The Spread of Cycad Aulacaspis Scale (CAS): Ecological Collapse and Cultural Erosion of *Cycas revoluta* in the Amami Islands, Japan

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Abstract:

The rapid spread of cycad aulacaspis scale (*Aulacaspis yasumatsui*; CAS) across the Amami Islands, Japan, represents one of the most significant ecological disruptions documented in the region in recent decades. As a result, *Cycas revoluta* is facing a critical existential threat, and the Amami cultural practices and traditions that have developed around this plant are likewise at risk of irreversible loss. This article presents the most comprehensive assessment to date of CAS-driven impacts across the northern Amami archipelago, combining botanical survey, genetic sampling, and ethnographic documentation. Our field results reveal increased spread, extensive mortality, and accelerating population collapse across Amami Ōshima, with early- and mid-stage infestations on neighboring islands suggesting that similar trajectories will soon affect the broader region. Complementary interviews and visual documentation register parallel losses in knowledge, practice, and sense of place, underscoring the deeply intertwined ecological and cultural dimensions of this crisis. Together, these data show how an invasive species can rapidly destabilize long-standing biocultural systems, raising urgent questions for conservation, heritage preservation, and the resilience of island ecosystems.

Key words: biocultural heritage, cycad aulacaspis scale, *Cycas revoluta*, ethnobotany, invasive species, *sotetsu* culture

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Introduction

Cycas revoluta Thunb., known in Japanese as *sotetsu* and in English as the sago palm, is native to southern Japan, and is abundant in the Ryukyu archipelago (Calonje *et al.* 2025, Osborne and Tomiyama 1995, Yamazaki 1995). As long-lived plants of striking appearance that were also an important food source, *sotetsu* have long held symbolic and utilitarian value in Ryukyuan and broader Japanese culture (e.g., Ankei and Tōyama 2015, Englehardt and Carrasco 2023, Sakae 2003). Although cycads are robust plants, the *Cycas* genus is particularly vulnerable to the scale insect *Aulacaspis yasumatsui* Takagi (cycad aulacaspis scale [CAS]) (Takagi 1977). Previous CAS invasions of cycad populations in Florida (1995) and Taiwan (2000) caused widespread damage (Bailey *et al.* 2011, Howard *et al.* 1999, Walters *et al.* 1997), and the introduction of CAS to Guam in 2003 led to the death of an estimated 88% of *Cycas micronesica* K.D. Hill within five years (Marler and Krishnapillai 2020, Marler and Lawrence 2012).

In June 2021, CAS was detected on Amami Ōshima (Amami Shimbun 2022,

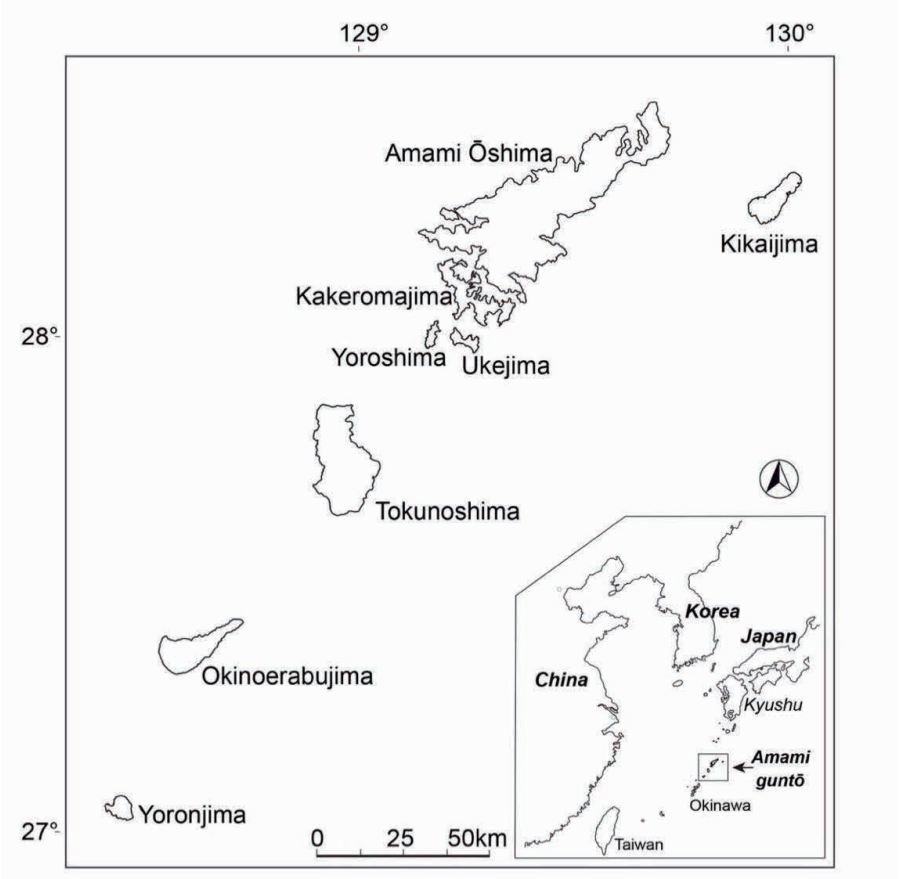

Figure 1. The Amami guntō, a subgroup of the Ryukyu archipelago that arcs southwest between the Japanese island of Kyushu and Taiwan (map by the authors).

Takagi 2023, see Figure 1), prompting urgent concern for the long-term survival of both plant populations and associated "*sotetsu* culture." Since then, researchers, government authorities, and community collaborators (Deloso *et al.* 2025, Englehardt *et al.* 2024, Englehardt *et al.* 2025, Amami City 2023, Kagoshima Prefecture 2025, Kawaguchi *et al.* 2024, Tsujimoto *et al.* 2024), have been tracking CAS spread and damage on Amami Ōshima and neighboring islands. Building on these early studies that first identified and monitored the emergence of CAS in the Amami Islands, our work extends this foundation by providing the most comprehensive island-wide survey to date, coupled with pre-collapse genetic sampling and systematic ethnographic documentation of cultural knowledge now at risk of disappearing. In studying this crisis, our goal has been to document a body of botanical and ethnographic evidence that may soon be unobtainable, at a moment in which cultural practices synergistically interact with biological realities, where changes in one element of the system affect the other.

This article details the results of recent (October 2025) ethnobotanical fieldwork conducted in the Amami Islands (*Amami guntō*). The objectives of this research were to: (1) map and quantify CAS impacts across the northern Amami Islands; (2) collect botanical samples to support future genetic analyses of population structure, human-mediated dispersal, and invasion-driven genetic loss; and (3) record and preserve Amami *sotetsu* culture via ethnographic interviews and visual documentation.

Botanical Survey of CAS Damage in the Northern Amami Guntō

During Fall 2025 we surveyed a total of 413 *C. revoluta* populations across four islands: 308 on Amami Ōshima, 49 on Kakeromajima, 30 on Kikaijima, and 26 on Tokunoshima. Survey work permitted us to ground-truth data provided by local collaborators (Englehardt *et al.* 2024: Fig. 12, Table 1, Englehardt *et al.* 2025) and to expand on the limited observations made by team members in 2023 and 2024 (Deloso *et al.* 2025). Fieldwork revealed that the damage to populations had increased exponentially since our last observations (see Deloso *et al.* 2025: Fig. 4). Nearly all populations across Amami Ōshima exhibited extensive mortality (Figure 2). Over 80% showed late-stage or terminal infestation, and 90% displayed minimal new growth, which was almost invariably infested or incompletely developed. The fact that several dozen populations that team members or local collaborators had observed as healthy or only moderately affected in 2023 and 2024 were now collapsing suggests that a critical threshold for widespread mortality among nearly all natural populations on Amami Ōshima has already been or will soon be crossed.

Among the approximately 200,000 plants in the populations surveyed on Amami Ōshima, only 22 completely healthy and uninfested specimens were documented (Figure 3). Five of these were in private gardens, and along with another eight decorative plants, had obviously been treated with chemical agents—since they were immediately adjacent to infested plants. The other nine healthy specimens observed were isolated individuals, generally located at higher altitudes and all but three of which were encountered near infested populations.

Kakeromajima exhibited an earlier stage of the pattern observed on Amami Ōshima.

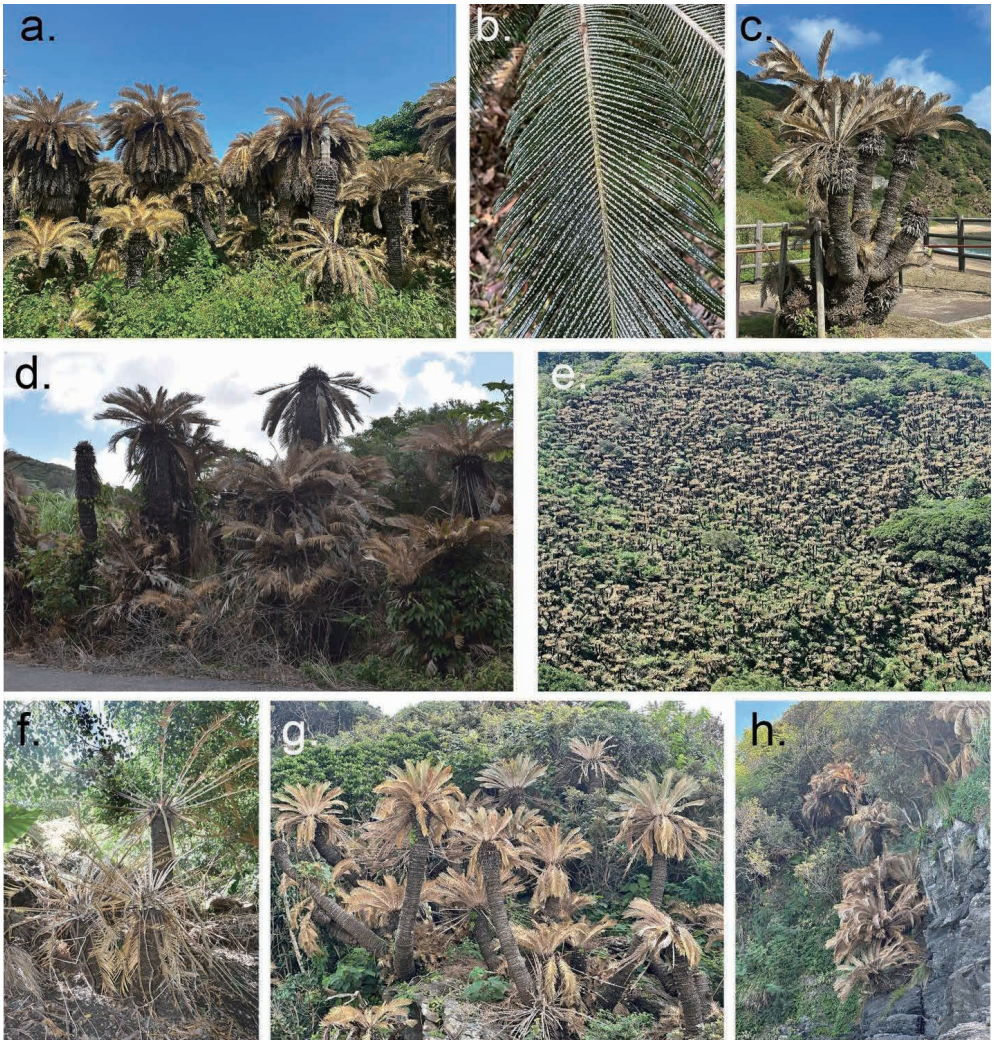

Figure 2. CAS-infested Cycas revoluta on Amami Ōshima: (a) Ayamaru Misaki, Amami-shi; (b) Imazato, Yamato-son; (c) Ōganekuturusu Park, Yamato-son; (d) Sani, Amami-shi; (e) Ankyaba, Tatsugo-chō; (f) Wase, Amami-shi; (g) Ashiken, Uken-son; (h) Yadorihama, Setouchi-chō (photos by Joshua D. Englehardt).

While healthy individuals remained more common, most were adjacent to infested plants, and mixed stands were widespread (Figure 4). Based on infestation density, Kakeromajima appears one to two years behind Amami Ōshima in the collapse curve.

Cycas revoluta populations on Kikaijima, in turn, were even healthier (Figure 5), as CAS was detected, and likely introduced, only in early 2025 (Matsubara personal observation 2025: Figure 6c). Currently, infested plants are concentrated around the Wan port and adjacent areas in the southwest of the island (Figure 6d), and infestations were evident in only seven of 30 (23%) observed populations. CAS appears to have begun spreading at a very rapid pace over the past ten months, northward along Kikai's west coast and southeastward along the southwest-south coast, as isolated populations in the early

Figure 3. Healthy Cycas revoluta plants observed on Amami Ōshima: (a) Shirahama, Setouchi-chō; (b) Uken, Uken-son (evidently treated); (c) Ōgachi, Tatsugo-chō; (d) Ōganeku, Yamato-son (photos by Joshua D. Englehardt).

stages of infestation were observed as far north as the Ikeji and Nakama neighborhoods on the west coast and those of Tekuzuku and Kamikatetsu in the south (Figure 6e-f). In those locales, infested plants were interspersed with healthy ones, and a great deal of new growth and coning was observed across all populations.

At present, Tokunoshima supports the healthiest *C. revoluta* populations in the Amami *guntō*. Tens of thousands of individual plants line roads, coastal bluffs, and agricultural boundaries, with dense concentrations particularly noticeable on the island's eastern and northern coasts. Across the 26 populations surveyed on Tokunoshima, crown density, leaflet health, and new flushes were far more robust than on any other island. Vast hedgerows and roadside clusters exhibited deep green color, full crowns, and plentiful coning (Figure 6). A particularly large number of female plants were observed in mid- or late-stage coning (Figure 7e-f), and remnants of male cones were likewise plentiful. However, we documented the first two confirmed CAS infestations on Tokunoshima, both within two km of the Kametoku

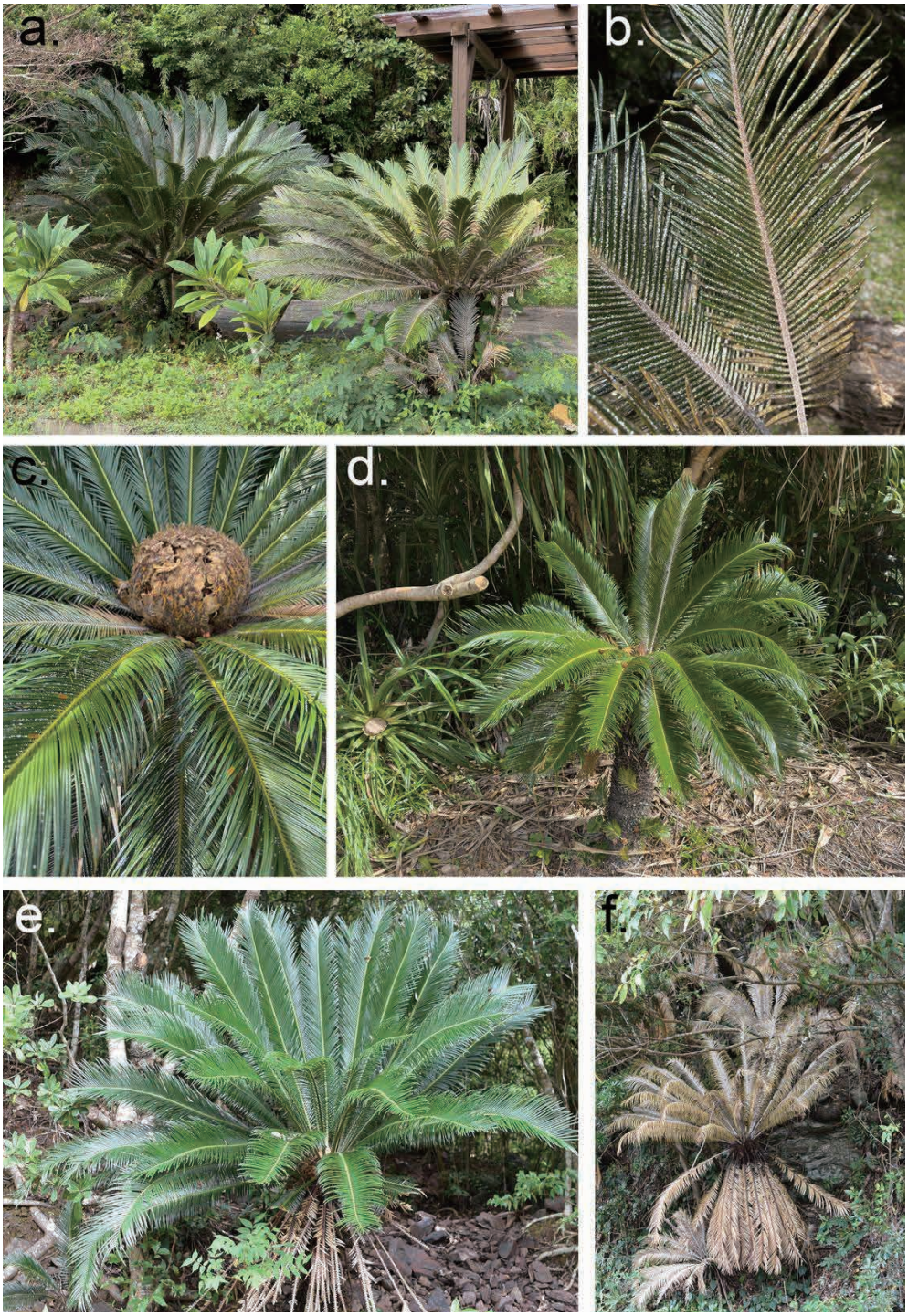

Figure 4. Mix of relatively healthy and infested Cycas revoluta on Kakeromajima: (a) Sesō roadside, relatively healthy; (b) Shimaotoshiobungakuhi Park, infested leaflets; (c) Nominoura, infested female with recent cone; (d) Izaneku-Oshikaku road, completely healthy; (e) Kanyū, early stages of infestation; (f) Sukomo hillside, infested (photos by Joshua D. Englehardt).

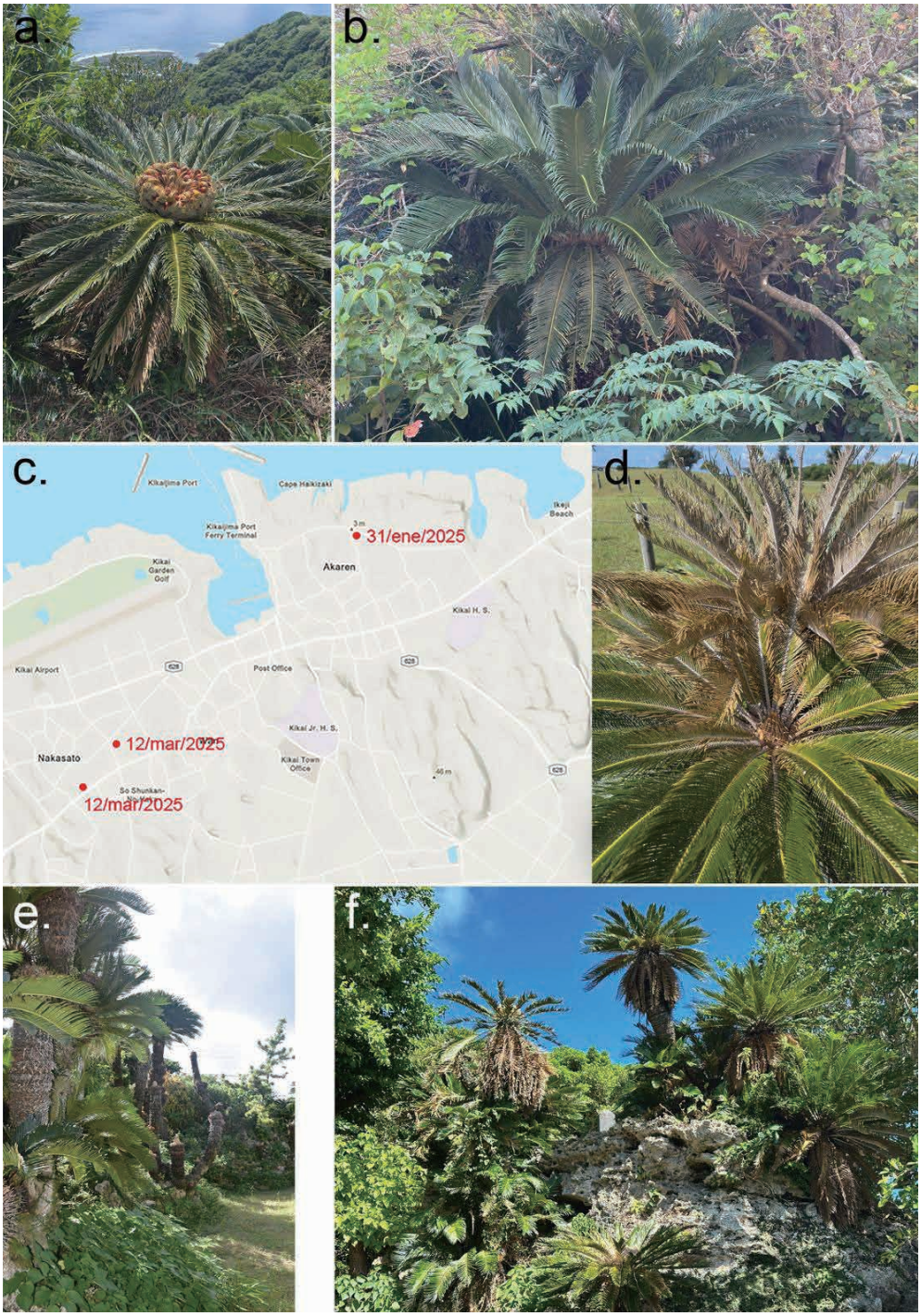

Figure 5. CAS and Cycas revoluta on Kikaijima: (a) Shichitoubana, completely healthy coning female; (b) Izaneku Itsukushima Jinja, completely healthy; (c) first detections of CAS on Kikai, January-March 2025; (d) Nakazato, infested, relatively healthy plants along golf course road; (e) Nakama private garden, designated municipal heritage, early stages of infestation (trimmed leaves); (f) Kamikatetsu cemetery, early stages of infestation (photos by Joshua D. Englehardt).

port area. Considering that CAS appears to have entered both Amami Ōshima and Kikaijima via the port areas, once again it would seem to be only a matter of time before CAS spreads outward to other Tokunoshima populations.

All survey data were georeferenced and visualized in an online ArcGIS StoryMap (https://storymaps.arcgis.com/stories/60e852443ed14e99b9ba49a4b5d6ceda). The mapping platform allows for the diachronic visualization and tracking of CAS spread across Amami Ōshima. The implications of our field observations are discussed more fully below.

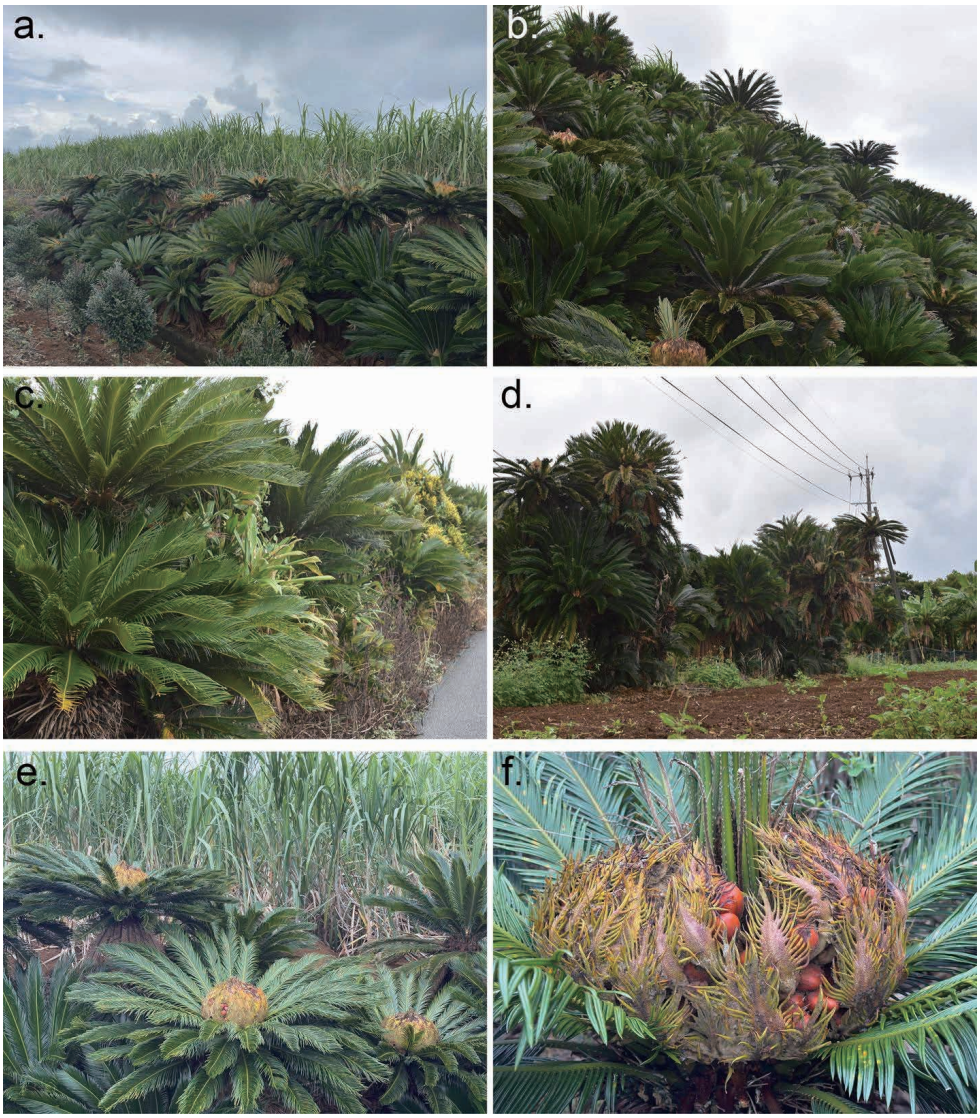

Figure 6. Healthy Cycas revoluta on Tokunoshima: (a) and (b) Kedoku Village; (c) Tokuwase Village; (d) Tete Village; (e) Kanami Village; (f) Kedoku Village (photos by Joshua D. Englehardt).

Botanical Sampling for Genetic Analyses

From 158 populations across the four islands surveyed we collected 271 georeferenced leaflet samples, each accompanied by photographs and field observations. Samples were silica-dried and logged daily. These botanical samples and associated data, in conjunction with recently released genetic datasets (Chang *et al.* 2019, Chang *et al.* 2022, Chang *et al.* 2023), lay the foundation for future genetic studies that may elucidate population structure and relatedness between plants within and among populations. These data, in turn, may reveal aspects such as the extent to which past human mediation—suggested by ethnographic data—has affected *C. revoluta* population structure, distribution, and dispersal as well as invasion-driven loss of genetic diversity among populations.

Given the high probability of extensive mortality as CAS continues to spread, the genetic samples obtained during our fieldwork may constitute the final documentation of pre-collapse population structure both among and within *C. revoluta* populations in the Amami Islands.

Ethnographic Documentation of Amami Sotetsu Culture

In addition to botanical survey and sampling, ethnographic fieldwork was also conducted. A total of 31 informal interviews with community members across all four islands were realized. Here, we focus on three of the most salient points: (1) local perceptions and accounts of the CAS invasion; (2) previously unreported manifestations and new perspectives of Amami *sotetsu* culture; and (3) recently discovered historical documents and photographs encountered during fieldwork.

Local Perceptions

In general, islanders, particularly those on Amami Ōshima, are acutely aware of the CAS invasion—it has been reported on extensively in local press. Many interviewees mentioned the lack of new growth on plants, saying they had seen only “just a little green [‘new growth’]”. An informant at the famous Ankyaba *sotetsu* grove reported that plants had not coned in 2025, and only partially in 2024. This fact likely explains the recent closure of the *nari* (cycad seed) miso factory in Uttabaru, Tatsugo-chō, since seeds have become scarce. Likewise, a clerk at the Aji-no-Sato store in Kasari reported that the paste currently on sale had been made from the previous year’s seeds. Many interviewees on Amami also inquired about treatment options or asked what could be done to save the *sotetsu*. It was upsetting to inform them that it is likely too late for any meaningful action and that the most effective available treatment options (e.g., biological control) are unlikely to make a difference at this point and in any case have not been tested or approved for use in Japan.

Some community responses appeared to be shaped by misconceptions. For example, six informants expressed the belief that cutting off the leaves of an infested plant would save it, even though such pruning is wholly ineffective in removing CAS infestations, since the insect also feeds on other parts of the plant (e.g., roots and trunks). Nevertheless, many

infested decorative or private garden plants whose leaves had been trimmed were observed during survey (e.g., Figure 6e). In that sense, it appears that the public outreach campaign to disseminate information on controlling CAS spread initiated by municipal and prefectural authorities has not been very effective. In fact, informational flyers prepared by prefectural authorities (Kagoshima Prefecture 2025) explicitly recommend cutting off infested leaves as one of several possible control measures. This recommendation has likely reinforced the misconception that pruning alone can save infested plants. One informant, encountered cutting off the leaves of several infested plants in a decorative hedgerow in Surigachi Village, mentioned that the plants had only been infested the previous year (2024) and that "in spite of cutting off all the leaves when [the infection was noticed], three of the plants had already completely died." A similar account was related by two interviewees in Kuninao, Yamato-son. This rate of mortality (within a year) squares with previously reported data (see Deloso *et al.* 2025: Fig. 4), a point to which we return below. Nonetheless, both informants seemed optimistic that the plants could survive, and pointed out that they had seen some new growth in 2025. When interviewing the individual at Surigachi, new leaf growth was indeed evident on one plant, although it had obviously been attacked almost immediately by remnant CAS in the plant crown.

Many interviewees likewise were cognizant of the muted response on the part of governmental authorities, as well as a lack of concern and pressure from local communities in general, in response to CAS. Ethnographic accounts revealed a crucial clue that may explain this situation: some informants analogized CAS to familiar but non-lethal pests such as pine wilt (Kameyama *et al.* 2024, Kuroda *et al.* 2006) or the cycad blue butterfly (*Luthrodes pandava* Horsfield; Marler *et al.* 2012), contributing to the perception that CAS would subside naturally. These reports may, in part, explain the lack of any meaningful local or regional response, to date, to the CAS outbreak and subsequent spread across the Amami *guntō*. That is, lack of concern could be due to the perception that CAS was like other outbreaks in that it would "go away on its own" without causing any real damage.

Nonetheless, when confronted with a mounting body of empirical evidence that CAS is indeed devastating insular *C. revoluta* populations, most informants expressed regret, repeating variants of the phrase *taihen desu ne* ("it's difficult, isn't it…?"). This fact suggests that local communities do indeed recognize the cultural and historical importance of *sotetsu* and take the *C. revoluta* populations as a marker of regional identity and point of local pride (Englehardt and Carrasco 2023, Hayward and Kuwahara 2012). Nevertheless, the notable lack of meaningful action at any level would seem to confirm the words of one informant: "Amami people don't care about cycads anymore, because now they are not so dependent on them."

New Perspectives on Amami Sotetsu Culture

Ethnographic interviews also revealed several manifestations of *sotetsu* culture, ranging from the whimsical to the ritual, that we had not previously encountered. One of these was related by an informant in Kanyū, Kakeromajima who, on a previous visit to Kuninao, Yamato-son, Amami Ōshima, had witnessed that village's *Hachigatsu odori*. During this

Figure 7. “Sotetsuman,” the cycad-themed mascot of Akitoku Village, Kakeromajima.

fall festival, participants dance to a *shima-uta* (“island song,” traditional folk songs of the Ryukyu Islands) called *Makkou no Merabe* (“Facing the Women”), an antiphonal (call-and-response) song in which women rhythmically call the men they are facing *yaki zuzutsu*[1] (“baked *sotetsu*”) as a kind of taunting jest. This is, according to the informant, because the men’s skin had darkened as a result of working in the fields under the tropical sun, and they therefore resembled the cone of a male *sotetsu* after it has been “baked” in the sun and withers, turning “black.”

Serendipitously, the same informant mentioned a dedicated “*sotetsu* park” in Akitoku, Kakeromajima, and in doing so introduced us to one of the more striking manifestations of Amami *sotetsu* culture: *Sotetsuman*, “cycad man” (Figure 7). The official mascot of Akitoku Village, *Sotetsuman* is modeled on the plant itself—its “flowers,” “seeds,” “leaves,” and “trunk”—and promoted as a local hero. The character appears in illustrated form in Akitoku, in a photo stand at the Amami Mangrove Park on Amami Ōshima, and has even been adapted into a costumed figure at community events. The imagery surrounding *Sotetsuman* underscores the deep-seated significance of *C. revoluta* in the Amami cultural imaginary and its renewal through contemporary popular media. As with other regional mascots, *Sotetsuman* refigures a local plant into a cute, anthropomorphized character, illustrating how *C. revoluta* continues to mediate identity and place-making even as the material basis of *sotetsu* landscapes is rapidly disappearing.

Another significant piece of ethnographic data was provided by a community leader in Ankyaba, Tatsugo-chō, who reported that, according to village oral history, the local *sotetsu* population had been intentionally brought from Yamato-son to the southwest. A subsequent

1 A locale-specific term for *C. revoluta*.

conversation in Naze, Amami-shi suggested that such movements may have reflected the historical abundance of *sotetsu* in Yamato-son, documented in ethnohistorical sources such as the *Nantōzatsuwa* and the earlier *Nōmuchō*, which emphasized the cultural importance and cultivation of cycads across the Ryukyu Islands (see Englehardt and Carrasco 2023: 284). Ankei (2023: 32) records a parallel account from Tete, Tokunoshima: after winning an archery contest in Shodon, Kakeromajima some 400 years ago, a man from Tete declined the prize of a gun and instead requested a *C. revoluta* plant, said to be the progenitor of all *sotetsu* in Tete. Because we sampled populations in Ankyaba, Yamato-son, Shodon, and Tete, forthcoming genetic analyses may help evaluate these oral histories of cycad movement.

Recently Uncovered Historical Evidence on Amami Cycads

Fieldwork also brought to light several important historical sources that illuminate past cycad distribution and the changing relationship between *sotetsu* use and agroecological practices. Chief among these is a trove of high-resolution aerial photographs taken by the United States Navy during World War II in preparation for a planned bombardment of the Amami Islands. Although previously examined by Hayaishi and Tōyama (2015), a renewed analysis may allow the identification of cycad-lined terraces, hillside plantings, and other forms of landscape management (see also AŌJRC 1956). These images may further provide evidence of sex ratios and spatial distributions within individual populations—an issue of interest given our observation that female plants appear to outnumber males in parts of the archipelago. This imbalance aligns with ethnographic accounts (Moriguchi and Ankei 2009) noting that seeds were the preferred food source, whereas the stems of male plants were also consumed, potentially reducing male abundance over time. New genetic sexing techniques (Yang *et al.* 2024) will be applied to our samples to investigate these patterns. Together, these historical and genetic data may help clarify how selective planting, terracing, and the intentional establishment of *sotetsu* in marginal areas contributed to the formation of managed landscapes that are often assumed to be "natural."

Discussion: Landscapes of Accelerating Decline

Tsujimoto *et al.* (2024:148) note that *Cycas revoluta* held "exceptional cultural importance on Amami Ōshima," forming part of a historical "*sotetsu* culture." We concur that *sotetsu* were more deeply integrated into daily life on Amami Ōshima than on any other island in the archipelago, a point echoed widely (e.g., Ankei and Tōyama 2015, Hayward and Kuwahara 2012, Moriguchi and Ankei 2009, Okuzaki 2008, Sakae 2003). As Tsujimoto and colleagues observe, this close cultural relationship, combined with the dense distribution of cycads, facilitated the rapid and extensive spread of CAS—an acceleration that our own longitudinal tracking since 2022 confirms.

Botanical survey revealed severe and island-wide infestation on Amami Ōshima, with minimal new growth or reproductive activity and very few healthy individuals. The pace of destruction appears to be increasing: districts that remained relatively unaffected in 2024,

particularly Uken-son and Setouchi-chō, showed dramatic declines in 2025, including a 410% increase in mortality in prefectural records (Amami Shimbun 2025, Kagoshima Prefecture 2025). Ethnographic accounts align with these observations, with informants reporting rapid die-offs following initial infestation. CAS now extends across the entire island, reshaping landscapes that, until recently, were defined by dense cycad groves. The five-year window from detection to collapse documented for Taiwan and Guam (Bailey *et al.* 2011, Deloso *et al.* 2025, Marler and Lawrence 2012) closely matches our four years of observations on Amami.

Although Kakeromajima and Kikaijima currently retain healthier populations, CAS is now firmly established on both islands. In the absence of effective control strategies, comparable mortality trajectories are likely. Further south, Tokunoshima remains comparatively robust, though the first infestations—detected near Kametoku port in October 2025—suggest that similar decline is imminent. No confirmed cases exist for Yoroshima, Okinoerabujima, or Yoronjima, but CAS is already widespread on Okinawa Island (Tsujimoto personal observation 2025).

Finally, our survey sheds light on mechanisms of introduction and dispersal. CAS was first detected near major ports on Amami Ōshima, Kikaijima, and Tokunoshima, strongly suggesting human-mediated transport. Yet infestations also occur in remote and uninhabited locations, implying secondary dispersal through wind or other vectors, including the butterfly *Luthrodes pandava*, observed in abundance during fieldwork. Given the speed and spatial reach of the invasion, our ability to collect pre-collapse genetic material in 2025 may represent the final opportunity to document population structure before widespread loss.

Conclusion

This contribution has detailed our efforts to document the unfolding CAS invasion in the Amami Islands and to record critical ethnobotanical knowledge from a biocultural system now in immediate jeopardy. The results are unambiguous: *Cycas revoluta* is experiencing widespread mortality across Amami Ōshima, with early stages of collapse beginning to appear across the wider archipelago. If current trends continue, the decline of *sotetsu* populations on Amami Ōshima, and eventually elsewhere in the Amami *guntō*, seems likely, with profound consequences for the survivability of *sotetsu* culture in anything resembling its historical form.

It is difficult to express our own sense of dismay at this situation. Within a span of five years, we have witnessed the near-total destruction of both the plants themselves and the millenary cultural systems with which they are intertwined. Our ethnographic work underscores how much remains to be understood about these traditions; yet if the plants from which they emerge disappear, so too will the practices, memories, and social relations they sustain. Whether future generations will know *sotetsu* as living presences or only as archival images remains deeply uncertain.

Our interlocutors on Amami Ōshima are themselves aware of this possibility. Many expressed concern at the prospect of losing a set of cultural traditions that once formed a

distinctive axis of local pride and identity. Our longitudinal observations over the past four years align closely with the five-year window from initial detection to collapse documented in Taiwan and Guam, suggesting that what we are witnessing on Amami Ōshima is not anomalous, but rather typical of CAS invasion dynamics in insular cycad systems.

A final conversation crystallized the disconnect between scientific evidence and official attitudes. During a dinner in Naze in October 2025, attended by many people intimately familiar with the CAS situation on Amami Ōshima, several guests voiced urgent concern and cited mortality patterns from other regions. Another, however, offered a telling comment: *shinpai shinai, sotetsu wa shinanai node*—"I'm not worried, because *sotetsu* don't die." If only that were the case.

Nonetheless, while the current situation is dire, some hope remains for long-term survival and possible recovery. Although only a few healthy, uninfested plants were observed during fieldwork, their presence suggests that some isolated natural populations may yet survive. Further, *C. revoluta* seeds from Amami Ōshima have been sent to botanical institutions for ex-situ conservation, which may allow for the restoration of insular *sotetsu* landscapes once the invasion has run its course. Finally, recent field observations on Guam have revealed increasing recovery of *Cycas micronesica* populations 20 years after CAS-driven collapse—although those plants have yet to begin naturally reproducing. If such resurgence is to occur in the Amami Islands, however, intensified conservation efforts and more robust CAS control and treatment strategies—such as those outlined by Deloso *et al.* (2025)—must begin immediately.

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