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Increased threat of island endemic tree's extirpation via invasion-induced decline of intrinsic resistance to recurring tropical cyclones

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Cycas micronesica populations in Guam have been threatened by the invasion of the armored scale *Aulacaspis yasumatsui*. I integrate four factors that illuminate an acute need for intervention to reduce an unprecedented threat caused by the invasion. First, mechanical failure of healthy *C. micronesica* trees during catastrophic winds is rare because of the cycad tree's unique pachycaulis stem design. Second, tree-winching and three-point bend stress tests revealed the natural resistance to damage from tropical cyclones has been compromised by the chronic feeding of this homopteran pest. Third, no typhoon event has occurred since the arthropod's invasion and its spread in the year 2005 to actually test extent of mechanical failure for the unhealthy remaining trees. Fourth, historical records indicate the probability that Guam will experience typhoon force winds is 0.51 in three years and 0.91 in 10 y. These four factors integrate to predict the next typhoon may eliminate the surviving *C. micronesica* trees and stewardship of this declining population requires intervention to counter this prediction.

Introduction

Tropical cyclones are defining of forest community structure in many geographic regions.[1,2] These large-scale infrequent disturbances are called typhoons in the Western Pacific, hurricanes in the Atlantic and Eastern Pacific and cyclones in the south Pacific regions. Resistance and resilience to catastrophic tropical cyclone damage vary greatly among sympatric taxa, and this heterogeneity mediates landscape-level changes following tropical cyclone damage.[1-4]

Stem herbivory by arthropods or ungulates can induce internal decay of stem tissues, and the resulting compromised mechanical integrity may increase incidence of stem failure.[5,6] Therefore, differential incidence of stem decay induced by herbivory partly defines community damage during tropical cyclones. The homopteran *Aulacaspis yasumatsui* invaded Guam in 2003,[7] and dispersed into native forest habitat by 2005.[8] The dominant *Cycas micronesica* served as its only native host species, and heavy infestations of the pest occurred on the surfaces of leaves, reproductive structures and stems. The armored scale insect employs a piercing, sucking approach to phytophagy and external stem appearance remains unchanged even after years of infestation. Therefore, any resulting change in susceptibility to mechanical failure generated by the stem herbivory would be direct, not mediated by stem decay.

This invasion has resulted in epidemic mortality of the cycad population, and the decline in survival elicited IUCN endangered status by 2006.[9] The homogeneous annual decline in population density from 2007 to 2011 predicts extirpation from Guam habitats will occur in 2019 if the unwavering decline is sustained in the upcoming years.[10] I set out to examine whether the chronic feeding habit of this pest has negatively affected stem biomechanical properties of the persisting unhealthy cycad trees. If validated, this phenomenon illuminates a magnified threat of *C. micronesica* extirpation on Guam and nearby Rota via removal of the innate resistance to naturally recurring typhoons, and justifies increased protective measures for remaining live trees. This example may serve to demonstrate that conservation of threatened plant populations in the context of invasive species may not always present straight-forward predictions and use of an integrated biology approach to identifying threats is warranted.

Results

Simultaneous measurements from different habitats. In winching experiments on standing stems, each force vs. displacement curve conformed to a negative exponential $Y = a - b^{*}e^{(-kx)}$. The main effect of pull direction was not significant for a (p = 0.1807), b (p = 0.1483) or k (p = 0.1298). Similarly, the interactive effect of pull direction and duration of scale infestation was not significant for a (p = 0.1335), b (p = 0.1129) or k (p = 0.1218). However, the main effect of scale infestation duration significantly decreased parameter a and b, and significantly increased

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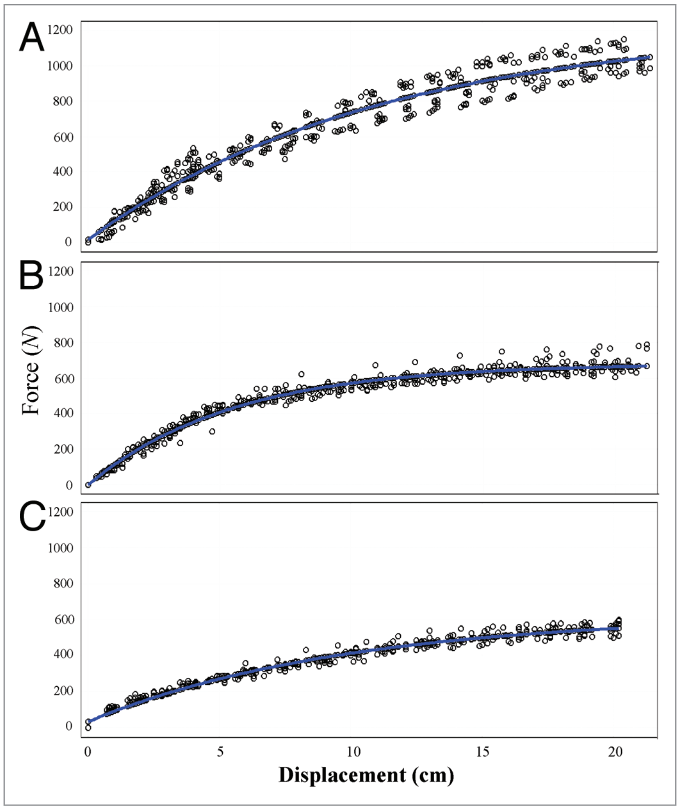

Figure 1. Force vs. displacement curves for *Cycas micronesica* tree-pulling experiments for un-infested trees and trees infested with *Aulacaspis yasumatsui*. (**A**) Control trees: force = 1221.41 – 1204.62*e $^{-0.09053*displacement}$. (**B**) Two years of infestation: force = 679.90 – 679.51*e $^{-0.18317*displacement}$. (**C**) Five years of infestation: force = 628.31 – 593.71*e $^{-0.10195*displacement}$.

parameter *k* ($p < 0.0001$). Therefore, one model was fitted for each of the three levels of scale infestation duration (**Fig. 1**).

Two years of scale infestation reduced parameter *a* to 55% of control trees and five years of infestation reduced *a* to 51% of control trees ($p < 0.0001$). Two years of infestation reduced parameter *b* to 56% of control trees and five years of infestation reduced *b* to 49% of control trees ($p < 0.0001$). Two years of infestation increased parameter *k* 102% above that of control trees, and five years of infestation increased *k* 13% above that of control trees ($p < 0.0001$). At the limits of displacement within this experiment, the absolute force required to displace the stem of cycad trees experiencing five years of scale infestation was 49% of that for healthy trees.

I also calculated turning moment at maximum displacement in the winching experiments for each of the three scale infestation duration levels. Healthy trees with no scale infestation history exhibited turning moment of 1838 ± 78 *N*m, trees following two years of scale infestation exhibited turning moment of 1206 ± 50 *N*m, and trees following five years of scale infestation exhibited turning moment of 976 ± 27 *N*m ($p \leq 0.0001$).

In three-point bending stress tests, each force vs. displacement curve conformed to a linear model. The three independent variables displacement, infestation duration and displacement × duration were significant ($p < 0.0001$) in the analysis of covariance. This confirmed that the scale infestation duration was significant and three separate regression models were warranted to describe the linear relationship between the force and displacement (**Fig. 2A**). Two years of scale infestation reduced the slope to 84% of control trees, and five years of scale infestation reduced the slope to 51% of control trees. The absolute force required to reach the maximum displacement of the stem of cycad trees experiencing five years of scale infestation was 45% of that for uninfested, healthy trees.

I also calculated stem rigidity from the three-point bend tests as $FL^3/48y$, where F = force, L = length between supports and y = deflection. Healthy trees with no scale infestation history exhibited rigidity of 11,527 ± 312 $N\text{m}^2$, trees following two years of scale infestation exhibited rigidity of 9,201 ± 87 $N\text{m}^2$ and trees following five years of scale infestation exhibited rigidity of 5,422 ± 67 $N\text{m}^2$ ($p \leq 0.0001$).

Sequential measurements on permanent population. Turning moment was not influenced by the main effect of pull direction ($p = 0.9935$) or the two-factor interaction between direction x month ($p = 0.9998$). In contrast, the duration of scale infestation influenced turning moment ($p < 0.0001$). Heavy scale infestation did not affect turning moment for the initial 9 mo, but by 15 mo of infestation turning moment declined to 88% of that for healthy trees (**Fig. 3**). My final measurements at 26 mo of infestation indicated stem strength had been compromised severely by the chronic feeding of this armored scale pest, as turning moment was 51% of that for trees prior to scale infestation.

Discussion

These results predict that most of the mature and tall specimens among the remaining *C. micronesica* trees will experience mechanical failure during the next typhoon if no form of intervention is implemented. In effect, ignoring the need for protection from mechanical failure may lead to extirpation of Guam's cycad populations in a single typhoon event. One approach to validating this prediction would be to wait for the next typhoon and document population damage thereafter. This approach would verify accuracy of the prediction, but would not allow these post-typhoon data to be used to argue the need for mitigating conservation protocols. Another approach for validating the prediction would be to use an integrative biology approach to stitch together an empirical argument. I will discuss four components to authenticate my statement. First, the autochthonic cycad population must be shown to possess inherent resistance to mechanical stresses imposed during the frequent typhoons that characterize the region. Second, the invasion must be shown to have compromised this resistance in some manner. Third, an accounting of Guam's typhoon history must reveal that the post-invasion cycad population has not been challenged by a typhoon to date such that no historical event can be used to validate the statement. And fourth, the risk of a recurring typhoon impacting the unhealthy cycad survivors must be high for this predicted threat to materialize prior to the projected 2019 extirpation of Guam's cycad population. Confirmation of these four components would provide evidence that unprecedented conservation measures are warranted to counter the increased risk of extirpation.

Component 1. The forests of Guam are so controlled by frequent typhoon damage that they have been dubbed "typhoon forests."[11] Indeed, Guam has that highest probability or risk of being hit by a tropical cyclone than any other region of the United States.[4] All native tree species on Guam evolved with tropical cyclone disturbance as a chronic driver of population development. *Cycas micronesica* cannot escape direct damage by major tropical cyclones,[12] however, the species is remarkably resilient following typhoon damage.[13] Furthermore, most direct damage to trees in the wake of the strongest of tropical cyclones was leaf damage, and mechanical failures in the form of stem snapping or uprooting accounted for a small percentage of documented damage.[12] Healthy *C. micronesica* trees are clearly resistant of tropical cyclone disturbance, especially in comparison to sympatric native and exotic taxa.

Component 2. Tree winching and three-point bend experiments are routinely used to quantify potential wind damage, as their findings correlate with actual windthrow damage for every species studied, and their response variables are used as metrics to build risk models.[14-16] Therefore, I used these established tests to determine how the duration of *A. yasumatsui* infestation affected *C. micronesica* stem biomechanics.

Chronic infestation of this invasive homopteran insect compromised the strength for *C. micronesica* stems. Furthermore, since stem strength decreased in accordance with duration of the scale infestation, it is an indication that delays in implementing protective conservation measures will increase the risk of extirpation should a typhoon event occur prior to intervention.

Component 3. Typhoon Chataan in July 2002, Typhoon Pongsona in December 2002, Typhoon Tingting in July 2004 and Typhoon Chaba in August 2004 were the most recent occurrences of damaging tropical cyclones on Guam.[17,18] Thus, four direct hits by damaging typhoons within 25 mo is not an unusual historical occurrence for Guam. *A. yasumatsui* was confined to urban landscapes until January 2005 when it dispersed into native forests.[8] By coincidence an unusual period of 8+ years without a direct hit by a typhoon has followed this invasion within in situ *C. micronesica* habitats. The opportunity to study the direct damage to scale-infested Cycas trees following typhoon-force winds has never materialized in human history. Therefore, direct assessments of windthrow cannot be employed to inform management decisions for this at-risk island population.

Component 4. Typhoon vulnerability for Guam was calculated based on 52 y of historical records.[19] These data reveal that tropical cyclone force winds recurred on average on Guam every 4.7 y, which translates to a 0.21 probability that Guam will experience typhoon-force winds within the next 12 mo. I used probability theory to generate a curve of the probability that Guam will receive tropical cyclone force winds over the next 10 y (**Fig. 2B**). This probability reached 0.51 within three years and 0.91 within 10 y. This extensive, long-term meteorological data set predicts an 81% chance the remaining *C. micronesica* trees will suffer direct damage by a tropical cyclone prior to the currently predicted extirpation in 2019. Therefore, management of this dwindling island cycad population must include protective measures to counter the physical damage that will accompany a tropical cyclone occurrence.

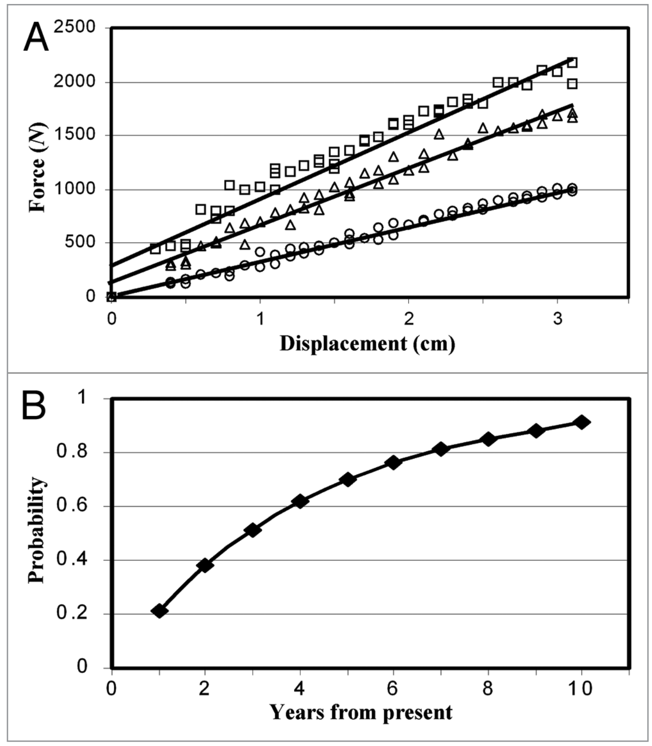

Figure 2. (**A**) Force vs. displacement curves for *Cycas micronesica* three-point strength experiments for un-infested trees and trees infested with *Aulacaspis yasumatsui* for two or five years. Control trees (□) force = 263.29 + 657.03*displacement; Two years (○) force = 100.17 + 552.79*displacement; Five years (△) force = -3.37 + 334.46*displacement. (**B**) Probability that Guam will experience direct impacts of tropical cyclone winds throughout the impending 10 y.

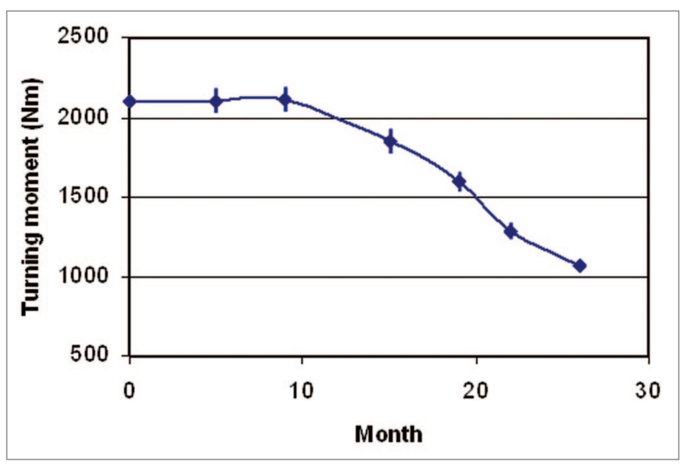

Figure 3. Turning moment of standing *Cycas micronesica* trees as influenced by number of months following infestation by *Aulacaspis yasumatsui.*

Conservation applications. All four components required to validate my statement have been satisfied. This integrative approach offers empirical evidence that this alien arthropod invasion has reduced the innate resistance of Guam's native cycad taxon to naturally recurring typhoons by altering the stem's mechanical properties and increasing the risk of mechanical failure. The combined outcomes of this study are a harbinger of imminent demise for this endangered island cycad population. They indicate as more time passes stem strength will continue to decrease. Without some form of conservation intervention, therefore, the next major typhoon may eliminate the remaining trees *Cycas* from Guam's forests.

For this taxon, our previous work revealed that the presence of epiphytes was associated with mechanical failure during a major typhoon.[12] The large pinnately compound leaves of *C. micronesica* are flexible and easily reconfigure in directional winds. Moreover, leaves of this taxon are disposed of with a clean abscission at the base of the petiole during high wind events. Both of these leaf characteristics enable a *C. micronesica* trees to lower the drag coefficient and thereby employ mechanical stress avoidance approaches to minimize mechanical failure during typhoons. The epiphyte loads compromised these stress avoidance strategies by increasing the drag coefficient and canopy weight, which then surpassed the ability of stems to resist damage by the increased mechanical stress. Therefore, during this impending period of anticipating Guam's next typhoon, stewardship of this important cultural and biological resource might include selective removal of epiphytes from surviving *C. micronesica* trees. A second approach might include installation of anchored guy wires to a subset of enduring live trees. The selection process for this procedure could include trees that represent all height categories throughout the height range of the surviving population, since height of this taxon is a surrogate for age, and conserving a population of various age classes may maximize genetic structure of the protected population. These efforts may allow the protected trees to avoid the mortality that my data foretell.

Invasions and large infrequent disturbances. The influence of abiotic disturbances on damage to forests imposed by subsequent disturbances is well-documented. For example, tropical cyclones are known to increase susceptibility to other abiotic disturbances such as subsequent fire.[20-22] Conversely, pre-hurricane fires influence the damage caused by a hurricane.[23] Abiotic disturbances such as tropical cyclones may also increase incidence of biotic disturbances, such as subsequent irruptions of insect pests.[23,24] However, I am unaware of a previous example where the invasion of an exotic arthropod has directly decreased resistance of a tree species to the large-scale disturbance imposed by tropical cyclones. My results add to the understanding of how tropical cyclones affect forests in today's prevalence of biological invasions, and conversely how biological invasions affect forest responses to large scale infrequent disturbances. Therefore, this study may improve our ability to understand how invasions and large, infrequent disturbances interplay to inform conservation management decisions.

As the Anthropocene[25] continues to unfold, biological invasions will assuredly increase and our resolve to understand all of the consequences should also increase. The occurrence of tropical cyclones is also projected to remain elevated in the upcoming decades,[26] so the need for increased understanding of how vulnerable species are threatened by catastrophic wind events cannot be over-emphasized.[27] This call for action is as important on Guam as any other location, considering the burgeoning military buildup and the increase in human and cargo traffic that will be required to support the buildup during the impending 10 to 15 y.[28]

Unfortunately, the mechanisms by which invasions threaten existing native species may not be overtly recognizable. My data highlight the importance of expecting these invasions to result in nuanced cascading events that have not been previously reported. Our tenacity to expect these unprecedented cascading events may improve efforts in risk analysis for predicting the ultimate consequences of future invasions. In this case study, the unique pachycaulis stem design of the native *C. micronesica* which uses primarily live stem tissue for biomechanical integrity[29] is largely responsible for the outcomes. Wood is the stiffest known plant tissue,[30] and stems comprised primarily of wood may sustain biomechanical integrity even after arthropod damage. Furthermore, wood properties confer resistance to tropical cyclone damage for rainforest canopy trees.[31] Perhaps the live tissue of cycad stems enabled the resource-depleting consequences of the alien pest's homopteran feeding style that compromised strength of the pachycaulis stem without any signs of intermediating stem decay.

Human history is laden with myriad examples of a conservation lesson learned after the lesson can actually be used. My intent is for this invasion-induced case study to serve as an example where a combination of empirical approaches can be stitched together to instill the sense of urgency needed to conserve a species before an anticipated natural disaster renders the lesson too late to use. It is fitting that a cycad species serves as the model in a conservation paper that argues for an unprecedented approach to assessing population threats, as cycads are the most threatened group of plant species on Earth.[32]

Materials and Methods

Simultaneous measurements from different habitats. I employed traditional tree winching and three-point bend experimental approaches. Control *C. micronesica* trees were located within an isolated forest fragment that had evaded *A. yasumatsui* scale immigration at the time of the field work. Two durations of scale infestation were employed by including trees located in habitat with direct scale infestations for two years and other trees located in a habitat with infestations for five years. The three habitats exhibited no difference in physiognomy or soils (clayey-skeletal, gibbsitic, nonacid, isohyperthermic Lithic Ustorthents), and the only observed difference was duration of scale infestation. I selected four monopodial trees in the control habitat with minimal difference in diameter along the columnar stem, then I scouted the other two habitats to find individuals that matched the stem height and diameter of each control replication. Despite epidemic tree mortality, the infested habitats still supported more than 300 trees per ha, so this approach was practicable. These methods standardized tree size to minimize complications in the comparative calculations.

Mean tree height was 2.36 meter and the tree-winching experiments used a cable strapped at 1.8 meter stem height and anchored at 15 meter. Stem diameter at height of the cable was 0.15 meter. Four force-vs.-displacement pulls were conducted at 90°, 180°, 270° and 360° aspect. The independent variable was lateral displacement of the stem in cm, and the dependent variable was the force required to achieve each displacement increment in Newtons. Displacement was executed in 19–23 incremental points and was terminated at about 20 cm maximum for each pull to ensure displacement did not approach tree failure. Within these displacement limits, each force vs. displacement curve conformed to a negative exponential $Y = a - b{*}e^{(-kx)}$. The model for each replication was calculated, then a SAS data set was created by including the three nonlinear model parameters *a*, *b* and *k* as the response variables. A Proc GLM model was fitted to determine the significance of scale infestation duration, pull direction and the interaction of these two sources of variation.

The three-point bend test was imposed on the standing trees. The span length was 2 meter and the load was applied at the midpoint. Mean diameter of the stem throughout the span was 0.16 meter. The independent variable was lateral displacement of the stem, and the dependent variable was the force required to displace the stem for each increment. Displacement was terminated before 3.5 cm maximum for each bending replication to ensure I did not damage stems, and 10 to 11 increment points were used per test. Within this displacement range, the regression model was linear. To determine whether the linear relationship between force and displacement was influenced by scale infestation duration, a GLM model was fitted in SAS GLM Procedure with force as a dependent variable and displacement, replications and the interaction of displacement and replications as independent variables. The P-values obtained were not significant, confirming that the replication effect was not significant and one single regression model could be used to describe the linear relationship between the force and displacement for each infestation duration level. Thereafter, GLM model was fitted using force as the dependent variable and displacement, infestation duration and the interaction of displacement and duration as independent variables to determine if scale duration significantly influenced force.

Sequential measurements on permanent population. In order to augment the chronosequence approach described above, I also employed sequential measurements on the same set of trees beginning prior to scale infestation. I located eight trees of similar size from a habitat in southern Rota simultaneous with *A. yasumatsui* immigration into the habitat in November 2009. Mean tree height was 2.46 min. I conducted tree-pull measurements as described above, then returned to the same trees for repeated measurements at various times up to 26 mo following scale infestation. Each of the trees were not infested with *A. yasumatsui* for the initial measurements, but were heavily infested for each of the 5 to 26 mo measurement periods. I calculated turning moment at 20-cm lateral displacement as force x height of the attached pulling cable. Then a repeated measures factorial ANOVA was performed using SAS GLIMMIX procedure in version 9.3. Pull directions and the months of infestation were treated as fixed factors and trees were treated as Random factor. The AR(1) covariance structure was selected as the suitable covariance structure among the repeated measure factor month.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Acknowledgments

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