

Opuntia drummondii

Dune Prickly-pear

Cactaceae



Opuntia drummondii by J. S. Dodds, 2023

***Opuntia drummondii* Rare Plant Profile**

New Jersey Department of Environmental Protection
State Parks, Forests & Historic Sites
Forests & Natural Lands
Office of Natural Lands Management
New Jersey Natural Heritage Program

501 E. State St.
PO Box 420
Trenton, NJ 08625-0420

Prepared by:
Jill S. Dodds
jsdodds@biostarassociates.com

April, 2025

For:
New Jersey Department of Environmental Protection
Office of Natural Lands Management
New Jersey Natural Heritage Program
natlands@dep.nj.gov

This report should be cited as follows: Dodds, Jill S. 2025. *Opuntia drummondii* Rare Plant Profile. New Jersey Department of Environmental Protection, State Parks, Forests & Historic Sites, Forests & Natural Lands, Office of Natural Lands Management, New Jersey Natural Heritage Program, Trenton, NJ. 19 pp.

Life History

Opuntia drummondii (Dune Prickly-pear) is also known as *O. pusilla* (see Synonyms section). It is one of four cacti native to New Jersey—all four are members of the *Opuntia humifusa* complex (Majure et al. 2017, Köhler et al. 2023). *Opuntia* stems are segmented, with individual segments referred to as cladodes, pads, or joints. Diagonal rows of areoles (small, roundish depressions) are present on each segment. The green stems are the primary photosynthetic organs because the small, cone-shaped leaves are ephemeral, being present only on first-year cladodes. Short barbed hairs (glochids) develop along the edges of the areoles: They are easily dislodged and upon contact they can become embedded in skin, causing irritation. Prominent spines are also produced in some species (Rebman and Pinkava 2001, Pinkava 2020).

All of New Jersey's prickly-pears have a low, sprawling growth form. The other three species (*Opuntia cespitosa*, *O. humifusa*, and *O. mesacantha* ssp. *mesacantha*) have flattened cladodes but those of *O. drummondii* may be flat or cylindrical. *O. drummondii* can be distinguished by its terminal stem joints, which are easily detached. Its segments are also small and narrow relative to those of other species, rarely exceeding 5 cm in length and 2.5 cm in width, although some can be up to 11.1 cm long and 3.4 cm wide. *O. drummondii* may produce 0–4 spines per areole but 1–2 are typical. Some of the species' morphological characteristics (e.g. presence of tuberous roots, proportion of cylindrical joints, abundance of spines) can differ considerably depending on habitat conditions. The inner tepals of *O. drummondii* flowers are bright yellow and 22–32 cm long and the outer tepals are green or yellow-green. Each flower has numerous stamens and a single style with a variable number of lobes. The fruits are fleshy, barrel or club-shaped, and reddish-purple at maturity; they have areoles but no spines. (See Graham 1846, Britton 1911, Coker 1918, Benson 1982, Kraus 1988, Majure 2007a, Majure and Ervin 2008, Holmes 2016, Majure et al. 2017, Pinkava 2020).



S. Maund, 1846.



J. S. Dodds, 2023.

Opuntia drummondii reproduces clonally. The ready disarticulation of the terminal cladodes facilitates vegetative dispersal, and when the joints land in favorable locations they can produce roots and develop into new plants (Majure 2007a, Majure et al. 2017). Small (1917, 1918a,

1920) observed that flowering was rare in some populations but frequent in others. In the southeastern states, *O. drummondii* may flower from April through June (Faucette 2016, Majure et al. 2017, Pinkava 2020, Weakley et al. 2024). Britton (1911) noted that cultivated plants at the New York Botanical Garden were blooming on May 12–13 but New Jersey plants have been observed in flower during June and July (iNaturalist 2025). The fruits usually mature between August and October (Kraus 1988, Faucette 2016, Weakley et al. 2024), although in some cases fruiting continues into the winter months (Majure et al. 2017). In one New Jersey population a few of the previous year's fruits could still be found during mid-May, including some that were releasing seeds and some that were still intact (pers. obs.). During the winter, stem segments may become reddish or cross-wrinkled (Majure 2007a) and a similar condition can result from stress.



Bradley Smith, 2023.



J. S. Dodds, 2023.

Opuntia drummondii is known from diploid, triploid, and tetraploid populations which are virtually indistinguishable. Polyploid populations are usually found in coastal areas or in the mountains, and may be associated with harsher conditions. Diploid populations are more widely distributed and sometime occur in close proximity to polyploid populations (Majure 2012, Majure et al. 2012a & 2017, Majure and Puente 2014). Hybridization is common in *Opuntia* and some likely hybrids involving *O. drummondii* have been reported (Benson 1982, Krauss 1988, Majure et al. 2017, Pinkava 2020).

Pollinator Dynamics

The majority of *Opuntia* species, including all of those in the *Humifusa* complex, are pollinated by insects and primarily by bees (DeFelice 2004, Mandujano et al. 2010, Majure et al. 2012b). Two bee species that exclusively visit *Opuntia* flowers are *Melissodes mitchelli* and *Lithurgopsis gibbosa* (Fowler and Droege 2020), although both of the specialists appear to be rare and limited to the southern states (BugGuide 2025, NatureServe 2025). Long-tongued and short-tongued bees have been reported as pollinators of other prickly-pears, including species of *Agapostemon*, *Apis*, *Ashmeadiella*, *Augochlorella*, *Bombus*, *Ceratina*, *Colletes*, *Diadasia*, *Dialictus*, *Halictus*, *Lasioglossum*, *Lithurge*, *Megachile*, *Melissodes*, *Perdita*, and *Xylocopa*. Medium to large bees appear to be the most effective pollinators (Grant et al. 1979, Osborn et al. 1988, McFarland et al. 1989, Stubbs et al. 1992, Hilty 2020). An assortment of beetles are also found on *Opuntia*

flowers but they are thought to play a negligible role in cross-fertilization (McFarland et al. 1989, Hilty 2020).

Many species of *Opuntia* are self-compatible, or partially so, but some are not (Osborn et al. 1988, McFarland et al. 1989, Mandujano et al. 2010). Although no specific studies were found for *O. drummondii*, the species' apparent capacity for hybridization may be indicative of some level of self-compatibility (Martínez-Ramos et al. 2024).

Seed Dispersal and Establishment

The grayish or tan seeds of *Opuntia drummondii* are rounded and flat, approximately 4–6 mm in diameter, and 1.5 mm thick (Benson 1982, Pinkava 2020). Graham (1846) noted that *O. drummondii* had numerous ovules but Small (1918a) described the fruits as few-seeded. Counts of seeds per fruit in other *Opuntia* spp. ranged from dozens to several hundred (López-Palacios et al. 2015, 2019). Small (1918a) observed that ripe *O. drummondii* fruits often fell from the stems but were then held in place by the surrounding stems and their spines.

Opuntia fruits are consumed by a wide variety of vertebrates including mammals, birds, and reptiles (Small 1920, DeFelice 2004, Waldstein 2010). Seeds that pass through mammalian digestive tracts remain viable (Riegel 1941, Spencer and Spencer 1941) and can have greater germinability (Potter et al. 1984). Rodents are more likely to be seed predators than dispersers, although Riegel (1941) observed that some seeds which had been buried by squirrels subsequently sprouted. Harvester ants sometimes carry *Opuntia drummondii* seeds to their nests (MacGown et al. 2008). The ants generally consume the seeds but some may be dispersed by accidental losses during transport (DeFelice 2004).

Prickly-pear seeds are generally slow to sprout, and their structure suggests that they may remain viable in the soil for long periods. Typical germination requirements for *Opuntia* species are likely to include warm temperatures and sufficient soil moisture (Potter et al. 1984). Literature reviews have indicated that many *Opuntia* spp. form mycorrhizae, at least under some circumstances (Whitcomb 2000, Wang and Qiu 2006), but it is not clear whether fungal associations play a role in seedling establishment.

The primary means of dispersal in *Opuntia drummondii* appears to be vegetative. As previously noted, the terminal joints are easily detached and can root readily. Cladodes that remain where they fall contribute to the expansion of established colonies (Majure and Ervin 2008). In some cases they may be moved to different locations by wind (Small 1920). Tiny backward-pointing barbs on the tips of *O. drummondii* spines frequently cause the cladodes to cling to the fur of passing animals or to human clothing and thus be carried to new sites (Small 1917, Rebman and Pinkava 2001, DeFelice 2004, Majure 2007a, Majure and Ervin 2008, Ward 2009). *Opuntia* cladodes can also remain afloat for long periods and still produce roots (DeFelice 2004). *O. drummondii* is known to spread vegetatively along watercourses (Majure et al. 2017), and flooding events or coastal storms are likely aid in the establishment of new populations (Majure 2007a, Majure and Ervin 2008, Majure et al. 2007).

Habitat

Opuntia drummondii may be found at elevations of 0–100 meters above sea level. It is most frequently associated with barrier islands, beaches, and dunes along the Atlantic and Gulf coasts but some occurrences extend much farther inland (Coker 1918, Hunt 1947, Richmond 1962, Benson 1982, Stalter and Lamont 1997 & 2015, Majure 2007a, Ward 2009, Pinkava 2020). Coastal habitats include beaches, dunes, swales, sand flats, shrub thickets, hammocks, clam shell middens, and salt marsh edges (Miller and Jones 1967, Anderson and Alexander 1985, Kraus 1988, Easley and Judd 1993, Stalter et al. 2018). Although *O. drummondii* has been reported on foredunes—where the plants may be subject to stresses from sand deposition, salt spray, and overwash (Blonder et al. 2018)—it is more commonly situated in stable substrate behind the primary dunes (Holmes 2016, Majure et al. 2017, Sorrie 2021). In New Jersey, *O. drummondii* has been found on oceanside and bayside dunes where its typical associates include scattered shrubs (*Prunus maritima*, *P. serotina*, *Myrica pensylvanica*), vines (*Toxicodendron radicans*, *Smilax rotundifolia*), and herbs (*Solidago sempervirens*, *Achillea millefolium*) (NJNHP 2024). When the species occurs further inland it is most likely to grow in well-drained, sandy soils along forest edges or riversides (Moldenke 1944, Benson 1982, Majure and Ervin 2008, Holmes and Amor 2010). However, it has occasionally been documented on rock outcrops, where it nearly always co-occurs with *O. mesacantha* ssp. *mesacantha* (Majure et al. 2017).

Opuntia drummondii occasionally colonizes anthropogenic habitats or disturbed areas such as roadsides, old fields, or cemeteries (Easley and Judd 1993, Holmes and Amor 2010, Faucette 2016, Philley 2019). Goldberg and Rillstone (2012) found that it was equally likely to be present on natural islands and those constructed from dredge spoils. *O. drummondii* has also been identified as a species that is potentially suitable for use in green roof designs (Buesching 2001, Henderson 2003).

Opuntia drummondii is most likely to thrive when growing in full sun (Weakley et al. 2024). When it occurs in scrub-shrub or hammock communities the plants are usually situated in gaps or clearings (Whitaker et al. 2004, Majure 2007b). Like many other species that grow in arid environments, *O. drummondii* is a CAM (Crassulacean Acid Metabolism) plant, so it can conserve water by keeping its stomata closed during the day and fixing carbon at night (Rebman and Pinkava 2001, Holmes 2016). Majure (2007a) found that *O. drummondii* plants in full sun developed nearly twice as many spines as shaded plants. Cactus spines generally aid in thermoregulation by reflecting or absorbing excess heat and in water collection by providing condensation sites for fog or dew (Aliscioni et al. 2021). When growing in shaded conditions, *O. drummondii* plants produce increasingly smaller cladodes but the process can be reversed by removal of the canopy (Majure 2007b, Majure and Ervin 2008).

Wetland Indicator Status

Opuntia drummondii is not included on the National Wetlands Plant List (NWPL). Any species not on the NWPL is considered to be Upland (UPL) in all regions where it occurs. The UPL designation means that it almost never occurs in wetlands (U. S. Army Corps of Engineers 2022).

USDA Plants Code (USDA, NRCS 2025)

The USDA code for *Opuntia drummondii* is OPDR. The USDA NRCS currently lists the species as *O. pusilla* (OPPU2).

Coefficient of Conservancy (Walz et al. 2020)

CoC = 6. Criteria for a value of 6 to 8: Native with a narrow range of ecological tolerances and typically associated with a stable community (Faber-Langendoen 2018).

Distribution and Range

The global range of *Opuntia drummondii* is restricted to the southeastern coast of the United States (POWO 2025). The map in Figure 1 depicts the historical extent of the species in North America. To date, it has only been found in one New Jersey County: Cape May County (Figure 2).

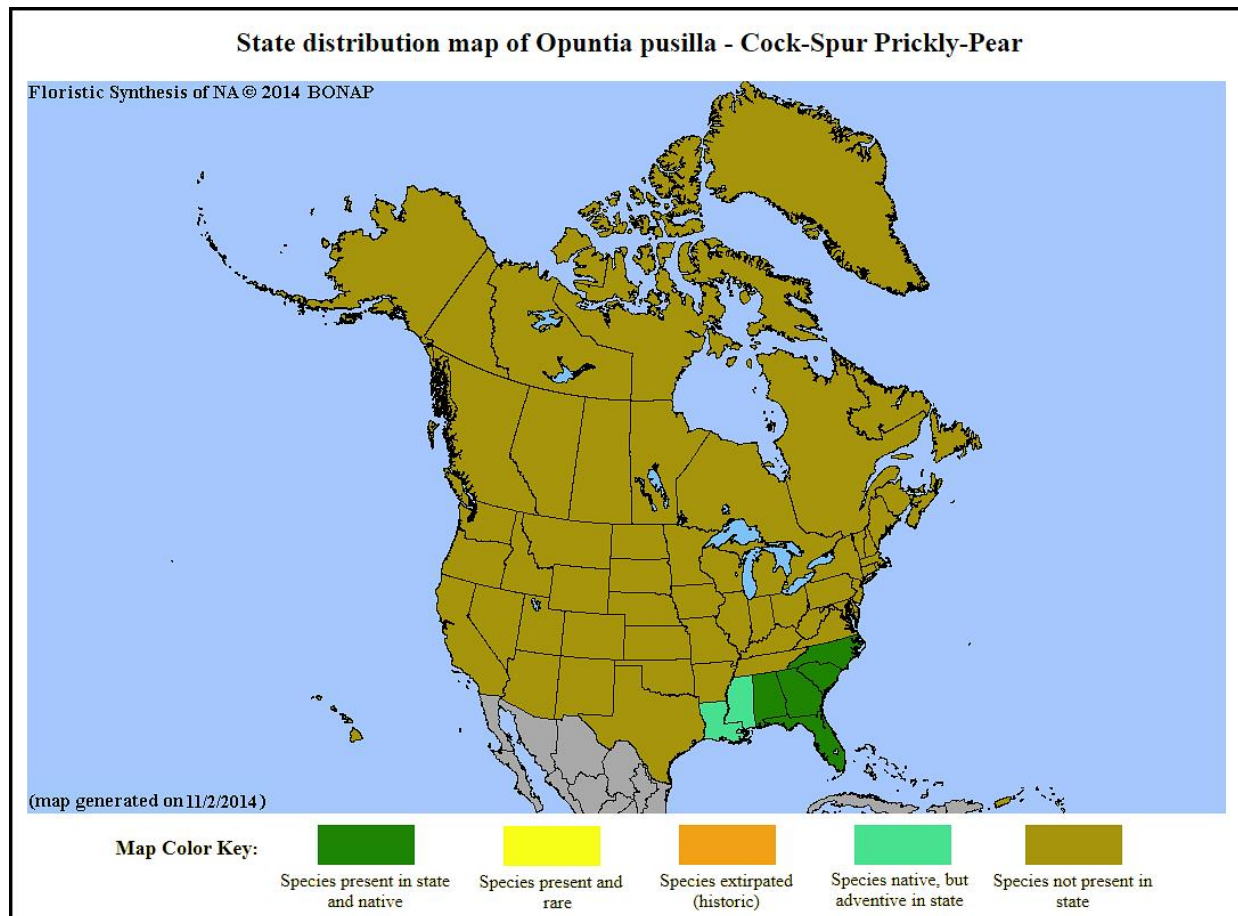


Figure 1. Distribution of *O. drummondii* in North America, adapted from BONAP (Kartesz 2015).

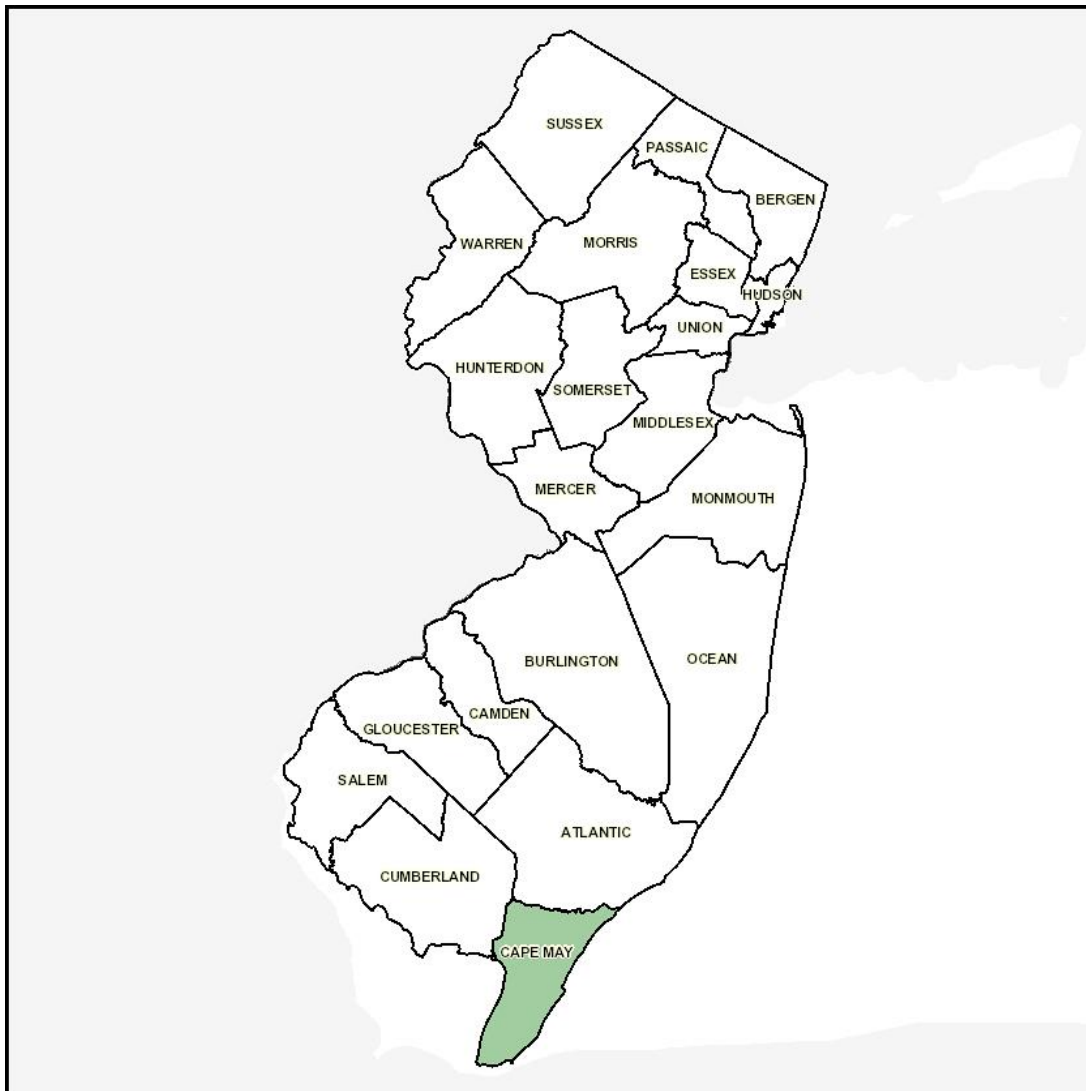


Figure 2. County records of *O. drummondii* in New Jersey (source data from NJNHP 2024).

Conservation Status

Opuntia drummondii is apparently secure at a global scale. The G4 rank means the species is at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, although there is some cause for concern as a result of recent local declines, threats, or other factors. The need for an updated review of its global status has been noted (NatureServe 2025). The map below (Figure 3) illustrates the conservation status of *O. drummondii* throughout its range. Dune Prickly-pear is apparently secure in Mississippi and is unranked in the other four states where it has long been known. Small (1920) predicted that *O. drummondii* would expand its range and that seems to be occurring. However, the cactus is still relatively rare in the states where it has recently established: It is listed as vulnerable (moderate risk of extinction) in one and critically imperiled (very high risk of extinction) in two.

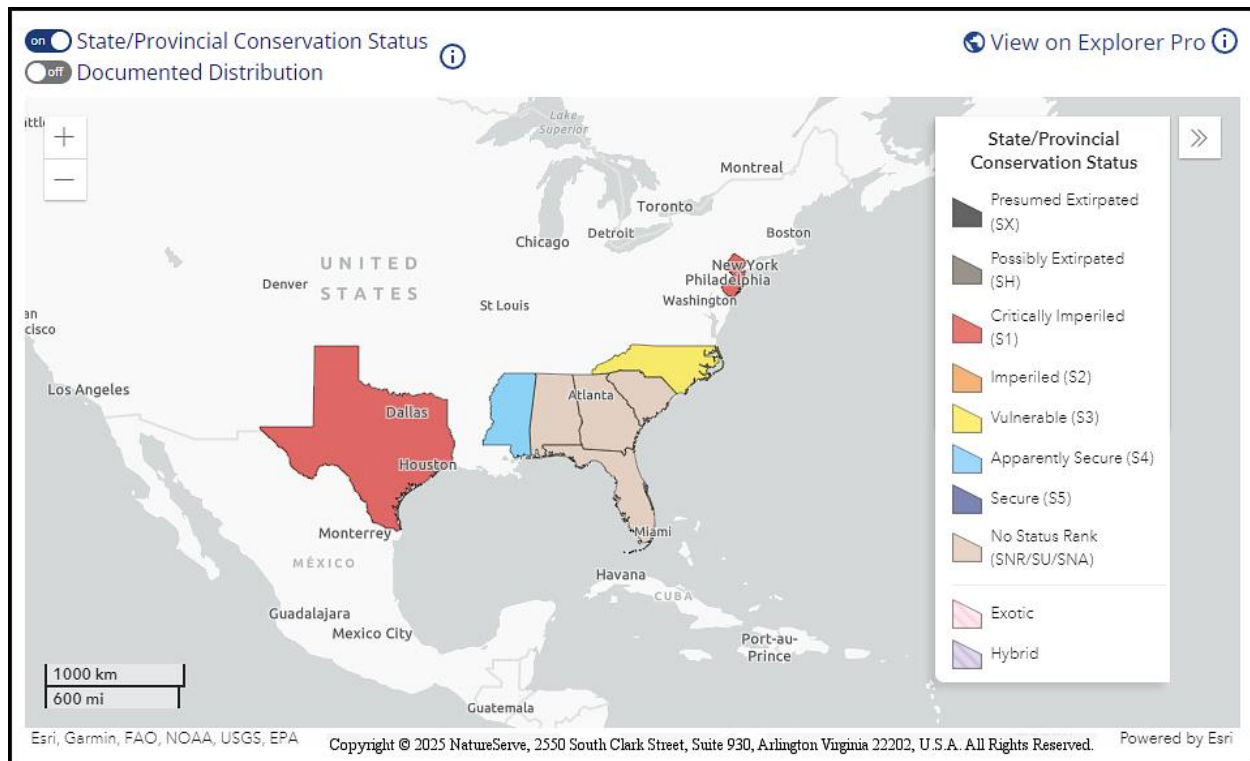


Figure 3. Conservation status of *O. drummondii* in North America (NatureServe 2025).

Opuntia drummondii is critically imperiled (S1) in New Jersey (NJNHP 2024). The rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. *O. drummondii* has also been assigned a regional status code of HL, signifying that the species is eligible for protection under the jurisdiction of the Highlands Preservation Area (NJNHP 2010). Dune Prickly-pear was not known in New Jersey prior to 2020 and to date it has only been documented in two locations (NJNHP 2024).

Threats

The primary threat to *Opuntia drummondii* is herbivory. The spines and glochids probably serve as a deterrent to most mammalian grazers (Small 1918a, Rheinhardt and Rheinhardt 2004). However, the larvae of certain moths can consume the cactus pads from the inside out. Two such species have been documented on *O. drummondii*: *Melitaria prodenialis*, the Eastern Cactus-boring Moth, and *Cactoblastis cactorum*, the Cactus Moth (Hight et al. 2002, Solis et al. 2004, Tate et al. 2009, Sauby et al. 2012, Schartel and Brooks 2018). *Melitaria prodenialis* is native to the eastern United States, including New Jersey, but *Cactoblastis cactorum* is native to South America. *C. cactorum* was first introduced into the Caribbean then somehow made its way to Florida, and it has continued to spread throughout the southeastern states (Solis et al. 2004, Simonson et al. 2005). To date, the Cactus Moth has been recorded as far north as South Carolina and west to Louisiana (NAMPG 2025), and it is so abundant in Florida that it is considered a threat to the survival of multiple *Opuntia* species (Zimmerman et al. 2000).



Melitaria prodenialis on *Opuntia humifusa* (J. S. Dodds, 2019).

Melitaria prodenialis and *Cactoblastis cactorum* moths are similar in appearance but their larvae are distinctive (Solis et al. 2004). The native moth, *Melitaria prodenialis*, has a lesser impact on prickly-pear populations because the females lay fewer eggs, the larvae are less tolerant of mucilage produced by host plants, and the species is more prone to pathogens (Stephens et al. 2012, Parisio et al. 2014). *C. cactorum*, on the other hand, has been known to eradicate entire *Opuntia* populations. It was deliberately introduced into Australia in an attempt to control the spread of invasive *Opuntia* species and the experiment was wildly successful—the moths destroyed millions of hectares of the cacti in less than five years (DeFelice 2004). The further spread of *C. cactorum* in North American is almost inevitable because the females are attracted to light and can travel in cars, trains, boats, or planes. Larvae within *Opuntia* cladodes may be transported across state lines in horticultural material, and they could also be dispersed to new locations by large storms (Zimmerman et al. 2000, Majure et al. 2007).

Climate Change Vulnerability

Information from the references cited in this profile was used to evaluate the vulnerability of New Jersey's *Opuntia drummondii* populations to climate change. The species was assigned a rank from NatureServe's Climate Change Vulnerability Index using the associated tool (Version 3.02) to estimate its exposure, sensitivity, and adaptive capacity to changing climactic conditions in accordance with the guidelines described by Young et al. (2016) and the state climactic computations by Ring et al. (2013). Based on available data *O. drummondii* was assessed as Less Vulnerable, meaning that climate change is not expected to have a notable detrimental impact on its extent in New Jersey by 2050. In fact, Dune Prickly-pear was viewed as a southeastern endemic quite recently (e.g. Estill and Cruzan 2001) and it is possible that the warming climate is facilitating its northward range expansion.

As the global climate continues to change, *Opuntia drummondii* is likely to experience higher temperatures, increasingly intense storm events, and rising seas in New Jersey (Hill et al. 2020). *O. drummondii* is well-adapted to high temperatures but low temperatures could be limiting. However, the species appears to have some tolerance for cold: Small (1917) observed that plants on dunes had not been damaged by temperatures low enough to freeze the water in adjacent swamps, and on another trip he found that a significant number of *O. drummondii* plants had survived a cold spell despite relatively high levels of mortality in within the population (Small 1918b). The species has been known to persist through severe hurricanes, even in one case where the plants were temporarily submerged (Stalter and Lamont 1993, Shiflett and Backstrom 2023). Some storms might even facilitate dispersal, and the cactus's ability to establish from stem segments may allow it to colonize new locations fast enough to keep pace with sea level rise.

Management Summary and Recommendations

Opuntia drummondii is a recent arrival in New Jersey and no threats to the known occurrences have been reported (NJNHP 2024). It would be advisable to monitor the success of the cactus at the sites where it has established and determine whether it is colonizing additional locations in the state. It would also be prudent to track the spread of *Cactoblastis cactorum* along the Atlantic coast. The invasive moths pose a significant threat to *O. drummondii* populations in the south so vigilance is recommended in order to identify new *C. cactorum* incursions and deal with them before they become devastating.

Synonyms

The accepted botanical name of the species is *Opuntia drummondii* Graham. Orthographic variants, synonyms, and common names are listed below (Majure et al. 2017, Weakley et al. 2024, POWO 2025). Graham (1846) named the species in honor of Thomas Drummond, who collected specimens from Florida in 1835 but died shortly thereafter (Small 1918b). The name *Opuntia pusilla* was published first and is still widely used but Majure et al. (2017) recently raised some questions about its validity and POWO (2025) has classified it as an unplaced name.

Botanical Synonyms

Opuntia pusilla (Haw.) Haw.
Opuntia frustulenta Gibbes
Opuntia pes-corvi Leconte ex Engelm.
Opuntia tracyi Britton
Cactus pusillus Haw.

Common Names

Dune Prickly-pear
 Little Prickly-pear
 Cockspur Pricklypear
 Sandbur Pricklypear
 Creeping Cactus
 Devil Joint

References

- Aliscioni, Nayla Luján, Natalia E. Delbón, and Diego E. Gurvich. 2021. Spine function in Cactaceae, a review. *Journal of the Professional Association for Cactus Development* 23: 1–11.
- Anderson, Loran C. and Laurence L. Alexander. 1985. The vegetation of Dog Island, Florida. *Florida Scientist* 48(4): 232–251.
- Benson, L. D. 1982. *The Cacti of the United States and Canada*. Stanford University Press. 1044 pp.
- Blonder, Barbara I., John M. Wooldridge, and Mary B. Garrard. 2018. Assessing postfire vegetative changes and implications for management in a northeast Florida coastal strand ecosystem. *Castanea* 83(1): 104–121.
- Britton, N. L. 1911. Shorter Notes. *Torreyia* 11: 152.
- Buesching, Jessica Mae. 2001. *Views From Above: Combining Green Roof Technology With Restorative Views of Nature*. Master's Thesis, University of Georgia, Athens, GA. 90 pp.
- BugGuide. 2025. An online resource for identification, images, and information about insects, spiders and their kin in the United States and Canada. Site hosted by Iowa State University Department of Entomology. Available at <https://bugguide.net/node/view/15740>
- Coker, W. C. 1918. A visit to Smith Island. *Journal of the Elisha Mitchell Scientific Society* 34(3): 150–153.
- DeFelice, Michael S. 2004. Prickly Pear Cactus, *Opuntia* spp.: A spine-tingling tale. *Weed Technology* 18(3): 869–877.
- Easley, M. Caroline and Walter S. Judd. 1993. Vascular flora of Little Talbot Island, Duval County, Florida. *Castanea* 58(3): 162–177.
- Estill, James C. and Mitchell B. Cruzan. 2001. Phytogeography of rare plant species endemic to the southeastern United States. *Castanea* 66(1–2): 3–23.
- Faber-Langendoen, D. 2018. *Northeast Regional Floristic Quality Assessment Tools for Wetland Assessments*. NatureServe, Arlington, VA. 52 pp.
- Faucette, Amanda Louise. 2016. *Guide to the Vascular Flora of Buxton Woods Coastal Reserve (Dare County, North Carolina)*. Master's Thesis, North Carolina State University, Raleigh, NC. 267 pp.
- Fowler, Jarrod and Sam Droege. 2020. Pollen specialist bees of the eastern United States. Available at https://jarrodfowler.com/specialist_bees.html

Goldberg, Nisse A. and Ryan J. Rillstone. 2012. Comparison of plant diversity on spoil and natural islands in a salt marsh habitat, northeastern Florida. *The Journal of the Torrey Botanical Society* 139(2): 226–231.

Graham, Robert. 1846. *Opuntia drummondii*. In B. Maund and J. S. Henslow (eds.), *The Botanist*, Volume 5. R. Groombridge, New York, NY.

Grant, Verne, Karen A. Grant, and Paul D. Hurd, Jr. 1979. Pollination of *Opuntia lindheimeri* and related species. *Plant Systematics and Evolution* 132: 313–320.

Henderson, Beau. 2003. Human-Driven Extensive Greenroof Design. Master's Thesis, Virginia Polytechnic Institute & State University, Blacksburg, VA. 60 pp.

Hight, S. D., J. E. Carpenter, K. A. Bloem, S. Bloem, R. W. Pemberton, and P. Stiling. 2002. Expanding geographical range of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America. *Florida Entomologist* 85(3): 527–529.

Hill, Rebecca, Megan M. Rutkowski, Lori A. Lester, Heather Genievich, and Nicholas A. Procopio (eds.). 2020. New Jersey Scientific Report on Climate Change, Version 1.0. New Jersey Department of Environmental Protection, Trenton, NJ. 184 pp.

Hilty, John. 2020. Flower visiting insects of *Opuntia humifusa*. Illinois Wildflowers. Accessed April 7, 2025 at https://www.illinoiswildflowers.info/flower_insects/plants/prickly_pear.htm

Holmes, Kirk. 2016. Morphological and Ecological Characterization of *Opuntia* Miller on the Coast of South Carolina. Master's Thesis, Clemson University, Clemson, SC. 101 pp.

Holmes, Walter C. and Brandi K. Amor. 2010. The vascular flora of a river bottom in east central Mississippi. *Phytologia* 92(2): 206–229.

Hunt, Kenneth W. 1947. The Charleston woody flora. *The American Midland Naturalist* 37(3): 670–756.

iNaturalist. 2025. *Opuntia drummondii* observation records. California Academy of Sciences website, accessed April 8, 2025 at <https://www.inaturalist.org/taxa/596540-Opuntia-drummondii>

Kartesz, J. T. 2015. The Biota of North America Program (BONAP). Taxonomic Data Center. (<http://www.bonap.net/tdc>). Chapel Hill, NC. [Maps generated from Kartesz, J. T. 2015. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP) (in press)].

Köhler, Matias, Marcelo Reginato, Jian-Jun Jin, and Lucas C. Majure. 2023. More than a spiny morphology: Plastome variation in the prickly pear cacti (Opuntieae). *Annals of Botany* 20: 1–16.

Kraus, E. Jean Wilson. 1988. A Guide to Ocean Dune Plants Common to North Carolina. University of North Carolina Press, Chapel Hill, NC. 71 pp.

López-Palacios, Cristian, Cecilia B. Peña-Valdivia, J. Antonio Reyes-Agüero, J. Rogelio Aguirre-Rivera, Hugo M. Ramírez-Tobías, Ramón Marcos Soto-Hernández, and Juan Francisco Jiménez-Bremont. 2015. Inter- and intra-specific variation in fruit biomass, number of seeds, and physical characteristics of seeds in *Opuntia* spp., Cactaceae. Genetic Resources and Crop Evolution 62(8): 1205–1223.

López-Palacios, Cristian, Juan Antonio Reyes-Agüero, Cecilia Beatriz Peña-Valdivia, and Juan Rogelio Aguirre-Rivera. 2019. Physical characteristics of fruits and seeds of *Opuntia* sp. as evidence of changes through domestication in the Southern Mexican Plateau. Genetic Resources and Crop Evolution 66(2): 1–14.

MacGown, J. A., J. G. Hill, L. C. Majure, and J. L. Seltzer. 2008. Rediscovery of *Pogonomyrmex badius* (Latreille) (Hymenoptera: Formicidae) in mainland Mississippi, with an analysis of associated seeds and vegetation. Midsouth Entomologist 1: 17–28.

Majure, Lucas Charles. 2007a. The Ecology and Morphological Variation of *Opuntia* (Cactaceae) Species in the Mid-South, United States. Master's Thesis, Mississippi State University, Starkville, MS. 101 pp.

Majure, Lucas C. 2007b. The vascular flora of the Chunky River (Mississippi). Journal of the Botanical Research Institute of Texas 1(2): 1179–1202.

Majure, Lucas C. 2012. The Evolution and Systematics of the *Opuntia humifusa* Complex. Doctoral Dissertation, University of Florida, Gainesville, FL. 255 pp.

Majure, Lucas C. and Gary N. Ervin. 2008. The Opuntias of Mississippi. Haseltonia 14: 111–126.

Majure, Lucas C. and Raul Puente. 2014. Phylogenetic relationships and morphological evolution in *Opuntia* s.str. and closely related members of tribe Opuntieae. Succulent Plant Research 8: 9–30.

Majure, Lucas C., Gary N. Ervin, and Pat Fitzpatrick. 2007. Storm-driven maritime dispersal of prickly pear cacti (*Opuntia* species). Poster prepared by the Department of Biological Sciences and GeoResources Institute, Mississippi State University, Mississippi State, MS. Available at https://www.cavs.msstate.edu/publications/docs/2007/05/3848Maritime_Dispersal_Phoenix_fitz.pdf

Majure, Lucas C., Walter S. Judd, Pamela S. Soltis, and Douglas E. Soltis. 2012a. Cytogeography of the *Humifusa* clade of *Opuntia* s.s. Mill. 1754 (Cactaceae, Opuntioideae, Opuntieae): Correlations with pleistocene refugia and morphological traits in a polyploid complex. Comparative Cytogenetics 6(1): 53–77.

Majure, Lucas C., Raul Puente, M. Patrick Griffith, Walter S. Judd, Pamela S. Soltis, and Douglas E. Soltis. 2012b. Phylogeny of *Opuntia* s.s. (Cactaceae): Clade delineation, geographic origins, and reticulate evolution. *American Journal of Botany* 99(5): 847–864.

Majure, Lucas C., Walter S. Judd, Pamela S. Soltis, and Douglas E. Soltis. 2017. Taxonomic revision of the *Opuntia humifusa* complex (Opuntieae: Cactaceae) of the eastern United States. *Phytotaxa* 290(1): 1–65.

Mandujano, María del Carmen, Israel Carrillo-Angeles, Concepción Martínez-Peralta, and Jordan Golubov. 2010. Reproductive biology of Cactaceae. In K. G. Ramawat (ed.), *Desert Plants*, Springer-Verlag, Berlin.

Martínez-Ramos, Linda M., Sonia Vázquez-Santana, José García-Franco, and María C. Mandujano. 2024. Is self-incompatibility a reproductive barrier for hybridization in a sympatric species? *American Journal of Botany* 111: e16309.

Maund, S. 1846. Illustration of *Opuntia drummondii* from *The Botanist*, Volume 5. R. Groombridge, New York, NY. Public domain image, courtesy of Biodiversity Heritage Library.

McFarland, J. D., P. G. Kevan, and M. A. Lane. 1989. Pollination biology of *Opuntia imbricata* (Cactaceae) in southern Colorado. *Canadian Journal of Botany* 67: 24–28.

Miller, G. J. and S. B. Jones, Jr. 1967. The vascular flora of Ship Island, Mississippi. *Castanea* 32(2): 84–99.

Moldenke, Harold N. 1944. A contribution to our knowledge of the wild and cultivated flora of Florida, I. *The American Midland Naturalists* 32(3): 529–590.

NAMPG (North American Moth Photographers Group at the Mississippi Entomological Museum, at Mississippi State University). 2025. Digital Guide to Moth Identification. Available online at <http://mothphotographersgroup.msstate.edu/>

NatureServe. 2025. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed April 4, 2025 at <https://explorer.natureserve.org/>

NJNHP (New Jersey Natural Heritage Program). 2010. Explanation of Codes Used in Natural Heritage Reports. Updated March 2010. Available at https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf

NJNHP (New Jersey Natural Heritage Program). 2024. Biotics 5 Database. NatureServe, Arlington, VA. Accessed March 15, 2024.

Osborn, Martha M., Peter G. Kevan, and Meredith A. Lane. 1988. Pollination biology of *Opuntia polyacantha* and *Opuntia phaeacantha* (Cactaceae) in southern Colorado. *Plant Systematics and Evolution* 159: 85–94.

- Parisio, Oulimathe, Trevor Randall Smith, Stephen D. Hight, and Bobbie Jo Davis. 2014. Rearing a native cactus moth, *Melitara prodenialis* (Lepidoptera: Pyralidae), on artificial diet and *Opuntia* cladodes: Preliminary comparisons. *The Florida Entomologist* 97(3): 1232–1236.
- Philley, Kevin D. 2019. The vascular flora of Choctaw County, Mississippi, U.S.A. *Journal of the Botanical Research Institute of Texas* 13(1): 319–348.
- Pinkava, Donald J. Page updated November 5, 2020. *Opuntia pusilla* (Haworth) Haworth. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Accessed April 4, 2025 at http://floranorthamerica.org/Opuntia_pusilla
- Potter, Robert L., Joseph L. Petersen, and Darrell N. Ueckert. 1984. Germination responses of *Opuntia* spp. to temperature, scarification, and other seed treatments. *Weed Science* 32(1): 106–110.
- POWO. 2025. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed April 4, 2025 at <http://www.plantsoftheworldonline.org/>
- Rebman, Jon P. and Donald J. Pinkava. 2001. *Opuntia* cacti of North America: An overview. *The Florida Entomologist* 84(4): 474–483.
- Rheinhardt, Richard D. and Martha Craig Rheinhardt. 2004. Feral horse seasonal habitat use on a coastal barrier spit. *Journal of Range Management* 57: 253–258.
- Richmond, E. 1962. The fauna and flora of Horn Island, Mississippi. *Gulf Research Reports* 1(2): 59–106.
- Riegel, Andrew. 1941. Some coactions of rabbits and rodents with cactus. *Transactions of the Kansas Academy of Science* 44: 96–103.
- Ring, Richard M., Elizabeth A. Spencer, and Kathleen Strakosch Walz. 2013. Vulnerability of 70 Plant Species of Greatest Conservation Need to Climate Change in New Jersey. New York Natural Heritage Program, Albany, NY and New Jersey Natural Heritage Program, Department of Environmental Protection, Office of Natural Lands Management, Trenton, NJ, for NatureServe #DDCF-0F-001a, Arlington, VA. 38 pp.
- Sauby, Kristen E., Travis D. Marsico, Gary N. Ervin, and Christopher P. Brooks. 2012. The role of host identity in determining the distribution of the invasive moth *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in Florida. *Florida Entomologist* 95(3): 561–568.
- Schartel, Tyler E. and Christopher P. Brooks. 2018. Biotic constraints on *Cactoblastis cactorum* (Berg) host use in the southern US and their implications for future spread. *Food Webs* 15 (June 2018): Article e00083.

Shiflett, Sheri A. and Joni T. Backstrom. 2023. Impacts of Hurricane Isaias (2020) on geomorphology and vegetation communities of natural and planted dunes in North Carolina. *Journal of Coastal Research* 39(4): 587–609.

Simonson, Sara E., Thomas J. Stohlgren, Laura Tyler, William Gregg, Rachel Muir, and Lynn J. Garrett. 2005. Preliminary assessment of the potential impacts and risks of the invasive cactus moth, *Cactoblastis cactorum* Berg, in the U.S. and Mexico. Final Report to the International Atomic Energy Agency. 32 pp.

Small, John K. 1917. Cactus hunting on the coast of South Carolina. *Journal of the New York Botanical Garden* 18(215): 237–246.

Small, John K. 1918a. A winter collecting trip in Florida. *Journal of the New York Botanical Garden* 19(220): 69–77.

Small, John K. 1918b. Collecting prickly pears at Apalachicola. *Journal of the New York Botanical Garden* 19(220): 1–6.

Small, John Kunkel. 1920. In quest of lost cacti: Cactus hunting in the Carolinas in winter. *Journal of the New York Botanical Garden* 21: 161–178.

Smith, Bradley. 2023. Photo of *Opuntia drummondii* from Florida. Shared via iNaturalist at <https://www.inaturalist.org/observations/158911323>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>

Solis, M. A., S. D. Hight, and D. R. Gordon. 2004. Tracking the cactus moth, *Cactoblastis cactorum* Berg., as it flies and eats its way westward in the US. *News of the Lepidopterists' Society* 46: 3–5.

Sorrie, Bruce A. 2021. Vascular flora of the Outer Banks, North Carolina, U.S.A. *Journal of the Botanical Research Institute of Texas* 15(2): 607–710.

Spencer, Donald A. and Alice L. Spencer. 1941. Food habits of the white-throated wood rat in Arizona. *Journal of Mammology* 22: 280–284.

Stalter, Richard and Eric E. Lamont. 1993. The vascular flora of Fort Sumter and Fort Moultrie, South Carolina, one year after Hurricane Hugo. *Castanea* 58(2): 141–152.

Stalter, Richard and Eric E. Lamont. 1997. Flora of North Carolina's Outer Banks, Ocracoke Island to Virginia. *The Journal of the Torrey Botanical Society* 124(1): 71–88.

Stalter, Richard and Eric E. Lamont. 2015. The vascular flora of Back Bay National Wildlife Refuge and False Cape State Park, Virginia. *International Biology Review* 3: DOI: <https://doi.org/10.18103/ibr.v0i3.437>

Stalter, Richard, John Baden, Chester DePratter and Paul Kenny. 2018. The vascular flora of coastal Indian clam shell middens in South Carolina, U.S.A. *Journal of the Botanical Research Institute of Texas* 12(2): 697–706.

Stephens, Faye A., Anastasia M. Woodward, and Travis D. Marsico. 2012. Comparison between eggsticks of two cactophagous moths, *Cactoblastis cactorum* and *Melitara prodenialis* (Lepidoptera: Pyralidae). *The Florida Entomologist* 95(4): 939–943.

Stubbs, C. S., H. A. Jacobson, E. A. Osgood, and F. A. Drummond. 1992. Alternative forage plants for native (wild) bees associated with lowbush blueberry, *Vaccinium* spp., in Maine. Maine Agricultural Experiment Station, Technical Bulletin 148, University of Maine, Orono, ME. 54 pp.

Tate, C. D., Steven Hight, and James Carpenter. 2009. Oviposition preference of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in caged choice experiments and the influence of risk assessment of F1 sterility. *Biocontrol Science and Technology*. 19(Supplement 1): 317–333.

U. S. Army Corps of Engineers. 2022. National Wetland Plant List, version 3.6. <https://nwpl.sec.usace.army.mil/> U. S. Army Corps of Engineers Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2025. PLANTS profile for *Opuntia pusilla* (Cockspur Pricklypear). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed April 4, 2025 at <http://plants.usda.gov>

Waldstein, Arielle Hopkins. 2010. Raccoon Ecology and Management on Cape Lookout National Seashore, North Carolina. Master's Thesis, North Carolina State University, Raleigh, NC. 138 pp.

Walz, Kathleen S., Jason L. Hafstad, Linda Kelly, and Karl Anderson. 2020. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservancy (CoC) Values for Species and Genera (update to 2017 list). New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ.

Wang, B. and Y. L. Qiu. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16(5): 299–363.

Ward, Daniel B. 2009. Keys to the flora of Florida: 23, *Opuntia* (Cactaceae). *Phytologia* 91(3): 383–393.

Weakley, A. S. and Southeastern Flora Team. 2024. Flora of the Southeastern United States. Edition of March 4, 2024. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2203 pp.

Whitaker, J. David, John W. McCord, Philip P. Maier, Albert L. Segars, Megan L. Rekow, Norm Shea, Jason Ayers, and Rocky Browder. 2004. An Ecological Characterization of Coastal

Hammock Islands in South Carolina. Final Report to Ocean and Coastal Resources Management, South Carolina Department of Health and Environmental Control. 15 pp.

Whitcomb, Sean A. 2000. Mycorrhizal Associations in *Opuntia humifusa* in Southern Illinois. Honors Thesis, Southern Illinois University, Carbondale, IL. 26 pp.

Young, Bruce E., Elizabeth Byers, Geoff Hammerson, Anne Frances, Leah Oliver, and Amanda Treher. 2016. Guidelines for Using the NatureServe Climate Change Vulnerability Index, Release 3.02, 1 June 2016. NatureServe, Arlington, VA. 65 pp.

Zimmermann, H. G., V. C. Moran, and J. H. Hoffmann. 2000. The renowned cactus moth, *Cactoblastis cactorum*: Its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. Diversity and Distributions, 6(5): 259–269.