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SPECIAL FEATURE REVIEW

Current topics on cycad biology: Deciphering the Rosetta Stone of plant evolution

Biological invasion by the cycad-specific scale pest *Aulacaspis yasumatsui* (Diaspididae) into *Cycas revoluta* (Cycadaceae) populations on Amami-Oshima and Okinawa-jima, Japan

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Abstract

The islands of the Ryukyu archipelago in Japan are biologically diverse, supporting numerous plant and animal taxa found nowhere else. One of the most iconic plants is *Cycas revoluta* Thunb., the only cycad native to Japan. At this moment, the community of cycad researchers is concerned about the impacts caused by the recent invasion of the cycad aulacaspis scale (*Aulacaspis yasumatsui* Takagi) into the wild populations of *C. revoluta* in the islands of Amami-Oshima and Okinawa-jima. Within the last three decades, this cycad-specific scale has been inadvertently transported outside its native range in southeastern Asia and is known to cause high mortality on both wild and cultivated cycad species that are not evolutionarily and ecologically adapted to the effects of its infestation. Currently, neither the extent of the spread in Japan nor the attendant ecological impacts are well characterized; thus, several recommendations to mitigate the potential threat are proposed here. Monitoring the impact of the scale pest and evaluating the use of native predators as biological control organisms for *A. yasumatsui* are recommended. Considering the already known genetic diversity and spatial genetic structure of *C. revoluta*, we recommend establishing in situ and ex situ colonies to assure the conservation of its genetic composition in case of loss of populations.

KEYWORDS

conservation, cycads, invasive species, island biogeography, pest control

1 | INTRODUCTION

Biological invasions are increasingly common during the Anthropocene as humans continue to vector species, either deliberately or inadvertently (Simberloff, 2013). These invasions can have dire impacts on local biodiversity and, through secondary impacts, can drive overall habitat degradation or loss. The associated management costs are likewise impactful, particularly in economically under-resourced regions (Diagne et al., 2021). Insular areas are typically more vulnerable to biological invasion, as such ecosystems have evolved in relative isolation and are hence less resilient to invasion than their continental counterparts (Fordham & Brook, 2010). Moreover, they tend to harbor more endemic species, so the potential for extirpation and extinction of native biodiversity is high.

Several islands in the Pacific Ocean harbor unique species of cycads. Collectively, cycads are one of the most imperiled groups of organisms globally (IUCN Red List, 2023, Brummitt et al., 2015; Fragniere et al., 2015), with roughly 70% of species assessed as threatened. In this article, we focus on *Cycas revoluta* Thunb. (Cycadaceae), the only native cycad from Japan. Described in 1782 by Swedish botanist Carl Thunberg, *C. revoluta* is the third oldest cycad to be formally described (Osborne, 2011) (Figure 1). Curiously, the Japanese common name *sotetsu* (蘇鉄) translates to "coming back from the death by iron," referring to the apparent phenomenon of driving a rusted iron nail into the trunk of a debilitated plant with the plant soon rejuvenating thereafter (Osborne & Tomiyama, 1995). At the time of Thunberg's description, *C. revoluta* had been cultivated in Europe for about 100 years (Osborne, 2011), but in the Ryukyu Islands, where this taxon is endemic, *C. revoluta* has been revered by people for centuries, forming part of the alimentary, agroecological, and symbolic identity of the local culture (Englehardt & Carrasco, 2023; see also Englehardt et al. 2024). For example, people from the Ryukyu Islands have used cycads as a source of food that was especially needed during times of famine, have used cycads as wind and sea breaks to protect fields and other food crops (Kira & Miyoshi, 2000; Kogure, 2022), and have given the cycads a symbolic and sacred significance that has been preserved to date. Nowadays, *C. revoluta* is cultivated in shrines, temples, public and private gardens, and as a container and bonsai subject. Young plants and seeds of *C. revoluta* are widely propagated for worldwide export. *Cycas revoluta* is found as an outdoor landscape plant in countries with an appropriate climate and as a potted plant in countries with cooler temperatures. Thus, *C. revoluta* is arguably the most cultivated cycad species globally (Donaldson, 2003; Thieret, 1958).

Cycas revoluta has become popular worldwide not only due to its aesthetic value as a garden plant, but also due to the unique and appraised set of biological characteristics shared with other cycads that evidence them as evolutionarily conservative plants (Gutiérrez-Ortega et al., 2024; Ito-Inaba et al., 2019). For example, many cycad species, including *C. revoluta*, can grow in soil conditions that might not be optimal for other plants (Marler & Calonje, 2020a). One physiological explanation for this resilience in poor soils is that all cycads employ symbiotic relationships with cyanobacteria, housed in root structures termed coralloid roots, which capture and convert atmospheric nitrogen into a useable form for plant use (Gutiérrez-García et al., 2019; Norstog & Nicholls, 1997). This function may also improve soil nutrient composition, benefitting other plants growing near cycads (Marler & Calonje, 2020a). Another feature that makes cycads attractive for biologists and ecologists

FIGURE 1 Healthy *Cycas revoluta* plants in habitat in Uken-son, Amami-Oshima. Credit: Jui-Tse Chang.

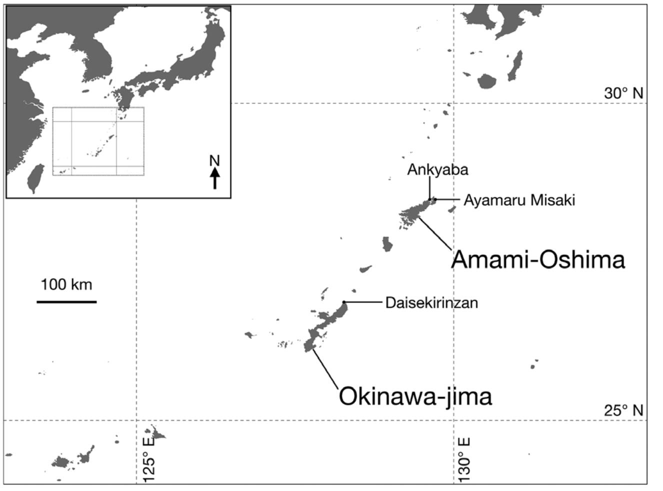

FIGURE 2 The Ryukyu Islands, Japan. The locations of Amami-Oshima, Okinawa-jima, and specific locations mentioned in the text are indicated.

is their association with insects. The association with thrips and beetles as brood–pollination mutualists has gained attention to clarify the evolutionary consequences of symbiosis (Salzman et al., 2020; Terry et al., 2012; Toon et al., 2020). Additionally, several herbivorous insects have co-evolved to feed specifically on cycad hosts (Prado, 2011).

In 1972, a new species of cycad-specific scale insect was discovered on cultivated *C. revoluta* plants in Thailand and formally described as *Aulacaspis yasumatsui* Takagi (Takagi, 1977). *A. yasumatsui* is commonly known as the cycad aulacaspis scale (CAS) and will hereafter be referred to as such. Cycad aulacaspis scale feeds on the sap of cycads. The infestation often begins by crawlers, the first instar of the insect, settling on the leaflets and progresses through the rachis and petiole until covering the whole body of the plant within a few months. All plant parts, including the coralloid roots, are attacked by the insect. Cycad aulacaspis scale causes damage by depleting the non-structural carbohydrates from all organs (Marler & Cascasan, 2018), causing stress that desiccates the plants until death. Cycad aulacaspis scale is native to Southeast Asia, ranging from the Andaman Islands to Vietnam (Marler et al., 2021). Within its native range, this insect usually does not cause plant mortality, and several of us (A. Lindström, B. Deloso, T. Marler, W. Tang, R.D. Cave) have observed parasitoids within this range that presumably have co-evolved with CAS and might control the populations. Outside its native range, CAS has become a serious threat to cycad diversity, as we explain below. A recent invasion by CAS on the islands of Amami-Oshima and Okinawa-jima (Figure 2, Figure 3) has prompted concern among cycad biologists and enthusiasts alike. Reports by the webpage of Kagoshima Prefecture (2024) confirm that CAS has been spreading in wild populations of *C. revoluta* since at least November 2022. Given the ability of CAS to rapidly spread among wild cycad populations, we expect that the pest will become a serious threat in several other islands if prompt action is not taken. This paper aims to direct attention to this potentially serious ecological threat and to make recommendations based on the knowledge obtained from previous CAS invasions in other countries.

2 | CYCAD AULACASPIS SCALE AND ITS PRIOR INVASIONS IN OTHER COUNTRIES

In 1995, CAS was detected in southern Florida, USA, where it decimated many cultivated *Cycas* species, including *C. revoluta*, with infestations rapidly covering leaves, stems, and reproductive parts (Walters et al., 1997). Within 2 years, tens of thousands of large, well-established specimens of cultivated *C. revoluta* in southern Florida were killed by this infestation (Howard

FIGURE 3 *Cycas revoluta* plants infested by cycad aulacaspis scale near Kuninao, Amami-Oshima. Photo taken on July 30th, 2024. Credit: Benjamin Deloso.

FIGURE 4 One of the wild *Cycas revoluta* populations in northern Amami-Oshima shows a possible ongoing local extinction. Photos were taken on (a) 15 June 2023 and (b) 11 February 2024. Credit: Jui-Tse Chang.

et al., 1999; Tang, pers. obs.). In 2000, CAS was detected in Taiwan, where 62% of adult plants in one population of the native *Cycas taitungensis* C.F.Shen, K.D.Hill, C.H. Tsou & C.J.Chen (= *C. revoluta*, as currently circumscribed [Chang et al., 2022]) were killed by CAS within a few years (Liao et al., 2018).

Because of the spread of CAS and its devastation to cycads in Florida and Taiwan, Marler (2000) predicted that CAS posed an imminent threat to *Cycas micronesica* K.D Hill populations on the island of Guam. Unfortunately, CAS was detected in 2003 in the tourist district of upper Tumon on Guam and quickly spread into nearby *C. micronesica* habitats. In Guam, 88% of mature wild *C. micronesica* plants were killed by CAS within 5 years (Marler & Krishnapillai, 2020). *Cycas micronesica* went from the most abundant tree in Guam's forests to being listed as endangered by the IUCN within 5 years of the invasion (IUCN Red List: Marler et al., 2010). This precedent serves as a cautionary tale for *C. revoluta* populations in Japan. Although the IUCN conservation status of *C. revoluta* is currently least concern (LC) (Hill, 2010), the situation may deteriorate without effective action.

3 | CYCAD AULACASPIS SCALE INVASION ON CYCADS IN JAPAN

The first record of CAS in Japan is from Amami-Oshima, and the scale is spreading across the island (Figure 3) (Kawaguchi et al., 2024; Takagi, 2023). Since March 2023, CAS is also present in Okinawa Prefecture (Okinawa Times, 2024). Based on the massive die-off of *C. revoluta* and *C. micronesica* plants caused by CAS in Florida and Guam, respectively, large numbers of this cycad in the Ryukyu Islands are expected to succumb in the coming years without intervention by Japanese conservationists and authorities. As it was in the case of Guam, there is expected to be a long debate on what to do about the invasion of CAS into *C. revoluta* habitats in Japan. There may be conflicting opinions about appropriate courses of action to take regarding this alien invasion of CAS. The insect has a life cycle from egg to adult female of 32–40 days at about 25°C; hence, CAS can quickly develop dense populations on *C. revoluta* (Cave, Sciacchetano, & Diaz, 2009; Howard et al., 1999). Temporal snapshots across 10 months in northern Amami-Oshima have already shown local extinction in some areas (Figure 4). There is an urgent need for an early, unified response to CAS.

4 | AVOIDANCE OF FURTHER SPREAD

One of the priority responses to manage invasion is to limit the spread of CAS. The first instar of armored scales (the crawler stage) is the developmental stage associated with medium- to long-distance dispersal via wind currents or passive hitchhiking on passing animals, including humans (e.g., carried on clothes), a process known as phoresis (Marler et al., 2020). Cycad aulacaspis scale also spreads to new localities via transport of infested plants. Therefore, we recommend the immediate prohibition of transport of cycad plants among islands, as we still do not know the source of the invasion (see also Takagi, 2023). Until the extent of the spread is better understood, we also recommend that visitors to cultivated or natural cycad groves (e.g., Ankyaba and Ayamaru Misaki in Amami-Oshima; Daisekirinzan in northern Okinawa-jima) be restricted so as to contain further spread of CAS. A drastic measure would be to remove individual cycads cultivated along roads in the Ryukyu Islands to avoid stepping-stone dispersal of CAS to wild populations.

5 | SMALL-SCALE USE OF PESTICIDES

Pesticides to treat infested cycad plants in the landscape have been used. The conventional pesticide pyriproxifen, an insect growth regulator that prevents immature insects from attaining adulthood and thus rendering them unable to reproduce, was reported to be effective in controlling CAS without damaging the host plant (Emshousen et al., 2004). In Costa Rica, tests with six brands of locally available soaps suggested that some brands were effective at killing adults and crawlers and reducing CAS infestations (Blanco-Metzler & Zúñiga Orozco, 2013). These treatments, although costly and time-consuming to apply, may be useful in controlling CAS in small-scale landscapes, and thus this is an area of research that should be expanded in the future. However, the impact of large-scale pesticide use on wild cycad populations is not recommended due to potential impacts on pollinating insects and the development of pesticide resistance in the target pest (Tang et al., 2005).

6 | ASSURANCE COLONIES

We recommend immediate seed collection from CAS-infested *C. revoluta* populations to preserve germplasm via ex situ conservation. The priority is to establish germplasm repositories within Japan, with accessions representing as many populations as possible. Additionally, several botanical gardens outside of Japan have extensive collections of cycads. These institutions include the Montgomery Botanical Center in Coral Gables, Florida, USA; the Francisco Javier Clavijero Botanical Garden in Xalapa, Mexico; and the Nong Nooch Tropical Botanical Garden in Chon Buri, Thailand, to name a few. These and other botanical gardens could assist in conserving *C. revoluta* genetic diversity from populations under threat from CAS, especially including both genetic diversity across the previously reported genetic boundary (Chang et al., 2022, 2023).

Cycad seeds are recalcitrant and generally cannot be stored long term in traditional seedbanks, although Nadarajan et al. (2018) suggested that some species may exhibit an orthodox response to brief storage periods at -20°C. This remains to be verified for seeds of *C. revoluta*. *Cycas revoluta* seeds have shown optimal germination when sown in temperatures ranging between 25°C and 30°C (Frett, 1987). Additionally, seeds of *C. revoluta* have been reported to have germination rates of 92% germination after 6 months of air-dry storage at 2°C, compared with 42% germination when stored at 22°C (Dehgan & Schutzman, 1989). Modest seed collection from wild populations has been suggested to have no negative demographic impacts; in fact, multiple seed collections over several years may be required to capture the most genetic diversity of a population destined for an ex situ collection (Griffith et al., 2017). Additionally, seeds from healthy parent plants are the most desirable. Experience from *C. micronesica* on Guam showed that seeds originating from plants infested with CAS displayed lower germination rates, and the resulting seedlings had reduced vigor and slower growth than those from uninfested seeds (Marler, 2021). The mechanisms that cause this disparity in seedling growth are unknown, but seedlings resulting from CAS-infested *C. revoluta* seeds may exhibit similar growth behavior. We therefore recommend seed collection from as many populations as possible before the health of the adult plants is further compromised. Any seeds collected from CAS-infested *C. revoluta* plants should be fully cleaned prior to transport to nursery locations.

Another approach to starting ex situ cycad populations is through stem cuttings. Cycads are easily propagated from stem cuttings (Deloso et al., 2020; Deloso, Paulino, & Marler, 2020; Marler et al., 2020). An advantage of this approach is that stem cuttings would better capture the overall genetic diversity of the population versus only seed collection (Griffith et al., 2015; Griffith et al., 2020). This is because the collection of seeds represents only the individuals that successfully reproduced during that particular reproductive cycle. Additionally, all cycad genera, except for members of the tribe Encephalarteae (*Encephalartos, Lepidozamia*, and *Macrozamia*), produce terminal male strobili and therefore undergo anisotomous branching (Stevenson, 1992). This subsequent male branching behavior in cycads may have conservation implications if the sex of a plant can be verified before stem cuttings are collected in situ to better represent a more balanced sex ratio in an ex situ collection (Marler & Calonje, 2020b). This branching behavior can formulate stem collection protocols in *C. revoluta* habitats for future ex situ conservation. Many *Cycas* populations display low genetic diversity at the population level (Wang et al., 2019; Xiao et al., 2005; Zheng et al., 2017). In *C. revoluta*, population genetic diversity was lower in the north of the genetic boundary, including Amami-Oshima, where the CAS outbreak occurred (Chang et al., 2022, 2023). We therefore urge higher priority for Amami-Oshima population conservation compared with Okinawa-jima due to this reduced genetic diversity and recommend collection of both seed and stem cuttings to ensure a more robust representation of the genetic diversity of *C. revoluta*. Stem cuttings taken from CAS-infested areas should be treated with pesticides prior to transport to nursery areas.

7 | ASSESSING THE POSSIBLE IMPACT OF CLIMATE CHANGE

In the context of ongoing climate change and globalization, the spread of invasive species, such as CAS, poses an emergent threat to the native ecosystems of the Ryukyu Islands. Populations of *C. revoluta* in the northern Ryukyu Islands appear more genetically distinct, while at the perspective of CAS invasion potential, populations south of the genetic boundary are more vulnerable, according to present and future climatic scenarios (Satishchandra & Geerts, 2020; Wei et al., 2018). In response, we advocate using species distribution models (SDMs) while considering the recently infested localities in Amami-Oshima and Okinawa-jima to predict potential future sites susceptible to CAS invasion in Japan (Bebber, 2015). These models, rooted in the relationships between current species distribution records and environmental variables, provide a spatial representation of areas with favorable conditions for the dispersion of the invasive species (Kearney & Porter, 2009). Their application would allow authorities and natural resource managers to anticipate and strategize for management and mitigation, focusing efforts on high-risk areas (West et al., 2009). Incorporating SDMs into these islands' conservation strategy is a proactive measure and a long-term investment in protecting biodiversity and the ecological balance of these delicate insular ecosystems (Pang et al., 2021).

8 | BIOLOGICAL CONTROL

We recommend the Japanese government fund a dedicated biological control program as the best approach to saving the *C. revoluta* populations in the long term. Chemical pesticides are expensive, labor intensive, and relatively ineffective for controlling CAS (Emshousen & Mannion, 2004); they are not recommended as a long-term control technique in wild cycad populations due to cost and adverse secondary effects in the ecosystem (Tang et al., 2005). Instead, two decades of research on classical biological control of CAS suggest that this is likely the best and perhaps only effective means to control this pest in infested areas into the future (Tang & Cave, 2016). However, research is still necessary to evaluate the effectiveness and risks of the biological control strategy in the Ryukyu Islands, and this may require an international, multiagency effort and the participation of biological control experts.

Classical biological control is an old and proven technique for the control of insect pests, especially scale insects (Rosen, 1973). In this technique, entomologists visit the native habitat of an insect pest and identify its natural enemies. These natural enemies are then studied in a quarantine facility to determine under what conditions, such as temperature and humidity, they are most effective. Also, these laboratory studies determine what, if any, nontarget plants and insects these natural enemies might eat. Classical biocontrol is safe with proper research and safeguards, with few to no significant negative side effects. For example, a historical review of biocontrol efforts in Florida involving the introduction of 59 arthropods and one nematode showed that this approach has had minimal documented effects on nontarget organisms (Frank & McCoy, 2007). Likewise, a global review of more than 5000 introductions, involving about 2000 species of arthropod agents for the control of arthropod pests in 196 countries and spanning 120 years (Van Lenteren et al., 2006), found that they rarely had negative environmental effects. We understand, however, that there are concerns regarding the application of biological agents as control for pests. Releasing exotic species in vulnerable ecosystems such as islands may result in irreversible ecological damage (Louda et al., 2003). Therefore, appropriate specificity tests, risk assessments, and attentive priority to host-specific biological control agents (over generalists) and native species (over exotic ones) should be considered before the application of this technique on *C. revoluta*. As a further safeguard, any release of biocontrol agents should be linked to long-term monitoring of the populations and a continuous evaluation of its effectiveness and any negative impacts.

Within the native range of CAS, several of us (A. Lindström, B. Deloso, T. Marler, W. Tang, R.D. Cave) have observed potential biological control agents that might prevent CAS from causing fatal injury to the plant. The lady beetle *Phaenochilus kashaya* Giorgi and Vandenberg (Coleoptera: Coccinellidae) was discovered in Thailand in 2007 (Cave, Nguyen, et al., 2009; Giorgi & Vandenberg, 2012). The cycads in the dipterocarp forests where the beetle occurs were sparsely infested with CAS or had no scales (R. D. Cave personal observation). Laboratory studies indicate the beetle is a voracious consumer of CAS and a quite fecund predator (Manrique et al., 2012). In contrast, *Rhyzobius lophanthae* Blaisdell (Coleoptera: Coccinellidae) consumes fewer scales and is less fecund (Thorson, 2009). This predaceous lady beetle was released on Guam in 2005 and had limited success in controlling CAS (Marler et al., 2013; Moore et al., 2005). No recent attempts have been enacted to augment the established biological control on Guam (Deloso, Terry, et al., 2020; Marler et al., 2021).

Song et al. (2012) proposed two Southeast Asian *Cybocephalus* species (Coleoptera: Cybocephalidae) as potential biological control agents for CAS in Taiwan. *Cybocephalus nipponicus* Endrödy-Younga has a wide distribution and is well known as a predator of armored scale insects (Hisamatsu, 2015), including CAS (Smith & Cave, 2006). This predator already exists in the Ryukyu Islands, including Amami-Oshima (Hisamatsu, 2015). The tiny beetle is widespread throughout eastern China, Vietnam, and Thailand but also occurs on southern Pacific islands, the eastern USA, the West Indies, and South Africa (Smith, 2022). Recently (July 2024), surveys on Amami-Oshima and Okinawa-jima found seven species of lady beetles and one species of Cybocephalidae on CAS-infested *C. revoluta* (R.D. Cave, B. Deloso, T. Marler, and S. Nagata personal observation) but no parasitoids nor evidence of parasitism. We recommend that additional CAS predator and parasitoid surveys be conducted on Amami-Oshima and Okinawa-jima to confirm if *C. nipponicus* or other predators and parasitoids of armored scales exist and how they might affect the population sizes and dynamics of CAS on these islands. After these surveys are conducted, the new findings may inform further recommendations for biological control.

Using history as a lesson, Taiwan's past experiences showed moderately successful management of CAS with biological control. After the invasion of CAS to *C. revoluta* populations in Taiwan, physical and chemical controls were applied first with some success in managing the invasion (Forestry and Nature Conservation Agency, 2016). Subsequently, in 2003, the non-native *C. nipponicus* was introduced from Thailand. Following a rigorous risk assessment, including greenhouse experiments to test host specificity and effectiveness, the beetles were reared in large numbers before being released into the natural habitat since 2006 (Hsu, 2008). High host specificity was observed in *C. nipponicus*, suggesting potentially low ecological impact on nontarget species. The release of approximately 410 600 *C. nipponicus* individuals over 5 years, accompanied by physical and chemical controls on 500 and 2000 *C. revoluta* individuals, respectively, resulted in the control of CAS but did not lead to its eradication (Ministry of Agriculture, 2011). In the meantime, further field surveys for native natural enemies found an additional species, *Cybocephalus politissimus politissimus* Reitter (= *Cybocephalus flavocapitis* T.R. Smith), although further evaluation was not performed (Hwang, 2008).

Castillo et al. (2011) tested the entomopathogenic fungus *Cordyceps javanicus* (Frieder. and Bally) Kepler, B. Shrestha and Spatafora (Hypocreales: Cordycipitaceae) (referred to as *Isaria fumosorosea* Wize [PFR97® strain] in the publication) against first instars of CAS at two temperatures in the laboratory. The LC_{50} at 20°C and 30°C were 6.1×10^6 and 5.3×10^6 blastospores/ml, respectively. The lethal time to kill 50% of the test population was shorter at 30°C than at 20°C. *Cordyceps javanicus* may be an additional tool for management of CAS, but field tests need to be conducted.

In summary, the biological control approach aims to understand the ecological conditions and natural biological control agents that are best for bringing natural environmental balance to a disturbed ecosystem. Alien pests are reunited with their natural enemies to re-establish a natural predator–prey system. So far, research has identified at least five natural enemies of CAS that may be effective biocontrol agents in the native *C. revoluta*

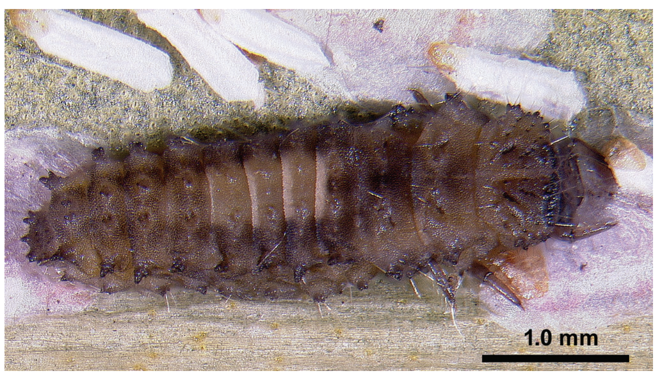

FIGURE 5 Larva of the lady beetle *Rhyzobius lophanthae*. Credit: Ronald D. Cave.

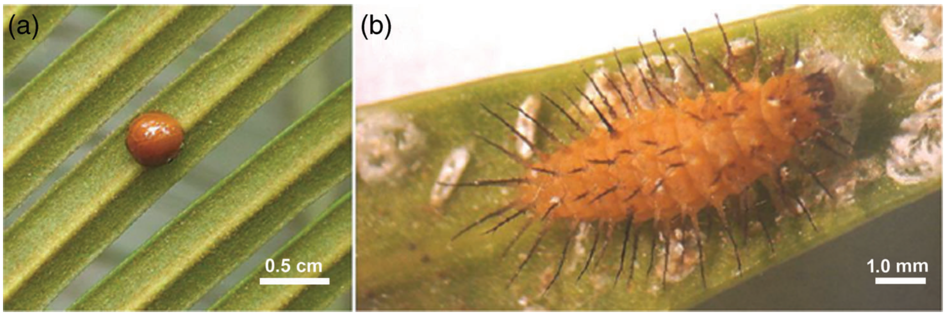

FIGURE 6 Adult (a) and larva (b) of the lady beetle *Phaenochilus kashaya*, a voracious feeder on cycad aulacaspis scale. Credit: Ronald D. Cave.

FIGURE 7 Mummified cycad aulacaspis scale with the parasitoid wasp *Coccobius fulvus* inside. Credit: Ronald D. Cave.

FIGURE 8 Inflated second instars of cycad aulacaspis scale parasitized by *Arrhenophagus chionaspidis*. Credit: Ronald D. Cave.

ecosystems of Amami-Oshima and Okinawa-jima. These natural enemies are the predatory lady beetles *R. lophanthae* (Figure 5) and *P. kashaya* (Figure 6), the minute predatory beetle *C. nipponicus*, and the parasitic wasps *Coccobius fulvus* (Compere & Annecke) (Figure 7) and *Arrhenophagus chionaspidis* Aurivillius (Hymenoptera: Encyrtidae) (Tang & Cave, 2016) (Figure 8). The two wasps are widespread throughout mainland Southeast Asia. *Phaenochilus kashaya* has not yet been tested outside of its native range on CAS-infested *Cycas* populations, but it holds promise.

Success or failure of a biological control agent in a specific region cannot be considered guaranteed success or failure in another region that experiences different ecological, climatological, and socioeconomic conditions. For untried agents that have been studied only in the laboratory, we cannot really know if they will establish and be effective in the field until they are properly introduced into the new environment and monitored. Therefore, it is imperative that all natural enemies of CAS be considered as candidates for introduction to the Ryukyus, and then carefully chosen candidates, whether or not they have achieved success elsewhere, should be released as soon as possible.

9 | CONCLUSION

The ongoing CAS invasion in Japan should be considered a serious threat to biodiversity and the local culture surrounding the species *C. revoluta*. The long-term ecosystem level effects of the CAS invasion are unknown and warrant more research. Evidence from other invaded islands demonstrates that delayed actions to manage CAS can have severe consequences. While ex situ conservation strategies are essential to ensure the species' long-term survival in case of total loss in the wild, preserving *C. revoluta* populations in situ should take priority. This means ensuring that CAS does not spread to other islands within the Ryukyu Islands and Kyushu. Because of its cosmopolitan use as a horticultural plant and its great importance in the history and ethnobiology of Japanese culture, *C. revoluta* is possibly the most iconic cycad species worldwide. In Japan, there is an opportunity for prompt, concerted intervention to ensure the future survival of this species in its native habitat.

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CONFLICT OF INTEREST STATEMENT

All authors declare that there are no financial/commercial conflicts of interest.

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