Localized Overabundance of an Otherwise Rare Butterfly Threatens Endangered Cycads

Authors: Whitaker, Melissa R. L., Salzman, Shayla, Gratacos, Xavier, and Tucker Lima, Joanna M.

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Localized overabundance of an otherwise rare butterfly threatens endangered cycads

Melissa R. L. Whitaker1,*, Shayla Salzman2, Xavier Gratacos3, and Joanna M. Tucker Lima3

The butterfly Eumaeus atala (Poey) (Lepidoptera: Lycaenidae) is native to southern Florida, the Bahamas, and Cuba, where the larvae feed on cycads in the genus Zamia (Zamiaceae). Though once so common as to be called “the most conspicuous insect” in Florida (Schwartz 1888), overharvesting of the butterfly’s only native food plant, Zamia integrifolia L.f. (Zamiaceae), led to drastic population declines in the early 1900s, and E. atala was considered locally extinct by the 1930s (Klots 1951). In 1959, a small breeding population was discovered in southern Miami, though unpublished “guarded reports” of sightings circulated earlier (Rawson 1961). Grassroots conservation efforts have since rallied around the butterfly’s recovery, and over 300 ephemeral populations have been documented across Florida since 2001, largely in urban and semi-natural habitats where Zamia are planted as ornamentals (Ramirez-Restrepo et al. 2017).

A large, persistent population inhabits the Montgomery Botanical Center, a research and conservation garden in Coral Gables, Florida, USA. During peak butterfly season, it is possible to find over 300 E. atala larvae on the 49 ha (120 acres) property in a single d, plus many more eggs, pupae, and adults. Given the rarity of E. atala and the limited success of reintroduction efforts across Florida, it is worth examining why the butterfly flourishes at the Montgomery Botanical Center.

Cycads have been cultivated at the Montgomery Botanical Center since 1932, and their collection has steadily grown in species richness and abundance, with new additions made annually. In 2020, the center cultivated 235 cycad species endemic to Asia, Africa, Australia, and the Americas, including many species that are considered threatened or endangered (IUCN 2020). We evaluated the species richness and abundance of Zamia plantings at the Montgomery Botanical Center between 2000 and 2020 and found a steady increase in both metrics (Fig. 1), with 2,838 Zamia plants belonging to 55 species as of Jan 2020.

Because E. atala populations never have been formally quantified or monitored at the Montgomery Botanical Center, we consulted the Center’s staff about the butterfly’s population dynamics on the property. We spoke with the Center’s director, current and former cycad curators, resident cycad biologist, and landscape designer, representing over 40 yr of cumulative experience at Montgomery Botanical Center. Long-term staff report that E. atala always have been present on the Center property in small numbers, with seasonal abundance fluctuating in typical boom or bust cycles. However, over the past approximately 10 yr, E. atala numbers have repeatedly reached outbreak levels with boom cycles becoming bigger, longer, and more frequent, such that Floridian and Caribbean Zamia plants are repeatedly defoliated and butterfly larvae are found feeding on an expanded host range.

In Aug 2018, Jan 2019, and Jan 2020, authors MRLW and SS spent an estimated 130 h (combined) inspecting the Center’s cycads for E. atala eggs and larvae. We estimate that 90% of the Center’s cultivated cycad species and 80% of individual cycad plants were inspected during these surveys. Eggs and larvae were found on more than 20 cycad species, while other authors have reported E. atala feeding on additional cycad species elsewhere in Florida (Table 1).

Eumaeus atala larvae feed gregariously (Fig. 1) and can cause severe damage to their slow-growing host plants, often completely defoliating large cycads. As part of the Center’s pest management strategy, Center staff conduct daily inspections of Zamia integrifolia plants to manually collect butterfly eggs, larvae, and pupae from leaves. All other Caribbean Zamia plants are cleaned during regular routine maintenance, and collected insects are sent to nearby education, conservation, and research groups, many of which are trying to establish breeding colonies elsewhere in Florida. The Center staff estimate that over 2,000 E. atala individuals were relocated in 2019, requiring approximately 4 to 8 h of dedicated effort per wk.

The abundance of E. atala at the Montgomery Botanical Center is at least partially attributable to the ample availability of host plants on the property; as of 2020 the Montgomery Botanical Center maintains 431 Zamia integrifolia individuals. More curious is why E. atala are not found in greater abundance in surrounding areas. There is no shortage of Z. integrifolia in the immediate vicinity of the Montgomery Botanical Center, because these plants are commonly found in residential and public gardens, and several large plantings of this species occupy road medians, parks, and other public spaces nearby. According to the Coral Gables Public Works Department, Coral Gables, Florida, USA, at least 220 Z. integrifolia plants are grown in public spaces within an 11 km radius of the Montgomery Botanical Center (Bob Boberman, Coral Gables Public Works Department, personal communication), with many more plants grown in neighboring home gardens and road medians. The Fairchild Tropical Garden is located less than 1 km from the Montgomery Botanical Center and grows 201 Z. integrifolia plants, 84 of which were planted in the last yr (Yisu Santamarina, Fairchild Tropical Garden, personal communication). Though E. atala butterflies are commonly found in small numbers in these areas, we have heard of no population explosions similar to the one at the Montgomery Botanical Center. These observations, while anecdotal, suggest that host plant abundance likely is not the only factor limiting butterfly abundance.

Given that E. atala larvae feed on many other non-native cycad species, host plant diversity likely influences local population dynamics. With 55 species in cultivation in 2020, the diversity of Zamia at the
Montgomery Botanical Center is higher than anywhere else in Florida. This expanded host range may enable the butterfly's continuous reproduction if seasonal differences across cycad species allow for year-round availability of key plant resources. The butterflies preferentially oviposit on young, tender cycad leaves because these are required by early larval instars. That most Zamia produce just 1 new leaf flush per yr may have historically constrained the butterfly's reproductive cycles, whereas increased plant diversity could confer yr-round availability of fresh new leaves. A systematic evaluation of leaf phenology across Zamia species at the Montgomery Botanical Center would shed light on this possibility.

Other factors influencing the butterfly's local population size might include availability of adult nectar sources or roosting sites, changes in regional climate, local adaptive evolution, or heterogeneity in host plant quality. Given the abundance of acceptable nectar plants in home gardens and public spaces near the Montgomery Botanical Center, nectar limitation seems unlikely to play a major role in constraining population size. Shelter plants at the Center may be important for adult butterflies, which are commonly seen roosting in native trees and shrubs such as Quercus virginiana Mill. (Fabaceae), Hamelia patens Jacq. (Rubiaceae), Psychotria nervosa Benth. (Rubiaceae), Metopium toxiferum (L.) Krug & Urb (Anacardiaceae), and Sabal palmetto (Walter) Lodd. ex Schult. & Schult.f. (Arecaceae). Cold temperatures limit many aspects of butterflies' biology, and monthly minimum temperatures have been steadily increasing in Florida (Fig. 1; NOAA 2020). Several Center staff members have noted that the butterflies are easier to manage in yr with a relatively cold winter. However, any effect of weather would presumably lead to similar E. atala population dynamics across Florida, not just at the Montgomery Botanical Center. Alternatively, depending on dispersal abilities and site fidelity of E. atala, there may be opportunities for local adaptive evolution, e.g., expanded host range. Finally, Zamia plants at the Montgomery Botanical Center may provide a higher quality food source than plants grown elsewhere, because horticultural practices such as irrigation and fertilization can affect plant nutritional quality dramatically by altering the ratios of water, nutrients, and phytotoxins within plant tissues (Couture et al. 2010). Perhaps the care that plants receive at the Montgomery Botanical Center makes them nutritionally superior or less chemically defended than plants grown offsite.

The increasing availability of non-native cycads as novel host plants for E. atala could lead to new population dynamics, even within the butterfly's native range. A similar scenario has been documented for Luthrodex pandava (Horsfield) (Lepidoptera: Lycaenidae), a cycad-feeding lycaenid butterfly native to southern Asia. As a specialist of paleotropical cycads in the genus Cycas (Cycadaceae), L. pandava has emerged as a chronic naturalized pest—even within parts of its native range—following widespread horticultural use of Cycas plants (Wu et al. 2010). The butterfly has been introduced to other parts of Asia, Africa, the Middle East, and Guam, where it threatens both introduced and endemic Cycas species (Feulner et al. 2014; Fric et al. 2014; Marler et al. 2012). Another cycad-feeding lycaenid butterfly, Theclinesthes onycho (Hewitson) (Lepidoptera: Lycaenidae), has attracted the attention of cycad conservationists due to increased outbreaks on native and introduced Cycas plants in Australia (Manners 2015).

### Table 1. Cycad species on which Eumaeus atala larvae have been observed feeding.

| Cycad species | IUCN status   | Native range                   | Source                      |
|---------------|---------------|--------------------------------|-----------------------------|
| Zamia integrifolia | Near threatened | Florida, Bahamas               | Authors' observations       |
| Zamia angustifolia | Vulnerable      | Bahamas                        | Authors' observations       |
| Zamia pumila | Near threatened | Cuba, Dominican Republic, Puerto Rico | Authors' observations       |
| Zamia lucayana | Endangered     | Bahamas                        | Authors' observations       |
| Zamia portoricensis | Endangered   | Puerto Rico                    | Authors' observations       |
| Zamia vazquezii | Critically endangered | Mexico                    | Authors' observations       |
| Zamia furfuracea | Endangered      | Mexico                         | Authors' observations       |
| Zamia decumbens | Not listed      | Belize                        | Authors' observations       |
| Zamia soconusensis | Vulnerable     | Mexico                        | Authors' observations       |
| Zamia neurophilidii | Vulnerable     | Costa Rica, Nicaragua, Panama | Authors' observations       |
| Zamia variegata | Endangered     | Belize, Guatemala, Mexico      | Authors' observations       |
| Zamia nana   | Not listed     | Panama                        | Authors' observations       |
| Zamia pseudomonticola | Near threatened | Costa Rica, Panama             | Authors' observations       |
| Zamia stevensonii | Not listed    | Panama                        | Authors' observations       |
| Zamia elegantissima | Endangered   | Panama                        | Authors' observations       |
| Zamia erosa | Vulnerable     | Cuba, Jamaica, Puerto Rico     | Authors' observations       |
| Zamia fischeri | Endangered     | Mexico                        | Authors' observations       |
| Zamia loddigesi | Near threatened | Mexico                       | Authors' observations       |
| Zamia inermis | Critically endangered | Mexico             | Authors' observations       |
| Zamia onan-reyesii | Not listed    | Honduras                      | Authors' observations       |
| Zamia pauciflora | Near threatened | Mexico                       | Authors' observations       |
| Zamia lindenii | Near threatened | Ecuador, Peru                 | Authors' observations       |
| Zamia pygmaea | Critically endangered | Cuba                      | Hammer 1996               |
| Zamia skinneri | Endangered     | Panama                        | Hammer 1996               |
| Zamia echenartoides | Vulnerable   | Colombia                      | Koi 2013                |
| Ceratozamia chamberlainii | Not listed | Mexico                        | Authors' observations       |
| Encephalartos villosus | Least concern | South Africa, Swaziland       | Hammer 1996               |
| Encephalartos hildebrandti | Near threatened | Kenya, Tanzania        | Hammer 1996               |
| Macrozamia lucida | Least concern   | Australia                     | Authors' observations       |
| Cycas caudata | Vulnerable     | Australia                     | Hammer 1996               |
| Cycas revoluta | Least concern   | China, Japan                  | Hammer 1996               |
Fig. 1. (A) Gregarious feeding by *Eumaeus atala* larvae on a *Zamia integrifolia* plant; (B) *Eumaeus atala* adult on a damaged *Zamia integrifolia* plant; (C) exemplary planting of *Zamia integrifolia* at the Montgomery Botanical Center photographed from the same vantage point in (top) Jan 2015 (photo by Joseph Hibbard) and (bottom) Jan 2020 (photo by Jessica Lambert), showing extensive damage inflicted by *Eumaeus atala* herbivory; (D) *Zamia* species richness and abundance have increased at the Montgomery Botanical Center between 2000 and 2020.
tional Lepidoptera feed on cycads (Whitaker & Salzman 2020) but their status as pests or conservation targets is largely unknown.

The Montgomery Botanical Center manages one of the world’s most important research and conservation collections of cycads, which are globally threatened by habitat loss, poaching, and insect pests. The fate of E. atala across the Caribbean is linked inextricably to the availability of suitable host plants. Conservation efforts that prioritize butterflies over plants (or vice versa) could have unintended consequenc-es, and effective conservation should prioritize the co-existence of these interacting species (Koi 2017). We suggest that host plant availability may not be the only factor underlying the localized abundance of E. atala, and we propose testable hypotheses regarding the abiotic and biotic forces that may constrain population size. Ultimately, a better understanding of the factors influencing local population dynamics will aid butterfly conservation across the native range of E. atala, while also informing pest management strategies at the Montgomery Botanical Center.

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Summary

Though once considered extinct in Florida, the Eumaeus atala butterfly (Poey) (Lepidoptera: Lycaenidae) has made a slow but steady recovery thanks to grassroots conservation efforts targeting the butterfly and its only native foodplant, the cycad Zamia integrifolia L.f. (Cycadales: Zamiaceae). A robust E. atala population occurs at the Montgomery Botanical Center, a research and conservation facility in Coral Gables, Florida, USA, that cultivates a living collection of global cycads, many of which are critically endangered in the wild. Since the early 2000s, the E. atala population at the Montgomery Botanical Center has grown and adopted an expanded host range, much to the detriment of the plants; both native and exotic cycads incur consistent and severe damage from larval herbivory. This presents a complex situation in which in situ butterfly conservation conflicts with ex situ cycad conservation. Here we describe the local population of E. atala at the Montgomery Botanical Center, suggest testable hypotheses for explaining the butterfly’s localized abundance, and discuss implications for butterfly and cycad conservation efforts in Florida.

Key Words: Eumaeus atala; Zamia integrifolia; coontie; conservation; pest management

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