Localized Overabundance of an Otherwise Rare Butterfly Threatens Endangered Cycads

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Localized overabundance of an otherwise rare butterfly threatens endangered cycads

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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 In 1959, a small breeding population was discovered in southern Miami, though unpublished "guarded reports" of sightings circulated earlier (Rawson 1961).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 (Ramírez-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 *Z. 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

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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 soconuscensis	Vulnerable	Mexico	Authors' observations
Zamia neurophyllidia	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 loddigesii	Near threatened	Mexico	Authors' observations
Zamia inermis	Critically endangered	Mexico	Authors' observations
Zamia onan-reyesii	Not listed	Honduras	Authors' observations
Zamia paucijuga	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 encephalartoides	Vulnerable	Colombia	Koi 2013
Ceratozamia chamberlainii	Not listed	Mexico	Authors' observations
Encephalartos villosus	Least concern	South Africa, Swaziland	Hammer 1996
Encephalartos hildebrandtii	Near threatened	Kenya, Tanzania	Hammer 1996
Macrozamia lucida	Least concern	Australia	Authors' observations
Cycas cairnsiana	Vulnerable	Australia	Hammer 1996
Cycas revoluta	Least concern	China, Japan	Hammer 1996

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 yr-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. (Aracaceae). 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 *Luthrodes 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 onycha* (Hewitson) (Lepidoptera: Lycaenidae), has attracted the attention of cycad conservationists due to increased outbreaks on native and introduced *Cycas* plants in Australia (Manners 2015). Several addi-

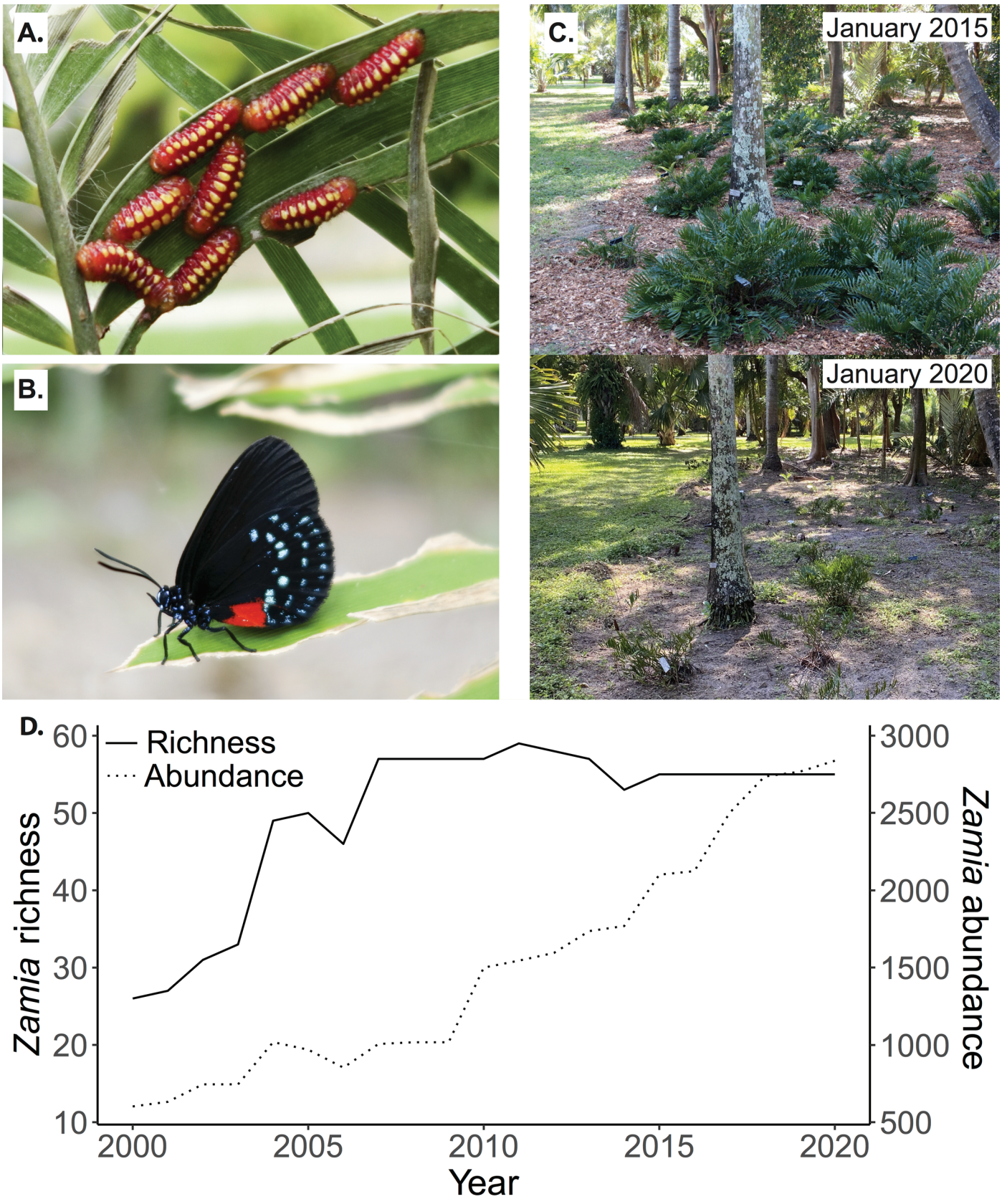

Fig. 1. (A) Gregarious feeding by *Eumaeus atala* larvae on a *Zamia integrifolia* plant; (B) *Eumaeus atala* adult on a damaged *Zamia integrifolia* plant; (C) exemplary planting of *Zamia integrifolia* at the Montgomery Botanical Center photographed from the same vantage point in (top) Jan 2015 (photo 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 consequences, 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

Sumario

Aunque se le consideró localmente extinta en la Florida, la mariposa *Eumaeus atala* (Poey) (Lepidoptera: Lycaenidae) ha tenido una recuperación lenta pero constante gracias a los esfuerzos de conservación dirigidos a la mariposa y su única planta alimenticia nativa, la cícada *Zamia integrifolia* L.f. (Cycadales: Zamiaceae). Una población robusta de *E. atala* se encuentra en el Centro Botánico de Montgomery, una instalación de investigación y conservación en Coral Gables, Florida, EE.UU., que cultiva una colección viviente de cícadas globales, muchas de las cuales están en peligro crítico en la naturaleza. Desde el principio de la década del 2000, la población de *E. atala* en el Centro Botánico de Montgomery ha crecido y ha adoptado un rango de hospederos mas amplio, en detrimento de las plantas; tanto las cícadas nativas como las exóticas sufren un daño constante y severo por la herbivoría de las larvas. Esto presenta una situación compleja en la que la conservación de mariposas in situ entra en conflicto con la conservación ex situ de las cícadas. Aquí describimos la población local de *E. atala* en el Centro Botánico de Montgomery, sugerimos hipótesis comprobables para explicar la abundancia localizada de mariposas y discutimos las implicaciones para los esfuerzos de conservación de mariposas y cícadas en Florida.

Palabras Clave: *Eumaeus atala*; *Zamia integrifolia*; sagú sagrado; conservación; manejo de plagas

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