

# The keystone saguaro (*Carnegiea gigantea*, Cactaceae): a review of its ecology, associations, reproduction, limits, and demographics

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Received: 17 November 2013 / Accepted: 25 March 2014 / Published online: 10 April 2014  
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**Abstract** This paper reviews the basics of a Sonoran Desert keystone cactus species, including the ecology of its establishment and high mortality, its association with nurse plants to provide ameliorated conditions for survival, and variability in longevity and reproduction over its range such as delayed reproduction in hotter and more arid populations where this delay is met with longer lifespans. The production of flowers, branches, and spines from areoles is reviewed, as well as current methods for estimating individual age despite great variability in growth rates, most notably linked to summer rainfall. Possible implications of anthropogenic influences that impact populations as well as global climate change are discussed as are implications for potential range shifts in the future. This paper also provides a table listing of over 100 birds, mammals, insects, reptiles, and other animal species that use *Carnegiea* and highlighting its keystone status.

**Keywords** Cactus · *Carnegiea gigantea* · Keystone species

The saguaro (*Carnegiea gigantea* (Engelm.) Britt. and Rose, Cactaceae) is a symbol and icon of the desert, as well as a keystone species, and considerable research has been focused on better understanding its ecology and biotic interactions. The aims of this review include (1) highlighting many of the known species interactions associated with *Carnegiea* including (1a) compiling a list of the services *Carnegiea* provides the ecosystem based on the published literature (which includes mutually beneficial associations such as pollination services) and (1b) its association with nurse plants and its dependence on such facilitative relationships. (2) Our current knowledge of *Carnegiea*'s ecology is reviewed including the importance of climate in shaping its populations, its geography, reproduction, and demographics, which rely on (3) new techniques that have been developed for age estimation, and (4) the species' future prospects are reviewed, particularly in light of global climate change and human impacts on its populations.

## A keystone species

The saguaro is a keystone species in the Sonoran Desert. Its importance for a wide variety of taxa is evident in the notably incomplete list of some of the species that use or rely on it (Table 1). This includes species mentioned in Steenbergh and Lowe (1977) who point out that the insect component of their list, for example, is “by no means complete” and that “a

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Communicated by Martin Nunez.

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**Table 1** Species known to (or likely to) utilize *Carnegiea gigantea* for food, shelter, and a variety of other purposes

Species	Common name	Reference	Use/association
Birds: Accipitriformes			
<i>Buteo jamaicensis</i>	Red-tailed hawk	Mader (1978)	N
<i>Cathartes aura</i>	Turkey vulture	Bennet and Kunzmann (1994)	R
<i>Parabuteo unicinctus</i>	Harris' Hawks	Dawson and Mannan (1991), Mader (1978)	R, M, N
Birds: Apodiformes			
<i>Calypte costae</i>	Costa's hummingbird	F96	Fl
Birds: Columbiformes			
<i>Zenaida asiatica</i>	White-winged doves	McGregor et al. (1962); S&L	Fl, Fr
<i>Zenaida macroura</i>	Mourning dove	WM03; S&L, F96	Fl, Fr
Birds: Falconiformes			
<i>Coragyps atratus</i>	Black vulture	Bennet and Kunzmann (1994)	R
<i>Falco sparverius</i>	American kestrels	Kerpez and Smith (1990b)	N
Birds: Galliformes			
<i>Callipepla gambelii</i>	Gambel's quail	WM03, S&L	Fr
Birds: Passeriformes			
<i>Amphispiza bilineata</i>	Black-throated sparrow	WM03	Fr
<i>Auriparus flaviceps</i>	Verdin	Sosa and Fleming (2002); WM03; F96	Fl, Fr
<i>Campylorhynchus brunneicapillus</i>	Cactus wren	S&L; WM03; Sosa and Fleming (2002)	Fr
<i>Cardinalis cardinalis</i>	Northern cardinal	WM03	Fr
<i>Carduelis psaltria</i>	Lesser goldfinches	WM03	Fr
<i>Carpodacus mexicanus</i>	House finch	F96	Fl
<i>Icterus parisorum</i>	Scott's oriole	WM03	Fr
<i>Molothrus ater</i>	Brown headed cowbirds	WM03	Fr
<i>Myiarchus cinerascens</i>	Ash-throated flycatcher	Sosa and Fleming (2002); WM03; Kerpez and Smith (1990b)	Fr, N
<i>Myiarchus tyrannulus</i>	Brown-crested flycatcher	WM03; Kerpez and Smith (1990b)	Fr, N
<i>Passerina versicolor</i>	Varied buntings	WM03	Fr
<i>Pipilo fuscus</i>	Brown towhee, canyon towhee	S&L; WM03	Fr
<i>Poliophtila melanura</i>	Black-tailed gnatcatcher	WM03	Fr
<i>Progne subis</i>	Purple martins	Kerpez and Smith (1990b)	N
<i>Psaltiriparus minimus</i>	Lloyd's bushtit	F96; Sosa and Fleming (2002)	Fl, Fr
<i>Toxostoma curvirostre</i>	Curve-billed thrasher	S&L; WM03; Sosa and Fleming (2002); F96	Fl, Fr, Sdlg
Birds: Piciformes			
<i>Colaptes auratus</i>	Northern flicker	F96; McAuliffe and Hendricks (1988), Kerpez and Smith (1990b)	Fl, N
<i>Colaptes chrysoides</i>	Gilded flicker	S&L; McAuliffe and Hendricks (1988); F96	Fl, Fr, Sdlg, N

**Table 1** continued

Species	Common name	Reference	Use/association
<i>Melanerpes uropygialis</i>	Gila woodpecker	McAuliffe and Hendricks (1988); S&L; WM03; F96	Fl, Fr, Sdlg, N
Birds: Strigiformes			
<i>Bubo virginianus</i>	Great horned owl	Baumgartner (1938), Mader (1978)	N
<i>Glaucidium brasilianum</i>	Ferruginous pygmy-owl	Flesch (2003)	R
<i>Micrathene whitneyi</i>	Elf owl	Goad and Mannan (1987); WM03; Kerpez and Smith (1990b)	Fr, N
<i>Otus kennicottii</i>	Western screech-owls	Kerpez and Smith (1990b)	N
Mammals: Chiroptera			
<i>Antrozous pallidus</i>	Pallid bat	F96; Fleming (2002)	Fl
<i>Choeronycteris mexicana</i>	Mexican long-tongued bat	Fleming (2002)	Fl
<i>Leptonycteris curasoae</i>	Southern long-nosed bat	Sosa and Fleming (2002); Fleming (2002)	Fl,Fr
<i>Leptonycteris nivalis</i>	Greater long-nosed bat	McGregor et al. (1962); S&L	Fl,Fr
<i>Leptonycteris yerbabuenae</i>	Lesser long-nosed bat	Simmons and Wetterer (2002)	Fl,Fr
Mammals: Lagomorpha			
<i>Lepus alleni</i>	Antelope jackrabbit	S&L	Sdlg, T
<i>Lepus californicus</i>	Black-tailed jackrabbit	Sosa and Fleming (2002); S&L	Fr, Sdlg, T
<i>Sylvilagus auduboni</i>	Desert cottontail	S&L	Sdlg
Mammals: Artiodactyla			
<i>Ovis canadensis</i>	Desert bighorn sheep	S&L	T
<i>Pecari tajacu</i>	Collared peccary	S&L	Fr
Mammals: Carnivora			
<i>Canis latrans</i>	Coyote	S&L; Sosa and Fleming (2002)	Fr
<i>Urocyon cinereoargenteus</i>	Gray fox	Sosa and Fleming (2002)	Fr
Mammals: Rodentia			
<i>Citellus harrisi</i>	Harris' antelope ground squirrel	S&L	Fr, Sdlg
<i>Citellus variegatus</i>	Rock squirrel	S&L	Sdlg
<i>Dipodomys deserti</i>	Desert kangaroo rat	S&L	Fr, Sdlg
<i>Dipodomys merriami</i>	Merriam kangaroo rat	S&L	Fr, Sdlg
<i>Dipodomys ordi</i>	Ord kangaroo rat	S&L	Fr, Sdlg
<i>Dipodomys spectabilis</i>	Bannertail kangaroo rat	S&L	Fr, Sdlg
<i>Eutamias dorsalis</i>	Desert cliff chipmunk	S&L	Sdlg
<i>Neotoma albigula</i>	White-throated woodrat	S&L	Fr, Sdlg, T
<i>Neotoma lepida</i>	Desert woodrat	S&L	Sdlg
<i>Neotoma phenax</i>	Sonoran woodrat	S&L	Sdlg
<i>Onychomys torridus</i>	Grasshopper mouse	Niering et al. (1963)	Sdlg
<i>Perognathus amplus</i>	Arizona pocket mouse	S&L	Fr, Sdlg
<i>Perognathus baileyi</i>	Bajada pocket mouse	S&L	Fr, Sdlg
<i>Perognathus goldmani</i>	Thornscrub pocket mouse	S&L	Fr, Sdlg
<i>Perognathus intermedius</i>	Rock pocket mouse	S&L	Fr, Sdlg

**Table 1** continued

Species	Common name	Reference	Use/association
<i>Perognathus longimembris</i>	Little pocket mouse	S&L	Fr, Sdlg
<i>Perognathus penicillatus</i>	Desert pocket mouse	S&L	Fr, Sdlg
<i>Perognathus pernix</i>	Sinaloa pocket mouse	S&L	Fr, Sdlg
<i>Peromyscus crinitus</i>	Canyon mouse	S&L	Sdlg
<i>Peromyscus eremicus</i>	Cactus mouse	S&L	Fr, Sdlg
<i>Peromyscus maniculatus</i>	Deer mouse	S&L	Sdlg
<i>Peromyscus merriami</i>	Riparian mouse	S&L	Sdlg
<i>Reithrodontomys burti</i>	Sonora harvest mouse	S&L	Sdlg
<i>Reithrodontomys fulvescens</i>	Fulvous harvest mouse	S&L	Sdlg
<i>Reithrodontomys megalotis</i>	Western harvest mouse	S&L	Sdlg
<i>Spermophilus tereticaudus</i>	Round-tailed ground squirrels	S&L	Fr, Sdlg
<b>Reptiles</b>			
<i>Dipsosaurus dorsalis</i>	Desert iguana	Sosa and Fleming (2002)	Fr
<i>Urosaurus ornatus</i>	Tree lizard	M'Closkey (1997)	R, O, “feeding”
Arachnids: Acarina	Mites, ticks	**Olson (2000)	D
<b>Arachnids: Araneae</b>			
<i>Loxosceles arizonica</i>	Arizona brown spider	Olson (2000)	D
Arachnids: Opiliones	Daddy long-legs	**Olson (2000)	D
Arachnids: Pseudoscorpiones	Pseudoscorpions	**Olson (2000)	D, M
<b>Arachnids: Scorpiones</b>			
<i>Centruroides exilicauda</i>	Bark scorpion	Olson (2000)	D
<i>Vejevois spinigeris</i>	Stripe-tailed scorpion	Olson (2000)	D
<b>Insects: Coleoptera</b>			
<i>Acrotichis</i> sp.	Beetle	Olson (2000)	D
<i>Agna capillata</i>	Beetle	Olson (2000)	D
<i>Aneflus protensu</i>	Beetle	S&L	Sdlg
<i>Belonuchus ephippiatus</i>	Beetle	Olson (2000)	D
<i>Cactophagus validus</i>	Weevil	S&L	T
<i>Cactopinus hubbardi</i>	Saguaro rhinoceros beetle	Olson (2000)	L
<i>Carcinops gilensis</i>	Beetle	Olson (2000)	D
<i>Carpophilus longiventris</i>	Saguaro sap beetle	Olson (2000)	Fl, L, O
<i>Dactylosternum cacti</i>	Beetle	Olson (2000)	D
<i>Gerstaeckeria turbida</i>	Weevil	Turner et al. (1966)	Sdlg
<i>Hololepta yucateca</i>	Cactus hister beetle	Olson (2000)	D
<i>Maseochara semivelutina</i>	Beetle	Olson (2000)	D
<i>Moneilema gigas</i>	Cactus longhorn beetle	Olson (2000)	Sdlg, L
<i>Nephanes</i> sp.	Beetles	Olson (2000)	D
<i>Tachyporus grossulus</i>	Beetle	Olson (2000)	D
<i>Trachyderes mandibularis</i>	Beetle	Goldsmith and Alcock (1993)	Fr, M
<b>Insects: Diptera</b>			
<i>Drosophila mettleri</i>	Fly	Meyer and Fogleman (1987)	D <sup>1</sup>
<i>Odontoloxozus longicornus</i>	Fly	Olson (2000)	D
<i>Volucella avida</i>	Fly	Olson (2000)	D

**Table 1** continued

Species	Common name	Reference	Use/association
Insects: Hymenoptera			
<i>Apis mellifera</i>	Honey bee	Olson (2000); F96	Fl, L
<i>Diadasia opuntiae</i>	Bee	Dimmitt (2000)	Fl
<i>Hemipepsis ustulata</i>	Tarantula hawk wasp	Alcock (2008)	R, M
<i>Lasius</i> sp.	Ants	S&L	Fr
<i>Leptothorax</i> sp.	Ants	S&L	Fr
<i>Pogonomyrmex barbatus</i>	Harvester ant	S&L	Fr
Insects: Isoptera			
<i>Gnathamitermes perplexus</i>	Desert encrusting termite	Olson (2000)	D,L
Insects: Lepidoptera			
<i>Cactobrosis fernaldialis</i>	Snout moth	S&L	Sdlg
<i>Feltia subterranea</i>	Cutworm	S&L	Sdlg
<i>Heliothis zea</i>	Corn earworm	S&L	Sdlg
<i>Hyles lineata</i>	White-lined sphinx	F96	Fl
<i>Orthodes alfkani</i>	moth	S&L	Sdlg
<i>Peridroma margaritosa</i>	Variegated cutworm	S&L	Sdlg
<i>Spodoptera exigua</i>	Beet armyworm	S&L	Sdlg
Insects: Orthoptera			
Gryllidae (2 spp.)	Crickets	S&L	Sdlg
<i>Heliasius</i> sp.		S&L	Sdlg
<i>Melanoplus</i> sp.	Grasshopper/locust	S&L	Sdlg
Nematoda			
<i>Diplogaster</i> sp.	Roundworm	Kiontke and Sudhaus (1996)	D

This is a partial list of species; the true number of species that benefit from *Carnegiea* is far larger. This partial list provides some of the scope of the diversity of organisms that use or rely on this keystone species. Many subspecies are also identified in sources, but listings here do not include multiple subspecies, varieties, etc. and are provided only to the species level. Steenbergh and Lowe (1977), Wolf and del Río (2003), and Fleming et al. (1996) are abbreviated S&L, WM03, and F96, respectively. \*\* Olson (2000) listed orders that include members who use *Carnegiea*, but did not list specific species. Abbreviations include Fl (use of flower components, i.e., pollen, nectar), Fr (use of fruit and/or seeds), Sdlg (consumption of seedlings or very small plants), T (consumption of tissue of established plants, e.g., adults), D (living inside of dead or rotting plant, using that material and/or proximal predators that consume these fauna), L [organisms identified as “insects of the living saguaro” by Olson (2000)], R (roosting or perching, often defensive against predators or territorial for mates), M (mate-seeking and/or mating), N (nesting), O (oviposition or egg laying)

*D*<sup>1</sup> Meyer and Fogleman (1987) note that *Drosophila mettleri* use substrate containing the juices from the decomposing *Carnegiea* for breeding, oviposition, and feeding

complete listing...would include additional families, and many times the number of species identified” (Steenbergh and Lowe 1977, p. 89). Many animals consume pollen, nectar, fruits, and seeds. *Carnegiea* flowers each secrete about 5 mL of nectar (McGregor et al. 1959), to which McGregor et al. (1962, p. 262) note that except for one study with similar values, they “are not aware of any other flower that approaches the saguaro in either nectar or pollen production.” Further, not only *Carnegiea* fruits are highly nutritious, but flowers and fruits are produced during the

hottest and driest time of year (the pre-monsoon period in late spring and early summer), making those resources even more valuable due to their timing (Wolf and del Río 2000).

In portions of their range, *Carnegiea* are the tallest entity in the community. They are heavily used for perching by a large number of species range wide to seek prey and avoid predation. Many species nest on the plant, such as at the base of branches, while others (e.g., Gila woodpeckers) excavate cavities within the stem and branches (Korol and Hutto 1984). After

abandonment, a large number of species that cannot themselves create such cavities compete for those nesting sites (Kerpez and Smith 1990a) that provide thermal protection and greater safety due to their height (Korol and Hutto 1984).

Despite the presence of oxalates (e.g., Schmidt-Nielsen 1964), some species, particularly when other food and water sources are scarce, will consume the flesh right off of a standing plant (e.g., Steenbergh and Lowe 1977). *Carnegiea* plants are also used for hiding, for shade, and even with death, a large community of arthropods and other life forms live within the humid plant as it decays (Olson 2000). Butterfield and Briggs (2009) found that soil fertility increases around a dead *Carnegiea*, though this was not the case for the other cacti they considered. In fact, *Carnegiea* even sequesters atmospheric carbon (Garvie 2003).

Finally, *Carnegiea* play an important role in many religions, ceremonies, cultures, and livelihoods of native peoples who have inhabited the region for thousands of years. The Papago (Tohono O'odham) and Pima nations, as well as their Hohokam ancestors have placed great cultural significance on the species, including the production of ceremonial wines from the fruits (Bruhn 1971; Booth 2005). The fruits were used for food, drink, and syrup; the ribs were used for making buildings, fences, splints, and arrows, and the callus tissue that forms around bird holes was used for cups and water containers. Many traditions, myths, and tales relate to this desert giant and it is a crime among the Papago people to cut one down (Bruhn 1971).

### Limits, range, and geological history

*Carnegiea gigantea* is one of over 50 columnar cactus species (Dávila-Aranda et al. 2002). Individual longevity varies from perhaps 150 years to, rarely, 250 or more years. *Carnegiea* are the largest cactus in the United States and among the largest in the world, as adults attain weights of as much as 6 tons and have dozens of branches (e.g., Berry et al. 1960) and typically reach heights of 8–12 m to as high as 16 m (Steenbergh and Lowe 1983). Its range limits to the north coincide with periods with regular freezing temperatures (Shreve 1911; Steenbergh and Lowe 1977; Turner et al. 1995). To the west, their range is

limited by inadequate summer rainfall, while to the south and east, their limits are less certain, but probably related to increased moisture associated with greater vegetation and competition (Turner et al. 1995).

Their greatest densities occur in places where summer rainfall is high (in the east), also coincident to higher densities of some of *Carnegiea*'s more effective nurses (Drezner 2006a, 2003a). An east to west gradient in elevation, temperature, and precipitation shapes dominant species distributions in the northern Sonoran Desert, which includes gradients in soil pH, calcium, and particle size (Medeiros and Drezner 2012).

The cactus family has a very poor fossil record, in part due to the poor preservation in the environments in which they are most commonly found (Van Devender 2002). Much of *Carnegiea*'s history in the Sonoran Desert is based on a limited fossil record, not dating back more than about 11,000 years reliably (Van Devender 2002). During the glacial periods of the Pleistocene, the northern Sonoran Desert was woodland. *Carnegiea* spent most of the last glaciation in small refugia, likely areas that had enough rainfall to support populations in southern and central Sonora, though packrat middens have not been located to confirm this hypothesis (Van Devender 2002). Around 11 ka, at the end of the last ice age, *Carnegiea* expanded into the current northern Sonoran Desert, and did so very rapidly, repeating what had likely occurred over the more than dozen interglacials during the Pleistocene (Van Devender 2002).

### The areoles: spines, flowers, fruits, and branches

Areoles, unique to the cactus family, are modified lateral buds (Anderson 2001). Spines are modified leaves growing from that bud (Rebman and Pinkava 2001). After establishment, plant growth occurs at the meristematic tissue at the stem apex, and growth, along with the production of new areoles and spines, occurs upward. While spines help protect *Carnegiea* from water-seeking desert animals (e.g., Stelfox and Vriend 1977; Steenbergh and Lowe 1983), this may not be their primary purpose or main advantage (Nobel and Loik 1999). Spines cast shade that can reduce the plant's surface temperature by several degrees (Lewis and Nobel 1977; Nobel 2002) and in areas with cooler

winters, spines can protect the plant from subfreezing temperatures on winter nights by trapping escaping longwave radiation (heat), thereby extending the range of some species to slightly cooler climates (Nobel 1980; Nobel and Bobich 2002; Lewis and Nobel 1977; Steenbergh and Lowe 1977).

As the plant gets older and taller, it begins producing flowers; these develop from young areoles up to a few years old near the top of the plant (Johnson 1924). The transition to adulthood, when a plant begins producing flowers and fruit, is variable over their range (Drezner 2008). In four sampled populations, reproduction began on average from 52 years of age (at a height of 2.44 m) in one population to 106 years of age (at a height of 3.28 m) at another (Drezner 2008). Because flowers and fruits form from new areoles, increasing reproductive output necessitates an increase in stem tips. Thus, *Carnegiea* begin to produce branches. A single branch essentially doubles fruit production, and further branching continues to increase seed production (Steenbergh and Lowe 1983; see also Schmidt and Buchmann 1986). Plants in drier microsites tend to produce fewer branches than those with greater access to water (Yeaton et al. 1980), thus utilizing extra water for increased reproduction.

In four sampled populations, the onset of branching ranged from 78 to 139 years of age on average, with faster growing populations starting to branch at a younger age (Drezner 2013a). By height, the fastest and slowest growing populations (also representing greatest and least annual rainfall) begin branching at similar heights (5.24 and 5.22 m, respectively), with the remaining two sites bracketing the range at 4.38 and 5.46 m (Drezner 2013a). This is likely the result of the interplay of winter and summer rain. Greater winter rain increases number of branches (Drezner 2003b), but greater summer rain drives up plant height, and so the two seasons of rainfall appear to counteract each other. As with spines and flowers, branches are also produced from areoles. Branches appear to emerge from areoles that have produced flowers in the past (Drezner 2013a).

A majority of columnar cacti are bat-pollinated. *Carnegiea* are the most northern of the columnar cacti and occurs where there is greater reliance on seasonal migrants (outside the main bat ranges), making bats less reliable for such services (Fleming et al. 2001). As a result, *Carnegiea* have shifted from the more ancestral reliance on bat pollination to a more

generalized pollination system that relies on a variety of taxa including birds and bees (Fleming et al. 2001) as shown in Table 1. Flowering occurs in May and June, with warmer locations beginning perhaps a few weeks earlier (Steenbergh and Lowe 1977). Flowers appear all over the stem apex, but are better developed on the east-facing side due to the higher temperatures there (Johnson 1924). Branches, however, are found disproportionately to the south of *Carnegiea* plants (Yeaton et al. 1980; Geller and Nobel 1986; Drezner 2003c), and are distributed on the plant to maximize receipt of photosynthetically active radiation (PAR) on branch surfaces and to minimize self-shading (Geller and Nobel 1986). Where plants are shaded, PAR interception is reduced (Franco and Nobel 1989). Branch direction shifts where shade is cast (Geller and Nobel 1986), and branches are more evenly distributed around shaded plants (Drezner 2003c). Although once thought to be related to summer or annual precipitation, Bowers (1996) observed that large November to March rain events influence flowering, despite the May–June flowering period, and Drezner (2003b) found that the number of branches in populations is similarly related to winter rainfall.

### The early years

Because of mammal, bird, and insect predation of seeds, it has been estimated that less than 0.1 % of seeds establish and survive (Steenbergh and Lowe 1977). *Carnegiea*'s small seeds are less able to tolerate drought than other cacti (Bowers and Pierson 2001). Use of the CAM (Crassulacean acid metabolism) photosynthetic pathway coupled with limited water storage capacity results in slow growth (Jordan and Nobel 1982). A seedling may only be 2–3 mm tall by 1 year of age (Steenbergh and Lowe 1983). Survival rates are low during the first years of life due to the extreme heat, periods without rainfall (Brum 1973; Steenbergh and Lowe 1977; Turner 1990), desiccation, ground surfaces of over 70 °C (Franco and Nobel 1988), winter subfreezing temperatures that result in fatal freezing, browsing animals that consume seedlings (Steenbergh and Lowe 1976; Niering et al. 1963), and wind-blown debris that can damage seedlings (Parker 1989), among others (Drezner 2004a). Adequate summer rains for germination and survival followed by adequate late spring rainfall for



the nearly year-old seedlings increases survivorship (Turner et al. 1966; Brum 1973; Turner 1990). Where rainfall is adequate and a population persists, summer temperature is a better predictor of survival than rainfall, likely due to decreased desiccation between rain events (Drezner 2004b). Plants become reliably established and mortality rates decrease in the absence of subsequent drought, severe freezes or other conditions in the few years that follow (Steenbergh and Lowe 1983). Freezing temperatures are the primary cause of premature saguaro mortality after the survivorship curve flattens and stabilizes (Steenbergh and Lowe 1983). Cold temperatures are a natural part of the climate regime of the northern Sonoran Desert (Steenbergh and Lowe 1983).

### Facilitation and nurse plants

To ameliorate the conditions outlined above, *Carnegiea* establish exclusively under the canopy of another plant (Turner et al. 1966), typically a perennial tree or shrub (Drezner 2004a) or less commonly a nurse rock which provides some benefits (Steenbergh and Lowe 1977; Bowers and Pierson 2001) also observed in other cacti (Sosa and Fleming 2002). Turner et al.'s (1966) classic study demonstrated that not one of 1,200 seedlings survived in the open, but 35 % of 1,200 seedlings that were shaded did. *Carnegiea* fruits ripen during the hot, pre-monsoon period when animals seek the fruits and consume and/or excrete them under cover of trees and shrubs (Bregmann 1988; Drezner 2004a), thus distributing seeds to suitable microsites just prior to the start of the summer rains. Although some species are predatory and destroy *Carnegiea* seeds, other species are efficient seed dispersers.

Although successfully nursed by a variety of species, *Carnegiea* are found less than expected under the open-canopied *Larrea tridentata* (Hutto et al. 1986; Parker 1989; Drezner 2006b) and more than expected under the dense-canopied *Ambrosia* spp. (Drezner 2006b), and in more marginal populations may prefer larger and more substantive nurses (Brum 1973). Microsite improvements are lessened in more open-canopied species making them less preferable (Drezner 2006b). The open-canopied *Larrea* is also allelopathic (Mahall and Callaway 1992) though evidence suggests that they may not be competitive

with *Carnegiea* (Yeaton et al. 1977). When *Carnegiea* do establish beneath *Larrea* canopies, their distribution is more tightly clustered around the base of the plant (Drezner 2006b). In colder areas, these cacti are found more to the nurse's warmer south side, while in warmer areas their distribution is not significantly biased (Drezner and Garrity 2003). The more southerly cactus *Coryphanta pallida* is distributed to the north and west of its nurse (Valiente-Banuet et al. 1991).

The elevated temperatures under the south side of a nurse's canopy may be due not only to solar direction, but also to the growth patterns of the nurse. The canopy of the common nurse *Parkinsonia microphylla* extends farther out to the south and west from the trunk (Drezner 2010), contributing to the higher numbers of *Carnegiea* under and the higher temperatures to the south sides of their nurses (Drezner and Garrity 2003; Drezner 2007). Nurse canopies can elevate nighttime winter ambient air temperatures by 4 °C or more (Drezner and Garrity 2003, Drezner 2007). Nurse plants may extend *Carnegiea*'s range into colder areas because of the temperature amelioration services they provide (Nobel 1980).

Because *Carnegiea* roots are laterally extensive (Cannon 1911), but shallow (20 cm or less), competition eventually ensues between *Carnegiea* and its nurse (McAuliffe 1984). This association begins as a commensal one, as the small cactus has little impact on the nurse plant. As it grows larger and its roots become more extensive, the *Carnegiea* protégé takes up an increasing fraction of the water that would have otherwise percolated down to the roots of the nurse (McAuliffe 1984). Where multiple cacti establish under the same nurse plant, this effect is amplified with the cacti taking up as much as half the rain water (McAuliffe and Janzen 1986), sometimes leading to the premature death of the nurse (McAuliffe 1984). This has been compared to predator–prey oscillatory cycles (Vandermeer 1980; McAuliffe 1984), where *Carnegiea* (predator) hastens the death of its nurse (prey), which reduces potential microsites for future generations of the cactus, thus lowering establishment of *Carnegiea* plants, which allows nurse populations to increase. Such dynamics have also been documented in other cacti (Flores-Martínez et al. 1994, 1998; Valiente-Banuet et al. 1991). However, for cacti, this process would operate at much longer time scales with intervening generations in between



(McAuliffe 1984), and protégé species can be successful under many different nurse species, complicating any such relationship (e.g., Drezner 2004a, 2006b).

Casual observation of *Carnegiea* in more arid sites hints at their greater presence in runnels (small channels of concentrated surface runoff). On closer inspection, however, much of this pattern is related to the increased presence of nurse species in runnels (Drezner 2013b). Surprisingly, *Carnegiea* are found disproportionately more on interfluves—a highly unexpected finding considering the aridity and marginality of that study site (Drezner 2013b). While only 20 % of the nurse trees were on interfluves, about half of the nursed cacti were on interfluves (Drezner 2013b). This is likely an example of seed-seedling conflicts (Schupp 1995) where one variable may favor success (or act upon the plant/seed) at one life stage, while another variable may be more beneficial in another stage of its life cycle. After rains, *Carnegiea* seeds may be transported and washed to unfavorable microsites, or destroyed or damaged in transport, while this may not be the case on interfluves, thus leading to their significant presence outside of runnels (Drezner 2013b).

### Age estimation and populations structure

With mortality near 100 % in many to most years (Niering et al. 1963; Steenbergh and Lowe 1983; Turner 1990; Pierson and Turner 1998), occasionally, a cohort may establish with adequate summer rainfall and relatively moderate winter temperatures and adequate spring rains. Some populations may only produce a cohort every 100 years, though other populations produce cohorts more frequently (e.g., Turner 1990; Drezner 2006c; Pierson et al. 2013). The regularity of cohorts and overall regeneration success in populations is highly dependent on the local climate conditions as these and other studies on individual populations have shown (Parker 1993; Pierson and Turner 1998; Drezner 2006c; Pierson et al. 2013).

Assessing the age of any individual is challenging as *Carnegiea* do not produce tree rings or other such features that can be dated with established methods, but they do grow upward from their apex. Age–height relationships have long been observed (Engelmann 1859). Long-term data have enabled age assessment in

a few locations (Turner 1990, Pierson and Turner 1998, Pierson et al. 2013). Shreve (1910), Hastings and Alcorn (1961), and Steenbergh and Lowe (1983) modeled age–height relationships for given locales. These relationships have subsequently been applied to other sites in the absence of local growth data (e.g., Brum 1973; Parker 1993). However, growth is highly variable. Steenbergh and Lowe (1983) reported that a 50-year-old plant is 90-cm tall at Organ Pipe Cactus National Monument, but 378-cm tall at Saguaro National Park’s Rincon Mountain District. Such variability raises questions about the applicability of such models across sites; Brum (1973) noted that there may have been error introduced into his results by doing so.

The pattern of growth is quite consistent in the species as at youth growth is naturally slow, increasing with plant size, until it begins to decline when branching commences and resources are redirected to reproduction (Steenbergh and Lowe 1983). Drezner (2003d) developed a general growth model to estimate age of individuals at any site. Individual heights are sampled in two different years and entered into the model. The growth rate that best fits the data to the growth model is calculated, yielding the population-specific multiplier (the *growth factor*), a unitless index value that represents the relative growth of that population. The fast growing population at the Rincon Mountain District of Saguaro National Park was arbitrarily set to a value of 1.0. Thus, a plant of a given height in a population with a growth factor of 0.50 grows half as much per year (e.g., 3 cm/year) at that height than a plant at Saguaro National Park (e.g., 6 cm/year at that height) (Drezner 2003d).

This model yields two inter-related tools. The first is the ability to estimate individual age in any population without a full census or long-term data. The second is the creation of an index value that can be used to compare growth across populations and/or growing conditions. Both have since been used. Growth in 10 populations showed a significant positive correlation between growth and July rainfall (Drezner 2005). Locally, growth slows in the shade in relatively mesic populations, while in hotter, drier populations shaded plants grow faster than those in full sun (Drezner, in review). Also, in xeric populations, growth is faster where greater surface water is available, but this relationship is not observed in a relatively mesic sites (Drezner, in review).

Studies have compared growth rates of a variety of species with that of *Carnegiea* (e.g., Bowers 2005; Pinto 2007; Halloy 2008), and population demographics have been assessed (e.g., Drezner 2006d; Danzer and Drezner 2010). Regional-scale trends across populations occur (i.e., the same years were favorable or unfavorable in all the sites) yet each site reflects its own environment, such as greater regeneration overall in wet and cool sites Drezner (2006c). Bowers (1997) linked the regeneration of *Ferocactus cylindraceus* with El Niño in northern Arizona, as Drezner and Balling (2002) did for *Carnegiea*. Subsequently, Drezner and Balling (2008) noticed that the dates of several cohort peaks correspond to known volcanic eruptions (such as Krakatau in 1883). Volcanic emissions drive changes in climate for the year to a few years following the eruption, such as cooler summers, elevated precipitation in the arid pre-monsoon period in spring and in winter, and milder winter temperatures (Drezner and Balling 2008). These changes would all benefit young *Carnegiea* by ameliorating climate in their favor during their earliest and most vulnerable year(s) of life. Drezner and Balling (2008) found that both at a marginal site and in a region-wide dataset, cohort establishment was significantly associated with eruptions, and this was later confirmed for two other populations on slopes (Donnermeyer and Drezner 2012). Interestingly, Adams et al. (2003) found that El Niño years were significantly associated with global volcanic eruptions.

Other approaches for assessing demography have been used, including linking climate records to height structure (Jordan and Nobel 1982), and the use of carbon and oxygen stable isotope ratios from spines (e.g., English et al. 2010). General change over time has been documented through repeat photography at the community level (Turner et al. 2003).

### The great necrosis scare and the role of freezing temperatures

Perhaps the greatest crisis associated with the species historically has been the bacterial necrosis scare. Many individuals were moribund and their diseased condition was blamed on *Erwinea carnegiana*, a bacterium. Despite earlier work that provided explanations for the observed blackening and so-called diseased conditions (e.g., Shreve 1911), many

research dollars were invested into studying the disease and strategies for curtailing its spread. Efforts included the removal of standing plants, with the accidental destruction of some healthy plants in the process (e.g., Lightle et al. 1942; Gill and Lightle 1942, 1946; Gill 1951; Steenbergh and Lowe 1983). The often cited study by Alcorn and May (1962) predicted the local extirpation of the saguaro in its namesake national park by the year 2000. Today, Saguaro National Park's western district alone is home to about 1.3 million *Carnegiea* plants (see Thornton 2008). The number of individuals in the wild, however, is a matter of speculation, and estimates fluctuate across three orders of magnitude, and have not been resolved, particularly including the Mexican portion of their range (Thornton 2008).

With a better understanding of the ecological processes at work, the disease hypothesis was eventually rejected. Severe freezes occur where Arctic air masses penetrate the northern Sonoran Desert, occurring several times a century (Turnage and Hinckley 1938). Because a *Carnegiea* plant may continue to stand erect and maintain its green coloring for a few years after a fatal freezing event (Steenbergh and Lowe 1977), the cause and effect were not always associated. *E. carnegiana* do not attack healthy plants; it is part of the natural decomposition process after the plant has already died, such as from a severe freeze (Steenbergh and Lowe 1977, 1983). In its northern populations, severe freezes are a natural part of the ecology of the species, as Steenbergh and Lowe (1983) have so emphatically argued to finally bring the necrosis scare to an end.

There were significant ecological ramifications of the bacterial necrosis scare including the collateral damage associated with the destruction of some healthy plants, and spraying the park with DDT was considered (to kill the moth vector of the so-called disease), though eventually rejected (McAuliffe 1996). There were also public and political ramifications. At one point, the Saguaro National Park was considered for closure by the National Park System, and was placed in lower priority for funding by the National Park System during the years that followed (Clemensen 1987; McAuliffe 1996). McAuliffe (1996) provides a good review and chronology of these events. Unfortunately, still today, there remains fear in parts of the general public that this species is in danger due to infection or disease.

## Climate change and the future

The long-term survival of populations can be difficult to assess with dramatic variations in cohort establishment found across populations (Pierson et al. 2013). Cold, northern populations compensate for lower individual density by producing more branches, and thus increasing their investment in seed production (Drezner 2006a). Eastern populations are highly dense and fast growing, but not as heavily branched (Drezner 2003b, 2004c). The onset of reproduction and of branching is much later in western; arid populations also characterized by slow growth (Drezner 2005, 2008, 2013a). Western populations exhibit both low individual density and low rates of branching (Drezner 2006a). Combined with delayed reproduction, these western populations appear disadvantaged. Recent work has shown, however, that slow growing populations in more arid areas live longer than their faster growing, taller counterparts farther east (Drezner 2014); and despite the delay (over multiple decades) in fruiting and reproduction, the number of years in which plants are reproductive is similar to that in faster growing easterly populations, though it is possible that slower growing populations exhibit reduced fitness (Drezner 2008).

The future of this keystone species is uncertain in the face of global climate change (e.g., see also Drezner and Lazarus 2008). Rehfeldt et al. (2006) considered a variety of temperature and precipitation variables with global warming and the impacts on communities and species in the western United States. *C. gigantea* was one of their focal species, and their results suggest that its range would shift northwestward by perhaps 500 km and move upslope perhaps 600 m relative to its current range. However, because they did not include more southern (Mexican) components in their study, they could not assess whether the species would experience an increase or decrease in its range size (Rehfeldt et al. 2006). However, these are broad generalizations, and the specifics of a new climate regime will provide unique conditions that may not be adequate for long-term population sustainability or germination (Thornton 2008). Caution should be used when evaluating such scenarios as biotic interactions are often ignored (Davis et al. 1998). Biotic interactions include pollinator quality and availability, seed dispersal services, the presence of competitors and the strength of the competitive interaction under new environmental

conditions, and interactions with herbivores. Species assemblages are crucial elements of ecosystems, and their splintering is sure to cause unpredictable consequences making any prediction difficult.

The role of increasing atmospheric carbon dioxide concentrations is also important but not always considered. *Carnegiea* are CAM photosynthesizers, and increasing atmospheric CO<sub>2</sub> concentrations would result in more efficient gas exchange and less water loss (Drennan and Nobel 2000; Nobel 1999). It is suggested that another CAM-photosynthesizing cactus, *Opuntia ficus-indica*, will likely extend its range substantially (Nobel 1988, Nobel and Israel 1994). As *Carnegiea*'s range is currently limited to the north by freezing temperatures (e.g., Shreve 1911; Steenbergh and Lowe 1977, 1983), northerly expansions are expected (e.g., Rehfeldt et al. 2006). This potential expansion combined with greater gas exchange efficiency that will reduce water loss including during drought (Drennan and Nobel 2000), gives hope for *C. gigantea*'s future; however, the species living within its new range may well be different from the ones in its current community (Rehfeldt et al. 2006), and species that currently utilize *Carnegiea* during their lives (e.g., Table 1) may exhibit range shifts that no longer place them with this species, while changes in available pollinators and seed dispersers may directly impact *Carnegiea* survival. In some cases, this alone may drive range contractions of potentially many other species currently living in and relying on this keystone cactus. Also, it is likely that other variables that may impact *Carnegiea* populations have not been isolated, and the saguaro's future range and numbers remain a matter of speculation.

In addition to global-scale changes in climate, more localized issues will also determine the future of this species. Thornton (2008) lists variables that threaten modern *Carnegiea* populations including cattle grazing, disturbances associated with the drug trade, urban development, cactus poaching, vandalism, and invasive species. Buffelgrass (*Pennisetum ciliare*) has become a problematic weed in the Sonoran Desert. Where present, it contributes to the presence of combustible ground cover and fire (Schiermeier 2005). *Carnegiea* mortality from fire can be very high (Rogers 1985), and where there is less ground cover, mortality is lower (Steenbergh and Lowe 1977). Even without fire, *Carnegiea* declines in the presence of *P. ciliare* (Olsson et al. 2012).

## Conclusions

Following the key works by Steenbergh and Lowe (1976, 1977, 1983, 1977, 1983) more than 30 years ago, many advancements have been made on *C. gigantea* ecology, including the complex dynamics of its association with nurse species and its demographic peaks and declines over space and time. That knowledge has been facilitated by new methods for establishing individual plant age with shifting environmental conditions, and better quantification of its relationships with its nurse plants.

Its role as keystone species has been alluded to (e.g., Steenbergh and Lowe 1977; Fleming 2002), and the current review of the literature yields a woefully incomplete listing of the extensive services *Carnegiea* provide to the fauna of the Sonoran Desert and to the ecosystem. Even a casual perusal of Table 1 shows the disjointed classifications among related species (e.g., depending on the source, some species may be listed as receiving one benefit or service, while the other species is only documented with another). This results from the gaps in the published literature, shedding light on how much we still have to learn about the role of this keystone species in the Sonoran Desert and the community-wide interactions that are tied to it.

Another uncertainty that merits further investigation is the future of this species in the face of changing climate. History (i.e., the bacterial necrosis scare) has shown us that poor assumptions and science can be highly detrimental to the long-term understanding and management of this (and other) species. Our data for future population and range shifts are limited and often speculative. We look to climate envelopes for direction, but we need to be cautious as other variables, such as biotic interactions, may not be included in such models (Davis et al. 1998). Thus, with limited knowledge about how species assemblages may change in future climate scenarios that are themselves not fully resolved, more questions remain than are answered about the future of this species, and ultimately, of the Sonoran Desert ecosystem.

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