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Cover: Mixed media with fine liners, colour pencils, and watercolour background of an Indian funnel web spider. © Elakshi Mahika Molur.



Decades of IUCN recommendations for biocontrol of invasive pest on the Guam cycad: you can lead policy-makers to conservation proposals but you cannot make them follow

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Abstract: Guam's cycad known as *Cycas micronesica* has been threatened by a coalition of invasive herbivore species, and the armored scale *Aulacaspis yasumatsui* has emerged as the primary threat. This lethal cycad pest invaded Guam in 2003, and the Species Survival Council of the International Union for Conservation of Nature (IUCN) began publishing recommendations addressing protection of the cycad population in 2005. Sustained epidemic mortality caused the addition of *C. micronesica* to the United States Endangered Species Act in 2015. The need to establish a sustainable coalition of biological control organisms has been the constant advice throughout almost two decades of recommendations, yet the decision-makers who controlled the direction of policy and funding have not responded to the advice with success. Therefore, we describe the history of publications in which the IUCN has asserted that this singular conservation action is urgently required to save the cycad species. We then summarize contemporary recommendations to address the ongoing threats to this and other insular cycad species.

Keywords: *Aulacaspis yasumatsui*, biological control, conservation science, *Cycas micronesica*, *Rhynchobius lophanthae*.

Abbreviations: CAS—Aulacaspis yasumatsui, Cycad Aulacaspis Scale | CSG—Cycad Specialist Group, Species Survival Council, IUCN | ESA—United States Endangered Species Act | GBF—The Kunming-Montreal Global Biodiversity Framework | IUCN—International Union for Conservation of Nature | USFWS—United State Fish & Wildlife Service.

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Author details & contributions: THOMAS MARLER is a conservation physiologist who has studied terrestrial plant species in western Pacific island nations for 30+ years. He has pioneered adaptive management research of the endangered *Cycas micronesica*, and wrote the original draft of the manuscript. ANDERS LINDSTRÖM is a cycad taxonomist and curator of the Living Plant Collections at Nong Nooch Tropical Botanical Garden, Chonburi, Thailand, was directly involved in manuscript conceptualization, and reviewed and edited several versions of the manuscript. IRENE TERRY is a pollination and conservation biologist who has studied the chemistry of cycad cone volatiles involved with pollination for 20+ years, including research on pollination and conservation of *Cycas micronesica*, and she worked on several drafts of the manuscript. BENJAMIN DELOSO is a botanist pursuing his PhD degree at Florida International University and is broadly interested in cycad biology and taxonomy, as well as the flora of the Pacific. He worked on several drafts of the manuscript. All four authors are contributing members of the Cycad Specialist Group of the IUCN Species Survival Council and have conducted in situ and ex situ research addressing *Cycas micronesica* biology, conservation, and ecology.

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INTRODUCTION

The cycad *Cycas micronesica* K.D.Hill grows among numerous disjunct ecological niches in the Mariana Islands, the Federated States of Micronesia, and the Republic of Palau (Hill 1994, Figure 1). The arborescent cycad species exhibits morphological traits that are typical of cycads, with large pinnately compound leaves radiating from the stem apex (Image 1). The species was the most abundant tree on Guam in 2002 when an estimated 1.57 million healthy mature trees existed (Donnegan et al. 2004). At that time, there were no identifiable threats throughout its indigenous range.

The absence of threats changed in 2003–2005 when Guam was invaded by the armored scale *Aulacaspis yasumatsui* Takagi (Cycad Aulacaspis Scale, CAS), the leaf miner *Erechthias* sp., and the *Cycas*-specific butterfly *Luthrodes pandava* Horsfield (Deloso et al. 2020). These specialist herbivorous insects arrived in Guam without their natural predators, finding an abundant population of hosts that evolved in the absence of native leaf herbivores. The rapid decreases in health of the attacked cycad trees generated unprecedented infestations by the native longhorn beetle *Acalolepta marianarum* Aurivillius, which employs the common stem borer behavior of preferentially attacking unhealthy trees (Marler 2013).

Plant mortality in the urban landscape was immediate, and plant mortality among in situ habitats began in 2005 (Marler & Lawrence 2012). A 2013 forest survey revealed only 624,000 *C. micronesica* trees remained alive, and most of these were heavily infested with CAS at the time (Lazaro et al. 2020). These findings indicated 60% of the mature tree population was killed within an eight year period. *Cycas micronesica* was listed as 'Endangered' under the IUCN Red List in 2006 (Bösenberg 2022a), only three years after the invasion. Members of the Cycad Specialist Group (CSG) within the Species Survival Commission of the IUCN have provided informal and formal published recommendations concerning the threats to and recovery needs of *C. micronesica* since 2005 when the CAS population began spreading into forest habitats on Guam. The decades of publications since the beginning of the invasion carry a common theme: exploit the successes of classical introduction biological control (Hoddle et al. 2021) of CAS has always been and continues to be the most important conservation action required for this species recovery.

Most nations do not possess the financial resources to lead the way in invasion biology adaptive

management research. When a wealthy nation such as the United States experiences a consequential invasion that foreshadows similar invasions in other nations, the global community looks to that wealthy nation for knowledge that evolved from their early adaptive management iterative learning process. Three recent documents highlight how misdirection of conservation activities since the 2003 Guam invasion has led to a failure to fully establish biological control of CAS. First, the United States Fish & Wildlife Service (USFWS) is required to publish a national recovery plan and five-year status reports informing taxpayers about how the Endangered Species Act (ESA) is being honored for each ESA-listed species. *Cycas micronesica* was added to the ESA in 2015 (USFWS 2015). The national recovery plan for *C. micronesica* has not been formulated to date despite published documentation of widespread ongoing mortality, and the first status report for *C. micronesica* was published in 2020 (USFWS 2020). This status report described the death of an estimated 947,556 Guam trees between 2002 and 2012 and highlighted the need for more research to reduce the impact of cycad pests. Unfortunately, the report did not list any ongoing or planned conservation actions addressing the emergency need to establish adequate biological control of CAS. Second, the United States military owns more land on the island of Guam than any other party, and the United States Sikes Act requires the publication of a multi-year Integrated Natural Resource Management Plan to steer conservation efforts. This plan guides federal resource managers with top-down directives that are used for developing funded projects. The current plan does not include any information concerning the emergency need to establish effective biological control of CAS in Guam (DON 2022). Third, a Habitat Conservation Plan for Guam is being developed by biologists in the island's territorial government agencies, and updates of the draft document are available for review (<http://www.guamhcp.com>). The current draft describes numerous expensive *C. micronesica* conservation actions including plant translocations and nursery operations, the need for more research on how to manage CAS, but again no plans for exploiting the heavily communicated best available science to establish an effective biological control program. Moreover, this plan includes the proposed creation of *C. micronesica* plants that are genetically resistant to CAS herbivory. While genetic resistance is a possible explanation for why some of Guam's *C. micronesica* trees are still alive today, this has not been verified to date. The current status of knowledge indicates that intraspecific or interspecific genetic

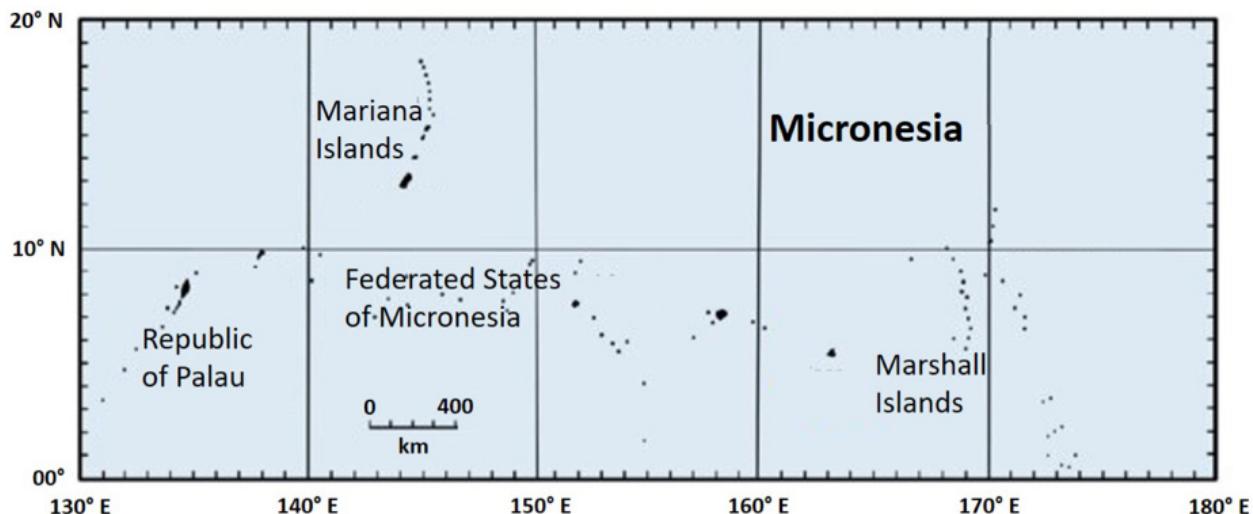


Figure 1. *Cycas micronesica* is the only cycad species native to Micronesia, and exhibits an indigenous range that includes the Mariana Islands, the western limits of the Federated States of Micronesia, and the Republic of Palau.

resistance to CAS herbivory within the *Cycas* genus has never been identified. In all countries where CAS is native, no genetic resistance among the host population has been detected. The CAS is always controlled by native predators and parasitoids in its native states. Clearly, the federal and territorial decision-makers who have been empowered to define the direction of Guam's recent and impending conservation actions have steered planning toward activities that have not honored the recommendations from the CSG since 2005.

These Guam developments have created a case study where the best available science has been ignored and evidence available to inform urgent conservation actions has been disregarded (Lindström et al. 2023). The recent invasion of Japan by CAS (Takagi 2023) has caused a repeat of the initial years following the Guam invasion, with entire crowns of leaves of the host *Cycas revoluta* Thunb. population being killed by the CAS herbivory as the first step in the process that ends in plant death (Image 2). We predict there will be sustained plant mortality that will endanger *C. revoluta* if the Japan decision-makers follow in the footsteps of the Guam decision-makers by failing to heed the IUCN's recommendation to establish immediate biological control of CAS.

Our objective herein is to plainly outline what was communicated within each of the publications that included germane recommendations from CSG members since the 2003 invasion in order to reemphasize that sustainably managing a classical biological control program of CAS remains the most important conservation endeavor needed to enable persistence of

C. micronesica. Every citation within the chronological review contained at least one member of the CSG on the authoring team, ensuring the collective knowledge from the international experts representing the IUCN directly informed the recommendations. Thereafter, we provide contemporary recommendations for funding informative adaptive management conservation actions that acknowledge the current best management practices based on evidence from the best available science.

Chronological review of recommendations prior to ESA-listing

2005

The invasions of Taiwan and Guam by CAS generated the first two case studies in which a native *Cycas* species was threatened by non-native CAS herbivory (Tang & Cave 2016). The threats to Taiwan's *Cycas taitungensis* C.F.Shen, K.D.Hill, C.H.Tsou & C.J.Chen and Guam's *C. micronesica* led the CSG to form a new subgroup in 2005 to address the growing threat to wild cycad populations posed by the artificial spread of insect pests and pathogens affecting cycads. This new subgroup immediately published a recommendation paper in hopes of informing decision-makers in Guam and other locations (Tang et al. 2005). In addition to respecting the need for employing methods that reduce the risk of spreading CAS, the need for immediate identification of biological control organisms was discussed in detail as the most important permanent response for establishing classical biocontrol in the location of every new CAS

invasion.

A commentary style article was authored by several resident biologists from Guam (Moore et al. 2005). This article detailed the initial attempts at establishing introduction biological control on Guam with the successful establishment of the predator *Rhyzobius lophantheae* Blaisdell and the unsuccessful introduction of the parasitoid *Coccobius fulvus* Compere & Annecke. The authors included the mandate that ultimate construction of effective multi-species biological control of CAS was the only conservation action that could ensure the survival of *C. micronesica*. A second commentary style article communicated the predicted demise of Guam's forests if CAS persisted without biological control into the future, the unfortunate lack of initial response by the conservation community which allowed the CAS population to become so well established by 2005, and that a multi-pronged approach rooted in biological control of CAS would be required to save the insular cycad species (Terry & Marler 2005).

2012

The Guam community operated during the first few years of conservation actions without local evidence or relevant data from other countries. Although numerous countries outside of the native range of CAS had been invaded prior to 2003 (Marler et al. 2021), no *in situ* *Cycas* habitats had been invaded prior to the Guam invasion. Several adaptive management projects were initiated which began to inform the conservation decisions by 2012. The first look at plant mortality from benchmarked permanent plots in northern Guam was published (Marler & Lawrence 2012), revealing 92% plant mortality within the first six years of CAS herbivory. This article pointed to the fact that *in situ* *Cycas* species that thrive within the native range of CAS do not experience lethal threats because of native biological control, and that *ex situ* *C. micronesica* plants growing in Thailand where CAS is controlled by natural enemies do not exhibit a decline in health despite experiencing CAS herbivory. The first of numerous recommendations to establish parasitoid biocontrol of CAS on Guam to augment the predator biocontrol was outlined.

Guam's urban landscape contained many *Cycas revoluta* Thunb. plants at the time of the 2003 invasion. The stem apex of this popular cycad species is covered with dense tomentum. This plant trait allowed CAS individuals to become established on cataphyll surfaces because the tomentum excluded the *R. lophantheae* predators (Marler 2012). The results verified that most *Cycas* plants contain microsites on various organ

surfaces within which CAS can become established where *R. lophantheae* cannot physically navigate (Marler et al. 2021). The recommendation to introduce a smaller biological control organism such as a parasitoid species was the primary actionable recommendation from this research, as these smaller CAS enemies may be able to navigate to all CAS infestation sites.

The failures to adequately pursue biological control of CAS led to the publication of a commentary article in which the ongoing negative cycad population developments were discussed (Marler & Terry 2012). Some of the limitations of the *R. lophantheae* predator were outlined along with the emergency recommendation of establishing at least one parasitoid species to augment the established *R. lophantheae* predation.

2013

The levels of infestation of CAS, *L. pandava*, *Erechthias*, and *A. Marianarum* were followed from 2005-2013 and the interplay among the four arthropod herbivores became more fully understood (Marler 2013a). Increases in CAS damage led to subsequent increases in *A. Marianarum* damage and subsequent decreases in *Erechthias* damage. Alternatively, increases in CAS damage led to concurrent decreases in *L. pandava* damage. The need for a parasitoid biological control organism was reiterated, along with the prediction that future improvements in CAS control may lead to increases in *L. pandava* damage.

Experimental elevation of container-grown *C. micronesica* seedlings within *in situ* forest settings revealed that the predator *R. lophantheae* was more effective at controlling CAS at higher strata and less effective at lower strata (Marler et al. 2013). The findings were discussed along with the recommendation of establishing parasitoid biological control organisms which may not be constrained by the same stratification issues.

A commentary article analyzed various issues regarding stratification of *R. lophantheae* predation success (Marler 2013b). The reasons for the persistence of greater prevalence of CAS on *C. micronesica* leaves close to the soil surface were discussed in length. Accurate sampling methods are required to fully assess biocontrol efficacy, and the vertical heterogeneity in CAS incidence one decade after the Guam invasion indicated *R. lophantheae* biocontrol efficacy was clearly impaired when cycad leaves persisted close to the soil surface.

A comprehensive listing of known biological control agents was published to provide the Guam decision-



Image 1. *Cycas micronesica* is an attractive, arborescent cycad species with large pinnately compound leaves that radiate from the stem apex.
© Thomas Marler.

makers the names of the organisms that could be pursued for immediate introduction to Guam (Cave et al. 2013). The need to introduce at least one parasitoid to augment the *R. lophantheae* biological control was repeated.

2014

The sustained lack of concern toward the need to biologically control CAS was addressed in another commentary style article (Marler & Lindström 2014). This opinion article proposed approaches to address stakeholder apathy or outright objection to the need for urgent conservation interventions when a native tree species is threatened with extinction. The limitations of

R. lophantheae biological control were discussed in the context of global invasion science, whereby the Guam case study unfolded as an example that may inform conservation efforts in other invaded islands within which initial biological control efforts were unsuccessful.

Summation of recommendations prior to ESA-listing

Preemptive conservation endeavors may be highly effective for ensuring a proposed species is not ultimately added to a national endangered list such as the ESA (Treakle et al. 2023; Stanley et al. 2024). The CAS invasion that caused the ultimate ESA-listing of *C. micronesica* was predicted in 2000 (Marler 2000) and occurred in 2003 (Deloso et al. 2020; Marler et al. 2021). As outlined



Image 2. The armored scale *Aulacaspis yasumatsui* has recently invaded natural habitats of *Cycas revoluta*. This 16 May 2024 photograph from Japan's Amami-Ôshima island reveals the rapid death of every pre-existing leaf as the first step that begins sustained damage that leads to ultimate plant death. © Thomas Marler.

above, the formal recommendations explicating the emergency conservation actions required to save *C. micronesica* from extinction risk began in 2005 and continued throughout the years prior to the ESA-listing. Moreover, the United States military was the landowner with the greatest number of *C. micronesica* plants within their custody at the time of the invasion. The deciders responsible for management decisions concerning federal lands are required by law to use evidence-based management decisions that respect the best available science. These deciders who controlled the policy and

budget directions were provided a full decade of IUCN recommendations based on best available science prior to the ESA-listing. The decisions instead directed planning and considerable funding into conservation actions that did not address the recommended biological control of CAS, ensuring the addition of *C. micronesica* to the ESA.

Chronological review of recommendations after the ESA-listing

Cycas micronesica was added to the United States ESA in 2015 (USFWS 2015). Based on United States Forest

Service surveys of mature tree populations, almost 100,000 of Guam's *C. micronesica* trees died each year within one decade after the CAS invasion (Donnegan et al. 2004; Lazaro et al. 2020) and during a timeframe in which the CSG had been recommending emergency establishment of multi-species biological control of CAS (Marler & Terry 2005; Moore et al. 2005; Tang et al. 2005). These explicit biocontrol recommendations from the scientific community continued into the years following the ESA-listing.

2016

The need to provide another detailed listing of potential biological control organisms led to another publication that enumerated the available CAS predators and parasitoids along with their attributes and limitations (Tang & Cave 2016). This publication provided the Guam deciders with the latest adaptive management recommendations derived from global biocontrol research concerning which organisms carried the greatest potential for introduction to save *C. micronesica* from continued CAS-induced mortality.

2017

The first project designed to evaluate methods of salvaging mature trees from military construction sites resulted in a description of the moderate success in producing adventitious roots on large *C. micronesica* stem cuttings obtained from CAS-damaged trees (Marler & Cruz 2017). In discussing the conservation implications, the authors noted the emergency need of establishing effective biological control of CAS on Guam, and due to limited conservation funds all available public funds should not be spent on expensive salvage projects unless efficacious classical biological control is first established.

The sustained lack of concern for the need to establish biological control of CAS was addressed in another opinion style article in which the ill-informed focus on salvage of *C. micronesica* trees from construction sites was discussed (Marler & Lindström 2017). Again, recommendations to refrain from spending more conservation funding on plant translocation projects were communicated along with the assertions that redirecting those funds to expanded biological control efforts such that "...the plant mortality will cease and the species can be removed from the ESA-listing." The need to collect parasitoids within the native range of CAS was discussed along with how to maneuver through the problem that many of these parasitoids would be new to science which would require that they be described

and named prior to introduction to Guam.

2018

The ongoing inability of *R. lophantheae* to adequately control Guam's CAS population led to an olfactometer study which demonstrated the preferential navigation of the predator toward mature leaves infested with CAS (Marler & Marler 2018). Guam's *C. micronesica* seedling population was rapidly killed by CAS herbivory (Marler & Lawrence 2012; Marler & Krishnapillai 2020), and the results of the olfactometer study illuminated another potential explanation for why the established predator had been ineffective in stopping the seedling mortality. The findings were discussed in the context that parasitoid biocontrol was urgently needed on Guam because parasitoids may not be constrained by the same issues that caused the predator biocontrol to be inadequate.

The results of a second study that refined methods to improve adventitious root formation on large stem cuttings were published (Marler 2018). The findings verified that reduced stem carbohydrates resulting from long-term CAS infestations were correlated with reduced asexual propagation success. Again, the recommendations included the need to refrain from expending human and budgetary resources on expensive salvage projects, as these resources should instead be spent on sustainably controlling the ubiquitous CAS infestations using classical biological control protocols.

2020

The influence of inadequate biological control of CAS on Guam was shown to reduce *C. micronesica* height increment among surviving trees (Marler et al. 2020). These data were combined with population-level mortality data to estimate that at least 70 years of demographic depth had been removed from Guam's *C. micronesica* population by 2020. Recommendations that developed from the study included the cessation of funding expensive salvage projects and that use of all available funds to "...launch biological control of the primary threats would establish the road to species recovery."

A comprehensive look at island-wide *C. micronesica* survival was published from benchmarked permanent plots (Marler & Krishnapillai 2020). The results confirmed the complete mortality of seedlings, saplings, and juveniles shortly after CAS herbivory, and 96% population mortality by 2020. The primary recommendation was to "...establish a complex integrated biological control program under the direction of scientists with appropriate international expertise" as the only conservation action

that may enable recovery of *C. micronesica*.

The adaptive management literature from Guam had continued to accumulate throughout the years since 2003, and the first of several formal review articles was published as a comprehensive outline of herbivore and omnivore threats to *C. micronesica* survival (Deloso et al. 2020). Although the list of cycad consumers had grown by this time, CAS was identified as the single greatest threat to Guam's cycad population. The need for the conservation community to stop funding salvage projects and instead invest unreservedly into classical biological control of CAS was repeated.

2021

A detailed look at how the Guam CAS invasion fit into the chronology and geography of CAS invasions throughout numerous countries was published (Marler et al. 2021). Enemy release occurs when an invasive species thrives within its invaded locations as a result of the lack of native biological control by enemies found within its native range (Heger et al. 2024). The long list of CAS invasions has revealed that the lack of natural enemies allowed CAS to kill its host plants until local biologists established biological control. Recommendations indicated that a dedicated search for fortuitous biological control organisms within newly invaded locations should be combined with the purposeful introduction of predators and parasitoids from other managed biocontrol programs which could provide advice and rapid responses.

2023

The results from another asexual propagation study were published which revealed that a CAS-infested plant may be killed by the added stress of transplantation or the take of stem cuttings for adventitious root formation (Marler 2023a). The findings indicated that salvage and propagation of CAS-damaged *C. micronesica* comprise an ill-informed conservation agenda and implementing sustainable biological control of CAS as recommended in 2005 remained the most important conservation agenda.

The fact that CAS herbivory reduces non-structural carbohydrates and this response to the herbivory decreases asexual propagation success was exploited to demonstrate that a visual starch stain technique could be useful for identifying CAS-damaged host trees that would yield the best chances of propagation success during salvage programs (Marler 2023b). The discussion of relevant conservation issues reiterated that "...species recovery would ensue without the need for expensive

propagation and translocation rescue projects" if conservationists would stop spending funds on salvage and nursery projects and instead direct all available funds to establishing a multi-species classical biocontrol program.

The influence of the Guam CAS invasion on *C. micronesica* female tree behavior was studied following benchmarked pre-invasion data, and revealed reproductive effort and output remained constrained two decades after the invasion (Marler & Terry 2023). The outcomes revealed that, if adequate establishment of classical biocontrol of CAS were to be achieved, species recovery may require conservation practitioners to proactively manage population-level regeneration and recruitment behaviors. The implementation of a coalition of biological control organisms to stop the CAS-induced population damage was discussed as the most important conservation agenda.

The May 2023 Typhoon Mawar imposed the strongest tropical cyclone windspeeds on Guam since the 2003 CAS invasion. A coalition of CSG members responded to this stochastic event by discussing how the tropical cyclone caused damage to the in situ *C. micronesica* population & interacted with the history of funded conservation actions (Lindström et al. 2023). The recommendations indicated that "...a dedicated multi-step procedure for establishing classical biological control" remained the most important conservation action for saving *C. micronesica*, and that a serious response to the 2005 biocontrol recommendations (Moore et al. 2005; Tang et al. 2005; Terry & Marler 2005) would have likely preemptively mitigated the CAS threat such that *C. micronesica* would have never been ESA-listed.

2024

Disparities in biotic and abiotic stressors among the Guam and Rota habitats that were invaded by CAS from 2005-2010 were exploited to reveal the *C. micronesica* population response to nascent CAS damage was remarkably homogeneous (Marler & Cruz 2024). The results indicated that all co-occurring threats can be ignored by conservationists who should focus exclusively on establishing immediate classical biocontrol of CAS to remove the primary threat to species survival.

Summation of recommendations after ESA-listing

The general tone of the recommendations within CSG publications during the years following the ESA-listing was essentially a continuation of the decade of recommendations that were published prior to the ESA-

listing. Funding from the U.S. military for *C. micronesica* conservation activities within Guam's forests was initiated in 2012, a project described by Marler & Cruz (2017). The amount of funding increased dramatically following the ESA-listing, resulting in the investment of more funds for cycad conservation than in any other location worldwide. These expensive projects were designed without any of the available public funds directed toward expanding biological control of CAS. Therefore, a new theme that began to define the CSG publications was the unfortunate misdirection of the millions of dollars of federal funding toward activities that were of no consequence to the primary threat of CAS herbivory.

Parallels

This devastating pest has steadily expanded its invasive range during the antecedent three decades. When CAS invaded Taiwan, the threat to the endemic *C. taitungensis* was immediate (Marler et al. 2021). Several years of CAS population expansion were required before CAS infested the in situ *C. taitungensis* localities, and the resulting plant mortality reached 62% by 10 years after the initial invasion (Liao et al. 2018). As a result, the status of this endemic island cycad was changed from Vulnerable to Endangered in 2010 (Bösenberg 2022b). The parallels to the Guam case study were striking, as the *C. micronesica* threat status was changed from Near Threatened to Endangered in 2006 (Bösenberg 2022a).

A remote ex situ germplasm collection of Guam's *C. micronesica* genotypes was constructed on the island of Tinian beginning 2006 and consisted of \approx 1200 healthy plants in 2018 (Brooke et al. 2024). The Implementation Plan for managing this valuable germplasm exploited the concepts of "proactive biological control" (Hoddle et al. 2018). This biological control approach differs from classical biological control in that available natural enemies are pre-selected and permitted for introduction and release prior to an anticipated invasion of a target invasive pest. Development of proactive biological control programs are analogous to purchasing insurance, since the initial lag phases of classical biological control are avoided (Hoddle 2024). The scale predator *R. lophantheae* was established on the nearby island of Rota at the time, and collection, transport to Tinian, and release in Tinian had been pre-approved in the event that CAS invaded Tinian at some time in the future. The plan mandated the cessation of all management activities until immediate introduction of *R. lophantheae* to Tinian had been successful, a process that should have required no more than 24–48 h. Unfortunately,

the military biologists responsible for managing this germplasm and the practitioners contracted to protect the germplasm did not follow the mandates of the plan, allowing the nascent CAS infestation to become firmly established. The lack of concern for following through with the proactive biological control plan caused 83% mortality of the germplasm within four years of the invasion (Brooke et al. 2024).

Recent invasions persist that threaten more iconic endemic *Cycas* species. For example, the 2006 predictions that an armoured scale invasion to India would threaten the endemic *Cycas circinalis* L. (Muniappan & Viraktamath 2006) have come to pass with the 2023 invasion of the closely related *Aulacaspis madiunensis* Zehnter (Joshi et al. 2023). Similarly, Amami-Oshima Island was invaded by CAS in 2022 (Takagi 2023), and the subsequent invasions of other Ryukyu Islands and initial mortality of the endemic *C. revoluta* populations have been alarming developments (Deloso et al. 2024).

The continuing expansion of the invasive range of CAS underscores the value of the lessons learned from Guam, where a native *Cycas* species was threatened by non-native armoured scale herbivory for the first time. These lessons call for resident scientists and conservation agents in newly invaded countries to embrace the recommendations from international experts and implement immediate adaptive management endeavors addressing every facet of biological control.

Contemporary observations and recommendations from Guam

Benchmarked permanent plots throughout Guam revealed 245 stems per ha were alive in some 2015 habitats when *C. micronesica* was federally listed (Marler & Krishnapillai 2020). These same plots revealed 157 stems per ha were alive in 2020 when the five-year species recovery status report was published (USFWS 2020), indicating 36% mortality of the 2015 population occurred during these five years of federal protection. All available evidence indicated that 100% of this mortality was a direct result of herbivory by CAS and the resulting increases in damage by native stressors such as *A. Marianarum* (Marler 2013a) and tropical cyclone winds (Marler et al. 2016). These native stressors were not damaging to the cycad population prior to the plant damage imposed by the CAS invasion. Yet the USFWS reviewed the first five years of ESA protection (USFWS 2020) with no mention of any biological control efforts designed to address the CAS threat. Similarly, the contemporary Integrated Natural Resource Management Plan crafted to define the ongoing conservation actions

of the U.S. military (DON 2022) failed to mention any plans to expand biocontrol of CAS on Guam. This Guam case study has unfolded to inform conservationists in other regions of the world that apathy toward recommendations of international specialists concerning the need for immediate biocontrol of CAS can rapidly impose irreversible damage to *in situ Cycas* populations and the ecosystem services that they provide.

What is needed to more fully understand the current status of *C. micronesica* population survival and desired species recovery? We recommend that biologists within federal funding and permitting agencies at least minimally begin to connect with knowledgeable input from international experts. The many mistakes made in the heavily funded conservation projects on Guam could have been avoided if the funding agencies had followed this recommendation. For example, the U.S. military has spent millions of U.S. dollars on *C. micronesica* conservation in the past decade, numbers that dwarf the amount of cycad conservation funding from all other sources worldwide, yet none of these funds have been devoted to expanding the coalition of predator and parasitoid species to enhance the control of CAS on Guam. Therefore, a fundamental shift in culture of the empowered conservation decision-makers will be required to enable a respect for the need to embed adaptive management research by qualified specialists within every conservation project. As early as 2008 this Guam case study was being highlighted as an example in which the lack of rapid establishment of biological control of a new herbivorous insect invasion could cause irreversible damage to ecosystems (Messing & Watson 2008), and yet today the lack of adequate CAS biological control continues to be the greatest threat to *C. micronesica* survival.

Parasites comprise an ancient life form that remains prevalent today (Poulin 2014). Parasitism is an integral component of ecosystem function (Hatcher et al. 2012). The exploitation of highly specific parasitoids as endoparasites to control damaging herbivore arthropods has been a successful component of managed biological control programs for decades (Eggleton & Belshaw 1992). We continue to believe that the managed construction of a coalition of biological control organisms that includes parasitoids will actively suppress Guam's CAS population and passively engineer the recovery of the *C. micronesica* population. The list of biocontrol organisms that are available to introduce to Guam is extensive (Cave et al. 2013; Tang & Cave 2016; Marler et al. 2021).

Numerous attempts to introduce the parasitoids *C. fulvus* and *Aphytis lingnanensis* Compere to Guam

from Florida and Hawaii were unsuccessful (Marler & Lindström 2017). The reasons for the lack of success remain elusive, but there was no parasitoid specialist included in those Guam activities. We recommend the inclusion of a parasitoid specialist to oversee a repeat of these endeavors, as both parasitoid species are readily available within the U.S.A. Dedicated trips to rear parasitoids from CAS-infested *Cycas* leaves within the CAS native range has led to collection of parasitoids that have not been described (Marler & Lindström 2017). These organisms cannot be imported to Guam until a taxonomist places a binomial on the animal, which is a prerequisite to applying for mandatory import permits. We have recommended a multi-stage program within which these parasitoids are described and named by taxonomic experts as part of the initial funding (Marler & Lindström 2017; Lindström et al. 2023), and we repeat this recommendation here. These conservation actions could have been completed between the 2003 invasion and the 2015 ESA-listing with a fraction of the funds that have been spent on *C. micronesica* salvage, transplantation, and nursery endeavors.

The fortuitous improvement in health of Guam's *in situ C. micronesica* population has been reported in the past few years (Lindström et al. 2023; Marler & Terry 2023). Some contemporary trees exhibit healthy leaves with no signs of herbivory, which is something that has not occurred since 2005. These observations point to a pivotal time period in which conservationists need to identify why reduced CAS herbivory is fortuitously occurring. Numerous geographic regions are characterized by native *Cycas* species, native CAS, and native biocontrol organisms coexisting in harmony. In these settings, the host plants are typically infested with CAS but remain unthreatened (Marler & Lindström 2017). Some *C. micronesica* trees in various Guam habitats exhibit general appearance that mimics the *Cycas* trees in these regions where native CAS is controlled by native natural enemies. These observations indicate that the likely cause of the recent decrease in CAS herbivory on Guam is a fortuitous improvement in biological control of the resident CAS population. An experienced cycad biologist would possess the wherewithal to experimentally determine if currently unidentified biocontrol of CAS has developed in recent years on Guam. The team of deciders empowered to define future conservation actions on Guam should include at least one cycad specialist who has worked within habitats containing sympatric native *Cycas*, CAS, and CAS enemies, as these biologists understand the gestalt traits of the cycad and CAS populations under

these sustainably controlled conditions.

We believe the CAS invasions of Guam in 2003, Rota in 2007, and Palau in 2008 were enabled by the frequent international flights in these three airports, flights from regions that contained *Cycas* populations that were heavily infested with CAS. We also believe that the infrequent flights to the Yap airport explain why Yap remains uninvaded by CAS to date, despite a thriving *C. micronesica* population. New investments of United States national security funding into Yap will likely ensure a CAS invasion of Yap in the near future. Indeed, an estimated US\$37 million is being spent to expand the Yap Island airport (Island Times 2023) and an estimated US\$3.3 billion will be spent on Yap and other FSM islands over next 20 years (Island Times 2024). The resulting increases in human travel to Yap indicate that *C. micronesica* conservationists need to be on the lookout for the probable Yap invasion by CAS in the near future.

The Guam and Rota cycad populations were decimated by the CAS invasions of those islands because of apathy toward the need to rapidly establish biocontrol. Yap's conservation community has an opportunity to be ready to construct the biological control program that will be required to save Yap's *C. micronesica* population from being decimated by CAS. Similarly, the conservation communities within the recently invaded *C. circinalis* and *C. revoluta* habitats have an opportunity to construct the biological control program that will be required to save these iconic cycad species. In so doing, they can emerge as the first location where successful conservation actions were implemented in compliance with evidence-based approaches based on the best available science as communicated by the CSG.

Global Biodiversity Targets

Lessons from every conservation case study are integral for informing the global biodiversity crisis. Legal instruments that create opportunities for international cooperation are useful for addressing declines in genetic diversity, compromises in ecosystem services, and the risk for localized ecosystem collapse. The Kunming-Montreal Global Biodiversity Framework (GBF) has been developed to operationalize global biodiversity targets (Convention on Biological Diversity 2022). Single species case studies in isolated island communities do not operate in isolation from global crises, and goals of the GBF will not be possible without commitments for compliance in these isolated biodiversity cases.

The GBF's four goals and 23 targets provide guidelines to mobilize resources to maintain the Earth's biodiversity. This Guam case study falls directly in line

with species and ecosystem conservation in goal A, with attention on threats that are driven by human activities. Implementation of this goal requires local conservationists to identify the factors that are known to threaten each species as the baseline for progress. As outlined in this review, the threats to *C. micronesica* are clearly understood and have been pointedly communicated in the primary literature for decades. Recovery actions in target 4 for species that require urgency necessitates the identification of the root causes of human-induced extinction. The consistent and ongoing expansion of the invasive range for CAS (Marler et al. 2021) has emerged as one of the greatest threats to cycad conservation (Tang et al. 2005), and the root causes of the threats are unambiguously understood as transport of CAS-infested plant materials and phoresis of CAS crawlers through human travel. This Guam case study falls directly under target 6 which calls for combatting the consequences of invasive species. The demise of Guam's 2005 *C. micronesica* population when CAS began killing in situ plants has been documented with 96% mortality as of 2020 (Marler & Krishnapillai 2020), and as outlined herein the causes have been a failure to implement a classical multi-species biological control program to mitigate the CAS threat.

Goals and targets are integral parts of the international solution to guide biodiversity policy reforms. Successful implementation, however, cannot occur without learning from past programs which provide successful and unsuccessful case studies. Bureaucracy and politics have been identified as institutional barriers, and staff turnover and limited use of available knowledge have been identified as organizational barriers to successful recovery of endangered species (Guerrero et al. 2024). Guam's government agency bureaucracy, inter-agency politics, lack of collaboration with international experts, violation of human rights of Guam's indigenous peoples, rapid turnover of consequential decision-makers, failures to respect the value of adaptive management, and waste of resources on inconsequential projects have been discussed as barriers to conservation of *C. micronesica* and as root causes of environmental destruction (Marler 2014, 2019; Marler & Lindström 2014, 2017; Marler & Cruz 2017, 2024; Lindström et al. 2023; Brooke et al. 2024; Deloso et al. 2024). These barriers have been successfully exploited to marginalize international experts from having a seat at Guam's decision-making table. They have also generated public condemnation by the United Nations of the violations of human rights of Guam's indigenous peoples (United Nations Commission

on Human Rights 2021) and an ongoing lawsuit from the Center for Biological Diversity for systemic violations of the tenets of the ESA (Center for Biological Diversity 2023). The contributions of this case study to future cycad conservation endeavors in particular and the GBF in general will require deciders in other countries which are invaded by CAS to avoid these same barriers.

SUMMATION

The 2003 CAS invasion of Guam created a case study that held the potential to develop mitigation protocols through biocontrol adaptive management research that could inform conservation planners in other nations where subsequent CAS invasions threatened native *Cycas* species. The deciders who hold power over the planning and funding of Guam's conservation actions have not exploited this opportunity. There is an urgent need to overhaul the manner in which Guam's policy and funding deciders view the input of relevant specialists. This Guam case study informs conservationists in other regions of the world that apathy toward inputs from international specialists concerning the need for immediate biocontrol of CAS can rapidly impose irreversible damage to *in situ* *Cycas* populations.

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Articles

Endemicity and diversity of birds of the Kuvempu University Campus, Shivamogga District, Karnataka: an updated checklist

– M.N. Harisha & B.B. Hosetti, Pp. 26063–26077

Unregulated wild orchid trade in Manipur: an analysis of the Imphal Valley markets from the Indo-Burma hotspot

– Kamei Kambuikhonlu Kabuini & Maibam Dhanaraj Meitei, Pp. 26078–26088

Watershed survey of streams in western Bhutan with macroinvertebrates, water chemistry, bacteria and DNA barcodes

– Juliann M. Battle, Bernard W. Sweeney, Bryan Currinder, Anthony Aufdenkampe, Beth A. Fisher & Naimul Islam, Pp. 26089–26103

Communications

Indian Leopard predation on the sub-adult Himalayan Griffon Vulture (Accipitridae: Accipitriformes)

– Soumya Sundar Chakraborty, Debal Ray, Apurba Sen, P.J. Harikrishnan, Nabi Kanta Jha & Rounaq Ghosh, Pp. 26104–26109

Diet composition and diet choice of Lesser Mouse-tailed Bat *Rhinopoma hardwickii* (Gray, 1831) (Rhinopomatidae: Chiroptera)

– Pawan Kumar Misra, Sayma Farheen, ShaktiVardhan Singh & Vadimalai Elangovan, Pp. 26110–26115

DNA barcoding and distribution of *Osteobrama peninsulae* (Teleostei: Cyprinidae) in India

– Boni Amin Laskar, Asha Kiran Tudu, Shibananda Rath & Laishram Kosygin, Pp. 26116–26123

Diving into diversity: aquatic beetles of Sukhna Wildlife Sanctuary, Chandigarh, India

– Karmannye Om Chaudhary, Pp. 26124–26130

Review

An updated checklist of snakes (Reptilia: Squamata) in northeastern India derived from a review of recent literature

– Bijay Basfore, Manab Jyoti Kalita, Narayan Sharma & Ananda Ram Boro, Pp. 26131–26149

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Viewpoint

Decades of IUCN recommendations for biocontrol of invasive pest on the Guam cycad: you can lead policy-makers to conservation proposals but you cannot make them follow

– Thomas E. Marler, Anders J. Lindström, L. Irene Terry & Benjamin E. Deloso, Pp. 26150–26162

Short Communications

Photographic record of Kashmir Gliding Squirrel *Eoglaucomys fimbriatus* (J.E. Gray, 1837) from the Gurez Valley, Jammu & Kashmir, India

– G. Mustufa Lone, Bilal A. Bhat, Mir Shabir Hussain & Arif Nabi Lone, Pp. 26163–26166

Winter population of raptor species in the Vellore dump yard of Coimbatore City, India

– V. Balaji & R. Venkitachalam, Pp. 26167–26171

Notes

Phenotypic variations in Mindoro Warty Pig *Sus oliveri* (Cetartiodactyla: Suidae)

– John Carlo Redeña-Santos, Anna Pauline O. de Guia, Nikki Heherson A. Dagamac & Fernando García Gil, Pp. 26172–26175

First photographic evidence of the Chinese Pangolin *Manis pentadactyla* (Linnaeus, 1758) in Raimona National Park, Assam, India

– Dipankar Lahkar, M. Firoz Ahmed, Bhanu Sinha, Pranjal Talukdar, Biswajit Basumatary, Tunu Basumatary, Ramie H. Begum, Nibir Medhi, Nitul Kalita & Abishek Harihar, Pp. 26176–26179

Habenaria spencei (Orchidaceae): rediscovery other than its type locality and new distribution record to Karnataka, India

– Shreyas Betageri & Katrahalli Kotresha, Pp. 26180–26184

Book Review

Fairies of the day and angels of the night

– Chitra Narayanasami, Pp. 26185–26186

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