# The Cascading Effects of *Ceratocystis fimbriata* on the ‘Ōhi‘a Montane Wet Forest Community

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*Lā‘au ‘ohi wai*, or the forest that gathers water, covers 11,796-hectares between ~1,000–2,000 m in elevation along the windward slopes of Hāleakalā on the Hawaiian island of Maui. The montane wet forest community is located below the orographic cloud zone and receives annual precipitation in excess of 300 cm (Culliney, 2006). Ricklefs & Miller (2000) emphasized that this ecoregion had “the highest productivity on Earth […] due to intense sunlight, warm temperatures, and abundant rainfall” (p. 192). For this reason, the plant populations of the montane wet forest community form the basis of the energy transfer system through the trophic levels and are vital facilitators in nutrient cycling and regeneration within the ecosystem.

The high productivity and widespread distribution of the montane wet forest community provide essential protection for the Island’s watersheds, critical habitat for Hawai‘i’s wildlife (Loope & Uchida, 2012), and supports "the strong links between native Hawai‘ian culture and the islands' environment" (Keith et al. 2015, p. 1277). The health and security of watersheds are essential to maximizing groundwater recharge in addition to rainfall interception and its subsequent evapotranspiration into the atmosphere to maintain water balance (Restom Gaskill, 2004). In Hawai‘i, "groundwater aquifers supply 99% of all drinking water and 50% of all freshwater used statewide" (Mair & Fares, 2010, p. 1454). The forest ecosystem preserves ecological services of instrumental value that include “the supply and purification of fresh water [...] the sequestering of carbon […] and the support of recreation and tourism” (Postel & Thompson, 2005, p. 98). The ‘Ōhi‘a forests also "provide habitat for most of the 35 native forest bird species in Hawai‘i, 21 of which are threatened or endangered, most of the over 900 species of endemic vascular plants, and many of the 5000 endemic species of insects" (Mortenson et al.

2016, p. 84). Culturally, the ʻŌhiʻa tree is "considered one of the *kinolau*, a physical manifestation of Kū, one of the four Hawaiian deities. Kū stands for strength and anchor [...] and can be translated into the ecological concept of keystone species" (Mueller-Dombois, et al. 2013, p. xiii).

This "cloud forest" is considered a zone of great intrinsic value with "islands of biodiversity [that support] a high proportion of endemic species" (Giambelluca et al. 2008, p. 230). The ʻŌhiʻa lehua (*Metrosideros polymorpha*) dominates the closed-canopy community and its companion understory is comprised of dozens of native plant species such as the ʻōlapa (*Cheirodendron spp*.), the hāpuʻu (*Cibotium spp*.), and the ʻōhā kēpau (*Clermontia spp*.) along with small pockets of non-native weeds like the Kāhili ginger (*Hedychium gardnerianum*), and strawberry guava (*Psidium cattleianum*). A suite of native and endemic fauna, many of them rare and endangered, can also be found in the montane wet forest community. Birds such as the ʻiʻiwi (*Drepanis coccinea),* and the kiwikiu (*Pseudonestor xanthophrys*), and the only native terrestrial mammal, the Hawaiian hoary bat (*Lasiurus cinereus semotus*), hold court with a multitude of invertebrates and snails that all add to the diverse, interconnected community.

The endemic ʻŌhiʻa lehua (*Metrosideros polymorpha*) is the foundational tree species within this forest and accounts for 50% of the basal area within almost every habitat and moisture zone found from sea level to the tree line at 2800 m (Mortenson et al. 2016). The jet stream was responsible for the initial transport of the tiny, wind-dispersed ʻŌhiʻa seeds that arrived in Hawaiʻi by way of the Marquesas around four million years ago (Ziegler, 2002). The success of the ʻŌhiʻa as an early colonizer is due to its high number of widely dispersed seeds, which are pollinated by insects and birds, that germinate under adverse conditions on a variety of substrates (Drake, 1993).

Flowering occurs throughout the year and the random dispersion of prolific seeds results in the exponential growth of dense seedling populations that are established on newly disturbed lava substrates, and in canopy gaps found in old-growth forests (Friday & Herbert, 2006). As the shade-intolerant seedlings mature, they experience increased mortality due to the density-dependent limiting process of self-thinning that is “concentrated among the smallest individuals in the stand, preventing continuous regeneration and recruitment into the canopy” (Drake, 1993, p. 32). The resulting local population, or “cohort stand” consists of individual trees that are born within a limited time span of 50 years and grow up together with a uniform tree structure throughout their life cycle (Mueller-Dombois, Jacobi, Boehmer, & Price, 2013).

After 400 years, the first generation of an ‘Ōhi‘a cohort, with a mean population density of 820 trees per hectare, experience a stand-level dieback that is triggered by large density-independent events at senescence due to “synchronized origin and site specific habitat constraints during stand demography,” (Boehmer, et al. 2013). The local population is then reestablished in about 30-40 yr with the same canopy species through auto-succession (Mueller-Dombois, & Boehmer, 2013). The process recurs for two – three generations over a 1,000+ yr before enough nutrients exist in the soil substrate to support an “old growth forest” composed of “limited tree flora” due to its evolution in geographic isolation (Mueller-Dombois, et al. 2013).

Hawai‘i is the most geographically remote group of islands on Earth, and as such has evolved to become host to a high number of endemic species. In fact, 19% of the 2,176 marine organisms and 64% of the 11,511 terrestrial biotas found in the archipelago are considered endemic (Ziegler, 2002). Despite its unique diversity, Hawai‘i is an ecological disaster. Devastating biological invasions introduced by humans into Hawai‘i's ecosystems are impoverishing island biodiversity (Loope & Medeiros, 1994). *Metrosideros polymorpha* is under threat from an onslaught of introduced organisms, pathogens, and habitat loss. Kāhili ginger (*Hedychium gardnerianum*), and strawberry guava (*Psidium cattleianum*) disrupt and displace the ‘Ōhi‘a canopy and lead to severe changes in the native trophic levels and nutrient cycles (Mueller-Dombois, et al. 2013). Pathogens such as *Ceratocystis fimbriata,* or Rapid ‘Ōhi‘a Death, threaten to extirpate local populations on Hawai‘i Island and alter forest composition, structure, and function (Mortenson, et al. 2016).

Since 2012, large stands of healthy *M. polymorpha* on Hawai‘i Island have been dying within days to weeks from *Ceratocystis fimbriata*, a fungal pathogen, and has "result[ed] in localized to extensive stands of predominantly dead ‘Ōhi‘a trees" (Mortenson et al. 2016, p. 84). The otherwise healthy trees "exhibit rapid, synchronized death of leaves on individual branches that eventually spreads to the entire canopy" (Keith et al. 2015, p. 1276). Current aerial surveys from 2017 estimate the range of mortality at hundreds of thousands of trees spread over ~30,000 ha throughout Hawai‘i Island ("Rapid ‘Ōhi‘a Death," 2018) with mortality rates averaging around 24% but increasing to 47% in some test plots (Mortenson et al. 2016). Other sources have reported up to 90% mortality in certain stands ("Rapid ‘Ōhi‘a Death," 2018). Mortenson et al. (2016) claimed that this pattern was distinct from the well-documented cases of *M. polymorpha* cohort senescence as described earlier.

Dark, radial staining within the xylem of the dead ‘Ōhi‘a trees shows evidence of *C. fimbriata,* with the darkest staining indicating the infection site, generally a wound ("Rapid

ʻŌhiʻa Death," 2018). As the fungus travels upwards, it interferes with the plant's ability to transport water and nutrients from the roots to the canopy through the xylem. The leaf stomata close in response to the stress, and transpirational pull is disrupted causing mortality in the tree.

Humans are thought to be the primary vector via transport of contaminated soil, wood, tools, and vehicles; additionally, there is a theory that fungal spores are also disbursed by the wind through contaminated wood-boring beetle frass that becomes mixed with spores (Brewer, 2017). Possible wind dispersion is concerning due to "the potential spread of the disease to other islands, which have not yet had any detections of Rapid ʻŌhiʻa Death" (Brewer, 2017). The ʻŌhiʻa is Hawaiʻi's most widespread tree and constitutes ~80% of all forest trees in Hawaiʻi's native forests and occupies about 400,000 ha across the State (da Silva et al. 2014). "Mortality of ʻŌhiʻa at this scale is of great concern as the understory in these forests is often occupied by invasive non-native plants capable of severely limiting ʻŌhiʻa regeneration" (Mortenson et al. 2016, p. 83).

The major competitors to the ʻŌhiʻa lehua are human introduced alien invaders. Mueller-Dombois et al. (2013) suggested that major threats to the ʻŌhiʻa are categorized as ʻŌhiʻa lifecycle disruptors, canopy displacers, and killer trees. The disruptors, dense undergrowth that prevents rebirth by blocking light, consist of princess flower (*Tibouchina urvilleana*) and Kāhili ginger (*Hedychium gardnerianum*). The canopy displacers, strawberry guava (*Psidium cattleianum*) and the faya tree (*Morella faya*), can penetrate the undergrowth and have distribution advantages over ʻŌhiʻa. Canopy trees that are shade and light tolerant and can overtop ʻŌhiʻa, thereby starving them of light, include the albizia tree (*Falcataria moluccana*), the ironwood tree (*Casuarina equisetifolia*), and the miconia tree (*Miconia calvescens*).

While some varietals of *M. polymorpha* have shown resistance to *Ceratocystis fimbriata*, even an average mortality of 24% as observed by Mortenson et al. (2016) would be enough to allow the invasive Kāhili ginger (*Hedychium gardnerianum*), and strawberry guava (*Psidium cattleianum*) to out-compete the shade-intolerant *Metrosideros polymorpha*. The ‘Ōhi‘a's ability to pioneer and recolonize disturbed marginal sites allows for great resiliency of the species (Mueller-Dombois et al. 2013). However, it cannot effectively recover in the presence of highly invasive exotics and the widespread mortality of ‘Ōhi‘a trees "will very likely transform these forests from native dominated to non-native dominated" (Mortenson et al. 2016, p. 90). The ecological impacts to forest composition, structure, and function would be devastating should the disease spread throughout the islands.

The transformation of ‘Ōhi‘a forest from native dominated to non-native dominated will result in lost plant-pollinator mutualisms, decreased carbon sequestration, and diminished hydrological services. The limiting factor of habitat loss, due to the eradication of large numbers of *M. polymorpha* and the subsequent encroachment of invasive species, will result in the extirpation and extinction of Hawai‘i's endemic birds (Reynolds et al. 2003). The mutualistic aspect of this relationship between the endemic Hawaiian honeycreepers [Drepanididae (Cabanis)] and bees [Hylaeus (Fabricius)] are "critical to the overall functioning of island ecosystems and are severely impacted by invasive species" (Hanna et al. 2013, p. 148). Although insects are capable of pollinating the weakly self-compatible hermaphroditic ‘Ōhi‘a flowers, their structure is adapted to bird pollination and thus endemic birds are adapted to them (Hanna et al. 2013). Neither species will prosper without the other.

The earth's storage of carbon is found within four compartments: the oceans, the atmosphere, terrestrial biomass (plants and soil), and fossil deposits. Ricklefs & Miller (2000) claimed, "Land plants take in more carbon from the atmosphere in the process of primary production than they return via respiration. However, terrestrial-atmospheric carbon exchange is roughly balanced in the long term" (p. 209). Nevertheless, terrestrial ecosystems have the potential to become carbon sinks or sources and in the case of Hawaiian forests Selmants et al. (2017) reported:

> Live-biomass carbon storage in native forests was estimated as 32 TgC, which was 51 percent of all carbon stored as live biomass (63 TgC), followed by invaded forests (21 TgC) and alien tree plantations (6 TgC) [...] Among ecosystem types, native forests represented the largest single terrestrial carbon sink with NEP of 1.26 TgC/yr, which accounted for 53 percent of total annual carbon sequestration. Alien grasslands were estimated to be a net carbon source to the atmosphere with NEP estimated at -0.56 TgC/yr, because ecosystem respiration exceeded GPP in large areas of alien dry grasslands. (p. 75)

Rates of evapotranspiration and throughfall characteristics of a forest stand are "a major component of the water balance in rain forest ecosystems" (Mair & Fares, 2010, p. 1453). This balance is important in understanding the contributions of a terrestrial ecosystem to the hydrological service of ground water recharge and the subsequent increase or decrease in fresh water resources. These established native forests are responsible for recycling most of the available freshwater through evapotranspiration and play an instrumental role in groundwater recharge by facilitating high infiltration rates (Restom Gaskill, 2004). Comparisons between a montane wet cloud forest of *M. polymorpha* with that of a non-native strawberry guava (*Psidium cattleianum*) and tropical ash (Fraxinus uhdei) forest found that evapotranspiration rates were 27% higher in the non-native site and that during dry periods, the evapotranspiration rate increased to 53% higher and total water use in stands dominated by *F. uhdei* were double that of *M. polymorpha* thus proving that non-native species are capable of altering the hydrology in Hawaiian forest ecosystems (Mair & Fares, 2010). Therefore, a loss of significant amounts of montane wet forest equates to a diminished capacity of our available fresh water resources.

The threat of Rapid ‘Ōhi‘a Death via the fungal pathogen *Ceratocystis fimbriata* is of such magnitude that it is beyond the scope of any single agency to address measures for the preservation of Hawai‘i’s most abundant native tree and its associated ecosystems. Rather, management strategies, based upon scientific research, must originate from the coordinated interdisciplinary effort of watershed partnerships, NGOs, government agencies, scientists, economists, political leaders, resource managers, and concerned citizens. Additionally, consensus building around common goals must be encouraged and facilitated through open lines of communication and group bonding conferences.

Currently, biosecurity measures prohibiting the export of soil, wood, and many plants from Hawai'i Island have been enacted and public educational campaigns on identifying infected trees and the current best management practices for the pathogen's containment have been well broadcasted. In addition, funding and awareness campaigns at the local, state, and federal levels must be organized to support the development of scientific modeling, experimentation, and data collection; the results of which can be used to develop a management plan and strategies to implement effective solutions; some of which might include fungicidal biocontrol measures, and plant hybridization resistant to *C. fimbriata.*

Unfortunately, all of these strategies need to have happened already. Every moment of every day is another step closer to the extinction of one of Hawai‘i’s most precious organisms and its associated ecosystem. In the meantime, land managers must continue their efforts at containing the damaging effects of invasive alien species on Hawai‘i’s insular biota in hopes that one day we find a steady state balance.

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