



Review

# *Aulacaspis yasumatsui* Delivers a Blow to International Cycad Horticulture

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**Abstract:** The literature covering the biology, invasion chronology, host plant responses, and control efforts of the armored scale *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae) is reviewed. The small size of this cycad pest and complex surface morphology of the host cycad organs combine to make visual detection of every cryptic infestation difficult or impossible to achieve. The international movement of *Cycas revoluta* Thunb. nursery plants and the presence of *C. revoluta* nursery industries in so many countries have enabled this pest to wreak havoc on the international cycad horticulture trade over the last 25 years. The short pre-oviposition period and considerable female fecundity lead to rapid population expansion on the plants initially infested in newly invaded regions. A depletion of non-structural carbohydrates accompanies long-term infestations and precedes plant death. Enemy escape within the invasive range allows the scale population growth to remain unchecked until anthropogenic efforts establish non-native biological control.

**Keywords:** biological control; cycad; *Cycas micronesica*; invasion biology



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## 1. Introduction

Cycad aulacaspis scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae), was first discovered in Thailand on *Cycas revoluta* plants in 1972, and was described in 1977 [1]. The scale was subsequently observed in other Southeast Asian countries and recognized as a *Cycas* L. pest. The accepted native range of *A. yasumatsui* is from the Andaman Islands to Vietnam [2], which includes Thailand, where the original collections were made that were used for the species description [1]. Within its native range, the infestations are not lethal to the host plants. The accidental introduction of *A. yasumatsui* to Miami, Florida in 1994 [2] led to widespread infestations; by the time the invasion had become common knowledge in 1996, the pest was recognized as a lethal threat to *Cycas* plants [3]. Typical horticultural protocols to control the scale were ineffective in Florida, and the insect rapidly extended its invasive range further [4].

Infestations of the scale in the presence of its natural enemies do not pose a serious threat to many cycad species, but in the absence of natural enemies, the infestations are lethal for most *Cycas* species. The international cycad horticulture nursery and landscape industries have been threatened by the pest's rapid invasion into many geographic regions. This continued expansion ultimately led to invasions into the native habitats of *Cycas micronesica* K.D. Hill [5] in Guam, and *C. taitungensis* Shen, Hill, Tsou and Chen [6] in Taiwan, immediately threatening the survival of both species. Within 10 years of the Florida invasion, the International Union for Conservation of Nature Cycad Specialist Group considered *A. yasumatsui* the single most important threat to natural cycad populations [2]. This single scale species demonstrates the immense cost and ecological impact associated with invasive species, which are increasing three-fold every decade [7].

These invasion events catalyzed the launch of research designed to understand the life history traits of *A. yasumatsui* and the responses of the host plants. Considerable effort has been invested in documenting the timing of the sequential invasions and various attempts at introducing biological control organisms. The objective of this review is to report on the *A. yasumatsui* literature produced over the last four decades since the organism was described. A review of the invasive nature of the pest since the Florida invasion may contribute to reducing the ongoing devastation of the cycad horticulture industry.

## 2. Search Methods

We conducted a Google Scholar search with “*Aulacaspis yasumatsui*” as the only query term. Based on a review of the search results, we sorted the articles into four broad categories, which defined the sections hereinafter. First, papers on the biology of *A. yasumatsui* were used to describe the traits unique to this insect (7 papers). Second, papers documenting the sequence of invasion in each country were tabulated in chronological order (30 papers). Third, papers on the plant responses by host plant individuals and populations were covered (39 papers). Finally, papers documenting the chemical or biological control programs in various countries were described (29 papers).

## 3. Biology

### 3.1. Life History

The first controlled trials conducted to understand the behavior of *A. yasumatsui* were carried out in Florida using clean *C. revoluta* plants exposed to the crawlers [3]. Under field conditions, scale densities of 70 per leaflet were observed after only 16 d of exposure, and females began egg production within 35 d. Total egg production was not assessed, but some female scale covers contained up to 110 eggs. Some eggs were incubated at 25 °C to determine the number of crawlers hatched in 8–12 d. This initial observational study revealed the high reproductive potential and speed with which the pest could threaten a host plant.

The first controlled study of *A. yasumatsui* ontogeny was conducted in Florida using *C. revoluta* as the host [8]. Use of a range of incubation temperatures revealed that an optimum temperature range of 30–32 °C resulted in an egg development time of 6.9–7.5 d. For females, nymphal development time was 19.7–21.6 d and total development time from egg to adult was 26.6–29.0 d. For males, the optimum temperature was 32 °C, at which nymphal development time was 18.0 d and total development time from egg to adult was 25.4 d. Extreme temperatures of 18 and 35 °C greatly inhibited development in the study. This experimental approach revealed that the scale’s temperature tolerance range was broad, but some geographic locations with natural or cultivated populations may experience temperatures that suppress the development of *A. yasumatsui*.

The second study was conducted in Taiwan using *C. taitungensis* as the host [9]. At a constant temperature of 24 °C, egg incubation time was 7.3 d, female nymphal development time was 28.7 d, and total development time from egg to adult was 35.9 d. For males, total development time from egg to adult was 19.0 d. Maximum longevity of adult females during the oviposition period was 67.0 d, and for adult males was only 1 d. The net reproduction rate was 112 offspring per adult female.

One more study in Taiwan used *C. revoluta* as the host and employed a range of temperatures [10]. The optimum temperature was found to be 28 °C, resulting in an egg incubation time of 7.8 d. The durations of other stages were similar to previous reports; for females, the total development time from egg to adult was 36.8–59 d. and maximum longevity was 44.7–57.4 d. For males, duration of the adult stage was 1.5–2.1 d. The net reproduction rate per adult female ranged from 46 offspring at sub-optimal temperatures to 96 at optimal temperatures.

Field observations in Shenzhen, China found that up to eight generations of *A. yasumatsui* occurred during the warmer months of the year [11]. An observational study in Florida revealed

that freezing temperatures of  $-6.7$  °C for 4 h were not lethal to *A. yasumatsui* on *C. revoluta* plants, and the scale infestations increased in density after the daily temperature rose [12].

### 3.2. Knowledge of Temperature Responses May Aid Cycad Conservation

Temperature-response studies [8,10] revealed that sub-optimal and supra-optimal temperatures were highly effective in reducing reproductive performance in *A. yasumatsui*. However, conservationists cannot rely on temperature extremes to eradicate this cycad pest, because it survives them even if it does not reproduce well at these temperatures. Still, planting ex situ germplasm collections in climatic zones with seasonal temperatures that are sub-optimal for the scale has been proposed as a passive approach for conserving endangered species such as *C. micronesica* and *C. taitungensis*, because adequate control of *A. yasumatsui* may be achieved with less control effort [10].

### 3.3. Organismal Research Needs

The combined results described in Sections 3.1 and 3.2 illuminate the ontogeny and fecundity traits of *A. yasumatsui* that cause such rapid lethal damage to the host plants. However, we believe there are several issues that require more research.

The two host plants used in the published studies were *C. revoluta* and *C. taitungensis*. These species are among the most susceptible in the context of rapidity of death after the initial scale infestation. In most botanic gardens and nurseries, the scale can be found feeding on other cycad taxa that are not at risk of lethal damage (see Section 5.1). Nothing is known to date about the performance of *A. yasumatsui* when feeding on one of the less palatable cycad taxa. Horticulturists and conservationists urgently need this information to define the most appropriate mitigation protocols in a common garden setting.

The phenotypic heterogeneity of *A. yasumatsui* appears to be greater than that of other *Aulacaspis* taxa [2,13]. This may be due to genetic diversity in *A. yasumatsui*, as has been shown in other insects. For example, study of the genetic structure of the cycad specialist butterfly *Luthrodes pandava* Horsfield has identified four distinct cryptic subspecies [14]. More studies are needed to determine whether this heterogeneity in *A. yasumatsui* is due to the existence of cryptic species, or differences in environmental factors or in the nutritional value between various host plants. Moreover, the scale's endosymbiont diversity is influenced by diet [15], and more research is needed to determine whether *A. yasumatsui* endosymbiont diversity may influence its phenotype.

Our understanding of the *A. yasumatsui* crawler stage is inadequate. This stage is of crucial importance for several reasons. *Cycas* plants infested with *A. yasumatsui* may develop high-density infestations as a result of crawler behavior. A peculiar result of this behavior is that plants that are initially infested in a newly invaded habitat may become completely covered by *A. yasumatui* before the adjacent plants begin to be infested [16]. The crawler is the only developmental stage in armored scales that can achieve medium- to long-distance passive locomotion by exploiting wind currents or by hitch-hiking on passing animals including humans, a process known as phoresis [17]. For example, after *A. yasumatsui* began rapidly expanding its range on Guam in 2005, new infestations developed that were disjunct such that wind or proximity to infested sites could not explain the pattern of population expansion [18]. Similarly, the island of Tinian has many *C. micronesica* and *C. revoluta* plants in the managed urban landscape and a large, publicly funded ex situ *C. micronesica* germplasm collection in a remote forest within a federally restricted area. The island was invaded by *A. yasumatsui* in August 2019 [19] and the initial infestation occurred in the remote protected area, on the access trail entering the expansive cycad collection. This Tinian invasion had been predicted [20] because the recent conservation decisions included sending a maintenance team from Guam, where *A. yasumatsui* infestations are ubiquitous, to Tinian every month. The only biological explanation for this island invasion and its initial location was that biologists with permission to enter the remote protected area had vectored phoretic crawlers into the site.

*Aulacaspis yasumatsui* crawlers become sessile within 1.0–1.7 d if suitable feeding sites are readily available [8,10]. However, nothing is known about how many days a crawler can remain viable if a suitable feeding site is not immediately available. This is undoubtedly less than the duration of the first nymphal instar, which may be as short as 9 d at optimal temperatures and as long as 31 d at sub-optimal temperatures [8,10]. Replicated trials are urgently needed to withhold host tissue from crawlers for various durations of time before providing them with host tissue in order to determine whether they can become established and reach maturity. Such trials would determine how long a crawler carried by wind or through phoresy may remain potentially infective.

#### 4. The Expanding Invasion Range

The movement of live cycad plants containing undetected infestations of *A. yasumatsui* is the means by which invasions have likely occurred in new geographic areas. The most popular cycad species for horticultural use is *C. revoluta*, and this versatile plant is ideal for many horticultural applications (Figure 1). The main reason that infestations may be undetected is because the small, sessile insects settle in crevices and convoluted surfaces that make direct observance of some individuals difficult or impossible [21]. A single, hidden gravid female could generate more than 100 offspring in several weeks after a *Cycas* plant is passed through quarantine. Unfortunately, *C. revoluta* is one of the species that provides *A. yasumatsui* with numerous cryptic feeding sites not observable during direct inspection of the intact plant (Figure 2a). Moreover, cycad roots can serve as feeding sites for *A. yasumatsui*, and infestations may occur down to 60 cm below the soil surface [4]. At the time of the initial Florida invasion, much of the *C. revoluta* horticulture industry was comprised of container-grown nursery plants [2], for which detection of root infestations within the container medium was not possible.

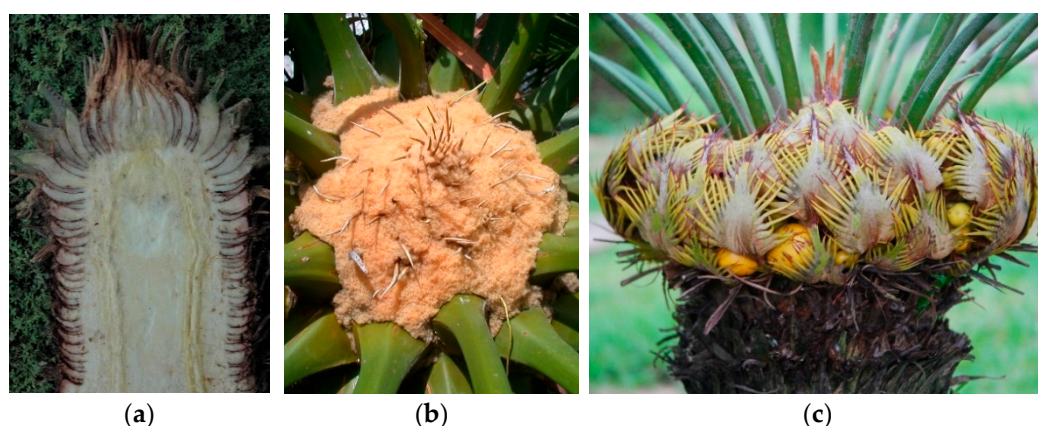


(a)



(b)

**Figure 1.** *Cycas revoluta* is shipped in high volumes to support the international horticulture industry. The species is used in numerous horticultural applications. (a) Containerized specimen plants are used as house plants, accent plants in the landscape, and bonsai. (b) Mass plantings of *C. revoluta* provide stunning landscapes.



**Figure 2.** *Aulacaspis yasumatsui* can infest many surfaces on *Cycas* host plants that are impossible to see during visual inspections. (a) *Cycas revoluta* stem section reveals the overlapping persistent leaf bases that create cavities where the armored scale may persist. (b) Apex of *C. tansachana* K.D. Hill and S.L. Yang stem covered by dense trichomes that can conceal scale infestations. (c) Mature megastrobilus of *C. nongnoochiae* K.D. Hill revealing numerous cavities in which scale infestations may be hidden.

Ambiguities have plagued the documentation of some country invasions, primarily because the live appearance of *A. yasumatsui* is similar to many other armored scale species [22]; this can lead to difficulty in diagnosis. Authoritative identification requires microscopic study of slide-mounted adult females. The case of Indonesia provides an example of the need for identification by a taxonomic authority; the probable invasion prior to the 1980s [23,24] remains equivocal because *A. yasumatsui* was not authoritatively identified in the country by a taxonomic expert until a 2011 outbreak [25]. This phenotypic similarity to other scale species may lead to identification mistakes by quarantine officers, so molecular diagnostic techniques have been developed to aid in species identifications [26].

The initial confirmed identification of *A. yasumatsui* on cycad plants outside the scale's native range occurred in 1994, when infested plants were observed in Miami, Florida [2] and 1995, when plants imported from Vietnam to the Netherlands were infested with the scale [6]. If the *A. yasumatsui* infestation on imported plants which caused the Florida outbreak had been detected at the port of entry, there is a chance that the Florida invasion could have been prevented. At the time of the invasion, the *C. revoluta* nursery industry in Florida was substantial, with container-grown plants being shipped to numerous other states and countries in high volumes [2]. The invasive range of the pest expanded dramatically within a few years as a result of this trade in whole plants. We list the many invasions and interceptions that have been reported by the year of first report (Table 1).

**Table 1.** List of geographic locations which have reported *Aulacaspis yasumatsui* on established cycad plants or on plants intercepted at a port of entry. The list does not include countries within the unambiguous native range of the scale.

Year	Location	Citation
1992	China	[27]
1994	Continental United States	[2]
1995	Netherlands	[6]
1998	Hawaii	[27]
1996	Cayman Islands	[2,28]
1996	Hong Kong	[2,27]
1996	U.S. Virgin Islands	[2,28]
1996	Puerto Rico	[2,29]
1996	Saint Kitts	[2]
1996	Singapore	[2,27]
1996	Taiwan	[2,6]
2001	France	[30,31]
2001	Singapore	[27]
2003	Barbados	[6]
2003	Guam	[32]
2003	Guadeloupe	[33]
2004	Costa Rica	[6]
2004	New Zealand	[6]
2006	Croatia	[34,35]
2006	Ivory Coast	[6]
2006	United Kingdom	[6]
2007	Rota	[18]
2008	Palau	[36]
2008	Philippines	[37]
2009	Bali	[24]
2009	Bulgaria	[38,39]
2009	Java	[24]
2009	Poland	[40]
2009	Timor	[24]
2012	Malaysia	[25]
2012	Sulawesi	[41,42]
2013	Cyprus	[43]
2014	Nigeria	[44]
2015	Mexico	[45]
2015	South Africa	[46]
2015	Turkey	[47]
2016	Guatemala	[48]
2018	Dominican Republic	[49]
2019	Tinian	[19]

This list of reported country invasions is assuredly incomplete because some invasions may have been reported in literature that was not identified in our systematic search; many infestations or quarantine confiscations may remain undetected or unreported; or the *A. yasumatsui* infestations were misidentified as another scale species. Moreover, in many cases the date of first publication is known but the initial date of invasion is impossible to determine because this was not reported. However, the list exemplifies several critical issues of importance to horticulture and invasion biology. First, when the recent pattern of expanding invasive range is studied, locations that are vulnerable to impending invasion risk may be apparent. The 2003 invasion of Guam [50] and 2019 invasion of Tinian [20] were both predicted before they were reported. Second, newly invaded geographic locations may serve as conduits through which continuing invasions occur; for example, exports from the continental United States and Costa Rica were the likely sources of invasions into Europe and Africa. Third, residents of isolated islands can be successful in keeping out invasive species when decision makers are informed and sound science is respected.

For example, the residents of the Mariana Island of Tinian were successful in keeping this lethal cycad pest from invading their island for decades after the international *A. yasumatsui* expansion began, and the invasion did not occur until 2019 as a result of an ex situ conservation project [19].

The considerable data available have been used to develop models of future invasion potential for *A. yasumatsui* [51,52]. These models and the 25-year history of documented invasions may be used to improve policy and action plans for managing the continuing expansion of the invasive range of this devastating horticultural pest.

## 5. Host Responses

### 5.1. Host Range

All cycad species within the native range of *A. yasumatsui* belong to the genus *Cycas*. The 25 years of interactions of this scale with many cycad species in the invasive range indicate *Cycas* species are the best quality hosts for *A. yasumatsui* growth and fecundity. *Cycas* species are also among the most susceptible to damage by the scale. The range in susceptibility among cycad taxa is relevant to the horticulture industry because maintaining a suitable-looking specimen is often difficult despite copious amounts of intervention. Without biological or chemical control, the susceptible cycad species die rapidly after the scale population reaches high densities. Many owners of cycad plants in non-commercial locations, after several years of unsuccessfully trying to maintain the beauty of the cycad specimen, give up and resort to removing the cycad plants. For these reasons, the full list of host species of *A. yasumatsui* should be understood by horticulturists and conservationists.

The current understanding of cycad diversity recognizes 364 distinct species, 120 of which belong to the monogeneric Cycadaceae family [53]. Every Cycadaceae species that has been observed is a suitable host for *A. yasumatsui*. We list the Zamiaceae species which are known hosts, based on direct observations (Table 2).

**Table 2.** List of Zamiaceae species that are reported as hosts for *Aulacaspis yasumatsui*. The list is developed from the literature and from the authors' personal observations.

Species	Taxonomic Authority
<i>Bowenia serrulata</i>	(W. Bull) Chamb.
<i>Ceratozamia robusta</i>	Miq.
<i>Dioon califanoi</i>	De Luca and Sabatori
<i>Dioon edule</i>	Lindl.
<i>Dioon merolae</i>	De Luca
<i>Dioon mejiae</i>	Standl. and L.O. Williams
<i>Dioon rzedowskii</i>	De Luca, Moreti, Sabatori and Vasquez
<i>Dioon sonorensis</i>	(De Luca et al.) Chemnick et al.
<i>Dioon spinulosum</i>	Dyer ex Eichler
<i>Encephalartos barteri</i>	Miguel
<i>Encephalartos ferox</i>	G. Bertol
<i>Encephalartos hildebrandtii</i>	A. Bran and C.D. Bouché
<i>Encephalartos manikensis</i>	Gilliland
<i>Encephalartos pterogonus</i>	R.A. Dyer and I. Verd
<i>Encephalartos whitelockii</i>	P.J.H. Hurter
<i>Macrozamia lucida</i>	L.A.S. Johnson
<i>Macrozamia miquelii</i>	F. Muell.
<i>Microcycas calocoma</i>	(Miq.) A. DC.
<i>Stangeria eriopus</i>	(Kunze) Baill.
<i>Zamia loddigesii</i>	Miq.
<i>Zamia integrifolia</i>	L. f.

### 5.2. Individual Plant Responses

The reserves of non-structural carbohydrates in *C. revoluta* leaves, stems, and roots decline increasingly in proportion to the length of exposure to *A. yasumatsui* herbivory [54]. Starch exhibits greater relative declines than sugars, and disaccharides exhibit greater

relative declines than hexoses. The ongoing depletion of carbohydrates with duration of herbivory is probably how *A. yasumatsui* kills the host plant.

In Guam, highly disparate germination performance of *C. micronesica* seeds among numerous habitats was observed, whereby the percentage germination of seeds that were free of *A. yasumatsui* infestation was six times greater than that of seeds directly infested by the scales [55]. These observations led to manipulative studies which determined that the carbohydrates in gametophyte and sarcotesta tissues were greatly affected by *A. yasumatsui* herbivory. The greatest relative decline in carbohydrates during *A. yasumatsui* seed infestation occurred in the sarcotesta tissue. Scale-infested seeds contained a gametophyte starch pool that was only 37% of that of uninfested seeds. The ability of *A. yasumatsui* to deplete the non-structural carbohydrates of host plants clearly affects consequential transgenerational phenomena.

Two cascading effects of reduced carbohydrate status due to long-term *A. yasumatsui* herbivory have been studied. First, the use of stem cuttings from scale-damaged trees for producing new *C. micronesica* plants is less successful. For example, the success rates for adventitious root formation on cycad stem cuttings is in excess of 90% for experienced cycad horticulturists if the source plants are healthy [56–59]; however, success rates declined to only 30–40% after the source trees had been damaged by *A. yasumatsui* for seven years [56,60]. Second, stem CO<sub>2</sub> efflux of scale-damaged *C. micronesica* plants was reduced when compared to that of healthy trees [61]. This simple non-destructive field measurement was proposed as an indirect approach for estimating the stem carbohydrate status of live but unhealthy trees, which may improve selection of the best candidates for obtaining stem cuttings for asexual propagation.

Height increment of cycad plants has not been adequately studied. The plants are relatively slow to increase in height when compared to most arborescent species. The height increment of uninfested *C. micronesica* was 2.5–3.0 cm·y<sup>-1</sup>; this was reduced by chronic *A. yasumatsui* damage to 1.6 cm·y<sup>-1</sup> [62].

Branching behaviors of cycad trees are unique, and many female trees remain unbranched for life. In contrast, most male trees exhibit several points of dichotomous branching [63]. The pre-invasion Guam populations of *C. micronesica* were comprised mostly of unbranched trees, but after 15 years of *A. yasumatsui* damage most of the remaining live trees contained three or more branches. The long-term mortality of this insular cycad species has revealed female trees were killed by *A. yasumatsui* more often than male trees.

### 5.3. Population and Habitat Responses

The most researched case study after an *A. yasumatsui* invasion has been that of *C. micronesica*. Three Guam studies used permanent plots to obtain population data over time. First, belt transects were established in a site in northwest Guam before *A. yasumatsui* invaded the site in early 2005. This was a high-density *C. micronesica* forest where many biochemistry and pollination studies were conducted; it contained the most genetically isolated *C. micronesica* stand on Guam [64]. Survival and regeneration data were obtained until 2011 to develop a Type I right-censoring approach [65]. This six-year study revealed for the first time that seedlings and small juvenile plants were killed by *A. yasumatsui* herbivory more rapidly than large plants. Seedlings were killed within nine months, and juvenile plants less than 100 cm tall were killed within 40 months. Some regeneration occurred in the earliest years, but every seedling was killed so by 2008, no recruitment was occurring [66]. Mortality of 92% occurred within the six years of *A. yasumatsui* infestation. The study site was abandoned in 2015 when *C. micronesica* was added to the United States Endangered Species Act [67], as the federal permitting and access regulations became inhibitory.

Second, numerous plots were positioned throughout Guam in 2005 prior to the arrival of *A. yasumatsui* in each area. All the research sites on federal property were abandoned in 2015 due to new federal restrictions on access, but the remaining 12 sites



were monitored annually until 2020 to provide 15 years of survival data [68]. These long-term data corroborated the results of the first study, in that seedling mortality was 100% by 2006, juvenile plant mortality was 100% by 2014, and the census after 15 years of *A. yasumatsui* damage revealed 96% mortality of the *C. micronesica* population.

The third study was a forest inventory conducted in 2002 [69] and repeated in 2013 [70]. The 2002 inventory revealed *C. micronesica* was the most abundant tree species on the island, with an estimated population of 1.57 million trees [69]. By 2013, the population had declined to 0.62 million trees, leaving 20 other arborescent taxa more abundant than *C. micronesica* [70]. Interestingly, *Cocos nucifera* L. was the second most abundant tree species on Guam in 2002, and this native species also declined in population such that by 2013, it ranked 15. This decline in the coconut tree population was a result of the 2007 *Oryctes rhinoceros* L. invasion [20]. Therefore, the two most abundant tree species on Guam in 2002 were decimated by non-native specialist insect invasions in the period 2003–2007 such that by 2013, neither ranked in the top ten. An estimated 93% of the *C. micronesica* trees exhibited *A. yasumatsui* infestations in 2013 [70].

The influence of *A. yasumatsui* on a host plant cannot be fully understood without attempting to understand the plant's interactions with other native or non-native herbivores [71]. For *Cycas* species, the most common co-occurring herbivores are the specialist butterfly *Luthrodes pandava* (synonym: *Chilades pandava* Horsfield) [71,72] and the mutualistic pollinator species [73–75]. The most researched *A. yasumatsui* invasion example is the Guam *C. micronesica* case study. The 2003 Guam invasion by *A. yasumatsui* was accompanied by other invasions, of *L. pandava* (which feeds on young, expanding leaf tissue), *Erechthias* sp. Meyrick moth (which mines old *Cycas* leaflets), and *O. rhinoceros* (which bores into the stems) [5,20,76]. Previously non-threatening damage to *C. micronesica* by the native stem borer *Acolepta marianarum* Aurivillius and feral pigs (*Sus scrofa* L.) added to the threats to the trees because their health was compromised by the invasive insects [20]. The direct interactions of *A. yasumatsui* and the native *Anatrachyntis* Meyrick pollinator [77,78] have not been studied; however, chronic damage by *A. yasumatsui* and the other non-native pests decimated the tree population [68], and this indirectly damaged the native pollinator because *Cycas* male cones provide brood sites for pollinator regeneration [5,77,78]. Historically, hundreds of *Anatrachyntis* adults emerged from each *C. micronesica* male cone after pollen dispersal, but recent attempts to rear pollinators from *C. micronesica* male cones on Rota Island have yielded no pollinators (unpublished, T.E.M.). These observations indicate that the pollinator population may have been extirpated on this island due to the infrequent production of male cones because of damage by invasive insects. The Guam case study provides examples of invasional meltdowns from the long list of invasive herbivores and coextinction threats due to loss of pollinator species [79].

Direct interactions of several insects have been studied in the Guam case study [20,80]. For example, *Erechthias* damage declined but *Acolepta marianarum* damage increased after *Aulacaspis yasumatsui* damage. Negative correlations between *A. yasumatsui* and *L. pandava* indicate that these two insects are in direct competition when *C. micronesica* is their only host.

*Cycas micronesica* associates with nitrogen-fixing endosymbionts and improves ecosystem health by introducing nitrogen into the soil food web and increasing heterogeneity in biogeochemistry [81]. One of the unique traits of the tree is slow leaf-litter decomposition compared to other sympatric tree species [82]. However, the litter quality of *C. micronesica* leaves was altered by *A. yasumatsui* herbivory such that nitrogen and potassium concentrations increased, changes that predicted an increase in the decomposition speed of the *C. micronesica* leaf litter [83].

The soils adjacent to *C. micronesica* trees damaged or killed by *A. yasumatsui* are plagued by a phytotoxic legacy that damages understory plant growth [84]. The soils may remain barren for years, and experimental manipulations indicate the presence of persistent organic substances may be causal. This legacy effect may be related to large numbers of persistent dead *A. yasumatsui* bodies and scale covers on the *C. micronesica* leaf litter [85].

Multiple stressors imposed on plants simultaneously may produce unique challenges for plants in a manner that cannot be predicted by studying individual stressor responses [86]. Interactions between pests and other forest disturbances are instrumental in driving many forest dynamics [87]. The Guam case study has contributed to the examples of these ecological phenomena, whereby the intrinsic resilience of *C. micronesica* trees to the region's frequent tropical cyclones [88] is compromised by chronic *A. yasumatsui* herbivory [89–91].

Consequential interactions between *A. yasumatsui*, the predator *Rhyzobius lophanthae* Blaisdell, and the host *Cycas* plants may influence the efficacy of the predator. The cryptic location of some *A. yasumatsui* infestations [21] may protect some *A. yasumatsui* individuals from access by the predator [92]. For example, the overlapping persistent leaf bases, dense trichomes, or long-lived reproductive structures on *Cycas* plants (Figure 2) provide small crevices where the armored scales can live but the predator cannot enter. This phenomenon increases the value of parasitoid biological control because the size differential between the scale and the ovipositing parasitoid is minimal. In addition, for unknown reasons the predator preferentially forages at higher levels, and prefers to avoid the strata near the soil surface [16,93]. This predator behavior may result in localized *A. yasumatsui* infestations on leaves near the soil surface on plants that exhibit no *A. yasumatsui* on leaves in the higher strata. Finally, when provided a binary choice in an olfactometer assay, this predator prefers *A. yasumatsui* on mature tree leaves versus seedling leaves [94].

## 6. Control Methods

### 6.1. Chemical Control

Numerous trials have been conducted to determine the efficacy of various insecticides for *A. yasumatsui* control; most have been ineffective in defining an economical approach. However, the crawler stage of this pest appears to be vulnerable to most contact insecticides including horticultural oils and soaps. Use of contact insecticides for controlling *A. yasumatsui* requires vigilance, with an application frequency of less than weekly, and attention to saturation of every plant surface with each scheduled spray in order to contact every crawler. The more efficacious active ingredients identified in the initial trials for use as frequent spray applications were pyriproxyfen [22] and dimethoate [95]. Soft approaches for suppressing *A. yasumatsui* infestations have been communicated also. For example, the use of coffee grounds for suppressing *A. yasumatsui* was promoted in Florida [96], but these assertions were not corroborated in a replicated trial [97]. Howard et al. [3] were the first to determine the efficacy of imidacloprid for controlling *A. yasumatsui*, and this systemic insecticide may require the least amount of labor for chemical control of the scale. This systemic insecticide has been used for *A. yasumatsui* control on *C. micronesica* to enable in situ research on horticultural and physiological questions [55,56,91,98].

### 6.2. Predator Control

The greatest concerns with the continuing international spread of *A. yasumatsui* involve conservation of in situ cycad populations, which must rely on biological control. Biologists in many geographic locations have indicated that pre-existing biological control organisms may fortuitously begin to attack the newly invaded *A. yasumatsui* populations. Other teams have purposefully introduced biological control organisms to control a new *A. yasumatsui* invasion. Organized efforts to introduce predators or parasitoids to locations that have been invaded by *A. yasumatsui* have been ongoing since 1997. The predators of the scale that have been reported are listed in Table 3.

**Table 3.** A list of predators known to feed on *Aulacaspis yasumatsui*.

Species	Family	Case Studies
<i>Chilocorus cacti</i>	Coccinellidae	[29,99]
<i>Chilocorus circumdatus</i>	Coccinellidae	[99]
<i>Chilocorus stigma</i>	Coccinellidae	[99]
<i>Curinus coeruleus</i>	Coccinellidae	[99]
<i>Cryptolaemus montrouzieri</i>	Coccinellidae	[29,99]
<i>Cybocephalus</i> sp.	Cybocephalidae	[100]
<i>Cybocephalus nipponicus</i>	Cybocephalidae	[25,33,99,101–111]
<i>Cybocephalus flavocapitis</i>	Cybocephalidae	[104,107,108]
<i>Cycloneda sanguinea</i>	Coccinellidae	[99]
<i>Diomus austrinus</i>	Coccinellidae	[99]
<i>Exochomus children</i>	Coccinellidae	[99]
<i>Harmonia axyridis</i>	Coccinellidae	[99]
<i>Hyperaspis ornatella</i>	Coccinellidae	[99]
<i>Hippodamia convergens</i>	Coccinellidae	[99]
<i>Microweisea coccidivora</i>	Coccinellidae	[99]
<i>Olla v-nigrum</i>	Coccinellidae	[99]
<i>Phaenochilus kashaya</i>	Coccinellidae	[109,110,112,113]
<i>Rhyzobius lophanthae</i>	Coccinellidae	[25,99,101,102,105,109,110,114,115]
<i>Zilus subtropicus</i>	Coccinellidae	[99]

### 6.3. Parasitoid Control

Entomologists are skilled at searching for predators and parasitoids within armored scale infestations, but most gardeners and horticulturists are not trained in detecting the signs that an armored scale has been parasitized. This may explain why the list of parasitoids that are known to parasitize *A. yasumatsui* is much shorter than the list of predators (Table 4).

**Table 4.** A list of parasitoids known to parasitize *Aulacaspis yasumatsui*.

Species	Family	Case Studies
<i>Alerus</i> sp.	Aphelinidae	[29]
<i>Aphytis lingnanensis</i>	Aphelinidae	[20,105,109,110]
<i>Coccobius fulvus</i>	Aphelinidae	[8,12,28,29,32,33,101,105,109,110,116,117]
<i>Encarsia</i> sp.	Aphelinidae	[99,118]
<i>Encarsia diaspidicola</i>	Aphelinidae	[119]
<i>Pteroptrix</i> sp.	Aphelinidae	[110]
<i>Arrhenophagus chionaspidis</i>	Encyrtidae	[8,20,25,109,110]
<i>Aprostocetus</i> sp.	Eulophidae	[118]
<i>Aprostocetus purpureus</i>	Eulophidae	[8,99]

### 6.4. Other Biological Enemies

In addition to these predators and parasitoids, the entomopathogenic fungus *Isaria fumosorosea* Wize infects *A. yasumatsui* and may be useful for controlling the scale [120]. Moreover, the nematodes *Steinernema feltiae* Filipjev, *Heterorhabditis indica* Poinar, Karunaka and David, *Heterorhabditis marelatus* Liu and Berry, and *Heterorhabditis bacteriophora* Poinar may be useful for suppression of *A. yasumatsui* [99,101].

## 7. Lessons Learned and Future Directions

Many geographic locations in tropical and subtropical regions have relied on *C. revoluta* as a ubiquitous part of the urban landscape. The species is famous for providing stunning specimen plants requiring minimal to no care. It is also famous for possessing a toolbox to thwart every threat; but within months of an *A. yasumatsui* invasion into one of these locations, *C. revoluta* and other *Cycas* species in the landscape lose their horticultural appeal. With a few exceptions (such as the original 1994 Florida invasion and the 2019

Tinian invasion, where publicly funded conservation projects were instrumental in the invasions), the international trade in infested horticultural plants was responsible for most of the other invasions.

Enacting a conservation action plan for an endemic *Cycas* population that becomes threatened by a new *A. yasumatsui* invasion requires an understanding of myriad interacting phenomena. Conservation mistakes can be made if decision-makers are not open to input from experienced experts. For example, most of the funds for conserving *C. micronesica* on Guam have been invested in expensive propagation and tree-rescue projects. However, the primary threat to the species is herbivory by non-native insect herbivores. This threat remains unchanged by the expenditure of the conservation funding [62,121] and if the public funds were instead directed toward control of the insect threats rather than tree-rescue projects, the chance of *C. micronesica* species recovery would improve.

*Aulacaspis yasumatsui* was thought to be the only member of *Aulacaspis* Cockerell associated with gymnosperm host plants. However, four other *Aulacaspis* species have been identified that use *Cycas* plants as hosts: *A. madiunensis* Zehntner, *A. mischocarpi* Cockerell and Robinson, *A. rosae* Bouché, and *A. zunyiensis* Wei and Jing [122–125]. *Aulacaspis madiunensis*, *A. mischocarpi* and *A. rosae* are oligophagous to polyphagous but the full host range for *A. zunyiensis* is not known. *Aulacaspis yasumatsui* appears to be host-specific to Cycadaceae and Zamiaceae taxa.

The heavily discussed native habitats of endemic cycad species that have been threatened by the international list of *A. yasumatsui* invasions were on the islands of Guam, Rota, and Taiwan. Lack of fortuitous biological control and the initial *C. micronesica* and *C. taitungensis* plant mortalities were well-documented following these invasions. Very little has been discussed about the interesting case of the Philippines, an archipelago that is outside the native range of *A. yasumatsui* but is home to 13 accepted *Cycas* species [53]. *Aulacaspis yasumatsui* is known to occur in the country [37] but the original invasion date is not known. Since the Philippines has unusually high *Cycas* diversity within a small geographic range, more research is needed to develop the necessary knowledge to conserve these unique cycad species [37].

Rapid identification of the armored scale in every newly invaded location should be conducted by an experienced taxonomist, and is mandatory for developing a rapid action plan. For example, the Miami invasion caught cycad conservationists and horticulturists by surprise because the initial anecdotal identifications indicated that the scale outbreak was the locally ubiquitous *Pseudaulacaspis cockerelli* Cooley [22]; this lessened the success of early attempts at control.

Rapid establishment of biological control is also required to thwart initial *A. yasumatsui* establishment, especially in insular settings. The Guam invasion was observed in 2003, but the first release of a predator was not permitted and enabled until 2005. The slow pace of the regulations for introducing biological control on Guam is an example of how delays in establishing biological control can contribute to ecosystem damage [126].

Initial reports suggested imidacloprid was effective in suppressing *A. yasumatsui* populations. However, long-term use appeared to generate resistance to this chemical. Observational knowledge that has accrued in Florida and Thailand cycad nurseries and private collections has revealed the use of pyrethroid insecticides such as bifenthrin and cypermethrin and/or organophosphate insecticides such as acephate and chlorpyrifos [127–129] are more efficacious (personal observation, A.L.). The development of resistance to any one insecticide appears to be rapid, and replicated trials are needed to determine an optimum interval for scheduling alternations among the efficacious insecticides.

Publicizing a new country invasion is required to enable the most effective international response [2]. An inadvertent or purposeful decision to withhold news of a new *A. yasumatsui* invasion from the international community is a decision to deny threatened cycad plants the international expertise and protection that they deserve. This recently occurred on the island of Tinian, where the news of an August 2019 invasion by *A. yasumatsui* was not made public until 19 months later [19]. The confusion about the date of

the first *A. yasumatsui* invasion of Indonesia [23–25] provides an example of how initial identification by a taxonomic authority and rapid communication to the international community are crucial steps to bring clarity to this international problem.

Most cycad species are remarkably resistant to threats, and resilient following abiotic or biotic damage in their native habitats. This is one of the endearing traits of the plant group that attracts plant collectors as they learn to cultivate cycad plants. Horticulturists that are new to cycads often kill their first few plants with too much attention, then become more knowledgeable about the need to leave the plants alone to appreciate their persistent traits [130]. However, when a *Cycas* population is invaded with *A. yasumatsui* the plants do not possess the tools to fight back, and the initial infestation often signals a one-way trip toward death. This acute host-herbivore bipartite system contains the answers to many questions of interest to biologists. However, Guam is only one of 39 reported invasions (Table 1), yet almost all of the studies to determine what this armored scale does to its host have been conducted on Guam (see Sections 5.2 and 5.3). These oversights should be corrected by biologists in other invaded regions in order to best understand how to conserve the host cycads from the threats imposed by this armored scale.

## 8. Conclusions

The invasion of Florida by *A. yasumatsui* 25 years ago initiated a sequence of invasions that have devastated horticulture industries based on *Cycas* species, and threatened the in situ populations of two *Cycas* species. Many lessons have been learned during this time, and the knowledge that has been generated is available to inform future conservation decisions. The small size of this cycad pest and the complex surface morphology of the host cycads make low-density infestations impossible to detect by visual inspection. The short pre-oviposition period and considerable female fecundity of *A. yasumatsui* lead to rapid population expansion on the plants that are initially infested in newly invaded regions. Host plants succumb to the herbivory through gradual depletion of non-structural resources. Enemy escape within the invasive range allows explosive scale population growth, requiring resident biologists to enact a rapid plan to search for fortuitous pre-existing natural enemies and to introduce predators or parasitoids from other invaded regions where biological control has been successful. International trade is responsible for many of the world's devastating invasions [131], and our case study provides a compelling example of how greater regulation of the international horticulture industry may aid in curbing the global risks of some invasive species.

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## References

1. Takagi, S. A new species of *Aulacaspis* associated with a cycad in Thailand (Homoptera: Coccoidea). *Insecta Matsumaruana New Species* **1977**, *11*, 63–72.
2. International Union for Conservation of Nature Cycad Specialist Group. *Report and Recommendations on Cycad Aulacaspis Scale, Aulacaspis Yasumatsui Takagi (Hemiptera: Diaspididae)*; IUCN: Gland, Switzerland, 2006.
3. Howard, F.W.; Hamon, A.; McLaughlin, M.; Weissling, T.; Yang, S.L. *Aulacaspis yasumatsui* (Hemiptera: Sternorrhyncha: Diaspididae), a scale insect pest of cycads recently introduced into Florida. *Fla. Entomol.* **1999**, *82*, 14–27. [[CrossRef](#)]

4. Weissling, T.J.; Howard, F.W.; Hamon, A.B. Cycad Aulacaspis Scale, Aulacaspis Yasumatsui Takagi (Insecta: Homoptera: Sternorrhyncha: Diaspididae); EDIS EENY-096. 2017. Available online: <http://edis.ifas.ufl.edu> (accessed on 23 April 2021).
5. Marler, T.; Muniappan, R. Pests of *Cycas micronesica* leaf, stem, and male reproductive tissues with notes on current threat status. *Micronesica* **2006**, *39*, 1–9.
6. Germain, J.F.; Hodges, G.S. First report of *Aulacaspis yasumatsui* (Hemiptera: Diaspididae) in Africa (Ivory Coast), and update on distribution. *Fla. Entomol.* **2007**, *90*, 755–756. [[CrossRef](#)]
7. Diagne, C.; Leroy, B.; Vaissière, A.C.; Gozlan, R.E.; Roiz, D.; Jarić, I.; Salles, J.-M.; Bradshaw, C.J.A.; Franck, C. High and rising economic costs of biological invasions worldwide. *Nature* **2021**. [[CrossRef](#)]
8. Cave, R.D.; Sciacchetano, C.; Diaz, R. Temperature-dependent development of the cycad aulacaspis scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae). *Fla. Entomol.* **2009**, *92*, 578–581.
9. Bailey, R.; Chang, N.T.; Lai, P.Y.; Hsu, T.C. Life table of cycad scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae), reared on *Cycas* in Taiwan. *J. Asia Pac. Entomol.* **2010**, *13*, 183–187. [[CrossRef](#)]
10. Ravuiwasa, K.T.; Tan, C.-W.; Bezirganoglu, I.; Hwang, S.-Y. Temperature-dependent demography of *Aulacaspis yasumatsui* (Hemiptera: Diaspididae). *J. Econ. Entomol.* **2012**, *105*, 1581–1590. [[CrossRef](#)]
11. Yang, W.X.; Wu, W.D.; Jiao, G.L.; Liu, F. Biology of *Aulacaspis yasumatsui* Takagi and its control test. *J. Fujian For. Sci. Technol.* **2009**, *36*, 127–129.
12. Duke, E.R.; Lorenzo, A.B.; Howard, F.W. Survival of the cycad aulacaspis scale in northern Florida during sub-freezing weather. *Proc. Fla. State Hort. Soc.* **2003**, *116*, 345–347.
13. Takagi, S.; De Faveri, S. Notes on scale insects of *Aulacaspis* associated with mangroves and cycads (Sternorrhyncha: Coccoidea: Diaspididae). *Insecta Matsumurana* **2009**, *65*, 101–129.
14. Wu, L.-W.; Yen, S.-H.; Lees, D.C.; Hsu, Y.-F. Elucidating genetic signatures of native and introduced populations of the cycad blue, *Childes pandava* to Taiwan: A threat both to sago palm and to native *Cycas* populations worldwide. *Biol. Invasions* **2010**, *12*, 2649–2669. [[CrossRef](#)]
15. Gruwell, M.E.; Wu, J.; Normark, B.B. Diversity and phylogeny of *Cardinium* (Bacteroidetes) in armored scale insects (Hemiptera: Diaspididae). *Ann. Entomol. Soc. Am.* **2009**, *102*, 1050–1061. [[CrossRef](#)]
16. Marler, T.E. Vertical stratification in arthropod spatial distribution research. *Commun. Integr. Biol.* **2013**, *6*, e25749. [[CrossRef](#)]
17. White, P.S.; Morran, L.; de Roode, J. Phoresy. *Curr. Biol.* **2017**, *27*, R578–R580. [[CrossRef](#)]
18. Marler, T.; Terry, I. The continuing demise of *Cycas micronesica*. *Cycad Newsl.* **2013**, *36*, 22–26.
19. NAVFAC Marianas. *Request for Statements of Interest: Cycad Monitoring at Andersen Air Force Base (AAFB) and Tinian Military Lease Area (MLA)*; Joint Region Marianas: Piti, GU, USA, 2021.
20. Deloso, B.E.; Terry, L.I.; Yudin, L.S.; Marler, T.E. Biotic threats to *Cycas micronesica* continue to expand to complicate conservation decisions. *Insects* **2020**, *11*, 888. [[CrossRef](#)] [[PubMed](#)]
21. Marler, T.E.; Moore, A. Cryptic scale infestations on *Cycas revoluta* facilitate scale invasions. *HortScience* **2010**, *45*, 837–839. [[CrossRef](#)]
22. Emshousen, C.; Mannion, C.; Glenn, H. Management of cycad aulacaspis scale, *Aulacaspis yasumatsui* Takagi. *Proc. Fla. State Hort. Soc.* **2004**, *117*, 305–307.
23. Haynes, J. Cycad aulacaspis scale: A global perspective. *Cycad Newsl.* **2005**, *28*, 3–6.
24. Lindstrom, A.J.; Hill, K.D.; Stanberg, L.C. The genus *Cycas* (Cycadaceae) in Indonesia. *Telopea* **2009**, *12*, 385–418. [[CrossRef](#)]
25. Muniappan, R.; Watson, G.W.; Evans, G.A.; Rauf, A.; Von Ellenrieder, N. Cycad aulacaspis scale, a newly introduced insect pest in Indonesia. *HAYATI J. Biosci.* **2012**, *19*, 110–114. [[CrossRef](#)]
26. Chiu, Y.; Wu, W.; Shih, C. Identification of three *Aulacaspis* species (Homoptera: Diaspididae) by PCR-RFLP analysis for quarantine application. *Formos. Entomol.* **2001**, *21*, 365–375.
27. Hodgson, C.; Martin, J.H. Three noteworthy scale insects (Hemiptera: Coccoidea) from Hong Kong and Singapore, including *Cribropulvinaria tailungensis*, new genus and species (Coccidae), and the status of the cycad-feeding *Aulacaspis yasumatsui* (Diaspididae). *Raffles Bull. Zool.* **2001**, *49*, 227–250.
28. Howard, F.W.; Weissling, T.J. Questions and answers about the cycad aulacaspis scale insect. *Proc. Fla. State Hort. Soc.* **1999**, *112*, 243–245.
29. Segarra-Carmona, A.E.; Pérez-Padilla, W. The cycad scale, *Aulacaspis yasumatsui* Takagi (Homoptera: Diaspididae): A new invasive pest to Puerto Rico. *J. Agric. Univ. Puerto Rico* **2008**, *92*, 123–129. [[CrossRef](#)]
30. Germain, J.-F. Scale insects (Homoptera: Coccoidea) from import interception in France (1997–2001). *Boll. Zool. Agr. Bachic. Ser. II* **2001**, *33*, 504.
31. Germain, J.F. *Aulacaspis yasumatsui* Takagi: A risk for *Cycas*. *PHM Rev. Hortic.* **2002**, *440*, 43–44.
32. Terry, I.; Marler, T. Paradise lost? Tipping the scales against Guam’s *Cycas micronesica*. *Cycad Newsl.* **2005**, *28*, 21–23.
33. Étienne, J. Pour la sauvegarde des *Cycas* en Guadeloupe. *L’Entomologiste* **2007**, *63*, 271–275.
34. Masten Milek, T.; Šimala, M.; Novak, A. Species of genus *Aulacaspis* Cockerell, 1836 (Hemiptera: Coccoidea: Diaspididae) in Croatia, with emphasis on *Aulacaspis yasumatsui* Takagi, 1977. *Entomol. Croat.* **2008**, *12*, 55–64.
35. Milek, T.M.; Šimala, M. *Aulacaspis yasumatsui* Tagaki, 1977 (Coccoidea: Diaspididae), a newly discovered scale insect in Croatia. *Glas. Biljn. Zaštite* **2008**, *8*, 239–242.

36. Marler, T.E.; Lawrence, J.H. Canopy and knowledge gaps when invasive alien insects remove foundation species. *Commun. Integr. Biol.* **2013**, *6*, e22331. [[CrossRef](#)] [[PubMed](#)]
37. Lindstrom, A.J.; Hill, K.D.; Stanberg, L.C. The genus *Cycas* (Cycadaceae) in the Philippines. *Telopea* **2008**, *12*, 119–145.
38. Trencheva, K.A.; Trenchev, G.E.; Tomov, R.U.; Wu, S. First report of *Aulacaspis yasumatsui* Takagi, 1977 (Hemiptera: Diaspididae) in Bulgaria. *Plant Sci.* **2010**, *47*, 206–209.
39. Trencheva, K.; Trenchev, G.; Tomov, R.; Wu, S.A. Non-indigenous scale insects on ornamental plants in Bulgaria and China: A survey. *Entomol. Hell.* **2010**, *19*, 114–123. [[CrossRef](#)]
40. Łabanowski, G. Pests of ornamental plants introduced to Polish glasshouses. *Prog. Plant Prot.* **2009**, *49*, 1714–1723.
41. Sembel, D.T.; Meray, E.R.; Kandowangko, D.S.; Dien, M.F.; Ratulangi, M.M. Distribution and status of newly introduced insect pests of Pakis Haji in North Sulawesi. *Eugenia* **2012**, *18*, 109–117.
42. Watson, G.W.; Muniappan, R.; Shepard, B.M.; Sembel, D.T.; Rauf, A.; Carner, G.R.; Benson, E.P. Sap-sucking insect records (Hemiptera: Sternorrhyncha and Thysanoptera: Thripidae) from Indonesia. *Fla. Entomol.* **2014**, *97*, 1594–1597. [[CrossRef](#)]
43. Ülgentürk, S.; Kaydan, M.B.; Hocali, S.Ş. New scale insect (Hemiptera: Coccoidea) records for the Turkish Republic of Northern Cyprus. *Türkiye Entomol. Bülteni.* **2015**, *5*, 59–68. [[CrossRef](#)]
44. Dimkpa, S.O.N.; Baraka, R.E.; Tobin-West, M.D.; Okwukwu, E. Cycad aulacaspis scale (CAS) *Aulacaspis yasumatsui* Takagi as a major pest of sago palm *Cycas* spp. in Nigeria. *Int. J. Entomol. Nematol. Res.* **2021**, *5*, 1–10.
45. González-Gómez, R.; Riverón-Giró, F.B.; García-González, A.; Martínez-Rosas, R.; Solís-Montero, L. First report of *Aulacaspis yasumatsui* (Hemiptera: Diaspididae) in Mexico. *Fla. Entomol.* **2016**, *99*, 583–584. [[CrossRef](#)]
46. Nesamari, R.; Millar, I.M.; Coutinho, T.A.; Roux, J. South African cycads at risk: *Aulacaspis yasumatsui* (Hemiptera: Coccoidea: Diaspididae) in South Africa. *Afr. Entomol.* **2015**, *23*, 196–206. [[CrossRef](#)]
47. Ülgentürk, S. *Cycas* palmiyelerinin kaçak yolcusu; *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae). *Türkiye Entomol. Bülteni* **2015**, *5*, 195–200. [[CrossRef](#)]
48. Normark, B.B.; Normark, R.D.; Vovides, A.; Solís-Montero, L.; González-Gómez, R.; Pulido-Silva, M.T.; Escobar-Castellanos, M.A.; Dominguez, M.; Perez-Farrera, M.A.; Janda, M.; et al. Cycad aulacaspis scale (*Aulacaspis yasumatsui* Takagi, 1977) in Mexico and Guatemala: A threat to native cycads. *BiolInvasions Rec.* **2017**, *6*, 187–193. [[CrossRef](#)]
49. Perez-Gelabert, D. The invasive armored scale *Aulacaspis yasumatsui* Takagi (Hemiptera: Coccoidea: Diaspididae) in the Dominican Republic. *Proc. Entomol. Soc. Wash.* **2019**, *121*, 525–528. [[CrossRef](#)]
50. Marler, T. Looking out for scale insects. *Pacific Sunday News*, 13 February 2000; p. 24.
51. Wei, J.; Zhao, Q.; Zhao, W.; Zhang, H. Predicting the potential distributions of the invasive cycad scale *Aulacaspis yasumatsui* (Hemiptera: Diaspididae) under different climate change scenarios and the implications for management. *PeerJ* **2018**, *6*, e4832. [[CrossRef](#)] [[PubMed](#)]
52. Satishchandra, K.N.; Geerts, S. Modeling the distribution of the invasive alien cycad aulacaspis scale in Africa under current and future climate scenarios. *J. Econ. Entomol.* **2020**, *113*, 2276–2284. [[CrossRef](#)]
53. Calonje, M.; Stevenson, D.W.; Osborne, R. The World List of Cycads. Available online: <http://cycadlist.org> (accessed on 23 April 2021).
54. Marler, T.E.; Cascasan, A.N. Carbohydrate depletion during lethal infestation of *Aulacaspis yasumatsui* on *Cycas revoluta*. *Int. J. Plant Sci.* **2018**, *179*, 497–504. [[CrossRef](#)]
55. Marler, T.E.; Cruz, G.N. Source and sink relations mediate depletion of intrinsic cycad seed carbohydrates by *Aulacaspis yasumatsui* infestation. *HortScience* **2019**, *54*, 1712–1717. [[CrossRef](#)]
56. Marler, T.E. Stem carbohydrates and adventitious root formation of *Cycas micronesica* following *Aulacaspis yasumatsui* infestation. *HortScience* **2018**, *179*, 497–504. [[CrossRef](#)]
57. Deloso, B.E.; Lindström, A.J.; Camacho, F.A.; Marler, T.E. Highly successful adventitious root formation of *Zamia* stem cuttings exhibits minimal response to indole-3-butyric acid. *HortScience* **2020**, *55*, 1463–1467. [[CrossRef](#)]
58. Deloso, B.E.; Paulino, C.J.; Marler, T.E. Leaf retention on stem cuttings of two *Zamia* L. species with or without anti-transpirants does not improve adventitious root formation. *Trop. Conserv. Sci.* **2020**, *13*, 1–8. [[CrossRef](#)]
59. Marler, T.E.; Deloso, B.E.; Cruz, G.N. Prophylactic treatments of *Cycas* stem wounds influence vegetative propagation. *Trop. Conserv. Sci.* **2020**, *13*, 1–6. [[CrossRef](#)]
60. Marler, T.E.; Cruz, G.N. Adventitious rooting of mature *Cycas micronesica* K.D. Hill (Cycadales: Cycadaceae) tree stems reveals moderate success for salvage of an endangered cycad. *J. Threat. Taxa* **2017**, *9*, 10565–10570. [[CrossRef](#)]
61. Marler, T.E. Stem CO<sub>2</sub> efflux of *Cycas micronesica* is reduced by chronic non-native insect herbivory. *Plant Signal. Behav.* **2020**, *15*, e1716160. [[CrossRef](#)]
62. Marler, T.E.; Griffith, M.P.; Krishnapillai, M.V. Height increment of *Cycas micronesica* informs conservation decisions. *Plant Sig. Behav.* **2020**, *15*, e1830237. [[CrossRef](#)] [[PubMed](#)]
63. Marler, T.E.; Calonje, M. Stem branching of cycad plants informs horticulture and conservation decisions. *Horticulturae* **2020**, *6*, 65. [[CrossRef](#)]
64. Cibrián-Jaramillo, A.; Daly, A.C.; Brenner, E.; DeSalle, R.; Marler, T.E. When North and South don't mix: Genetic connectivity of a recently endangered oceanic cycad, *Cycas micronesica*, in Guam using EST-microsatellites. *Mol. Ecol.* **2010**, *19*, 2364–2379. [[CrossRef](#)]

65. Marler, T.E.; Lawrence, J.H. Demography of *Cycas micronesica* on Guam following introduction of the armoured scale *Aulacaspis yasumatsui*. *J. Trop. Ecol.* **2012**, *28*, 233–242. [[CrossRef](#)]
66. Marler, T.E.; Terry, L.I. Arthropod invasion disrupts *Cycas micronesica* seedling recruitment. *Commun. Integr. Biol.* **2011**, *4*, 778–780. [[CrossRef](#)]
67. United States Fish & Wildlife Service. Endangered and threatened wildlife and plants; endangered status for 16 species and threatened status for 7 species in Micronesia. *Fed. Regist.* **2015**, *80*, 59424–59497.
68. Marler, T.E.; Krishnapillai, M.V. Longitude, forest fragmentation, and plant size influence *Cycas micronesica* mortality following island insect invasions. *Diversity* **2020**, *12*, 194. [[CrossRef](#)]
69. Donnegan, J.A.; Butler, S.L.; Grabowiecki, W.; Hiserote, B.A.; Lintiacio, D. *Guam's Forest Resources, 2002*; Resource Bulletin PNW-RB-243; Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2004.
70. Lazaro, M.; Kuegler, O.; Stanton, S.; Lehman, A.; Mafnas, J.; Yatskov, M. *Guam's Forest Resources: Forest Inventory and Analysis, 2013*; Resource Bulletin PNW-RB-270; Department of Agriculture, Forest Service, Pacific Northwest Research Station: Portland, OR, USA, 2020.
71. Marler, T.E.; Lindström, A.J.; Terry, L.I. *Chilades pandava* damage among 85 *Cycas* species in a common garden setting. *HortScience* **2012**, *47*, 1832–1836. [[CrossRef](#)]
72. Marler, T.E.; Lindström, A.; Terry, L.I. Information-based or resource-based systems may mediate *Cycas* herbivore interactions. *Plant Signal. Behav.* **2012**, *7*, 760–762. [[CrossRef](#)] [[PubMed](#)]
73. Terry, L.; Tang, W.; Marler, T.E. Pollination systems of island cycads: Predictions based on island biogeography. *Mem. N. Y. Bot. Gard.* **2012**, *106*, 102–132.
74. Skelley, P.; Xu, G.; Tang, W.; Lindström, A.J.; Marler, T.; Khurajam, J.S.; Singh, R.; Radha, P.; Rich, S. Review of *Cycadophila* Xu, Tang & Skelley (Coleoptera: Erotylidae: Pharaxonothinae) inhabiting *Cycas* (Cycadaceae) in Asia, with descriptions of a new subgenus and thirteen new species. *Zootaxa* **2017**, *4267*, 1–63. [[PubMed](#)]
75. Tang, W.; Xu, G.; Marler, T.; Khurajam, J.S.; Singh, R.; Lindström, A.J.; Radha, P.; Rich, S.; Nguyen, K.S.; Paul, S. Beetles (Coleoptera) in cones of cycads (Cycadales) of the northern hemisphere: Diversity and evolution. *Insecta Mundi* **2020**, *0781*, 1–19.
76. Marler, T.E.; Matanane, F.C.; Terry, L.I. Burrowing activity of coconut rhinoceros beetle on Guam cycads. *Commun. Integr. Biol.* **2020**, *13*, 74–83. [[CrossRef](#)]
77. Terry, L.; Roe, M.; Tang, W.; Marler, T.E. 2009. Cone insects and putative pollen vectors of the endangered cycad, *Cycas micronesica*. *Micronesica* **2009**, *41*, 83–99.
78. Marler, T.E. Cycad mutualist offers more than pollen transport. *Am. J. Bot.* **2010**, *97*, 841–845. [[CrossRef](#)]
79. Marler, T.E.; Lindström, A.J. The value of research to selling the conservation of threatened species: The case of *Cycas micronesica* (Cycadopsida: Cycadales: Cycadaceae). *J. Threat. Taxa* **2014**, *6*, 6523–6528. [[CrossRef](#)]
80. Marler, T.E. Temporal variations in leaf miner, butterfly, and stem borer infestations of *Cycas micronesica* in relation to *Aulacaspis yasumatsui* incidence. *HortScience* **2013**, *48*, 1334–1338. [[CrossRef](#)]
81. Marler, T.E.; Krishnapillai, M.V. *Cycas micronesica* trees alter local soil traits. *Forests* **2018**, *9*, 565. [[CrossRef](#)]
82. Marler, T.E. Perennial trees associating with nitrogen-fixing symbionts differ in leaf after-life nitrogen and carbon release. *Nitrogen* **2020**, *1*, 111–124. [[CrossRef](#)]
83. Marler, T.E.; Dongol, N. Three invasive insects alter *Cycas micronesica* leaf chemistry and predict changes in biogeochemical cycling. *Commun. Integr. Biol.* **2016**, *9*, e1208324. [[CrossRef](#)]
84. Marler, T.E.; Dongol, N. Do phytotoxic compounds in soils after scale-infested *Cycas micronesica* litter deposits explain reduced plant growth? *HortScience* **2013**, *48*, 1571–1573. [[CrossRef](#)]
85. Watson, G.; Marler, T.E. Does cycad aulacaspis scale (*Aulacaspis yasumatsui*, Hemiptera: Diaspididae) play a direct role in causing soil phytotoxicity? *Commun. Integr. Biol.* **2014**, *7*, 1571–1573. [[CrossRef](#)]
86. Zandalinas, S.I.; Sengupta, S.; Fritschi, F.B.; Azad, R.K.; Nechushtai, R.; Mittler, R. The impact of multifactorial stress combination on plant growth and survival. *New Phytol.* **2021**, *230*, 1034–1048. [[CrossRef](#)] [[PubMed](#)]
87. Canelles, Q.; Aquilué, N.; James, P.M.A.; Lawler, J.; Brotons, L. Global review on interactions between insect pests and other forest disturbances. *Landsc. Ecol.* **2021**, *36*, 945–972. [[CrossRef](#)]
88. Hirsh, H.; Marler, T. Damage and recovery of *Cycas micronesica* after Typhoon Paka. *Biotropica* **2002**, *34*, 598–602. [[CrossRef](#)]
89. Marler, T.E. Increased threat of island endemic tree's extirpation via invasion-induced decline of intrinsic resistance to recurring tropical cyclones. *Commun. Integr. Biol.* **2013**, *6*, e22361. [[CrossRef](#)] [[PubMed](#)]
90. Marler, T.E.; Lawrence, J.H. Phytophagous insects reduce cycad resistance to tropical cyclone winds and impair storm recovery. *HortScience* **2013**, *48*, 1224–1226. [[CrossRef](#)]
91. Marler, T.E.; Lawrence, J.H.; Cruz, G.N. Topographic relief, wind direction, and conservation management decisions influence *Cycas micronesica* K.D. Hill population damage during tropical cyclone. *J. Geogr. Nat. Disast.* **2016**, *6*, 178. [[CrossRef](#)]
92. Marler, T.E. Boomeranging in structural defense: Phytophagous insect uses cycad trichomes to defend against entomophagy. *Plant Signal. Behav.* **2012**, *7*, 1484–1487. [[CrossRef](#)]
93. Marler, T.E.; Miller, R.; Moore, A. Vertical stratification of predation on *Aulacaspis yasumatsui* infesting *Cycas micronesica* seedlings. *HortScience* **2013**, *48*, 60–62. [[CrossRef](#)]
94. Marler, T.E.; Marler, P.N. *Rhyzobius lophanthae* behavior is influenced by cycad plant age, providing odor samples in a Y-tube olfactometer. *Insects* **2018**, *9*, 194. [[CrossRef](#)]



95. Caldwell, D.L. The cycad aulacaspis scale, *Aulacaspis yasumatsui*: Management approaches and pesticide trial updates. *Proc. Fla. State Hort. Soc.* **2003**, *116*, 347–350.
96. Broome, T. Coffee, cycads' new best friend? *Cycad Newsl.* **2007**, *30*, 44–46.
97. Magellan, T.M.; Husby, C.; Cuestas, S.; Griffith, M.P. Spent coffee grounds do not control cycad aulacaspis scale. *HortTechnology* **2013**, *23*, 201–206. [[CrossRef](#)]
98. Marler, T.E.; Cruz, G.N. *Cycas micronesica* stem carbohydrates decline following leaf and male cone growth events. *Plants* **2020**, *9*, 517. [[CrossRef](#)] [[PubMed](#)]
99. Cave, R.D. Biological control agents of the cycad aulacaspis scale, *Aulacaspis yasumatsui*. *Proc. Fla. State Hort. Soc.* **2006**, *119*, 422–424.
100. Sembel, D.T.; Meray, E.M.; Rante, C.S.; Kandowangko, D.S.; Ratulangi, M.; Dien, M.F. Distribution of new crop pests in North Sulawesi, Indonesia. *Int. J. Arts Sci.* **2013**, *6*, 151–160.
101. Cave, R.D. Biological control of *Aulacaspis yasumatsui*. *Cycad Newsl.* **2005**, *28*, 8–9.
102. Smith, T.R.; Cave, R.D. Pesticide susceptibility of *Cybocephalus nipponicus* and *Rhyzobius lophanthae* (Coleoptera: Cybocephalidae, Coccinellidae). *Fla. Entomol.* **2006**, *89*, 502–507. [[CrossRef](#)]
103. Smith, T.R.; Cave, R.D. Life history of *Cybocephalus nipponicus* Endrödy-Younga (Coleoptera: Cybocephalidae), a predator of *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae). *Proc. Entomol. Soc. Wash.* **2006**, *108*, 905–916.
104. Smith, T.R.; Bailey, R. A new species of *Cybocephalus* (Coleoptera: Cybocephalidae) from Taiwan and a new distribution record for *Cybocephalus nipponicus*. *Coleopt. Bull.* **2007**, *61*, 503–508. [[CrossRef](#)]
105. Flores, D.; Carlson, J. Fortuitous establishment of *Rhyzobius lophanthae* (Coleoptera: Coccinellidae) and *Aphytis lingnanensis* (Hymenoptera: Encyrtidae) in South Texas on the cycad aulacaspis scale, *Aulacaspis yasumatsui* (Hemiptera: Diaspididae). *Southwest. Entomol.* **2009**, *34*, 489–492. [[CrossRef](#)]
106. Smith, T.R.; Cave, R.D. The Cybocephalidae (Coleoptera) of the West Indies and Trinidad. *Ann. Entomol. Soc. Am.* **2007**, *100*, 164–172. [[CrossRef](#)]
107. Bailey, R.; Chang, N.T.; Lai, P.Y. Two-sex life table and predation rate of *Cybocephalus flavocapitis* Smith (Coleoptera: Cybocephalidae) reared on *Aulacaspis yasumatsui* Takagi (Hemiptera: Diaspididae), in Taiwan. *J. Asia Pac. Entomol.* **2011**, *14*, 433–439. [[CrossRef](#)]
108. Song, S.Y.; Tan, C.W.; Hwang, S.Y. Host range of *Cybocephalus flavocapitis* and *Cybocephalus nipponicus*, two potential biological control agents for the cycad aulacaspis scale, *Aulacaspis yasumatsui*. *J. Asia Pac. Entomol.* **2012**, *15*, 595–599. [[CrossRef](#)]
109. Cave, R.D.; Chao, J.-T.; Kumashiro, B.; Marler, T.; Miles, J.; Moore, A.; Muniappan, R.; Watson, G.W. Status and biological control of cycad aulacaspis scale. *Biocontrol News Inf.* **2013**, *34*, 1N–4N.
110. Tang, W.; Cave, R.D. Recent advances in the biological control of cycad aulacaspis scale. *Encephalartos* **2016**, *123*, 16–18.
111. Perez-Gelabert, D.E. First record of *Cybocephalus nipponicus* Endrödy-Younga (Coleoptera: Cybocephalidae), a natural enemy of the cycad scale *Aulacaspis yasumatsui* Takagi (Coccoidea: Diaspididae) in the Dominican Republic. *Proc. Entomol. Soc. Wash.* **2020**, *122*, 248–250. [[CrossRef](#)]
112. Giorgi, J.A.; Vandenberg, N.J. Review of the lady beetle genus *Phaenochilus* Weise (Coleoptera: Coccinellidae: Chilocorini) with description of a new species from Thailand that preys on cycad aulacaspis scale, *Aulacaspis yasumatsui* Takagi (Hemiptera: Sternorrhyncha: Diaspididae). *Zootaxa* **2012**, *3478*, 239–255. [[CrossRef](#)]
113. Manrique, V.; Mancero-Castillo, D.A.; Cave, R.D.; Nguyen, R. Effect of temperature on the development and consumption of *Phaenochilus kashaya* (Coleoptera: Coccinellidae), a predator of the cycad aulacaspis scale, *Aulacaspis yasumatsui*. *Biocontrol Sci. Technol.* **2012**, *22*, 1245–1253. [[CrossRef](#)]
114. Anonymous. White cycad scale update. *Hawaii Hort.* **2000**, *3*, 13.
115. Moore, A.; Marler, T.; Miller, R.H.; Muniappan, R. Biological control of cycad aulacaspis scale on Guam. *Cycad Newsl.* **2005**, *28*, 6–8.
116. Hodges, G.S.; Howard, F.W.; Buss, E.A. Update on Management Methods for Cycad Aulacaspis Scale. EDIS ENY-680. 2003. Available online: <http://edis.ifas.ufl.edu> (accessed on 23 April 2021).
117. Wiese, C.; Amalin, D.; Coe, R.; Mannion, C. Effects of the parasitic wasp, *Coccobius fulvus*, on cycad aulacaspis scale, *Aulacaspis yasumatsui*, at Montgomery Botanical Center, Miami, Florida. *Proc. Fla. State Hort. Soc.* **2005**, *118*, 319–321.
118. Emshousen, C.; Mannion, C. Taming Asian cycad scale (*Aulacaspis yasumatsui*). *Cycad Newsl.* **2004**, *21*, 8–10.
119. Neumann, G.; Follett, P.A.; Hollingsworth, R.G.; De Leon, J.H. High host specificity in *Encarsia diaspidicola* (Hymenoptera: Aphelinidae), a biological control candidate against the white peach scale in Hawaii. *Biol. Control* **2010**, *54*, 107–113. [[CrossRef](#)]
120. Castillo, J.A.; Avery, P.B.; Cave, R.D.; Montemayor, C.O. Mortality of the cycad aulacaspis scale (Hemiptera: Diaspididae) by the entomopathogenic fungus *Isaria fumosorosea* Wize under laboratory conditions. *J. Entomol. Sci.* **2011**, *46*, 256–264. [[CrossRef](#)]
121. Marler, T.E.; Lindström, A.J. First, do no harm. *Commun. Integr. Biol.* **2017**, *10*, e1393593. [[CrossRef](#)] [[PubMed](#)]
122. Chen, F.G. *The Chionaspini (Diaspididae, Coccoidea, Homoptera) from China*; Science & Technology Publishing House: Sichuan, China, 1983.
123. Watson, G.W. *Arthropods of Economic Importance: Diaspididae of the World*; (Series Title: World Biodiversity Database); Expert Center for Taxonomic Identification: Amsterdam, The Netherlands, 2002.
124. Wei, J.; Jing, X.; Zhang, H. A new species of *Aulacaspis* Cockerell, 1893 from China with a key to Chinese species (Hemiptera, Coccoidea, Diaspididae). *ZooKeys* **2016**, *619*, 13–24. [[CrossRef](#)]

125. Suh, S.-J. Armoured scale insects (Hemiptera: Diaspididae) intercepted at the ports of entry in the Republic of Korea over the last 20 years. *Bull OEPP/EPPO* **2016**, *46*, 313–331. [[CrossRef](#)]
126. Messing, R.H.; Watson, T.K. Response to Holland et al.; Biocontrol in Hawaii: More bureaucracy is not the answer. *Proc. Hawaii. Entomol. Soc.* **2008**, *40*, 85–87.
127. United States Environmental Protection Agency. *Bifenthrin Pesticide Fact Sheet*; Office of Pesticide Programs, U.S. Government Printing Office: Washington, DC, USA, 1988.
128. United States Environmental Protection Agency. *Reregistration Eligibility Decision (RED) Acephate*; EPA 738-R-01-013; Office of Pesticide Programs, U.S. Government Printing Office: Washington, DC, USA, 2006.
129. Zhou, S.; Duan, C.; Michelle, W.H.; Yang, F.; Wang, X. Individual and combined toxic effects of cypermethrin and chlorpyrifos on earthworm. *J. Environ. Sci.* **2011**, *23*, 676–680. [[CrossRef](#)]
130. Marler, T.E.; Cruz, G.N. Best protocols for cycad propagation require more research. *J. Threat. Taxa* **2017**, *9*, 10738–10740. [[CrossRef](#)]
131. Hulme, P.E. Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. *One Earth* **2021**, *4*, 666–679. [[CrossRef](#)]