Pacific Cooperative Studies Unit

UNIVERSITY OF HAWAIʻI AT MĀNOA

3190 Maile Way, St. John #408

Honolulu, Hawai‘i 96822

Technical Report # 206

An Overview of the Status and Protection of Maui's Watershed Forests

September 2024

Arthur C. Medeiros PhD [1], Erica von Allmen [1]

[1] Auwahi forest Restoration Project, P.O. Box 652, Makawao, Maui, 96768

Organization Contact Information:

Arthur C. Medeiros. Program Manager. artcmedeiros@gmail.com Auwahi Forest Restoration Project, P.O. Box 652, Makawao, Maui, 96768

Erica von Allmen. Program and Research Coordinator. auwahioffice@gmail.com Auwahi Forest Restoration Project, P.O. Box 652, Makawao, Maui, 96768

Recommended Citation:
Medeiros A., von Allmen, E. 2024. An Overview of the Status and Protection of Maui's Watershed Forests. Technical Report #206. Pacific Cooperative Studies Unit, University of Hawai‘i, Honolulu, Hawai‘i. 93 pp.

Keywords:
Rapid ‘Ōhi‘a Death, invasive species, watersheds, endangered species

Place Keywords:
Maui County, Hawai‘i

Abbreviations:
ROD – Rapid ‘Ōhi‘a Death
DWS – Maui County Department of Water Supply
HAWP – Hawai‘i Association of Watershed Partnerships
LAC – Latin American clade
AAC – Asiam-American clade
qPCR – Quantitative Polymerase Chain Reaction
DLNR – Department of Land and Natural Resources
cm – Centimeters
m – Meters
ft – Feet
DBH – Diameter at Breast Height

Table of Contents

EXECUTIVE SUMMARY

Today and likely into the future, pure freshwater resources are one of Maui's greatest gifts and greatest needs, an essential element to existing ways of life, the island's economy, and a requirement if we are ever to achieve food independence. Though often unrecognized in this role, native watersheds provide one of Maui's most important natural resources, essential for life as we now know it.

The watershed forests of windward exposures of Maui that receive the bulk of the island's precipitation are still functionally intact over great expanses, retaining their multi-layered, largely native tree and fern dominated forest systems. Because of this, despite the fact that Maui's native watershed forests have been greatly modified and reduced, windward forests above 3,000 feet to tree line remain fundamentally intact and functionally vital for water extraction purposes.

Despite this relatively apparent state of richness currently found in these windward forests, there are factors in motion which appear to threaten the status of this critical natural capitol resource for future generations. Given the current status of Maui's watersheds and their management, the best-case scenario for windward forests is to maintain a type of ecological stability as time progresses.

The unusual and near complete dominance of windward Hawaiian watershed forests by a single tree species, *ʻōhiʻa lehua* (Metrosideros polymorpha), creates ecological vulnerability for rapid and dramatic changes to forest structure if the health of that dominant tree species is threatened.

Other factors that threaten this forest type are climate change and invasive species. Climate change predictions for Hawaiʻi forecast decreasing precipitation, increasing heat, and greater number and frequency of drought and storm events. Invasive species are non-native species of plant, animal, and pathogen deliberately or incidentally introduced to a new region. A recent dramatic example of pathogen impact on Hawaiian watershed forests was the recent emergence of two Metrosideros-specific pathogenic fungi, collectively known as Rapid *ʻŌhiʻa* Death.

Decline of the dominant tree species of Hawaiian watersheds, *ʻōhiʻa lehua*, would likely trigger successional changes involving the explosive spread of invasive plant species responding to an increase in light and resource availability. Potentially these changes could initiate a cascade of ecological processes that would challenge the long-term stability of watershed forests and water extraction and cause fundamental changes in the ways future generations conduct our lives and manage limited water supplies

The degradation and potential loss of native Hawaiian watershed forests is an excellent example of the 'tragedy of the commons.' Originally an economic theory, 'tragedy of the commons' describes how highly valued community resources can be degraded or even lost because, without direct ownership, no one entity appears to have singular responsibility for the resources' fate. Studying the interaction of people and ecosystems, Elinor Ostrom, Stanford University, demonstrated that if appropriate systems are instituted, valuable community resources can, in contrast, be responsibly managed and utilized by stakeholders, as well as play a key role in protecting and perpetuating these resources. The community- and partner-based protection and

restoration of Maui County's watershed forests has the potential to be hailed as a classic example of 'restoration of the commons', where, with community awareness and support, public and private groups work together to cooperatively provide stewardship for an invaluable community asset.

On Maui, watershed forest degradation accelerated dramatically after European contact, approximately 250 years ago, with the introduction of non-native animals and plants. On leeward slopes, wildfires and feral cattle herds were the primary drivers for the near-complete loss of watershed forests on the islands of Maui, Molokaʻi, Lānaʻi, and Kahoʻolawe. From 1790 to 1850, native forests which formerly occurred from near sea level to tree line on leeward exposures were decimated and replaced largely by suites of African, Australian, and Central and South American plant species.

Upper elevation native windward *ʻōhiʻa lehua* (Metrosideros polymorpha) forests, where most potable water gathering systems are based, receive the bulk of tradewind-associated precipitation in Maui County. Worldwide, native forests, with their diverse, multi-layered canopies and understories, are the most efficient natural systems in processing, filtering, and storing precipitation.

Methods to protect Hawaiian windward watershed forests were developed in the 1980s and have remained the primary standard practices for today's watershed managers. Sadly, despite this, even priority watershed areas are progressively being degraded (especially up to moderately high elevations, ca. 4,500 feet (1,370 m) by landscape-level plant invasions. Conversion of native forests to non-native forests decreases overall aquifer recharge and has reduced ability to manage sediment and sheet flow during torrential rain events.

Rapid *ʻŌhiʻa* Death (ROD) likely constitutes the worst invasive pathogen threat ever encountered by Hawaiian watershed forests. This assessment is partially regarding the importance of *ʻōhiʻa lehua* making up 80% of the trees in our watershed forests, and partially on the impact of ROD, killing over an estimated one million *ʻōhiʻa lehua* trees over a four-year period (2017-2021), largely on Hawaiʻi Island.

In addition to Rapid *ʻŌhiʻa* Death, two other drivers, invasive species and climate change, also threaten to upset the status quo of native windward forests of Maui County and potentially reduce water quantity and quality.

Prior to the arrival of humans, the Hawaiian Islands received a new plant species about once every 30,000 years. Since humans first arrived, 20,000-30,000 non-native plant species have been introduced to the islands. Currently, a new non-native plant species arrives about every five days. Without rigorous quarantine measures, threats from new species continue to mount.

Despite the fact that they are among the most intact of remaining native Hawaiian ecosystems, windward *ʻōhiʻa lehua* forests are vulnerable to large-scale displacement by certain notoriously invasive tropical plant species. Plant invasions at this scale cause drastic changes in species composition and reduced resistance to natural and climatic disturbances, as well as alterations to nutrient, carbon, and water cycles. With yet uncertain implications, climate change is an additional stressor of Hawaiian watershed forests, both independently as well as synergistically interacting with other stressors like diseases and invasive plants.

1. Global introduction

Global human populations, currently at 7.9 billion, continue to grow rapidly, virtually unchecked. By 2050, the global human population is predicted to reach 9.8 billion, postulated by many experts to be near the human carrying capacity for the planet, given available technologies (UN DESA 2015). According to U.N. estimates, approximately 10% of the human population, largely in African countries, lacks access to improved sources of drinking water. Given its limited availability and value as a component for economic prosperity, potable water has been identified as a likely potential source for serious future global conflicts, so called 'water wars.'

Potable water, a critical limiting factor for human populations and economies, is becoming an increasingly scarce commodity due to overuse, large-scale land modifications, and climate change. Though approximately 71% of the planet's surface is covered by water, the great majority of that (96.5%) is salt water held in the world's oceans, hence largely unusable by terrestrial life forms, including humans. Of the world's total water, only 0.4% is potable freshwater available to humans (Gleick 1993). As global populations create greater demand for potable water, solutions deemed too expensive to be practical at a large scale are increasingly viable. Compounding problems of finite supply, burgeoning human populations, and climatic changes will likely decrease already limited potable water supplies.

An article in Fortune magazine in 2000 established a new paradigm in the way non-polluted freshwater resources are regarded, stating, "Water promises to be to the 21st century what oil was to the 20th century: the precious commodity that determines the wealth of nations." As human populations burgeon toward an estimated 9.8 billion in 2050, there is an inevitable and perennial conflict with limited freshwater resources.

Water availability for growing human populations has many critical components: precipitation amount and intensity (a combination of duration and frequency), the land's ability to receive, filter, and store incoming precipitation, water storage and transport systems, and location of demands. Based on global trends, it is likely, barring a technological breakthrough, that all these factors will be evaluated to increase efficacy and meet demands, including mandatory daily water restrictions.

The emerging global freshwater crisis can be illustrated by the situation in Cape Town, South Africa. Several successive drought years combined with high water use placed the city in a severe and growing crisis. Despite dwindling water supplies, initial 'Think Water' media campaigns encouraging voluntary cutbacks alone were ineffective. In late 2017, South Africa declared a national emergency and launched a multi-focused effort to re-establish water security. Cape Town reached a breaking point in the crisis – declaring April 12, 2018, 'Day Zero' – the day the city's municipal water supply would be cut off (Wallace 2021). Christine Colvin of World Wildlife Fund South Africa observed, "It's going to be terrifying for many people when they turn on the tap and nothing comes out."

What is clear here is that potable water, an essential component of human well-being and economies, will gain increasing attention and value on isolated, oceanic high-elevation islands,

such as Maui County. As awareness grows of the need for potable water, inevitably, attention will be focused on those parts of the supply-demand chain that are capable of being managed, such as water use. Perhaps more critically, attention should be drawn to the acreage of high-quality watersheds that Maui County possesses to maintain and potentially increase our water supplies.

In general, the term 'watershed' refers to areas of land that receive, filter, and store water. Within watersheds, precipitation is utilized by plants, absorbed into the ground, evaporated back into the atmosphere, and fed into rivers, streams and ground water. Watershed forests optimize water infiltration and aquifer recharge, moderate storm runoff, and reduce soil erosion. Forests with multiple-layered canopies, especially characteristic of high diversity native forests, generally offer the highest degree of ecosystem services in terms of water quantity and quality (Hua et al. 2022).

On isolated oceanic islands with large resident human populations, such as those of the Hawaiian archipelago, the extent and quality of watershed forests are especially important in maximizing water availability for human activities. Multi-layered, high diversity native Hawaiian forests are much more likely to support efficient watershed functioning than the more simply structured vegetation types with relatively few species, as is characteristic of watershed areas invaded by non-native species (Kagawa-Viviani 2020, Kagawa-Viviani and Giambelluca 2020, Perkins et al. 2018, Cavaleri et al. 2014).

As will be detailed in this report, extensive native forests of Maui Island, and for that matter, all major islands of the Hawaiian archipelago, have been decimated historically by land use change, wildfire, and invasive species, especially on leeward and lower elevation areas. Today, the remaining stands of native Hawaiian forests continue to be displaced by rampant growth of invasive species degrading the forests' potential to receive, process, and store water resources suitable for human needs.

2. Hawai′i's watershed forests, essential for Hawai′i's way of life and economy

On highly isolated oceanic islands like Maui, fresh potable water is essential for human occupation. The importance of water as the fundamental resource from which wealth and security can be derived was not lost on early Hawaiian populations who linked the word *wai* for freshwater with the word *waiwai*, often defined as wealth or prosperity.

At the time of discovery by the first human voyagers, watershed forests of Maui and other islands extended from near the shoreline to the summits, or in the case of Haleakalā, to the treeline at 7,600-8,000 feet (2,315-2,440 m) elevation. Since then, human development and agriculture have displaced nearly all these native forests in low to middle elevation leeward areas and, to a lesser extent, windward areas.

Tradewind-associated rainfall gathered from windward *ʻōhiʻa lehua* (Metrosideros polymorpha) forests forms the bulk of precipitation in Maui County. As such, potable water gathering and transport systems are centered on windward 'wet' forests. These windward forests are distinct from most other tropical forests in that their canopies are often dominated by a single species of native tree which is often considered a keystone species, *ōhiʻa lehua*. Native forests dominated by a single species are extremely uncommon in the Pacific and ecologically create a potentially catastrophic vulnerability.

Barring technological development capable of providing a long-term sustainable and economical water source, Maui's watersheds represent the sole-source provider of this critical element of economic and human well-being. The composition of watershed forest vegetation determines how much water will run off, how much sediment will transfer off-site, and how much water will infiltrate to recharge the aquifer. In terms of water resources provided by native forest-dominated watersheds for human use, in 2020, the Maui County Department of Water Supply (DWS) processed approximately 4 billion gallons (15 billion liters), 11.3 million gallons (42.8 million liters) a day through 780 miles (1,255 km) of water transmission and distribution lines.

The historic loss of native watershed forests has left Maui in a challenging position as we enter coming eras of unstable climate (DeMaagd and Roberts 2020). It is clear that Maui County's watershed forests are at a pivotal point in their history. Forest tracts remaining on windward slopes, which constitute the great majority of Maui County watershed forests, have been in chronic decline since first human contact, accelerating with the introduction and spread of feral cattle in the 1840s. Despite their decline, windward forest canopies remain largely native in their mid- to high-elevation cores. In contrast, on leeward exposures, native forests which formerly occurred from near sea level to treeline were decimated, reduced by 90%.

Droughts have increased in frequency on Haleakalā over the last twenty years and are predicted to increase in both frequency and duration (www.drought.gov, Leong et al. 2014) moving into the future. Recently, drought conditions have spurred significant mandated cutbacks of water use by many Maui residents.

Figure 1. Even at a flood stage such as this, healthy, multi-layered native watershed forests have the capacity to regulate and store precipitation, producing water of high clarity and purity. Upper Waimoku falls, Kīpahulu Valley, Haleakalā.

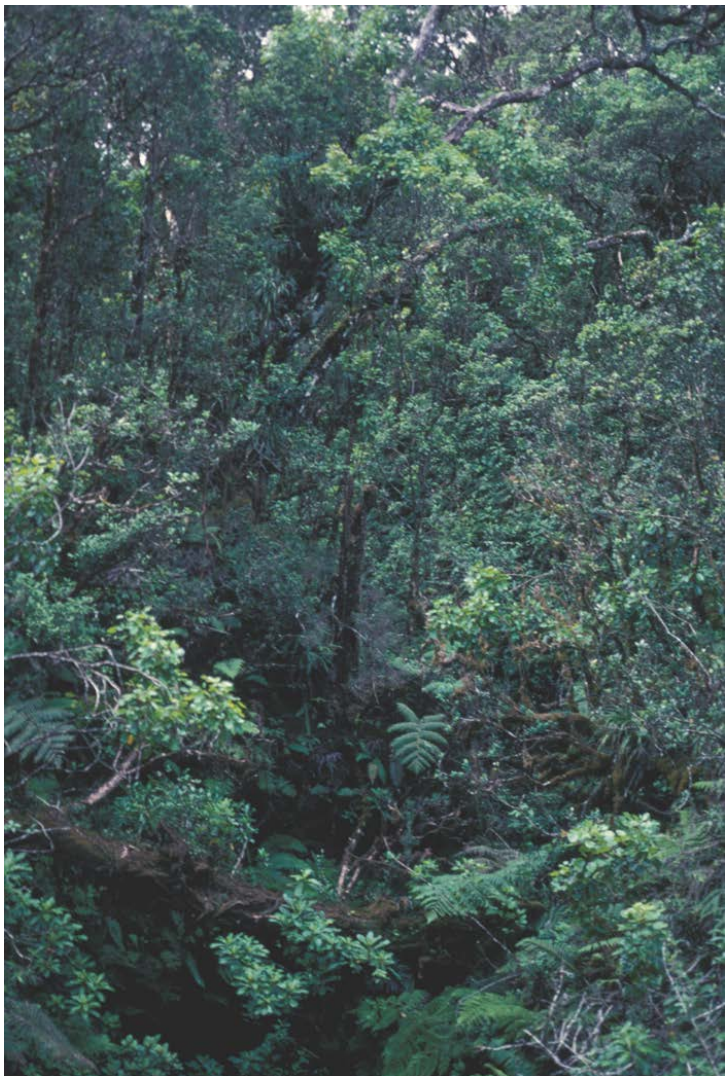

Figure 2. Multiple layers of vegetation from canopy through smaller trees, shrubs, ferns, herbs, and mosses that act to slow, filter, and store precipitation are typical characteristics of intact native Hawaiian watershed forests. Shown here is a small periodic stream in an *'ōhi'a lehua* forest, 4,700 feet (1,430 m) elevation, Kīpahulu.

Today, native species still dominate windward forests' canopies; however, there is a pervasive shift occurring in the understory toward non-native tree species. The gradual invasion of the understory of windward forests by invasive trees and shrubs is progressively replacing native *'ōhi'a lehua* forests with woody species primarily originating from Central and South America. The resulting vegetation has far less layering, species diversity, and structural complexity, all of which will likely have detrimental effects on the ability of these forests to intercept, store, and filter incoming precipitation as fundamental hydrology is shifted. A few studies exploring the impacts of non-native species on hydrologic function suggest this shift to non-native vegetation may severely impact water resource availability (Cavaleri et al. 2014, Perkins et al. 2012, 2014, and 2018, Kagawa-Vivani 2020). Given this change in forest composition coupled with continuously increasing human populations, it is only a matter of time until water, especially potable water, becomes scarce and increasingly inaccessible.

Figure 3. Uppermost native forest of parts of Maui County rank globally as among the rainiest regions on the planet, with precipitation exceeding 400-500 inches (10,000-12,700 mm) annually. Upper Hāna rainforest, 6,300 feet (1,920 m) elevation, Haleakalā.

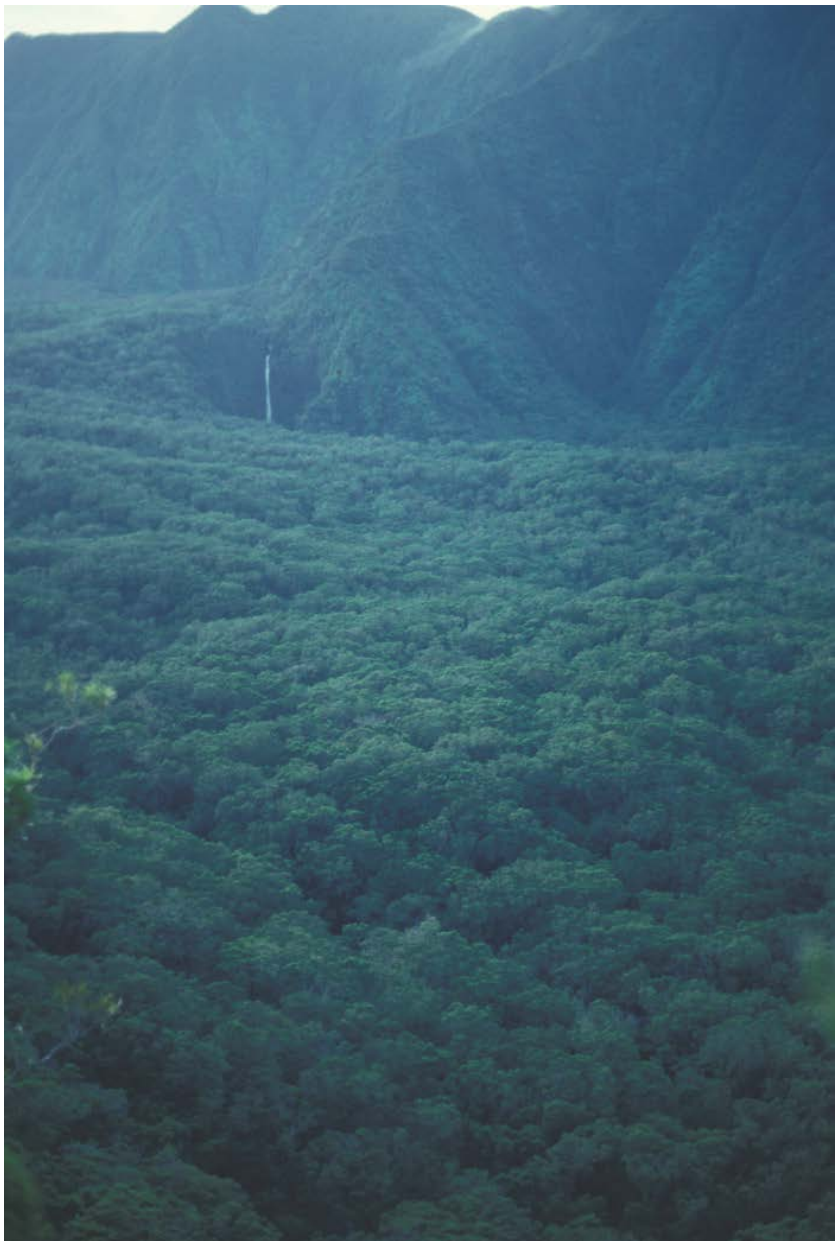

Figure 4. Currently, Maui Island retains a core of native *ʻōhiʻa lehua* forest, concentrated primarily in the rainiest elevations of windward slopes from where most of the island's potable water is gathered. Upper Kīpahulu, 3,800 feet (1,160 m) elevation, Haleakalā.

A study on the economic value of ecosystem services provided by tropical watershed forests estimated the Koʻolau mountain range of Oʻahu contributed a minimum value of $1.4 billion for aquifer recharge (Kaiser and Roumasset 2002). When including other ecosystem services in addition to water (species habitat benefits, biodiversity benefits, subsistence benefits, hunting-related benefits, aesthetic values, commercial harvests, and ecotourism), the value of the watershed forests of the Koʻolau range was estimated at $7.4-14 billion (Kaiser et al. 1999, Kaiser et al. 2008) and the related value to the downstream coral reefs was estimated at an additional $10 billion (Cesar and van Beukering 2004).

Studies of the Ko'olau watershed also estimated that forest degradation, largely due to invasive species impacts, reduced the extracted value of aquifer recharge by approximately $41 million, with larger disruption-based losses estimated at $4.6-8.5 billion per year (Kaiser et al. 2008). Invasive species have been documented to have significantly higher evapotranspiration rates and reduced fog interception, both contributing to decreases in aquifer recharge (Giambelluca et al. 2009, Kagawa et al. 2009). A recent modeling study conducted on a watershed on Haleakalā estimated the degree to which the rate of spread of invasive species dramatically affected the economic resources required to obtain groundwater resources for human use (Bremer et al. 2019).

Figure 5. In contrast to native Hawaiian forests, watershed forests that have been heavily invaded by non-native species have much simpler stand structures, with the ground often exposed to mineral soil by rainfall, accelerating erosion and runoff. Understory of heavily invaded area, now transformed into a highly invasive single-species Miconia calvescens stand, central Tahiti.

Despite their progressive displacement by non-native species, *'ōhi'a lehua*forests, which dominate the windward slopes of Haleakalā and the upper valleys of West Maui, receive the bulk of precipitation and are the primary source of our drinking water. In contrast, Maui's leeward slopes currently provide little water for human populations. These leeward native forests have been deforested to such a degree that only about 10% remain (Medeiros et al. 2014). On the southwest slopes of Haleakalā, native forests have been completely replaced by non-native tree plantations and non-native pastures. On southeastern Haleakalā, in some areas, fragments of native forests remain among oceans of non-native pasture grasses, while in other areas, there is no vegetation, and extreme erosion has removed significant quantities of topsoil.

Unlike windward watershed forests, the few remaining tracts of leeward native watershed forests are known for high tree diversity and multi-layered canopies. Despite degradation, the Auwahi Forest Restoration Project (auwahi.org) has demonstrated that badly degraded native leeward forests can be successfully restored and recover biotic resilience and hydrologic function in relatively short time frames (Medeiros et al. 2014, Perkins et al. 2012, 2014).

A potentially important target area for ecological restoration for the County of Maui DWS is the western slope of Haleakalā from ʻUlupalakua to Makawao because of its potential as a source for future water resources and the current lack of water transport and storage, treatment, and facilities. Implementing a tremendous restoration effort like this could result in improved water capture, potentially providing important contributions to water supply, especially considering growing human populations and uncertain climatic changes. However, there are significant limitations in the current available funding and time required for this scale of ecological restoration and rehabilitation (10-30 years after restoration is initiated). If watershed forests were to be rehabilitated on Haleakalā's western slopes, emphasis could be placed on creating novel forests that would maximize future water recharge while being relatively resilient to impacts of invasive species and climate change.

Across Maui County, the impacts of over two centuries of deforestation and land disturbance in soil types with fine transportable substrates have created a severe secondary issue, topsoil erosion, which can be particularly extreme during heavy rainfall events. The sediment transfer from upland areas not only impacts inshore water quality, reduces coral reef health and marine life, but also directly reduces aquifer recharge, facilitates non-native species invasion, decreases ecosystem services, and degrades land in such a way that future restoration potential is diminished. Particularly vulnerable areas of Maui County are notorious for their tendencies for erosion and inundation of inshore marine waters following heavy rains; these areas include southern Haleakalā, south and western West Maui, leeward Molokaʻi, Kahoʻolawe, and Lānaʻi.

In conclusion, watershed forests on isolated islands like the Hawaiian archipelago are of almost incalculable value for the water reserves they supply, vital to the economic well-being, health, and standard of living of the residents. As can be seen from this report, watershed forests of Maui County have historically been reduced to a fraction of their historic extent, and remaining watershed forests face a complex assemblage of threats to their continued existence.

Primary responsibility lies in doing all that is feasible to protect and even enhance existing native watersheds, primarily windward *ʻŌhiʻa-lehua* (Metrosideros polymorpha) forests. An important part of this responsibility can be addressed through direct pro-active management and targeted management-focused research. Research topics in this regard could include classic biological control for priority habitat-modifying invasive plants, the development of disease-resistant watershed canopy species, and exploring protection and restoration corridors. Besides the essential task of protecting existing watersheds, supplemental research could evaluate the economic and ecological feasibility of restoration or rehabilitation of upslope leeward areas where there may be potential for potable water extraction. In leeward areas, landscape-level native forest rehabilitation to maximize water resources could also provide substantial benefits to the perpetuation of both biological and cultural resources. In doing so, the potential exists for greater cost-sharing funding possibilities, as well as a broader scope and depth of public support.

In coming times, the hand of resource managers may be forced (either by lack of funding or by uncertainty of outcomes of dynamic, costly management) to accept whatever changes come with future situations. Another approach, however, is to continue to synthesize and evaluate available information on watershed management globally with the intention of creating new standard operating procedures. In the future, technology will likely bring new tools into ecosystem stewardship as we advance new adaptive approaches in evaluating and assisting natural systems to become more resilient, to conserve and even increase their contributions of potable water for future generations.

3. Role of Hawai‘i’s watershed forests as biological and cultural sanctuaries

Watershed forest areas of Maui County, which receive and process incoming precipitation, in many cases, are the same forests noted for their biological and cultural significance. This is important purely from an informational point of view for forest managers when considering responsible management actions and their implications. It also allows for both economic and social partnering opportunities to achieve mutually adventitious results.

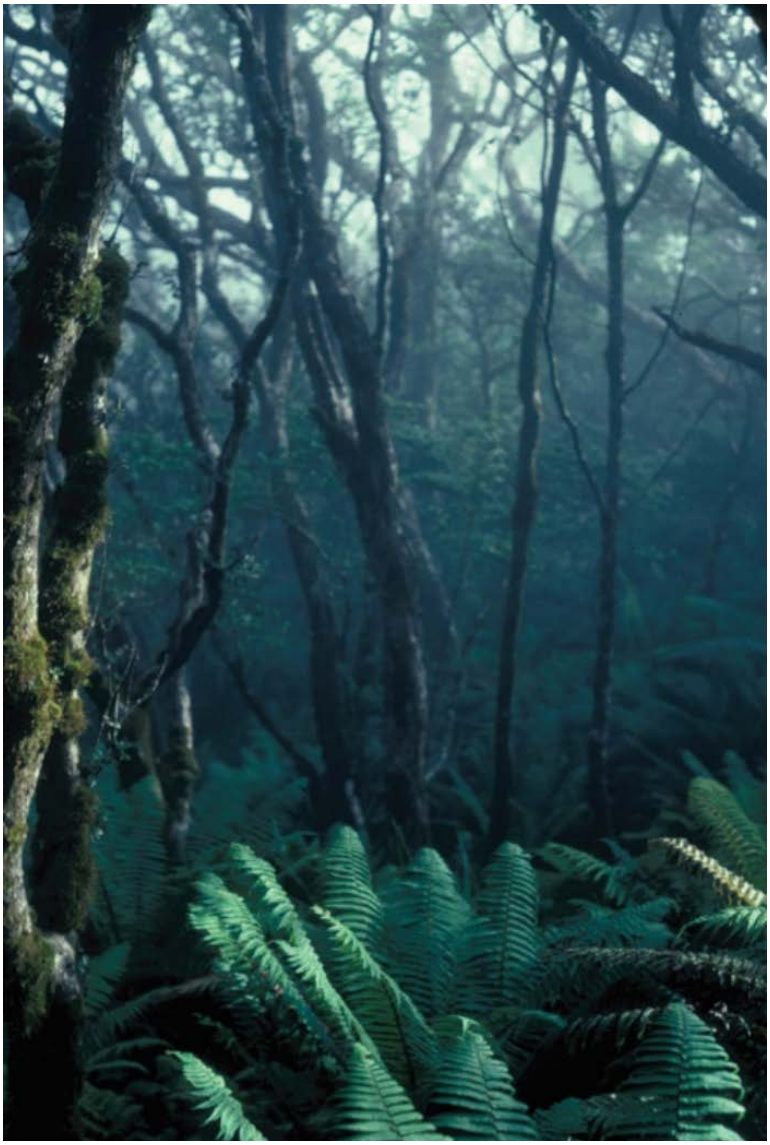

Figure 6. The combination of extreme isolation, substantial age (ca. 40my), and high elevation of Hawaiian volcanoes (taller than most in the Pacific) has yielded a globally renowned and extraordinary endemic biota (i.e., found only here). Certain native forest areas within Maui County easily rank among the most diverse forests in the United States, harboring a disproportionately high percentage of the nation’s biodiversity. Upper northeast rift, 6,300 feet (1,920 m) elevation, Haleakalā.

In terms of their biological significance, native plants and animals in Hawai‘i arose in an evolutionary crucible generated by the unique combination of an extremely isolated location

(2,300 miles), the significant age of the archipelago (60-80 million years), and the uncommon range of ecological habitats developed over an extremely limited land area. Over millions of years, these forces yielded a native biota nearly exclusively comprised of plant and animal species (95-99%) endemic (found only here) to the Hawaiian Islands and often found only on a particular island or even only in a restricted area within an island.

Figure 7. *ʻōhiʻa lehua*(Metrosideros polymorpha) is easily the most abundant and most dominant tree species of Hawaiian watersheds. Though the genus Metrosideros is found throughout the southern Pacific, in Hawaiʻi, the endemic species dominates wet forests, making up 9 out of every 10 trees. Pollen and nectar resources of *ʻōhiʻa lehua*flowers are primary food sources of the renowned Hawaiian honeycreeper finches, as well as other critically important pollinator species. Kīpahulu Valley, ca. 4,100 feet (1,250 m) elevation, Haleakalā.

Globally, Hawaiʻi is known for the biological phenomenon of adaptive radiation where a single colonizing species, initially arriving millions of years ago, speciated into an incredible array of related forms which differ wildly in their morphologies (ways they look), behaviors, and ecologies, far beyond normal continental standards. The result can be a spectacular array of individual species that, despite being very closely related species, remarkably often bear little resemblance to each other. One world-renowned example is the extraordinary radiation of the Hawaiian honeycreepers, a frequent topic of biological textbooks. For many spectacular species clusters, including the Hawaiian honeycreepers, surviving species are now concentrated in areas that also serve as the core of Hawaiʻi's functional watersheds.

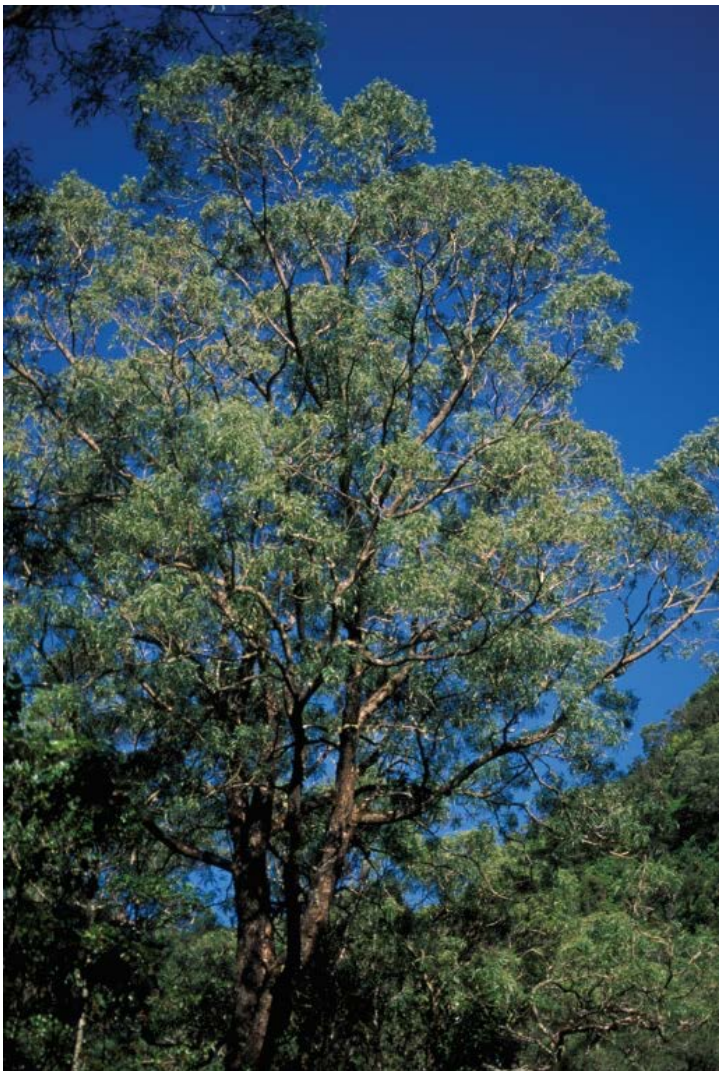

Figure 8. *Koa* (Acacia koa) is the second most common tree of Hawaiian wet forests and a nitrogen fixer providing essential nutrients that support vigorous understory vegetation, consequently playing a key role in both intact and disturbed forest systems. Kīpahulu Valley, 4,000 feet (1,220 m) elevation, Maui.

Due to their biological, cultural, and legal importance, Hawaiian honeycreepers are discussed here in detail as an example of adaptive radiation. The Hawaiian honeycreepers (Drepanidae, Carduelinae) all likely evolved from a single flock of small birds driven offshore by a storm that arrived at the Hawaiian Islands sometime between 5.8 to 7.2 billion years ago (Lerner et al. 2011). From this, an incredible array of honeycreepers evolved. In total, at least 59 species of Hawaiian honeycreeper existed when humans first arrived in Hawai‘i about 1,000 years ago, but currently, only 17 species survive (Farmer 2020, Fortini et al. 2015). Six species occur in Maui watersheds, three of which are Federally-listed as Endangered by the U.S. Fish and Wildlife Service. They are listed here from most common to most rare: *‘apapane* (Himatione sanguinea), *‘amakihi* (Chlorodrepanis virens), *‘i‘iwi* (Drepanis coccinea), ‘*alauahio* or Maui creeper (Paroreomyza montana newtoni), *‘akohekohe* (Palmeria dolei), and Maui parrotbill (Pseudonestor xanthophrys) with Drepanis, Palmeria, and Pseudonestor being the Endangered species.

Figure 9. Shown here, Cyanea aculeatiflora, bird-pollinated lobelia endemic to East Maui, 4,400 feet (1,340 m) elevation, Kīpahulu Valley, Haleakalā. Certain groups of Hawaiian plants have diversified explosively, over time evolving from a single ancestor into numerous endemic Hawaiian species, such as the Hawaiian lobelia.

The primary threats to Hawaiian honeycreepers, which have driven their endangerment, are the losses to habitat quality and quantity, invasive predators, and susceptibility to introduced diseases (avian pox and malaria carried by the house mosquito (Culex quinquefasciatus)). As such, their populations are now restricted to high elevation native forest areas, where this mosquito does not currently thrive.

The high diversity of endemic plants and animals in Hawai‘i is often limited to geographic areas with specific biotic and abiotic attributes. As such, when these sites are modified, be it through land-use change or deforestation, suitable habitats may be severely limited or completely

eliminated. As of 2016, the island cluster of Maui Nui (including Maui, Molokaʻi, Lānaʻi and Kahoʻolawe) has 157,002 acres (635 km^2) of designated critical habitat protecting for 125 listed plant and animal species (120 species of plants, three species of birds, and two species of snails). Of these designated critical habitats, 20% are on federal lands, 55% are on state lands, and 25% are on private lands (Fish and Wildlife Service 2016).

In addition to the significant value as biological sanctuaries, native Hawaiian forests, their animals, and plants are *haku* (interwoven) into the lives and origins of the Hawaiian people. When Polynesian explorers first touched their canoe prows onto the sand, theirs were the first human footprints ever in Hawaiʻi. The native animals and plants of these islands, along with the 28 species of plants they originally brought with them, were to become their entire world. As such, these forests provided the resources for Hawaiian people to survive and thrive. Native Hawaiian knowledge systems integrate understanding of social, psychological, and spiritual linkages between people and species. To *kanaka maoli* (native Hawaiians, literally 'native or real people'), native species are more than just items for consumption or utilization; they are ritualized, woven into all life, including *hula* (dance), literature, *mele* (song), and *oli* (chant).

In current times of cultural revival and renaissance of traditional Hawaiian practices, watershed rainforests serve an increasing role as the sole potential gathering site for natural materials important in cultural practices, like the *ōhiʻa lehua*, *maile* (Alyxia oliviformis), and ferns associated with attire of *hula* dancers or construction of the *kuahu*, the 'altar' of specific plants associated with the *hula*. Less often gathered native components of watershed forests include *wauke* (Broussonetia papyrifera) and *māmaki* (Pipturus albidus) for *kapa* (bark cloth) production, *olonā* (Touchardia latifolia) for cordage (documented as the strongest natural cordage in the world (MacCaughey 1918)), and specific woods and plant materials for dyeing *kapa*.

Few Hawaiian plants have as important a role in the cosmology of the Hawaiian culture as does *ōhiʻa lehua*. This most common of forest trees is the *kino lau* (body form) of the deity Pele. Wood, branches, and leaves of *ʻōhiʻa lehua*were regarded as having spiritual or religious value to native Hawaiians and as such, were used in the construction of certain parts of *heiau*, such as special houses and, in some cases, branches with leaves serving as a loose roof (Papa ʻĪʻī 1958, Kamakau 1976). Regarding its early ethnobotanical uses in Hawaiʻi, Hillebrand (1888) states, "The wood is very hard, furnishes the best fuel, and is also used for building houses. Many of the old idols were made of it."

In spite of the degree of environmental perturbation in Hawaiʻi, watershed lands have retained landscapes similar to those before the arrival of Europeans. The abundance of native plants and animals in upland watersheds, compared to the rest of the islands, makes them the only places, in most cases, which resemble pre-European contact settings for native Hawaiian life, ethnobotany, cosmology, and spiritual beliefs.

4. Historic loss and degradation of Hawai‘i’s watershed forests

The Hawaiian Islands have occupied their current position for at least 40 million years, long preceding human evolution. The powerful volcanism associated with the twin hot spots that have created the Hawaiian Islands is the mechanism behind the generation of high elevation islands greater than 13,000 feet (3,960 m), the tallest in the Pacific. The blocking of predominant northeast trade winds significantly increases background rainfall rates generally associated with open ocean in this region of 25-30 inches (600-900 mm) annually to nearly 600 inches (1,500 mm) in some Hawaiian mountain areas. Over time, unique forest types entirely dissimilar from the forests of any other high islands in the Pacific began to develop on both windward and leeward slopes.

Today, when we refer to watershed forests in Hawai‘i, we are almost always referring to upland forests above human habitations, especially on the windward or summit regions. However, prior to discovery by human voyagers, the ‘watershed’ forests of Maui County virtually covered the islands, in many cases growing nearly to the seashore. On West Maui, Moloka‘i, Lāna‘i, and Kaho‘olawe, watershed forests likely extended from near the shoreline to the summits of these islands. On Haleakalā, native forests once extended from near sea level to treeline at 7,600-8,000 feet (2,300-2,440 m) elevation, where rainfall is limited by a temperature inversion.

From a water-centric perspective, it is worth noting that the near-complete forest cover of the Hawaiian Islands before human discovery allowed hydrologic and aquifer systems to function at their maximum potential unimpaired. Based on paleontological evidence of plants and birds present at that time, perhaps some of the most obvious hydrologic differences between then and now is the greater moisture levels of leeward region lowlands, where forest cover once moderated seasonal aridity levels.

The arrival of the first humans, Polynesians from Tahiti and the Marquesas, occurred approximately 1,000 years ago (Wilmshurst et al. 2010). After discovery, repeated voyages occurred between Hawai‘i and their homelands to the South when voyaging between Hawai‘i and the South Pacific ceased, presumably due to human factors. Approximately 1,000 years of occupation by native Hawaiians allowed population numbers to grow relatively large, prompting the development of unique, often landscape-scale agricultural ventures centered around taro in windward areas, and sweet potatoes with other more drought-tolerant crops in leeward areas.

Prior to human contact, natural sources of ignition were uncommon, and even fire-prone dry forests likely grew for long periods between natural fire events (Abrahamson 2013). Following human contact, early Hawaiian populations used fire to help clear forest lands for sweet potato cultivation, especially on leeward slopes (Kirch 1982).

The synergistic impacts of fire, ungulates, and invasive plants which displaced lower elevation leeward forests continued upslope in the 20th century, causing the loss and degradation over extensive areas of native watershed forests on leeward slopes, for example on Haleakalā, from Makawao to Kaupō (Medeiros et al. 1984).

Native Hawaiians introduced about 30-50 plant species, some as important food sources, others for utilitarian resources, and apparently some arrived incidentally as 'hitchhikers' (St John 1978, Nagata 1985). Of all the plants that Polynesians introduced, none had a significant ecological impact on watersheds, with the exception of *kukui*, or candlenut tree (Aleurites moluccanus). *Kukui*, with its habit of dominating riparian habitat, its abundant leaf fall resistant to natural degradation processes, and the tendency for leaves to clog deeper stream channels, likely had an ecosystem-level impact.

The arrival of Europeans in 1778 brought about very rapid and dramatic changes to Hawai'i's natural environment, in particular, to widespread native forests that dominated the plains of central and southern Maui.

Europeans arriving in the Hawaiian Islands introduced domestic cattle, both bulls and cows, which were released to freely-forage and establish cattle populations for economic benefit. Cattle were released into upland areas with abundant food and water resources, where the resident human population had no knowledge of cattle management. Inevitably this led to cattle becoming feral and establishing rapidly growing populations in relative isolation from scattered human habitations. As herd sizes of feral cattle grew, so did their impacts on the extents and structural integrity of watershed forests, and eventually on Hawaiian subsistence gardens. Early attempts to herd or harvest large unmanaged herds were largely unsuccessful until cattle hunting and cowboy skills were acquired in the islands. These skills were essential to managing what had become both a resource and a threat. The feral cattle issue had profound effects on native forests and native Hawaiian ways of life, already threatened in this same time period by the smallpox epidemic. In the first few decades after cattle population expansion, a number of human deaths were reported due to encounters with aggressive feral cattle. Perhaps the most notorious of these encounters resulted in the death of famous American naturalist David Douglas, who was trampled by a feral bull on Mauna Kea in 1832.

Unlike feral goats, cattle require substantial quantities of water daily to remain healthy. The movements of herds seeking water, shade, and feeding areas quickly eliminates herbaceous and shrub vegetation layers in the forest. Death of trees by the trampling of roots combined with the lack of future reproduction by seed (due to browsing of seedlings) began to thin canopies and create a matrix of forest pockets from what once were continuous forest extents.

In addition, *koa* (Acacia koa) and other native trees were a ready source of wood, both as fuel and for building materials. Regarding the logging of remnant *koa* left by cattle and fire, Lydgate (1883) stated, "In early times, *koa* sawing was a regular and flourishing business, largely because of the difficulty of obtaining any other kind of lumber and many of the older houses and churches – with what seems to us now almost reckless extravagance – were built of the finest furniture *koa*."

The dramatic increase in feral cattle, combined with deliberate forest clearing to supply timber, decimated intact forests in areas such as the lower and upper slopes of Haleakalā, such as Kula, likely within decades. Of the loss of watershed forests between current day Makawao and 'Ulupalakua, Gifford in 1904 observed, "More marked examples of declining forests can scarcely be imagined than exists in the districts of Hamakua on Hawai'i and of Kula in Maui, in

which one may pass through thousands of acres of totally dead forest into equal areas in a dying condition, and from these into the small remnant that yet remains thrifty."

Many times, the most catastrophic impacts on a natural system occur when more than one invasive element or change-inducing factor occur in sequence. In this case, impacts from cattle on native Hawaiian watershed forests were magnified by subsequent introductions of numerous non-native plants, especially grass and other fire-adapted plant species. In continental tropical areas where ungulates are native to those regions, there is often a dynamic balance between grazing, fuel levels, and wildland fire frequency and intensity. The introduction of both ungulates and invasive fire-adapted grass species to Hawai‘i initiated what has been termed the "grass-fire cycle" (D'Antonio and Vitousek 1992), with dire implications for native leeward watershed forests.

When compared to introduced species from fire-prone areas, native Hawaiian trees have few, if any, adaptations to deal with wildland fire. As a result, episodic large wildland fires in Hawai‘i can burn substantial tracts of native forests in a very short time, sometimes with dramatic forest loss over just a few days. Following fires that kill native trees, fire-adapted non-native species with abundant seeds and rapid growth rates become increasingly common. This process usually repeats until formerly forested lands are left not only without native trees but lacking almost all evidence that forests ever occurred there.

As Hosmer (1912) stated, "Prior to about 25 years ago (1887), there was a belt of heavy forest with dense undergrowth in the Kula district between the elevations of 3,500 and 5,000 feet (1,070-1,525 m), that is throughout the section immediately above the corn belt. Gradually, this forest was opened up by grazing until now it has practically disappeared save as its former extent can still be traced."

Despite considerable forest degradation, there are ways that the Hawaiian Islands are fortunate when considering watershed forests. First, Hawaiian watershed forests are currently largely centered on windward rain forests, which are the most intact native ecosystems remaining in the archipelago. Secondly, in many other parts of the world, native forest areas with high biological value are often pitted in direct opposition to commercial and economic ventures, such as natural resource extraction. For example, commercial logging and Endangered spotted owls in the northwest US have antagonistic objectives. In contrast, the compelling and unique biota of Hawai‘i has great biocultural value to the general public, and the protection of watershed forests is widely seen as vital for the preservation of these important resources.

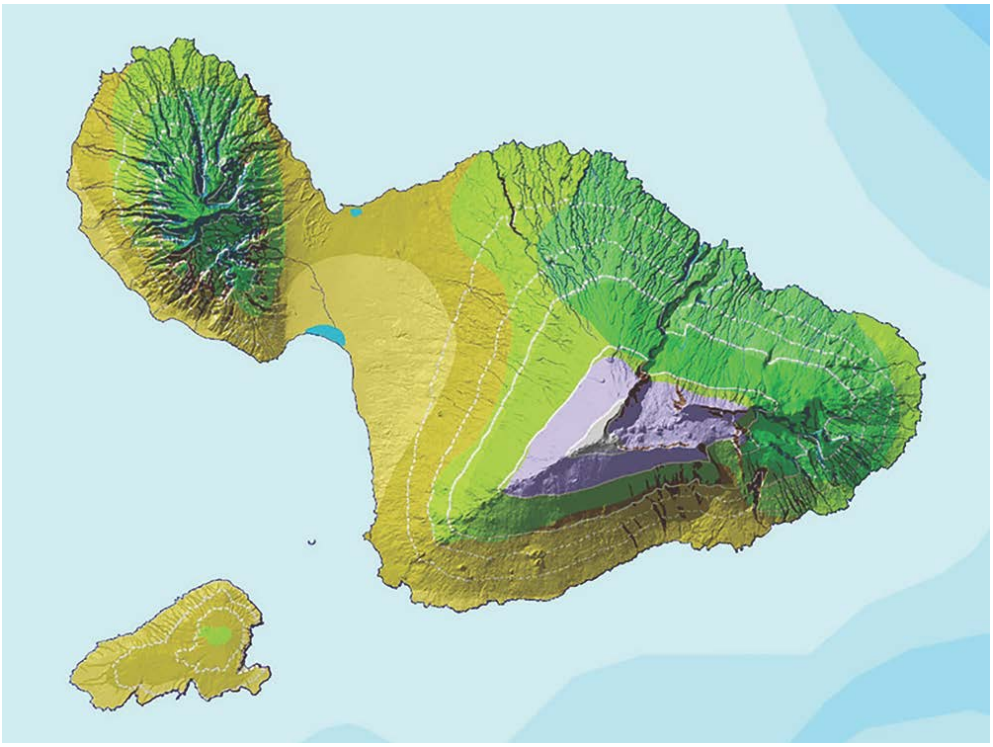

Figure 10. Likely pre-human contact vegetation of Maui island, with green designating *ʻōhiʻa lehua*windward forests and yellow marking leeward forests. Image courtesy of The Nature Conservancy.

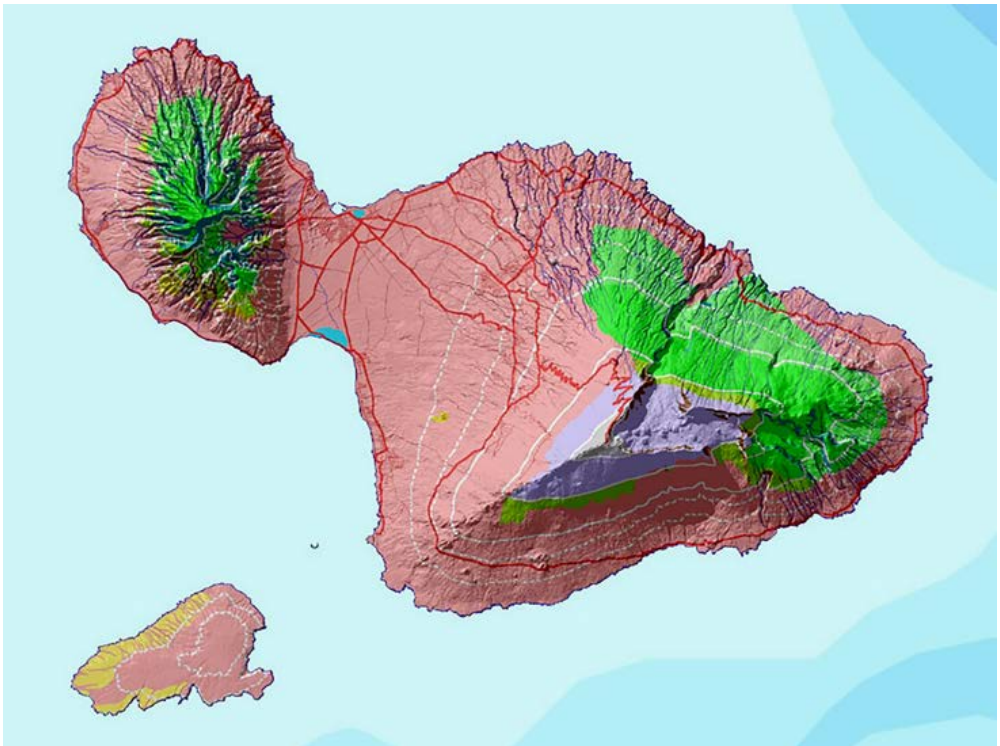

Figure 11. Modern vegetation map of Maui, with colors as in Figure 10, but here with non-native vegetation marked in red. Image courtesy of The Nature Conservancy.

5. Vulnerability of Hawai‘i’s watershed forests

The fundamental nature of watershed management has shifted over recent decades, evolving to meet increasingly complex threats to watersheds nearly everywhere on the planet. We live in a time of unprecedented global changes, both ecological and climatic. Watershed basins, even those on relatively stable continental systems, have been besieged over the past century by land clearing, invasive species, evolving forest diseases, unsustainable forestry extraction, and now climate change. These complex and interrelated stressors have brought us to a point where no watershed system globally can be presumed safe from some threat or degrading force.

On each of the Hawaiian Islands, potable water for human use is derived from watershed forests via surface water and aquifers. On all islands, potable water is sourced primarily from upland windward forests, which receive the greatest rainfall, generally where *‘ōhi‘a lehua*(Metrosideros polymorpha) dominates. ‘ōhi‘a lehuaforests make up about 80% of Hawai‘i’s remaining native forests and are the core of remaining watershed forests.

Five primary factors threaten Hawaiian watershed forests:

1. Characteristic single canopy tree species dominance of *‘ōhi‘a lehua*forests
2. Invasive non-native ungulates, especially post-1950 by feral pigs
3. Invasive non-native plants, generally from the Neotropics
4. Growing impact of non-native diseases of *‘ōhi‘a lehua*trees (ROD, Myrtle rust, etc.)
5. Climate change

The first factor threatening Hawaiian watershed forests is the single tree canopy species dominance in ‘ōhi‘a lehuaforests, which will be discussed in this chapter. This relatively uncommon ecological trait among tropical forests leaves them less resilient to the many stressors that are occurring in our changing world. Three other factors (2, 3, and 4) which involve invasive species, many an indirect result of Hawai‘i’s relatively porous quarantine system, will be discussed in the following chapters. Though uncertain in the manifestation of its impacts, the last threat, climate change, also discussed later, has the potential to generally reduce the fitness of Hawaiian watershed forests, and synergistically increase the impacts of the previous four drivers.

Ecosystems of oceanic islands are notoriously more vulnerable than continental ecosystems to degradation and destruction due to non-native animal and plant invasions. The greater the isolation and age of the islands in question, the greater the vulnerability to plant and animal invasion from continents. As the Hawaiian Islands are easily the most isolated ancient island group on the planet, theory suggests, and history demonstrates, that this isolation comes at the price of predisposition to potentially catastrophic impacts caused by invasive plants and animals (Denslow 2003).

This vulnerability of Hawaiian ecosystems is strongly influenced by the island biota heritage being derived from few ancestor species, compounded by the fact that evolution here occurred in isolation from key groups of plant and animal species which, through antiquity, have hardened and shaped continental biota through competition and herbivory. In addition, small population sizes, climatic niches, low habitat availability, and low functional redundancy are other factors contributing to the vulnerability of Hawaiian ecosystems. As such, the evolutionary forces that

shaped the Hawaiian biota are the same forces that make Hawai‘i highly vulnerable to invasive species impacts.

In addition, windward Hawaiian watershed forests, the most intact and extensive remaining forest type in the islands, have single species canopy dominance, another ecological trait uncommon in other tropical forests. Despite understory diversity and layering, the canopy of native Hawaiian windward watershed forests is characteristically composed primarily (ca. 80%) of a single canopy tree species, *‘ōhi‘a lehua*(M. polymorpha).

In evolutionary terms, recent genetic sequencing determined that Metrosideros likely had an ancient origin of 3.9 million years before present (range 2.6-6.3 million years ago). These data suggest the ancestral form arrived on Kaua‘i island, likely from the Marquesas or Austral islands, based on genetic similarities (Percy et al. 2008).

In the Hawaiian Islands, there are five endemic species of Metrosideros, though the marked but sometimes overlapping variation of M. polymorpha encompasses an enormous range of morphological growth forms. Three species are endemic to the island of O‘ahu (M. macropus, M. rugosa, M. tremuloides) and one species (M. waialealae) is rare on Kaua‘i, Lāna‘i, and Moloka‘i (Dawson and Stemmermann 1990).

From an ecological perspective, M. polymorpha is unusually adaptive. Different races of the same species simultaneously act as pioneers on new lava, as an early successional stage species, and become a dominant canopy species (late successional stage) of old-growth forests. Though M. polymorpha trees can grow in a variety of habitats from near sea level to over 7,550 feet (2,300 m) elevation on both windward and leeward exposures, M. polymorpha is more dominant in Hawaiian windward forests, far outnumbering any other tree species that occur in the wettest mountain areas of each island’s north to northeast slopes.

Metrosideros polymorpha evolved to fill an extraordinary proportion of the habitat matrix of the archipelago, and in doing so, became important for much of Hawai‘i’s other endemic flora and fauna. The term ‘keystone species’ refers to species that are disproportionately important to the stability and resilience capacity of the systems they occupy, to the degree that their loss would likely severely destabilize ecological functioning. Metrosideros polymorpha is often referred to as a keystone species due to its dominance throughout a variety of habitats as well as the support it provides to many forest species that depend on it. Metrosideros polymorpha provides year-round nectar resources for native moths, bees, thrips, nectivorous birds, and provides habitat for other native plants (Gagne 1979, Gruner 2004). Studies conducted from 1996 to 2001 surveying arthropods on M. polymorpha detected 711 insect species, with 495 species that were native specifically (endemic) to Hawai‘i, including several host-specific to M. polymorpha (Gruner 2004). Playing such a critical ecological role, it is likely that M. polymorpha supports more threatened and endangered taxa than any other species in the US (Gruner 2004, Paxton et al. 2018, Fortini et al. 2019).

Windward forests of M. polymorpha are often composed of trees representing a series of age cohorts, that is, groups of trees of similar ages and sizes. This robust pattern of cohorts suggests

that M. polymorpha has an evolutionary history of cohort senescence or periodic die back, another factor that might signal vulnerability to invasive species (Mueller-Dombois 1985).

Forests with a low diversity of canopy species are more vulnerable to perturbations than forests with multiple canopy species due to the lower resiliency of their simple biotic systems (Kennedy et al. 2002, Conti et al. 2017). In forests with multiple canopy species, the loss of a single species does not necessarily result in forest destabilization and likely displacement by invasive species. However, in cases where a single species dominates a forest canopy, such as M. polymorpha in Hawai‘i, the loss or reduction in fitness of that species initiates a cascade of ecological impacts leading to instability of the ecosystem, impacting a multitude of organisms that are dependent on the structural integrity provided by the forest canopy.

Since M. polymorpha forest canopies are fairly dense, and the trees are relatively resilient to high winds and storm impacts, this canopy layer forms a protective layer over a variety of smaller trees, native shrub layers, through fern layers all the way to the moss-covered ground. The understory vegetation layers protected by M. polymorpha canopies are not tolerant to drastic changes either increasing or decreasing the amount of sunlight that filters through to these lower vegetation layers. In the worst-case scenario, the loss or significant modification to M. polymorpha would likely trigger displacement of existing native forest communities by rapid colonization of light-loving, disturbance-adapted invasive plant species, which can lead to complete native forest loss over a relatively short time.

As an example, canopy loss and catastrophic defoliation in Hawaiian watershed forests associated with hurricanes have triggered explosive growth of invasive species, driving landscape-level changes in forest structure, composition, and function. The dramatic increase of light reaching the previously darkened forest floor led to increased invasion by light-loving non-native plants, such as Miconia calvescens and introduced grasses. Following persistent defoliation of a single-species canopy, the resulting vegetation can be altered through progressive tree mortality, reduction of total vegetation height, dramatic reduction in species diversity, and loss of structural complexity. The resulting increase in non-native vegetation has been shown to cause changes in ecosystem function, such as nutrient cycling (Hughes and Denslow 2005) and hydrologic function (Cavaleri et al. 2014).

As mentioned in previous sections, the loss of structural complexity of a watershed forest results in the reduced ability of vegetation to mitigate heavy rainfall events without erosion and topsoil loss. More critically, in hydrologic terms, the resultant vegetation community replacing *‘ōhi‘a lehua*watersheds will probably have a dramatically reduced ability to store and process precipitation, resulting in quantifiable reductions in extractable water quantity and quality.

Based on recent evidence, financial investment intended to protect Maui County’s water resources may be better spent on preventing impacts rather than attempting to remediate impacts after they have occurred. Effective restoration of damaged or displaced *‘ōhi‘a lehua*forests may be problematic based on the recent discovery of the surprisingly old age of mature trees that compose our watershed forests and the length of time required for these trees to reach maturity (Hart 2010). Utilizing carbon-14 dating methods, Hart (2010) estimated the age of 27 Metrosideros polymorpha trees on Hawai‘i island as ranging from 50-720 years, impressive

compared to many other tree species. The oldest tree in the study, dated by carbon-14, had a median age of 647 years before present, placing it among the oldest documented angiosperm trees in the northern hemisphere (Hart 2010). In this study, a fairly large 24-inch (61 cm) DBH (diameter at breast height) *ʻōhiʻa lehua*tree was estimated to be approximately 422-433 years old.

At the writing of this report, Hawaiʻi is still fortunate to have large tracts of native (and most efficient) watershed forests comprised largely of M. polymorpha. These surviving forests remain relatively more intact than any other native plant community in Hawaiʻi. However, over the past decades, the ecological stability of Hawaiʻi's watershed forests have gradually eroded. Though they continue to function today, producing abundant, clean potable and agricultural water, their future long-term status must be regarded as vulnerable.

6. Entities engaged in management of Maui County's watershed forests

One important development in the protection and management of Hawaiian watershed forests that first began in the 1990s was the concept of watershed partnerships. Watershed partnerships are voluntary alliances of public land managers and agencies and private landowners committed to the common value of protecting forested watersheds for water recharge, conservation, and other ecosystem services through collaborative management. The strength of this approach is the potential for agile, cooperative management actions conducted across land boundaries for a common purpose. In addition, unlike State and Federal agencies, watershed partnerships are more flexible and efficient in terms of quick hiring and application of human power to required tasks. Perhaps the primary limitation of watershed partnerships is that in working with a broad range of private and public landowners with differing priorities and budgets, it is difficult to fully implement this strategy.

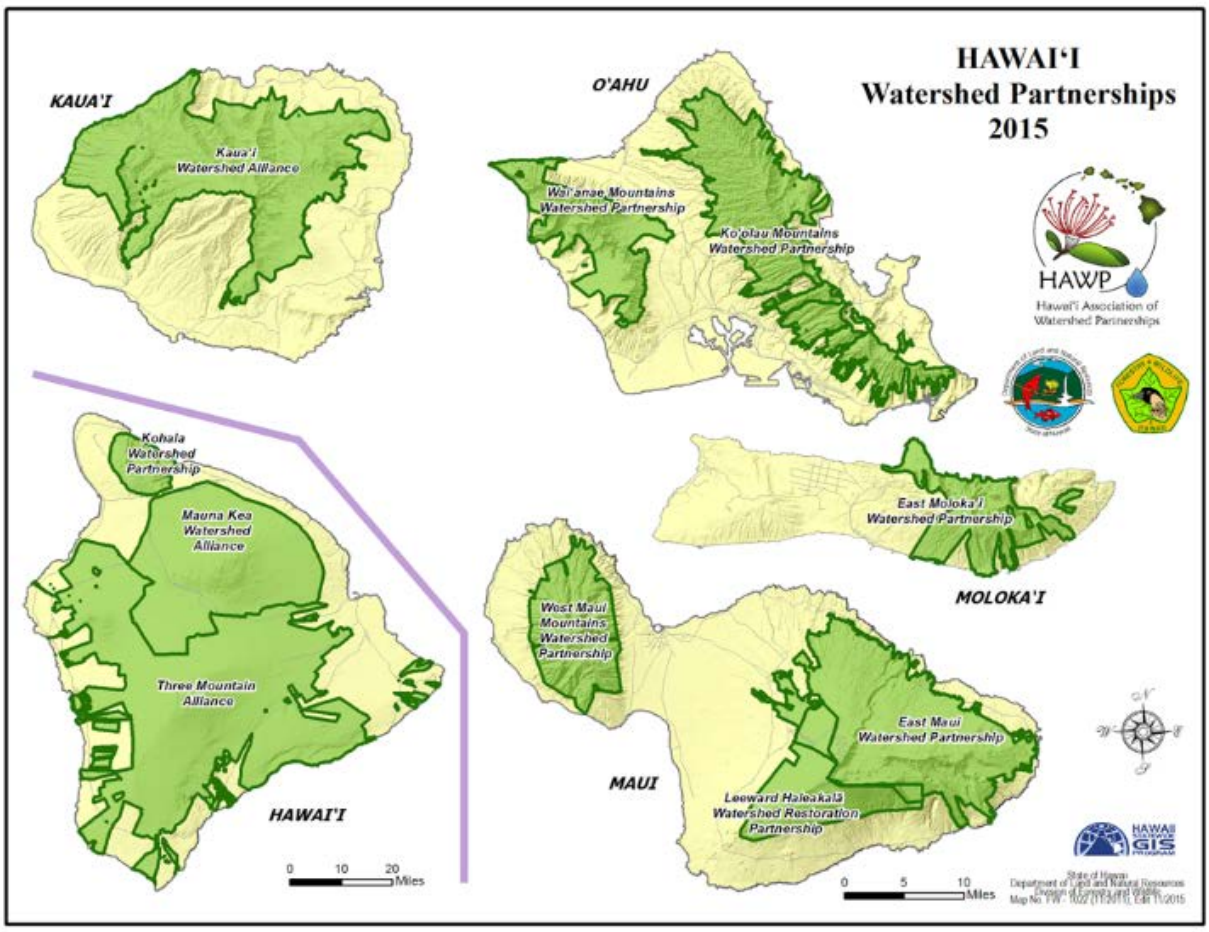

Figure 12. Map of Hawaiian Islands with eleven watershed partnerships on six main islands shown in green.

In Hawai‘i, the first watershed partnership was formed in 1991 on East Maui by several public land managers and private landowners, recognizing the advantages of working together to

attempt to meet the complicated needs required for the conservation of a large, shared watershed area that provides billions of gallons of fresh water.

To address statewide issues, the Hawai‘i Association of Watershed Partnerships (HAWP) was formed in 2003 to help organize the growing number of watershed partnerships and build collaborative support for watershed protection. Currently, HAWP is comprised of eleven watershed partnerships statewide that assist State and Federal agencies in managing and protecting Hawai‘i‘s last remaining native forested watersheds.

In Maui County, Maui Island has three watershed partnerships (Mauna Kahalawai or West Maui Mountains Watershed Partnership, East Maui Watershed Partnership, and Leeward Haleakalā Watershed Restoration Partnership). Moloka‘i’s watershed partnership, the East Moloka‘i Watershed Partnership, works on the forested eastern end of the island. On Lāna‘i, the Lāna‘i Forest and Watershed Partnership has, in recent years, become inactive.

Elsewhere in the State, Hawai‘i Island has three watershed partnerships (Three Mountain Alliance, Mauna Kea Watershed Alliance, and Kohala Watershed Partnership), O‘ahu two (Ko‘olau Mountains Watershed Partnership and Wai‘anae Mountains Watershed Partnership), and Kaua‘i one (Kaua‘i Watershed Alliance).

Statewide, the eleven watershed partnerships work collaboratively with 74 public and private partners to protect and manage approximately 2.2 million acres of upper elevation watershed forests. These lands are a combination of native forests, non-native and native mixed forests, and deforested lands that still have potential for forest recovery.

The strengths of the watershed partnership model currently being utilized throughout Hawai’i come primarily from its communal informational and decision-making capacities. In the future, this regional watershed partnership model may evolve into one that assists government agencies with the gathering and processing of monitoring data and other science-based information. Such information can contribute to science-based decision making and land management practices that best protect native watershed forests and optimize their hydrologic functioning.

7. Threats posed by invasive animals

During the entire 40 million plus year history of the Hawaiian Islands prior to the arrival of any humans, except for *ʻōpeʻapeʻa* (Lasiurus cinereus semotus), the native bat, and *ʻīlioholoikauaua* (Neomonachus schauinslandi), the Hawaiian monk seal, Hawaiian biota evolved over millions of years in total isolation from mammals, one of the planet's most dominant and influential life forms. As a result, native Hawaiian plants gradually dropped the energy-requiring defenses that had evolved in their continental forbearers to protect them, especially against two important mammal groups: ungulates and rodents. Leaves and stems stopped producing bitter chemicals, thorns, and irritating hairs, instead focusing on maximizing growth and reproduction. Without adaptations to grazing animals, rats, wildfires, or any other factors that had shaped continental biotas, when certain animal species from the continents such as cattle (Bos taurus), feral goats (Capra hircus), or even black rats (Rattus rattus) were introduced, their impacts on native Hawaiian biota were devastating. With abundant naïve food resources available and a lack of natural predators and pathogens, the ungulates and rats introduced with European explorers in the late 1790s very quickly spread and began having deleterious ecosystem-level impacts.

During the Polynesian period (approximately from 1,000 AD until 1778), early Polynesians imported early Polynesian forms of pigs (Sus scrofa) and the Polynesian rat (Rattus exulans). Both of these species' impacts, though largely undocumented, are thought to be minimal in comparison to later European introductions of larger varieties of these species and other mammal species which were free to roam and reproduce abundantly.

Today, four ungulate species continue to threaten Maui's watershed forests: feral cows, pigs, goats, and axis deer (Axis axis), all of which still contribute significantly to the degradation of watershed forests. The combined effect of these ungulates has led to decimated vegetation through significant increases in invasion by non-native plants, severe decreases in native species recruitment, and accelerated levels of erosion. These ungulate-induced changes have been shown to negatively affect soil infiltration capacity across the wide moisture and substrate age gradients (Fortini et al. 2021). These cumulative impacts have left many leeward slopes completely denuded, and in some cases, soil so severely degraded that it can no longer support plant life without amendments.

7.1 Feral cattle (Bos taurus)

Likely the single most devastating period of destruction of watershed forests on Maui occurred from 1790 to 1850 on leeward slopes by rapidly growing populations of feral cattle after first European contact. Introduced cattle quickly became feral and developed large upslope populations that damaged native forests of all elevations. Following an introduction by Captain George Vancouver in 1793, on the island of Hawaiʻi, feral cattle rapidly built huge populations due to the legal protection given to the animals by Kamehameha I (Tomich 1969). By 1830, there were an estimated 20,000 wild cattle on Hawaiʻi island alone (Wolman and Smith 2019). Though there is less documentation of feral cattle population increases on Maui, by 1806, an American ship captain reported longhorns on Maui were chasing people and digging up gardens and patches of sugar cane (Wolman and Smith 2019). The US Exploring Expedition in 1841 reported 'bullock tracks' near the summit of Haleakalā. That same year, one visitor noted, "The

bullocks of the mountains were…very numerous and savage so that traveling among the mountains was attended with great danger."

As early as 1856, Hillebrand (in an address to the Royal Hawaiian Agricultural Society) warned of the consequences of overpopulation by cattle to Hawaiian forests in the islands (Tomich 1969). Early 20th century foresters also began to report the scale of the problem. Lyon (1909), writing about O'ahu, stated that "Feral cattle have been the greatest factor in pushing the forests back to their present narrow limits, and at certain vital points cattle are still allowed to penetrate the remaining forests." In the early 1900s, botanist Joseph Rock referred to feral cattle as the "archenemy of Hawaiian forests."

Judd (1918), reviewing the effects of cattle and goats on Hawaiian forests, stated: "The continued grazing of cattle today in the native forest for the pecuniary benefit of a few .... is very short-sighted." Forbes (field notes) encountered feral cattle in Kīpahulu Valley, Ko'olau Gap, and below Hosmer's Grove in 1919-20. Cattle grazed on private lands throughout much of what is now Haleakalā National Park until the 1920s. Tomich (1969) states that "uncontrolled cattle were known on Maui until about 1930, in the Kula Forest Reserve, particularly in Pu'u Keokea and Polipoli areas." Though these cattle were finally extirpated under incentive permits, feral cattle are still common in watershed forests of Kahikinui as of the writing of this report. Even when occurring in relatively low numbers, feral cows are especially damaging, quickly trampling and destroying fern and shrub forest understories in search of forage, water, and shady resting areas.

During the 150-year period from 1790-1940, feral cattle severely damaged and destroyed large areas of native watershed forests on Maui, especially on lowland and leeward areas, including dense watershed forests between current day Makawao and 'Ulupalakua. Though at least two populations of feral cows still occur on Maui to the present, the current impact to the island's watersheds is relatively minimal, especially to the core of Maui's wetter windward watershed forests.

Figure 13. Hundreds of feral cattle continue to impact watershed forests both in East and West Maui. Feral cattle, 3,800 feet (1,160 m) elevation, Kahikinui, Haleakalā.

7.2 Feral pigs (Sus scrofa)

Feral pigs uproot and eat native plants. In their rooting for invertebrates and vegetable material, they upturn the ground surface, disturbing and destroying existing plant cover. Pig behavior is especially damaging to native fern understories. Like feral cattle, they prefer shady, ferny gulches where many rare plant species occur. In these disturbed pig-rooting sites, introduced plant species replace native species and become well-established (Mueller-Dombois and Spatz 1975, Jacobi 1981). By disturbing the integrity of native understory, pigs threaten the reproduction of overstory tree species.

Figure 14. Feral pig populations on Maui are derived nearly exclusively from European stock released from piggeries in the 1930's rather than from smaller Polynesian-type pigs introduced by Hawaiians. Digging, plowing, and consumption of selected plants damage native watersheds, facilitating increased erosion and invasion of non-native plants, as well as being vectors for several diseases potentially damaging to humans. Feral pig, upper Hāna, 5,600 feet (1,700 m) elevation, Haleakalā.

In addition, feral pigs excavate the burrows and consume the young birds and tending adults of the Endangered *ʻuʻau* (Hawaiian petrel, Pterodroma phaeopygia sandwichensis). Before protection from feral pigs, hunters utilizing the Kalapawili grasslands noted that the flesh of feral pigs harvested from that area had a distinctive fishy odor, presumably from the consumption of *ʻuʻau* (Winston Banko, personal communication).

Although pigs were brought to Hawaiʻi by Polynesians as early as 3,000 years ago, the current severe environmental damage caused by pigs began more recently due to the release of domestic, non-Polynesian genotypes (Diong 1982). Polynesian pigs, transported through the Pacific with colonizing Polynesians, are much smaller, more docile, and less prone to taking up feral existence than those introduced in historical times (Tomich 1969). The effect of feral pigs can be particularly severe in remote sites where hunting cannot control their populations. In such areas, the impact of feral pigs is the destruction of understory vegetation and the transformation of these sites into bare, plowed soil prone to invasion and erosion.

Pigs are also important seed dispersers of some invasive plant species, most conspicuously the habitat-modifying forest pest, strawberry guava (Psidium cattleianum), of which feral pigs may be their most effective dispersal agent. Individual droppings of feral pigs may contain hundreds of strawberry guava seeds that germinate readily (Medeiros 2004).

Figure 15. By consuming fruit and distributing seeds in their droppings, in Hawai`i, feral pigs are the primary vector for upslope movement of strawberry guava, one of the most serious invasive threats to watershed forests. Shown here, cohort (even-aged grouping) of strawberry guava seedlings sprouting from feral pig dropping, upper Haleakalā watershed forest.

Today, feral pigs must be regarded as the most serious ungulate threat to Maui watersheds. In their targeted herbivory of native plants, their highly effective dispersal of seeds of damaging invasive plant species, and their 'roto-tilling' or churning of the soil, sometimes over extensive areas, pigs greatly facilitate invasive weed spread and the degradation of the core of Maui's remaining windward watershed forests.

7.3 Feral goats (Capra hircus)

Often introduced by early European voyagers, feral goats (Capra hircus), such as the type found on Maui today, are renowned for their potential to be extremely damaging to native forests worldwide. The damage caused by feral goats is most extreme where they are outside their native range, not controlled by predators, and in areas where they can achieve high population densities, such as on oceanic islands. A great deal of literature exists on the damage of feral goats to native vegetation and watersheds throughout the world (e.g., Coblentz 1980).

Goats were released on nearly all major Hawaiian Islands soon after first European contact with Hawai'i in 1778 (Tomich 1969). Without natural predators to control them and with abundant native forests composed of plants without evoluntionary adaptations to deter herbivory by mammals, feral goat populations in Hawai'i increased explosively. Within 70 years (by

1850), feral goats had increased to the point that 26,500 goat skins were exported from the Hawaiian Islands (Marques 1905).

On Maui Island, feral goats have been established for over 240 years and have been abundant in native leeward forests for much of that time. The first record of feral goats on Maui occurred in 1841 with the report that the US Exploring Expedition had encountered "a few goats near the summit of Haleakalā" (Wilkes 1845), likely released in 1780-1790. In 1920, early Hawaiian botanist CN Forbes recorded that feral goats were "common in the uplands" of Maui, referring to native *ʻōhiʻa lehua*and *koa* forests now considered the heart of the Kahikinui watershed.

In the 1800s, throughout Hawaiʻi, feral goat populations decimated native shrublands, grasslands, and forests (e.g. Yocum 1967, Baker and Reeser 1972, and Mueller-Dombois and Spatz 1975). During this time, feral goat impacts were mixed with those posed by feral cattle. However, though some relict feral cattle populations exist today, the magnitude of their impacts in Hawaiʻi has diminished dramatically over the last century. In contrast, during the same period, feral goats, capable of occupying habitat without water resources, gradually became extremely common, especially in areas remote from humans and hunting.

Feral goats are extremely damaging, especially because of their locally high population densities. Though preferential in diet, the high numbers of animals tend to devour nearly all plant materials, even extremely unpalatable species such as Styphelia and Dodonaea, leaving only the green portions of Pteridium ferns unconsumed. Their omnipresent herbivory, especially of the keystone canopy species *koa* is extremely damaging to native vegetation. As an example, goat herbivory of *koa* includes foliage, young branches, bark, seedlings, and even roots (Medeiros et al. 1984).

The first serious conservation efforts to curb this loss of Hawaiian plants and animals were undertaken in the 1970s and 1980s at Hawaiʻi Volcanoes and Haleakalā National Parks. On Hawaiʻi island at Kealokomo-Pānau, feral goat round-ups were held semi-annually throughout the early 20th century by local residents for food and trade. By 1931, 75,000 goats were estimated to occur on Hawaiʻi island (Williams 1986). From 1938-1974, more than 44,000 animals had been removed from Hawai'i Volcanoes National Park on Hawaiʻi to protect native vegetation (Williams 1986). That largely, goat-free habitat status at Hawaiʻi Volcanoes National Park has been maintained to this day.

After the successful removal of feral goats from Hawaiʻi Volcanoes National Park and the resulting recovery of vegetation, other public and private land managers began ungulate exclusion programs to protect native ecosystems. Beginning in the 1980s, Haleakalā National Park on Maui initiated an effort to achieve a similar goal and eliminate ungulates from the Crater District of the Park where they had become very common and were damaging native vegetation. Prior to control of ungulates at Haleakalā National Park, large herds of several hundred feral goats were commonly encountered on hikes in remote sections of the Park (Medeiros personal observation). After ungulate exclusion at Haleakalā National Park on Maui, the recovery of native vegetation at that time was rapid and heartening.

Though feral goats remain the most destructive ungulate of remnant native watersheds of leeward Maui, especially in *koa* and *koa-'ōhi'a lehua*forests. As they prefer drier habitats, their current impacts on the critical core of Maui's watersheds on wetter northern slopes remains minimal.

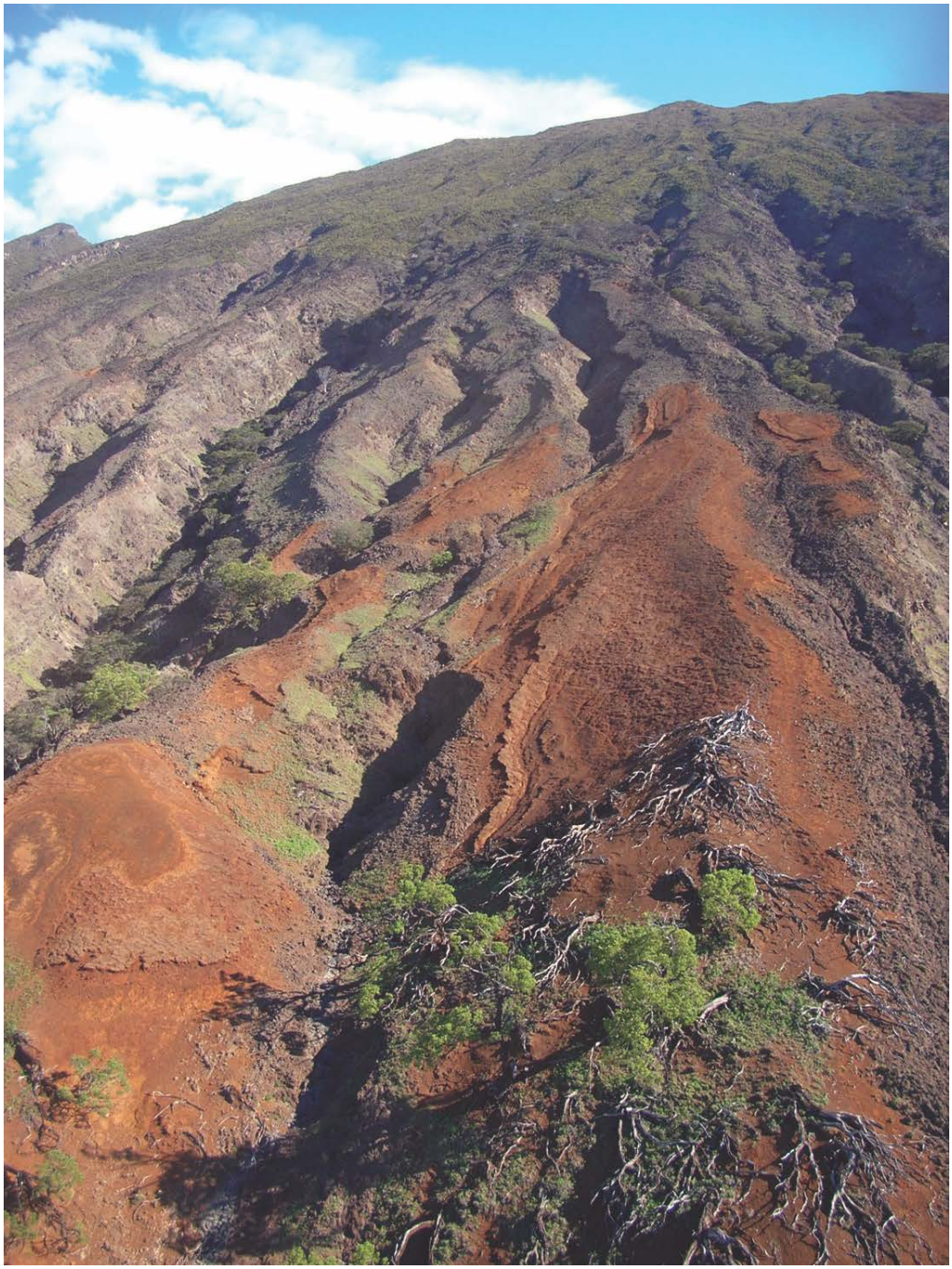

Figure 16. Historically, feral cattle have been the most damaging animal to Maui's native watersheds. However, currently feral goats (Capra hircus), especially in more remote areas of leeward East and West Maui, are the introduced ungulate most responsible for ongoing deforestation. Upper Nu'u, southeast Haleakalā.

Figure 17. Within the last 200 years, the combination of feral goat, cattle, and wildfire impacts have nearly destroyed diverse, closed-canopy *ōhi'a lehua-koa* forest that occurred throughout leeward Maui. In many ways, the ecological situation depicted here may be similar to how the area from Makawao to ʻUlupalakua appeared in the mid-1800s. Waiopai, 3,800 feet (1,158 m) elevation, southern Haleakalā.

7.4 Axis deer (Axis axis)

Among feral animals in Hawai'i, Axis deer (Axis axis) are somewhat unique in that, never having been truly domesticated, they are exceedingly cryptic and difficult to herd (Alan Kaufman, and Steve Hess, personal communication). As such, Axis deer pose a serious and largely unprecedented challenge for land managers, perhaps especially when attempting eradication or exclusion from protected areas of any significant size. Deer damage plants by

browsing, grazing, bark chewing, and antler rubbing, the latter sometimes resulting in the death of shrubs and small trees. In addition, the trampling, browsing, and up-rooting of native plants, especially native trees, leads to the elimination of successful seedling recruitment and subsequent forest decline. Axis deer are still in an exponential population growth phase, and though this species does not favor cooler, higher elevation climes, they can occur above treeline on Haleakalā.

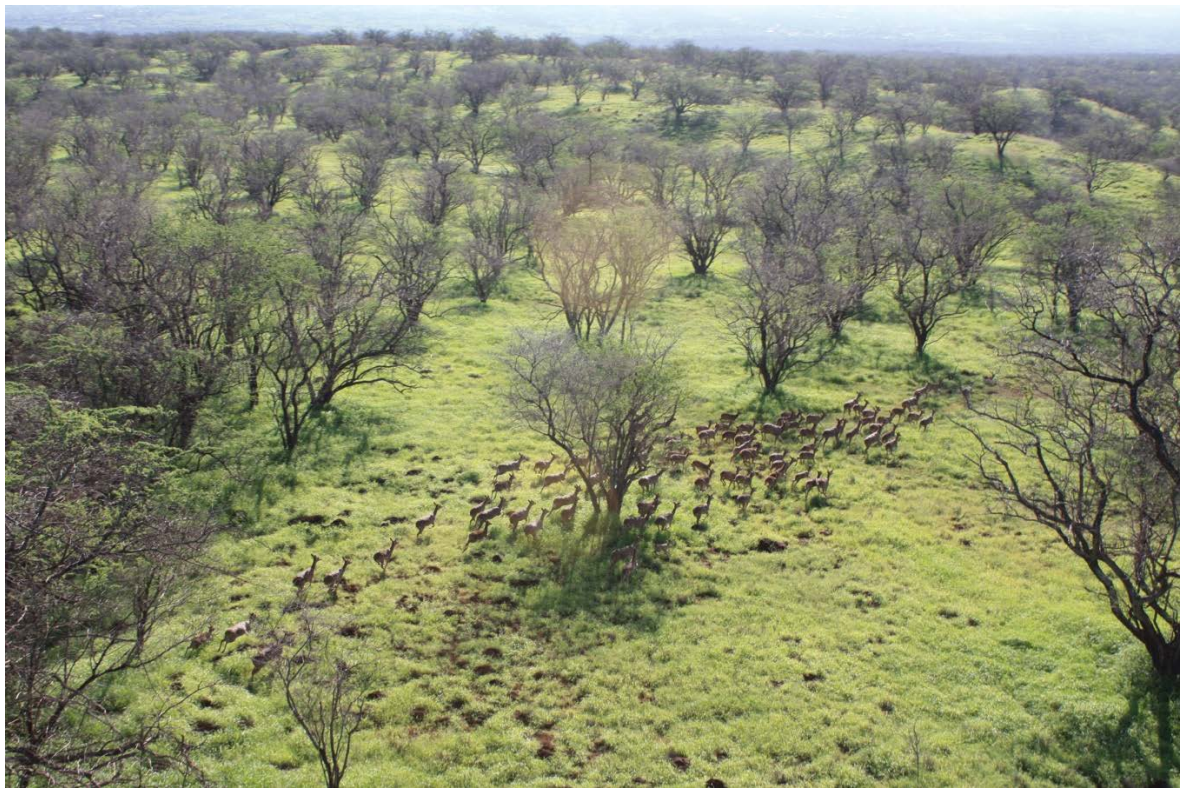

Figure 18. Axis deer (Axis axis), native to India and Sri Lanka, were introduced to Maui by the State of Hawai‘i in the 1950‘s as a game animal. Without legal hunting for decades, axis deer have multiplied to an estimated 35,000-50,000 individuals on Maui and become a threat to native vegetation, agriculture crops, as well as the cause of vehicular collisions. Axis deer herd near original introduction site on Maui near Kīhei.

Axis deer were first introduced to the Hawaiian Islands in 1867 on Moloka‘i from their native range in India and Sri Lanka (Tomich 1969). Despite objections by some biologists and ranchers, axis deer were first introduced as a game animal on East Maui in 1959-60 in the Pu‘u o Kali and Makena areas (Kramer 1971).

Based on estimates of population increases of axis deer elsewhere in its introduced range, the population size of axis deer on Maui was originally 32 animals in 1965 and increased to 167 animals in 1975, 882 animals in 1985, 4,657 animals in 1995, over 25,000 animals by 2005 (Medeiros 2004), and most recently in 2020, up to 35,000-50,000 (Jake Muise from https://www.mauinews.com/news/local-news/2020/01/axis-deer-on-the-rise-experts-say/). Unfortunately, this recent survey conducted by Muise also found high numbers of axis deer on Lāna‘i (25,000-30,000) and Moloka‘i (50,000-70,000).

Winter food for this burgeoning population primarily consists of non-native grasses. However, each summer, when the non-native buffelgrass (Cenchrus ciliaris) and other grasses go dormant, and no feed is available in the buffelgrass-kiawe (Prosopis pallida) non-native woodland, axis deer move onto the rough ʻaʻā lava flows to feed on native plants and move upslope into wetter areas. With increasing population numbers, deer have stripped low elevation lava flows of native species, many of which represent irreplaceable genetic and cultural resources. Degradation was particularly severe during four years of El Niño drought (1998-2001), when some vine and shrub species declined by 80-90% (A. Medeiros, personal observation).

As of now, populations of axis deer appear to be expanding in leeward parts of Maui, especially in middle to lower elevation regions. As such, their impacts on the critical core of Maui's watersheds on wetter northern slopes remain minimal to this point. It should be noted that on Lānaʻi and Molokaʻi, axis deer appear to reside more frequently in thickly vegetated forest areas than on Maui, warranting future monitoring on Maui to detect movements of axis deer into forested areas.

7.5 Black rat (Rattus rattus)

Globally, rodents are among the most important vertebrate predators of seeds (Jensen 1985; Jensen and Nielsen 1986; Ridley 1930). On isolated tropical islands, rodents have driven species extinctions and modified entire ecosystems (Shiels 2010). Since the Hawaiian Islands have no native rodents, the native biota has not developed defensive adaptations to prevent ecological damage, perhaps especially the devastating levels of seed predation, which often has striking ecological consequences.

The first rat species brought to the islands was the Polynesian rat (R. exulans). Introduced approximately 1,000 years ago by Polynesians to Hawaiʻi, this species now occupies a wide elevation range (Tomich 1969, Charles Stone, personal communication). More recently, the black or roof rat (Rattus rattus), the global super-invader from Asia, was introduced. Black rats probably arrived in Hawaiʻi around 1870 (Atkinson 1977) and rapidly expanded to occupy a wide range of habitats from sea level to high elevation (Tomich 1969).

Studies of ecology, paleoecology, and archeology suggest direct and indirect impacts of rat species on native plants and animals have led to tremendous impacts on Hawaiian ecosystems and have transformed many island environments (Atkinson 1985, Athens et al. 2009, Athens et al. 2002). In the absence of predators and competitors, black rat populations increased exponentially with devastating impacts, through their consumption of endemic birds, insects, land snails, and native plants, especially their seeds (Hadfield and Saufler 2009, Shiels et al. 2013, Shiels et al. 2017). Black rats have been attributed as a primary driver in the decline of native Hawaiian forests, responsible for initiating ecological impacts contributing to ecosystem collapse (Athens et al. 2002).

In certain areas, especially in restoration sites and conservation efforts focused on bird species, suppression of black rat populations appears to be a necessary step in the full recovery of native

ecosystems, especially native avifauna, large-seeded tree species, and other biological elements such as tree snails, all vulnerable to rat predation (Shiels 2010, Shiels et al. 2017).

8. Threats posed by invasive plants

The ongoing degradation of Maui's watershed forests is not due to a single factor, but rather a synergistic mix of factors, each of which has been discussed in previous chapters of this report. The mutualistic combination of vulnerability of the forests of highly isolated islands and the exposure to an increasingly large number of non-native plants, animals, and diseases has led to long-term, persistent degradation of watershed forests, their composition, structure, and function.

Prior to the arrival of humans, a new plant species arrived once every 35,000-40,000 years, which evolved slowly into the native Hawaiian plant flora. As of 2004, approximately 13,000-15,000 non-native plant species had been introduced to Hawai‘i, some intentionally, and many unintentionally. Although many non-native plant species are introduced into Hawai‘i, it takes a very specialized series of ecological traits to leave cultivation and become naturalized. Another series of traits is required to become invasive and abundant to the point of threatening existing forest vegetation. As a result, only about 100 species of all these introduced plants are considered highly invasive and habitat-modifying (Smith 1985). Overall, a new plant species introduced to Hawai‘i has a 1:130 to 1:150 chance of becoming a serious invader.

One of the most serious long-term threats to Hawaiian watershed forests is the gradual displacement of native plant species by invasive plant species, with a potentially dramatic decline in the forest's ability to provide functional hydrologic services.

A combination of several factors is required for a non-native plant to become so invasive that it replaces existing native vegetation. The first has been called the "enemy release hypothesis," where the newly arriving species is freed from the suppressing factors, such as co-evolved insects and pathogens, which keep them in check in their native habitat (Keane and Crawley 2002). The second factor is that many invasive species are pioneer species that evolved in competitive dark tropical forests where they colonize ephemeral light gaps and high disturbance areas such as streambanks and treefall gaps. Compared to the dark understory of more equatorial tropical rainforests, native Hawaiian forests are relatively well-lit, with quite a lot of light reaching the forest floor, making them vulnerable to species adapted for rapid colonization and growth in light gaps. The third factor is that one in every 130-150 non-native plants introduced to Hawai‘i become highly invasive species because of their evolution within very large, diverse, and competitive continental tropical gene pools. These plants are invasive super-species that have often been selected by the horticultural industry as 'new' and 'easy to grow.' These species are often adapted to grow in disturbed sites within moist forest systems at numerous tropical locales worldwide.

As each decade passes, our watershed forests face increasing numbers of invasive plant species in diverse guilds ranging from trees to shrubs to vines and herbs with a wide variety of ecological strategies. For example, in *‘ōhi‘a lehua*watershed forests of upland regions of

Kīpahulu Valley, the number of non-native plant species recorded increased from five species in 1945 (Fagerlund 1945) to 22 in 1967 (Lamoureux 1968), 55 in 1980 (Yoshinaga 1980), and 81 non-native plant species in 1998 (Medeiros et al. 1998). This represents a 1520% increase of non-native invaders in a protected watershed forest on Maui in just over five decades.

One of the most critical ecological changes that accompany the invasion of our native windward watershed forests by invasive plant species is the disruption of seedling establishment by native canopy trees, especially the dominant species *ōhi'a lehua*. Seeds of Metrosideros are tiny and wind-dispersed, producing seeds smaller than a typical letter on a printed page. Though capable of eventually growing to over 100 feet (30 m) in height with trunks several feet (>1 m) in diameter, the tiny seedlings require protected, moist sites that are very stable over many years to establish. This need for protected habitat for the establishment of seedlings and the development of *'ōhi'a lehua*trees is due to their extremely slow growth rate at just 0.05 inches (1.3 mm) diameter growth annually (Hart 2010). Protection from ungulates and from competition with invasive plants is necessary for seedlings to survive and grow up to replace the adult cohort generations of *'ōhi'a lehua*trees that currently form the canopy of nearly all of the Hawaiian watershed forests.

By altering species composition and diversity, these highly invasive species can profoundly alter our watershed forests' nutrient, carbon, and water cycles. This changes the forests' successional trajectories from stable, semi-resilient, highly diverse systems to more chaotic and disturbance-driven systems, with simplified structure and low species diversity.

Models have predicted that the conversion of native Hawaiian forests to non-native forests will decrease aquifer recharge and transfer more water and sediment as sheet flow during significant rain events (Kagawa et al. 2009). The ecological dysfunction resulting from the displacement of *'ōhi'a lehua*watershed forests at the landscape scale inevitably will lead to ecological stochasticity, degraded hydrologic function, and progressive reduction of extractable water resources.

Conversion of native canopy vegetation to non-native species has happened at numerous sites in Oceania, usually occurring at lower elevations and typically accompanied by the presence of introduced ungulates, especially cattle and feral goats. Probably the most dramatic example of loss of native watershed system and replacement with an invasive plant community on a Pacific island has occurred on Tahiti and other islands of French Polynesia with miconia (Miconia calvescens).

Introduced to Tahiti in 1937, the spread of miconia occurred rapidly, displacing two-thirds of the native watershed forest within a relatively short 50-60 year period (Meyer 1996). This invasion was greatly facilitated by abundant seed dispersal by small generalist passerine birds, both native and alien species, but especially the silvereye (Zosterops lateralis) attracted to miconia's small sweet berries. Over a few decades, and aided by canopy disruption caused by two hurricanes, miconia came to dominate extensive areas, usurping the original canopy and covering highly dissected ridges and valleys with largely monospecific miconia thickets up to 4,500 feet (1,220 m) elevation in the mountains of Tahiti, coming to occupy more than 270 square miles (699 km^2; Meyer 1996).

The invasion and landscape-level displacement of the native watershed forests of Tahiti are used globally as a cautionary tale regarding the potential magnitude of invasive species' impact on a natural system. With similar volcanic origins, ages, and distance from the equator, both the Hawaiian and French Polynesia archipelagos have high endemism and are vulnerable to disturbance (Medeiros et al. 1997). Based on the loss of watershed forests in Tahiti, the worst-case scenario for Hawaiian watersheds regarding extractable water resources would be the loss of the *ʻōhiʻa lehua*canopy layer that currently exists over landscape-scale areas.

Figure 19. Mejiro or Japanese white-eye (Zosterops japonicus), a small Asiatic passerine introduced to Hawaiʻi in 1929, has become Hawaiʻi's most common bird species. In addition, Japanese white-eye have invaded Hawaiian rainforests and, in an example of mutualistic interaction between invasive species, have

become an important disperser of the seeds of many invasive weeds, including Miconia, Clidemia, strawberry guava, Himalayan ginger, and others. Photo taken of wild-caught bird from Hawaiian rainforest.

Table 1. Invasive plant species considered threats to Maui's watershed forests with proven track records in Hawai'i as ecological de-stabilizers.

Name	Common name	Guild	Country of Origin
Angiopteris evecta (Marattiaceae)	king fern	giant fern with frond up to 30 ft (9 m) long and rhizome-forming trunk up to 3 feet (1 m) wide	New Guinea, Australia, Melanesia, Micronesia, Polynesia
Bocconia frutescens (Papaveraceae)	tree poppy	medium tree up to 20 ft (6 m) tall	Central and South America and West Indies
Clidemia hirta (Melastomataceae)	Koster's curse	perennial shrub up to 15 ft (5 m) tall	Central and South America
Cortaderia jubata (Poaceae)	pampas grass	giant bunch grass up to 10 ft (3 m) tall	South America
Sphaeropteris (Cyathea) cooperi (Cyatheaceae)	Australian tree fern	tree fern up to 13 ft (4 m) tall	North-eastern Australia
Falcataria moluccana (Fabaceae)	Moluccan albizia	fast-growing canopy tree up to 115 ft (35 m) tall	Indonesia and Papua New Guinea
Hedychium gardnerianum (Zingiberaceae)	Himalayan ginger, kahili ginger	thicket-forming perennial herb	Eastern Himalayas
Macaranga mappa (Euphorbiacea)	bingabing	tree up to 30 ft (9 m) tall	Phillippines
Miconia calvescens (Melastomataceae)	miconia	tree up to 40 ft (12 m) tall	Central and South America

Morella (Myrica) faya (Myricaceae)	firetree	free up to 25 ft (8 m) tall	Macaronesian
Passiflora tarminiana Synonym: P. mollisima (Passifloraceae)	banana passionfruit; banana poka	woody climbing vine	South America
Psidium cattleianum (Myrtaceae)	strawberry guava, *waiwi*	trees up to 30 ft (9 m) tall	South America-Brazil to Uruguay
Rubus argutus (Rosaceae)	prickly Florida blackberry, sawtooth blackberry	thicket-forming woody erect shrub to arching or trailing vine up to 10 ft (3 m) tall	Central and Eastern U.S.
Rubus ellipticus (Rosaceae)	yellow Himalayan raspberry	thicket-forming shrub up to 10 ft (3 m) tall	Southeast Asia
Schefflera actinophylla (Araliaceae)	umbrella tree	fast-growing thicket forming tree up to 40 ft (12 m) tall	Queensland Australia, New Guinea, Java
Spathodea campanulata (Bignoniaceae)	African tulip tree	medium to large fast-growing tree up to 80 ft (25 m) tall	Africa
Tibouchina herbacea (Melastomataceae)	cane tibouchina	herb or subshrub up to 3 ft (1 m)	South America

8.1 Vignettes of three of Maui's worst forest invaders

A book could be written summarizing the origin, distribution, ecology, potential threat, and management strategies for each of the invasive plant species which poses a serious threat to Maui's watersheds. However, vignettes are presented here for four of Maui's most serious watershed threats: strawberry guava, *waiwi, waiwi'ula* (Psidium cattleianum), Himalayan or kahili ginger (Hedychium gardnerianum), and the melastomes Clidemia hirta and Miconia calvescens.

8.1.1 Strawberry guava, waiwi, waiwi'ula (Psidium cattleianum)

Strawberry guava (Psidium cattleianum, Myrtaceae) is a small tree up to 30 feet (9 m) in height, native to a relatively small area of southeast Brazil and northern Uruguay. It has been broadly distributed globally as a novelty fruit tree and is now widespread and considered an invasive plant throughout the tropics and subtropics.

The taxonomic status of the variations between forms of P. cattleianum in its native range and the dominant forms in invaded ranges is far from well-defined. Psidium cattleianum is native to the Atlantic Forest from Espiritu Santo, Brazil, to northern Uruguay, South America (Wikler et al. 2000). Psidium cattleianum has been used to describe a polymorphic assemblage of types with distinctive fruit, leaf, and habit characteristics. In Hawai‘i, two yellow-fruited forms (forma lucidum and var. littorale) and one red-fruited form (var. cattleianum *sensu stricto*) have become invasive (Wagner et al. 1990).

In its native habitat of Brazil, yellow-fruited trees attributed to P. cattleianum are the dominant form found in coastal forests (*restinga*) up into lower montane forests. In contrast to Hawai‘i, the red-fruited form found in Brazil is relatively uncommon, and its known distribution is restricted to certain localized regions (Charles Wikler, personal communication). In Brazil, both red- and yellow-fruited forms are grown in home gardens. One hypothesis of local Brazilian biologists is that the red-fruited form is of hybrid origin with another Psidium species, perhaps P. longi.

Strawberry guava tends to naturalize wherever introduced and has become widely established and invasive on islands of the Pacific, Atlantic, and Indian Oceans, and in Australia, Central America, Asia, Africa, the Caribbean, and North America (Medeiros 2004). Though the species is highly variable and adaptable, strawberry guava has become particularly problematic in wet forest systems as well as oceanic islands of the Pacific and Indian Oceans.

Compared to many other invasive species of Hawai‘i, strawberry guava was introduced to the islands at an uncommonly early date, shortly after the first European contact, in 1825. It is now commonly found growing on all main islands, except Ni‘ihau and Kaho‘olawe, from near sea level to 4,000 feet (1,220 m) elevation and occasionally up to 4,600 feet (1,400 m) elevation. Without the pressure from natural predators found in its home range, in Hawai‘i the species has more resources allowing for accelerated growth and reproduction.

Though strawberry guava naturalized quickly, initially, it was restricted to areas near habitations and disturbed lower forests. Strawberry guava has been shown to be dispersed infrequently by our common forest birds, both native and non-native, perhaps because of the fruit’s thick rind. However, strawberry guava invaded upper elevation *‘ōhi‘a lehua*forests on Maui after domestic pigs, released in the 1930s, became feral and abundant, and started upslope movement to colonize the middle and upper elevation *‘ōhi‘a lehua*forests (Medeiros 2004).

At the peak of fruiting in strawberry guava stands, the ground is covered with strawberry guava fruits so densely that the air becomes strongly scented. Feral pigs take advantage of these strawberry guava fruiting periods and gorge on their fruits, often returning to more upland forests where they are safer from hunting pressure. During this season, it is relatively common to see feral pig droppings entirely composed of strawberry guava fruits and seeds. Large droppings

contain hundreds of strawberry guava seeds that, if undisturbed, will germinate, producing up to a hundred or so seedlings as the dropping decomposes in the wet conditions (Medeiros 2004).

An example of upslope movement of strawberry guava has been documented in Kīpahulu Valley, Haleakalā National Park. There, in the 1850s, strawberry guava was confined to pasture edges and lower elevation non-native forests. By the early 1960s, strawberry guava began to spread upslope, likely aided by the upslope movement of feral pigs (Diong 1982). By 1967, strawberry guava was observed up to 2,200 feet (670 m) elevation (Lamoureux 1968); by 1980, to 3,800 feet (1,160 m) elevation (Yoshinaga 1980); and by 1998, to 4,600 feet (1,400 m) elevation (Medeiros et al. 1998).

On Maui, in lower to middle elevation forests (1,600-3,000 ft or 490-915 m), strawberry guava is overwhelmingly the most common tree species creating extensive, dense monotypic stands with a darkened understory. In these areas, strawberry guava excludes nearly all other plant species, perhaps aided by allelopathy (chemical inhibition of one plant by another). For example, highly invaded sites occur on Haleakalā's northern slopes from Haʻikū to Hāna and around through Kaupō.

Extensive stands of strawberry guava have become established at numerous sites spreading from lower elevations. Notable expansions of these populations upslope to 3,000-4,000 feet (915-1,220 m) elevation range occur in Koʻolau Gap, Nāhiku, and Kīpahulu Valley. Based on observations of potential spread elsewhere on Maui, it is likely that the strawberry guava, though proceeding slowly, is capable of further upslope invasion, likely to approximately 4,700 feet (1,430 m) elevation (Medeiros 2004). One key factor in the continued range expansion of this highly invasive tree is the mutualism with an effective seed disperser such as feral pigs. However, one notable situation is the stalled spread of strawberry guava on Haleakalā's northern slopes near Kaupō, apparently due to the substrate and lack of moisture.

Along with the notorious invader miconia, strawberry guava is frequently named by experienced Hawaiian biologists and managers as the most serious threat to Hawaiʻi's watersheds and other natural resources. The generalized ecological patterns seen in most invasive species in Hawaiʻi are to produce high numbers of seeds, have excellent dispersal systems, grow very rapidly, and thrive, at least at first, in disturbed areas within the forest. In contrast to miconia, strawberry guava produces low to moderate numbers of seeds, disperses only moderately well, and grows more slowly than most Hawaiian watershed forest weeds.

Figure 20. Introduced worldwide for its edible fruits, strawberry guava or *waiwi* (Psidium cattleianum) is known globally as one of the world's worst weeds, and in Hawai'i, one of the most serious invaders of Hawaiian watershed forests. Pictured here is a strawberry guava tree (+30 feet (9 m) tall), invading otherwise near intact *'ōhi'a lehua*forest at approximately 4,400 feet (1,340 m) elevation. For scale, note the person with a yellow notebook standing at the base of the tree.

Unlike most other invasive species which are soft wooded, strawberry guava is a medium-sized hard wooded tree. As an early successional, pioneer species it spreads through clonal sprouting and new sapling establishment, allowing it to dominate a site completely. In doing so, strawberry guava swamps out other species and generally eliminates native plant reproduction by smothering seedlings in their dark understories. With this ecological strategy, strawberry guava

can, over time, come to dominate large areas of watershed forest, replacing *ʻōhiʻa lehua*in windward forests with simplified forest structure, devoid of diversity and marked by erosion. Even today, upslope movement of strawberry guava continues with its upward sprawl and with feral pig movements.

The dynamic processes that are ongoing and critical to preserving our island's natural capital often lack significant data-driven research. An example of this is the need to quantify the impact on water resources due to the loss of *ʻōhiʻa lehua*forests being replaced with simplified stand structure characteristic of invaded systems.

However, some studies have been conducted on the impacts of strawberry guava on Hawaiian watershed ecohydrology. Evapotranspiration is the transfer of water from the land to the atmosphere via evaporation by soil and other surfaces as well as transpiration by plants. Compared to a fairly intact *ʻōhiʻa lehua*forest in the same cloud forest zone, heavily invaded strawberry guava forest had 27% higher evapotranspiration rates, with up to 53% higher evapotranspiration recorded during a dry period (Giambelluca et al. 2008). Fast-growing strawberry guava transpires significantly more water than native trees during the day and also transpires on hot, dry nights after recent rains (Kagawa-Viviani 2020). The high rates of evapotranspiration of strawberry guava equates to losses of water back to the atmosphere rather than retention of the moisture in the canopy, absorbent ground cover, soil, and aquifer.

In addition to these losses, strawberry guava moves water droplets through the canopy (as throughfall and stem water) at much higher velocities than *ōhiʻa lehua*, due to tree architecture. Strawberry guava characteristics such as smooth bark, glabrous leaves, and steep leaf and branch angles funnel water directly to the tree's base, where deep undecomposed leaf litter prevents it from infiltrating or being available for other understory species (Safeeq and Fares 2014). This accelerated movement of water from the canopy to the forest floor can cause overland flow and soil erosion during large rain events. In contrast, the complex structure of *ʻōhiʻa lehua*canopies with broad, meandering branches, textured bark, aerial roots, and complex leaf whirls retain the moisture in the canopy, some of which eventually gets soaked into the soil.

In response to the growing awareness that strawberry guava is threatening our watershed forests, preliminary surveys began in Brazil to first identify potential biological control candidates found in association with strawberry guava in its native range. This was followed by over a decade of testing, much done in Brazil to reduce costs. As a result of this work, 133 insect species in 80 families representing 12 orders were identified as associated and perhaps limiting the vigor of strawberry guava (Loope 2011). In 2012, after extensive field and laboratory research centered around testing, a Brazilian scale insect, Tectococcus ovatus, was approved and released in Hawaiʻi as a biocontrol to slow down the growth and reproduction of strawberry guava in Hawaiian forests. Tectococcus ovatus is a small scale insect that suppresses strawberry guava by inducing the plant to produce large conspicuous galls, sometimes in abundance, causing its leaves, stems, and fruits to deform and reduce function. Heavy infestations of T. ovatus can decrease growth rates, inhibit fruit production, reduce photosynthesis, and cause premature leaf drop and potentially large-scale defoliation (Vitorino et al. 2000, Wessels et al. 2007).

Although T. ovatus can provide meaningful suppression of strawberry guava, it does not disperse well on its own. Dispersal generally occurs with the wind-aided movement of the minute non-flying insects from plant to plant and into new areas. Especially in dense forest sites protected from wind, the spread rate of T. ovatus is predicted to be slow, with an associated lag in strawberry guava suppression. In Hawai‘i, once established, T. ovatus is predicted to take seven to eight years to spread to the point that strawberry guava’s vigor and rate of spread are reduced significantly and begin to provide long-term holistic suppression of strawberry guava (State of Hawai‘i, 2010). As a result, an augmentation effort centered around the targeted release of T. ovatus in and throughout any extensive strawberry guava populations on Maui would likely greatly facilitate spread and accelerate the timeline for suppression of strawberry guava. A technology-based management approach, such as GPS-guided delivery by drone, would likely have a high impact per dollar invested, taking advantage of decades of previous work and considerable financial investment.

As with most cases of biological control, how much the target plant is impacted by the introduced biological control, in this case T. ovatus, is not assured. Often numerous biological control agents utilizing different life strategies and attacking different parts of the plant are required for holistic efficacy. The combined synergistic control of multiple biocontrol agents needed to control serious pest plants has already been achieved with panini (Opuntia megacantha) and lantana (Lantana camara), with research developed in Hawai‘i and now used globally.

In conclusion, strawberry guava is now the second most common tree in Hawai‘i and is nearly universally recognized as one of the most serious weeds in Hawai‘i and at numerous other sites worldwide where it has invaded. In Hawai‘i, it is found from near sea level to 4,000 feet (1,220 m) elevation commonly, and to 4,600 feet (1,400 m) elevation occasionally, on all main islands except Ni‘ihau and Kaho‘olawe. In many sites, strawberry guava is overwhelmingly the most common tree species creating extensive monotypic stands, usually in middle elevation watershed forests, especially on Haleakalā’s northern slopes from Ha‘ikū to Hāna and around through Kaupō, with darkened understory that excludes other plant species. The recently released biocontrol agent T. ovatus may level the playing field between invasive strawberry guava and native forest species.

8.1.2 Himalayan ginger (Hedychium gardnerianum)

Hedychium gardnerianum, hereafter Himalayan ginger, is a very large (up to 7 feet (2 m) tall), clump-forming, rapidly growing rhizomatous herb. Himalayan ginger is native to the eastern Himalayas (India, Nepal, and Sikkim), but is now widely introduced and naturalized in tropical, sub-tropical, and warm temperate regions. Besides Hawai‘i, this species is recognized by the Center for Agriculture and Bioscience International (CABI 2022) as a problematic forest invader in New Zealand and the Azores, and as naturalized and spreading in Australia (Queensland), Ecuador, and South Africa.

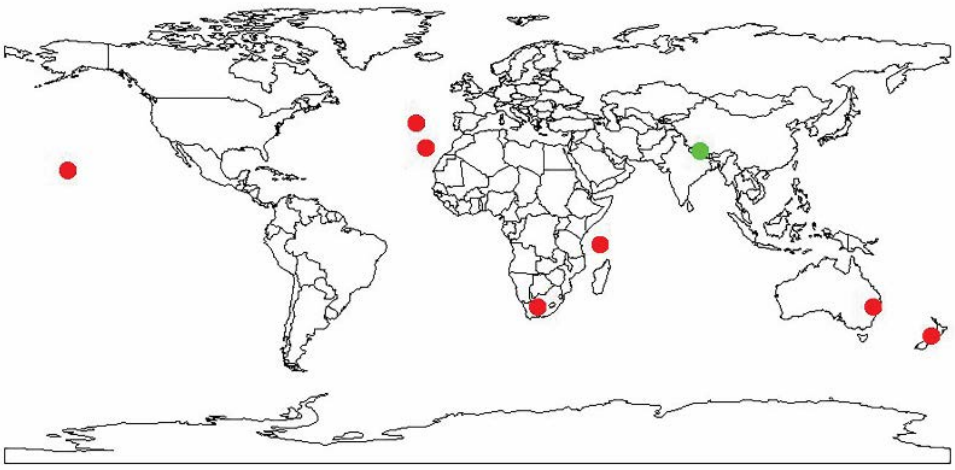

Figure 21. Distribution of invasive populations of Himalayan ginger (Hedychium gardnerianum) in red, with the approximate center of its native distribution marked green (Medeiros 2004).

Himalayan ginger was first recorded in the Hawaiian Islands relatively late, around 1940 (Wagner et al. 1990) and was previously referred to as kahili ginger. Despite that, it has become naturalized in native rain forest on Kauaʻi, Lānaʻi, Maui, and Hawaiʻi Island near Hawaiʻi Volcanoes National Park (Stone and Pratt 1994). On Maui, Himalayan ginger has established dense and spreading populations in areas of remote watershed forest in Makawao Forest Reserve, Nāhiku, Hāna, and Kīpahulu Valley. Himalayan ginger spreads primarily by vegetative regeneration of rhizomes. It can reproduce from small root fragments, resulting in limited efficacy of control through mechanical removal. It is worth noting that despite intensive traditional management efforts (mechanical and chemical) by Haleakalā National Park staff, Himalayan ginger populations in Kīpahulu are still fairly extensive.

Seed production of Himalayan ginger is moderate, with each 7 feet by 7 feet square area (4 m^2) of Himalayan ginger producing a range of 858 to 34,997 seeds/year, averaging 8,096 seeds/year (Medeiros 2004). The bright red seeds are relatively large, with conspicuous bright red attached aril, an adaptation to attract birds and facilitate seed dispersal. The primary dispersers of the seeds of Himalayan ginger in Maui watershed forests are two common, small, non-native, passerine birds, the Japanese white-eye (Zosterops japonicus) and the Red-billed leiothrix (Leiothrix lutea). These birds disperse Himalayan ginger seeds, yielding from 1 to 10 seeds recovered per bird capture (Medeiros 2004). Black rats consume and destroy Himalayan ginger seeds without dispersing them, an unusual case where one invasive species competes with another rather than the usual mutualistic interactions.

Figure 22. With its brightly colored, sweet-smelling spikes of flowers, Himalayan ginger (Hedychium gardnerianum) was introduced through the horticultural trade to numerous sites globally, including Hawai‘i, where it has often become problematically invasive in wet forests.

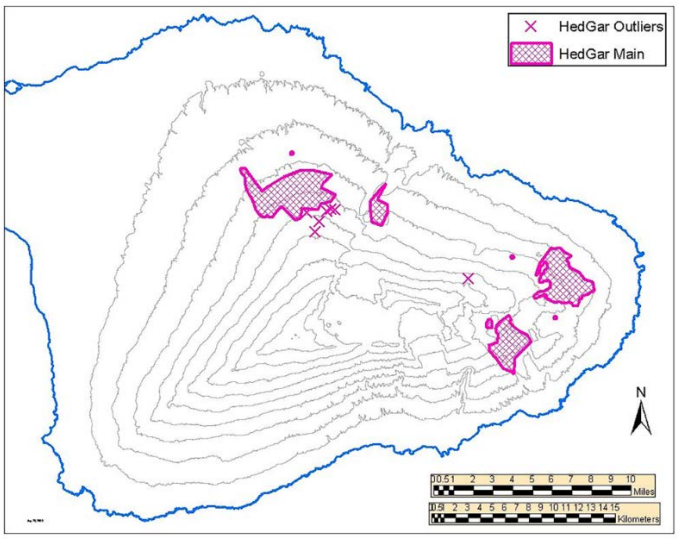

Figure 23. Distribution of Himalayan ginger (Hedychium gardnerianum) invasions in watershed forests of Haleakalā. As elsewhere globally, the species disperses by birds from lower elevation human habitation areas where it was introduced into near pristine *`ōhi`a lehua* watershed forests fairly far upslope (Medeiros 2004).

Most invasive plant species that are problematic in Hawaiian watershed forests are of tropical origins, usually Central and South America, and prefer warm, wet conditions. As such, when invading Maui watershed forests, the majority reach an upper elevation limit due to decreasing temperatures (for many species approximately 4,000-4,500 feet (1,220-1,370 m) elevation), beyond which the species does not successfully establish. However, in its native Himalayan range, Himalayan ginger occurs at high elevations, up to 6,200 feet (1,890 m) (Stainton 1997). Based on this, it seems likely that the range of Himalayan ginger could even expand to near the tree line limit of Haleakalā, Maui, at approximately 6,400-6,800 feet (1,950-2,070 m) elevation. With its uncommon ability to invade high elevation forest and completely smother native understory vegetation, Himalayan ginger is one of the most damaging and invasive non-native plant pests of Hawaiian watershed forests.

Besides Hawai‘i, Himalayan ginger has also spread to unmanageable levels and is causing serious environmental impacts in New Zealand. In 2008, exploratory work conducted by the highly respected international group CABI resulted in the collection of numerous species of natural enemies of Himalayan ginger in several orders (Rojas-Sandoval 2023). This search effort was funded by a collaboration of Hawai‘i and New Zealand agencies and groups. This study identified a large guild of natural enemies on H. gardnerianum populations in India which are being evaluated as natural enemies through host specificity testing in the UK (Rojas-Sandoval 2023). However, disappointingly, none possessed the characteristics essential to be considered as a biocontrol candidate, i.e., attacking only Himalayan ginger (and no other species), as well as causing significant damage.

Another form of biocontrol is augmentative biological control. This involves identifying a pathogen or predator already present within the invasive range of the target pest species and *ex situ* increasing the quantity of the identified biocontrol, then applying this biocontrol or releasing it into the pest populations in the invaded habitat to maximize its impact. When the biocontrol agent is a pathogen, applied in a spray or similar, it is referred to as bioherbicide. One advantage of augmentative biocontrol is that it does not require the extensive testing and approval process that classical biological control involves.

Figure 24. Though apparently uncommon in its native range, without its natural enemies to keep it in check, Himalayan ginger into Hawaiian forests develops very dense stands. Stands such as these displace and stall reproduction of native plants, including critically important canopy tree species. Himalayan ginger population shown here at Waikamoi, Haleakalā.

An almost textbook example of augmentative biological control can be found with early attempts to control Himalayan ginger in a more natural, sustainable way than herbicide application. In Hawai‘i, a naturally occurring bacterial wilt is caused by the ginger strain of Ralstonia (Pseudomonas) solanacearum. This bacterium infects edible and ornamental ginger and causes wilt in infected plants. When applied as a bioherbicide on Hawai‘i island, Ralstonia bacterium causes irreversible chlorosis, severe wilting, decay of rhizomes, and eventually death of treated Himalayan ginger (Anderson and Gardner 1999). Though the Ralstonia strain used was reportedly specific for Himalayan ginger and nonpathogenic to important ornamental gingers and common plant species in Hawai‘i (Anderson and Gardner 1999), additional further testing identified a vulnerability in certain ornamental gingers (Paret et al. 2006). Ralstonia is an important potential biological control agent, but the use of the identified strain was discontinued as a result of this research. One project that would increase the number of management options with Himalayan ginger is further investigation to find or develop a host-specific form of Ralstonia to control Himalayan ginger in Hawaiian watersheds.

Figure 25. Though manual control clearly has a role in the management of invasive plant species, it is most effective at the very beginning of an invasion. Mechanical control can be effective in eradicating the first incipient populations, or later, in slowing or checking invasive spread by strategically controlling and/or eradicating founder populations in new regions of invasion. However, if the invasion proceeds to landscape level, the cost-benefit analysis of manual and chemical control methods, likely increasingly ineffective in any case, should be re-evaluated.

Figure 26. Native to the eastern Himalayas, kahili or Himalayan ginger was introduced to Hawai`i in the 1940s. Without assistance from humans, it dispersed from garden settings invading Maui watershed forests, developing extensive colonies even in surprisingly remote areas. Himalayan ginger presents a somewhat unique threat in its ability to thrive at higher elevation than most other invasive plants in Hawai`i. Invasive Himalayan ginger population shown here in Koukouai drainage, ca. 3,500 feet (1,065 m) elevation, Kīpahulu Valley.

8.1.3 The melastomes: Miconia calvescens and Clidemia hirta,

The family Melastomataceae is one of the largest, most important plant groups of tropical forests, especially in Central and South America. Since some of the species are relatively easy to grow and have showy leaves and flowers, a number of species in the melastome family have been introduced to Hawai‘i into botanical gardens and horticultural practices as ornamentals. Over the past few decades, many species of this family have left their initial planting within gardens and become naturalized. With time, these escaped ornamentals become nuisance species, invading and harming native biodiversity and forest functioning. As such, the Melastomataceae family has developed a reputation as problematic to import and is widely identified as a quarantine target worldwide.

In their native ranges, many melastomes ecologically are considered pioneers, colonizing landslides, pastures, forest edges, and gaps created by treefall within forests. Melastomes have evolved life-history traits associated with being pioneer species, which have proven to be key elements in their ability to rapidly spread and cause perturbations in their invaded range. Specifically, melastomes often include adaptations such as rapid growth, very high levels of production of tiny seeds, short-time to first fruiting, fleshy and often bird-dispersed fruits, efficient seed dispersal, and high germination rates.

Though several melastomes have the potential to become invasive, and several additional taxa occur in the Hawaiian Islands, Clidemia hirta (hereafter referred to as clidemia) and Miconia calvescens (hereafter referred to as miconia) have become case examples of the potential for tropical weeds to invade and degrade natural ecosystems.

Both species are capable of invading intact forests and forming dense monotypic stands of trees of miconia, and shrubby thickets of clidemia, progressively suppressing and replacing native biota. Once established, they have the ability to spread rapidly with rank growth, smothering native understory species and tree seedlings, eventually completely dominating these areas. Thickets formed by either species increase soil erosion and can cause mass-transfer landslides, ultimately severely damaging watershed function. As such, these two species are the most notorious habitat-modifying invasive plant species of Hawaiian rain forests.

Clidemia is a shrub usually 6-12 feet (2-4 m) in height, native to Mexico, West Indies, Central America, and northern South America to Bolivia and southern Brazil (Smith 1992). It is a serious forest pest that has become widely naturalized around the world from approximately 20 degrees south longitude to 22 degrees north latitude on Pacific and Indian Ocean islands, Indonesia, Malaysia, Southeast Asia, and Africa (Medeiros 2004).

Miconia is a relatively small tree characterized by large leaves (up to 36 inches (90 cm) long, 18 inches (45 cm) wide) with purple undersides. It can grow up to 60 feet (18 m) tall in its native range of South and Central America but usually is between 20-40 feet (6-12 m) tall in the introduced range. Miconia thrives in light gaps and can also tolerate deep shade and moist conditions. Though only introduced to Maui in the early 1970s, by the late 1990s miconia had established populations in low elevation (sea level to 1,400 feet (430 m) elevation) wet forests of northeastern Haleakalā from Huelo through Hāna to Kaupō (Medeiros et al. 1997).

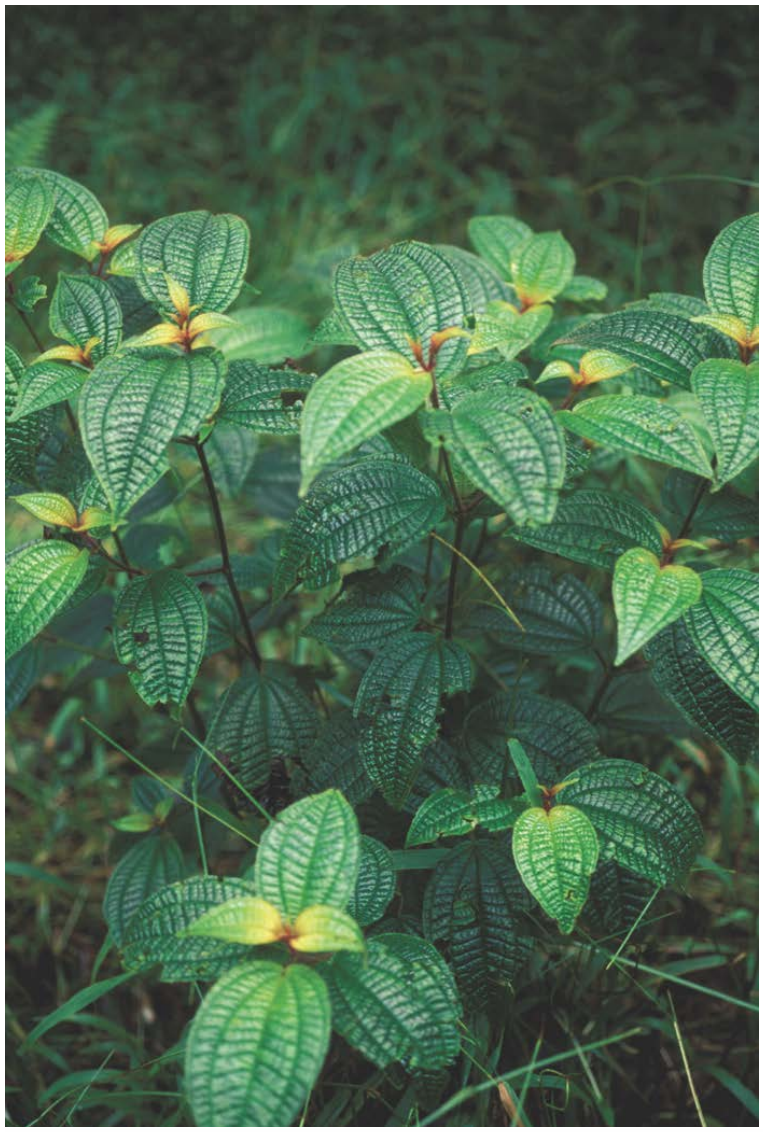

Figure 27. Clidemia, sometimes called Koster's curse (Clidemia hirta), along with miconia, are members of the important tropical plant family Melastomataceae (the melastomes), that have developed a notorious reputation as invaders of tropical forests worldwide.

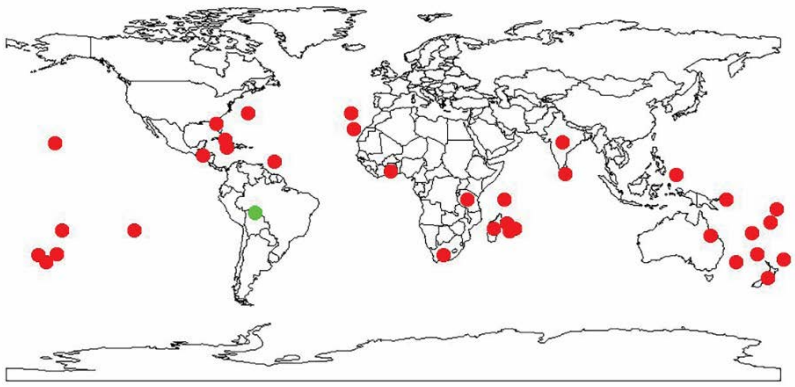

Figure 28. Distribution of invasive populations of clidemia (Clidemia hirta) in red, with the approximate center of its native distribution marked with green (Medeiros 2004).

These two highly invasive melastome species are characterized by their high rate of successful (greater than 90%) and rapid germination (15-20 days) in favorable conditions, fast growth (3.3 feet (1m)/year height increase for miconia), and early reproduction or sexual maturity (2-3 years for clidemia; 4-5 years for miconia; Medeiros 2004). Freedom from coevolved predators and pathogens in their native ranges has also heightened their fitness in invaded ranges.

The reproductive system of the most invasive melastomes, including clidemia and miconia, are self-compatible (not requiring cross-pollination with another individual, therefore able to self-fertilize). This is significant because it means that a single, isolated melastome plant can produce fruits and seeds abundantly after a handful of years. This trait allows a single individual plant to start new, fast-spreading populations that begin to colonize new forest areas rapidly.

Another key characteristic that contributes to clidemia and miconia as super-invaders is their capacity to produce incredibly large crops of seeds. For example, smaller individuals (1 ft^2) of clidemia in high-quality watershed forests on Haleakalā, Maui, were estimated to produce an average of 3.8 million seeds/year (Medeiros 2004). In similar habitat in Tahiti, large miconia individuals were estimated to produce 80 million seeds/year, with three fruiting seasons per year (Meyer and Fourdrigniez 2011).

The tiny melastome seeds (<1mm diameter) are easily spread in long-distance transport in infested soils carried by humans and associated with agriculture, vehicles, bulldozers, and hoofed animals such as feral pigs and goats. Melastome seeds, though small, have hard testa (seed coats) and are often long-lived, forming dense and persistent soil seed banks. Miconia has been observed to germinate for 16 years in the soil bank, while clidemia was observed germinating for up to 10 years in the soil bank (Brooks and Setter 2011). These seed banks can lie dormant under shaded conditions, and are stimulated to germinate by light from openings in the canopy.

Melastomes' self-compatible trait paired with high growth rates, high seed production, and extensive bird dispersal allows melastome populations to expand at an astonishing rate. They are notable among the most invasive of plants in Hawai‘i due to their rapid spread and ability to quickly become abundant at multiple locales throughout the Hawaiian Islands. For example, clidemia was first reported in Hawai‘i on O‘ahu (1941), then on Hawai‘i island (1972), Moloka‘i (1973), Maui (1976), Kaua‘i (1982), and Lāna‘i (1988) (Smith 1992).

In 1976, clidemia first became established on Maui in the Nāhiku district and spread rapidly from the lower disturbed wet forests into the native rain forests, apparently facilitated through copious seed dispersal by common non-native resident passerines (Medeiros 2004). By the early 1990s, clidemia had become widely established in watershed forests of Nāhiku and Hāna at 2,700-3,400 feet (820-1040 m) elevation, spreading much faster than either Himalayan ginger or strawberry guava (Medeiros et al. 1998). In 1988, the first discovery of a single clidemia plant was made in Kīpahulu Valley in Haleakalā National Park at 2,800 feet (850 m) elevation. By the early 1990s, clidemia had become widely established and, despite Haleakalā National Park control efforts, had begun to dominate areas in Kīpahulu rain forest from 2,700-3,400 feet (820-1040 m) elevation (Medeiros et al. 1998).

Figure 29. Quick growing and with high seed production, clidemia is a serious invader, in part due to its ability to efficiently disperse its seeds and establish multiple populations in nearly undisturbed native Hawaiian watershed forests. Within a surprisingly short time, scattered clidemia populations have the ability to coalesce and expand to the point where they form near-continuous cover, smothering native vegetation. Clidemia population shown here at Nāhiku, Maui.

The invasion of Maui's watershed forests by clidemia and miconia is being facilitated by abundant seed dispersal largely carried out by two common, small, non-native, frugivorous passerine birds, the Japanese white-eye (Zosterops japonicus) and Red-billed leiothrix (Leiothrix lutea). In Hawai'i, the Japanese white-eye is abundant from low elevations up to high elevation native rainforests and acts as a pervasive vector. In a study conducted in a high-quality watershed forest in Kīpahulu Valley, Haleakalā near fruiting clidemia patches, common forest birds were mist-netted, held in cloth bags for 20 minutes, released, and then the feces in the bags were examined for weed seeds. Japanese white-eye appeared to be the predominant seed disperser of clidemia, yielding an average of 314 clidemia seeds (ranging from 67 to 1,000) recovered per bird capture. Red-billed leiothrix yielded an average of 102 clidemia seeds (ranging from 3 to 289) recovered per bird capture (Medeiros 2004).

The ability to produce abundant quantities of viable seed by clidemia is unmatched by any other Hawaiian weed invader except miconia. A square meter (roughly 40 inches square) of clidemia has the potential to produce over 10 million (10,312,292) seeds annually compared to 2,024 seeds of Himalayan ginger or 568 seeds of strawberry guava produced in equal-sized areas (Medeiros 2004). Clidemia seeds are smaller than the period on a printed page, ca. 0.7 x 0.5mm. For context, if the clidemia seeds produced annually from an 8 feet square (0.75 m^2) area were laid end-to-end, they would form a line about 11 miles (17 km) long (Medeiros 2004).

Figure 30. Both of Hawai‘i’s highly invasive melastomes, Miconia calvescens and Clidemia hirta, are notable for their remarkably high levels of seed production, even moderate-sized individuals can produce millions of seeds annually. Embedded in small sweet fruits, seeds are quickly distributed by small non-native birds, an excellent example of mutualisms among invasive species. Shown here is a fallen *hapu‘u* log, nearly completely covered with hundreds of seedlings of dark green Miconia calvescens sprouts, photo taken in forest above Hāna.

The take-home message of this scale of seed production is that the only reasonable way to eradicate a clidemia population is before its first fruiting, which typically occurs within 2-3 years after establishment. Continued attempts at manual and chemical control of clidemia, especially in difficult-to-access areas, will likely have few if any long-term benefits.

In heavily invaded sites, miconia forms monotypic stands of dense thickets, so dense that there is no remaining vegetation in its dark understory, leaving the ground barren. The large leaves of miconia not only shade out understory species but also provide enough surface area to gather rain and accelerate it off the leaf's edge. This produces heavy droplets of water (7mm diameter) that fall through the canopy, picking up enough velocity to exceed that of typical raindrops (2mm diameter) and landing on the ground with greater force, causing erosion of the understory's barren soil (Giambelluca et al. 2009). Fine soil particles released during these events can block pores in the soil column, reducing infiltration and creating overland flow of water (Giambelluca et al. 2009). In some cases, in Tahiti, shallow-rooted miconia thickets have become saturated during heavy rain events and resulted in large landslides. Overall, the potential hydrological impacts of miconia are increased flooding, diminished groundwater supply, loss of topsoil, and siltation of coral reefs.

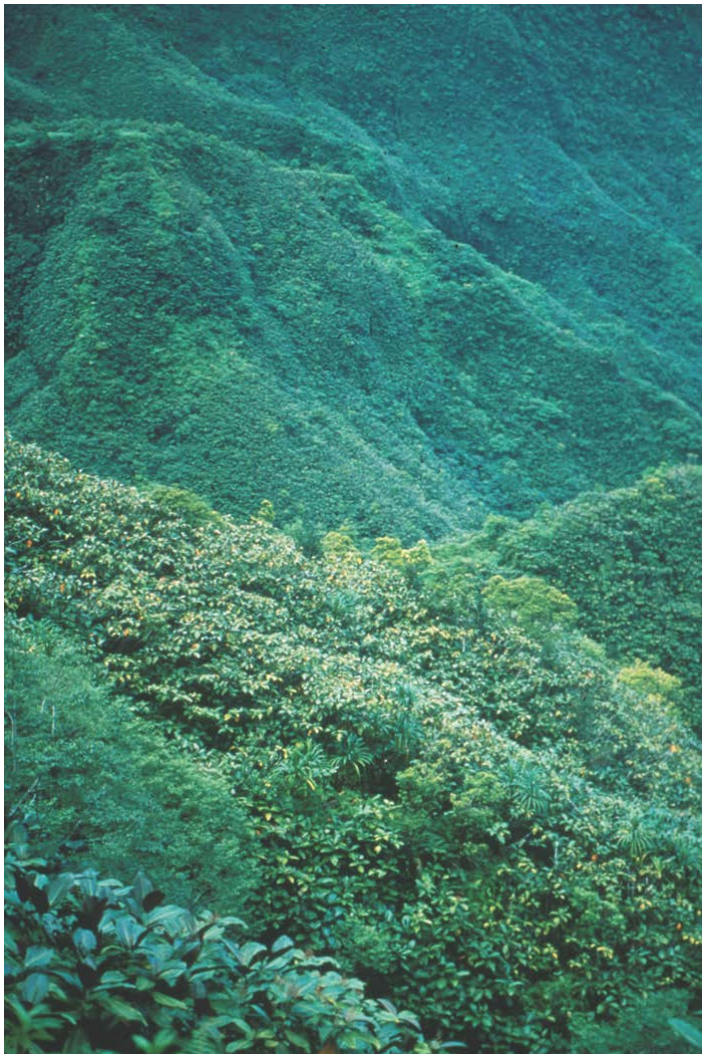

Figure 31. Miconia invasion shown here near Vaihiria, rough geographical center of watersheds of Tahiti Island, ca, 2,500-3,000 feet (760-910 m) elevation. The loss and conversion of the native watershed forests of Tahiti by the Central and South American tree, miconia, beginning around 1940, is among the cases of most forest-damaging species invasion known.

Figure 32. Landslide within central watershed, Lac Vaihiria region, central Tahiti. Landslides such as this occur frequently in wet regions on steep slopes heavily invaded by high biomass, shallow-rooted, dense stands of invasive plant species, in this case, Miconia calvescens, the same species invading Maui.

For miconia and clidemia, once they are established, controlling their spread is extremely challenging, borderline impossible, given current management tools. As such, the development of safe, i.e., host-specific, biological control from their native ranges appears to be the best option for suppressing established populations and reducing their impacts on regional native biota and ecosystem functioning.

The first biological control agent for clidemia was a thrip (Liothrips urichi), released in 1952 in Hawai‘i after successful suppression of C. hirta in Fiji. Since then, five insect species (including the thrip) and one pathogen have been released in Hawai‘i specifically as natural enemies of clidemia (Conant et al. 2002).

To date, however, there has been only minimum success, as no biocontrol agent or combination of agents have suppressed clidemia to the point that it has stopped or even slowed range expansion. Populations of clidemia in Hawai‘i remain vigorous, with highly reproductive individuals establishing new populations and developing denser thickets where already established. Research suggests that theoretically, it should be possible to suppress clidemia populations in Hawai‘i. However, unfortunately, so many parasitoids have been introduced to Hawai‘i to benefit agricultural crops over the decades that a number of species introduced as biocontrol, including the Liothrips thrip, have been parasitized to the point that they disappear entirely or have little to no impact on intended target organisms.

Figure 33. Biological control is complicated, expensive, controversial, sometimes ineffective, but often the last viable tool in the somewhat limited tool-box of options available for managers of Hawaiian watershed forests. Here, the buprestid beetle, Lius poseidon, introduced as biological control in Hawai‘i, perches on Clidemia hirta leaf, its intended target species.

Figure 34. A host-specific form (f. sp. Clidemiae) of the fungus Colletotrichum gloeosporioides has been introduced to help control clidemia in Hawai‘i’s watershed forests. In the image above, the characteristic darkening and circular splotching on this clidemia leaf are typical impacts of the biological control C. gloeosporioides f. sp. clidemiae.

Classic biological control for miconia has been explored for over three decades. The first species tested and approved for release was fungus, Colletotrichum gloeosporioides, f. sp. miconiae. In 1997, after required testing, this fungus was approved as a biocontrol agent for release in Hawai‘i (Killgore et al. 1999). Colletotrichum primarily affects leaves, splotching them, and causing a reduction of photosynthetic area and vigor. Unfortunately, Colletotrichum in Hawai‘i has had only a modest effect, with the best results of controlling miconia in drier sites, in both shaded and open habitats, but much less impact in wetter areas.

In contrast, Colletotrichum has performed much better in Tahiti, where five years of monitoring demonstrated that Colletotrichum-induced defoliation of miconia canopy trees ranged from 6% to 36%. This led to the significant recruitment of light-demanding pioneer species and the appearance of some semi-shade and shade-tolerant rare endemic species, with the total native and endemic species richness and plant cover increased in all sites and plots (Meyer et al. 2012).

Many additional biocontrol agents have been and are currently being studied and tested for miconia. One which has been approved for release is a small butterfly, Euselasia chrysippe, whose caterpillars feed on the tough leaves of several species of miconia. This butterfly, native to southeastern Mexico to northern Columbia, has a high degree of host specificity for miconia species, showing no capacity to impact native or economic plants in Hawai‘i (Allen 2012). The eggs are laid in masses on the underside of the leaves, and groups of up to 100 caterpillars feed, rest, molt, and pupate in unison (Nishida 2010, Allen 2010). Euselasia chrysippe is successful at

suppressing miconia largely due to its gregarious habits, which help defend the butterflies from predators such as parasitoids that often suppress other lepidopteran biocontrol agents in Hawai‘i (Allen 2010).

As with strawberry guava biocontrol, the damage to miconia in Hawai‘i is expected to cause partial defoliations, decreasing plant growth and reproduction, and increasing light in the understory for other plants to establish. Establishing self-sustaining populations of the butterfly likely would happen within a year after release. As of 2023, the release of this butterfly is waiting for final environmental assessment and permits for entry into the state.

Additionally, there are two candidate biocontrol gall wasps, specific to clidemia (Allorhogas clidemiae) and miconia (Allorhogas granivorus), which could significantly decrease seed production and associated dispersal. In both cases, the gall wasps lay eggs in the flower buds, altering fruit development and displacing seeds with wasp larvae. Trials are currently underway to measure host specificity of each of these gall wasps.

As of 2020, miconia can be found across 45,000 acres (182 km^2) of East Maui Watershed, from Kīpahulu to Huelo, and continues to invade native forests that receive more than 70-80 inches (1,800-2,000 mm) annual precipitation. After 27 years of mechanical and chemical control, currently, the infestation of miconia is not continuous, but a patchwork of scattered populations, some densely infested. As a result of this level of infestation, although O‘ahu and Kaua‘i are attempting eradication, on Maui, the goal for miconia is, through continued maintenance, to help assure that these populations do not spread into more pristine *‘ōhi‘a lehua*forests upslope.

Since miconia has already caused the destruction of one watershed system on a large high island in the Pacific, a critical question is, now that miconia appears beyond control at this point on Maui, how much of Maui’s watersheds will be displaced in the future in a similar fashion to Tahiti?

A recent modeling report suggests that over half (56.9%, >148,260 acres (600 km^2)) of East Maui watersheds appears to have the ecological and meteorological conditions suitable for invasion and displacement by miconia (Jorgensen et al. 2021).

In conclusion, both miconia and clidemia pose severe threats of further displacement of Maui’s watershed forests. The critical components of the relative invasive potential of these melastomes and the difficulty in controlling and managing them compared to other invasive plants of Hawaiian watersheds are: 1) rapid growth rates, 2) short time to first seed set, 3) the high levels of seed production, 4) the efficient seed dispersal, generally with non-native bird species, and 5) the longevity of seed survival in the seedbank. Despite control through traditional chemical and mechanical means, these melastomes continue to spread. The release of a few biocontrol agents (including the Euselasia chrysippe butterfly and potentially the Allorhogas clidemiae and Allorhogas granivorus gall wasps) could provide enough suppression for these two species to begin to limit their expansion in Maui’s watershed areas. With numerous other attractive melastomes growing in the tropics, quarantine efforts to limit their importation are critical to avoid another highly invasive, habitat-modifying plant from arriving in Hawai‘i.

8.2 Summary of efforts to control invasive plant species of Maui's watersheds

The cost-effective way to manage invasive species is to prevent indiscriminate species introductions. Once established, the cost of controlling or eradicating early introductions of highly invasive plant species can be surprisingly high. At the historical rate at which new invasive species are introduced, coupled with the cadre of highly invasive species already established on Maui, the available financial resources fall short of what is needed to protect our essential watershed forests and assure their natural capital benefits into the future.

Before the 1980s, there had been no scalable attempts to protect Hawaiian rainforests, and management was perceived to be too expensive to attempt with only a tenuous chance of success. In the 1980s, having achieved a positive environmental response after fencing out ungulates from dry shrublands, resource managers, first at Hawai‘i Volcanoes National Park, and then Haleakalā National Park, focused on developing new methods to protect Hawaiian rainforests through extensive research.

Though the standard toolbox of management techniques used by watershed managers today continues to evolve, the primary methodology fundamentally remains close to the original set of techniques developed in the 1980s. The series of techniques is as follows: enclose the area to be protected with ungulate-exclusion fencing, eliminate and/or drive feral animals out of the newly fenced area, and control the most invasive plant species.

In addition, in most cases, some form of vegetation or biological monitoring is implemented and periodically reassessed to help determine the degree of which recovery goals are being achieved through management actions. In concept, the technique is simple, but in practice, quantification of vegetation values in complex, multi-layered forest systems are difficult to repeatedly sample, either with direct or estimation-based assessment. In addition, the remote, hostile field locations accessible primarily by helicopter, often in cold, rainy weather, and steep, muddy, thickly vegetated terrain, are physically demanding and costly. As a result, ironically, despite often complex monitoring schemes, post-data collection analysis is often complicated by sampling and statistical challenges to the point that data is left without analysis, or at best, citing results with only coarse information about changes in major vegetation categories.

Given the scale of the threats, the diversity of landowners, and minimal funding levels, even priority watershed areas protected for decades, such as those within National Parks, are now becoming degraded by ungulate incursions and landscape-level invasive plant proliferation.

Though there are no inexpensive solutions or magic silver bullets to the challenge of invasive species, the most cost-effective strategy for change comes in educating the public about the status of our watershed forests, their threats, what is currently being done, and developing strategies and support for change. Secondly, encourage State, Federal, and private groups to assist, partner, and raise awareness of the importance of watershed integrity and support for implementing more effective management.

Four priority topics to increase options for future generations that will live on Maui are to: 1) investigate biological control options for the most damaging habitat-modifying invasive plants of Maui's watersheds, 2) implement effective quarantine and inspection for incoming commerce and transportation, 3) raise awareness among the general public and commercial partners through education about the global issue of invasive species and collaborative solutions to prevent future invaders from arriving, and 4) conduct applied research and management of Maui's most watershed-damaging invasive plant species.

9. Threats posed by invasive pathogens

Since the European discovery of Hawai‘i and the consistent levels of trade from global destinations, Hawaiian forests and native plant species have been plagued by near-continuous arrivals of pathogens and invasive insect species capable of producing ecosystem level impacts. With the advent of modern travel and commerce, animals, plants, and even forest pathogens began to be transported around the globe with shipments by boat and eventually more rapidly by airplanes. Over the last few decades, Hawai‘i’s increasing dependence on externally sourced food, equipment, and supplies, combined with the lack of sufficient quarantine, has resulted in continual arrivals of non-native pathogens and insects into Hawai‘i. Within the last 50 years, many non-native forest pathogens have arrived with the continual importation of goods, especially plant material, with devastating impacts on native forest ecosystems (Liebhold et al. 2012). As an example, the native dominant of our watershed forests, Metrosideros polymorpha, is a member of the Myrtaceae, a plant family which is also an important component of the global cut flower industry. Importations of plant material from species of the Myrtaceae family have been the source of pathogens which have established in Hawai‘i that seriously threaten our native watershed forests (Loope and La Rosa 2008). As of 2020, the state of Hawai‘i enacted a rule prohibiting the import of new Myrtaceae plant materials commonly used in the floral, nursery, landscaping, and food industry.

Disruption of canopy cover in Hawaiian forests has historically been associated with the highly accelerated spread of invasive understory trees and shrubs, triggered by sudden increases in light availability. The culmination of non-native pathogen impacts on forest trees paired with incipient invasive tree species could cause an ecological cascade, leading to a rapid shift from native to non-native forest. Transforming vast tracts of windward forests would have unprecedented and potentially dramatic adverse impacts on future water resources.

Several times in modern history, two of the most dominant Hawaiian watershed forest tree species, *‘ōhi‘a lehua*and *koa* have been impacted catastrophically across landscapes, resulting in widespread defoliation and/or mortality (Lyon, 1909, Perkins, 1913, Swezey, 1926, Gardner 1980, Mueller-Dombois 1985, Haines et al. 2009).

The greatest invasive pathogen that threatens *koa*, is *koa* wilt, first recorded in 1980 as a newly arrived lethal vascular wilt resulting from fungal infections by Fusarium oxysporum (Gardner 1980). Fusarium oxysporum is found in soils worldwide and can form pathogenic or non-pathogenic relationships with a broad range of plant hosts, including important agricultural crops and ecologically important tree species (Gordon and Martyn 1997). In fact, F. oxysporum represents some of the most abundant and widespread microbes of the global soil microflora (O’Donnell and Cigelnik 1997). The pathogen reproduces asexually with spore types that can survive in dead plant tissues, roots, and soils, with the longest survival in soils (Gordon and Martyn 1997). Fusarium oxysporum is known to display high levels of host-specificity, such as that formed with *koa* called F. oxysporum f. sp. koae. Though its origin is unknown, F. oxysporum f. sp. koae is believed to have been brought to Hawai‘i on an ornamental acacia plant (Friday and Dudley et al. 2015).

Fusarium oxysporum f. sp. koae causes failure of the vascular system and wilting of entire *koa* tree crowns, usually resulting in tree mortality. *Koa* wilt can cause mortality in all developmental stages of *koa*, in both managed and natural forest ecosystems (Gardner 1980). The pathogen's virulence is influenced by temperature, water availability, soil type, and interactions with other soil organisms (Anderson et al. 2002). As the second most abundant native tree in Hawai‘i, *koa* is an important component of native watershed forests. Currently, F. oxysporum f. sp. koae is the most serious threat to surviving *koa* across its native range, especially at mid to low elevations (below 2,000 feet (600 m), Gardner 1980, Dudley et al. 2017).

In regards to *ōhi‘a lehua*, the two primary invasive pathogen threats are Rapid *‘Ōhi‘a* Death or ROD (discussed in depth in the following sections), and the plant pathogen called *‘Ōhi‘a* rust, caused by Austropuccinia (formerly Puccinia) psidii.

First observed in Hawai‘i in 2005, a single genotype of *‘Ōhi‘a* rust (Austropuccinia psidii) spread throughout all main Hawaiian Islands within six months, causing declining health and extent of *‘ōhi‘a lehua*stands (Loope and La Rosa 2008). The rust is native to South America and has an unusually large host infection range (445 species within 73 genera) within the family Myrtaceae, including *ōhi‘a lehua*, guava, and eucalyptus (Carnegie and Giblin 2020). Austropuccinia psidii currently impacts commercially and ecologically important plant species globally with environmental and economic impacts. Rust-infected native trees develop lesions on new growth, including shoots, leaves, buds, and fruits, causing defoliation and destruction of buds, flowers and fruits (Glen et al. 2007).

The damage of Austropuccinia psidii to Hawaiian watershed forests, through the direct defoliation of *‘ōhi‘a lehua*stands and indirect impacts of accelerated invasion of non-native tree species, is of utmost concern for reasons previously discussed in this report. However, Austropuccinia psidii also poses a grave threat to the survival of fewer than 100 individual *nīoi* (Eugenia koolauensis) trees, a federally listed Hawaiian endemic, historically found on Moloka‘i and O‘ahu, but currently only persisting on O‘ahu (Keir 2018).

Prior to human arrival to Maui, without the presence of light-loving invasive plant species in the past, the regeneration of *‘ōhi‘a lehua*stands after high mortality events likely came naturally from resprouting and establishment of new seedlings from wind-dispersed ‘ōhi‘a lehuaseeds. Today, the primary threat of pathogens lies not in a single disease event, but rather the defoliation or loss of vigor in canopy tree species, which triggers a cascading series of invasions and transformation of the understory. This results in potentially a sudden shift from nearly entirely native to a nearly exclusively non-native forest.

9.1. Important forest pathogen (Ceratocystis spp.), Rapid *‘Ōhi‘a* Death

The most recent, and in all likelihood, most serious pathogens Hawaiian forests have ever been exposed to are the two fungal species, Ceratocystis lukuohia and Ceratocystis huliohia. While the pathogens cause different diseases, the collective pathogenic effect is referred to as Rapid *‘Ōhi‘a* Death, or ROD. Neither species has been recorded outside of the Hawaiian Islands, and both appear restricted to tree species in the Metrosideros genus in Hawai‘i, indicating an origin within

Hawai‘i. Rapid *‘Ōhi‘a* Death poses a severe threat to all 800,000 acres (3237 km^2) of Metrosideros forests occurring statewide.

Rapid *‘Ōhi‘a* Death potentially constitutes the worst invasive pathogen threat ever to occur in the Hawaiian Islands because of the degree (spread and mortality rates) of impact on the native Metrosideros genus. Especially concerning are the impacts to *‘ōhi‘a lehua*(Metrosideros polymorpha complex), as the primary and dominant component of 80% of the archipelago's remaining native watershed forests. The vulnerability of *ōhi‘a lehua*-dominated windward forests combined with the rapid spread of ROD and associated tree mortality is, in a way, the worst-case scenario for Hawaiian watersheds.

The scale of this threat has been recognized internationally in a global review of forest-damaging pathogens as the most recent addition to nine other highly significant invasive forest pathogens that have historically been recorded throughout the world (Poland et al. 2021). One reason for this international awareness is the recognition that Rapid *‘Ōhi‘a* Death threatens the well-being of Hawai‘i's critical water supplies since *‘ōhi‘a lehua*dominates forests where current potable water supplies are derived.

Ceratocystis (family Ceratocystidaceae), the group from which Rapid *‘Ōhi‘a* Death has originated, is a complex of fungi species, including serious pathogens which have proven to cause devastating diseases of trees. Globally, Ceratocystis species have been responsible for the severe loss of native forest trees as well as timber resources. Pertinent to biosecurity concerns about future tree pathogens, Ceratocystis fungi are easily moved in soil, on plant material, and with the insects with which they are associated. Because of this relative ease of transport, their often wide host range, and their ability to undergo host shifts, Ceratocystis fungi represent a very significant global quarantine threat (Roux et al. 2001, Wingfield et al. 2001, 2017).

In 2010, an alarming number of *‘ōhi‘a lehua*trees were dying rapidly in the Puna District of Hawai‘i Island. In 2014, diseased and dying *‘ōhi‘a lehua*trees from that area were identified as being infected with Ceratocystis, the first documented occurrence of what was to become known as Rapid *‘Ōhi‘a* Death (Keith et al. 2015). Continued studies concluded that two new-to-science species of Ceratocystis were the pathogens responsible for the Rapid *‘Ōhi‘a* Death phenomenon. These were given the names, Ceratocystis lukuohia and Ceratocystis huliohia (Barnes et al. 2018).

9.1.1 Origin of Rapid ‘Ōhi‘a Death

Ceratocystis is a complex of poorly delineated fungi species that includes serious plant pathogens, including those which cause damage to trees worldwide. During the past two decades, the number of reports of tree diseases caused by species in the Ceratocystis fimbriata complex, as defined by phylogenetic interference, has increased more than three-fold (Roux and Wingfield 2009). Despite the magnitude of the threat the Ceratocystis genus poses to forests worldwide, the study of this group of pathogens is limited because of difficulties in clearly defining and delineating between species (Barnes et al. 2001). The genetic boundaries of the group remain under review.

Globally, Ceratocystis species that have proven to cause devastating diseases of trees include: C. acaciivora in Asia; C. albifundus in Africa; C. fimbriata *sensu lato* (in the broad sense) and C. cacaofunesta in the Caribbean, Central, and South America; C. manginecans in the Middle East; and C. platani in Europe (Wingfield et al. 2001).

Dutch Elm Disease (C. ulmi) killed an estimated 10% of European elms and a greater portion of the more vulnerable American elms (CABI 2022). Ceratocystis ulmi has also been included among the world's most invasive plants and animals, categorizing them as 'ecosystem engineers', or species having strategic ecological roles with significant impacts and the potential to trigger cascading effects for native biota (Crooks 2002).

Ceratocystis fungi are generally pests of native tree species worldwide but have recently been implicated as pathogens of agroforests of Acacia and Eucalyptus from Africa, South America, and Brazil (Roux and Wingfield 2009). Emergent strains of Ceratocystis fimbriata *sensu lato* and other Ceratocystis species have been reported as serious pathogens of plantation forests with modus operandi and impacts strikingly similar to ROD, spreading with beetle frass (insect excrement including wood debris) into the plant through fresh wounding and resulting in significant mortality (Roux and Wingfield 2009). Based on this global trend, imported or locally derived strains of Ceratocystis could emerge as significant pests on other Hawaiian species. Of particular concern is the potential for an emergent Ceratocystis species which could infect *koa* (Acacia koa).

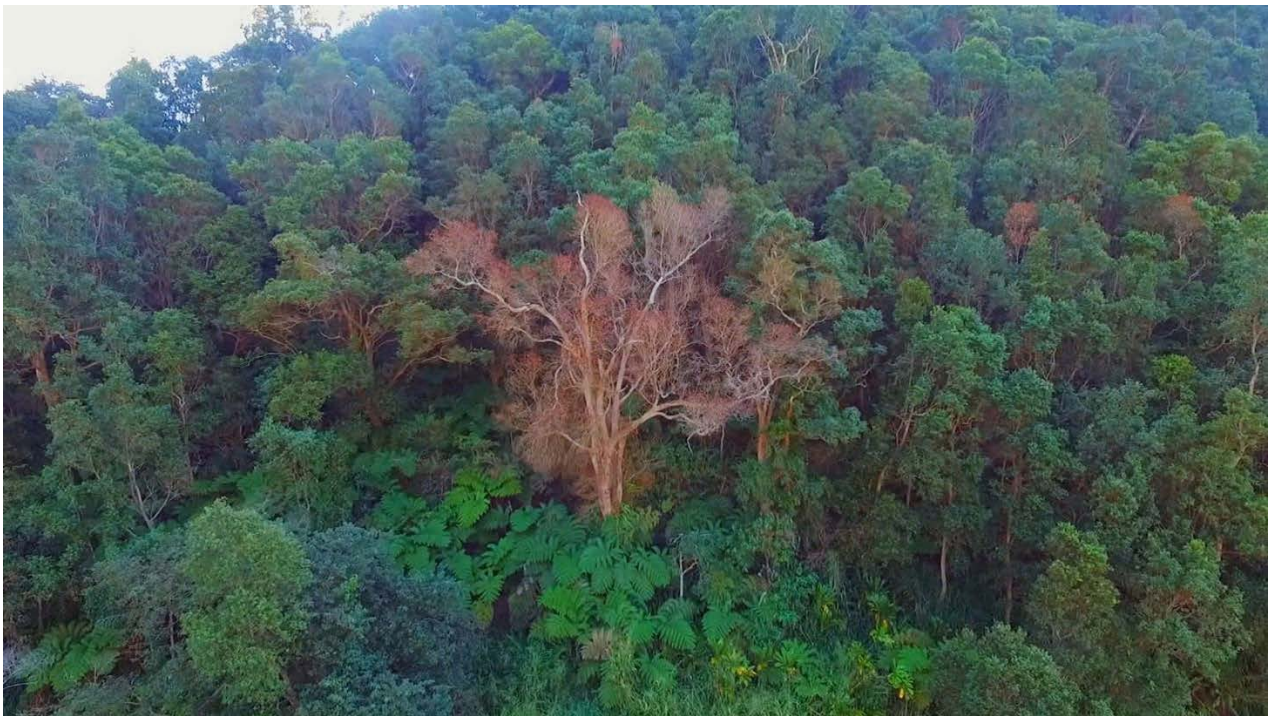

Figure 35. *ʻōhiʻa lehua*tree killed by ROD in watershed forest of Kaʻu, Big Island (photo from the Nature Conservancy).

After high numbers of rapidly dying trees were reported in Puna, the first diseased ʻōhiʻa lehuawere sampled and tested for Ceratocystis DNA. Initially, the fungi causing this rapid tree death was identified as C. fimbriata (Keith et al. 2015). Ceratocystis fimbriata was already known to occur in Hawaiʻi as a pathogen impacting sweet potato, taro, and Syngonium (Luiz 2017). Further analysis revealed two pathogens were causing Rapid *ʻŌhiʻa* Death, C. lukuohia and C. huliohia, each causing distinctive symptoms (Barnes et al. 2018).

Based on morphology and genetic sequencing, the two causative pathogenic species, C. lukuohia and C. huliohia, belong to discrete lineages with differing sites of origin. Ceratocystis lukuohia is speculated to be part of the so-called Latin American clade (LAC) with origins in the Caribbean, while C. huliohia is thought part of the Asian-Australian clade (AAC), native to Asia (Barnes et al. 2018). Interestingly, the two ROD-associated Ceratocystis species appear unique to Hawaiʻi, yet genetic sequencing suggests origins from two widely separated parts of the planet. This suggests the possibility that each species arrived independently and evolved locally, possibly through hybridization. If so, this likely occurred on the windward side of Hawaiʻi island and perhaps involved a greenhouse or similar facility and imported plant and/or organic materials.

Genetic analysis of C. lukuohia from multiple sites on Hawaiʻi and Kauaʻi islands revealed little genetic variation, indicating a more recent and likely, single introduction. In comparison, C. huliohia, detected on all of the main Hawaiian Islands, has more diversity between and among populations, suggesting an earlier introduction (Perroy et al. 2021).

Ceratocystis expert Thomas Harrington commented in a personal conversation to the senior author that the odds of a complicated hybrid Ceratocystis forming to attack a native species was ‘one in a million’ and that the odds against developing two from the same area during the same rough time period were ‘incalculable’. At this point, it is improbable to be able to determine the true origin of the two *ōhiʻa lehua*-damaging Ceratocystis species that make up Rapid *ʻŌhiʻa* Death. However, the importation of organic material from far-flung tropical locations could have been an important primary factor fundamental to the development of Rapid *ʻŌhiʻa* Death. With better biosecurity measures, it is possible, ROD may not have developed, and this entire event would not be taking place.

9.1.2 Impact of Rapid ʻŌhiʻa Death in native Hawaiian watershed forests

In just four years, 2017- 2021, it is estimated that ROD has infected and killed more than a million mature *ʻōhiʻa lehua*trees in native Hawaiian watershed forest, the majority on Hawaiʻi Island (ROD working group, written communication). Based on 2019 survey data, more than 180,000 acres ((728 km^2) approximately one-fifth of the total of Hawaiʻi’s remaining watershed forests) of *ʻōhiʻa lehua*forest were infected with Rapid *ʻŌhiʻa* Death disease on Hawaiʻi island.

As the first place ROD was documented, Hawaiʻi Island has suffered by far the greatest losses of any of the islands, with an average of four out of every ten trees dead in impacted stands, ranging from 24-47% (Mortenson et al. 2016). Certain areas of the Puna district on Hawaiʻi Island have had mortality as high as 90% within 2-3 years (Friday et al. 2015). Trees of all ages, across all environmental conditions, in native forests and residential areas, are currently affected, with

mortality ranging from 10–90 % in certain areas (Barnes et al. 2018). ROD has killed trees in all districts of Hawai‘i Island and has the potential to kill *‘ōhi‘a lehua*trees statewide. Of the sampled trees impacted by ROD, 82% were infected with C. lukuohia, the more virulent species.

Because of the broadly distributed and well-established status of the ROD infestation on Hawai‘i Island, lead government agencies (State of Hawai‘i Department of Land and Natural Resources, the US Forest Service, and US Department of Agriculture) have made the realistic, but unfortunate, decision to move from a policy of eradication and control to monitoring. There is special emphasis placed on preventing additional long-distance transport of the disease within Hawai‘i Island and from Hawai‘i Island to other islands in the archipelago.

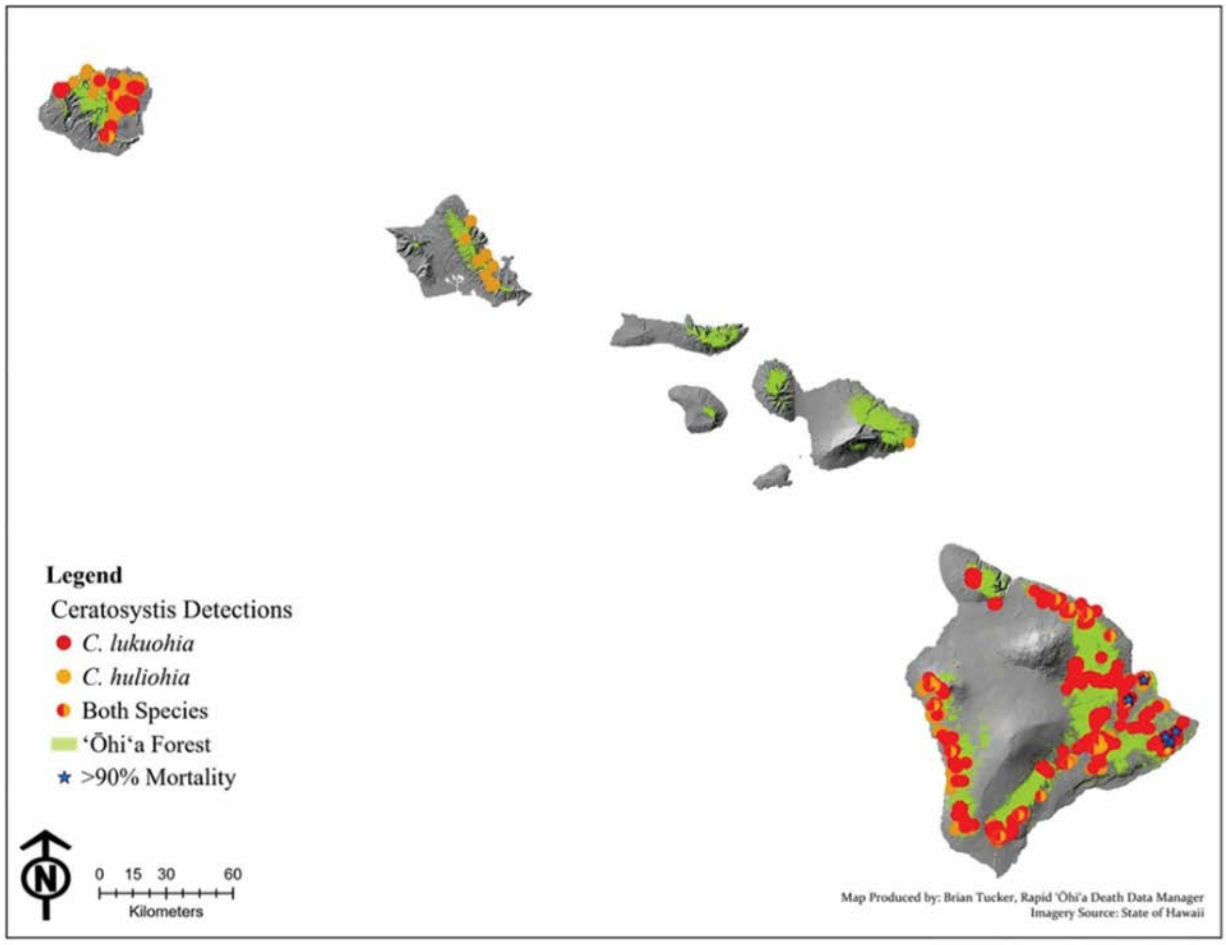

Figure 36. Statewide distribution of windward ‘ōhi‘a lehuaforests marked in green overlaid with verified ROD detections, Ceratocystis lukuohia with red dots and C. huliohia with orange dots. Six blue stars in eastern Hawai‘i Island mark areas where mortality of *‘ōhi‘a lehua*exceeds 90% (from Luiz et al. 2022).

The first record of Rapid *‘Ōhi‘a* Death on Maui occurred in July 2019 at the Koali area of Hāna, on Haleakalā. A private landowner identified the tree as showing rapidly browning and dying canopy and was identified as infected with C. huliohia. After confirmation of infection, the tree was cut to the ground, and all parts of the tree were destroyed by burning. Since 2019, though more than 75 suspect trees have been sampled, no other infections of Rapid ‘Ōhi‘a Death have

been confirmed on Maui (ROD SRP 2020). Though some trees on Molokaʻi or Lānaʻi have shown apparent symptoms and, as a result, been sampled for lab analysis, as of the writing of this report, Rapid *ʻŌhiʻa* Death has yet to be confirmed on those islands.

On Kauai, ROD was initially detected in a few trees in 2018 at Moloaʻa State Forest Reserve. Since then, hundreds more trees infected with C. lukuohia and C. huliohia have been detected in each sector of the island on the north, east, and south sides of the island, with elevations from 550 to 1,600 feet (170-490 m, www.kauaiisc.org/rod/). In 2021, ROD was confirmed in the leeward Kōkeʻe region, as well as one infected individual on the Alakaʻi plateau. On Oʻahu, the first record of a ROD-infected tree was in July 2019. Since then, over 365 trees have been sampled for the presence of ROD; only twelve individual trees were confirmed to be infected with C. huliohia. In rapid response, all of the infected trees were cut down and covered with tarps. There have been no positive detections of C. lukuohia infected trees on Oʻahu.

9.1.3 Biology of Rapid ʻŌhiʻa Death in native Hawaiian watershed forests

Most vascular wilt diseases in woody species require a wound site on the host tree for fungi spores to inoculate a tree and gain access to the tree's vascular system (Green 1981, Gibbs 2001). In Hawaiʻi, for an ʻōhiʻa lehuatree to become inoculated with either Ceratocystis species associated with ROD, there must be some wound allowing access to the tree's vascular system.

Wounding to ʻōhiʻa lehuatrees in Hawaiian forests most often occurs from high-intensity wind events and damage to trees inflicted by non-native ungulates. A primary source of tree wounding in Hawaiian forests likely to increase ROD impacts is the widespread presence of feral pigs, notorious for root-damaging rooting and plowing (Campbell and Long 2009, Murphy et al. 2014). Fortini et al. (2019) found the presence of feral ungulates was correlated with frequency of C. lukuohia infections and resultant tree mortality. In ROD infested areas, both fenced and unfenced, soil samples contain some Ceratocystis inoculum. However, unfenced forest areas with high levels of ungulate activity have higher densities of ROD infected trees and a greater proportion of soil samples containing Ceratocystis inoculum (Perroy et al. 2021). As such, when an ungulate incursion happens in the protected forest area due to a break in the fence, wounding and Ceratocystis infection increase. Confirming this, Perroy et al. (2021) found ʻōhiʻa lehuamortality was up to 69 times greater in the presence of ungulates.

In addition to wounding of trees by non-native ungulates, the structure of ʻōhiʻa lehuatrees may make them exceptionally vulnerable to wounding and infection. The characteristic growth forms of ʻōhiʻa lehuatrees which make them susceptible to damage are 1) their upper parts protrude above the forest canopy and are therefore exposed to the full force of wind gusts; 2) upper branches tend to fork at acute (narrow) angles to the main trunk(s); and 3) they commonly have split (codominant) main trunks with "included bark" (Loope et al. 2016, Lonsdale 2000).

Once the Ceratocystis fungi is inside the tree, it colonizes living ray parenchyma and moves outward into the inner phloem of inoculated trees long before the host becomes moribund (Hughes et al. 2020). Inoculations of M. polymorpha with isolates of C. lukuohia and C. huliohia resulted in visible wilt symptoms in 2–4 weeks in inoculated seedlings (Barnes et al.

2018). Wilt symptoms associated with Ceratocystis fungi include rapid death of the entire canopy or partial crown death. It has been reported that there is a strong banana-like odor associated with infected M. polymorpha trees. This characteristic could be used by scent dogs to detect early-phase infection.

Ceratocystis lukuohia, by far the more virulent and lethal of the two novel species, responsible for 80-90% of ROD mortality, spreads throughout the entire tree, colonizing the sapwood with visible brown and black stains. This vascular attack eventually leads to rapid wilt of the crown and kills the tree within two months (Hughes et al. 2020, Fortini et al. 2019, Barnes et al. 2018). Canker-forming C. huliohia locally colonizes phloem, cambium and outer xylem, resulting in much slower mortality only when multiple cankers form and girdle the tree (Barnes et al. 2018, Heller et al. 2019). In reference to the distinctive symptoms, the disease caused by C. lukuohia and C. huliohia are now more specifically referred to as 'Ceratocystis wilt of *'Ōhi'a*' and 'Ceratocystis canker of *'Ōhi'a'* respectively (Hughes et al. 2020).

Regarding the influence of temperature and moisture, ROD is most prevalent at warmer, wetter sites, with less tree mortality in high elevation cooler and dryer forests. The windward sides of the main Hawaiian Islands offer areas of high suitability for C. lukuohia. As the dispersal of the pathogen continues and has not yet reached its full potential, the actual range of this pathogen has yet to be fully realized (Fortini et al. 2019). Though C. lukuohia occupies nearly the driest and wettest parts of the known *'ōhi'a lehua*distribution, it generally is more prevalent in the hotter and wetter portions of *'ōhi'a lehua*distribution. Fortini et al. (2019) showed increase pathogen prevalence with increased mean annual rainfall.

In terms of elevation, ROD is most prevalent at lower elevations. Early in its spread, C. lukuohia reached the higher limits of the mean temperatures of *'ōhi'a lehua*distribution on Hawai'i Island. In the last few years, C. lukuohia has not changed its lower mean annual temperature limit of 56.5 °F (13.6 °C, with few detections below 59°F (15 °C)) and remains well above the 46.4 °F (8 °C) *'ōhi'a lehua*minimum mean annual temperature limit (Fortini et al. 2019).

9.1.4 Dispersal of Rapid 'Ōhi'a Death

Understanding the Ceratocystis pathological system, especially dispersal mechanisms, is key to effective, pro-active management and predictive modeling. The scientific community continues to research and better understand the complex mechanisms that drive the spread and influence the environmental limits of ROD. Transmission of ROD appears to involve complex interactions between Ceratocystis spore viability and the abundance and strength of multiple possible vectors such as insects, ungulates, humans, and wind (Fortini et al. 2019).

In its role as a serious forest pathogen, worldwide, the fungus Ceratocystis has repeatedly developed effective spore dispersal methods through mutualistic relationships with various subfamilies of weevils (Coleoptera: Curculionidae), especially ambrosia beetles (subfamilies Scolytinae and Platypodinae). Ambrosia beetles farm specialized fungi in sapwood tunnels and use pocket-like organs called mycangia to carry propagules of the fungal cultivars (Mayers et al. 2020). Ambrosia fungi selectively grow in mycangia, which is central to the symbiosis, avoiding

competition from phloem-feeding bark beetles and other insects in the nutritious inner bark by using fungal agriculture to exploit the nutrient-poor sapwood (Harrington 2010). Harrington (2013) documented that inoculum from Ceratocystis species may be carried directly by ambrosia beetles, but also on tools and equipment, in frass of ambrosia beetles or other wood-boring insects, and in sawdust. Also relevant to their significant role in the ROD pathological pathway, wood-boring beetles, like ambrosia, are direct pathogen vectors, creating entry wounds as sites for sporulation and emitting pheromones that attract conspecific individuals leading to heavy infestations of beetles.

In recent years, it has become understood that in Hawai‘i, Ceratocystis is spreading with the frass of ambrosia beetles. These beetles bore into infected Metrosideros wood during and after infection and expel frass harboring viable spores of Ceratocystis from gallery entrances (Roy et al. 2019, 2020). The frass is light and buoyant enough to drift in the wind and potentially infect other trees. This dispersal mechanism has been recorded primarily in the cluster of Latin American species of the C. fimbriata clade, including serious pest species C. cacaofunesta and C. plantani (Harrington 2009). Harrington (2009) notes that “The sawdust and fungal propagules expelled by the trees…may be dispersed by wind or rain splash for relatively short distances.”

Ceratocystis lukuohia and C. huliohia utilize at least five species of ambrosia beetles, Xyleborus (Curculionidae; Xyloborini). Of these, four are introduced and invasive species (X. ferrugineus, X. ferrugineus, X. saxesenii, and X. affinis) and one is a native species (X. simillimus). The introduced beetle X. saxesenii is the most common of these species and is recorded to emerge and spread frass from the greatest tree heights, and thus may likely spread frass great distances. The native ambrosia, X. simillimus, is less common; however, it has a higher elevation range and may facilitate the spread of ROD to higher elevations. The invasive X. ferrugineus is of particular concern, as it is prevalent across a broad range, including high elevations, and produces abundant frass (4 times more than X. simillimus, Roy et al. 2020).

In addition to transmitting fungi in their frass, beetles also directly vector viable Ceratocystis propagules from tree to tree, though the contribution of each of these modes in spreading these pathogenic fungi is not well understood (Roy et al. 2019, 2020). A large amount of frass also falls to the forest floor and can become attached to and dispersed by animals, shoes, gear, tools, and vehicles.

Beetles have been recorded to emit viable Ceratocystis propagules into the environment for at least 133 days (Roy et al. 2020). The viability of Ceratocystis propagules does not appear to be dependent on beetle species (Roy et al. 2020). Factors determining spore viability are not well known, however physical characteristics of the tree, such as time since infection, or abiotic factors such as temperature, humidity, and rainfall may all influence longevity. Due to the prevalence of certain ambrosia species at low heights on the tree, the frass of some species (X. ferrugineus and X. simillimus) are more likely to be transported via soil (Roy et al. 2020).

9.1.5 Detection and monitoring of Rapid ‘Ōhi‘a Death

Globally, methods for remote detection, mapping, and monitoring of forest fungal pathogens are poorly developed. In Hawai‘i, to understand the biology and spread of Rapid *‘Ōhi‘a* Death and assess the potential for management, containment, and reduced transmission, it is necessary to accurately detect, map, and monitor ROD (Ceratocystis fungi) presence across extensive populations of *ōhi‘a lehua*. Recent advances in detection and monitoring of ROD have been made, primarily on Hawai‘i Island, utilizing a combination of remote sensing and on-the-ground field work.

In Hawai‘i, a number of factors contribute to the ongoing formidable challenge of detecting and monitoring ROD: 1) microscopic Ceratocystis fungi spores are impossible to visually track, 2) *‘ōhi‘a lehua*trees may be infected without visible signs of damage for over a year, 3) aerial detection of ROD is complicated by other factors that can cause death of *‘ōhi‘a lehua*trees, 4) samples from symptomatic ‘ōhi‘a lehuatrees are required for confirmation of the presence of Ceratocystis DNA, and 5) populations of ‘ōhi‘a lehuaoccur across vast landscapes, many in remote areas, making sampling challenging, sometimes impossible.

Four types of surveillance of ‘ōhi‘a lehuaforests have been innovated and applied across the archipelago to detect and monitor ROD: 1) aerial surveillance by helicopter and small unmanned aircraft systems (sUAS) such as drones, 2) analysis of remote imagery (such as LiDAR, Pictometry and LandSat), 3) analysis of hyperspectral imagery (obtained by fixed-wing aircraft surveys) coupled with chemical composition data analysis, and 4) remote sampling to detect airborne spores from Ceratocystis. The goal with all these techniques is to facilitate the detection of Ceratocystis-infected populations, gather data, apply management, and then monitor response to management over time.

The most efficient and often used method of ROD detection and monitoring is aerial surveillance by helicopter. Helicopters facilitate close observation of *‘ōhi‘a lehua*tree canopies over large acreage in relatively short periods of time, providing auxiliary imagery and GPS location data. Drones supplement helicopter surveys with secondary surveys to determine the extent of infected individuals in surrounding areas after a primary contact (Loope et al. 2016). Despite the fact that monitoring for ROD by helicopter is expensive and imperfect, this technique has not yet been replaced by a better technique.

Once an *‘ōhi‘a lehua*population has been detected with ROD symptoms, field crews need to locate trees and obtain wood samples for Ceratocystis DNA testing. In 2017, a portable molecular quantitative polymerase chain reaction (qPCR) diagnostic test was designed, which cut the time required to determine the presence of Ceratocystis infection from weeks to hours (ROD SRP 2020).

When an *‘ōhi‘a lehua*population is confirmed as infected with either C. lukuohia or C. huliohia, a standardized decision-tree is used to assess the best management to minimize disease. In cases of single or few infected individuals, the infected tree(s) are cut down and either burned or contained with plastic covers or tarps to prevent further spread of Ceratocystis spores. If ROD is affecting a large stand of trees, the area is monitored, and specific decontamination protocols are recommended for people, equipment, and vehicles moving in and out of the area (ROD SRP 2020).

On Hawai‘i Island, the state Department of Land and Natural Resources (DLNR) conducts quarterly helicopter flights. Two of these flights survey the entire island, and two other flights are conducted in priority areas (North Kona, Hualalai, Kohala, and Hamakua). On Maui Island, DLNR conducts quarterly helicopter surveys of East Maui watershed areas and semi-annual surveys of West Maui, Lāna‘i, and Moloka‘i.

Hyperspectral imagery assessments have been used to detect forest pathogens elsewhere and, in some cases, have proved to be a powerful tool to survey large landscapes and detect early-stage infections prior to the onset of visible symptoms. Hyperspectral imagery has been used to successfully detect early-stage infections in global forest pathogens including oak wilt (Everitt et al. 1999, Fallon et al. 2020), laurel wilt (Hariharan et al. 2019, Abdulridha et al. 2016, 2018), and myrtle rust (Heim et al. 2019). Utilizing chemical and spectral differences defined in lab work, hyperspectral imagery has been analyzed for ROD infestations across large areas of *‘ōhi‘a lehua*forest (Asner et. al. 2018). By the end of the year 2017, fixed-wing aircraft had successfully obtained georeferenced, 3-D hyperspectral imagery for the entire range of *‘ōhi‘a lehua*forests (>500,000 acres (2,020 km^2) with data for all tree crowns over 5 feet (1.5 m) tall on Hawai‘i Island (Vaughn et al. 2018). This hyperspectral imagery was assessed for ROD infections across all of Hawai‘i Island. Unfortunately, however, due to *‘ōhi‘a lehua*leaf characteristics, it was determined that hyperspectral imaging did not allow early detection of ROD with enough lead time to prevent spread (Perroy et al. 2020).

Data from these large-scale mapping efforts have been valuable in determining the extent of *‘ōhi‘a lehua*mortality. However, identifying new outbreaks and proactively stopping the spread of ROD is limited by the frequency of obtaining and analyzing imagery data.

Air and waterborne spread of infectious spores may play an important role in the spread of ROD to new and distant locations. As previously mentioned, ambrosia frass contributes to the airborne dispersal of inoculated particles and is likely a significant vector in the spread of ROD. In efforts to understand the role of wind-dispersed frass, airborne samplers were innovated and placed in locations with high-density of ROD infected trees (Atkinson et al. 2019). This technique resulted in no significant detections of C. lukuohia and C. huliohia; adjustments to techniques are required to better understand this pathway.

The limited ability to detect Ceratocystis infections in real time across extensive *‘ōhi‘a lehua*forests, combined with the fact that ROD-diseased *‘ōhi‘a lehua*trees are now known to be infectious for up to a year before they display detectable ROD symptoms, has proved fundamentally problematic in preventing the continued spread of ROD on Hawai‘i island, as well as its movements within the Hawaiian Islands.

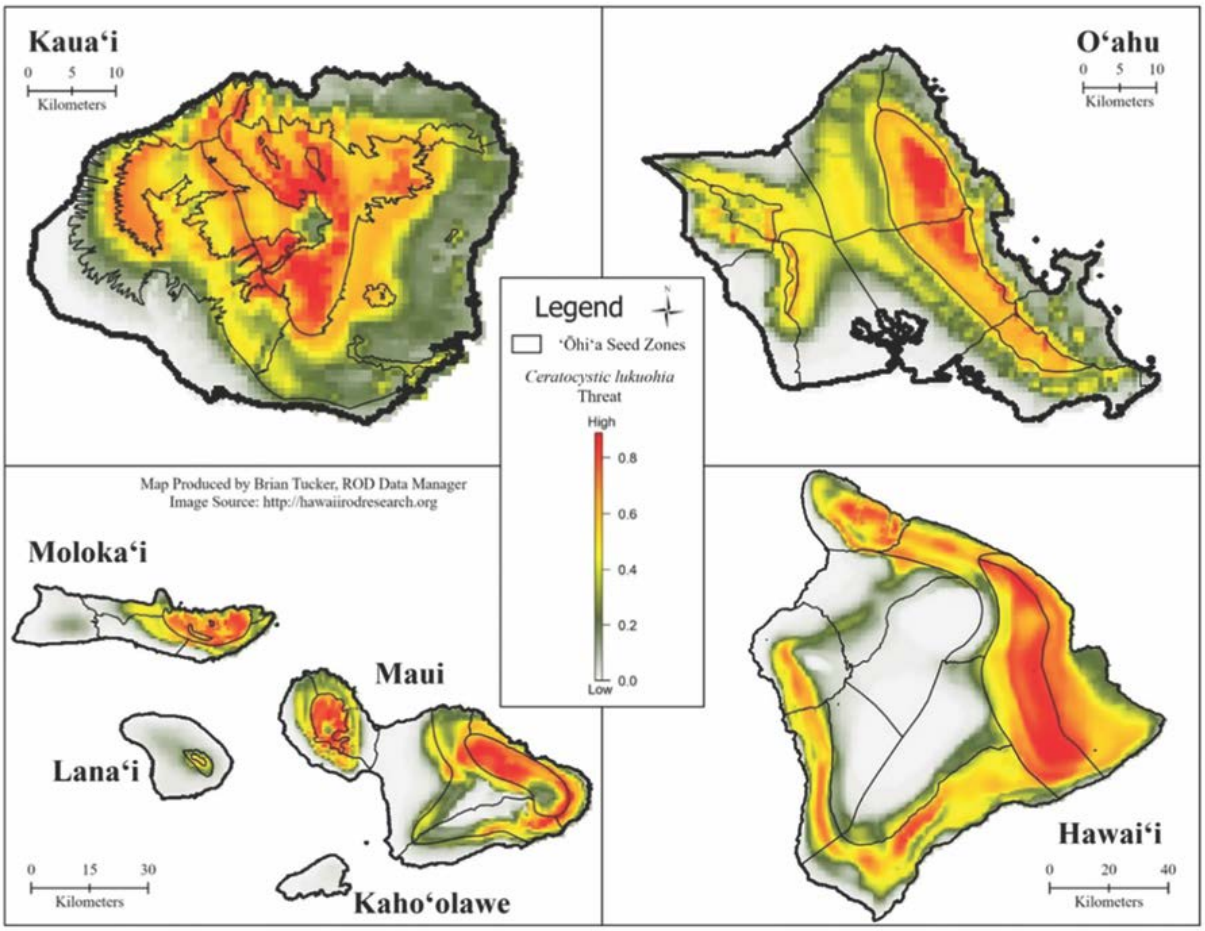

Figure 37. Map of main Hawaiian Islands predicting suitability and likely areas of future invasions of C. lukuohia, the more virulent and tree-killing of the two ROD fungi species. On this map, yellow indicates low, but existing potential for invasion, with red indicating the highest degree of site vulnerability (from Luiz et al. 2022).

9.1.6 Conclusions regarding Rapid ‘Ōhi‘a Death

There is still much unknown regarding the biology of Rapid *‘Ōhi‘a* Death caused by two Ceratocystis species. Hence, there is also considerable uncertainty regarding the potential scale of the ultimate impacts on ‘ōhi‘a lehuaforests and their ability to function as efficient watersheds. However, based on the Ceratocystis-induced death of over a million ‘ōhi‘a lehuatrees on Hawai‘i Island just in recent years, the threat to all ‘ōhi‘a lehuaforests on all Hawaiian Islands, the bulk of our watersheds, is grave.

Recognizing that ROD is difficult to manage, and even track, has shifted efforts to mitigate ROD impacts with large-scale, zone-by-zone collection and banking of ‘ōhi‘a lehuaseeds from across the Hawaiian Islands. There has also been an increased focus on the development of ROD-resistant ōhi‘a lehua. In addition, the emphasis statewide has shifted to focus on research intended to fill critical information gaps.

A core part of the current strategy articulated in the 2020 strategic plan (ROD SRP 2020) is the focus on developing disease screening and resistance breeding programs to attempt to evaluate lineages of ʻōhiʻa lehuathat express natural resistance to ROD and pass on this trait to their progeny. The planned approach is based on, and very similar to, disease screening and resistance breeding programs developed to address invasive blight impact on some important North American tree species (Sniezko 2006, Sniezko et al. 2012a, 2012b). Disease screening and resistance breeding programs are not quick or simple, nor do they produce guaranteed results.

Natural resistance to ROD has already been identified in some ʻōhiʻa lehuaindividuals in preliminary screening (Luiz et al. 2022). This experimental study supports field observations that it is rare for 100% of the ʻōhiʻa lehuatrees, even in heavily impacted areas, to be killed by ROD. In certain areas, even with high exposure to ROD, numerous ʻōhiʻa lehuatrees remain surprisingly healthy and appear resistant to ROD. The next stage will be to evaluate the degree of resistance, select resilient gene lineages, raise them to seed production stage (likely with cuttings to reduce time), and determine heritability of ROD resistance in their resultant offspring. If those efforts are successful, presumably in exposure to both ROD species, the operation will be scaled up to seed farms. When these ʻōhiʻa lehuatrees in seed farms reach reproduction, at least theoretically, they will produce increasingly prodigious amounts of seeds which will yield ROD-resistant ʻōhiʻa lehua(Luiz et al. 2022).

The development of ROD-resistant ʻōhiʻa lehuawould be a critical breakthrough, and one that would even potentially save resistant ʻōhiʻa lehuafrom extinction. However, given the scale, rate of movement, and damage from ROD in recent decades, it is the extant ʻōhiʻa lehuaforests, with trees of apparently great age, and all the other plant and animal species these forests support that may be in much greater peril.

In part, this is due to the role ROD has in defoliating ʻōhiʻa lehuaforests, becoming a classic ʻecosystem engineer' (Crooks 2002) as the driver in a cascading series of ecological events that defoliation triggers, usually ending in the loss of native species commensurate with the invasion and replacement by aggressive, light-loving non-native plant species.

Sudden and widespread defoliation of the rain forest canopy causes rapid increases in both light and temperature of formerly shaded understories, reducing the fitness of native shrub, fern, and herb species in that habitat. Invasive plant species, on the other hand, forged in intense competition regimes of continental tropical forests, are often superbly adapted for exploiting disturbances such as canopy loss. Under these circumstances, invasive plant species can displace native species relatively quickly across broad landscapes, leading to wholesale vegetation transformation, with related shifts in ability of the forest to absorb and retain moisture.

Defoliation and disturbance to the native forest canopy on the island of Tahiti by successive tropical typhoons in the 1980s appear to have been critical in the explosive spread of the invasive tree Miconia calvescens (Melastomataceae), resulting in the loss of two-thirds (over 160,620 acres 650 km^2) of that island's watershed forests in a few decades (Medeiros et al. 1997). Similarly, after Hurricane ʻIniki impacted Kauaʻi in 1992, the loss of forest canopy and suddenly increased light levels in Limahuli Valley triggered a rapid increase of the invasive weed

Clidemia hirta, resulting in a fifty-fold increase within just a few years (Steve Perlman, personal communication).

These examples of previous disturbance events leading to vegetation transformation of native forests to non-native dominated forests illustrate the potential for the impacts of ROD on Hawaiian watershed forests. The defoliation of extensive tracts of ʻōhiʻa lehuaforests may ultimately be the tipping point that leads to the transformation of Hawaiian watershed forests into non-native dominated vegetation, with associated changes in hydrologic function.

If ROD-resistant seed stocks of ʻōhiʻa lehuabecome available, scaled-up seed production would likely not become available for decades. As such, two questions will become critical. First, what will the ecological status of Hawaiian watershed forests be when ROD-resistant ʻōhiʻa lehuaseeds come on line? Related to that, what will the role of these seeds be, and how will they be applied to watershed forest situations in a manner which would allow ROD-killed trees to be replaced by ROD-resistant ʻōhiʻa lehuatrees?

In ethnobotanical and cultural terms, the loss of ʻōhiʻa lehuawould be a tragedy. Even today, common cultural practices by native Hawaiians involve the gathering and presentation of ʼōhiʻa lehua(a sacred *hula* plant) as a fundamental part of the *hula*. Recently, these practices have needed to be radically modified so as not to further disperse ROD. This loss would be compounded in that it is not just the potential loss of the species itself, but also a critically important keystone species that supports a whole community of associated plants and animals.

Also in jeopardy, no matter what course is taken, is the loss of the amazing genetic variation currently reflected in ʻōhiʻa lehuain Hawaiʻi. ōhiʻa lehua, Metrosideros polymorpha, is regarded globally as an amazing evolutionary story, as the species appears in the midst of rapid evolution into multiple species (Aradhya et al. 1991). As such, ʻōhiʻa lehuafar exceeds the usual bounds of appearance and specific habitat type for tree species by developing an extraordinary range of types of ōhiʻa lehua. Even though it is likely that much of this variation may be lost with ROD impacts, ironically, it is this very variation that is threatened that might be the natural source for developing future ROD-resistant strains of ōhiʻa lehua. Of course, there are four other less common species of native Metrosideros in Hawaiʻi also now at risk, as well as economically important species of Metrosideros outside of Hawaiʻi, especially in New Zealand, where it is also a crucial native forest component.

If, over the next decades, the ʻōhiʻa lehuaforests of Hawaiʻi decline precipitously and are replaced with simpler vegetation communities dominated by non-native species, this will have profound hydrologic, cultural, and biological consequences. On the other hand, it is also very possible that we have just entered into a long, complicated series of events that will be necessary to save both ʻōhiʻa lehuaas a species and ʻōhiʻa lehuaforests as self-sustaining natural forests supporting optimum watershed functioning.

Conclusion

Perhaps, the clearest overall conclusion that can be drawn from this type of examination is that while human populations are exponentially increasing, the original native highly efficient watershed forests that receive, process, and store precipitation have been greatly modified and reduced. Though deforestation is largely historic, with damage and displacement by feral animals and fire peaking in ca. 1820-1880, forest degradation continues to this day. In addition, climate change predictions for Hawai‘i forecast decreasing precipitation, increasing heat, and greater number and frequency of drought and storm events – additional factors that challenge the long-term stability of watershed forests and water extraction for human use.

An unusual characteristic of Hawai‘i’s windward forests is that the great majority of trees belong to a single species – *’ōhi‘a lehua*(Metrosideros polymorpha). This creates a vulnerability for their future efficacy as efficient watersheds. Deforestation, displacement by humans, occupation by invasive species, and climate change challenge intact *‘ōhi‘a lehua*forests, and compound as factors that will shift the system towards greater degradation if *‘ōhi‘a lehua*is compromised as a species.

Given the current circumstances of the status of Maui’s watersheds and their management, the best-case scenario for windward forests is to maintain a type of stability as time progresses, with only moderate displacement and alteration of function by invasive species. Perhaps, the more likely worst-case scenario would be the gradual or rapid loss of health for the dominant tree species, *ōhi‘a lehua*, with accompanying loss of forest canopy cover. Such an event, or series of events, would likely trigger successional changes involving the explosive spread of invasive plant species responding to an increase in light and resource availability. This change would likely initiate a cascade of ecological processes that could cause the irreversible loss of *‘ōhi‘a lehua*as a dominant canopy tree species for windward Hawaiian watersheds. A clear example of this type of tipping point threat became evident with the appearance of two Metrosideros-specific pathogenic fungi, collectively known as Rapid *‘Ōhi‘a* Death.

Considering these facts, some historic and some currently developing, an obvious question is, what can be done by decision makers and system managers now to maximize the chances of the best-case scenario occurring for as long as feasible? Barring future technological developments, one of the primary answers is as simple as it is difficult to maintain in a modern world – the development of a highly functional quarantine and postal regulation system that would protect Hawai’i from further damage by non-native invasive species. Invasive species imports pose novel mixes of species and even develop new strains, as has been seen globally on a continual basis. Even with good quarantine, the number of invasive plant, animal, and disease threats currently established in Hawai’i is formidable, with enough destructive agents currently here to provide daunting management challenges.

Maximizing the best-case scenario also includes the restoration of now deforested leeward watershed forest areas on Maui. One of the major, if not primary functions of these restored forests would be water capture, storage, and extraction for potable and agricultural purposes. Other natural capital benefits in the targeted restoration of watershed forest areas could include the creation of habitat for native species with cultural and biological value, as well as green

spaces, serving as outdoor places for human health and recreation activities. Ecological rehabilitation and forest restoration options for Maui will be explored in a future report, in process.

ACKNOWLEDGEMENTS

We thank Maui County and the Department of Water Supply (DWS) for their support and the early discussion of problems and possibilities of the future of Maui watersheds that led to this report. Besides being biologists, we are also taxpayers and residents of Maui. As such, we are deeply appreciative and proud of the forward-thinking awareness of the importance of watershed stewardship within Maui County DWS, as well as the many individuals within that group who take authentic responsibility for a critical natural resource that is requisite for our future well-being.

Prepared by the Auwahi Forest Restoration Project for County of Maui Department of Water, this report assesses the history, status, and characteristics of Maui‘s watersheds, as well as historic degradation and loss, current threats, and potential management responses to them. This report gives special attention to the newly arrived, forest-damaging invasive fungi known as Rapid *‘Ōhi‘a* Death, a pathogen of dominant watershed tree species *‘ōhi‘a lehua*(Metrosideros polymorpha).

This report was written by Arthur Medeiros, PhD and Erica von Allmen of the Auwahi Forest Restoration Project (hereafter synonymous with Auwahi project), based on over seven combined decades of experience in research, management, and ecological restoration in Maui watershed forests. In addition, Dr. Medeiros’ dissertation, Phenology, reproductive potential, seed dispersal and predation, and seedling establishment of three invasive plant species in a Hawaiian rain forest, is an important research effort documenting the spread and impact of the most invasive plant species degrading Maui’s watersheds. Erica von Allmen received her Master of Science in ecohydrology with focused research on water use by trees. Medeiros and von Allmen are amongst a limited number of professionals in Hawai‘i who have both undergone training and evaluations and are now certified as having achieved state of the science expertise in this field through the Certified Ecological Practitioner Program (CERP). This certification is offered by the Society for Ecological Restoration International in efforts to standardize practices, protocols, and definitions while training and accrediting restoration practitioners worldwide. Unless credited elsewhere, all photos were taken by the senior author. We thank reviewers Laura Arnold, Jennnifer Higashino, Hanna Lilley, and Amber Thompson.

LITERATURE CITED

2020–2024. https://gms.ctahr.hawaii.edu/gs/handler/getmedia.ashx?moid=66598&dt=3&g=12. Accessed 15 Sept 2020.

Abdulridha, J, Y. Ampatzidis, R. Ehsani, and A.I. De Castro. 2018. Evaluating the performance of spectral features and multivariate analysis tools to detect laurel wilt disease and nutritional deficiency in avocado. Comput. Electron. Agric. 155: 203–211.

Abdulridha, J., E. Ehsani, and A. De Castro. 2016. Detection and differentiation between Laurel Wilt Disease, Phytophthora Disease, and Salinity Damage using a hyperspectral sensing Technique. Agriculture. 6: 56.

Abrahamson, I. L. 2013. Fire regimes in Hawai'ian plant communities. In: Fire Effects Information System, www.fs.usda.gov/database/feis/fire_regimes/Hawaii/all.html. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Allen, P. E. 2012. Survival patterns under Costa Rican field conditions of the gregarious caterpillar Euselasia chrysippe (Lepidoptera: Riodinidae), a potential biological control agent of Miconia calvescens (Melastomataceae) in Hawai‘i. Journal of Research on the Lepidoptera, 45: 77-84.

Allen, P.E. 2010. Group size effects on survivorship and adult development in the gregarious larvae of Euselasia chrysippe (Lepidoptera, Riodinidae). Insect. Soc. 57: 199–204.

Anderson, R. C., D.E. Gardner, C.C. Daehler, and F.C. Meinzer. 2002. Dieback of Acacia koa in Hawai‘i: ecological and pathological characteristics of affected stands. Forest Ecology and Management, 162(2-3), 273-286.

Anderson, R.C, and D.E. Gardner. 1999. An Evaluation of the Wilt-Causing Bacterium Ralstonia solanacearum as a Potential Biological Control Agent for the Alien Kahili Ginger (Hedychium gardnerianum) in Hawaiian Forests. Biological Control 15(2): 89-96. https://doi.org/10.1006/bcon.1999.0705.

Aradhya, K. M., D. Mueller-Dombois, and T.A. Ranker. 1991. Genetic evidence for recent and incipient speciation in the evolution of Hawaiian Metrosideros (Myrtaceae). Heredity, *67*(2): 129-138.

Asner, G.P., R.E. Martin, L. Keith, W. Heller, M.A. Hughes, N. Vaughn, R.F. Hughes, and C. Balzotti. 2018. A Spectral Mapping Signature for the Rapid *‘Ōhi‘a* Death (ROD) Pathogen in Hawaiian Forests. Remote. Sens. 10: 404.

Athens, J.S. 2009. Rattus exulans and the catastrophic disappearance of Hawai‘i‘s native lowland forest. Biological Invasions 11: 1489-1501.

Athens, J.S., H.D. Tuggle, J.V. Ward, and D.J. Welch. 2002. Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai‘i. Archaeology in Oceania 37: 57-78.

Atkinson, C.T., K. Roy, and C. Granthon. 2019. Economical environmental sampler designs for detecting airborne spread of fungi responsible for Rapid *ʻŌhiʻa* Death. Hawaiʻi Cooperative Studies Unit Technical Report HCSU-TR087.

Atkinson, I.A.E. 1977. A reassessment of factors, particularly Rattus rattus L., that influenced the decline of endemic forest birds in Hawaiian Islands. Pacific Science 31: 109-133.

Atkinson, I.A.E. 1985. The spread of commensal species of Rattus to oceanic islands and their effect on island avifaunas. In 'Conservation of Island Birds'. (Ed. P.J. Moors). pp 35-81. ICBP Technical Publication No.3, Cambridge.

Baker, J.K. and D.W. Reeser. 1972. Goat management problems in Hawaiʻi Volcanoes National Park. US Nat Park Serv., Nat. Resour. Rep, (2), p. 62.

Barnes, I., A. Fourie, M.J. Wingfield, T.C. Harrington, D.L. McNew, L.S. Sugiyama, B.C. Luiz, W.P. Heller, and L.M. Keith. 2018. New Ceratocystis species associated with rapid death of Metrosideros polymorpha in Hawaiʻi. Persoonia 40: 154-181.

Barnes, I., A. Gaur, T. Burgess, J. Roux, D.B. Wingfield, and M.J. Wingfield. 2001. Microsatellite markers reflect intra-specific relationships between isolates of the vascular wilt pathogen Ceratocystis fimbriata. Molecular Plant Pathology, 2(6): 319-325.

Bremer, L.L., C.A Wada, S. Medoff, J. Page, K. Falinski, and K.M. Burnett, 2019. Contributions of native forest protection to local water supplies in East Maui. Sci. Total Environ. 688: 1422-1432.

Brooks, S.J. and S.D. Setter. 2011. Soil seed bank longevity information for weed eradication target species. Proceedings of the 23rd Asian-Pacific Weed Science Society Conference, Vol 1, pp. 69-77.

CABI. 2022. Centre for Agriculture and Bioscience International. https://www.cabi.org/isc/datasheet/12165

Campbell, T.A., and D.B. Long. 2009**.** Feral swine damage and damage management in forested ecosystems. For. Ecol. Manag., 257(12): 2319–2326.

Carnegie, A.J., and Giblin, F.R. 2020. Austropuccinia psidii (myrtle rust). Invasive species compendium. https://www.cabi.org/isc/datasheet/45846.

Cavaleri, M.A., R. Ostertag, S. Cordell, and L. Sack. 2014. Native trees show conservative water use relative to invasive trees: results from a removal experiment in a Hawaiian wet forest. Conserv Physiology, 2(1): cou016. https://doi.org/10.1093/conphys/cou016.

Cesar, H.S.J. and P.J.H. van Beukering. 2004. Economic valuation of the coral reefs of Hawaiʻi. Pacific Science 58: 231–242.

Coblentz, B.E. 1980. A unique ungulate breeding pattern. J. Wildl. Manage. 44: 929.

Conant, P., C.W. Smith, J.S. Denslow, and S. Hight. 2002. Classical biological control of Clidemia hirta (Melastomataceae) in Hawai‘i using multiple strategies. In Workshop on biological control of invasive plants in native Hawaiian ecosystems. Technical Report, Vol. 129, pp. 13-20.

Conti L, Block S, Parepa M, Münkemüller T, Thuiller W, Acosta ATR, van Kleunen M, Dullinger S, Essl F, Dullinger I, Moser D, Klonner G, Bossdorf O, Carboni M (2017) Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. J Ecol 12:3218–3221. https://doi. org/10.1111/1365-2745.12928

Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. – Oikos 97: 153–166.

D’Antonio C.M. and P.M. Vitousek. 1992. Biological Invasions by Exotic Grasses, the Grsss/Fire Cycle and Global Change. Annu. Rev. Ecol. Syst. 23: 63-87.

Dawson, J.W. and L. Stemmermann. 1990. Metrosideros Banks ex. Gaertn. In Manual of the flowering plants of Hawai‘i, Vol. 1 (eds W.L. Wagner, D.R. Herbst and S.H. Sohmer) pp. 964-970. Honolulu, HI: University of Hawai‘i Press.

DeMaagd, N. and M.J. Roberts. 2020. How Will Climate Change Affect Water Demand? Evidence from Hawai‘i Microclimates. University of Hawai‘i at Mānoa, Department of Economics.

Denslow, J.S. 2003. Weeds in Paradise: Thoughts on the invasibility of tropical islands. Annals of the Missouri Botanical Garden 90 (1): 119-127. https://doi.org/10.2307/3298531.

Diong, C.H. 1982. Population biology and management of the feral pig (Sus scrofa) in Kīpahulu Valley, Maui. PhD dissertation. University of Hawai‘i Mānoa, Hawai‘i.

Drought.gov. 2022. Drought Conditions for Maui County. https://www.drought.gov/states/hawaii/county/maui

Dudley, N., T. Jones, R. James, R. Sniezko, J. Wright, C. Liang, P.F. Gugger, and P. Cannon. 2017. Applied genetic conservation of Hawaiian Acacia koa: An eco-regional approach. In: Sniezko, Richard A.; Man, Gary; Hipkins, Valerie; Woeste, Keith; Gwaze, David; Kliejunas, John T.; McTeague, Brianna A., tech. cords. 2017. Gene conservation of tree species—banking on the future. Proceedings of a workshop. Gen. Tech. Rep. PNW-GTR-963. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 963, 78–91.

Everitt, J.H., D.E. Escobar, D.N. Appel, W.G. Riggs, and M.R. Davis. 1999. Using airborne digital imagery for detecting oak wilt disease. Plant Disease. 83: 502-505.

Fagerlund, G.0. 1945. An account of an inspection of Kīpahulu Valley. Typewritten report, Haleakalā National Park, Makawao, Hawai‘i. Pp. 8.

Fallon, B., A. Yang, A. Lapadat, C., I. Armour, J. Juzwik, R.A. Montgomery, J. Cavender-Bares. 2020. Spectral differentiation of oak wilt from foliar fungal disease and drought is correlated with physiological changes. Tree Physiol., 40: 377–390.

Farmer, C. 2020, November 11. Mosquito Birth Control and the fight to save Hawaiian honeycreepers. American Bird Conservancy. https://abcbirds.org/blog20/save-hawaiian-honeycreepers/#:~:text=Detecting%20avian%20fossils%20and%20pre,which%20only%2017%20survive%20today

Fish and Wildlife Service. 2016. Endangered and Threatened Wildlife and Plants; Designation and Nondesignation of Critical Habitat on Molokaʻi, Lānaʻi, Maui, and Kahoʻolawe for 135 Species. Available online: https://www.federalregister.gov/documents/2016/0 3/30/2016-06069/endangered-and-threatened-wildlife-and-plants-designation-and-nondesignation-of-critical-habitat-on. Accessed 5 February 2022.

Fortini, L., L. Christina, K. Perkins, O. Chadwick, S. Yelenik, J. Jacobi, K. Bishaw, and M. Gregg. 2021. Landscape level effects of invasive plants and animals on water infiltration through Hawaiian tropical forests. Biol. Invasions. 23: doi:101007/s10530-021-029494-8.

Fortini, L.B., A.E. Vorsino, F.A. Amidon, E.H. Paxton, and J.D. Jacobi. 2015. Large-Scale range collapse of Hawaiian forest birds under climate change and the need 21st Century Conservation Options. PLoS ONE 10(10): e0140389. doi:10.1371/journal.pone.0140389.

Fortini, L.B., L.R. Kaiser, L.M. Keith, J. Price, R.F. Hughes, J.D. Jacobi, and J.B. Friday. 2019. The evolving threat of Rapid ʻŌhiʻa Death (ROD) to Hawaiʻi's native ecosystems and rare plant species. For. Ecol. Manag. 448: 376–385.

Friday J.B., L.M. Keith, and F. Hughes. 2015. Rapid *ʻŌhiʻa* Death (Ceratocystis Wilt of *ʻŌhiʻa*). UH-CTAHR Research Extension Series PD-107.

Gagne, W.C. 1979. Canopy-associated arthropods in Acacia koa and Metrosideros tree communities along an altitudinal transect on Hawaiʻi Island. Pacific Insects, 21: 56–82.

Gardner, D.E. 1980. Acacia koa seedling wilt caused by Fusarium oxysporum f. sp. koae, f. sp. nov. Phytopathology 70: 594– 97.

Giambelluca, T.W., H.F. Diaz, and M.S.A. Luke. 2008. Secular temperature changes in Hawaiʻi. Geophys. Res. Lett. 35: L12702, doi:10.1029/2008GL034377.

Giambelluca, T.W., R.A. Sutherland, K. Nanko, R.G. Mudd, and A.D. Ziegler. 2009. Effects of Miconia on hydrology: a first approximation. In Proceedings of the International Miconia Conference, Keanae, Maui, Hawaiʻi, USA.

Gibbs, N.J. 2001. Vascular wilt diseases of trees – An Anglo-American perspective. In: Ash CL, ed. Shade Tree Wilt Diseases. St Paul, MN, USA: American Phytopathological Society Press, 15–28.

Gleick P.H. Ed. 1993. Water in Crisis: A guide to the Worldʻs Fresh Water Resources. New York: Oxford University Press.

Glen, M., A.C. Alfenas, E.A.V. Zauza, M.J. Wingfield, and C. Mohammed. 2007. Puccinia psidii: A threat to the Australian environment and economy—A review. Australas. Plant Pathol. 36: 1-16.

Gordon, T.R., and R.D. Martyn. 1997. The evolutionary biology of Fusarium oxysporum. Annual review of phytopathology, 35(1): 111-128.

Green, R.J. Jr. 1981. An overview. In Fungal Wilt Diseases of Plants (Eds M.E. Mace, A.A. Bell and C.H. Beckman). Pp. 1-24. Academic Press, New York.

Gruner, D.S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology, 85: 3010–3022.

Hadfield M.G. and J.E. Saufler. 2009. The demographics of destruction: isolated populations of arboreal snails and sustained predation by rats on the island of Moloka'i 1982-2006. Biol Invasions 11: 1595-1609.

Haines, W.P., M.L. Heddle, P. Welton, and D. Rubinoff. 2009. A recent outbreak of the Hawaiian *koa* moth, Scotorythra paludicola (Lepidoptera: Geometridae), and a review of outbreaks between 1892 and 2003. Pacific Science 63: 349–369.

Hariharan, J., J. Fuller, Y. Ampatzidis, J. Abdulridha, and A. Lerwill. 2019. Finite difference analysis and bivariate correlation of hyperspectral data for detecting laurel wilt disease and nutritional deficiency in avocado. Remote Sens., 11(15): 1748, doi:10.3390/rs11151748.

Harrington, T.C. 2009. The genus Ceratocystis. Where does the oak wilt fungus fit? In: Billings, R.F. and Appel, D.N. (eds) National Oak Wilt Symposium, June 4–7, 2007, Austin, Texas. The Proceedings of the Second National Oak Wilt Symposium. Texas Forest Service Publication 166, College Station, Texas, pp. 21–35.

Harrington, T.C. 2013. 11 Ceratocystis Diseases'. Infectious forest diseases, 230-255.

Harrington, T.C., D.N. Aghayeva, and S.W. Fraedrich. 2010. New combinations in Raffaelea, Ambrosiella, and Hyalorhinocladiella, and four new species from the redbay ambrosia beetle, Xyleborus glabratus. Mycotaxon 111: 337–361.

Hart, P.J. 2010. Tree growth and age in an ancient Hawaiian wet forest: vegetation dynamics at two spatial scales. Journal of Tropical Ecology 26: 1-11.

Heim, R., I.J. Wright, A. Allen, I. Geedicke, and J. Oldeland. 2019. Developing a spectral disease index for myrtle rust (Austropuccinia psidii). Plant Pathol. 68: 738–745.

Heller W.P. and L.M. Keith 2019. Real-Time PCR Assays to Detect and Distinguish the Rapid ʻŌhiʻa Death Pathogens *Ceratocystis lukuohia* and *C. huliohia.* Disease Control and Pest Management. Published Online:17 Oct 2018 https://doi.org/10.1094/PHYTO-09-17-0311-R

Hillebrand, W. 1888. Flora of the Hawaiian Islands. Williams and Norgate.

Hosmer, R.S. 1912. Creation of Kula Reserve: Report of the Superintendent of Forestry. In: Logan, Daniel, editor. The Hawaiian Forester and Agriculturalist Vol. IX, No. 9. Honolulu: Hawaiian Gazette Co., Ltd., Publishers, pp. 274-281.

Hua, F., L.A. Bruijnzeel, P. Meli, P.A. Martin, J. Zhang, S. Nakagawa, X. Miao, W. Want, C. McEvoy, J.L. Pena-Arancibia, P.H.S. Brancalion, P. Smith, D.P. Edwards, and A. Balmford. 2022. The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. *Science*, doi:10.1126/science.abl4649.

Hughes R.F. and J.S. Denslow. 2005. Invasion by a N2-fixing tree alters function and structure in wet lowland forests of Hawai‘i. Ecological Applications 15: 1615–1628.

Hughes, M. A., J. Juzwik, T. Harrington, and L. Keith. 2020. Pathogenicity, symptom development and colonization of Metrosideros polymorpha by Ceratocystis lukuohia. Plant Dis. doi:10.1094/PDIS-09-19-1905-RE.

Jacobi, J. D. 1981. Vegetation changes in a subalpine grassland in Hawaii following disturbance by feral pigs. Technical Report 41. Cooperative National Park Resources Studies Unit. University of Hawaii at Manoa, Honolulu, Hawaii.

Jacobi, J.D. 1981. Vegetation changes in a subalpine grassland in Hawai‘i following disturbance by feral pigs. Technical Report 41. Cooperative National Park Resources Studies Unit. University of Hawai‘i at Mānoa, Honolulu, Hawai‘i.

Jensen, T.S. 1985. Seed–seed predator interactions of European beech, Fagus silvatica and forest rodents, Clethrionomys glareolus and Apodemus flavicollis. Oikos, 149–156.

Jensen, T.S. and O.F. Nielsen. 1986. Rodents as seed dispersers in a heath–oak wood succession. Oecologia 70, 214–221.

Jorgensen, N., J. Leary, M. Renz, and B. Mahnken. 2021. Characterizing the suitable habitat of Miconia calvescens in the East Maui Watershed. Management of Biological Invasions, 12(2): 313-330. https://doi.org/10.3391/mbi.2021.12.2.07

Judd, C.S. 1918. Forestry as applied in Hawai‘i. The Hawai‘i Forester and Agr. 15(5): 117-133.

Kagawa A., L. Sack, K. Duarte, S.A. James. 2009. Hawaiian native forest conserves water relative to timber plantation: species and stand traits influence water use. Ecol. Appl. 19:1429-1443.

Kagawa-Viviani, A.K. 2020. Ecohydrology of Change: Dynamics of Climatological, Hydrological, and Ecological Change across Hawai‘i's Landscapes. Doctoral dissertation, University of Hawai‘i at Mānoa.

Kagawa-Viviani, A.K. and T.W. Giambelluca. 2020. Spatial patterns and trends in surface air temperatures and implied changes in atmospheric moisture across the Hawaiian Islands, 1905-

2017. Journal of Geophysical Research: Atmospheres 125(2) e2019JD031571. https://doi.org/10.1029/2019JD031571

Kaiser, B. and J. Roumasset. 2002. Valuing indirect ecosystem services: the case of tropical watersheds. Environ Dev Econ 7: 701–14.

Kaiser, B., B. Pitafi, J. Roumasset, and K. Burnett. 2008. The economic value of watershed conservation. Coastal watershed management; Fares. A., El-Kadi, Al, Eds, 299-329.

Kaiser, B., B. Pitafi, J. Roumasset, and K. Burnett. 2009. The Economic Value of Watershed Conservation. WIT Transactions on State of the Art in Science and Engineering. Vol 33, Ch. 11. WIT Press doi:10.2495/978-1-84564-091-0/11.

Kaiser, B., N. Krause, and J. Roumasset. 1999. Environmental Valuation and the Hawaiian Economy. University of Hawai‘i Economic Research Organization Working Paper.

Kamakau, S.M. 1976. The Works of the People of Old - *Na Hana a ka Po‘e Kahiko*. Bishop Museum Press, Honolulu, 170 pp.

Keane, R.M. and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17: 164–170.

Keir, M. 2018. Eugenia koolauensis. The IUCN Red List of Threatened Species 2018.

Keith, L.M., Hughes, F.R., Sugiyama, L.S., Heller, W.P., Bushe, B.C., Friday, J.B. 2015. First Report of Ceratocystis Wilt on Ohia (Metrosideros polymorpha). Plant Dis. 99, 1276. https://doi.org/10.1094/PDIS-12-14-1293-PDN.

Kennedy, T.A., S. Naeem, K.M. Howe, J.M. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature, 417(6889): 636-638.

Killgore, E.M., L.S. Sugiyama, R.W. Barreto, and D.E. Gardner. 1999. Evaluation of Colletotrichum gloeosporioides for biological control of Miconia calvescens in Hawai‘i. Plant Disease, 83(10): 964-964.

Kirch P.V., 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pacific Science 36:1-14.

Kramer, R. J. 1971. Hawaiian land mammals. Charles E. Tuttle, Rutland, VT.

Lamoureux, C.H .1968. The vascular plants of Kīpahulu valley, Maui. Scientific report of the Kīpahulu Valley expedition, 23-54.

Leong, J.A., J.J. Marra, M.L. Finuncane, T. Giambelluca, M. Merrifield, S.E. Miller, J. Polovina, E. Shea, M. Burkett, J. Campbell, P. Lefale, F. Lipschulz, L. Loope, D. Spooner, and B. Wang. 2014. Hawai‘i and U.S. Affiliated Pacific Islands. Climate Change Impacts in the United States:

The Third National Climate Assessment, J.M. Melillo, Terese (T.C.) Richmond, and G.W. Yohe, Eds. U.S. Global Change Research Program, 537-556. Doi:10.7930/JOW66HPM.

Lerner H.R.L., M. Meyer, H.F. James, H.F. Hofreiter, and R.C. Fleischer. 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. Curr. Biol. 21: 1838–1844. doi:10.1016/j.cub.2011.09.039.

Liebhold, A.M., E.G. Brockerhoff, L.J. Garrett, J.L. Parke, and K.O. Britton. 2012. Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Frontiers in Ecology and the Environment, 10(3): 135-143.

Lonsdale, D. 2000. Hazards from Trees: A General Guide. UK Forestry Commission. 28pp. http://www.forestry.gov.uk/pdf/fcpg13.pdf

Loope, L., F. Hughes, L. Keith, T. Harrington, R. Hauff, J.B. Friday, C. Ewing, and M. Melzer. 2016. Guidance document for Rapid *ʻŌhiʻa* Death: background for the 2017-2019 ROD Strategic Response Plan. University of Hawaiʻi: College of Tropical Agriculture and Human Resources.

Loope, L.L. 2011, September 11. Biocontrol precision is weapon against invaders. https://mauiinvasive.org/2011/09/06/biocontrol-precision-is-weapon-against-invaders/

Loope, L.L. and A.M. La Rosa. 2008. An Analysis of the Risk of Introduction of Additional Strains of the Rust Puccinia psidii Winter (*ʻŌhiʻa* Rust) to Hawaiʻi. US Geological Survey Open-File Report 2008: 1008.

Luiz, B. 2017. Understanding Ceratocystis species A: growth, morphology, and host resistance Doctoral dissertation, University of Hawaiʻi at Hilo.

Luiz, B.C., C.P. Giardina, L.M. Keith, D.F. Jacobs, R.A. Sniezko, M.A. Hughes, J.B. Friday, P. Cannon, R. Hauff, K. Francisco, M.M. Chau, N. Dudley, A. Yeh, G. Asner, R.E. Martin, R. Perroy, F.J. Tucker, A. Evangelista, V. Fernandez, C.M. Keliʻihoʻomalu, K. Santos and R. Ohara. 2022. A framework for establishing a Rapid *ʻŌhiʻa* Death resistance program. New Forests, 1-24.

Lydgate J.M. 1883. Hawaiian Woods and Trees, Hawaiian Almanac and Annual for 1883. Honolulu.

Lyon, H.L. Saddle Road. 1909. The forest disease on Maui. Hawaiian Planters' Record 1: 92-95; 15: 1-159.

MacCaughey, V. 1918. The Olona, Hawaii's Unexcelled Fiber-Plant. Science 48*:* 1236, 236–238. http://www.jstor.org/stable/1641963.

Marques, A. 1905. Goats in Hawaiʻi. In Thrums Hawaiian Almanac and Annual for 1906: 48-55. Honolulu.

Mayers, C.G, T.C. Harrington, H. Masuya, B.H. Jordal, D. McNew, H-H. Shih, F. Roets, and G.J. Kietzka. 2020. Patterns of coevolution between ambrosia beetle mycangia and the

Ceratocystidaceae, with five new fungal genera and seven new species. Persoonia 44: 41– 61. https://doi.org/10 .3767/persoonia.2020.44.02.

Medeiros, A.C. 2004. Phenology, reproductive potential, seed dispersal and predation, and seedling establishment of three invasive plant species in a Hawaiian rainforest. PhD dissertation, University of Hawai‘i at Mānoa, Honolulu.

Medeiros, A.C., E.I. von Allmen and C.G. Chimera. 2014. Dry forest restoration and unassisted native tree seedling recruitment at Auwahi, Maui. Pacific Science 68: 33-45.

Medeiros, A.C., L.L. Loope and C.G. Chimera. 1998. Flowering plants and gymnosperms of Haleakalā National Park. Cooperative National Park Resources Studies Unit, University of Hawai‘i, Department of Botany, Technical Report 120. 181 pp.

Medeiros, A.C., L.L. Loope, P. Conant, and S. McElvaney. 1997. Status, ecology and management of the invasive plant Miconia calvescens D.C. (Melastomataceae) in the Hawaiian Islands. Bernice P. Bishop Museum Occasional Papers, 48: 23–26.

Medeiros, A.C., Loope, L.L. and Hobdy, R., 1984. Vegetation and flora of a lowland leeward site near Kihei, Maui. In Proc. Fifth Conf. in Natural Sciences, Hawai’i Volcanoes National Park. Cooperative National Park Studies Unit, Department of Botany, University of Hawaii: pp. 78-82.

Meyer, J.Y. 1996. Status of Miconia calvescens (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pacific Science 50: 66-76.

Meyer, J.Y. and M. Fourdrigniez. 2011. Conservation benefits of biological control: the recovery of a threatened plant subsequent to the introduction of a pathogen to contain an invasive tree species. Biol. Conserv. 144: 106–113. http://dx.doi.org/10.1016/j.biocon.2010.08.004.

Meyer, J.Y., M. Fourdrigniez, and R. Taputuarai. 2012. Restoring habitat for native and endemic plants through the introduction of a fungal pathogen to control the alien invasive tree Miconia calvescens in the island of Tahiti. BioControl. 57(2): 191-198.

Mortenson, L.A., F. Hughes, J.B. Friday, J.B., L.M. Keith, J.M. Barbosa, N.J. Friday, Z. Liu, and T.G. Sowards. 2016. Assessing spatial distribution, stand impacts and rate of Ceratocystis fimbriata induced *‘Ōhi‘a* (Metrosideros polymorpha) mortality in a tropical wet forest, Hawaii Island, USA. For. Ecol. Manag. 377: 83–92.

Mueller-Dombois, D. 1985. *‘Ōhi‘a* dieback in Hawai‘i: 1984 synthesis and evaluation. Pacific Science 39(2): 150-170.

Mueller-Dombois, D. and G. Spatz. 1975. Application of the relevé method to insular tropical vegetation for an environmental impact study. Phytocoenologia 2: 417- 429.

Murphy, M.J., F. Inman-Narahari, R. Ostertag. and C.M. Litton. 2014**.** Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian Forest. Biol. Invasions, 16: 63–71.

Nagata, K. M. 1985. Early Plant Introductions in Hawai'i. The Hawaiian Journal of History, vol. 19: 35-61.

Nishida, K. 2010. Description of the immature stages and life history of Euselasia (Lepidoptera: Riodinidae) on Miconia (Melastomataceae) in Costa Rica. Zootaxa, 2466(1): 1-74.

O'Donnell K. and E. Cigelnik. 1997. "Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus Fusarium are nonorthologous". Molecular Phylogenetics and Evolution. 7 (1): 103–16. doi:10.1006/mpev.1996.0376.PMID9007025.

Papa ʻĪʻī, J. 1958. Fragments of Hawaiian History. Bernice P. Bishop Museum Spec. Publ. 70. Bishop Museum Press, Honolulu, Hawaiʻi, 202 pp.

Paret, M. L., A.S. De Silva, and A.M. Alvarez. 2006. Ornamental plants in the Zingiberaceae and Costaceae families susceptible to Ralstonia solanacearum, race 4 biovar 4. Phytopathology, 96 (6).

Paxton, E.H., M. Laut, J.P. Vetter, and S.J. Kendall. 2018. Research and management priorities for Hawaiian forest birds. Condor 120: 557–565.

Percy, D.M., A.M. Garver, W.L. Wagner, H.F. James, C.W. Cunningham, S.E. Miller and R.C. Fleischer. 2008. Progressive island colonization and ancient origins of Hawaiian Metrosideros (Myrtaceae). Proceedings of the Royal Society 275: 1479-1490.

Perkins, K. S., J. R. Nimmo, A. C. Medeiros, D.J. Szutu, and E.I. von Allmen. 2014. Assessing effects of native forest restoration on soil moisture dynamics and potential aquifer recharge, Auwahi, Maui. Ecohydrology. doi: 10.1002/eco.1469.

Perkins, K. S., J.R. Nimmo, and A.C Medeiros. 2012. Effects of native forest restoration on soil hydraulic properties, Auwahi, Maui, Hawaiian Islands. Geophysical Research Letters, 39(5).

Perkins, K.S., J.D. Stock and J.R. Nimmo. 2018. Vegetation influences on infiltration in Hawaiian soils. Ecohydrology, 11(5): e1973.

Perkins, R.C.L. 1913. Introduction to Fauna Hawaiiensis. Vol. 1. D. Sharp (editor), Cambridge University Press, Cambridge.

Perroy, R.L., M. Hughes, L.M. Keith, E. Collier, T. Sullivan and G. Low. 2020. Examining the utility of visible near-infrared and optical remote sensing for the early detection of Rapid *ʻŌhiʻa* Death. Remote Sens. 11: 1846.

Perroy, R.L., T. Sullivan, D. Benitez, R.F. Hughes, L.M. Keith, E. Brill, K. Kissinger, and D. Duda. 2021. Spatial patterns of *ʻŌhiʻa* mortality associated with Rapid *ʻŌhiʻa* Death and ungulate presence. Forests 12: 1035. https://doi.org/10.3390/f12081035.

Poland, T.M., T. Patel-Weynand, D. Finch, C.F. Miniat, D.C. Hayes, and V.M. Lopez. 2021. Invasive species in forests and rangelands of the United States: A comprehensive science synthesis for the United States forest sector. pp. 455. Springer Nature.

Ridley, H.N. 1930. The Dispersal of Plants Throughout the World. Reeve, Ashford.

ROD Strategic Response Plan. 2020. Rapid ʻŌhiʻa Death strategic response plan. https://www.cgaps.org/wp-content/uploads/2020-ROD-Strategic-Response-Plan-final-compressed.pdf

Rojas-Sandoval, J. 2023. CABI Compendium. Hedychium gardnerianum online datasheet. https://www.cabidigitallibrary.org/doi/pdf/10.1079/cabicompendium.26679

Roux, J. and M.J. Wingfield. 2009. Ceratocystis species: Emerging pathogens of non-native plantation Eucalyptus and Acacia species. Southern For. 71: 115-120.

Roux, J., B.D. Wingfield, and M.J. Wingfield. 2001. Ceratocystis species: Taxonomic challenges in a group of pathogens of increasing global importance.

Roy, K., C.P. Ewing, M.A. Hughes, L. Keith, and G.M. Bennett. 2019. Presence and viability of Ceratocystis lukuohia in ambrosia beetle frass from rapid *ʻŌhiʻa* death-affected Metrosideros polymorpha trees on Hawaiʻi Island. Forest Pathology, 49(1): e12476.

Roy, K., K.A. Jaenecke, and R.W. Peck. 2020. Ambrosia beetle (Coleoptera: Curculionidae) communities and frass production in *ʻŌhiʻa* (Myrtales: Myrtaceae) infected with Ceratocystis (Microascales: Ceratocystidaceae) fungi responsible for Rapid *ʻŌhiʻa* Death. Environmental Entomology, 49(6): 1345-1354.

Safeeq, M. and A. Fares. 2014. Interception losses in three non-native Hawaiian forest stands. Hydrol. Process. 28: 237–254.

Shiels, A.B. 2010. Ecology and impacts of introduced rodents (Rattus spp. and Mus musculus) in the Hawaiian Islands. PhD dissertation, University of Hawaii at Mānoa, Honolulu, Hawaiʻi.

Shiels, A.B., A.C. Medeiros, and E.I. von Allmen. 2017. Shifts in an invasive rodent community favoring black rats (Rattus rattus) following restoration of native forest. Restoration Ecology 25: 759–767.

Shiels, A.B., C.A. Flores, A. Khamsing, P.D. Krushelnycky, S.M. Mosher, and D.R. Drake. 2013. Dietary niche differentiation among three species of invasive rodents (Rattus rattus, R. exulans, Mus musculus). Biol. Invasions 15: 1037–1048.

Smith, C.W. 1985. Impact of alien plants on Hawaiʻi's native biota. In: C.P. Stone and J.M. Scott (eds) Hawaiʻi's terrestrial ecosystems: preservation and management. University of Hawaiʻi Press, Honolulu, pp. 180-250.

Smith, C.W. 1992. Distribution, status, phenology, rate of spread, and management of Clidemia in Hawai‘i. Pages 241–253 in C. P. Stone, C.W. Smith, and J.T. Tunison, editors. Alien plant invasions in native ecosystems of Hawai‘i. University of Hawai‘i Cooperative National Park Resources Studies Unit, Honolulu.

Sniezko, R.A. 2006. Resistance breeding against nonnative pathogens in forest trees—current successes in North America. Can J Plant Pathol 28: S270–S279.

Sniezko, R.A., J. Hamlin, and E.M. Hansen. 2012a. Operational program to develop Phytophthora lateralis resistant populations of Port-Orford-cedar (Chamaecyparis lawsoniana). In: R. A. Sniezko, R.A., A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel. 2012b. Proceedings of the 4th international workshop on genetics of host-parasite interactions in forestry: Disease and insect resistance in forest trees. Gen Tech Rep. PSW-GTR-240. Albandy, CA: Pacific Research Station, Forest Service, US Department of Agriculture. 372 p. 240.

St. John, H. 1978. The first collection of Hawaiian plants by David Nelson in 1779. Pac. Sci. 32 (3): 315-324.

Stainton, A. 1997. Flowers of the Himalayas: A Supplement. Oxford University Press, Delhi.

State of Hawai‘i. June 2010. Draft Environmental Assessment: Biocontrol of Strawberry Guava by its Natural Control Agent for Preservation of Native Forests in Hawaiian Islands. 131 pp. Available from: http://oeqc.doh.hawaii.gov/ Shared% 2 ODocuments /EA_and_EIS_ O nline_Library / Statewide/20lOs/2010-06-23-ST-DEA-Biocontrol-StrawberryGuava. pdf [Accessed September 2014

Stone, C.P. and L.W. Pratt. 1994. Hawai‘i‘s Plants and Animals: Biological Sketches of Hawai‘i Volcanoes National Park. Hawai‘i Natural History Association, National Park Service, and Cooperative National Park Resources Studies Unit, University of Hawai‘i at Mānoa, Honolulu.

Swezey, O. H. 1926. Recent introductions of beneficial insects in Hawai‘i. J. Econ. Entomol. 19: 714–720.

Tomich, P.Q. 1969. Mammals in Hawai‘i: a synopsis and notational bibliography. Spec. Pub. Bernice P. Bishop Mus. 57. 238 pp.

United Nations Department of Economic and Social Affairs. 2015. World population projected to reach 9.7 billion by 2050. http://www.un.org/en/development/desa/news/population/2015-report.html. Accessed: 8 February 2022.

Vaughn, N., G.P. Asner, P. Brodrick, R.E. Martin, J. Heckler, D.E. Knapp, and R.F. Hughes. 2018. An approach for high-resolution mapping of Hawaiian Metrosideros forest mortality using Laser-Guided Imaging Spectroscopy. Remote. Sens. 10: 502.

Vitorino, M.D., J.H. Pedrosa-Macedo, and C.W. Smith. 2000. The biology of Tectococcus ovatus Hempel (Heteroptera: Eriococcidae) and its potential as a biocontrol agent of Psidium cattleianum (Myrtaceae). In Proceedings of the X International Symposium on Biological Control of Weeds. pp. 651-657. Bozeman (MT): Montana State University.

Wagner, W.L., D.R. Herbst and S.H. Sohmer. 1990. Manual of the Flowering Plants of Hawai‘i. B.P. Bishop Museum and University of Hawai‘i Presses, Honolulu.

Wallace, B. 2021. Avoiding Day Zero: How Cape Town cut its water usage by 50% in three years.

Wessels, F. J., J.P. Cuda. M.T. Johnson, and J.H. Pedrosa-Macedo. 2007. Host specificity of Tectococcus ovatus (Hemiptera: Eriococcidae), a potential biological control agent of the invasive strawberry guava, Psidium cattleianum (Myrtales: Myrtaceae), in Florida. BioControl 52(4):439-449. https://doi.org/10.1007/s10526-006-9043-3

Wikler, C., J.H., Pedrosa-Macedo, M.D. Vitorino, M.G. Caxambú, and C.W. Smith. 2000. Strawberry guava (Psidium cattleianum) - prospects for biological control. In Proceedings of the X international symposium on biological control of weeds. pp. 659-665.

Wilkes, C. 1845. Narrative of the United States Exploring Expedition during the Years 1838, 1839, 1840, 1941, 1942. Charles Wilkes, U.S.N. v. IV, pp. 252-256.

Williams, J. 1986. Native vs. exotic woody vegetation recovery following goat removal in the eastern coastal lowlands of Hawaii Volcanoes National Park. In: Smith CW, editor. Proceedings of the Third Conference in Natural Sciences Hawaii Volcanoes National Park; 1980 June 4-6; Honolulu. Honolulu (HI): University of Hawaii at Manoa, Department of Botany. p 373-382.

Wilmshurst, J.A., T.L. Hund, C.P. Lipo, and A.J. Anderson. 2010. High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. Proceedings of the National Academy of Sciences. 108(5), 1815-1820. https://doi.org/10.1073/pnas.1015876108.

Wingfield, M. J., B. Slippers, J. Roux, and B.D. Wingfield. 2001. Worldwide movement of exotic forest fungi, especially in the tropics and the southern hemisphere: This article examines the impact of fungal pathogens introduced in plantation forestry. Bioscience 51(2): 134-140.

Wingfield, M.J., I. Barnes, Z. Wilhelm de Beer, J. Roux, B.D. Wingfield, and S.J. Taerum. 2017. Novel associations between opiostomatoid fungi, insects and tree hosts: current status-future prospects. Biological Invasions 19: 3215-3228.

Wolman, D. and J. Smith. 2019. Aloha Rodeo: Three Hawaiian cowboys, the world's greatest Rodeo, and a hidden history of the American West.

Yocum, C.F. 1967. Ecology of feral goats in Haleakalā National Park, Maul, Hawai‘i. Amer. Midl. Nat. 77: 418.

Yoshinaga, A.Y. 1980. Upper Kīpahulu Valley weed survey. Honolulu (HI): Cooperative National Park Resources Studies Unit, University of Hawai‘i at Mānoa, Department of Botany. PCSU Technical Report, 33.