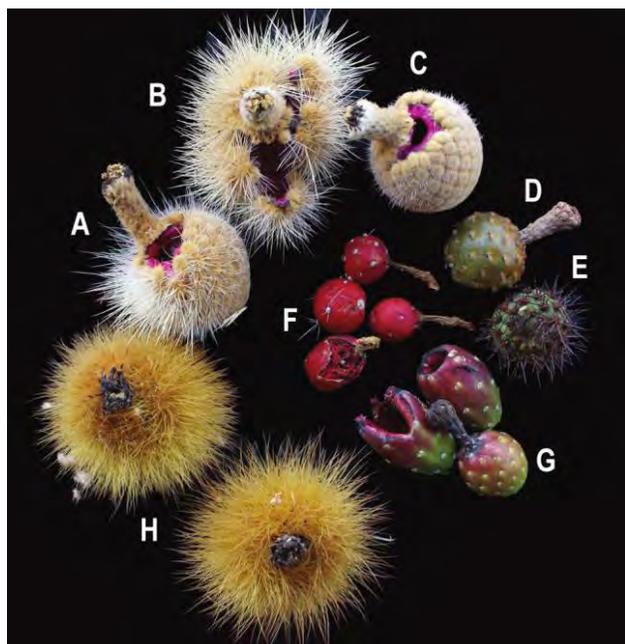


Fig. 2 Endozoochorous fruits of some Sonoran Desert columnar cacti. A–C, Cardon (*Pachycereus pringlei*); D, E, organ pipe cactus (*Stenocereus thurberi*); F, octopus cactus (*Stenocereus alamosensis*); G, saguaro (*Carnegiea gigantea*); H, hairbrush cactus (*Pachycereus pectenaboriginum*).

sects can have significant impacts on plants at the individual, population, and community levels (Crawley 1989; Maron and Crone 2006), but this lack of research leaves us without a systematic understanding of the roles insect herbivores play in regulating plant populations and communities in the Sonoran Desert. The few studies that have documented the impacts of insect herbivores on plants are reviewed below.

The leaf miner (*Buccalatrix thurberiella*) feeds on both cultivated cotton (*Gossypium hirsutum*) and desert cotton (*Gossypium thurberi*). In cultivated cotton this insect can cause significant reduction in boll production and even mortality (McGregor 1916; Morrill 1927), but experimental research has provided no evidence of impacts on the fitness of desert cotton (Karban 1993). In contrast, although the beetle known as the mesquite twig girdler (*Oncideres rhodosticta*) feeds on mesquite, the interaction may be mutualistic, in that girdling stimulates young mesquite trees (*Prosopis glandulosa*) to increase stem density, which increases the resource-capture ability of the plant, but the potential impacts on plant fitness have not been examined (Duval and Whitford 2008). Finally, Miller et al. (2009) examined the impacts of insect herbivory on population density of the tree cholla cactus (*Opuntia imbricata*) across an elevation gradient in the Chihuahuan Desert, finding evidence that the nature of the interaction varies with environmental context. Through a combination of observational, experimental, and modeling work, they showed that herbivory limits density at lower elevations, where levels of herbivory are greatest.

The Sonoran Desert is home to two species of leafcutter ants (*Acromyrmex versicolor* and *Atta mexicana*) that cut fresh leaves

and collect dead plants to serve as a substrate for growing basidiomycetous fungi, which they subsequently consume (Gamboa 1975; Aylward et al. 2012). Although leafcutter ants do not directly ingest the vegetation they collect, they are considered to be the dominant herbivores in the Neotropics (Hölldobler and Wilson 2010). *Acromyrmex versicolor* and *Atta mexicana* are two of the most conspicuous plant-damaging insects in the Sonoran Desert. Both species are generalists. They collect primarily dried vegetation, which is available year-round, but also seasonally available resources, such as dried and fresh flowers, seeds and fruits, and fresh young leaves (Wetterer et al. 2001). Colonies may forage over a very large area, as great as 8,000 m² (Mintzer 1979), but their potential impacts on plant fitness and communities have not been examined.

Florivory

Florivory can yield plant, population, and community outcomes different from those of herbivory on leaves, shoots, and stems (McCall and Irwin 2006). Desert flowers offer relatively undefended, watery tissue and so should be a prime resource for consumers, but in the Sonoran Desert florivory has been the focus of little research. In his volume on cactus-feeding insects and mites, Mann (1969) recorded several instances of florivory in the Sonoran Desert. Nearly all florivores in this account were larvae of Lepidoptera. More recently, McIntosh (2002) found that the barrel cactus *Ferocactus cylindraceus* was heavily attacked by the flower-eating caterpillar *Pseudoschinia elautalis* (Crambidae), which destroyed 23%–29% of flowers and buds.

Ants are common visitors to cactus flowers in the Sonoran Desert. They consume nectar and pollen and may also interact with other flower visitors. For example, Ness (2006) showed that the reproductive success of the close relative *Ferocactus wislizeni* was negatively affected by aggressive ants foraging on pollen and discouraging (sometimes even attacking) pollinators from visiting flowers. Conversely, in the senita cactus (*Pachycereus schottii*) the presence of ants foraging in flowers did not significantly deter the cactus's pollinators, the senita moths (*Upiga virensens*; Lepidoptera: Crambidae), but increased pollination (Holand et al. 2011).

Nectar Robbing

Nectar robbers acquire nectar from flowers via holes in petals rather than legitimate floral openings. Nectar robbers reduce plant reproductive success by removing floral nectar without providing pollination services. In addition, nectar robbers may lessen floral attractiveness to legitimate pollinators, resulting in further reproductive losses for the plant. Although nectar robbing describes a typically antagonistic interaction, impacts on plant reproduction vary among systems (Irwin et al. 2010). In the Sonoran Desert, nectar robbing by carpenter bees (*Xylocopa californica*) does not alter floral visitation of the effective pollinator, the bumblebee *Bombus sonorus*, to desert willow (*Chilopsis linearis*) and thus does not influence female reproductive success in terms of fruit set, and it may even increase male reproductive success by increasing the distance and the number of flowers to which pollen is dispersed (Richardson 2004a, 2004b).

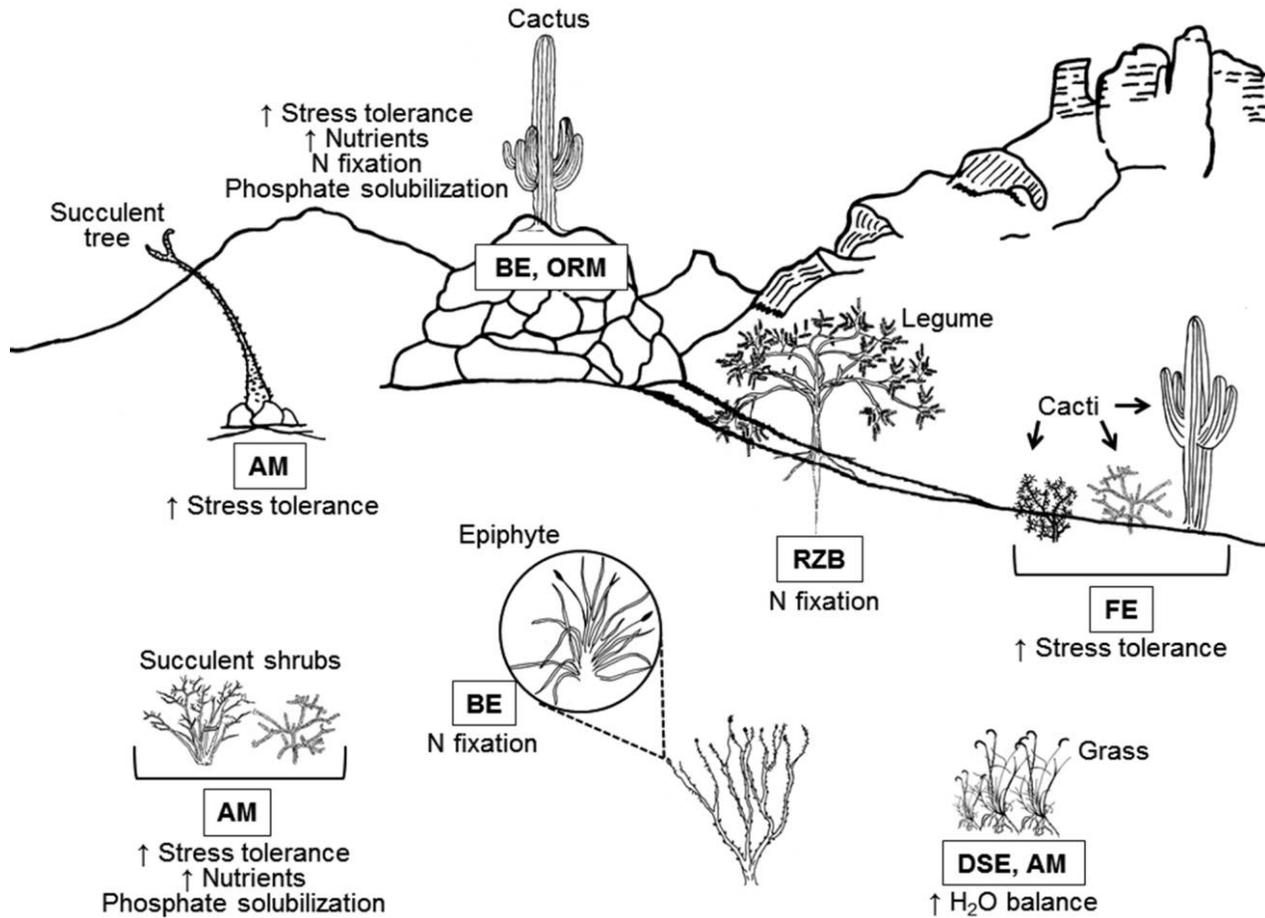


Fig. 3 Illustration of positive plant-microbe interactions referred to in the text. Positive interactions among plants and microbes help plants overcome drought by improving water balance ($\uparrow H_2O$ balance) and low nutrient availability of soils by nutrient acquisition (\uparrow nutrients), mostly through nitrogen (N fixation) and phosphorous (phosphate solubilization). Traits such as salinity tolerance and wide temperature tolerance and pathogen resistance are also conferred by association with microbes (\uparrow stress tolerance). The networks of interactions occurring belowground are drivers of biogeological processes, including soil formation and hydrological and nutrient cycles. AM = mycorrhizal fungi; BE = bacterial endophytes; DSE = dark septate endophytes; FE = fungal endophytes; ORM = other beneficial rhizosphere microbes; RZB = nodulating rhizobacteria.

Granivory and Seed Predation

The primary granivores of the Sonoran Desert are ants and rodents (Mares and Rosenzweig 1978), and most of the published literature has examined one or both of these groups. Seed predation is considered a central structuring factor in plant communities (Inouye et al. 1980; Price and Joyner 1997). In a classic study in Portal, Arizona, Brown (1998) manipulated rodent populations and observed large changes in plant density and community structure following decreases in particular rodent guilds. For example, when kangaroo rats (*Dipodomys* spp.) were removed from plots, the abundance of the large-seeded plants they preferentially consume increased by several thousand times, and the abundance of small-seeded species decreased. The plant community was further transformed by the removal of all rodents as granivores (Brown 1998).

Although ants and rodents compete for available seeds, resource partitioning may allow them to coexist (Brown and Da-

vidson 1977; Reichman 1979; Davidson et al. 1984). Ants and rodents partition available seeds by size, with ants selectively harvesting smaller seeds and rodents showing preferences for larger seeds (Davidson et al. 1984). Subdivision occurs within these guilds, as well. For example, smaller ant species selectively harvest smaller seeds than larger species (Davidson 1977). Rodents also partition seeds resources, not by seed size (Stamp and Ohmart 1978) but rather by microhabitat and seed patch densities (Brown 1998). Ants and rodents also partition them by depth. Whereas rodents can access both surface and buried seeds, ants are restricted to foraging on seeds lying on the soil surface (Reichman 1979).

Few studies have examined other groups of potential seed predators in the Sonoran Desert. Bruchid beetles (family Bruchidae) foraging in the canopy of palo verde (*C. microphyllum*) trees fed upon and killed seeds, whereas seeds on the ground were frequently cached by rodents and exhibited some survival (McAuliffe 1990). Although they have the potential to act as

seed predators, other groups of Sonoran Desert seed consumers, such as birds, larger mammals, and tortoises, appear more frequently in seed-dispersal studies (see “Plant–Seed Disperser Interactions (M-II)”) and have not been recorded to take large amounts of seed relative to rodents and ants. Notably, however, research on seed consumption by these species has been sparse.

Plant Host–Parasite Interactions (A-II)

Parasitic interactions can be defined as systems in which an organism (the parasite) lives on or in another organism (the host) for a prolonged time (e.g., Combes 2001). Two common and easily observable forms of parasitism in the Sonoran Desert involve parasitic plants and gall-inducing insects, or gall formers, and in both cases, the parasite harms the host plant as it draws nutrients from it (see details below).

Plant Host–Plant Parasite

A plant parasite extracts photosynthate and water through the haustorium, a specialized root appendage, and can be hemiparasitic, in that it supplements its own photosynthesis or depends completely on the host, respectively (Scott 2008). The most common plant parasite in the Sonoran Desert is the hemiparasitic desert mistletoe, *Phoradendron californicum*, found on branches of woody shrubs and trees, mostly leguminous (Glazner et al. 1988; Aukema and Martínez del Rio 2002; Aukema 2003, 2004; fig. 1C). The Sonoran Desert is also home of two root holoparasites: the rare sandfoot (*Pholisma sonora*) and the widespread broomrape (*Orobancha ludoviciana*). The sandfoot attaches to the roots of a diversity of desert shrubs, such as *Ambrosia* spp., and is found only in the dune systems near Yuma and in southeastern California, where it is highly threatened by habitat destruction and off-road vehicle activity (Nabhan 1980). The broomrape parasitizes a diversity of species, including composites and crops, and requires the presence of a host root for germination (Musselman 1980).

Effects of plant parasites on their hosts are barely documented. Infection by *P. californicum* is rarely fatal to the host plant, even though infestation levels can become very high (Aukema and Martínez del Rio 2002). No studies exist on infestations by root holoparasites, probably because it is difficult to study them, given that these plants remain cryptic most of their lifetime and emerge only during flowering and reproduction.

Plant Host–Gall-Inducing Insects

Gall formers do not directly damage host tissues but act as phloem parasites by inducing the host plant to allocate resources to gall development and feeding of the gall formers (Weis and Kapelinski 1984; Larson and Whitham 1991; Fay et al. 1996). Wasp or midge galls develop on leaves where insects have laid their eggs; the gall is produced by the plant in response to the insect infestation and nourishes the developing larvae. This explains why gall formers are also considered an underrepresented type of herbivore in studies of herbivory (Larson 1998), although the relationship is parasitic (Price et al. 1987).

In the Sonoran Desert, galls are common on shrubs such as creosote (*Larrea tridentata*), saltbush (*Atriplex* spp.), and other species (Fernandes and Price 1988; Joy and Crespi 2007). An in-

vestigation of gall characteristics on *Atriplex canescens* found that larvae of the midge *Asphondylia atriplicis* were more likely to survive when they were associated with larger galls (Marchosky and Craig 2004). Other Sonoran Desert galls are found on riparian species, such as willow (*Salix* spp.; Price et al. 1994). The galls can be harmful to some plants, impeding their photosynthetic rate and potentially their growth, but appear to have little effect on others (Larson 1998). This plant–insect interaction is underappreciated in the Sonoran Desert.

Plant–Plant Interactions (C-I)

Interactions of plants with other plants are assumed to be antagonistic unless there is confirmatory evidence otherwise (Bronstein 2009), but here we focus on the most visible plant–plant interactions in the Sonoran Desert, nurse plant–seedling interactions, which are associations of seedlings with adult plants. These are commonly considered to be commensalisms, because seedlings (or protégés, “protected ones” in French) benefit from the microenvironment created by the adult plants but there is no effect on the latter. Nurse plants are perennial plants that create microenvironments, termed “resource islands,” within the reach of their roots and branches, providing shade, nutrients, and increased soil moisture (Halvorson et al. 1994). These resource islands are mounds that originate from the deposition and subsequent stabilization of wind-borne soil particles under plant canopies (Armbrust and Bilbro 1997). Soil formation by certain nurse trees is a critical factor for seedling establishment, and the presence of particular microbes (competing or beneficial) may have additional effects on seedling growth (Carrillo-García et al. 2000). In the Sonoran Desert, specific cacti–nurse tree interactions and their associated beneficial microbes may even facilitate restoration of degraded arid habitats (Bashan et al. 2012). The fine-textured soils they create become habitat for entire communities of organisms. Worldwide, there are about 147 described nurse species, from 98 genera and 40 families, and 429 protégé species, from 273 genera and 84 families, which occur in many different environments, especially arid and semiarid environments (Flores and Jurado 2003).

Sonoran Desert perennial plants differ in their ability to create resource islands. In a comparison of 46 potential nurse-plant species, mesquite (*Prosopis* spp.) and ironwood (*Olneya tesota*) supported the largest number of protégé species (Carrillo-García et al. 1999). Smaller-sized plants, such as the perennial bunchgrass *Hilaria rigida*, and small shrubs, such as ragweed (*Ambrosia* sp.), may also serve as nurse plants (see below).

Most research has focused on the interactions between cacti and their nurse plants. The best documented are interactions between the saguaro cactus and its nurse shrubs and trees (*Ambrosia deltoidea*, *Ambrosia dumosa*, *Cercidium microphyllum*, *Larrea tridentata*, *Prosopis* spp., and *O. tesota*; see fig. 1G; e.g., Medeiros and Drezner 2012; see Drezner 2014 and references therein). These interactions were noted more than 100 years ago by Forrest Shreve (1910, 1931) and then further studied by other researchers (e.g., Niering et al. 1963; Turner et al. 1966; Steenbergh and Lowe 1969, 1977). Nurse plants ameliorate harsh desert conditions and are critical to saguaro seedling survival, while other factors, such as herbivory, may have a smaller impact on seedling survival (Turner et al. 1966). Thus, factors that affect the abundance of nurse plants (e.g., grazing, climate change) may

exert a strong influence on saguaro population dynamics. The potential effects of the protégé on its nurse plant have rarely been examined, but in the case of the saguaro, one study provides evidence that saguaros may increase the mortality of their common nurse plants, the foothill palo verde (*Cercidium microphyllum*), through competition for water, with the potential for significant effects on the dynamics of the desert plant community (McAuliffe 1984). Competition for water has also been documented between the barrel cactus *Ferocactus acanthodes* and its associated nurse plant *H. rigida*, a perennial bunchgrass (Franco and Nobel 1989).

Less studied cactus–nurse plant interactions involve other large cacti. The giant cardon (*Pachycereus pringlei*) is associated with ironwood (*O. tesota*) and mesquite (*Prosopis glandulosa*) trees (e.g., Suzán et al. 1996). While its seedlings perform better under mesquite than under ironwood, cardon establishment is more strongly spatially associated with ironwood, most likely as a result of the preference of its primary seed disperser, *Auriparus flaviceps*, to nest in ironwood (Suzán-Azpiri and Sosa 2006). These same nurse-plant species were found to play a key role in increasing seedling recruitment of the senita cactus (*Pachycereus schottii*) by reducing granivory, but this reduction was conditional on rainfall, which highlights how the positive effects of facilitation may vary with context (Holland and Molina-Freaner 2013). Research on the rare night-blooming cereus *Peñiocereus striatus* and its nurse plants has also shown that the benefits of nurse plants are dependent on context (Suzán et al. 1994).

Plant-Pollinator Interactions (M-I)

The plant-pollinator interaction is by far the best-studied mutualism (Bronstein et al. 2006). In the Sonoran Desert, hummingbirds, bats, bees, moths, and wasps are well known for their pollination services (see Chambers et al. 2004). A large diversity of plants and pollinators, coupled with the open landscape and sparse vegetation cover, provides an ideal setting for the study of pollination and plant reproduction. Although the Sonoran Desert boasts an exceptional diversity of pollinators, the best-studied systems involve large, conspicuous flowers, large, high-energy floral visitors, or unique plant-pollinator relationships (fig. 1D, 1E). Indeed, most attention has been directed toward the obligate mutualisms between yuccas and yucca moths and between figs and fig wasps, as well as vertebrate pollination of the iconic columnar cacti of the Sonoran Desert, all of which have become textbook examples of mutualisms (see below). Other taxa have received relatively little attention.

Although the Sonoran Desert region is a center of both bird and bee diversity in North America, there have been few well-documented studies of bird or bee pollination. In particular, research from the plant perspective is scarce. In regard to birds, one exception is a study of migratory hummingbirds and ocotillos (*Fouquieria splendens*), which documented the selective force exerted by the arrival time of migratory hummingbirds on the flowering phenology of ocotillo (Waser 1979). Other bird-pollination studies have been limited to hummingbirds and other migratory pollinators, including white-winged doves (*Zenaidura macroura*) and the monarch butterfly (*Danaus plexippus*; Scobell and Scott 2002; Nabhan 2004).

Bee diversity peaks in the xeric regions of southwestern United States and northwestern Mexico (see Timberlake in Michener 1979, p. 283; Minckley 2008; Minckley and Asher 2013), and bees are responsible for pollinating the majority of flowering plants, yet studies focusing on bee pollination are relatively scarce in the literature on Sonoran Desert pollination systems (but see Waser 1979; McIntosh 2005; Cane et al. 2013). Much of the research has taken the perspective of the bees rather than that of the plants and is focused on the evolution of pollen specialists (McIntosh 2005; Minckley and Roulston 2006). Pollen specialists, bees that forage for nectar from a wide diversity of plants but collect pollen from only one or several closely related plant species, are well represented in the desert bee fauna, but the flowers visited by specialist bees are often visited by an even greater number of generalist bees (Minckley et al. 2000). For example, more than 120 bee species have been recorded visiting creosote (*Larrea tridentata*), of which 21 are specialists and the rest generalists (Minckley et al. 2000). Comparing the efficacy of pollen specialists and generalists, McIntosh (2005) found that the barrel cacti *Ferocactus wislizeni* and *Ferocactus cylindraceus*, which are visited by a wide diversity of bees, are pollinated primarily by pollen specialists rather than by other floral visitors.

Other research on mutualistic plant-pollinator interactions has focused on large flowers or large, high-energy pollinators. Such are the cases of the pioneer work by Gregory (1963, 1964) on the pollination of *Oenothera*, and other, more recent work with hawk moths (e.g., Willmott and Búrquez 1996; Raguso and Willis 2003, 2005; Riffell et al. 2008). Below we discuss the best-known pollination systems from the Sonoran Desert and their implications in the specialization/generalization paradigm of pollination.

Columnar Cacti: Mixed Strategies

Plant-pollinator interactions are currently one of the most studied topics in columnar cactus research. Columnar cacti in the Sonoran Desert exhibit both specialized and generalized pollination systems, although an evolutionary trend toward generalization is evident (Fleming et al. 2001). For many cactus species, pollinators from distantly related taxa contribute to the reproductive success of plants. The degree of specialization and generalization varies among and within species and also has a strong spatial component. These interactions can be organized under the pollination syndromes put forth by van der Pijl (Faegri and van der Pijl 1979), in which different groups of plants converge on one type of flower and reward that are appropriate to only one type of pollinator. Likewise, there are groups of animals that also exhibit morphological and behavioral convergence in the use of flowers as a resource.

A variety of pollination systems are represented across the diversity of columnar cactus species in the Sonoran Desert. The migratory lesser long-nosed bat *Leptonycteris yerbabuenae* is the most effective pollinator of *Carnegiea gigantea* (saguaro), *Stenocereus thurberi* (organ pipe cactus), *Pachycereus pringlei* (cardon), and *Pachycereus pecten-aboriginum*, all of which possess classic bat-pollinated flowers (Fleming et al. 2001; Bustamante et al. 2010). The relationship between columnar cacti and New World nectarivorous bats may be as old as 30 million years (Fleming and Kress 2011), and they have developed extensive coevolutionary linkages (Simmons and Wetterer 2002). Never-

theless, there has been local differentiation (Bustamante et al. 2010), as evidenced by some populations of *C. gigantea* and *S. thurberi*, which are also pollinated by hawk moths, hummingbirds, and other birds (Fleming et al. 2001; Bustamante et al. 2010), including the white-winged dove (*Z. asiatica*), which is an important pollinator of saguaro (McGregor et al. 1962).

Stenocereus alamosensis, with red tubular flowers, has morphological and functional traits associated with pollination by hummingbirds (fig. 1E). The spring bloom occurs during the northward migration of several hummingbirds species through the Sonoran Desert (Johnsgard 1983; A. Búrquez and E. Bustamante, unpublished data). *Stenocereus gummosus*, with a split distribution between the Baja California peninsula and the Sonoran coast, and *Stenocereus eruca*, a prostrate columnar cactus known only from central Baja California Sur, have flowers adapted to pollination by hawk moths (*Hyles lineata* and *Erinnyis ello*), their main pollinators (Clark-Tapia and Molina-Freaner 2003, 2004). In the absence of hawk moths, native bees are the primary flower visitors to *S. eruca*, but they are less effective pollinators, leading to low reproductive success in years with low hawk moth abundance (Clark-Tapia and Molina-Freaner 2004). In some cases the plant-pollinator interaction is more specialized, such as the interaction between senita cacti (*Lophocereus schottii*) and their pollinating moths, *Upiga virescens* (Holland and Fleming 1999), which is another seed-eating mutualism in the Sonoran Desert.

With the exception of *P. pringlei*, a trioecious cactus (Fleming et al. 1994), the columnar cacti of the Sonoran Desert are hermaphrodites and have autoincompatibility mechanisms (Fleming et al. 2001; Clark-Tapia and Molina-Freaner 2003, 2004; Bustamante et al. 2010). Therefore, spatial and temporal variability in the presence of specific pollinators may limit the transfer of pollen, with consequences for the reproductive success of these species. However, recent work has shown that for cactus species believed to be primarily pollinated by bats, the absence of bats does not appear to limit reproduction as much as expected (Valiente-Banuet et al. 2004; Bustamante et al. 2010). For example, simple adjustments in the closing time of the flower allow the successful production of fruit and seeds by diurnal pollinators, suggesting a bet-hedging strategy for the persistence of populations, or what Herbert Baker (1961) called safeguard pollination mechanisms.

Highly Specialized Systems

Yucca and yucca moths. A classic example of coevolution is the obligate mutualism between yuccas (*Yucca* and *Hesperoyucca*, Agavaceae) and yucca moths (*Tegeticula* and *Parategeticula*, Prodoxidae, Lepidoptera). Yucca moths serve as the exclusive pollinators of their hosts, and their larvae in turn require yucca seeds for their development (Pellmyr 2003). Sixteen species of pollinating yucca moths are known, 15 in the genus *Tegeticula* and one in the monospecific genus *Parategeticula*. Most of the 16 described moth species feed on a single host species, but some use as many as seven species across their geographic range (Pellmyr 1999). The genus *Yucca* includes an estimated 49 species (Good-Avila et al. 2006), four of which are present in the Sonoran Desert. *Yucca arizonica* is widely distributed in Sonora and Arizona, *Y. baccata* is present in Arizona and California, *Y. schidigera* occurs in the southern Mojave Desert

and extends southward into the Sonoran Desert in Baja California along the west base of the Sierra Juarez, and *Y. valida* is a peninsular species and is one of the most frequent large perennial species in the northern Vizcaino Plain (Turner et al. 1995, 2005). All of them are pollinated exclusively by *Tegeticula yuccasella*, a species complex (Pellmyr 1999). Female yucca moths actively gather pollen from yucca anthers, then oviposit into the floral ovary, and subsequently use some of the pollen load to actively pollinate the flower. The developing moth larvae feed on yucca seeds but do not destroy the entire crop; only 3%–5% of the seeds in a *Y. schidigera* capsule (Keeley et al. 1984) and only about 18% in *Y. baccata* (Addicott 1986) are eaten. As there are no other documented pollinators, active pollination by the female moth is critical for ensuring the reproductive success of yuccas (Pellmyr 2003).

Hesperoyucca whipplei (previously *Yucca whipplei*) is also distributed in the Sonoran Desert and is pollinated exclusively by *Tegeticula maculata* (Kiester et al. 1984). *Hesperoyucca whipplei* occurs more or less continuously in mountainous areas from southwestern California to northern Baja California, with some scattered and rather restricted southern populations (Turner et al. 1995). In addition to hosting the mutualistic seed-eater pollinator yucca moths, *H. whipplei* is a host plant of another three species of yucca moths of the genus *Produxus*, one commensalistic fruit feeder and two commensalistic stalk feeders (Althoff et al. 2007). This system has been used to study the influence of species interactions and feeding location on phylogenetic structure in insect lineages (e.g., Althoff et al. 2007).

Figs and fig wasps. The interaction between figs (*Ficus*, Moraceae) and their pollinating wasps (multiple genera, Agaonidae) is another classic plant and seed-eating-pollinator mutualism present in the southern range of the Sonoran Desert. In this case, habitat rarity and small plant populations have led to asynchronous reproduction that allows the persistence of the interaction. One fig species, *Ficus petiolaris* (subsp. *palmeri* and *petiolaris*), is endemic to the Sonoran Desert and is obligately associated with a pollinating and seed-eating wasp in the genus *Pegoscapus* (unnamed species, family Agaonidae). Two more species reach the desert edge, *F. insipida* and *F. pertusa*, and are found primarily in canyons, such as the Cañon de Nacapule north of San Carlos (Sonora, Mexico), and are pollinated by the wasps *Tetrapus costaricanus* and *Pegoscapus silvestrii*, respectively (Bronstein 1988).

Ficus petiolaris has the northernmost range of New World figs and is the only fig species widely distributed across xeric environments in northwestern Mexico, where it typically occurs in small, naturally fragmented populations in mainland Sonora, Mexico, the Gulf of California islands, the Baja California peninsula, and Arizona (Felger et al. 2001). Low inbreeding levels and high outcrossing rates are characteristic of *F. petiolaris*, even in small, peripheral populations (Gates and Nason 2012), with its obligate pollinator playing an important role in mediating high rates of pollen gene flow. The same happens in *F. insipida* and *F. pertusa* (Smith and Bronstein 1996).

In conclusion, the Sonoran Desert region is well known for several iconic floral mutualisms that involve a small sample of animal and plant taxa, but most pollination interactions remain poorly known. Yet the Sonoran Desert is an ideal place for pollination research, as it allows accessible and relatively easy and manageable flower manipulation and pollinator observation. Pollination studies in the region have proven fruit-

ful in uncovering the danger of simplifying interactions, through the use of pollination syndromes, and the evolutionary significance of reliance on several agents of pollen transport (e.g., Riffell et al. 2008). Also evident is the widespread generalization within pollination systems, largely driven by spatiotemporal variation in the abundance of resources, pollinator assemblages, and visitation rates (Herrera 1996; Ollerton 1996; Waser et al. 1996; Waser 1998; Thompson 2005).

Remaining gaps in our knowledge offer opportunities to continue to contribute to vanguard pollination research. For instance, the study of bee interactions and their effects on plant reproduction, particularly the study of small bee–plant interactions, promises a fruitful harvest of new data and theory. Butterfly and beetle pollination is also a promising field for documenting new interactions, as these taxa are also abundant and diverse in the desert. Finally, although full of anecdotal accounts, bird pollination (including both hummingbird and perching-bird pollination) is awaiting more formal studies, especially in the context of the generalist-specialist paradigm.

Plant–Seed Disperser Interactions (M-II)

Animal-mediated seed dispersal offers several notable benefits for desert plants (Howe and Miriti 2004; Bronstein et al. 2007). Dispersed seeds escape from their parental neighborhood, where both intraspecific competition (with siblings and parent) and enemy attack (from species-specific predators, parasites, and pathogens) are prevalent (Janzen 1970; Connell 1971; Howe and Smallwood 1982; Howe 1986). Vertebrate gut passage can scarify seeds and promote germination (Traveset and Verdú 2002). Typical disperser behaviors can result in “directed dispersal,” where seeds are deposited in microsites (e.g., beneath bird perch trees or in ant refuse piles) where nutrients and moisture are elevated (Wenny 2001; Purves et al. 2008). Resources such as water and nutrients can be extremely patchy in deserts (Austin et al. 2004), creating patchy plant regeneration sites that act as islands in a matrix of hostile conditions. Seeds depend on dispersers to reach these islands and to take advantage of these variable resources. The process of seed dispersal is therefore likely of high importance to Sonoran Desert plant recruitment, yet it has been remarkably little studied (but see Bronstein et al. 2007).

Seed Dispersal by Bats and Other Mammals

Although rodents are generally considered seed predators, their caching behaviors can result in seed dispersal for a proportion of seeds (Jensen and Nielsen 1986). Cached seeds are generally buried or otherwise protected from desiccation and predation; if forgotten by the rodent, such seeds may germinate and grow (e.g., McAuliffe 1990). Some plant species exhibit specialized traits for rodent dispersal. Jojoba (*Simmondsia chinensis*), for example, possesses a toxic seed coat that affects several rodent species but not Bailey’s pocket mouse (*Perognathus baileyi*), the plant’s likely primary disperser (Sherbrooke 1976). However, for cacti in the Sonoran Desert, it is generally assumed that rodents act as seed predators (Rojas-Aréchiga and Vázquez-Yanes 2000).

Dispersal of all columnar cacti of the Sonoran Desert is accomplished by endozoochory (seed dispersal via ingestion by vertebrate animals; see examples of fruits in fig. 2). Reptiles,

birds, bats, and other mammals, including terrestrial species (such as coyotes [*Canis latrans*], lagomorphs, peccary [*Pecari tajacu*], and foxes [*Urocyon cinereoargenteus*]) as well as humans, are known to act as dispersal agents (Steenbergh and Lowe 1977; Fleming and Sosa 1994; Rojas-Aréchiga and Vázquez-Yanes 2000), depositing seeds regularly in their feces. Bats are very important cactus seed dispersers, in terms of numbers of genera of columnar cacti that provide food for bats (Fleming and Sosa 1994), and bat gut passage may contribute to enhanced germination (Naranjo et al. 2003). Cactaceae is in the top five families providing fruit to frugivorous/nectarivorous phyllostomid glossophagine bats, including those in the genus *Leptonycteris*, the migratory, threatened long-nosed bats (Muscarella and Fleming 2007; see also fig. 2). For most desert plants, the importance of seed dispersal to seedling recruitment (i.e., rates of seed dispersal, comparisons of disperser species) has not been studied. In recent observations of barrel cactus (*Ferocactus wislizeni*) fruit removal under differing densities of mid- to large-sized terrestrial mammals, it was found that fruits were stripped from plants most rapidly in open desert, where they were accessible to larger terrestrial mammals (e.g., deer, javelina, lagomorphs, and rodents), whereas they remained substantially longer on plants in a fenced garden (accessible to birds, small lagomorphs, and small rodents) and even longer in urban environments with lowest density and diversity of wildlife (Leland 2014; C. E. Aslan, unpublished data).

Seed Dispersal by Birds, Reptiles, and Ants

There has been little research on birds as seed dispersers in the Sonoran Desert, although they are major dispersers in many other systems (Howe and Smallwood 1982). In several instances, birds have been shown to deposit seeds in areas protected by nurse plants. In Sonoran Desert grasslands, birds provided directed dispersal for wild chiltepin peppers by depositing them beneath trees that then served as nurse plants (Carlo and Tewksbury 2014). Similarly, an examination of four columnar cactus species (*Pachycereus pringlei*, *Carnegiea gigantea*, *Stenocereus thurberi*, and *Lophocereus schottii*) found that birds and a single lizard (*Dipsosaurus dorsalis*) were the primary dispersers, again placing seeds beneath nurse plants, where litter accumulation was critical for seedling protection (Sosa-Fernandez 1997).

The best-studied case of bird-mediated seed dispersal in the Sonoran Desert involves the hemiparasitic desert mistletoe (*Phoradendron californicum*). In this case, a strongly specialized seed-dispersal relationship exists between mistletoe and the phainopepla (*Phainopepla nitens*). The bird possesses a modified gut able to separate and deposit mistletoe seeds and to maximize the recruitment potential of the plant (Aukema 2004). Seeds are deposited in small, sticky clumps that adhere to host-plant branches. Although other bird species will also consume mistletoe fruits, the phainopepla successfully disperses significantly more seeds than do nonspecialist bird species (Larson 1996). A relationship so specialized and coevolved is highly unusual in the realm of seed dispersal.

It seems reasonable that desert tortoises may provide dispersal for many desert plants, but this interaction appears understudied in the Sonoran Desert, although the related *Gopherus polyphemus* in the southeastern United States is a known seed

disperser (Carlson et al. 2003). Similarly, ants are notably absent from the seed-dispersal literature from the Sonoran Desert.

Plant–Protective Agent Interactions (M-III)

Many plants engage in mutualistic interactions with ants, which provide plants with protection against insect herbivores (Rico-Gray and Oliveira 2007; Chamberlain and Holland 2009). These plants possess extrafloral nectaries (EFNs) that secrete a carbohydrate-rich reward to attract ants (see Marazzi et al. 2013). While in a few cases the mutualism is obligate, with ants nesting on the plants, as in the well-known ant acacias (Janzen 1967), the majority of protection mutualisms are facultative, with the ants nesting elsewhere.

In the Sonoran Desert, at least 30 genera include members possessing actively secreting EFNs, with the majority being cacti and legumes (B. Marazzi, unpublished data; fig. 1F). EFN-bearing plants can represent a crucial source of nutrients and water to a diversity of arthropods, such as flies, butterflies, beetles, and wasps, but ants are the most common consumers, with up to 12 species in some systems (e.g., Rudgers and Gardener 2004; Chamberlain and Holland 2008). Furthermore, ant colonies include these resources when staking their territories (Lanan and Bronstein 2013).

EFN-mediated mutualisms with Sonoran Desert ants are facultative. Studies on these interactions have focused on desert cotton (*Gossypium thurberi*; e.g., Rudgers et al. 2003; Rudgers 2004) and especially on cacti. Among the latter, the interaction between ants and the fishhook barrel cactus (*Ferocactus wislizeni*) is by far the best-known system (e.g., Ness 2006; Ness et al. 2009; Lanan and Bronstein 2013; fig. 1F). Other documented interactions among ants and cacti include the barrel cacti *Ferocactus cylindraceus* (as *Ferocactus acanthodes* in Ruffner and Clark 1986), *Ferocactus gracilis* (Blom and Clark 1980), and *Ferocactus viridescens* (Ludka 2009; Ludka et al. 2015), the buckhorn cholla *Cylindropuntia acanthocarpa* (as *Opuntia acanthocarpa* in Pickett and Clark 1979), and the senita cactus *Pachycereus schottii* (Holland et al. 2009).

Experiments on fishhook barrel cactus with artificial addition of *Manduca sexta* (Lepidoptera: Sphingidae) larvae to simulate herbivore presence have shown that not all desert ant species are equally efficient mutualists. In fact, of the four most common ants visiting the EFNs, *Solenopsis xyloni* was the most effective at removing the larvae, followed by *Solenopsis aurea* and *Crematogaster opuntiae*, while *Forelius* sp. was the least effective (Ness et al. 2006). However, although *S. xyloni* was the most effective protector, it was also the most disruptive when visiting flowers for pollen, frequently disturbing pollinators (Ness et al. 2009). Cactus flowers are easily accessible to ants, but by providing nectar in EFNs, cacti can limit ant visitation to flowers. For example, in the mutualism between ants and the senita cactus, flower visitation by four common ant species (*Camponotus ocreatus*, *Crematogaster depilis*, *Forelius mccooki*, and *Pheidole obtusospinosa*) decreased as the extrafloral nectar supply satiated and distracted them from floral resources, therefore limiting their interference with the obligate pollinating senita moth (Chamberlain and Holland 2008; see also “Plant–Pollinator Interactions (M-I)”).

At the community level, the mutualistic networks formed between Sonoran Desert EFN-bearing plants and ants have been

investigated in only one study in the Ironwood Forest National Monument, Arizona. These EFN-mediated mutualistic networks were found to be symmetric, meaning that ant species and EFN-bearing plant species exerted roughly equal effects on one another (as measured by their frequency of interaction; Chamberlain et al. 2010).

Plant–Microbe Interactions (M-IV)

Over the past decade, the notion of the microbe-free plant as the norm has been replaced with an understanding that virtually all plants host a wide variety of microbes (Partida-Martínez and Heil 2011). In addition, we now also know that the nature of nearly all plant–microbe interactions is highly dependent on environmental conditions, which can cause interactions to shift along a spectrum from antagonistic to mutualistic (Partida-Martínez and Heil 2011). While plant pathology continues to be an important field of study, most research is confined to agricultural settings. We limit our review of plant–microbe interactions to the mutualistic interactions that are more common in wild plants.

Beneficial microbes mediate the interactions between plants and the abiotic and biotic environment, enabling plants to survive in stressful environments (Rodríguez et al. 2004; Philippot et al. 2013). Association with beneficial microbes can increase drought and salinity tolerance, enhance disease resistance, and improve plant nutrition through increased nutrient and water uptake (Rodríguez et al. 2004, 2009; Mandyam and Jumpponen 2005; Rosenblueth and Martínez-Romero 2006; Yang et al. 2009; Pineda et al. 2010; Willis et al. 2013; fig. 3). In addition, these microbes can have significant indirect effects on plants by influencing aboveground plant–animal interactions (Wardle et al. 2004; Wolfe et al. 2005).

The interactions between plants and mycorrhizal fungi, rhizobial bacteria, and myriad other archaea, bacteria, and fungi take place in the rhizosphere, the zone of soil immediately surrounding plant roots (Philippot et al. 2013). In addition, an important group of symbionts known as endophytes spend at least a portion of their lives entirely within plant tissues (Partida-Martínez and Heil 2011). These microbes can be placed into four categories based on taxa and the location of the plant–microbe interface: (1) mycorrhizal fungi that live in symbiotic relationships with plant roots; (2) bacteria that live in symbiotic relationships with plant roots, inducing morphological structures called nodules; (3) other beneficial rhizosphere microbes, such as archaea, bacteria, and fungi, associated with plants; and (4) endophytic bacteria and fungi that live entirely within plant tissues for at least some part of their life cycle.

Arbuscular Mycorrhizal and Dark Septate Endophytic Fungi

Mycorrhizae are symbiotic associations of fungal mycelia with plant roots. Conventional mycorrhizal fungi include the arbuscular endomycorrhizal (AM) fungi, which have been found in upward of 80% of terrestrial plant species (Smith and Read 2010), and ectomycorrhizal fungi (EM), which are found in ca. 2% of species. The hyphae of AM fungi penetrate the cell walls of root cells, forming specialized structures known as arbuscules and vesicles, and extend into the soil, forming the mycelium; EM

fungi form a hyphal sheath surrounding plant roots and a hyphal net that extends into the intracellular spaces in plant roots (Smith and Read 2010). Dark septate endophytes (DSEs) are sterile root endophytes that form mutualistic associations functionally similar to mycorrhizae (Jumpponen 2001). They are rarely included in discussion of mycorrhizae because their morphology differs from conventional mycorrhizal morphology (Barrow and Aaltonen 2001; Jumpponen 2001).

AM fungi feature more prominently than EM fungi in arid ecosystems (Smith and Read 2010) and are abundant in the Sonoran Desert (Carrillo-Garcia et al. 1999; Bashan et al. 2007; Bills and Stutz 2009). While all AM fungal species contribute inorganic phosphorus to their hosts, they also perform a wide variety of other ecological functions that benefit plants, such as increased resistance to pathogens and herbivores and improved plant water balance (Philippot et al. 2013; Willis et al. 2013). These benefits can be significant and nearly always contribute to plant fitness (Willis et al. 2013). For example, association with AM fungi improved the water balance of *Bouteloua gracilis*, one of the dominant grasses in the arid Southwest, which allowed plants to increase carbon fixation by 40% over that in plants without such an association (Allen et al. 1981). In a study of the recolonization of highly disturbed sites in the Sonoran Desert, the first plant species (*Caesalpinia pinnosa*, *Jatropha cinerea*, *Jatropha cuneata*, and *Opuntia cholla*) to become established consistently showed high degrees of colonization by AM fungi, suggesting that association with AM fungi increases the chances of establishment in these stressful environments (Carrillo-Garcia et al. 1999).

DSEs can colonize roots simultaneously with AM fungi. Although DSEs have been the focus of little research, they appear to be abundant in stressed environments and may be nearly ubiquitous in the dominant plants in arid rangelands (Barrow and Aaltonen 2001; Mandyam and Jumpponen 2005). A growing number of studies from the Southwest, most from the Chihuahuan Desert, suggests that DSEs may be even more prevalent than AM fungi in arid ecosystems (Barrow et al. 1997b; Green et al. 2008; Herrera et al. 2010; Khidir et al. 2010; Porras-Alfaro et al. 2011). DSEs, rather than AM fungi, appear to be the primary fungal symbionts associated with fourwing saltbush (*Atriplex canescens*), a dominant shrub in the arid Southwest (Barrow et al. 1997a, 1997b). The fungi, which colonize the seedling immediately upon germination, were found to solubilize inorganic phosphorus and increase the phosphorus use efficiency of plants. To our knowledge, only one survey of DSEs has been undertaken in the Sonoran Desert, reporting a high degree of colonization in all 13 screened plant species, and is the first to record the presence of DSEs in the roots of many succulent species (Ontiveros-Valencia 2009).

Rhizobia-Legume Interactions

Limited availability of nitrogen represents a major challenge for plant survival. Plants have overcome this challenge through interactions with nitrogen-fixing microbes that provide them with nitrogen in exchange for photosynthetically fixed carbon compounds (Whitford 2002; Oldroyd and Downie 2008). In deserts, where soils are often nitrogen limited, biological nitrogen fixation represents the main source of nitrogen to the eco-

system (Waldon et al. 1989; Zahran 2001; Green et al. 2008). Although symbiotic nitrogen fixation in desert plants may occur by interaction with rhizobacteria, actinobacteria, and a variety of endophytic bacteria (Puente et al. 2004b; Lopez et al. 2011), here we focus on the interaction between rhizobia and leguminous plants, a symbiosis that has been the focus of much research in arid ecosystems (e.g., Hirsch et al. 2001; Long 2001; Whitford 2002; Oldroyd and Downie 2008; Sprent 2009).

Rhizobia are symbiotic nitrogen-fixing bacteria that induce the formation of and live within structures known as nodules on the roots of legumes, providing the plant with nitrogen in exchange for photosynthetically fixed carbon (Long 2001). The importance of the rhizobia-legume symbiosis in arid lands lies in the great impact that biological nitrogen fixation has on the nitrogen cycle (Zahran 1999). In the Sonoran Desert in California, estimates of natural ^{15}N suggest that 40%–70% of N inputs in mesquite woodlands results from symbiotic activity (Virginia et al. 1984, 1989). In particular, the mesquite-rhizobia mutualism is recognized as a source of soil fertility and represents a promising source of novel types of rhizobia for food crops in harsh environments (Jenkins 2003).

Four genera of rhizobia (*Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, and *Mesorhizobium*) have been isolated from the root nodules of wild legumes (Wang et al. 1999; Zahran 2001). A wide diversity of rhizobia have been found in arid regions (Perret et al. 2000; Zahran 2001), but to date, in the Sonoran Desert only a few legume species are known to host rhizobia. Among these are members of the genera *Lupinus*, *Dalea*, *Astragalus*, and *Lotus* (Shearer et al. 1983). It is likely that many additional taxa also form relationships with rhizobia. More comprehensive investigations have focused on widespread species, mainly *Prosopis glandulosa* (honey mesquite) and *Psoraleum spinosus* (smoke tree), that dominate desert washes and arroyos in the Sonoran Desert of California (Shoushtari and Pepper 1985; Jenkins et al. 1987, 1988). The composition of the rhizobial communities associated with these woody legumes varies with root depth (Jenkins et al. 1987, 1988). Physiological studies of these rhizobia suggest that differential growth rates, tolerance to salinity, high temperatures, and capacity to respire NO_3^- at phreatic depths are survival mechanisms that promote effective mesquite-rhizobia interactions and result in long-term productivity in desert soils (Shoushtari and Pepper 1985; Jenkins et al. 1987; Jenkins 2003). Studies of the smoke tree suggest that root stimulation by rhizobial populations is an important factor in the establishment of seedlings in N-limited desert arroyo systems (Jenkins et al. 1988). We still lack basic research on the impacts of rhizobia on plants in arid systems.

Other Beneficial Rhizosphere Microbes

Plant roots attract and feed the microbiota of the rhizosphere with sloughed-off root cells, mucilage, and other exudates, and in return the microbiota provide the plant with numerous benefits, such as increased supplies of limiting nutrients, reduced susceptibility to disease, and greater tolerance to abiotic stress (Pineda et al. 2010; Philippot et al. 2013). Little is known of the microbiota inhabiting the rhizosphere in arid ecosystems in terms of either taxonomic or functional diversity (Andrew et al. 2012). Recent findings suggest that the bacterial communities in both the rhizosphere and the bulk soil in the Sonoran Desert

are diverse and share a group of taxa representing a core microbial community characteristic of Sonoran Desert soils (Andrew et al. 2012). The common taxa across sites and habitats (rhizosphere and bulk soil) are dominated by members of the class Thermoprotei (Archaea, Crenarchaeota), suggesting that this class of organisms plays a significant but still unknown role in the microbial ecology of arid ecosystem soils.

Other work has focused on the bacterial communities of the rhizoplane, the zone of soil immediately adjacent to plant roots, including the root epidermis (Estermann and McLaren 1961). In the Sonoran Desert, rock-weathering and nitrogen-fixing rhizoplane bacteria may play an important role in the establishment and survival of several species of cacti (e.g., *Pachycereus pringlei*, *Stenocereus thurberi*, *Cylindropuntia cholla*) and the wild fig *Ficus palmeri* (Puente et al. 2004a). Furthermore, bacteria isolated from the rhizoplane of several native Sonoran Desert cactus species have been shown to fix nitrogen, dissolve phosphorus, and mobilize other essential minerals (Puente et al. 2004b). When used to inoculate sterile seeds of the cardon cactus (*P. pringlei*), these rhizobacteria enabled cactus seedlings to survive an extended period with no other source of nutrients (Puente et al. 2004b).

Fungal and Bacterial Endophytes

The term “endophyte” refers to any microbe that develops within living plant tissue (Partida-Martínez and Heil 2011). Until recently, these microbes had received little attention, but with advances in molecular techniques researchers are uncovering a tremendous diversity of both fungal and bacterial endophytes, which some studies suggest may contribute habitat-specific stress tolerance that enables plants to survive in environments where otherwise they could not (Rodríguez and Redman 2008). Here, we discuss mutualistic interactions between foliar endophytes and their plant hosts.

Mounting evidence suggests that nearly all plants host fungal endophytes (Rodríguez et al. 2009). Fungal endophytes confer many of the same benefits as mycorrhizal fungi (Rodríguez et al. 2009). The exploration of fungal endophytes in the Sonoran Desert has thus far been limited to studies of their taxonomic diversity and the factors that influence their distribution across plant species and habitats. A survey of fungal endophytes from a wide variety of cacti across six sites in the Sonoran Desert demonstrates a consistently high frequency of colonization (Suryanarayanan et al. 2005). The abundance of fungal endophytes in other types of vegetation appears to be more variable (Lau et al. 2013; Massimo et al. 2015). Most cacti appear to be dominated by a single fungal species (Suryanarayanan et al. 2005), while the diversity within nonsucculent, woody plants appears to be significantly higher (Lau et al. 2013; Massimo et al. 2015).

Bacterial endophytes are equally ubiquitous and can promote plant growth by means similar to those of other microbial plant symbionts (Rosenblueth and Martínez-Romero 2006). There have been a handful of studies of bacterial endophytes in the Sonoran Desert. Nitrogen-fixing bacteria have been isolated from the Sonoran Desert epiphyte *Tillandsia recurvata*, suggesting a symbiotic relationship (Puente and Bashan 1994). More conclusive studies of endophytic bacteria living in the roots of cardon (*P. pringlei*) have demonstrated that these bacteria promote seedling establishment on rocky substrate through weath-

ering of rock, mineralization of essential minerals in the substrate, and nitrogen fixation (Puente et al. 2009a, 2009b). Similarly, *Mammillaria fraileana*, which colonizes barren rock, is aided by rock-weathering bacteria, which mobilize inorganic nutrients in the rocky substrate (Lopez et al. 2011, 2012).

Perspectives and Future Research

This review reinforces our notion that most plant biotic interactions in the Sonoran Desert are poorly studied. We note a lack of studies of certain taxa, including plant-insect and plant-microbe interactions. We know surprisingly little about insect herbivory in the Sonoran Desert. In addition, although pollination has received more study than most interactions, bees have been the focus of relatively little research, despite their abundance, diversity, and importance as pollinators. In the case of plant-microbe interactions, new molecular tools offer tremendous opportunity to facilitate further research, resulting in renewed efforts to characterize the microbial populations associated with native plants. New approaches, such as the whole-community approach by multiple “omic” techniques, should be considered, as they have the potential to reveal the hidden diversity of microbial assemblages and their roles in ecosystem function (Morales and Holben 2011). Finally, while iconic Sonoran Desert species, such as the saguaro, have been the focus of much attention, we should begin to fill gaps in our current knowledge about less charismatic Sonoran Desert species, including rare endemics (e.g., Clark-Tapia et al. 2005).

The outcomes of species interactions with regard to plant fitness are of fundamental importance in plant ecology, evolution, and conservation. Certain interactions have been well documented from an evolutionary perspective (e.g., pollination of columnar cacti) and others from an ecological perspective (e.g., nurse plant–protégé interactions), but the link to plant fitness is a glaring gap in our understanding of plant biotic interactions. In part, this may be due to the difficulty of tracking the impact of interactions on the growth and reproduction of long-lived Sonoran Desert plants, but without this knowledge we have limited capacity to predict the outcome of changing interactions, lost partners, or specific management approaches.

Interactions are highly variable in time and space, and the outcomes of interactions are notoriously context dependent. Plant-animal and plant-microbe interactions in the Sonoran Desert have largely been studied in isolation, rather than in the context of the larger ecological community, and most of these studies took place at single locations and over short periods of time. With increasing human-driven environmental change, understanding of the factors that govern this context dependency has never been more important. Such an understanding requires studying interactions at broad temporal and spatial scales (e.g., Pierson et al. 2013). Long-term studies of interactions in permanent plots in the Sonoran Desert have often revealed unexpected changes in plant communities over time (e.g., Goldberg and Turner 1986; Angert et al. 2007; Butterfield et al. 2010). Large-scale initiatives involving citizen science, such as the Phenology Network (<https://www.usanpn.org/>), represent another possibility or source of data for long-term projects (e.g., Swann et al. 2011). Remote sensing offers tools for expanding the spatial scale and, in some cases, also the temporal scale of research (e.g., Olsson et al. 2012).

Furthermore, although we have presented these categories 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, forming a complex mosaic of interaction webs. This mosaic varies in space and time and shapes the very existence of individuals and communities.

Climate change is already influencing plant communities in the Sonoran Desert (Brusca et al. 2013). We need to uncover the thermal limits of individual desert organisms and how these limits may affect their interspecific interactions and the broader ecological community. The clearest documentation of temperature-sensitive interactions to date involves ants, organisms that play dominant ecological roles in the Sonoran Desert. Experiments at the Desert Laboratory in Tucson show that the most thermally tolerant ant associated with the ant-barrel cactus protective mutualism (see “Plant-Protective Agent Interactions (M-III)”) is also an exceptionally poor defender of this cactus (Ness et al. 2006; Fitzpatrick et al. 2014). This could be a major concern, because the dominant herbivore at the study site, a plant-sucking bug, has a thermal tolerance higher than that of any of the ants (Fitzpatrick et al. 2013). Thus, if barrel cacti were able to tolerate considerably warmer temperatures, they could well be confronted with this herbivore but have as their only defender a very poor mutualist.

Scenarios like this one are unlikely to be unique to ants and the plants they defend. For example, in other habitats, differential phenological responses to warming temperatures are leading to coflowering plant communities that differ from communities in the recent past (CaraDonna et al. 2014), a phenomenon that is likely affecting plant-pollinator mutualisms in unpredictable ways. There is every reason to think that such no-analog communities (Williams and Jackson 2007) lie in the Sonoran Desert’s future as well.

Finally, on the basis of our review of interactions in the Sonoran Desert, we observe that research has primarily focused on the use of plant traits by the interacting (mutualistic or antagonistic) animal consumer, whereas comparative morphological, anatomical, developmental, ontogenetic, and phenological

studies are scarce, as are studies that analyze the diversity of such traits in an evolutionary context, reconstructing their evolutionary history in a time-calibrated phylogenetic framework. Comparisons with traits in their relatives in nondesert habitats would allow us to investigate how such traits evolved to function in desert conditions and what evolutionary role they are playing in the diversification of lineages possessing these traits. These are fundamental questions that could motivate needed research about the natural history of interactions.

Concluding Remarks

We are just beginning to grasp the complexity of the web of species interactions in desert ecosystems. Interactions are an important means by which species meet the challenges of survival in extreme environments, such as the Sonoran Desert, but interactions, like species themselves, face numerous anthropogenic threats, such as habitat degradation and fragmentation and climate change. The region should prioritize the conservation of interactions, which will require knowledge of their diversity, ecology, evolution, and natural history. Documenting the impact of interactions on plant fitness and unraveling the context-dependent nature of these impacts should be priorities for future research. These types of data are needed to grapple with growing anthropogenic threats to both species and interactions (Marazzi et al. 2015) and to provide the scientific support to effectively protect and restore desert ecosystems.

Acknowledgments

We would like to thank the N-Gen Sonoran Desert Researchers Editorial Committee for motivating us to carry out this review and the Brown Foundation, of Houston, for their generous support. Thank you also to Kelsey Yule for providing us the photograph of desert mistletoes taken by Jonathan Knighton/Wisor, and Michele Lanan for her photograph of ants on EFNs of barrel cactus. Finally, special thanks go to the two anonymous reviewers for their highly constructive comments and suggestions.

Literature Cited

- Addicott JF 1986 Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. *Ecology* 70:486–494.
- Allen MF, WK Smith, TS Moore, M Christensen 1981 Comparative water relations and photosynthesis of mycorrhizal and nonmycorrhizal *Bouteloua gracilis* H.B.K. Lag ex Steud. *New Phytol* 88:683–693.
- Althoff DM, GP Svensson, O Pellmyr 2007 The influence of interaction type and feeding location on the phylogeographic structure of the yucca moth community associated with *Hesperoyucca whipplei*. *Mol Phylogenet Evol* 43:398–406.
- Andrew DR, RR Fitak, A Munguia-Vega, A Racolta, VG Martinson, K Dontsova 2012 Abiotic factors shape microbial diversity in Sonoran Desert soils. *Appl Environ Microbiol* 78:7527–7537.
- Angert AL, TE Huxman, GA Barron-Gafford, KL Gerst, DL Venable 2007 Linking growth strategies to long-term population dynamics in a guild of desert annuals. *J Ecol* 95:321–331.
- Anthony RG 1976 Influence of drought on diets and numbers of desert deer. *J Wildl Manag* 40:140–144.
- Armbrust DV, JD Bilbro 1997 Relating plant canopy characteristics to soil transport capacity by wind. *Agron J* 89:157–162.
- Aukema JE 2003 Vectors, viscin, and Viscaceae: mistletoes as parasites, mutualists, and resources. *Front Ecol Environ* 1:212–219.
- 2004 Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography* 27:137–144.
- Aukema JE, C Martínez del Rio 2002 Where does a fruit-eating bird deposit mistletoe seeds? seed deposition patterns and an experiment. *Ecology* 83:3489–3496.
- Austin AT, L Yahdjian, JM Stark, J Belnap, A Porporato, U Norton, DA Ravetta, SM Schaeffer 2004 Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235.
- Aylward FO, CR Currie, G Suen 2012 The evolutionary innovation of nutritional symbioses in leaf-cutter ants. *Insects* 3:41–61.
- Baker HG 1961 The adaptation of flowering plants to nocturnal and crepuscular pollinators. *Q Rev Biol* 36:64–73.
- Barrow JR, RE Aaltonen 2001 Evaluation of the internal colonization of *Atriplex canescens* (Pursh) Nutt. roots by dark septate fungi

- and the influence of host physiological activity. *Mycorrhiza* 11: 199–205.
- Barrow JR, KM Havstad, J Hubstenberger, BD McCaslin 1997a Seed-borne fungal endophytes on fourwing saltbush, *Atriplex canescens*. *Arid Soil Res Rehabil* 11:307–314.
- Barrow JR, KM Havstad, BD McCaslin 1997b Fungal root endophytes in fourwing saltbush, *Atriplex canescens*, on arid rangelands of southwestern USA. *Arid Soil Res Rehabil* 11:177–185.
- Bashan Y, T Khaosaad, BG Salazar, JA Ocampo, A Wiemken, F Oehl, H Vierheilig 2007 Mycorrhizal characterization of the boojum tree, *Fouquieria columnaris*, an endemic ancient tree from the Baja California Peninsula, Mexico. *Trees* 21:329–335.
- Bashan Y, BG Salazar, M Moreno, BR Lopez, RG Linderman 2012 Restoration of eroded soil in the Sonoran Desert with native leguminous trees using plant growth-promoting microorganisms and limited amounts of compost and water. *J Environ Manag* 102:26–36.
- Bentley BL 1977 Extrafloral nectaries and protection by pugnacious bodyguards. *Annu Rev Ecol Syst* 8:407–427.
- Bills RJ, JC Stutz 2009 AMF associated with indigenous and non-indigenous plants at urban and desert sites in Arizona. Pages 207–220 in C Azcón-Aguilar, JM Barea, S Gianinazzi, V Gianinazzi-Pearson, eds. *Mycorrhizas: functional processes and ecological impact*. Springer, Berlin.
- Blom PE, WH Clark 1980 Observations of ants (Hymenoptera: Formicidae) visiting extrafloral nectaries of the barrel cactus, *Ferocactus gracilis* Gates (Cactaceae), in Baja California, Mexico. *Southwest Nat* 25:181–195.
- Bronstein JL 1988 Mutualism, antagonism, and the fig-pollinator interaction. *Ecology* 69:1298–1302.
- 2009 The evolution of facilitation and mutualism. *J Ecol* 97: 1160–1170.
- 2015 The study of mutualism. Pages 3–19 in JL Bronstein, ed. *Mutualism*. Oxford University Press, New York.
- Bronstein JL, R Alarcón, M Geber 2006 Tansley review: the evolution of plant-insect mutualisms. *New Phytol* 172:412–428.
- Bronstein JL, I Izhaki, R Nathan, JJ Tewksbury, O Spiegel, A Lotan, O Altstein, AJ Dennis, E W Schupp, RJ Green 2007 Fleshy-fruited plants and frugivores in desert ecosystems. Pages 148–177 in AJ Dennis, EW Schupp, RA Green, DA Westcott, eds. *Seed dispersal: theory and its application in a changing world*. CAB International, Wallingford.
- Brown JH 1998 The desert granivory experiments at Portal. Pages 71–95 in WL Reseratis Jr, J Bernardo, eds. *Issues and perspectives in experimental ecology*. Oxford University Press, Oxford.
- Brown JH, DW Davidson 1977 Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196:880–882.
- Brown JH, GA Lieberman, WF Dengler 1972 Woodrats and cholla: dependence of a small mammal population on the density of cacti. *Ecology* 53:310–313.
- Brown KW, RM Lee, RP McQuivey 1976 Observations on the food habits of desert bighorn lambs. *Desert Bighorn Counc Trans* 20:40–41.
- Brusca RC, JF Wiens, WM Meyer, JA Eble, KA Franklin, J Overpeck, W Moore 2013 Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona mountain plant transect revisited. *Ecol Evol* 3:3307–3319.
- Bustamante E, A Casas, A Búrquez 2010 Geographic variation in reproductive success of *Stenocereus thurberi* (Cactaceae): effects of pollination timing and pollinator guild. *Am J Bot* 97:2020–2030.
- Butterfield BJ, JL Betancourt, RM Turner, JM Briggs 2010 Facilitation drives 65 years of vegetation change in the Sonoran Desert. *Ecology* 91:1132–1139.
- Cane JH, LH Kervin, R McKinley 2013 Sensitivity of systematic net sampling for detecting shifting patterns of incidence and abundance in a floral guild of bees at *Larrea tridentata*. *J Kans Entomol Soc* 86:171–180.
- CaraDonna PJ, AM Iler, DW Inouye 2014 Shifts in flowering phenology reshape a subalpine plant community. *Proc Natl Acad Sci USA* 111:4916–4921.
- Carlo TA, JJ Tewksbury 2014 Directness and tempo of avian seed dispersal increases emergence of wild chiltepins in desert grasslands. *J Ecol* 102:248–255.
- Carlson JE, ES Menges, PL Marks 2003 Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. *Fla Sci* 66: 147–154.
- Carrillo-García Á, Y Bashan, GJ Bethlenfalvay 2000 Resource-island soils and the survival of the giant cactus, cardon, of Baja California Sur. *Plant Soil* 218:207–214.
- Carrillo-García Á, JL León de la Luz, Y Bashan, GJ Bethlenfalvay 1999 Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. *Restor Ecol* 7:321–335.
- Chamberlain SA, JN Holland 2008 Density-mediated, context-dependent consumer-resource interactions between ants and extrafloral nectar plants. *Ecology* 89:1364–1374.
- 2009 Quantitative synthesis of context dependency in ant-plant protection mutualisms. *Ecology* 90:2384–2392.
- Chamberlain SA, JR Kilpatrick, JN Holland 2010 Do extrafloral nectar resources, species abundances, and body sizes contribute to the structure of ant-plant mutualistic networks? *Oecologia* 164:741–750.
- Chambers N, Y Gray, SL Buchmann 2004 Pollinators of the Sonoran Desert: a field guide. Arizona-Sonora Desert Museum, Tucson.
- Clark-Tapia R, MC Mandujano, T Valverde, A Mendoza, F Molina-Freaner 2005 How important is clonal recruitment for population maintenance in rare plant species?: the case of the narrow endemic cactus, *Stenocereus eruca*, in Baja California, México. *Biol Conserv* 124:123–132.
- Clark-Tapia R, F Molina-Freaner 2003 The genetic structure of a columnar cactus with a disjunct distribution: *Stenocereus gummosus* in the Sonoran Desert. *Heredity* 90:443–450.
- 2004 Reproductive ecology of the rare clonal cactus, *Stenocereus eruca*, in the Sonoran Desert. *Plant Syst Evol* 247:155–164.
- Combes C 2001 Parasitism: the ecology and evolution of intimate interactions. University of Chicago Press, Chicago.
- Connell JH 1971 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in PJ den Boer, G Gradwell, eds. *Dynamics of populations*. Pudoc, Wageningen.
- Crawley MJ 1989 Insect herbivores and plant population dynamics. *Annu Rev Entomol* 34:531–562.
- Davidson DW 1977 Species diversity and community organization in desert seed-eating ants. *Ecology* 58:712–724.
- Davidson DW, RS Inouye, JH Brown 1984 Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* 65:1780–1786.
- Davidson DW, D McKey 1993 Evolutionary ecology of symbiotic ant-plant relationships. *J Hymenoptera Res* 2:13–83.
- Dimmitt MA, PW Comus, LM Brewer, eds 2015 A natural history of the Sonoran Desert. 2nd ed. Arizona-Sonora Desert Museum Press, Tucson.
- Drezner TD 2014 The keystone saguaro (*Carnegiea gigantea*, Cactaceae): a review of its ecology, associations, reproduction, limits, and demographics. *Plant Ecol* 215:581–595.
- Duval BD, WG Whitford 2008 Resource regulation by a twig-girdling beetle has implications for desertification. *Ecol Entomol* 33:161–166.
- Estermann EF, AD McLaren 1961 Contribution of rhizoplane organisms to the total capacity of plants to utilize organic nutrients. *Plant Soil* 15:243–260.
- Faegri K, L van der Pijl 1979 The principles of pollination ecology. Pergamon, Oxford.
- Fay PA, RW Preszler, TG Whitham 1996 The functional resource of a gall-forming adelgid. *Oecologia* 105:199–204.

- Felger RS, MB Johnson, MF Wilson 2001 The trees of Sonora. Oxford University Press, New York.
- Fernandes GW, PW Price 1988 Biogeographical gradients in galling species richness. *Oecologia* 76:161–167.
- Fitzpatrick G, G Davidowitz, JL Bronstein 2013 An herbivore's thermal tolerance is higher than that of the ant defenders in a desert protection mutualism. *Sociobiology* 60:252–258.
- Fitzpatrick G, MC Lanan, JL Bronstein 2014 Thermal tolerance affects mutualist attendance in an ant-plant protection mutualism. *Oecologia* 176:129–138.
- Fleming TH, JW Kress 2011 A brief history of fruits and frugivores. *Acta Oecol* 37:521–530.
- Fleming TH, S Maurice, SL Buchmann, MD Tuttle 1994 Reproductive biology and relative male and female fitness in a trioecious cactus, *Pachycereus pringlei* (Cactaceae). *Am J Bot* 81:858–867.
- Fleming TH, CT Sahley, JN Holland, JD Nason, JL Hamrick 2001 Sonoran Desert columnar cacti and the evolution of generalized pollination systems. *Ecol Monogr* 71:511–530.
- Fleming TH, VJ Sosa 1994 Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *J Mammal* 75:845–851.
- Flores J, E Jurado 2003 Are nurse-protégé interactions more common among plants from arid environments? *J Veg Sci* 14:911–916.
- Franco AC, PS Nobel 1989 Effect of nurse plants on the microhabitat and growth of cacti. *J Ecol* 77:870–886.
- Futuyama DJ, AA Agrawal 2009 Evolutionary history and species interactions. *Proc Natl Acad Sci USA* 106:18043–18044.
- Gamboa GJ 1975 Foraging and leaf-cutting of the desert gardening ant *Acromyrmex versicolor versicolor* (Pergande) (Hymenoptera: Formicidae). *Oecologia* 20:103–110.
- Gates DJ, JD Nason 2012 Flowering asynchrony and mating system effects on reproductive assurance and mutualism persistence in fragmented fig-fig wasp populations. *Am J Bot* 99:757–768.
- Glazner JT, B Devlin, NC Ellstrand 1988 Biochemical and morphological evidence for host race evolution in desert mistletoe, *Phoradendron californicum* (Viscaceae). *Plant Syst Evol* 161:13–21.
- Goldberg DE, RM Turner 1986 Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* 67:695–712.
- Good-Avila SV, V Souza, BS Gaut, LE Eguiarte 2006 Timing and rate of speciation in *Agave* (Agavaceae). *Proc Natl Acad Sci USA* 103:9124–9129.
- Green L, A Porras-Alfaro, RL Sinsabaugh 2008 Translocation of nitrogen and carbon integrates biotic crusts and grass production in desert semiarid grassland. *J Ecol* 96:1076–1085.
- Gregory DP 1963 Hawkmoth pollination in the genus *Oenothera*. *Aliso* 5:357–384.
- 1964 Hawkmoth pollination in the genus *Oenothera*. *Aliso* 5:385–419.
- Halvorson JJ, H Bolton Jr, JL Smith, RE Rossi 1994 Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. *Great Basin Nat* 54:313–328.
- Hayes CL, WA Talbot, BO Wolf 2013 Woodrat herbivory influences saguaro (*Carnegiea gigantea*) reproductive output. *J Arid Environ* 89:110–115.
- Herrera CM 1996 Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. Pages 65–87 in DG Lloyd, SCH Barrett, eds. *Floral biology: studies on floral evolution in animal-pollinated plants*. Chapman & Hall, New York.
- Herrera CM, O Pellmyr 2002 Plant-animal interactions: an evolutionary approach. Blackwell Science, Oxford.
- Herrera J, HH Khidir, DM Eudy, A Porras-Alfaro, DO Natvig, RL Sinsabaugh 2010 Shifting fungal endophyte communities colonize *Bouteloua gracilis*: effect of host tissue and geographical distribution. *Mycologia* 102:1012–1026.
- Hirsch AM, MR Lum, JA Downie 2001 What makes the rhizobia-legume symbiosis so special? *Plant Physiol* 127:1484–1492.
- Holland JN, SA Chamberlain, KC Horn 2009 Optimal defence theory predicts investment in extrafloral nectar resources in an ant-plant mutualism. *J Ecol* 97:89–96.
- Holland JN, SA Chamberlain, TE Miller 2011 Consequences of ants and extrafloral nectar for a pollinating seed-consuming mutualism: ant satiation, floral distraction or plant defense? *Oikos* 120:381–388.
- Holland JN, TH Fleming 1999 Mutualistic interactions between *Upiga virescens* (Pyralidae), a pollinating seed-consumer, and *Lophocereus schottii* (Cactaceae). *Ecology* 80:2074–2084.
- Holland JN, F Molina-Freaner 2013 Hierarchical effects of rainfall, nurse plants, granivory and seed banks on cactus recruitment. *J Veg Sci* 24:1053–1061.
- Hölldobler B, EO Wilson 2010 The leafcutter ants: civilization by instinct. Norton, New York.
- Holt BS, WH Miller, BF Wakeling 1992 Composition and quality of mountain sheep diets in the Superstition Mountains, Arizona. *Desert Bighorn Counc Trans* 36:36–40.
- Howe HF 1986 Seed dispersal by fruit-eating birds and mammals. Pages 123–189 in DR Murray, ed. *Seed dispersal*. Academic Press, Sydney.
- Howe HF, MN Miriti 2004 When seed dispersal matters. *BioScience* 54:651–660.
- Howe HF, J Smallwood 1982 Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228.
- Inouye RS, GS Byers, JH Brown 1980 Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61:1344–1351.
- Irwin RE, JL Bronstein, JS Manson, L Richardson 2010 Nectar robbing: ecological and evolutionary perspectives. *Annu Rev Ecol Evol Syst* 41:271–292.
- Janzen DH 1967 Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *Kans Univ Sci Bull* 47:315–558.
- 1970 Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528.
- Jenkins MB 2003 Rhizobial and bradyrhizobial symbionts of mesquite from the Sonoran Desert: salt tolerance, facultative halophily and nitrate respiration. *Soil Biol Biochem* 35:1675–1682.
- Jenkins MB, RA Virginia, WM Jarrell 1987 Rhizobial ecology of the woody legume mesquite (*Prosopis glandulosa*) in the Sonoran Desert. *Appl Environ Microbiol* 53:36–40.
- 1988 Depth distribution and seasonal populations of mesquit-nodulating rhizobia in warm desert ecosystems. *Soil Sci Am J* 52:1644–1650.
- Jensen TS, OF Nielsen 1986 Rodents as seed dispersers in a heath-oak wood succession. *Oecologia* 70:214–221.
- Johnsgard PA 1983 The hummingbirds of North America. Smithsonian Institution Press, Washington, DC.
- Joy JB, BJ Crespi 2007 Adaptive radiation of gall-inducing insects within a single host species. *Evolution* 61:784–795.
- Jumpponen A 2001 Dark septate endophytes: are they mycorrhizal? *Mycorrhiza* 11:207–211.
- Karban R 1993 Costs and benefits of induced resistance and plant density for a native shrub, *Gossypium thurberi*. *Ecology* 74:9–19.
- Keeley JE, SC Keeley, CC Swift, J Lee 1984 Seed predation due to the yucca-moth symbiosis. *Am Midl Nat* 112:187–191.
- Khidir HH, DM Eudy, A Porras-Alfaro, J Herrera, DO Natvig, RL Sinsabaugh 2010 A general suite of fungal endophytes dominate the roots of two dominant grasses in a semiarid grassland. *J Arid Environ* 74:35–42.
- Kiester AR, R Lande, DW Schemske 1984 Models of coevolution and speciation in plants and their pollinators. *Am Nat* 124:220–243.

- Krausman PR, AJ Kuenzi, RC Etchberger, KR Rautenstrauch, LL Ordway, JJ Hervert 1997 Diets of desert mule deer. *J Range Manag* 50:513–522.
- Lanan MC, JL Bronstein 2013 An ant's-eye view of an ant-plant protection mutualism. *Oecologia* 172:779–790.
- Larson DL 1996 Seed dispersal by specialist versus generalist foragers: the plant's perspective. *Oikos* 76:113–120.
- Larson KC 1998 The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. *Oecologia* 115:161–166.
- Larson KC, TG Whitham 1991 Manipulation of food resources by a gall-forming aphid: the physiology of source-sink interactions. *Oecologia* 88:15–21.
- Lau MK, AE Arnold, NC Johnson 2013 Factors influencing communities of foliar fungal endophytes in riparian woody plants. *Fungal Ecol* 6:365–378.
- Leland AJ 2014 Effects of urbanization on seed dispersal and plant characteristics of the fishhook barrel cactus. MS thesis. University of Arizona, Tucson.
- Long SR 2001 Genes and signals in the *Rhizobium*-legume symbiosis. *Plant Physiol* 125:69–72.
- Lopez BR, Y Bashan, M Bacilio 2011 Endophytic bacteria of *Mammillaria fraileana*, an endemic rock-colonizing cactus of the southern Sonoran Desert. *Arch Microbiol* 193:527–541.
- Lopez BR, C Tinoco-Ojanguren, M Bacilio, A Mendoza, Y Bashan 2012 Endophytic bacteria of the rock-dwelling cactus *Mammillaria fraileana* affect plant growth and mobilization of elements from rocks. *Environ Exp Bot* 81:26–36.
- Ludka JT 2009 Protection and reliability: an examination of the quality and quantity of ant protection in the food-for-protection mutualism between *Ferocactus viridescens*, *Crematogaster californica* and the invasive *Linepithema humile*. MS thesis. University of California, San Diego, La Jolla.
- Ludka JT, KE Levan, and DA Holway 2015 Infiltration of a facultative ant-plant mutualism by the introduced Argentine ant: effects on mutualist diversity and mutualism benefits. *Ecol Entomol* 40:437–443.
- Mandyam K, A Jumpponen 2005 Seeking the elusive function of the root-colonising dark septate endophytic fungi. *Stud Mycol* 53:173–189.
- Mann J 1969 Cactus-feeding insects and mites. *US Natl Mus Bull* 256:1–158.
- Marazzi B, S Koptur, JL Bronstein 2013 The diversity, ecology, and evolution of extrafloral nectaries: current perspectives and future challenges. *Ann Bot* 111:1243–1250.
- Marazzi B, PN Sommers, BR López, JL Bronstein, E Bustamante Ortega, A Búrquez, RA Medellín, C Aslan, K Franklin 2015 Plant biotic interactions in the Sonoran Desert: conservation challenges and future directions. *J Southwest* 57:457–501.
- Marchosky RJ, TP Craig 2004 Gall size-dependent survival for *Asphondylia atriplicis* (Diptera: Cecidomyiidae) on *Atriplex canescens*. *Environ Entomol* 33:709–719.
- Mares MA, Rosenzweig ML 1978 Granivory in North and South American deserts: rodents, birds, and ants. *Ecology* 59:235–241.
- Maron JL, E Crone 2006 Herbivory: effects on plant abundance, distribution and population growth. *Proc R Soc B* 273:2575–2584.
- Massimo NC, MM Nandi Devan, KR Arendt, MH Wilch, JM Riddle, SH Furr, C Steen, JM U'Ren, DC Sandberg, AE Arnold 2015 Fungal endophytes in aboveground tissues of desert plants: infrequent in culture, but highly diverse and distinctive symbionts. *Microb Ecol* 70:61–76. doi:10.1007/s00248-014-0563-6.
- McAuliffe JR 1984 Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia* 64:319–321.
- 1986 Herbivore-limited establishment of a Sonoran Desert tree, *Cercidium microphyllum*. *Ecology* 67:276–280.
- 1990 Paloverdes, pocket mice, and bruchid beetles: interrelationships of seeds, dispersers, and seed predators. *Southwest Nat* 35:329–337.
- McCall AC, RE Irwin 2006 Florivory: the intersection of pollination and herbivory. *Ecol Lett* 9:1351–1365.
- McGregor EA 1916 *Buccalatrix thurberiella*, a pest of cotton in the Imperial Valley. *J Econ Entomol* 9:505–512.
- McGregor SE, SM Alcorn, G Olin 1962 Pollination and pollinating agents of the saguaro. *Ecology* 43:259–267.
- McIntosh ME 2002 Plant size, breeding system, and limits to reproductive success in two sister species of *Ferocactus* (Cactaceae). *Plant Ecol* 162:273–288.
- 2005 Pollination of two species of *Ferocactus*: interactions between cactus-specialist bees and their host plants. *Funct Ecol* 19:727–734.
- Medeiros AS, TD Drezner 2012 Vegetation, climate, and soil relationships across the Sonoran Desert. *Ecoscience* 19:148–160.
- Michener CD 1979 Biogeography of the bees. *Ann Mo Bot Gard* 66:277–347.
- Miller TEX, SV Louda, KA Rose, JO Eckberg 2009 Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. *Ecol Monogr* 79:155–172.
- Minckley R 2008 Faunal composition and species richness differences of bees (Hymenoptera: Apiformes) from two North American regions. *Apidologie* 39:176–188.
- Minckley RL, JS Ascher 2013 Preliminary survey of bee (Hymenoptera: Anthophila) richness in the northwestern Chihuahuan Desert. Pages 138–143 in G Gottfried J, PF Ffolliott, BS Gebow, LG Eskew, LC Collins, eds. Merging science and management in a rapidly changing world: biodiversity and management of the Madrean Archipelago III; May 1–5, 2012; Tucson, AZ. Proceedings. RMRSP-67. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Minckley RL, JH Cane, and L Kervin 2000 Origins and ecological consequences of pollen specialization among desert bees. *Proc R Soc B* 267:265–271.
- Minckley RL, TH Roulston 2006 Incidental mutualisms and pollen specialization among bees. Pages 69–98 in NM Waser, J Ollerton, eds. Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago.
- Mintzer A 1979 Foraging activity of the Mexican leaf-cutting ant *Atta mexicana* (F. Smith) in a Sonoran Desert habitat (Hymenoptera: Formicidae). *Insectes Soc* 26:364–372.
- Morales SE, WE Holben 2011 Linking bacterial identities and ecosystem processes: can “omic” analyses be more than the sum of their parts? *FEMS Microbiol Ecol* 75:2–16.
- Morrill AW 1927 Observations on *Buccalatrix gossypiella*, a new and important cotton pest. *J Econ Entomol* 20:536–544.
- Muscarella R, TH Fleming 2007 The role of frugivorous bats in tropical forest succession. *Biol Rev* 82:573–590.
- Musselman LJ 1980 The biology of *Striga*, *Orobancha*, and other root-parasitic weeds. *Annu Rev Phytopathol* 18:463–489.
- Nabhan G 1980 *Ammobroma sonora*, an endangered parasitic plant in extremely arid North America. *Desert Plants* 2:188–196.
- Nabhan GP, ed 2004 Conserving migratory pollinators and nectar corridors in western North America. University of Arizona Press, Tucson, Arizona.
- Naranjo ME, C Rengifo, PJ Soriano 2003 Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus* (Cactaceae). *J Trop Ecol* 19:19–25.
- Ness JH 2006 A mutualism's indirect costs: the most aggressive plant bodyguards also deter pollinators. *Oikos* 113:506–514.
- Ness JH, WF Morris, JL Bronstein 2006 Integrating quality and quantity of mutualistic service to contrast ant species visiting *Ferocactus wislizeni*, a plant with extrafloral nectaries. *Ecology* 87:912–921.
- 2009 For ant-protected plants, the best defense is a hungry offense. *Ecology* 90:2823–2831.
- Niering WA, RH Whittaker, CH Lowe 1963 The saguaro: a population in relation to environment. *Science* 142:15–23.

- Noy-Meir I 1973 Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–51.
- Oldroyd GE, JA Downie 2008 Coordinating nodule morphogenesis with rhizobial infection in legumes. *Annu Rev Plant Biol* 59:519–546.
- Ollerton J 1996 Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant-pollinator systems. *J Ecol* 84:767–769.
- Olsson AD, J Betancourt, MP McClaran, SE Marsh 2012 Sonoran Desert ecosystem transformation by a C₄ grass without the grass/fire cycle. *Divers Distrib* 18:10–21.
- Ontiveros-Valencia AV 2009 Arbuscular mycorrhizal and dark septate endophytic fungi in urban preserves and surrounding Sonoran Desert. MS thesis. Arizona State University, Phoenix.
- Partida-Martínez LP, M Heil 2011 The microbe-free plant: fact of artifact? *Front Plant Sci* 2:1–16.
- Pellmyr O 1999 A systematic revision of the yucca moths in the *Tegeticula yuccasella* complex north of Mexico. *Syst Entomol* 24:243–271.
- 2003 Yuccas, yucca moths, and coevolution: a review. *Ann Mo Bot Gard* 90:35–55.
- Perret X, C Staehelin, WJ Broughton 2000 Molecular basis of symbiotic promiscuity. *Microbiol Mol Biol Rev* 64:180–201.
- Philippot L, JM Raaijmakers, P Lemanceau, WH van der Putten 2013 Going back to the roots: the microbial ecology of the rhizosphere. *Nat Rev Microbiol* 11:789–799.
- Pickett CH, WD Clark 1979 The function of extrafloral nectaries in *Opuntia acanthocarpa* (Cactaceae). *Am J Bot* 66:618–625.
- Pierson EA, RM Turner, JL Betancourt 2013 Regional demographic trends from long-term studies of saguaro (*Carnegiea gigantea*) across the northern Sonoran Desert. *J Arid Environ* 88:57–69.
- Pineda A, SJ Zheng, JJA van Loon, CMJ Pieterse, M Dicke 2010 Helping plants to deal with insects: the role of beneficial soil-borne microbes. *Trends Plant Sci* 15:507–514.
- Porras-Alfaro A, J Herrera, DO Natvig, K Lipinski, RL Sinsabaugh 2011 Diversity and distribution patterns of soil fungal communities in a semiarid grassland. *Mycologia* 103:10–21.
- Price MV, JW Joyner 1997 What resources are available to desert granivores: seed rain or soil seed bank? *Ecology* 78:764–773.
- Price PW, KM Clancy, H Roininen 1994 Comparative population dynamics of the galling sawflies. Pages 1–11 in PW Price, WJ Mattson, YN Baranchikov, eds. *Ecology and evolution of gall-forming insects*. US Department of Agriculture, St. Paul, MN.
- Price PW, GW Fernandes, GL Waring 1987 Adaptive nature of insect galls. *Environ Entomol* 16:15–24.
- Puente ME, Y Bashan 1994 The desert epiphyte *Tillandsia recurvata* harbors the nitrogen-fixing bacterium *Pseudomonas stutzeri*. *Can J Bot* 72:406–408.
- Puente ME, Y Bashan, CY Li, VK Lebsky 2004a Microbial populations and activities in the rhizoplane of rock-weathering desert plants. I. Root colonization and weathering of igneous rocks. *Plant Biol* 6:629–642.
- Puente ME, CY Li, Y Bashan 2004b Microbial populations and activities in the rhizoplane of rock-weathering desert plants. II. Growth promotion of cactus seedling. *Plant Biol* 6:643–650.
- 2009a Endophytic bacteria in cacti seeds can improve the development of cactus seedlings. *Environ Exp Bot* 66:402–408.
- 2009b Rock-degrading endophytic bacteria in cacti. *Environ Exp Bot* 66:389–401.
- Purves DW, JW Lichstein, N Strigul, SW Pacala 2008 Predicting and understanding forest dynamics using a simple tractable model. *Proc Natl Acad Sci USA* 105:17018–17022.
- Raguso RA, MA Willis 2003 Hawkmoth pollination in Arizona's Sonoran Desert: behavioral responses to floral traits. Pages 43–65 in CL Boggs, WB Watt, PR Ehrlich, eds. *Evolution and ecology taking flight: butterflies as model systems*. University of Chicago Press, Chicago.
- 2005 Synergy between visual and olfactory cues in nectar feeding by wild hawkmoths, *Manduca sexta*. *Anim Behav* 69:407–418.
- Reichman OJ 1979 Desert granivore foraging and its impact on seed densities and distributions. *Ecology* 60:1086–1092.
- Richardson SC 2004a Are nectar-robbers mutualists or antagonists? *Oecologia* 139:246–254.
- 2004b Benefits and costs of floral visitors to *Chilopsis linearis*: pollen deposition and stigma closure. *Oikos* 107:363–375.
- Rico-Gray V, PS Oliveira 2007 The ecology and evolution of ant-plant interactions. University Chicago Press, Chicago.
- Riffell JA, R Alarcón, L Abrell 2008 Floral trait associations in hawkmoth-specialized and mixed pollination systems *Datura wrightii* and *Agave* spp. in the Sonoran Desert. *Commun Integr Biol* 1:6–8.
- Rodriguez R, R Redman 2008 More than 400 million years of evolution and some plants still can't make it on their own: plant stress tolerance via fungal symbiosis. *J Exp Bot* 59:1109–1114.
- Rodriguez RJ, RS Redman, JM Henson 2004 The role of fungal symbioses in the adaptation of plants to high stress environments. *Mitig Adapt Strateg Glob Change* 9:261–272.
- Rodriguez RJ, JF White Jr, AE Arnold, R Redman 2009 Fungal endophytes: diversity and ecological roles. *New Phytol* 182:314–330.
- Rojas-Aréchiga M, C Vázquez-Yanes 2000 Cactus seed germination: a review. *J Arid Environ* 44:85–104.
- Rosenbluth M, E Martínez-Romero 2006 Bacterial endophytes and their interactions with hosts. *Mol Plant-Microbe Interact* 19:827–837.
- Rudgers JA 2004 Enemies of herbivores can shape plant traits: selection in a facultative ant-plant mutualism. *Ecology* 85:192–205.
- Rudgers JA, MC Gardener 2004 Extrafloral nectar as a resource mediating multispecies interactions. *Ecology* 85:1495–1502.
- Rudgers JA, JG Hodgen, JW White III 2003 Behavioral mechanisms underlie an ant-plant mutualism. *Oecologia* 135:51–59.
- Ruffner GA, WD Clark 1986 Extrafloral nectar of *Ferocactus acanthodes* (Cactaceae): composition and its importance to ants. *Am J Bot* 73:185–189.
- Schoonhoven LM, JJA van Loon, M Dicke 2005 Insect-plant interactions. 2nd ed. Oxford University Press, New York.
- Scobell SA, PE Scott 2002 Visitors and floral traits of a hummingbird-adapted cactus (*Echinocereus coccineus*) show only minor variation along an elevational gradient. *Am Midl Nat* 147:1–15.
- Scott P 2008 Physiology and behavior of plants. Wiley, Chichester.
- Shearer G, DH Kohl, RA Virginia, BA Bryan, JL Skeeters, ET Nilsen, MR Sharifi, PW Rundel 1983 Estimates of N₂-fixation from variation in the natural abundance of ¹⁵N in Sonoran desert ecosystems. *Oecologia* 56:365–373.
- Sherbrooke WC 1976 Differential acceptance of toxic jojoba seed (*Simmondsia chinensis*) by four Sonoran Desert heteromyid rodents. *Ecology* 57:596–602.
- Shoushtari NH, IL Pepper 1985 Mesquite rhizobia isolated from the Sonoran Desert: physiology and effectiveness. *Soil Biol Biochem* 6:797–802.
- Shreve F 1910 The rate of establishment of the giant cactus. *Plant World* 13:235–240.
- 1931 Physical conditions in sun and shade. *Ecology* 12:96–104.
- Shreve F, IL Wiggins 1964 Vegetation and flora of the Sonoran Desert. Vol 1. Stanford University Press, Stanford, CA.
- Simmons NB, AL Wetterer 2002 Phylogeny and convergence in cactophilic bats. Pages 87–121 in TH Fleming and A Valiente-Banuet, eds. *Columnar cacti and their mutualists: evolution, ecology, and conservation*. University of Arizona Press, Tucson.
- Smith CM, JL Bronstein 1996 Site variation in reproductive synchrony in three Neotropical figs. *J Biogeogr* 23:477–486.
- Smith SE, DJ Read 2010 Mycorrhizal symbiosis. Academic Press, San Diego, CA.
- Sosa-Fernandez VD 1997 Dispersal and recruitment ecology of columnar cacti in the Sonoran Desert. PhD diss. University of Miami, Coral Gables, FL.

- Sprent J 2009 Legume nodulation: a global perspective. Wiley-Blackwell, Oxford.
- Stamp NE, and RD Ohmart 1978 Resource utilization by desert rodents in the lower Sonoran Desert. *Ecology* 59:700–707.
- Steenbergh WF, CH Lowe 1969 Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology* 50:823–834.
- 1977 Ecology of the saguaro II: reproduction, germination, establishment, growth, and survival of the young plant. Scientific Monograph 8. National Park Service, Washington, DC.
- Suryanarayanan TS, SK Wittlinger, SH Faeth 2005 Endophytic fungi associated with cacti in Arizona. *Mycol Res* 109:635–639.
- Suzán H, GP Nabhan, DT Patten 1994 Nurse plant and floral biology of a rare night-blooming cereus, *Peniocereus striatus* (Brandege) F. Buxbaum. *Conserv Biol* 8:461–470.
- 1996 The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. *J Veg Sci* 7:635–644.
- Suzán-Azpiri H, VJ Sosa 2006 Comparative performance of the giant cardon cactus (*Pachycereus pringlei*) seedlings under two leguminous nurse plant species. *J Arid Environ* 65:351–362.
- Swann DE, AC Springer, K O'Brien 2011 Using citizen science to study saguaros and climate change at Saguaro National Park. *Park Sci* 28:69–72.
- Thompson JN 2005 The geographic mosaic of coevolution. University of Chicago Press, Chicago.
- Traveset A, M Verdú 2002 A meta-analysis of gut treatment on seed germination. Pages 339–350 in DJ Levey, M Galetti, WR Silva, eds. Frugivores and seed dispersal: ecological, evolutionary and conservation issues. CAB International, Wallingford.
- Turner RM, SM Alcorn, G Olin, JA Booth 1966 The influence of shade, soil, and water on saguaro seedling establishment. *Bot Gaz* 127:95–102.
- Turner RM, JE Bowers, TL Burgess 1995 Sonoran Desert plants. University of Arizona Press, Tucson.
- 2005 Sonoran Desert plants: an ecological atlas. University of Arizona Press, Tucson.
- Valiente-Banuet A, F Molina-Freaner, A Torres, M del Coro Arizmendi, A Casas 2004 Geographic differentiation in the pollination system of the columnar cactus *Pachycereus pecten-aboriginum*. *Am J Bot* 91: 850–855.
- van Dam NM 2009 How plants cope with biotic interactions. *Plant Biol* 11:1–5.
- Virginia RA, LM Baird, JS LaFavre, WM Jarrell, BA Bryan, G Shearer 1984 Nitrogen fixation efficiency, natural ¹⁵N abundance and morphology of mesquite (*Prosopis glandulosa*) root nodules. *Plant Soil* 79:273–284.
- Virginia RA, WM Jarrell, PW Rundel, G Shearer, DH Kohl 1989 The use of variation in the natural abundance of ¹⁵N to assess symbiotic nitrogen fixation by woody plants. Pages 375–394 in RA Virginia, WM Jarrell, PW Rundel, G Shearer, DH Kohl, eds. Stable isotopes in ecological research. Springer, New York.
- Waldon HB, MB Jenkins, RA Virginia, EE Harding 1989 Characteristics of woodland rhizobial populations from surface- and deep-soil environments of the Sonoran Desert. *Appl Environ Microbiol* 55:3058–3064.
- Wang ET, MA Rogel, A García-de los Santos, J Martínez-Romero, MA Cevallos, E Martínez-Romero 1999 *Rhizobium etli* bv. *Mimosae*, a novel biovar isolated from *Mimosa affinis*. *Int J Syst Bacteriol* 49:1479–1491.
- Ward D 2009 The biology of deserts. Oxford University Press, New York.
- Wardle DA, RD Bardgett, JN Klironomos, H Setälä, WH van der Putten, DH Wall 2004 Ecological linkages between aboveground and belowground biota. *Science* 304:1629–1633.
- Waser NM 1979 Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). *Oecologia* 39:107–121.
- 1998 Pollination, angiosperm speciation, and the nature of species boundaries. *Oikos* 82:198–201.
- Waser NM, L Chittka, MW Price, NM Williams, J Ollerton 1996 Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060.
- Weis AE, A Kapelinski 1984 Manipulation of host plant development by the gall-midge *Rhabdophaga strobiloides*. *Ecol Entomol* 9:457–465.
- Wenny DG 2001 Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evol Ecol Res* 3:51–74.
- Wetterer JK, AG Himler, MM Yospin 2001 Foraging ecology of the desert leaf-cutting ant, *Acromyrmex versicolor* (Hymenoptera: Formicidae). *Sociobiology* 37:633–649.
- Whitford WG 2002 Ecology of desert systems. Academic Press, San Diego, CA.
- Williams JW, ST Jackson 2007 Novel climates, no-analog communities, and ecological surprises. *Front Ecol Environ* 5:475–482.
- Willis A, BF Rodrigues, PJ Harris 2013 The ecology of arbuscular mycorrhizal fungi. *Crit Rev Plant Sci* 32:1–20.
- Willmott AP, A Búrquez 1996 The pollination of *Merremia palmeri* (Convolvulaceae): can hawk moths be trusted? *Am J Bot* 83:1050–1056.
- Wolfe BE, BC Husband, JN Klironomos 2005 Effects of a below-ground mutualism on an aboveground mutualism. *Ecol Lett* 8:218–223.
- Yang J, JW Kloepper, CM Ryu 2009 Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci* 14:1–4.
- Zahrán HH 1999 Rhizobium-legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. *Microbiol Mol Biol Rev* 63:968–989.
- 2001 Rhizobia from wild legumes: diversity, taxonomy, ecology, nitrogen fixation and biotechnology. *J Biotechnol* 91:143–153.