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Canopy and knowledge gaps when invasive alien insects remove foundation species

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The armored scale *Aulacaspis yasumatsui* invaded the northern range of the cycad *Cycas micronesica* in 2003, and epidemic tree mortality ensued due to a lack of natural enemies of the insect. We quantified cycad demographic responses to the invasion, but the ecological responses to the selective removal of this foundation species have not been addressed. We use this case to highlight information gaps in our understanding of how alien invasive phytophagous insects force cascading adverse ecosystem changes. The mechanistic role of unique canopy gaps, oceanic island examples and threatened foundation species with distinctive traits are three issues that deserve research efforts in a quest to understand this facet of ecosystem change occurring across multiple settings globally.

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Introduction

Alien invasions are one of the critical means by which anthropogenic activities are altering biodiversity, and the direct and indirect effects of biological invasions on ecological processes are manifold.[1] Despite a growing interest in this subject, the extent of ecosystem change in response to invasions may be much greater than is often assumed.[2] A recent literature survey of invasive alien insects and consequential ecological changes revealed that almost two thirds of published reports were constricted to North America case studies, and the vast majority of these were restricted to responses of native biodiversity.[3] The authors pointed out that effects of invasive insects on ecosystem processes were rarely explored.

Cycas micronesica is an island endemic cycad species[4] that was the most abundant tree species on Guam[5] prior to the invasion of *Aulacaspis yasumatsui*.[6] *Cycas micronesica* was assigned endangered status by the IUCN[7] only three years after the invasion due to the epidemic mortality of the plant population.[8] It is arguably already functionally extinct as a consequence of failure to recruit.[9]

Mechanisms that mediate the impacts of exotic plant invasions are weakly understood,[10] and the knowledge gap is possibly more daunting for the impacts of exotic insect invasions on plant communities.[3] Here, we use the *A. yasumatsui* invasion into island habitats and the resulting widespread loss of *C. micronesica* trees to discuss three issues deserving focused attention for future research on the ecosystem responses to invasive alien insects.

Canopy Gaps

While light is a source of energy, it is also the language that plants use to decide how to grow. We propose that the role of increased light penetration following the selective removal of a common tree species by an alien phytophagous insect has not been adequately studied as a mediator of ecosystem change. While gap formation has been described as a consequence of European gypsy moth[11-13] and hemlock woolly adelgid[14,15] invasions into the United States, the specific mechanisms by which light influenced ecosystem changes

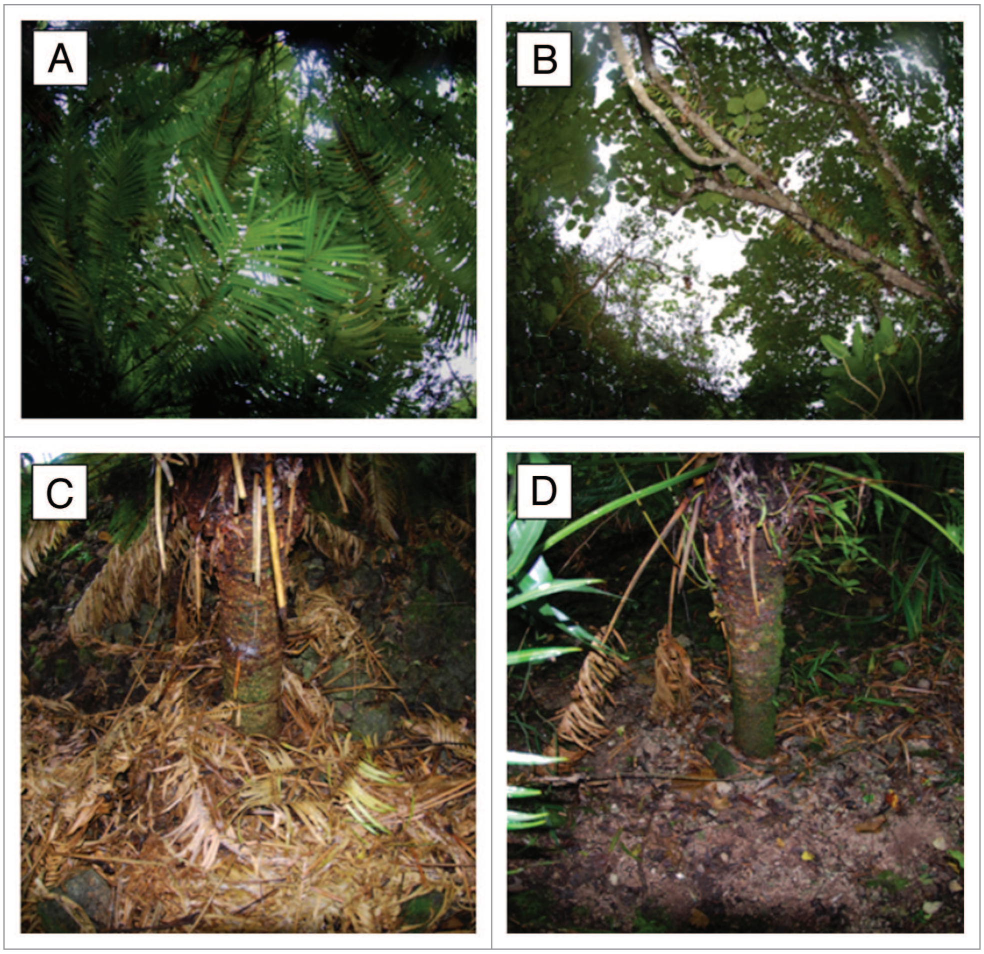

Figure 1. Vertical fisheye images from 1 meter elevation in *Cycas micronesica* habitat; (**A**) before the invasion of *Aulacaspis yasumatsu*; (**B**) the same location after selective loss of the *C. micronesica* trees. Litter layer appearance; (**C**) typical robust litter layer beneath undisturbed *C. micronesica* trees before the invasion; (**D**) nearly absent litter layer beneath *C. micronesica* trees four years after the invasion.

such as shifts in forest species composition or alterations in biogeochemistry were not anatomized.

Ecological processes following the formation of tree-fall gaps have been extensively studied.[16] However, gap formation through selective mortality of a single common forest tree species by an invasive phytophagous insect exhibits unique traits, and therefore general attributes of gap formation and subsequent closure may not translate fully to this form of disturbance. Our model species is a mid-story tree, and after widespread tree mortality the gap dynamics defined by the overstory tree species remain intact (see **Fig. 1A and B**). In contrast, gap formation by non-catastrophic defoliation during wind events is generally less selective, with most trees experiencing defoliation regardless of species. Moreover, small to moderate wind events deposit woody debris with the leaf litter layer and leaf re-growth in the canopy is rapid, enabling rapid re-establishment of canopy shade. These phenomena do not occur during selective gap formation by invasive phytophagous insects. Tree-fall gaps generated by catastrophic wind events or other causes lead to extensive soil disturbance as a component of gap formation. The pits and mounds associated with uprooting can mediate the changes in community structure following a tree-fall gap.[17] Alternatively, invasive herbivorous insect damage to a single forest taxon creates gaps with standing dead trees and no immediate disturbance of the soil surface.[13] These changes in light environment without concomitant disturbance of the soil surface pose interesting scenarios for comparing various means by which gap formation occurs and how light regimes are influenced by those gaps.

Light quality. Contemporary research is beginning to show that UV radiation delivers highly specific information that orchestrates plant metabolism and morphology[18,19] and directly modulates the relations of plants and herbivores.[20] UV light is substantially reduced by plant canopy cover, so understory plants that persist through the formation of herbivory-induced canopy gaps will experience drastic shifts in UV radiation. Similarly, recent evidence reveals that green light is a discrete signal that affects plant biology, including counteracting the signaling from blue or red wavebands.[21,22] Green and far-red light pass through the plant canopy with greater efficiency than red and blue light, therefore, gap formation during mortality of a dominant canopy tree species will exert acute shifts in green, blue, red and far-red signals to the understory community. These shifts in light quality mediate many of the subsequent community changes following gap formation, and we contend that gap formation by phytophagous insect removal of a foundation canopy species may exhibit light quality alterations that differ drastically from that of other forms of gap formation.

Sunflecks. Effective use of sunflecks for carbon gain is critical for growth and survival of understory plants. Pearcy and Way[23] propose more research on sunfleck use by plants in context of factors influencing global climate change, and specifically discussed heat, drought and elevated CO_2.[24] We assert that alien insect invasions are another critical global change factor and the sunfleck regimes created by selective removal of a single foundation tree species by an invasive insect are distinct from sunfleck regimes in undisturbed forests or those created by other forms of canopy disturbance.

Insolation. Selective loss of a foundation species alters the dynamics of forest ecosystems, including biogeochemical features.[15,25] Learning from descriptive papers reporting on biogeochemical changes following disturbances is maximized by identifying the functional or mechanistic basis for these changes. Furthermore, we have noticed that the post-invasion pulse of leaf litter decomposes rapidly, and subsequent to this initial litter pulse the soils in areas with high density dead *C. micronesica* trees exhibit an impoverished litter layer for several years (**Fig. 1D**). We suggest that increased insolation is one mediator of biogeochemical changes following alien phytophagous insect invasion that deserves further study. Exposure of soil surfaces to solar radiation increases the rate of litter decomposition.[26,27] Mechanisms may be direct effects on litter such as photodegradation of lignin[28] or rendering litter nitrogen more available to the detritus microorganism consortium.[29] Alternatively, landscape-scale soil warming as a result of greater insolation may mediate litter decomposition dynamics.[30] Seeking a greater understanding of the direct roles of changes in light quality and sunfleck dynamics along with increased insolation following the loss of a foundation species due to an invasion of an alien phytophagous arthropod should be of importance to modelers and ecologists.

Island Biology

Endemic flora on islands are acutely vulnerable to alien invasions,[31-34] as exemplified by our report.[8] Despite this defining characteristic of island biology, to our knowledge there are no published reports on ecosystem-level responses to alien phytophagous insect invasions on any island worldwide. For example, Kenis et al.[3] reviewed 403 primary research publications on invasions of alien insects of all types and the subsequent ecological responses. This list included 102 publications that addressed phytophagous insect invasions. Of these, only six investigations were conducted on islands, and none of these included ecosystem level data. The authors noted that the few accessible primary research reports on ecosystem processes following phytophagous insect invasions were restricted to only three insect genera invading North America. The remainder of the globe has not avoided ecological changes following invasions of phytophagous insects. Clearly, these are global impacts that deserve vetting in case studies outside of North America.

Species migrations occur continuously, and the movement of a species into new territory does not necessarily lead to an invasion. A complex set of factors collide to determine if an exotic species will become invasive following purposeful or inadvertent entry into a new geographic region.[35,36] A troublesome facet of some invasions is the subsequent regional spread from the initial successful population.[37] We predicted that *A. yasumatsui* would invade Guam three years prior to the 2003 invasion, a prediction that was founded on the invasion of Hawaii by the armored scale. Similarly, the nearby island of Rota was invaded in 2007 and the island nation of Palau was invaded in 2008. These islands fall within the endemic range of *C. micronesica*,[4] and are connected to Guam by daily airplane flights.

Manipulative experiments offer powerful approaches for clarifying ecological mechanisms, but they are limited for assessing cascading and compounding effects because manipulations are possible at scales smaller than ecological processes. In this light, Sagarin and Pauchard[38] argued that ecologists should be poised to take advantage of 'natural' experiments that may arise from localized declines of certain species or groups of species. Because islands are insular and offer disjunct biological populations for comparison, island studies offer powerful interpretive results for understanding how introduced predators exterminate native prey species.[33,39,40]

We suggest that our case study serves as an example of how valuable islands may be for filling information gaps in how invasive phytophagous insects can decimate native host plant species,[8] then how the loss of those species affects ecosystem change. Our continual reconnaissance efforts have allowed us to pinpoint the date that the spreading *A. yasumatsui* population entered the various *C. micronesica* populations in Guam and Rota, a process that spanned five years. By comparing the localized cascading effects of these sequential invasions with the *C. micronesica* habitats in Yap, which have not experienced the armored scale invasion to date, we can exploit a clearly defined natural experiment.

Unique Case Studies

According to the mass-ratio hypothesis,[41] controls on function are in proportion to abundance of a species. In this light, many dominant tree species are widely considered as foundation species where they exert a disproportionate control over ecosystem dynamics. Indeed, several case studies have documented ecosystem changes following the loss of foundation species.[14,15,25,42] If an invasion purges a foundation tree species possessing unique functional traits that are not redundant among sympatric tree species, the community-level ecological changes following the invasion may be greater than for cases where a foundation species possesses traits similar to the remaining species. Our model species, *C. micronesica*, is the only native gymnosperm in the Mariana Islands and the only widespread native tree supported by nitrogen-fixing endosymbionts. Prior to the armored scale invasion, the population greatly exceeded 3,500 trees per hectare in some locations. At least two arthropods depend on the *C. micronesica* population; the endemic stem borer *Dihammus marianarum* exploits cycad stem tissue for larval food, and the cone borer *Anatrachyntis* sp requires microstrobili for larval food.[6] The tree's ability to resist damage during and resilience after the frequent tropical cyclones[43] that define forest physiognomy of the region[44] render it an important food source following major tropical cyclone damage.[45]

Nitrogen cycling. Of particular interest is the influence of *C. micronesica* on nitrogen cycling in the forests it occupies. Although all cycads associate with nitrogen-fixing cyanobacteria endosymbionts,[46] we are aware of only one attempt to quantify the rate of nitrogen fixation. For the Australian *Macrozamia riedlei*, annual nitrogen fixation was up to 8.4 kg nitrogen per hectare, and was sufficient to fully replace natural volatilization losses of nitrogen in the cycad habitat.[47] The literature on plant invasions and their influence on ecosystem processes is extensive.[48-51] The disruption of established nitrogen cycling by alien plant invasions is acute for species that associate with nitrogen-fixing symbionts, a notion that has been verified by studying invaded habitats[52,53] and recovery of altered communities following restoration of sites that were formerly occupied by invasive tree species.[54] Our case study represents a previously unstudied inverse of this phenomenon, in that an endemic nitrogen-fixing foundation tree species is being selectively removed from natural communities. We are unaware of any published reports on the consequences to nutrient cycling and other ecosystem traits during widespread mortality of a foundation species with these characteristics. Our case study also highlights the risk of co-extinction of the organisms that depend on the tree for survival, and a clear understanding of how widespread mortality of this dominant plant species will damage mutualisms may support more successful future restoration programs.

Benchmarking. Understanding the direction and magnitude of change in any ecosystem trait in response to any driver is enabled by appropriate benchmarks. The population of *A. yasumatsui* insidiously floated and crawled across the island of Guam with unexpected rapidity and in patterns that defied explanation. During the onset of this invasion and subsequent occupation we received funds for mitigation efforts from many federal and conservation entities, but we were unsuccessful in convincing any of them to provide funds for research. This unfortunate Guam experience was due to the wholesale focus on eradication attempts, and likely occurs all too often in other newly invaded regions. In our case, the changes in ecosystem properties ensued and progressed to a point that effectual benchmarking was unachievable for many habitats. The invasion of Guam Island by coconut rhinoceros beetle (*Oryctes rhinoceros*) was detected in 2007 and by the Little Fire Ant (*Wasmannia auropunctata*) in 2011. These two insects possess characteristics that predict immense detrimental ecological responses to their invasions. We experienced the same phenomenon as with the *A. yasumatsui* invasion where funds were available for surveys and attempts at containment or eradication, but funds for establishing benchmarks or any other form of ecological research could not be acquired. We are now forced to rely on the isolated Yap Island *C. micronesica* populations as our benchmark for some long-term community-level changes because we have no data from many invaded habitats that have already experienced many ecological changes. We recommend that agencies interested in supporting conservation projects recognize that benchmarking during the nascent stages of an invasion is an endeavor worthy of funding.

Conclusions

The increasing rates in which alien insect invasions are modifying Earth's forests highlight the urgency and necessity to increase our understanding of how invasions influence ecosystem function.[55] Predicting how plant communities will respond to global changes then how the community responses feedback to ecosystem processes is of great importance,[56] yet most available information is anecdotal and restricted to effects addressing biodiversity while ignoring ecosystem function and processes. Herein we argue that a priority on case studies that exhibit unique traits may better fill the current void in knowledge and enable our ability to define generalizations across systems. The goal of being able to identify dominant forest species that are vulnerable and to anticipate the consequences of an invasion with at least some predictive power may be best achieved by prioritizing these unique case studies.

Canopy gaps created by the selective removal of a dominant tree species are distinct from canopy gaps created by other means, and the role of changes in light quality, sunfleck dynamics and total insolation are subjects that deserve further study. Oceanic islands offer insular living laboratories for studying disturbance, yet we are unaware of any published reports on how ecosystem processes have responded to an alien phytophagous insect invasion's removal of an island foundation forest species. The invasion of *A. yasumatsui* has selectively removed a foundation species that was not only the most abundant tree at the time of the invasion, but one that exhibited many unique characteristics such as association with a nitrogen-fixing endosymbiont. The remaining taxa that will define the recovery of canopy structure exhibit few functional redundancies with the cycad species. Therefore, we predict the changes to ecosystem processes will be vast and if documented adequately will serve to inform the current information void on how invasive phytophagous insects alter ecosystem properties.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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