Hawai'i forest review: Synthesizing the ecology, evolution, and conservation of a model system

Kasey E. Barton [a],[*], Andrea Westerband [a],[1], Rebecca Ostertag [b], Elizabeth Stacy [c], Kawika Winter [d],[e],[f], Donald R. Drake [a], Lucas Berio Fortini [g], Creighton M. Litton [f], Susan Cordell [h], Paul Krushelnycky [i], Kapua Kawelo [j], Kealoha Feliciano [a], Gordon Bennett [k], Tiffany Knight [l],[m],[n]

[a] School of Life Sciences, University of Hawai'i at Mānoa, Honolulu, HI, USA
[b] Department of Biology, University of Hawai'i, Hilo, HI, USA
[c] School of Life Sciences, University of Nevada, Las Vegas, NV, USA
[d] National Tropical Botanical Garden, Kaua'i, HI, USA
[e] Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Honolulu, HI, USA
[f] Department of Natural Resources and Environmental Management, University of Hawai'i at Mānoa, Honolulu, HI, USA
[g] U.S. Geological Survey, Pacific Island Ecosystems Research Center, Honolulu, HI, USA
[h] U.S. Forest Service, Institute of Pacific Islands Forestry, Hilo, HI, USA
[i] Department of Plant and Environmental Protection Sciences, University of Hawai'i at Mānoa, Honolulu, HI, USA
[j] Army Natural Resources Program, O'ahu, U.S. Army Garrison, Hawai'i, Schofield Barracks, HI, USA
[k] Life and Environmental Sciences Unit, University of California, Merced, CA, USA
[l] Department of Community Ecology, Helmholtz Centre for Environmental Research-UFZ, Halle, Saale, Germany
[m] Martin Luther University Halle-Wittenberg, Halle, Saale, Germany
[n] German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany

ABSTRACT

As the most remote archipelago in the world, the Hawaiian Islands are home to a highly endemic and disharmonic biota that has fascinated biologists for centuries. Forests are the dominant terrestrial biome in Hawai'i, spanning complex, heterogeneous climates across substrates that vary tremendously in age, soil structure, and nutrient availability. Species richness is low in Hawaiian forests compared to other tropical forests, as a consequence of dispersal limitation from continents and adaptive radiations in only some lineages, and forests are dominated by the widespread *Metrosideros* species complex. Low species richness provides a relatively tractable model system for studies of community assembly, local adaptation, and species interactions. Moreover, Hawaiian forests provide insights into predicted patterns of evolution on islands, revealing that while some evidence supports "island syndromes," there are exceptions to them all. For example, Hawaiian plants are not as a whole less defended against herbivores, less dispersible, more conservative in resource use, or more slow-growing than their continental relatives. Clearly, more work is needed to understand the drivers, sources, and constraints on phenotypic variation among Hawaiian species, including both widespread and rare species, and to understand the role of this variation for ecological and evolutionary processes, which will further contribute to conservation of this unique biota. Today, Hawaiian forests are among the most threatened globally. Resource management failures – the proliferation of non-native species in particular – have led to devastating declines in native taxa and resulted in dominance by novel species assemblages. Conservation and restoration of Hawaiian forests now rely on managing threats including climate change, ongoing species introductions, novel pathogens, lost mutualists, and altered ecosystem dynamics through the use of diverse tools and strategies grounded in basic ecological, evolutionary, and biocultural principles. The future of Hawaiian forests thus depends on the synthesis

* Corresponding author at: School of Life Sciences, University of Hawai'i at Mānoa, 3190 Maile Way, Room 101, Honolulu, HI, 96822, USA.
  E-mail address: kbarton@hawaii.edu (K.E. Barton).
[1] Current affiliation: Department of Biological Sciences, Macquarie University, Sydney, Australia.

of ecological and evolutionary research, which will continue to inform future conservation and restoration practices.

1. Introduction

The eight main Hawaiian Islands (Hawaiʻi, Maui, Lānaʻi, Kahoʻolawe, Molokaʻi, Oʻahu, Kauaʻi, Niʻihau) have inspired biologists for centuries, serving as a living laboratory and a model study system for ecology and evolution. Owing to their extreme isolation and steep environmental gradients, the Hawaiian Islands provide unparalleled opportunities to investigate biogeography, community ecology, assembly theory, biogeochemistry, and adaptive radiations. Increasingly, the global threats of habitat loss, non-native species, and climate change are radically altering the abundance and distributions of the highly endemic biota, inspiring new research in restoration ecology and conservation biology. Whereas previous reviews have synthesized specific aspects of Hawaiian biology, including forest population dynamics (Mueller-Dombois et al., 2013), invasion biology (D'Antonio et al., 2017), nutrient cycling (Vitousek, 2004), carbon cycling (Selmants et al., 2017), and forest restoration ecology (Friday et al., 2015), none have explicitly tried to integrate broadly across fields, leaving the literature on evolutionary processes largely separated from that on global threats and conservation. Moreover, while earlier reviews often encompass multiple ecosystems, we focus here on forests because of their dominance in terrestrial Hawaiʻi. Our goal is to synthesize forest research broadly across evolution, ecology, and conservation because these fields are inherently linked, and new insights may be gained by considering them simultaneously.

Hawaiian forests have served as a biological microcosm in part because their evolutionary and ecological processes are amenable to study. Features of Hawaiian forests that facilitate study include younger lineages distributed across a well-characterized island-age gradient, less complex trophic webs, and more simplified species interactions, at least among the native species (Gruner, 2004). Especially noteworthy is that most Hawaiian forest overstories, particularly on Hawaiʻi Island, are dominated in large part by a singular tree species, *Metrosideros polymorpha*, across broad environmental gradients and sharp ecotones. Although several other dominant and co-dominant canopy species occur in forests, dominance is high and diversity is low in Hawaiʻi compared to tropical forests elsewhere (Craven et al., 2018; Ostertag et al., 2014). With their simple species composition and structure, and partitioning across islands of known ages, Hawaiian forests offer an opportunity to explore the patterns and processes of speciation (Choi et al., 2020; Gillespie, 2016; Roderick and Gillespie, 1998), community formation (Gillespie, 2004; Shaw and Gillespie, 2016), the roles of niche versus neutral processes in structuring plant diversity in tropical forests (Hubbell, 2006; Kraft et al., 2008; Leibold and McPeek, 2006), and the importance of biodiversity for ecosystem functioning (Poorter et al., 2017).

We focus on native forests because they are an extensive ecosystem type in the main Hawaiian Islands (Appendix A), harboring a largely endemic biota and dominating the islands' watersheds and nutrient cycling (Selmants et al., 2017). While there is a vast literature on Hawaiian forests, we do not aim to include every study in our review. Instead, our purpose is to highlight key areas of discovery in Hawaiian forest research, and to identify gaps in knowledge that should serve as a basis for future study. We first provide a brief overview of the physical environment in order to provide context for subsequent discussions of adaptive radiations, forest diversity, tree demography, and the evolution of island syndromes. Species interactions are less well studied in Hawaiian forests, perhaps owing to dramatic shifts in native species abundances and distributions over recent centuries. Throughout this review, we will highlight gaps in our knowledge about historical native species interactions and discuss how invasions have led to novel

interactions, often with cascading effects on population dynamics, community patterns, and ecosystem function. We then discuss how restoration and conservation scientists have addressed global threats such as climate change and invasions, expanding our understanding of Hawaiian forests. Given that Hawaiʻi's Indigenous people (Native Hawaiians) have complex and dynamic relationships with forests and native biodiversity (Winter et al., 2020a, c), we also consider how biocultural perspectives shed new light on Hawaiian forest ecology and function, particularly in the context of restoration and conservation.

2. Physical environment

Understanding the physical environment is paramount to any discussion of Hawaiʻi's vegetation. Of fundamental importance is the volcanic substrate, which changes with age and interacts with climate and vegetation to provide the chemical and physical soil structure on which plants grow (Chadwick et al., 1999; Vitousek, 2004). The volcanic nature of the Hawaiian Islands and high surface water flow lead to the formation of steep elevation gradients and sharp ecotones that interact with trade-winds and disturbances such as seasonal storms and wildfires to establish the complex and striking environmental heterogeneity that underlies the forest structure and function.

2.1. Volcanic origin and soils

The Hawaiian Islands are born from an oceanic hotspot where magma emerges through the earth's crust, producing new submarine volcanoes that eventually emerge as basaltic shield volcanoes (Appendix B). As plate tectonics shift the Pacific Plate towards the northwest at 7−10 cm per year, a young volcano eventually moves beyond the hotspot and transitions from the shield-building stage to a post-shield stage where subsidence and erosional processes dominate (MacDonald et al., 1983; Ziegler, 2002). The combination of near-constant eruption of magma from the hotspot and tectonic movement has created an archipelago of 132 land formations—including islands, atolls, and seamounts—spanning > 2500 km from Lōʻihi Seamount to Kure Atoll (Eakins et al., 2003). Importantly, the bathymetry shows that many of the individual islands of today were historically connected during times of lower sea levels (e.g., Maui, Kahoʻolawe, Lānaʻi, and Molokaʻi, known as Maui Nui (Price, 2004)), and that over time, the sizes and degree of isolation of islands have changed, influencing the distributions of species (Funk and Wagner, 1995; Price and Elliott-Fisk, 2004).

The islands and volcanic substrates of Hawaiʻi have been dated with considerable certainty (Sherrod et al., 2007), yielding an unusually precise temporal context for studies of the evolution and assembly of biological communities. For example, the dates of formation of the Hawaiian Islands provide fairly robust calibration points for performing molecular dating analyses (Baldwin and Sanderson, 1998). These data enable a detailed understanding of the tempo and mode of lineage diversification in response to local biological, climatological, and geographical conditions or events, and permit researchers to piece together the order of community assembly across the islands (Rominger et al., 2016).

The gradient in substrate age, in combination with complex variability in climate, topography, and assemblages of colonizing organisms, has led to remarkably diverse soils across the main Hawaiian Islands (Appendix C). Ten of the twelve global soil orders and at least 250 distinct soil series are represented. The most widespread soils are Andisols (39 %), Histosols (26 %), Oxisols (10 %), and Mollisols (8%), with the six other orders making up the remaining 17 % (Deenik and McClellan, 2007). The soil orders are not uniformly distributed across

the islands. Volcanically derived Andisols are most common on the younger islands of Maui (40 %) and Hawai'i (52 %), whereas highly weathered Oxisols are common on the older islands of Kaua'i (44 %), O'ahu (37 %), Moloka'i (39 %), and Lāna'i (48 %). Soils with high organic matter content, Histosols, make up a large proportion of Hawai'i Island substrate (39 %) but are rare on the older islands (0–4 %) (Deenik and McClellan, 2007). Andisols develop from ash, cinder, pumice or other ejecta, and weather into soils that hold high amounts of organic matter and water; they support the most productive and carbon-dense woody ecosystems (Deenik and McClellan, 2007). Histosols form on lava flows as early successional vegetation decays, and thus have high organic matter that can support vast *M. polymorpha*-dominated forests, spanning dry to wet environments. Oxisols support somewhat less productive woody ecosystems as a result of nutrient limitations that occur over long substrate-weathering gradients, which explains why they are more common on older islands (Vitousek, 2004).

Nutrient availability in the three most abundant soil types is strongly related to soil order and climate. All soils in Hawai'i start out limited by nitrogen (N), owing to the lack of N in the initial volcanic substrate (Crews et al., 1995). Over time, N accumulates in the ecosystem through atmospheric deposition and biological N fixation (Crews et al., 1995). In wetter areas, the Andisols and Histosols on the younger islands experience significant loss of nutrients, especially N, calcium (Ca), and potassium (K), and these conditions can lead to soil acidification, accumulation of aluminum (Al), and binding of phosphorus (P) into forms that are not readily available for plant uptake (Deenik and McClellan, 2007). Over time, this leads to a shift in the ratio of N and P across the Hawaiian Islands as well as other chronosequences globally (Wardle et al., 2004). These infertile conditions also characterize Oxisols, in which considerable weathering has led to high levels of Al and iron (Fe) oxides and low cation exchange capacity (Deenik and McClellan, 2007). How forest productivity is maintained as rock-derived nutrients such as P, Ca, magnesium (Mg), and K weather away was not well understood until recently, when isotopic tracer techniques were able to demonstrate that cations arrive as marine aerosols while P is imported via dust from Asia (Chadwick et al., 1999) and northern Africa (Vogel et al., 2021). Much remains to be learned, however, about how these atmospherically derived nutrients, especially P, cycle within Hawaiian soils and interact with climate (Helfenstein et al., 2018), as well as other nutrient inputs such as those from seabirds (Mulder et al., 2011).

2.2. Climate

The climate of the Hawaiian Islands is characterized by wide and steep gradients in both temperature (Appendix D) and precipitation (Appendix E). Owing to the high and steep topography of the main islands, mean annual temperature varies from 4 to 24 °C, with temperature gradients up to 8 °C per kilometer (e.g., Northern Moloka'i, Central Kaua'i, and Waipi'o Valley on Hawai'i Island). Seasonal temperature variability is low, however, because of the tropical latitude and the buffering effects of the ocean. In contrast to temperature, for much of Hawai'i, rainfall is seasonal and occurs primarily between October and April. Mean annual precipitation (MAP) varies from 204 to 10,200 mm across the islands, with precipitation gradients as steep as 2200 mm per kilometer. Due to orographic lift of the northeasterly trade-winds across Hawai'i's mountainous terrain, windward areas receive on average twice as much rainfall (2400 mm) as leeward areas (1200 mm). Yet not all precipitation in Hawai'i is trade wind-driven, with other weather patterns contributing to total precipitation and extreme rainfall events (Kodama and Barnes, 1997). Southerly Kona storms that typically occur in the winter, for instance, provide 20 % of MAP on average for leeward areas (Kaiser, 2014). Elevational gradients in climate relate to the occurrence of the trade wind inversion on the taller islands, which inhibits cloud formation above roughly 2000 m above sea level. Reduced clouds above the inversion lead to greater insolation and lower

precipitation and relative humidity at high elevations (Cao et al., 2007). The trade wind inversion has a major effect on moisture availability for plants, effectively setting the maximum elevation limit of forests (Kitayama and Mueller-Dombois, 1994; Loope and Giambelluca, 1998). Beyond local factors, Hawai'i's climate is also partly determined by naturally occurring inter-annual variability including the El Niño-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the Pacific/North American teleconnection pattern (PNA) (Frazier et al., 2018).

Hawai'i's climate is in a state of flux. Long-term climate records show an increasing number of days with no rain and a substantial drying trend, particularly in dry forests (Frazier and Giambelluca, 2017; Timm et al., 2015). Drying effects on forests are likely to be exacerbated by significant warming trends for the entire archipelago (Kagawa-Viviani and Giambelluca, 2020). On the windward sides of the islands, a recently documented increase in trade wind inversion days could mean steeper precipitation gradients near the top of the forest line (Krushelnycky et al., 2016), and there is some evidence that a lifting cloud base in at least part of the archipelago may be driving declines in mean annual precipitation in low- to mid-elevation forests (Kagawa-Viviani and Giambelluca, 2020).

Beyond these inter- and intra-annual trends, projecting long-term climate shifts for Hawaiian forests is challenging and requires consideration of both regional and local dynamics. The existing precipitation projections for the state have generally agreed on a future in which wet areas remain stable or become wetter, and dry areas become drier (Timm et al., 2015; Zhang et al., 2016). However, these patterns are based on a limited number of models, and a broader set of regional climate models is needed to understand the robustness of these projections. Beyond shifts in mean precipitation, emerging research indicates changes in climate extremes as well. Notably, tropical cyclones, or hurricanes, only rarely reach the Hawaiian Islands compared to other islands, particularly those in the Caribbean, but the frequency of hurricane occurrence is projected to increase with global warming (Murakami et al., 2013). Ongoing climate shifts may also lead to either increasingly intense or frequent ENSO events, which generally lead to drier winter conditions in Hawai'i (Cai et al., 2018; Freund et al., 2019; Lu et al., 2020). Changes in storm tracks may lead to more frequent high-intensity storms over the islands than has historically been the case (Sugi et al., 2017; Tamarin-Brodsky and Kaspi, 2017).

These shifts in climate are likely to disproportionately influence Hawai'i's native flora as island species tend to have more narrow distributions and small population sizes than their continental counterparts (Harter et al., 2015). Hawaiian forest species vary in their abundances and distributions, making it difficult to predict how climate change will influence their persistence in the future (Box 1, Fig. 1). Given the limited potential for species on islands to shift their distributions latitudinally, Hawaiian forest species are largely restricted to shifting distributions in elevation. Pollen records indicate historical shifts in Hawaiian forests as a result of climate change (Hotchkiss and Juvik, 1999). Recent research indicates that expecting simple warming-related upslope shifts in species and forest communities is overly simplistic (Crimmins et al., 2011; Gibson-Reinemer and Rahel, 2015). For example, the upper elevation forest limit in Maui is determined not only by temperature, but also moisture (Crausbay et al., 2014). A study of changing species distributions over time on Mauna Loa, Hawai'i Island showed that between 1970 and 2010, native species contracted their low-elevation range limits without expanding at their upper range limits, likely because they had already reached the upper limit set by the trade wind inversion (Koide et al., 2017). This finding contrasted with the trend observed for non-native species, which inhabited lower elevations in 1970, and have since expanded upward, presumably as a result of suitable habitats at high elevations. Whereas both native and non-native plants are likely similarly limited by the trade wind inversion, increasing abundances of non-native species at high elevations may restrict the ability of native species to adapt or shift ranges in response to climate change.

Box 1

Conserving Hawaiian forest under a changing climate.

Hawaiian forests include species that vary considerably in their spatial distributions (Section 4, Figure 1). Managing Hawaiian forests under a changing climate to maximize persistence of species that vary so dramatically in climate niche breadth is complex and likely to require multiple strategies rather than a single one-size-fits-all approach. An important first step was a recent vulnerability assessment, which found that the future climatic niches of hundreds of Hawaiian plant species may not coincide with their current ranges, and furthermore, that many native plant species currently occupy ranges that by 2100 will not match their optimal observed climatic niche (Fortini et al., 2013). Because these assessments did not incorporate potential intraspecific variation in climate stress tolerance or account for discrepancies between the current distributions used to quantify climate envelopes and historical distributions before human activities and invasive species altered species distributions, additional research is still needed.

For widespread species, it is generally assumed that populations that span steep climatic gradients are locally adapted, leading to ecotypes. While population genetic differentiation and evidence for local adaptation has been detected for some species in parts of their ranges, especially for *M. polymorpha* (Section 4), most Hawaiian plant species have not been examined for local adaptation to climate variables. For microendemics with narrow climate ranges, even less is known about climate stress tolerance to inform management under changing climates. Because assisted migration is likely to be required to translocate species to suitable future climates, precise population-scale data on climate-stress tolerance is needed to ensure suitable matching between seed source and out-planting sites. Growing mismatches between current and historical climates may already contribute to reduced seedling emergence of *M. polymorpha* across a precipitation gradient on Oʻahu Island (Barton et al., 2020), emphasizing the urgency of research in this area. Finally, phenotypic plasticity and genetic variation available for local adaptation to changing climate may be viable strategies for short-lived forest species, but these data are generally absent for most Hawaiian plant species (Leopold and Hess, 2019; Westerband et al., 2020; Westerband et al., 2019).

It has remained difficult to scale up species-specific predictions of future distributions to the entirety of Hawaiʻi's forests. This is partly due to the poor fit of current, widely used ecosystem models that were originally developed for continental systems (Bachelet et al., 2015; Maguire et al., 2015). Nevertheless, recent ecological models for Hawaiʻi indicate a possible expansion of climatic conditions suitable for the dry and wet extremes of forests, and narrowing of areas currently most suitable for the more mesic forests, which are the most diverse of Hawaiʻi's forest types (Fortini and Jacobi, 2018). Whereas drier conditions have been linked to increased tree mortality and decreased growth in some tropical forests (Allen et al., 2017; Engelbrecht and Kursar, 2003; McDowell et al., 2018), little is known about how forests in Hawaiʻi's dry areas will respond to increased drying trends. Depending on the scale and species' responses, it is plausible that future changes in Hawaiʻi's climate could trigger dramatic shifts in plant community composition and ecosystem processes. For example, a study of native plant mortality on Mauna Loa during an El Niño drought suggests that severe drought can cause a shift in dominance from woody to herbaceous species (Lohse et al., 1995), often with cascading effects on wildfire regimes (see next section).

2.3. Disturbance

Physical disturbances are regular, natural features of island ecosystems (Mueller-Dombois and Fosberg, 1998). Typically, the spatial extent and intensity of disturbance are inversely correlated with frequency (e. g., limbfalls are more common than island-wide cyclones). Although Hawaiʻi Island is well known for patterns of disturbance and plant succession associated with volcanic eruptions and earthquakes, the most common disturbances in forests are flooding and landslides caused by extreme rainfall events, wind damage from tropical cyclones, and wildfire (Box 2, Fig. 2).

The Hawaiian Islands regularly experience localized, extreme rainfall events, e.g., 940 mm in 24 h on Hawaiʻi Island in 2000 and 254 mm in 12 h on Oʻahu in 2004 (Chu et al., 2009), which can cause landslides owing to Hawaiʻi's steep topography (MacDonald et al., 1983). In 2018, a national rainfall record was set on Kauaʻi with 1262 mm within a 24 -h period (Arndt et al., 2018), causing widespread landslides and flooding. Aside from these extreme events, little is known about landslide frequency or severity in Hawaiʻi (Restrepo and Vitousek, 2001; Restrepo et al., 2003). The most comprehensive assessment, based on 50 years of aerial photographs from southeast Oʻahu, estimated that landslides

range in size from $10-5860\,m^2$ (median $111\,m^2$, mean $291\,m^2$), are typically triggered by heavy rainfall, and affect about 0.6 % of the susceptible landscape per year (Peterson et al., 1993). For Hawaiʻi Island, however, landslide disturbance rates as high as 15 % biomass loss per century have been reported (Restrepo et al., 2003).

Tropical cyclones (formally called hurricanes in the Central North Pacific) can affect terrestrial ecosystems in several ways; high winds blow down limbs and trees, heavy rains cause landslides and flooding, and storms flood coastal lowlands (Lugo, 2008; Smith et al., 2012). The Central North Pacific experiences an average of three hurricanes per year (range 0–10), with frequencies during El Niño years three times as high as in La Niña years (Clark and Chu, 2002). Because the main Hawaiian Islands occupy only a small portion of this region, they experience strong hurricanes at relatively long intervals, although the frequency is expected to increase with global warming (Murakami et al., 2013). Models estimate that the islands experience hurricanes with wind speeds of 230, 204, 185, and 148 km/h at intervals of 137, 59, 33, and 12 years, respectively (Chu and Wang, 1998). In contrast to storm damage to other tropical forests (Chazdon, 2003), storm damage to Hawaiian forests from tree mortality and increased litterfall has not been well documented. An exception is Hurricane Iniki on Kauaʻi (Asner and Goldstein, 1997; Harrington et al., 1997; Herbert et al., 1999). Efforts to determine the effects of major historical storms on present forest structure could capitalize on the extensive Hawaiian language newspaper record of over 125,000 printed pages from 1834 to 1948 (Businger et al., 2018). These newspapers detail weather and geophysical events such as hurricanes and earthquakes, for example, the Category-3 Hurricane in 1871 that devastated the islands of Hawaiʻi and Maui (Businger et al., 2018).

Wildfires are a disturbance commonly associated with volcanic activity, although there is also evidence of non-volcanic fires in Hawaiʻi from charcoal aged >7300 years old, well before Polynesians arrived (Kinney et al., 2015). Studies of soil charcoal demonstrate that wildfires occurred historically in evergreen broadleaf wet forests (Smith and Tunison, 1992), with a mean fire return of 700–1000 years (Mueller-Dombois et al., 1977). Naturally occurring wildfires in Hawaiʻi were likely localized, of low intensity, and initiated by lightning or lava after extended periods of drought (Ainsworth and Kauffman, 2010; Mueller-Dombois, 1981; Sorenson, 1979; Vogl, 1969). As a result, native Hawaiian plants tend to have limited adaptations to wildfire as a frequent natural disturbance (LaRosa et al., 2008), although re-sprouting following fire, and heat- and smoke-tolerant seeds indicate historical
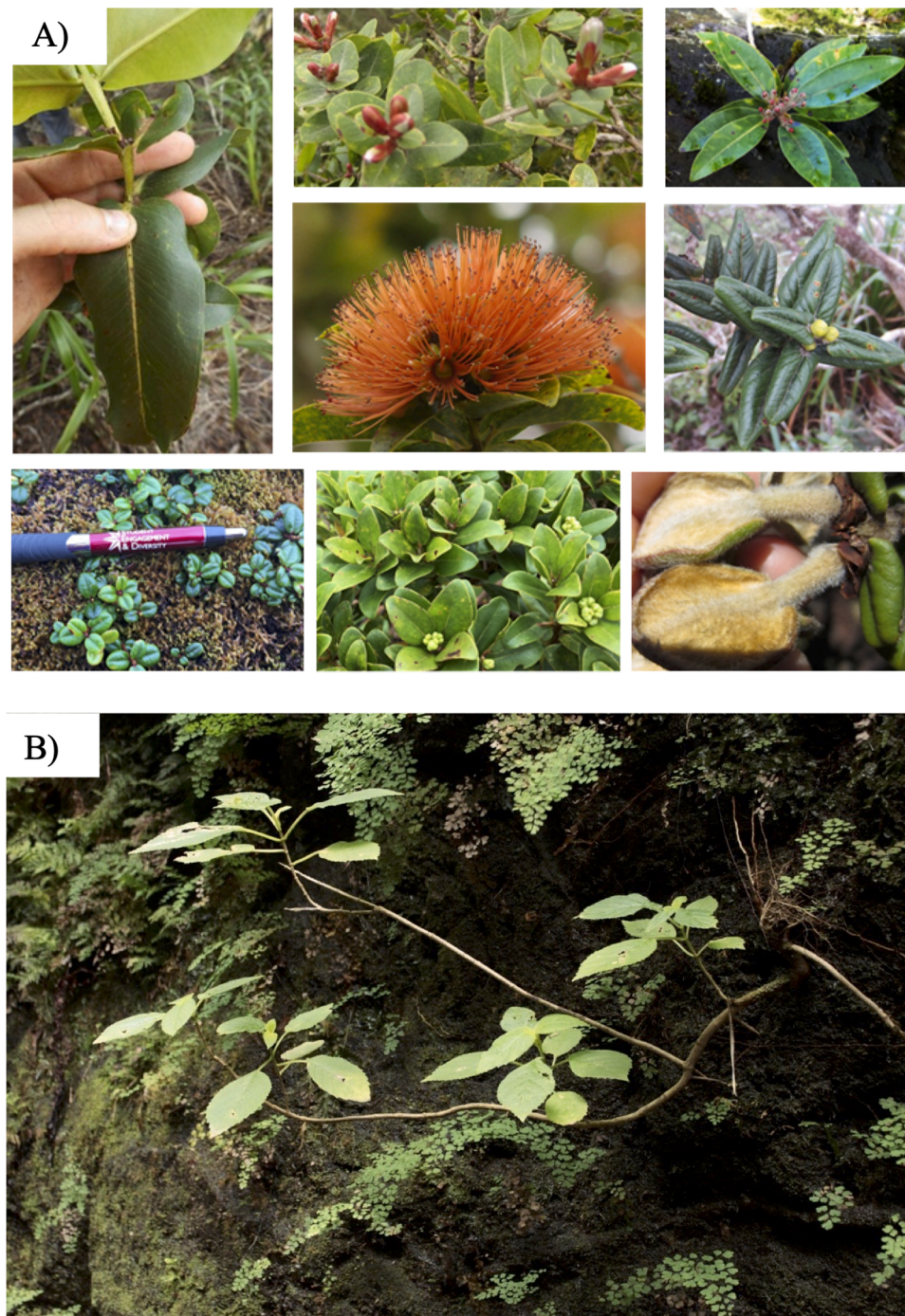
Fig. 1. Hawaiian forests include widespread abundant species such as the foundational *Metrosideros polymorpha* (A), as well as micro-endemics with highly constrained distributions, such as *Cyrtandra dentata* (B), restricted to gulches on Oʻahu Island. Photo credits: Elizabeth Stacy (A) and Adam Williams (top left image in A), Kapua Kawelo (B).

or *in situ* evolution of fire tolerance in at least some native trees and shrubs (Ainsworth and Kauffman, 2009; Loh et al., 2009).

The Hawaiian Islands have undergone drastic changes in wildfire dynamics due to the introduction and spread of non-native plants and humans themselves who ignite fires at a much greater rate than has occurred naturally (Trauernicht et al., 2015). The non-native species-wildfire cycle (D'Antonio and Vitousek, 1992) has been widely studied in Hawaiʻi and is one of the more important causes of native forest degradation, particularly in dry and mesic habitats (D'Antonio et al., 1998; Ellsworth et al., 2014; Mack and D'Antonio, 1998). For

example, wildfires fueled by non-native C_4 grasses have resulted in the loss of >60 % of seasonally dry sub-montane native forest (D'Antonio et al., 2000; Hess et al., 1999; Hughes and Vitousek, 1993; Hughes et al., 1991), greatly reducing the occurrence of *Acacia koa - Deschampsia nubigena* parklands (Karpa and Vitousek, 1994; LaRosa et al., 2008), and contributing to the loss of more than 90 % of the lowland forests in dry regions (Bruegmann, 1996; Cabin et al., 2002; Litton et al., 2006). Grass-fueled wildfires greatly increase fire frequencies by amplifying fine fuel loads and changing microclimatic conditions (D'Antonio and Vitousek, 1992; Freifelder et al., 1998). Over the past century in Hawaiʻi

Box 2
Disturbance regime change in Hawaiian forest.

Physical disturbances are regular, natural features of island ecosystems, and while lava flows are commonly associated with Hawai'i, they are relatively rare at the archipelago-scale compared to hurricanes and flooding (Figure 2). The frequency of big storms is expected to increase in Hawai'i as a consequence of climate disruption (Murakami et al., 2013). Intense storms disturb forest habitats by causing flooding and land-slides, by causing damage to trees through limb breakage and treefall, and by altering biogeochemical dynamics (Herbert et al., 1999). Such disturbances have cascading effects on forest dynamics by exposing substrate for invasive plant spread (Ostertag and Verville, 2002), reducing habitat for associated rare and threatened birds and snails, and potentially spreading invasive pathogens (Barnes et al., 2018). In addition to shifts in storm frequencies and severities, fire has increased dramatically in recent years, with devastating consequences for Hawaiian forests (Trauernicht et al., 2015). Contemporary fires in Hawai'i are largely human-caused due to military and recreational activities (Figure 2). Other small-scale disturbances due to invasive animals and human-caused habitat modifications are widespread and can have disproportionately large effects on forest dynamics. For example, invasive pigs alter soil structure with their rooting behavior, with cascading effects on seedling recruitment.

One of the primary challenges following disturbances such as landslides, fire, or even small-scale events is that cleared substrate provides an opportunity for displacement of native plants by fast-growing invasive species. Mitigation of these threats under changing disturbance regimes is challenging, particularly due to the remote location of many remaining native forests, and by the limited availability of native seeds to disperse (naturally or by managers) into disturbed sites to facilitate native forest regeneration (Friday et al., 2015). Production of native seeds for restoration requires knowledge of plant phenology, seed dormancy, and seedling establishment, which while increasing in scope, remain unknown for most native Hawaiian forest species, illustrating the value of explicit integration of basic ecology with conservation and restoration sciences.

Volcanoes National Park on Hawai'i Island, there has been a more than three-fold increase in the number of fires and a 60-fold increase in average fire size (Tunison et al., 2000), and these trends are characteristic of changes in wildfire activity across the entire archipelago (Trauernicht et al., 2015). While non-native grasses have received most of the attention in studies assessing the invasion-wildfire regime change, invasion by other plant forms may also change wildfire dynamics by altering fine fuels and microclimate (Ainsworth and Kauffman, 2009). Continued research on the non-native species-wildfire cycle would increase the capacity to restore and conserve native ecosystems archipelago-wide (Ellsworth et al., 2015; Trauernicht, 2019).

3. Distribution, classification, and structure of Hawaiian forests

3.1. Distribution

Hawai'i's forests are distributed across a range of environments (Appendix A), and currently cover approximately 34 % of the main islands, occurring in dry (6%), mesic (10 %), and wet (18 %) environments (Jacobi et al., 2017). Forests also occur across almost the full spectrum of soils present in Hawai'i (Appendix C). Due to biogeographic and evolutionary patterns of the flora (Section 4), many of the same woody species are abundant across a variety of soil types and climates. This situation is rare in continental tropical forests and presents an
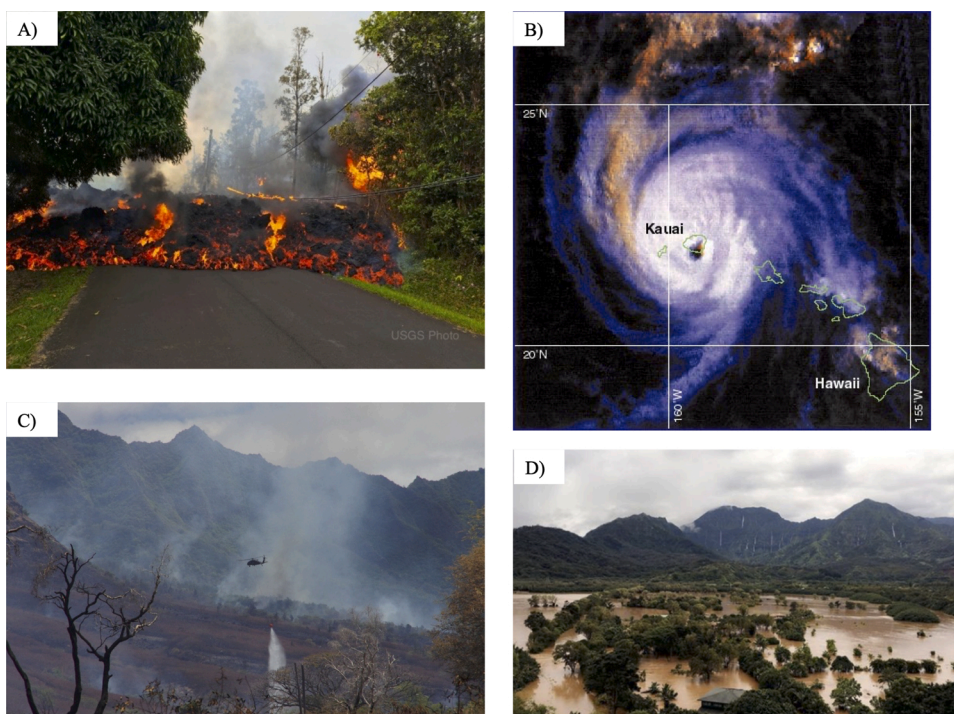
Fig. 2. Physical disturbances are regular, natural features of island ecosystems and can include lava flows (A, Kīlauea volcano, Hawai'i Island. 3 May 2018; photo credit: USGS); hurricanes (B, high resolution infrared image of Hurricane Iniki making landfall on Kaua'i. 11 Sept 1992; photo Credit: NOAA); fires (C, 2018 West Side Fires on O'ahu Island, which burned approx. 6,000 acres; photo credit: P. Trauernicht); and flooding (D, Hanlalei Valley, Kaua'i following heavy rains. April 2018; photo credit: T. Rex).

Box 3
Indigenous resource management (IRM) in Hawai 'i.

Indigenous resource management (IRM) is the body of philosophies, strategies, and practices employed by Indigenous Peoples to systematically manage abundance in context of habitats at the scale of landscapes and seascapes. IRM in Hawai'i involved the dividing of each island vertically – from mountains to sea – into social-ecological regions (*moku*), each of which were further subdivided into social-ecological communities (*ahupua'a*) that also typically extended from the mountains to the sea (Figure 3). The islands were also divided horizontally into social-ecological zones, which spanned across regions and connected communities to one another in a contiguous manner via managed habitats. While each island had a different suite of zones to manage resources, each community had to have at least one type of forest zone in order to properly function while most communities managed several. One of the zones that was managed on each of the high islands, but not in every community, was a sacred forest zone (wao akua), which is a zone of cloud forest managed as a refuge for endemic biodiversity that maintained core watershed function. Within this system freshwater, nutrients, and sediment were managed vertically within each community; while species abundance and connectivity were managed horizontally on a regional scale. This system of Hawaiian IRM began to break down in the 19th century after European contact, with the last vestiges of it enduring into the middle of the 20th century (Winter et al., 2018). However, this system of IRM is currently being revived in some communities under the auspices of biocultural restoration (Winter et al., 2020b; Winter et al., 2020c) and is seen as a viable model to solve issues of sustainability and conservation at both local and global scales (Gon and Winter, 2019; Winter et al., 2020b).

---

opportunity to investigate the role of soil and climate in driving plant ecological processes and ecophysiological function.

While there are still large, contiguous regions of forest across the islands, changes in resource management over the last two centuries have led to a dramatic reduction in the percentage of area covered by forests. During Hawai'i's pre-contact era, Indigenous resource management strategies aimed to maintain forested landscapes (Box 3, Fig. 3) (Winter et al., 2018, 2020a). Post-contact, these methods gave way to an approach that prioritized plantations and pasturelands. The proliferation of non-native species has further shrunk the footprint of native-dominated forest. Of the remaining forested area, Hawai'i Island has the highest percentage of native-dominated forests, whereas human-modified forests now dominate much of the landscape on the other islands, particularly on O'ahu (Jacobi et al., 2017). Furthermore, on each of the islands, more than half of the land area is covered by plant communities of primarily non-native plant species (Jacobi et al., 2017).

3.2. Classification

Given the extreme variation in Hawai'i's physical environment (Section 2), developing a classification system for vegetation that works across the islands is notoriously difficult (Mueller-Dombois and Fosberg, 1998). First, most vegetation classifications do not account for substrate

age and corresponding soil properties, which are known to influence forest structure and composition. Second, the most common way to characterize Hawaiian landscapes, and thus their plant communities, is by climate, particularly mean annual temperature and rainfall (Appendices D, E). While convenient, using climate as the primary means for delineating communities is overly simplistic in Hawai'i. For example, although mean annual precipitation is a key predictor of plant communities on a global scale (Holdridge, 1947), some Hawaiian regions show no association between mean annual rainfall and soil moisture, as the latter is also greatly influenced by fog, topography, seasonality, soil texture, and soil age (Price et al., 2012). In addition, rainfall is difficult to measure with high spatial resolution given Hawai'i's orographically driven rainfall and topographic complexity (Frazier and Giambelluca, 2017; Giambelluca et al., 2013).

Considering the extreme environmental heterogeneity of the Hawaiian Islands, a system for classifying plant communities (Appendix F) was developed based on elevation (a proxy for temperature), moisture, and dominant physiognomy (Wagner et al., 1999). According to this system, there are 58 unique woody plant communities in Hawai'i, excluding the coastal zone (Gagne and Cuddihy, 1990). Rather than further delineate Hawai'i's woody plant communities, we take a holistic view here, synthesizing research carried out in all of Hawai'i's native forest types. In some communities, plants are of low stature, and these
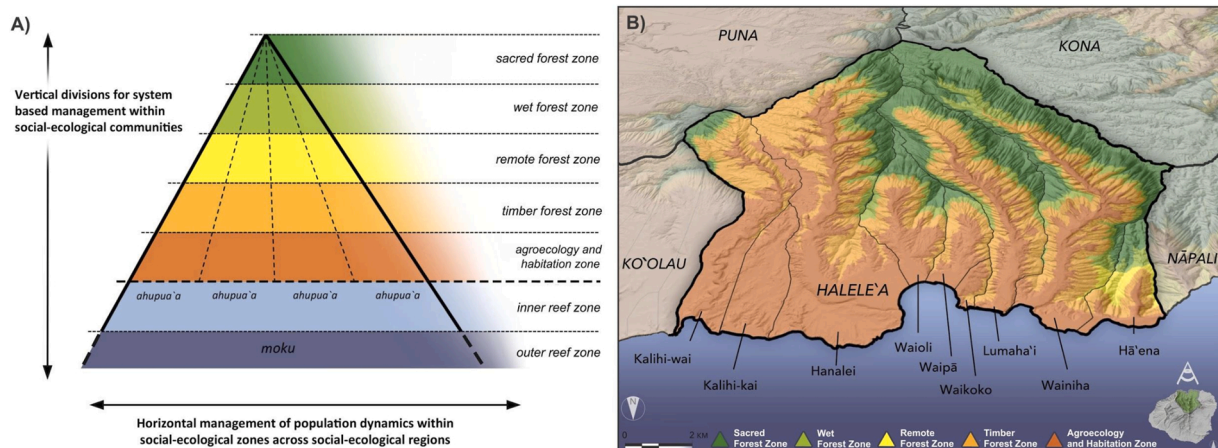
Fig. 3. Reproduced from Winter et al. 2018: A schematic model (A) and a spatial model (B) depicting the layout of a single social-ecological region (*moku*) based on the Hawaiian social-ecological system on the island of Kaua'i. (A) The terrestrial and oceanic social-ecological zones and their subcategories are oriented horizontally. *Ahupua'a* or social-ecological communities are oriented vertically. (B) The *moku* of Halele'a encompasses numerous *ahupua'a*, each with jurisdiction over a full spectrum of terrestrial and oceanic social-ecological zones within its boundaries.
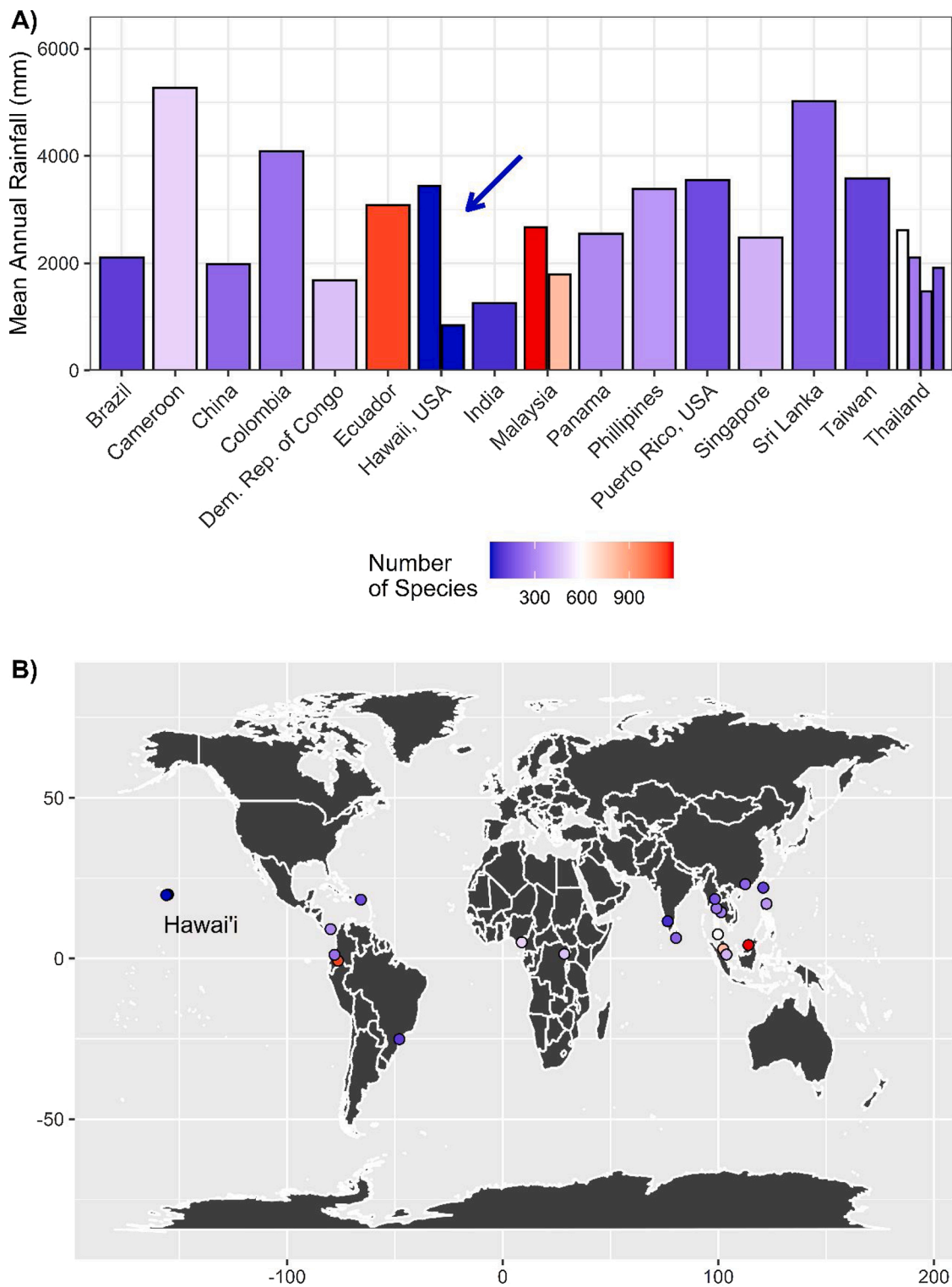
Fig. 4. Comparisons of species diversity and mean annual rainfall for tropical forests that form part of the ForestGeo network (https://forestgeo.si.edu/), based on previously published data (Davies et al., 2021; Ostertag et al., 2014). Species richness was calculated from species area curves, generated by plotting the cumulative number of species against the number of 20 m x 20 m quadrats sampled (area) in each 4-ha (200 m x 200 m) plot until the entire plot was sampled. A) Hawaiʻi is similar to other tropical forests in mean annual rainfall but has B) dramatically lower species richness compared to forests on continents and islands at similar latitudes. Multiple bars represent different sites within each country or region.

might arguably be referred to as shrublands; we include those here as forests because they are often contiguous with higher-statured forest stands.

As mentioned above, Hawaiian forests differ from many tropical forests in having dominance by relatively few tree species and overall low species richness (Fig. 4) (Ostertag et al., 2014). Some of the most

Table 1
Ranked species list of the ten most and least abundant plant species surveyed in the 530 forest plots compiled in the OpenNahele database (Craven et al., 2018). Plots are situated across all the main Hawaiian Islands, with the greatest sample area on Hawai'i Island. Relative abundance is the proportion of individuals for that species among the total 43,590 individuals sampled across all plots.

Species	Origin	Rank Abundance	Relative Abundance
Metrosideros polymorpha	native	1	0.330
Psidium cattleyanum	non-native	2	0.204
Cibotium glaucum	native	3	0.090
Cibotium menziesii	native	4	0.050
Cheirodendron trigynum	native	5	0.035
Schinus terebinthifolia	non-native	6	0.029
Leucaena leucocephala	non-native	7	0.022
Acacia koa	native	8	0.016
Psidium guajava	non-native	9	0.011
Ardisia elliptica	non-native	10	0.011
Dracaena aurea	native	174	5.73E-06
Dracaena konaensis	native	175	5.73E-06
Dubautia plantaginea	native	176	5.73E-06
Melicope anisata	native	177	5.73E-06
Myrsine lanaiensis	native	178	5.73E-06
Pittosporum glabrum	native	179	5.73E-06
Wikstroemia furcata	native	180	5.73E-06
Euphorbia multiformis	native	181	2.72E-06
Senna gaudichaudii	native	182	8.59E-07
Pittosporum terminalioides	native	183	1.43E-07

common woody genera in Hawai'i, which occur as dominants or co-dominants in multiple community types and across elevation and moisture gradients, include *Acacia, Diospyros, Dodonaea, Metrosideros, Leptecophylla, Nestegis, Sapindus, Cheirodendron, Bobea, Psychotria,* and *Vaccinium* (Appendix F). For some of these taxa, dominance appears to be driven by the large number of ecologically diverged forms that exist and whose physical traits allow them to establish over a range of

substrate ages and environmental conditions (Appendix G). For example, *Metrosideros polymorpha* (Myrtaceae) is the most abundant and widespread tree (Table 1), and it dominates many of the woody plant communities across a range of substrate age (including recent lava flows), precipitation, and elevation, as well as various successional stages from pioneer to climax communities. *Metrosideros* likely arrived in the Hawaiian Islands 3–4 mya when the oldest main islands, Kaua'i and O'ahu, were still forming (Dupuis et al., 2019; Percy et al., 2008), thus providing a source of wind-dispersed seeds (Drake, 1992) for the colonization of each younger island as it arose. Today, *Metrosideros* (predominantly *M. polymorpha*) accounts for approximately one-third of all tree stems in forest monitoring plots (Craven et al., 2018). More work remains to be done to clarify why *Metrosideros*, a genus of slow-growing species, have come to dominate Hawai'i's forests, although tolerance of a wide range of environmental conditions seems to be key.

3.3. Structure

The structural characteristics of Hawaiian forests, such as stand density, basal area, and biomass, are diverse and influenced by climatic, substrate age, and soil properties. A combined approach of remote sensing and plot-level data indicate that there are higher proportions of aboveground biomass and lower proportions of litter and downed woody debris in forests that occur in wet environments (Asner et al., 2011, 2016; Hughes et al., 2014; Selmants et al., 2017). Total biomass generally increases with precipitation (Ostertag et al., 2014), but not with temperature in mature wet forests (Selmants et al., 2014). Even within similar climates, aboveground biomass can vary considerably: from 14 to 108.1 Mg/ha in forests on the drier end and 200–958.9 Mg/ha in wetter forest environments (Imhoff, 1995; Litton et al., 2006; Ostertag et al., 2014). In addition, live and detrital biomass in wetter conditions generally increases with substrate age (Aplet and Vitousek, 1994; Kitayama et al., 1997b). The variation in biomass values is certainly due to factors other than climate, but should be evaluated carefully due to inconsistencies among studies in how biomass is measured and estimated. Thus, the abiotic factors underlying aboveground biomass accumulation in Hawai'i's forests are complex, and

Table 2
Characteristics of the ForestGeo forest dynamics plots arranged from low to high mean annual precipitation. Elevation, MAP, plot size, and number of trees reported in (Davies et al., 2021); other variables reported in (Ostertag et al., 2014).

Site	Plot Code	Land Type	MAP (mm)	Dry Season Months	Mean Elevation (m)	Plot Size (ha)	No. of Trees	Trees/ha	Basal area (m2/ha)	Aboveground biomass (Mg/ha)
Palamanui, HI, USA	PLN	Island	835	12	265	4	15,652	3913	8.6	29.4
Mudumalai, India	MUD	Mainland	1255	6	1050	50	25,500	510	25.5	174.2
Huai Kha Khaeng, Thailand	HKK	Mainland	1476	6	596	50	72,500	1450	31.2	211.2
Ituri, D.R. Congo	ITU	Mainland	1682	3.5	775	40	288,000	7200	35.4	
Pasoh, Malaysia	PAS	Mainland	1788	1	80	50	300,211	6004.22	31	339.8
Doi Inthanon, Thailand	DOI	Mainland	1908	6	1670	15	73,269	4884.6	39.8	
Dinghushan, Guangdong, China	DIN	Mainland	1985	0	350	20	71,617	3580.85		
Ilha do Cardoso, Brazil	ILH	Mainland	2100	1	6	10.2	40,000	3921.569	29	
Mo Singto, Thailand	MOS	Mainland	2100	5	770	30.5	134,942	4424.328	31.77	
Bukit Timah, Singapore	BUK	Island	2473	0	99	4	17,239	4309.75	34.5	
Barro Colorado Island, Panama	BCI	Mainland	2551	3	120	50	208,400	4168	32.1	306.5
Khao Chong, Thailand	KHA	Mainland	2611	3	235	24	121,500	5062.5		
Lambir, Malaysa	LAM	Island	2664	0	174	52	359,600	6915.385	43.5	497.2
Yasuni, Ecuador	YAS	Mainland	3081	0	230	50	297,778	5955.56	33	282.4
Palanan, Philippines	PAL	Island	3380	4.5	97	16	78,205	4887.813	39.8	290.1
Laupahoehoe, HI, USA	LAU	Island	3440	1	1160	4	14,641	3660.25	67.3	247.9
Luquillo, Puerto Rico	LUQ	Island	3548	0	381	16	154,177	9636.063	38.3	276.1
Nanjenshan, Taiwan	NAN	Island	3582	0	320	5.88	12,133	2063.435	36.3	
La Planada, Colombia	LPL	Mainland	4087	0	1818	25	105,400	4216	29.8	177.6
Sinharaja, Sri Lanka	SIN	Island	5016	0	500	25	193,400	7736	45.6	357.9
Korup, Cameroon	KOR	Mainland	5272	3	195	50	329,000	6580	32	

characterizing the interactions among these factors warrants consideration of local environmental properties but also, the component of plant structure measured.

A hallmark of ecological and biogeochemical studies in Hawai'i has been the ability to isolate the impact of single or multiple driving variables on the structure and function of terrestrial ecosystems by examining natural environmental gradients. The advantage of examining these gradients in Hawai'i is two-fold; the islands comprise extreme variation in environmental conditions, yet because species richness is low, species turnover is not nearly the confounding factor it is in other locations. For example, the use of chronosequences – substrate-age gradients – to infer processes such as substrate development, forest succession, and ecosystem development over time – is best done in systems like Hawai'i that have low biodiversity and disturbances of low frequency and severity (Walker et al., 2010). The long substrate-age gradient across the island chain, ranging in age from *ca.* 300 to >4.1 million years (Crews et al., 1995), has been used to study ecosystem development including soil nutrient availability (Crews et al., 1995; Vitousek et al., 1988), ecosystem productivity (Herbert and Fownes, 1999), plant resource-use efficiency (Treseder and Vitousek, 2001), fine root dynamics (Ostertag, 2001), decomposition (Hobbie and Vitousek, 2000), and forest succession (Kitayama and Mueller-Dombois, 1995). This space-for-time substitution approach has helped to define our understanding of ecosystem development over long time periods and has been generalized to far-removed ecosystems (Selmants and Hart, 2010). Resource gradient studies have also yielded important insights. For example, the Mauna Loa matrix gradient includes a series of sites that together can disentangle effects of elevation from temperature and precipitation, as well as lava flow age and lava type (Aplet and Vitousek, 1994; Crews et al., 1995; Kitayama et al., 1995). Other studies have focused on rainfall (Austin and Vitousek, 2000; Schuur, 2001; Schuur et al., 2001) and mean annual temperature gradients (Bothwell et al., 2014; Giardina et al., 2014; Iwashita et al., 2013; Litton et al., 2011; Pierre et al., 2017; Selmants et al., 2014).

It can be instructive to examine Hawaiian forests in the context of other tropical forests. Hawai'i has two long-term forest dynamics plots on Hawai'i Island as part of the Smithsonian's ForestGeo network, in which all plots employ the same standardized methods, mapping and measuring all stems ≤ 1 cm diameter at breast height. Laupāhoehoe is a montane wet forest at 1160 m elevation, with a mean annual temperature (MAT) of 16 °C and mean annual precipitation (MAP) of 3440 mm. Pālamanui is a lowland dry forest at 265 elevation, 20 °C MAT and 835 mm MAP. The two Hawaiian plots have strikingly low species richness, with only 21 species at Laupāhoehoe and 15 species at Pālamanui (Fig. 4). When forest structure is compared to the four sites within ±300 mm rainfall (Table 2), the montane wet forest site is similar in biomass, in the intermediate range in terms of tree density, and high in basal area (due to its high tree fern abundance, while other sites do not have tree ferns). Thus, low species richness does not seem to constrain many of the typical structural attributes found in this climatic zone, and the structure of the Laupāhoehoe forest is also similar to other montane wet forests in Hawai'i that are not part of this global network (Ostertag et al., 2014). At the drier end of the spectrum, however, Hawai'i's forests stand out in two ways: 1) very low basal area and biomass, and 2) dry periods that are year-round rather than a wet/dry seasonality. One indicator of a forest's dryness is the number of dry-season months, defined as months with < 100 mm rainfall (Mooney et al., 1995). A global comparative study of climate relationships in dry forests from Central America, South America, Africa, Asia, and Australia catalogued dry seasons ranging from 0.6 to 5.9 months per year (Malhi and Wright, 2004). However, several of the forests in Hawai'i experience 12 dry season months per year (Ostertag et al., 2014; Sandquist and Cordell, 2007). None of the other ForestGeo plots have such dry year-round conditions (Table 2). Even the sites with the greatest seasonality (6-months dry season at DOI, HKK, MUD) are not similar in terms of diameter distributions or basal area, but the Hawaiian forest

structure may be confounded by lava flow age.

There are several attributes of Hawaiian forests that may be extremely consequential and that deserve more study in a comparative framework. First, despite having a stem density similar to that of other tropical wet forests (Table 2), the canopy of Hawaiian forests tends to be quite open (Funk and McDaniel, 2010; McDaniel and Ostertag, 2010), which influences understory vegetation dynamics including recruitment and may be partially responsible for high invasion rates (see Section 5). Second, Hawaiian climatic records show extreme inter-annual variability in precipitation, especially in drier sites (Frazier and Giambelluca, 2017; Sandquist and Cordell, 2007). The low predictability of rainfall in Hawaiian forests likely affects plant function, and future studies could examine how this variability shapes the evolution of seed production and seedling regeneration, similar to approaches applied in fire-prone ecosystems (Keeley et al., 2011).

3.4. Human-induced regime shifts

Island forests have been profoundly affected by humans. A number of plants, mammals, and pathogens introduced by humans have adversely influenced native biodiversity and led to various waves of extinctions, each of which has had profound ecological ramifications in island systems (Wood et al., 2017). Hawai'i is no exception, being first impacted when seafaring Polynesians discovered the islands *ca.* 1000 years ago (Wilmshurst et al., 2011). The Polynesians brought with them a suite of plants and animals (including most notably the dominant food crops *kalo* (taro, *Colocasia esculenta*) and 'uala (sweet potato, *Ipomoea batatas*) as well as the Polynesian pig), which collectively comprised a portable biocultural toolkit (*sensu* Winter et al., 2018b) that ensured their survival in their new island home and allowed them to perpetuate their cultural traditions. Using Indigenous resource management, Hawaiians employed their biocultural toolkit to create mosaicked cultural landscapes (Box 3, Fig. 3), including areas dedicated to agroforestry that combined native and introduced species within highly managed novel plant communities (Winter et al., 2018, 2020a). A modeled prototypical land division from the ancient Hawaiian period (Box 3, Fig. 3) showed that as much as 40 % of the land area in low-elevation regions was dedicated to these cultural landscapes and novel forests (Winter and Lucas, 2017), with an even smaller percentage of area representing forested landscapes that were converted to field agro-ecology for the cultivation of crops such as taro and 'uala (Kurashima et al., 2019). The remaining 60 % was dedicated to maintaining various native forest types, including the wao akua (sacred forest), a zone of montane cloud forests that functioned as source populations for native species and preserved core watershed areas (Winter et al., 2018; Winter and Lucas, 2017).

Paleoecological data indicate that forests in the Hawaiian Islands have transitioned through a series of stable states over time (Athens et al., 2002; Burney et al., 1995, 2001; Hotchkiss and Juvik, 1999), punctuated by species turn-over driven by human-caused species introductions and referred to as "regime shifts" (Folke et al., 2004). Polynesian arrival is thought to have led to one of these regime shifts, largely driven by the introduction of the Pacific rat (*Rattus exulans*), which led to the initial collapse of lowland forest through seed depredation, a pattern observed following rat introductions to islands globally (Drake and Hunt, 2009). For example, in the mid-Holocene, lowland forests of O'ahu were dominated by *Pritchardia* palms, the leguminous shrub *Kanaloa kahoolawensis*, and *Dodonaea viscosa*, but seed depredation by Pacific rats led to rapid collapse of these lowland forests and conversion to grasslands within the span of 50–100 years (Athens et al., 2002). Radiocarbon data indicate that human settlement into these disturbed lowland habitats occurred after collapse of the forests, supporting the conclusion that the Pacific rat was the primary driver of this regime shift (Athens et al., 2002). Various native animal species similarly declined during the period after Polynesian arrival, including the large birds such as the moa nalo (*Thambetochen chauliodous*) and Big Island Goose (*Branta rhuax*) (James et al., 1987; Paxinos et al., 2002).

Box 4
Community assembly of Hawaiian forest: the kīpuka model system.

Community assembly at the archipelago-scale reflects long-distance dispersal to the Hawaiian Islands followed by diversification and inter-island migration, as discussed in Section 4. In addition, local-scale community assembly processes have been relatively well studied in Hawai'i, particularly on Hawai'i Island where forest fragments of various sizes occur throughout a landscape dominated by young lava flows (Figure 5). These remnant forest fragments, the kīpuka system, provide a model system for investigating classic ideas about assembly processes with respect to habitat size and isolation from source communities as originally formalized by the Island Biogeography Theory (MacArthur and Wilson, 1967) and later refined to account for matrix features affecting dispersal and meta-population dynamics (Laurance, 2008). Diversity across the kīpuka system corroborates general patterns reported elsewhere – higher species richness in larger kīpuka with relatively lower edge/area ratios, and more similar community composition among more connected kīpuka for birds (Flaspohler et al., 2010), spiders (Vandergast and Gillespie, 2004), and root-associated fungi (Vannette et al., 2016). However, links between kīpuka size, connectivity and diversity are not always observed, suggesting that dispersal across the lava matrix may not be a hard barrier to more mobile forest organisms, such as canopy arthropods (Petillon et al., 2020; Tielens et al., 2019).

The kīpuka system may provide insights into forest responses to novel sources of fragmentation associated with agriculture, animal husbandry, forestry plantations, suburbanization, and urbanization, which have reduced forest habitat and dissected previously large tracts of forest into fragments of varying size and connectivity. How these landscape modifications intersect with invasive species and climate change to affect Hawaiian forests are likely to be devastating to the future persistence of native island forest species, both in Hawai'i and globally (Gillespie et al., 2008). For example, invasive species are becoming so abundant in Hawaiian kīpuka that they dilute any potential relationship between native species richness and kīpuka size or connectivity in birds and spiders (Flaspohler et al., 2010; Petillon et al., 2020), and invasive rats can alter kīpuka food web dynamics (Wilson Rankin et al., 2018). Notably absent from kīpuka community assembly research are studies of plant diversity, most likely as a consequence of the dominance of *Metrosideros polymorpha* within these forest fragments. However, the extrapolation of kīpuka research as a model for understanding forest fragmentation dynamics in Hawai'i is limited by the absence of plant diversity studies, particularly for the older Hawaiian Islands where community assembly is not dominated by *M. polymorpha*. Considering the negative effects of fragmentation on forest canopy structure (Vaughn et al., 2014), cascading effects on plant diversity are likely.

The loss of these species eliminated the guild of large browsing herbivores from the Hawaiian Islands (see Section 7.1 for further discussion), with cascading effects on forest food webs (James and Burney, 1997). Although evidence reveals that over time, *R. exulans* spread into higher elevations, forests remained dominated by native species for centuries, likely because Hawaiians limited activity in montane areas (Athens et al., 2002; Burney et al., 1995, 2001). This altered stable state was in place for centuries until the arrival and proliferation of other non-native species in the 19th century, including the black rat (*Rattus rattus*), mosquitoes (*Culex* spp.), and Eurasian pigs (*Sus scrofa*), which interbred with the Polynesian pig and then became feral (Burney and Kikuchi, 2006). These arrivals triggered the current regime shift and led to widespread declines in native-dominated forests at all elevations. In short, extinction events and ecological changes started with the arrival of Indigenous peoples in Hawai'i, then increased significantly in the colonial and post-colonial periods with further species introductions and altered land-management strategies, a pattern common within island systems globally (Wood et al., 2017).

Indigenous resource management strategies and practices limited the human footprint to low elevations (Gon et al., 2018) and promoted connectivity throughout species distributions in the Hawaiian era (Winter et al., 2018). The abandonment of those practices, along with the proliferation of large-scale agriculture (e.g., cattle ranching and monotypic plantations) in the 19th century, led to the rapid loss and degradation of native ecosystems through increasing dominance by non-native plants. This process has accelerated in the modern era (Gon
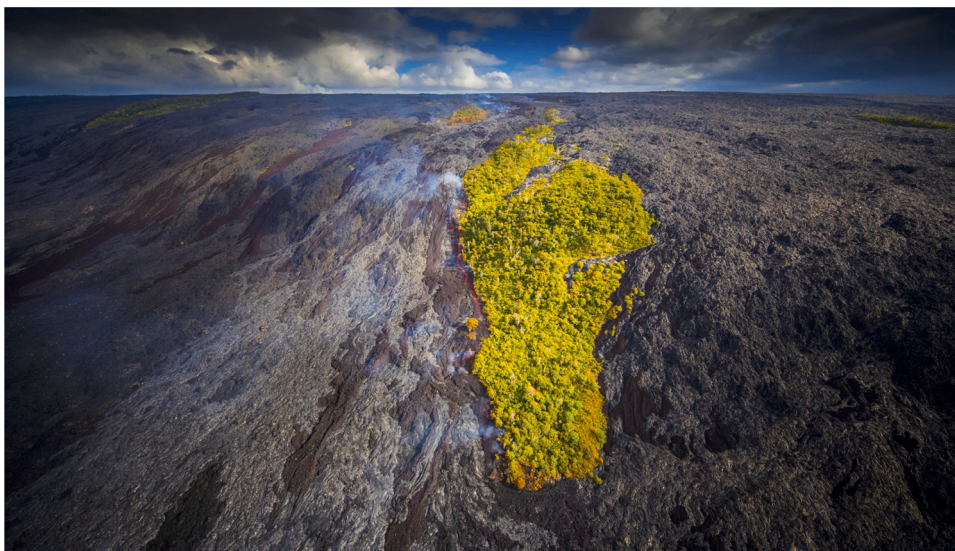

Fig. 5. Hawai'i Island Kīpuka. Photo credit: Andrew Richard Hara.

et al., 2018). In addition, the Hawaiian landscape has become more fragmented since human settlement. Whereas fragmentation is a natural consequence of the active volcanoes that make up the younger Hawaiian Islands (Vaughn et al., 2014), human-caused fragmentation is particularly important on the older islands where volcanism is millions of years in the past (Box 4, Fig. 5). Forest fragmentation likely influences plant community dynamics via negative effects on reproduction and fitness (Aguilar et al., 2006), by increasing conduits for non-native species, and by altering the physical environment. Although natural fragmentation caused by lava flows has been extensively researched in Hawai'i (Flaspohler et al., 2010; Vaughn et al., 2014), the consequences of anthropogenic fragmentation on Hawaiian forests has not been studied.

4. Diversity patterns and processes

The Hawaiian Islands have long been held as a model study system for disentangling the roles of community assembly and evolutionary processes in biodiversity (Emerson and Gillespie, 2008). As established in the previous section, the archipelago comprises a geographically isolated chronosequence of volcanic islands of known age (Sherrod et al., 2007) and striking structural and climatological complexity. This combination of features allows the study of the tempo and mode of lineage diversification in response to local biological, climatological, and geographical conditions and allows the tracking of community assembly and whole-ecosystem evolution across islands (Rominger et al., 2016).

Habitat suitable for colonization has existed on the islands for roughly 30 million years (Clague, 1996), but the vast majority of extant lineages derive from colonists that arrived within the past five million years (Price and Clague, 2002). While the focus of this review is on forests, in this section on diversity patterns, it is difficult to limit our discussion only to forests, because almost all studies have been conducted on an archipelago-scale. Studies focusing on diversity patterns by habitat type would be extremely fruitful, given variation in selective pressures across environments.

4.1. Biotic disharmony

As a result of Hawai'i's striking isolation from continental landmasses, its biota is characterized by striking *in situ* species radiations and the notable absence of whole groups that are widespread outside of the islands. Strong barriers to dispersal have led to a biota comprising predominantly angiosperms, ferns, arthropods, gastropods, and birds (Carr, 1987). The islands' endemic biota is derived almost entirely by *in situ* speciation of a limited number of lineages, which allows researchers to study the ecological and geographic drivers (Gillespie and Baldwin, 2009) and life history correlates (Price and Wagner, 2004) of biodiversity. Some Hawaiian lineages are hyper-diverse following spectacular radiations within the islands (e.g. lobeliads, honeycreepers, some insect groups) while many lineages that are well represented on continents are absent from Hawai'i (e.g., mangroves, figs, parrots, doves, terrestrial mammals except bats). Endemism is a common feature of island biotas, and thus the diversity patterns and processes characterized in the Hawaiian Islands may be represented of those of other systems (Gillespie et al., 2013).

The origin of the Hawaiian flora is global. A recent update of Fosberg's classic study (Fosberg, 1949) reports that of the 259 Hawaiian plant lineages examined, 78 are of widespread origin, whereas other common sources of the Hawaiian flora are Indo-Malayan (31), Neotropical (34), North American (30), Australasian (28), East Asian (10), and unknown (48) (Price and Wagner, 2018). A substantial number of lineages arrived in Hawai'i via previous dispersal from other Pacific Islands (Price and Wagner, 2018), indicating the importance of

stepping stones in colonization process. The younger islands were typically seeded by initial colonizations from older islands following Funk and Wagner's progression rule (Funk and Wagner, 1995; Shaw and Gillespie, 2016). The widely observed unidirectional colonization of, and subsequent diversification on, younger islands is likely the consequence of limited niche availability and strong competition with resident populations constraining colonization of older islands. Several counter-examples exist, however, of successful back-colonization of older islands, such as species of *Schiedea* (Wagner et al., 1995), *Cyrtandra* (Johnson et al., 2017), *Clermontia* (Givnish et al., 2013), and *Metrosideros* (Percy et al., 2008; Stacy and Sakishima, 2019).

Natural colonization of the Hawaiian Islands by plants requires high dispersibility and occurs via three major dispersal modes in increasing order of importance: abiotic dispersal (water and wind), external bird dispersal through adhesion of small seeds, and internal bird dispersal via ingestion (Carlquist, 1974; Price and Wagner, 2004, 2018; Sakai et al., 1995). These dispersal types show geographic patterning; external dispersal by bird is proportionally higher from North American taxa and lower in Pacific taxa, whereas internal bird dispersal is proportionally higher in Austral and Pacific taxa, and lower in widespread taxa (Price and Wagner, 2018). Because, on average, seed size is smaller for herbaceous plants than for forest trees, Hawai'i's colonizing angiosperms were likely predominantly herbaceous (Carlquist, 1974).

The native angiosperm flora found in all biomes across the main islands comprises 1039 species derived from just 259 presumed colonists (Price and Wagner, 2018). The exceptional endemism of Hawai'i's angiosperms (90 % at the species level) is due to dramatic radiations within just a handful of these lineages. Indeed, the ten largest lineages represent just 4% of original colonists yet comprise 41 % of Hawai'i's angiosperm species (Price, 2004). In ferns and lycopods, diversification is more modest, presumably due to the greater passive dispersibility (and thus broader species distributions) of ferns, multiple colonizations to the same island, and lower speciation rates (Driscoll and Barrington, 2007), but there is still remarkably high endemism at 78.1 % of the 210 species (Ranker et al., 2019).

Hawai'i is also home to a disharmonic animal biota that plays important roles in forests, including snails, spiders, and insects (Cowie and Holland, 2008; Gillespie and Roderick, 2002; Holland and Cowie, 2009). For example, it has been estimated that there are approximately 10,000 native insect species derived from a mere ~350−400 colonization events from around the Pacific (Eldridge and Miller, 1995; Howarth and Mull, 1992). Conversely, the only terrestrial vertebrates native to Hawai'i are birds and one insectivorous bat species; reptiles, amphibians, and non-volant mammals are absent from the native fauna, likely reflecting the barriers to dispersal of large, non-flying animals. The presence of such a disharmonic animal biota led to distinct plant-animal interactions in Hawaiian forests compared to continental forests, interactions which are now severely threatened by extinctions and altered by invasions (discussed below).

4.2. Diversity patterns

Patterns of plant diversity at the scale of whole archipelagoes have received extensive theoretical and empirical attention. According to the dynamic theory of island biogeography, species richness is expected to have a hump-shaped pattern with island age (Borregaard et al., 2017; Lim and Marshall, 2017; Whittaker et al., 2017, 2008). Young islands are expected to have low species richness that increases over time as colonization from the older islands occurs; speciation rates are also highest on young islands, as a consequence of high niche availability. As islands age, they subside and lose size, eventually leading to a decline in richness, and these trends on young and old islands is expected to result in a peak in species richness on intermediate-aged islands. The latter

prediction is well supported by datasets from the Azores, Canaries, Galápagos, Marquesas, and Hawaiian Islands (Whittaker et al., 2008). For the current main Hawaiian Islands, species richness of plants is greatest on Kaua'i, and lowest on Hawai'i Island (Craven et al., 2019; Price, 2004), indicating that Kaua'i is currently at the intermediate age of Whittaker's model and will lose species richness in the future. This pattern of diversity extends to individual clades as well (Price, 2004), with a majority of angiosperm lineages having peak richness on the oldest island, Kaua'i (seven of the ten richest lineages), and the lowest species richness on the youngest island, Hawai'i Island (true for nine of the ten richest lineages).

Diversity patterns of Hawai'i's non-flowering plants are not as well-characterized as those of flowering plants, although there are island checklists for ferns and fern allies (Palmer, 2003; Ranker et al., 2019) and mosses (Staples et al., 2004). Unlike angiosperms, ferns and lycophytes tend to be widespread across all of the main islands (Ranker et al., 2019), and thus do not appear to follow Whittaker's model. Relatively few studies have examined patterns of functional diversity among ferns and lycophytes (Waite and Sack, 2010, 2011), and this is an important gap in our knowledge as these are dominant members of the Hawaiian forest understory.

Extant plant diversity in Hawai'i is heavily represented by naturalized non-native species, which are abundant and widespread in Hawaiian forests (Table 1, Fig. 6), with several of the most abundant also occurring across diverse forest types (Ainsworth and Drake, 2020). Between 1840 and 1999, 7866 ornamental species were brought to the islands; of these, 420 have naturalized, 141 are listed as invasive, and 39 of those are identified as noxious (Schmidt and Drake, 2011). A more recent estimate on the native and naturalized non-native plant species in all Hawaiian biomes lists 1365 native and 1470 non-native species (Wagner et al. 2005). A forest-specific inventory revealed that the relative abundance of non-native plants varies considerably across islands (Craven et al., 2018). Some non-native plants in Hawaiian forests have clearly reached the final stages of invasion in which they contribute to declines in native flora and fauna and disrupt ecosystem function (Blackburn et al., 2011). Nonetheless, even with these examples, it remains difficult to predict which of the more recent arrivals will spread and disrupt Hawaiian forests in the future.

4.3. Diversity processes: adaptive radiations

As mentioned above, a majority of Hawai'i's biodiversity stems from adaptive radiations of relatively few colonizing lineages. These radiations are shaped by the striking environmental heterogeneity of the islands and facilitated by the disharmonic nature of Hawai'i's biota, which is thought to leave open niches (Carr, 1987). Through adaptation to contrasting environments, many Hawaiian plant groups display great morphological diversity (Appendix G) and occur across a much broader array of habitats than their mainland counterparts (Baldwin and Sanderson, 1998; Carlquist, 1974; Funk and Wagner, 1995; Ganders and Nagata, 1984). Whereas some lineages provide evidence for the importance of pollination mode and growth forms (woody versus herbaceous) as drivers of adaptive radiation (Weller et al., 2017), mode of seed dispersal is the most important correlate (Price and Wagner, 2004). Specifically, lineages with seeds that are internally dispersed by birds are the most speciose, and those with abiotically dispersed seeds are the least species-rich. Moreover, Price and Wagner (2004) found that broadly distributed lineages comprising isolated populations derived through internally-bird-dispersed seeds are most likely to have undergone radiations. While this pattern indicates that stochastic processes in small populations may contribute substantially to plant speciation in Hawai'i, the importance of genetic drift and mutation in these adaptive radiations is not known. Further, with just a few exceptions (Ekar et al., 2019; Givnish et al., 2004; Morrison and Stacy, 2014), the specific abiotic factors associated with, and likely responsible for, species diversification across Hawai'i's heterogeneous landscape have not been examined.

Because of the recency of most colonization events, variation at molecular markers used for plant phylogenetic analyses is low despite high morphological diversity in many Hawaiian groups (Appendix G). This problem is expected for recent and rapid radiations, and it frustrates attempts for species-level phylogenies and thus robust tests of evolutionary hypotheses in Hawaiian plants. For example, high cross-fertility and frequent hybridization among closely related taxa may have contributed to many Hawaiian plant radiations (Dunbar-Co et al., 2008; Johnson et al., 2019; Nepokroeff et al., 2003; Wagner et al., 1999). Natural hybridization that results in high fertility of first-generation
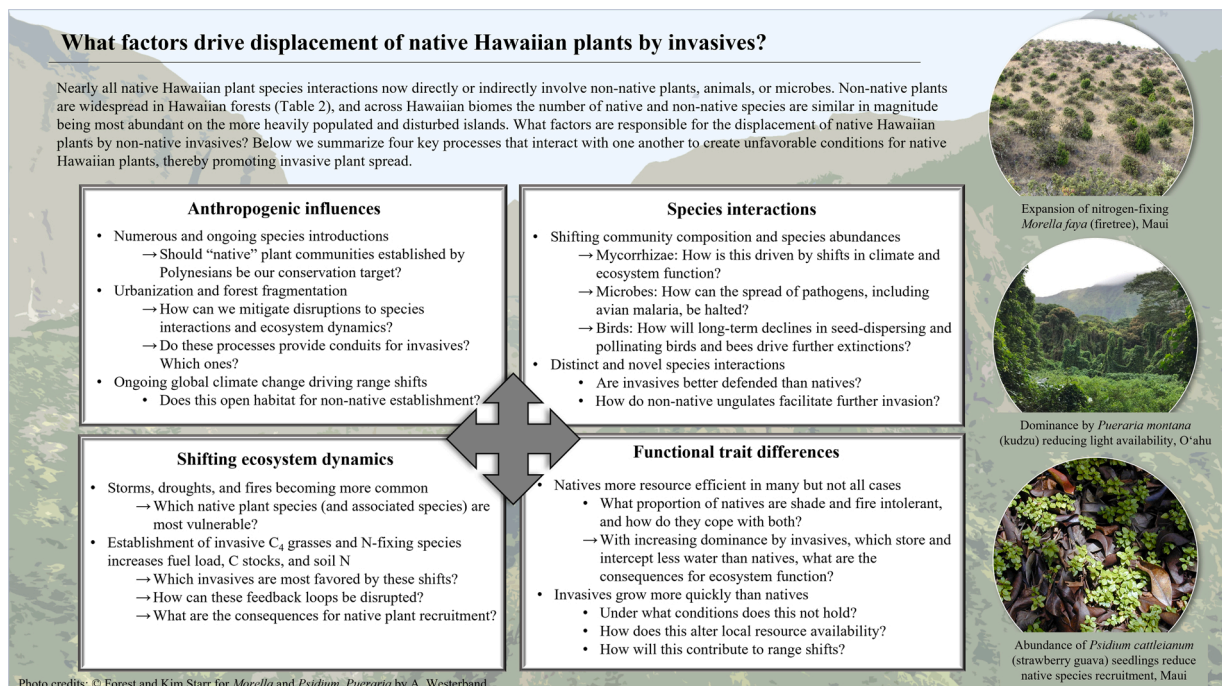

What factors drive displacement of native Hawaiian plants by invasives?

Nearly all native Hawaiian plant species interactions now directly or indirectly involve non-native plants, animals, or microbes. Non-native plants are widespread in Hawaiian forests (Table 2), and across Hawaiian biomes the number of native and non-native species are similar in magnitude being most abundant on the more heavily populated and disturbed islands. What factors are responsible for the displacement of native Hawaiian plants by non-native invasives? Below we summarize four key processes that interact with one another to create unfavorable conditions for native Hawaiian plants, thereby promoting invasive plant spread.

Anthropogenic influences
- Numerous and ongoing species introductions
  - → Should "native" plant communities established by Polynesians be our conservation target?
- Urbanization and forest fragmentation
  - → How can we mitigate disruptions to species interactions and ecosystem dynamics?
  - → Do these processes provide conduits for invasives? Which ones?
- Ongoing global climate change driving range shifts
  - • Does this open habitat for non-native establishment?

Species interactions
- Shifting community composition and species abundances
  - → Mycorrhizae: How is this driven by shifts in climate and ecosystem function?
  - → Microbes: How can the spread of pathogens, including avian malaria, be halted?
  - → Birds: How will long-term declines in seed-dispersing and pollinating birds and bees drive further extinctions?
- Distinct and novel species interactions
  - • Are invasives better defended than natives?
  - • How do non-native ungulates facilitate further invasion?

Shifting ecosystem dynamics
- Storms, droughts, and fires becoming more common
  - → Which native plant species (and associated species) are most vulnerable?
- Establishment of invasive C_4 grasses and N-fixing species increases fuel load, C stocks, and soil N
  - → Which invasives are most favored by these shifts?
  - → How can these feedback loops be disrupted?
  - → What are the consequences for native plant recruitment?

Functional trait differences
- Natives more resource efficient in many but not all cases
  - • What proportion of natives are shade and fire intolerant, and how do they cope with both?
  - → With increasing dominance by invasives, which store and intercept less water than natives, what are the consequences for ecosystem function?
- Invasives grow more quickly than natives
  - • Under what conditions does this not hold?
  - • How does this alter local resource availability?
  - • How will this contribute to range shifts?

Expansion of nitrogen-fixing *Morella faya* (firetree), Maui

Dominance by *Pueraria montana* (kudzu) reducing light availability, O'ahu

Abundance of *Psidium cattleianum* (strawberry guava) seedlings reduce native species recruitment, Maui

Photo credits: © Forest and Kim Starr for *Morella* and *Psidium*, *Pueraria* by A. Westerband

Fig. 6. Simultaneous and interacting factors underly the displacement of native by non-native plants in Hawaiian forests.

hybrids and thus allows for introgression between taxa appears to be a regular feature in species-rich lineages such as *Bidens* (Ganders and Nagata, 1983), as well as the forest trees *Euphorbia* (Koutnik, 1990), and *Cyrtandra* (Carr, 1987; Ziegler, 2002). Introgressive hybridization among incipient forms creates novel gene combinations that may promote adaptation to novel environments (Carr, 1987; Lewontin and Birch, 1966) and thus adaptive radiation (Seehausen, 2013). Consistent with this mechanism, recently evolved species of *Scaevola* originating from hybridization have been confirmed through molecular data (Howarth and Baum, 2005). In addition, intraspecific hybridization within the hypervariable *M. polymorpha* (Stacy et al., 2016) has been suggested as a source of some of the many varieties of this species (Ziegler, 2002). The recency of evolutionary diversification of Hawaiian plant groups and their propensity for hybridization make them ideal systems for investigating the role of introgression in the evolution of exceptional species richness (Meier et al., 2017).

Recent applications of next-generation DNA sequencing, are allowing much improved insight into plant evolution in Hawai'i (Choi et al., 2020; Izuno et al., 2017; Knope et al., 2020). As these new techniques allow for the construction of more accurate phylogenies, there is now an opportunity to investigate intersections between functional traits (Medeiros et al., 2019) and community diversity patterns. While such research is flourishing in other geographic regions (Cadotte et al., 2019), these synthetic approaches, merging community ecology and evolution, are lacking for Hawai'i.

4.4. Diversity processes: incipient plant radiations and non-radiating lineages

While the most species-rich groups have attracted the greatest attention from evolutionary biologists, there are many widespread species with tantalizing morphological variation that have received little attention (Appendix G). Such species are especially interesting because they offer the best opportunity for studying divergence and speciation in progress (Ramsey et al., 2003; Via et al., 2000).

The best example of a lineage undergoing incipient radiation is Hawaiian *Metrosideros*. Only five species of *Metrosideros* are recognized in Hawai'i, and all are likely derived from a single colonist to the islands 3.1 ± 0.6 mya (Dupuis et al., 2019) to 3.9 ± 2.5 mya (Percy et al., 2008). Yet studies of the most ecologically and geographically dominant member of this genus, *M. polymorpha*, reveal considerably more taxa than the eight varieties currently described (Dawson and Stemmermann, 1990). These varieties and tentative races are distinguished through vegetative characters and are non-randomly distributed across Hawai'i's heterogeneous landscape, from wet forests and bogs to new lava flows, deserts, subalpine zones, riparian zones, and windy cliffs (Stacy et al., 2020). On Ko'olau Volcano, O'ahu, leaf micromorphological characters differentiate six of seven infraspecific taxa of *M. polymorpha* (Sur et al., 2018), and all taxa examined to date on Hawai'i and O'ahu show evidence of local adaptation to particular environments or isolated abiotic features of these environments (Cordell et al., 2000, 1998; Ekar et al., 2019; Kitayama et al., 1997a; Morrison and Stacy, 2014; Stemmermann, 1983). The three most abundant varieties of *M. polymorpha* on Hawai'i Island also show heritable variation in floral characters consistent with biotic selection across elevational and successional gradients (Stacy and Johnson, 2021). The partial but significant reproductive isolating barriers observed between taxa within islands (Rhoades, 2012; Stacy et al., 2017) and the broad variation in the extent of genetic isolation of these forms (DeBoer and Stacy, 2013; Izuno et al., 2017; Stacy et al., 2014; Stacy and Sakishima, 2019; Stacy et al., 2020) are consistent with ongoing adaptive radiation in Hawaiian *Metrosideros* (Stacy et al., 2014), including the emergence of a riparian variety through incipient sympatric speciation (Choi et al., 2020). Evidence from across the genus suggests that *Metrosideros* may have a high capacity for adaptation to extreme environments, as evidenced by four independent origins of stenophyllous rheophytes in Hawai'i, New Caledonia (Dawson, 1992),

Lord Howe Island (Green, 1990), and South Africa (Van Steenis, 1981).

In spite of Hawai'i's spectacular radiations, most angiosperm lineages comprise single species (Price, 2004). While some of these monotypic groups display intriguing morphological variation (Appendix G), at least 15 endemic species appear monomorphic despite being widely distributed throughout the islands (St. John, 1946). These species may have evolved to become generalists as a consequence of ecological release, although the reason for the failure of speciation in these groups, many of which are species-rich in other parts of the world, is unknown.

4.5. Diversity processes: non-adaptive radiations

In some species-rich lineages, divergence does not seem to correspond to abiotic or biotic variation, suggesting that diversification occurred allopatrically through drift (i.e., that radiations are non-adaptive). Among angiosperms, the species-rich genus *Cyrtandra* may result from largely non-adaptive diversification (Carlquist, 1974). *Cyrtandra* is a species-rich genus distributed throughout the Pacific with recent diversification in the Hawaiian Islands (Johnson et al., 2017). Nearly all *Cyrtandra* species are narrowly distributed within wet upland forest understories; 57 of 60 species in Hawai'i are single-island endemics (treating Maui Nui as a single island) with many described as micro-endemics. Speciation within this group appears to have occurred predominantly through geographic isolation of small populations following founder events (Cronk et al., 2005; Johnson et al., 2017), with associated phenotypic divergence through drift, and hybridization in sympatry limited by postzygotic barriers (Johnson et al., 2015). Purported examples of non-adaptive radiations should be viewed with caution, however, as they may result from agents of selection that are more difficult to measure.

4.6. Adaptive shifts in phenotypes

The preponderance of adaptive radiations in Hawai'i offers a unique opportunity to investigate the evolution of phenotypic diversity and ecological release. Some of the phenotypic trends observed in Hawaiian plants are consistent with trait syndromes predicted for other island biotas (Burns, 2019; Patiño et al., 2017), while others are not.

Shifting species interactions and migrations from coastal to inland habitats are thought to have driven phenotypic shifts in native Hawaiian plants. Most plant colonizations to Hawai'i occurred in open, dry, or coastal areas, with many groups secondarily expanding into and adapting to wet forests (Carlquist, 1974). Altered dispersibility associated with shifts in dispersal vectors have been described. For example, in *Bidens*, there was loss of seed structures that attach to bird feathers, and in *Euphorbia*, there was an increase in fruit and seed size and loss of stickiness, both of which possibly reduced dispersibility (Wagner et al., 2005); in contrast, the mints (*Phyllostegia, Stenogyne*) and some lobeliads (*Clermontia, Delissea, Cyanea*) evolved fleshy fruits that attract birds (see Section 6), which likely increased dispersibility (Givnish et al., 2009; Lindqvist et al., 2003). Moreover, many of the largest-fruited (or –seeded) species are restricted to the oldest islands of O'ahu and Kaua'i (Carlquist, 1974), consistent with an evolutionary trend of increasing fruit size over time. Distributions of floral traits indicate evolutionary shifts as well, such as the evolution of moth pollination in *Brighamia* within the otherwise bird-pollinated lobeliads (Walsh et al., 2019).

Evolution of woodiness from herbaceous ancestors is common in Hawaiian angiosperms and has led to the highest global proportion of woody species of any flora in the world (Carlquist, 1974). An excellent example is the species-rich genus *Euphorbia*, with species transitions from sprawling and prostate plants in dry, coastal scrublands to tall trees in mid-elevation forests on O'ahu (Yang and Berry, 2011). In *Plantago*, woodiness has evolved twice, alongside the incursion into forest and shrubland habitats from bogs (Dunbar-Co et al., 2008). The reasons underlying increased woodiness in Hawai'i's flora are unknown, but likely include the recurring evolution of wet-habitat forest species from

coastal or dry habitat forest species, high rainfall in some forests favoring trees or shrubs, and the islands' relatively benign climate in some regions, which promotes continued growth year round and the perennial habit (Burns, 2019; Carlquist, 1974).

4.7. Effects of disharmony

Frontiers for future research involve understanding the effects of disharmony on forest community composition, functional composition and ecosystem functioning. For example, highly polymorphic species such as *M. polymorpha* are widespread and abundant in Hawaiian forests (e.g., present in 435/534 forest plots sampled across the islands (Craven et al., 2018)), whereas species from the diverse adaptive radiation of *Cyrtandra* are present in just two plots. Future examination of the interconnections among plant traits and the effects of disturbances on species, community, and ecosystem scale processes would provide new insights into the dynamics of a highly endemic biota to changing assembly and physical conditions, as has been shown elsewhere (Comita et al., 2018).

5. Demography, life history, and functional ecology

Research on the population dynamics and ecology of Hawaiian forest plants is heavily biased toward *M. polymorpha*, the most abundant and widespread tree species, and Hawai'i Island where the largest tracts of intact native forest remain (Jacobi et al., 2017). Less is known about the demography, functional ecology, and life history of Hawai'i's other forest trees and forests on the older islands.

5.1. Hawaiian tree demography

Studies of tree demography in Hawai'i are limited. Assessments of stage- and size-class distributions have been conducted for a few of Hawai'i's dominant species (Drake and Mueller-Dombois, 1993), but these data have rarely been used to quantify population growth rates and dynamics. Moreover, few studies have estimated growth and mortality rates across multiple ontogenetic stages or environments, instead providing snap-shots for a single ontogenetic stage and location. Recent demographic studies have revealed that consumption by non-native animals strongly influences the population dynamics of three endangered Hawaiian forest shrubs (Bialic-Murphy and Gaoue, 2018; Bialic-Murphy et al., 2017, 2018), but that each species is also affected by different environmental factors such as precipitation (Bialic-Murphy and Gaoue, 2018) and the availability of suitable germination sites (Bialic-Murphy et al., 2017). These studies showcase the value of long-term monitoring and demographic modeling for understanding the factors regulating Hawaiian forest plant population dynamics and for identifying key threats to endangered plant sustainability (Aguraiuja et al., 2008; Wong and Ticktin, 2015).

Growth rate estimates for Hawai'i's woody species reveal considerable variation among species. For example, for eight species on Hawai'i Island, annual increases in trunk diameter ranged from 0.5 mm/yr for *Vaccinium calycinum*, a understory shrub/small tree, to 4.0 mm/yr for the canopy dominant *A. koa*; *M. polymorpha* was close to the lower end of that range at 1.3 mm/yr (Hart, 2010). Faster growth rates have been reported for some forest trees in dry sites on Hawai'i Island, peaking with the shrub/small tree *Psydrax odorata* at 8.9 mm/yr (Sandquist and Cordell, 2007). In comparison, median growth rates of tropical tree species outside of Hawai'i range from 0.35 to 13.41 mm/yr in Costa Rica (Lieberman et al., 1985), from 6.0–75 mm/yr in Puerto Rico (Lugo et al., 1990), and 3.2–9.4 mm/yr in Venezuela (Worbes, 1999), indicating that Hawaiian species are within the range of growth rates reported for other topical forests, but may cluster at the slow end of the spectrum. Surprisingly few studies have compared growth rates of native and non-native forest species, with some evidence that non-native species have higher growth rates than native trees (Pattison et al., 1998;

Stratton and Goldstein, 2001). Additional research comparing a diverse suite of growth metrics of native and non-native species throughout ontogeny could elucidate the stage at which non-native trees appear to out-compete native species, providing crucial insights into the displacement of native by non-native species in Hawaiian forests.

Apart from the well-documented episodic mortality of *M. polymorpha* (canopy dieback events), data on mortality rates are scarce for Hawaiian forest species. In montane wet sites on Hawai'i Island, annual mortality ranged from 0.98 % for *Ilex anomala* to 5.82 % for *Coprosma ochracea*, and annual mortality for *M. polymorpha* was 1.1 % (Hart, 2012). As expected, mortality rates varied across ontogenetic stages (not considering seed and seedling stages) for both *M. polymorpha* and *A. koa*, with the highest rates in the largest (oldest) trees (Hart, 2012). Mortality rates and sources of mortality across the archipelago and across gradients, including climate, disturbance, and species interactions (e.g. novel diseases and natural enemies), are needed to better understand how Hawai'i's plant populations may cope with future changes in the environment.

5.2. Seedling recruitment in Hawaiian forests

Seedlings growing in Hawai'i's forests experience environmental conditions that are distinct from other tropical forests for multiple reasons. First, owing to the relatively open canopy of Hawaiian forests, light levels in Hawaiian forest understories tend to be considerably higher, at 6.4 % transmitted irradiance (Inman-Narahari et al., 2013), than those of other evergreen rainforests, which typically range from 0.01–3.0% (Coomes and Grubb, 2000). In addition, Hawai'i's volcanic substrate presents several challenges for seedling establishment, including low nutrient availability and minimal water retention in young substrates. The substrate-age gradient leads to different recruitment dynamics across the archipelago, where young substrates are dominated by episodic recruitment leading to even-aged stands, and older substrates are dominated by gap-phase recruitment.

Seed dormancy, longevity (in storage), and germination patterns are well described for many Hawaiian plants due to a focus over the past 20 years on seed banking for conservation (Baskin and Baskin, 2014; Chau et al., 2019), although the extent to which these patterns reflect variation under natural conditions is unknown. Seed rain studies reveal dominance by *M. polymorpha*, which deposits thousands of minute, wind-dispersed seeds per m^2 per year (Cordell et al., 2009; Drake, 1992, 1998; Inman-Narahari et al., 2013). Typically, less than 20 % of these seeds are embryo-filled (Burton, 1982; Drake, 1992), at least partially due to pollen limitation (Stacy et al., 2017). Other native species may be seed-limited with exceptionally low germination rates (Cordell et al., 2009). Whether poor seed germination of Hawaiian forest plants is a characteristic of the flora or a consequence of altered pollinator and disperser communities is not known. Phenological patterns of flowering and seed production remain poorly described for Hawaiian forest trees, although many species are reported to have ripe fruits coinciding with the wet season (Wagner et al., 1999). Upon maturation, seed consumption by non-native rodents poses a serious threat to native plant regeneration (Chimera and Drake, 2010; Pender et al., 2013; Shiels and Drake, 2011). With the exception of species with physical dormancy such as *A. koa* and *Sophora chrysophylla*, and a few other exceptions such as *Pipturus albidus*, many native species do not form a persistent seed bank (Drake, 1998).

Regeneration of Hawaiian forest plants occurs in various ways, including seed germination on the ground and aerial substrates, sprouts of individual trees, and simultaneous recruitment of whole stands following periodic, widespread dieback. Coarse woody debris (CWD) colonized by mosses during decomposition has relatively high nutrient availability (Nadkarni and Matelson, 1992), and in montane wet sites on both well-drained and water-logged soils, bryophyte-covered CWD is a primary substrate for native seedling recruitment (Burton and Mueller-Dombois, 1984; Cooray, 1974; Iwashita et al., 2013;

Mueller-Dombois, 2000; Santiago, 2000). In water-logged soils, CWD may also alleviate anaerobic conditions by elevating seedlings off the substrate (Santiago, 2000). When CWD is far off the ground, as in nurse logs, seedlings also gain the advantage of reduced disturbance by non-native ungulates, such as feral pigs, or falling tree fern leaves (Busby et al., 2010; Drake and Pratt, 2001). Many seeds germinate on tree ferns (Cole et al., 2012; Drake and Pratt, 2001; Inman-Narahari et al., 2013), which presumably offer similar protection from disturbance. Because most previous seedling recruitment studies were conducted in unfenced areas where ground recruitment is limited by ungulate disturbance, it is likely that recruitment directly in the soil is more common than previously thought, as demonstrated by recruitment patterns in fenced areas (Cole and Litton, 2014).

Light quantity and quality are important factors in Hawaiian forest seedling recruitment. In general, seedling survival is higher under high-light conditions, although high conspecific seedling density can outweigh the benefits of high light (Inman-Narahari et al., 2016; Schulten et al., 2014). Although Hawaiian forests tend to have a relatively open canopy, understory light levels in Hawaiian montane wet forest sites can be quite low where tree and ground ferns such as *Dicranopteris linearis* form dense canopies (Russell et al., 1998), and the increased light provided by treefall gaps may be important for seedling recruitment in such forests, particularly for shade-intolerant canopy species like *A. koa* (Burton and Mueller-Dombois, 1984; Drake and Mueller-Dombois, 1993; Hart, 2010). Dry-adapted forest species likely recruit under relatively high light conditions, and non-native grasses constrain native recruitment in Hawaiian dry forests by reducing light and soil moisture (Thaxton et al., 2010, 2012). Where grass invasions have occurred, light levels have been reduced to the extent that native seedling recruitment is almost entirely absent (Cordell et al., 2009; Denslow et al., 2006). Weeding to remove the grasses can increase native seedling recruitment (Cordell et al., 2009; Denslow et al., 2006), but because it is highly labor-intensive, this is unlikely to be a viable long-term management strategy. Shading treatments that effectively limit grass growth while allowing recruitment of shade-tolerant native species (Funk and McDaniel, 2010; McDaniel and Ostertag, 2010) may be a more cost-effective plan. However, because many Hawaiian forest species are relatively shade intolerant, native species may be quickly displaced by more shade-tolerant invaders once there is canopy closure (McDaniel and Ostertag, 2010; Schulten et al., 2014). This pattern is in stark contrast to most native-invader dynamics in continental forests, and is driven by the high light availability that characterizes the understory of Hawaiian forests.

In general, non-native species are recruiting at high rates in Hawaiian forests (Cordell et al., 2009; Mascaro et al., 2008). While the forest canopy is still dominated by native trees, more successful recruitment by non-native than native seedlings could portend dramatic shifts in community composition to dominance by non-native species as the canopy trees die (Fig. 6). Persistent soil seed banks (Drake, 1998), high seed production (Cordell et al., 2009), preferential dispersal by non-native birds (Vizentin-Bugoni et al., 2021, 2019), vigorous seedling growth (Lurie et al., 2017), and low susceptibility to damage by non-native herbivores (Joe and Daehler, 2008; Shiels et al., 2014) likely all contribute to high seedling establishment of non-native plants in Hawaiian forests. Because our understanding of native species recruitment derives from studies on Hawai'i or Maui Islands, these results may not be representative of patterns on the older, more eroded (steeper) and species-rich islands of O'ahu and Kaua'i, where non-episodic gap phase recruitment is more likely. Additional research spanning more species, forest types, and substrate ages is thus needed to more broadly understand and identify the conditions optimal for recruitment. Because of ongoing changes to the substrate and overstory of many forests by non-native species (Box 5, Fig. 7), more information about recruitment requirements could shed light on factors constraining *in situ* germination rates of native forest species, and inform management efforts aimed at enhancing natural recruitment as a conservation goal (Chazdon and

---

Box 5
Novel and hybrid ecosystems

In this era of the Anthropocene (Braje and Erlandson, 2013), many of Hawai'i's landscapes are human-dominated and, due to global trade and transport, contain new mixes of species. Novel ecosystems were first defined as persistent new ecosystem configurations formed by introduced species (Hobbs et al., 2006). Hybrid ecosystems represent an intermediate condition where there are mixtures of native and introduced species (Hobbs et al., 2014). Disturbances and degradation can easily convert a historically native-dominated forest into a hybrid or novel ecosystem (Figure 7A, blue arrows). While restoration is possible (Figure 7A, red arrows), it is labor intensive and expensive, and arguably increasingly difficult to return from hybrid to historical, and perhaps no longer logistically feasible to return from novel to historical directly (Cordell et al., 2016; Ostertag et al., 2009; Suding et al., 2004). Thus, a strong argument can be made that the remaining mostly-native Hawaiian ecosystems should be prioritized for conservation. Acceptance of the idea that some environmental changes create hybrid and novel ecosystems that are irreversible is a paradigm shift (Hobbs et al., 2014).

Understanding the functioning of hybrid and novel ecosystems is vital. Critical questions that need to be addressed in Hawaiian forests relate to the beneficial functional roles that non-native species may play (Ewel and Putz, 2004). Introduced trees may serve as nurse plants, as perches for seed recruitment, as nitrogen-fixers, as phytoremediators, or as fuel for prescribed burns (Ewel and Putz, 2004). Introduced fauna may serve as seed dispersers for native species (Cole et al., 1995; Foster and Robinson, 2007), but are not always dispersing native seeds (Chimera and Drake, 2010; Pejchar, 2015). In addition, humans must make value judgments about the ecosystem properties most desired. For example, novel forests on Hawai'i Island had greater species richness, diversity, and rates of aboveground productivity and nutrient cycling than native forest sites (Mascaro et al., 2012), but are those conditions desirable on an island that has been constrained by low nutrients and limited long-distance dispersal for its evolutionary history? The ecosystem services being provided and the interactions occurring among species must be examined on a case-by-case basis in specific locations, because there is no common rulebook for these novel conditions.

One approach to evaluate the costs and benefits of novel and hybrid ecosystems is through deliberate construction of these ecosystems, either in the field or through modeling. Self-assembled vs. designed ecosystems can be distinguished, with that latter having a human-centered goal (Higgs, 2017). In a hybrid restoration experiment in Hilo, Hawai'i called Liko Nā Pilina (Figure 7B), four different mixes of native and non-native non-invasive species are being evaluated in terms of plant growth, survival, and reproduction, community assembly of leaf litter arthropods, and ecosystem properties (Ostertag et al., 2020; Ostertag et al., 2015). In a hypothetical study based on Kaua'i, the relative costs of forest restored to pre-rat conditions (all native), pre-European (with Polynesian introductions), and a hybrid state were compared. The hybrid restoration stood out as moderate in cost, supportive of native plant regeneration and native insect abundance, cultural importance, and resilience to disturbance (Burnett et al., 2019). More research is needed on whether these hybrid ecosystems maintain these services in the long term.
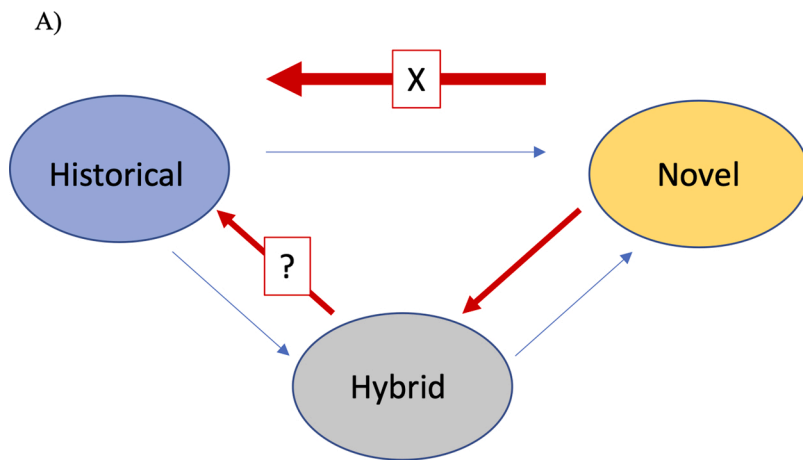
A)

B)

Fig. 7. Hawaiian forests include native-dominated communities that resemble historical pre-human contact assemblages as well as communities composed of a combination of native and introduced species, referred to as hybrids. Increasingly, species turn-over and modification of habitats and ecosystem dynamics are leading to novel ecosystems that are persistent and not easily converted back to historical conditions (A). Restoration efforts influence shifts between ecosystem types with variable success (Box 5). On Hawai'i Island, a hybrid restoration experiment called Liko Nā Pilina (B) investigates how four different mixes of native and non-native non-invasive species influence plant growth, survival, and reproduction, as well as community assembly of leaf litter arthropods, and ecosystem properties. Photo credit: Rebecca Ostertag.

Guariguata, 2016).

5.3. Tree physiology and morphology

The dominance of *M. polymorpha* across such a broad range of environments coincides with remarkable genetic and phenotypic variation, as highlighted in the previous section. Less attention has been paid to intraspecific variation in traits of other native species, although this is changing in recent years (Givnish et al., 2004; Scoffoni et al., 2015; Waite and Sack, 2010). In general, plants in low-diversity forests such as those in Hawai'i are predicted to be slow-growing and conservative in their leaf economic traits (Wright et al., 2004), strategies thought to lead to weak competitive ability compared to continental plants (Simberloff, 1995). Consistent with these predictions, native species have been documented to have higher leaf mass per area, lower leaf nitrogen and phosphorus concentrations and photosynthetic rates, and higher leaf construction costs compared to non-native species in Hawai'i (Baruch and Goldstein, 1999; Funk et al., 2013; Gleason and Ares, 2004; Pattison et al., 1998). Native species also typically have low stomatal conductance and high water-use efficiency at the leaf and whole-tree levels (Cavaleri et al., 2014; Cordell et al., 2002; Kagawa et al., 2009; Santiago et al., 2000; Stratton et al., 2000), resulting in the now widely held claim that Hawai'i's native tree species are 'water savers' and non-natives are 'water spenders.' Most of these studies were restricted to relatively few species on Hawai'i Island, however, and differences in allocation strategies were often not considered. For example, photosynthetic rates in native species can be higher than those of non-native species when considered on an area rather than a mass basis (Funk et al., 2013), and when integrated over the total leaf lifespan, photosynthetic nitrogen-use efficiency is similar between native and non-native tree fern species (Durand and Goldstein, 2001). Considering the extensive environmental gradients that occur within Hawaiian forests, it is not surprising that climate contributes to leaf functional trait expression and adds complexities to these patterns. For example, an archipelago-wide study of 91 species found that non-native woody plants tend to be more resource acquisitive (higher photosynthetic rate, leaf N and P concentrations) in cool, wet habitats whereas native woody plants tend to be more acquisitive in hot, arid habitats (Westerband Knight and Barton, 2021). Other studies have similarly found that climate and resource availability can influence native versus non-native trait differences in Hawai'i (Funk and Vitousek, 2007; Henn et al., 2019), and in some instances, differences in functional trait space may be driven by shifts in community composition following invasion, from woody- to herbaceous-dominated communities. Clearly, the "syndrome" that island plants are more conservative in their leaf ecophysiology and economics has only partial support among studies on Hawaiian trees, and much of our current knowledge regarding trait differences stems from studies conducted primarily on Hawai'i Island (Funk and Vitousek, 2007; Henn et al., 2019). How these patterns of leaf ecophysiology influence plant performance and population dynamics are unclear but would benefit from

additional research, particularly for rare species that may be vulnerable to extinction.

6. Positive interactions

Pollination and seed dispersal in Hawai'i's forests involve interactions with insects and birds. Birds are the only native vertebrate pollinators and frugivores in Hawai'i, which further distinguishes Hawai'i from other tropical islands, where bats and reptiles are also important pollinators and seed dispersers (Fleming and Kress, 2013). Because many birds went extinct before being studied by western scientists, much of what has been published regarding their roles as pollinators and frugivores has been inferred from the morphology of birds' bills and tongues, and from observations by early naturalists and descriptions in mo'olelo (Hawaiian oral histories); there has been surprisingly little effort to document the effectiveness of the remaining birds as pollinators. Given the limited number of extant native bird species that serve as pollinators, this task is tractable, and would be a valuable contribution to studies that compare the simplified pollination webs of Hawai'i to continental systems. In addition, recent research has documented climate-mediated decreases in the population sizes of Hawaiian forest birds that are likely pollinators and dispersers of many forest plant species (Benning et al., 2002; Paxton et al., 2016), which would contribute to an accelerated regime shift in Hawaiian forests.

6.1. Pollination

Information on specific plant-pollinator relationships in Hawai'i is fairly limited, but floral morphology suggests that 67 % of native plants are likely pollinated by insects, 19 % by birds, and 14 % by wind (Sakai et al., 2002). Although bees are most important pollinator group at the global scale, they are represented in Hawai'i by a single lineage of about 60 species in the genus *Hylaeus* (Colletidae) (Zimmerman, 1948), which occurs in virtually all habitat types, including forests (Daly and Magnacca, 2003). Although *Hylaeus* bees were among the most common native insects around the turn of the 20th century, today their populations are severely reduced, and many species are now rare or extinct owing to their heavy reliance on native plant resources and sensitivity to non-native insects (Magnacca, 2007; Miller et al., 2015; Wilson and Holway, 2010).

Hylaeus bees have been recorded on the flowers of over 60 native plant species, but they are thought to utilize community-dominant species most heavily (Daly and Magnacca, 2003; Magnacca, 2007). For example, these bees frequently visit and carry the pollen of *M. polymorpha* and *A. koa* flowers (Hanna et al., 2013; Koch and Sahli, 2013; Lach, 2008). *Hylaeus* may be important pollinators for other native plants that tend to receive few other regular visitors (Magnacca, 2007), especially species that, unlike *M. polymorpha*, are not also highly attractive to birds. Quantitative assessments of *Hylaeus* floral visitation rates and networks, however, are few and concentrated in coastal (Shay et al., 2016) and high-elevation ecosystems (Wilson et al., 2010). Interactions of *Hylaeus* with native plant communities in mid-elevation, closed-canopy forests in mesic to wet sites have yet to be characterized.

Even less is known about the roles of other insects in the pollination ecology of native Hawaiian plants. Many moths, for example, visit flowers nocturnally, and these interactions are not often observed. One recent series of studies discovered that two endangered *Schiedea* species occurring in forests with intermediate rainfall are pollinated only in the evening, and only by one to several species of small native moths, some of which remain undescribed (Weisenberger et al., 2014; Weller et al., 2017). Neither of the two native butterfly species (*Vanessa tameamea* and *Udara blackburnii*) has been confirmed to pollinate native trees, although adults of both species feed on *A. koa* nectar. One common conclusion to date is that native pollinating insects are strongly reliant on native plant resources, but whether the converse is equally true remains poorly understood. Floral visitation is now dominated by

non-native insects in many Hawaiian ecosystems, and these insects tend to visit a wider range of native and non-native plants than native pollinators (Aslan et al., 2019; Kuppler et al., 2017). Whereas non-native species like European honey bees may be replacing lost pollination services in some cases (Hanna et al., 2013), their more generalist behavior may reduce pollination effectiveness in others via heterospecific pollen transfer (Miller et al., 2015).

Native flower-visiting birds are restricted to two monophyletic endemic lineages. The honeyeaters (Mohoidae) consist of five extinct species, all of which were specialist nectar feeders with relatively large, curved bills (Fleischer et al., 2008). The honeycreepers (Fringillidae, Drepanidini) consist of over 50 species, most of which are now extinct. At least five of these were specialist nectar feeders, and several others were generalists that occasionally consumed nectar (Banko and Banko, 2009; Pratt, 2005, 2009). The strongest inferences on bird pollination have been made for the lobeliads (Campanulaceae), a radiation of over 120 endemic species of shrubs and small trees (Givnish et al., 2009). Nearly all species in the lineage bear large, tubular flowers that appear adapted to pollination by birds, and all species examined produce the relatively dilute, hexose-dominated nectar commonly found in passerine-pollinated plants (Lammers and Freeman, 1986; Pender et al., 2014). Reproduction in some lobeliads may now be limited owing to the extinction of all honeyeaters and most honeycreepers (especially the nectar specialists with long, curved bills), and the decline of most remaining nectar-feeding honeycreepers. Native birds are increasingly infrequent visitors to lobeliads in many Hawaiian forests, especially at low and mid elevations where introduced avian malaria has decimated native bird populations (Cory et al., 2015). The introduced, generalist warbling white-eye (*Zosterops japonicus*) visits lobeliads, acting as an effective pollinator for species with small, accessible flowers, but species with deeper, more strongly curved flowers are either avoided or nectar-robbed by these birds (Aslan et al., 2014a, b). The role of self-pollination across lobeliad species remains unclear, but the decline of most species within this lineage suggests that a lack of pollinators may be one factor limiting regeneration, and that co-extinctions of plants and specialist pollinators have occurred and are in progress in Hawaiian forests.

6.2. Seed dispersal

Approximately 40–50 % of Hawaiian flowering plants produce fleshy fruits (Sakai et al., 2002), most of which are presumably adapted for dispersal by vertebrates. At least two major lineages of plants evolved fleshy-fruitedness after arriving in the islands: Campanulaceae and Lamiaceae. In addition to their roles as pollinators, birds are Hawai'i's only native vertebrate frugivores. This again distinguishes Hawai'i from most tropical islands, where seed-dispersing frugivores commonly include birds, bats, and reptiles (Fleming and Kress, 2013). The single native bat species, 'ōpe'ape'a (*Aeorestes semotus*), is insectivorous (Gorresen et al., 2018).

Birds that feed primarily on fruit include only two of the honeycreepers (though several generalist honeycreepers occasionally consume fruit), all five species of thrush (Turdidae), and all three crows (Corvidae) (Banko and Banko, 2009). Three of the five thrushes (*Myadestes*) are now extinct, and one rare species is restricted to montane rain forest on Kaua'i (Pratt, 2009). The single remaining common species (*M. obscurus*, 'ōma'o) occurs in montane forests on Hawai'i Island (Pejchar, 2015). Two of Hawai'i's three species of crows (*Corvus*) are known only from sub-fossil remains, and the remaining species (*C. hawaiiensis*) currently exists only in captivity. In addition to these frugivorous birds, which were almost certainly seed dispersers, at least six species of honeycreepers that consumed fruits and seeds had heavy bills specialized for crushing seeds and likely functioned more as seed predators than seed dispersers (Banko and Banko, 2009; Carpenter et al., 2020; Olson, 2014; Walther and Hume, 2016). Most of these species are extinct, and their effects on plant reproduction are unknown. The remaining species, *Loxioides bailleui* (palila), is now restricted to

high-elevation forests on Mauna Kea, where it relies heavily on seeds of *Sophora chrysophylla* and the insect larvae they contain (Hess et al., 2014).

Inferences regarding the roles of extinct species in seed dispersal in Hawai'i are largely speculative, and even for the extant frugivores, little is known about dispersal beyond information on diets (Banko and Banko, 2009). The only published estimates of seed dispersal distances by native birds are for the 'ōma'o (Pejchar, 2015; Wu et al., 2014). Current frugivore communities also include several non-native birds that differ from native species in consuming smaller fruits, potentially driving selection for smaller fruits and thus a shift in community composition toward small-fruited species (Sperry et al., 2021). For example, the 'ōma'o inhabits montane forests on Hawai'i Island where it co-occurs with two generalist, non-native species: the warbling white-eye (*Zosterops japonicus*) and red-billed leiothrix (*Leiothrix lutea*) (Pejchar, 2015). The 'ōma'o consumes significantly larger fruits than either of the non-natives, and hence a greater range of species (Pejchar, 2015), but likely disperses them over shorter distances than the warbling white-eye (Wu et al., 2014). Similarly, the 'alalā (*Corvus hawaiiensis*), extinct in the wild, is the largest remaining native forest bird and consumes larger seeds than all other extant birds (Culliney et al., 2012; Matsuoka, 2020). A more recent study that focused on diet diversity in the field found that plant species richness of 'ōma'o was significantly greater than leiothrix, and that the warbling white-eye had the lowest diet diversity and was the least frugivorous (Matsuoka, 2020).

There is increasing evidence that many introduced bird species, including at least 45 passerines and 12 gamebirds, may be at least partially filling the roles of extinct native dispersers (Foster, 2009), particularly for small-seeded native plants in the wet-montane (Foster and Robinson, 2007; Matsuoka, 2020) and dry-lowland (Chimera and Drake, 2010) forests. However, recent studies in seven forests on O'ahu found that 93 % of seed dispersal events involved alien birds dispersing small-seeded alien plants (Vizentin-Bugoni et al., 2021, 2019), even in native-dominated forest. Matsuoka (2020) suggests that if the two native frugivores become extinct, the forest community would shift towards smaller-seeded species such as *Vaccinium* spp. and *R. hawaiensis*.

The recent, near-complete extinction of native fruit-eating birds has resulted in seed dispersal networks composed entirely of novel dispersers (Case and Tarwater, 2020; Vizentin-Bugoni et al., 2021, 2019), which are expected to result in altered patterns of seed dispersal for a majority of species. In particular, the Hawaiian flora includes several species with large ($\geq$ 5 cm diameter), fleshy fruits that have no known seed disperser, e.g., *Pritchardia martii* (Arecaceae), *Ochrosia* spp. (Apocynaceae), and *Alectryon macrococcus* (Sapindaceae) (Wagner et al., 1999). Potential dispersers in prehistoric times include the larger crows and possibly some species of moa-nalo, an extinct lineage of large, flightless waterfowl (Walther and Hume, 2016), though the latter might also have destroyed some of the seeds they ingested, if they consumed them at all (Carpenter et al., 2020). Research in montane mesic forest suggests that two of the four species examined were dispersal limited (Denslow et al., 2006). In Hawai'i's dry-habitat forests, where the fruits of native species tend to be larger, the effects of the loss of native seed dispersers are potentially even more severe. Whereas nearly 60 % of native forest tree species in a dry site had fleshy fruits, the predominant seed disperser of today, the warbling white-eye, overwhelmingly disperses non-native seeds (>92 % of seeds carried) rather than native seeds (<8% carried; Chimera and Drake, 2010), thereby contributing to the spread of nonnative plants in Hawaiian forests. The mismatch in size between historical native bird dispersers and extant non-native bird dispersers thus constrains dispersal for some large-seeded forest plants, likely contributing to a decline in recruitment and constriction in distribution. Whether plants can adapt to attract novel dispersers quickly enough to out-pace non-native species spread, or the confounding effects of other global threats such as global warming and habitat conversion, is unknown but relevant for conserving Hawaiian forests.

6.3. Plant-microbe interactions

Microbial diversity across Hawai'i's environmentally heterogeneous islands remains relatively uncharacterized, although previous studies have revealed interesting patterns. Contrary to predictions about limited fungal dispersal to the Hawaiian Islands, there is evidence for high mycorrhizal diversity and specialized interactions with mycoheterotrophic plants (Hayward and Hynson, 2014; Koske and Gemma, 1990). Most native and non-native Hawaiian plants form associations with mycorrhizal fungi (Koske et al., 1992), which enhance their performance (Gemma et al., 2002; Koske and Gemma, 2006; Miyasaka et al., 1993). Furthermore, there is evidence that mycorrhizae play a role in the establishment and spread of non-native plants (Allison et al., 2006; Hynson et al., 2013), although whether native mycorrhizae provide biotic resistance to the spread of non-native plants remains unclear. In addition to mycorrhizae, microbial interactions that improve nutrient access for host-plants include symbioses with *Rhizobium* bacteria for nitrogen. Although relatively few native trees have this symbiosis, a few common and widespread species, *A. koa*, *S. chrysophylla*, and *Erythrina sandwicensis*, develop nodules and likely play important roles in nutrient availability in Hawaiian forests (Pearson and Vitousek, 2001). Nitrogen fixation by non-native species, such as *Morella faya*, has been implicated in their successful establishment, with cascading effects on soil nitrogen and carbon cycling in Hawaiian forests (Asner et al., 2010; Vitousek et al., 1987).

Recent work has expanded from a focus on mycorrhizae and *Rhizobium* to demonstrate that soil fungal, bacterial, and archaeal diversity on Hawai'i Island co-vary in a complex and lineage-specific manner with precipitation and soil nutrient density (Peay et al., 2017), and that endophytic fungal communities within Hawaiian plants are highly diverse (Darcy et al., 2020; Datlof et al., 2017; Vega et al., 2010; Zimmerman and Vitousek, 2012). Microbial diversity can relate to the abiotic environment, as has been shown by the fungal endophyte communities within *M. polymorpha* with respect to rainfall and temperature (Zimmerman and Vitousek, 2012), and evapotranspiration (Darcy et al., 2020).

There are few functional studies of forest microbes, but they reveal that microbes have positive effects on forest plant species beyond their contributions to nutrient cycling. For example, the application of microbes extracted from healthy relatives to leaves of endangered *Phyllostegia kaalaensis* plants reduced the incidence of non-native powdery mildew and enhanced survival of out-plantings (Zahn and Amend, 2017). Forest microbes are also involved in food-web dynamics, as evidenced by epiphytic fungi on native Hawaiian trees serving as the primary food source for highly endangered tree snails in the genus *Achatinella* (O'Rorke et al., 2015; Price et al., 2017). Microbial ecology remains understudied in Hawaiian forests and is likely to be a fruitful area for future research.

7. Antagonistic interactions

The decline in Hawai'i's native fauna makes it difficult to characterize antagonistic species interactions in food webs or other interaction networks that are now dominated by non-native species. Nonetheless, there are still some native animals in Hawaiian forests, and insights can also be gained by examining interactions with novel natural enemies.

7.1. Herbivory

Native plant-herbivore interactions in Hawaiian forests are not well studied, and we know little about the specificity of interactions, temporal or spatial variability in those interactions, cascading consequences for upper trophic levels, effects on plant fitness, or the role of plant defenses in reducing or mitigating negative effects of herbivory. In part, this lack of research results from the pervasive assumption that island plants lack defenses due to a relaxation in selection pressure by

(presumably absent) island herbivores (Bowen and VanVuren, 1997; Carlquist, 1974; Ziegler, 2002). Comparisons of native versus non-native plants in Hawai'i, however, have provided mixed or weak support for this idea. Although non-native species are reported to have higher levels of terpenes than native species (Sardans et al., 2010), concentrations of total phenolics are similar between native and non-native plants (Funk and Throop, 2010; Peñuelas et al., 2010), and leaf toughness (Funk and Throop, 2010) and prickle density (Hoan et al., 2014) are higher in native plants. Comparisons of herbivory as an indirect metric of defense (e.g., greater herbivory should reflect lower defense in focal plants) have similarly revealed mixed support, with no detectable difference between non-native and native Hawaiian plants in leaf damage by insects (Funk and Throop, 2010), and variable damage by non-native gastropods (Shiels et al., 2014).

Clearly, native Hawaiian plants are not uniformly less well defended than continental plants, a pattern corroborated by recent meta-analyses comparing defenses in island versus continental plants globally (Meredith et al., 2019; Moreira et al., 2021). Future research is needed to improve on previous methods and more robustly characterize the variation in defenses in the Hawaiian flora. For example, multiple defense types should be measured simultaneously (Barton, 2014), including resistance via chemical and physical traits, indirect defense via natural enemies, and tolerance to herbivory, the last of which is typically overlooked and has been shown to vary among native and non-native Hawaiian seedlings (Barton, 2016; Barton and Shiels, 2020; Lurie et al., 2017). Finally, specificity in plant defenses should be examined as this likely explains the variable results among previous studies. Most studies concluding that island plants lack defenses have focused on mammalian herbivory (Bowen and VanVuren, 1997; Burns, 2014; Moreira et al., 2021), but because defenses are usually highly specific (Ali and Agrawal, 2012; Tanentzap et al., 2011), island plants may be poorly defended against mammalian herbivores while simultaneously being well defended against other guilds, such as piercing-sucking insects or browsing birds, of which Hawai'i had many (Walther and Hume, 2016).

The emphasis on weak defenses against mammalian herbivores in Hawaiian plants has unfortunately masked interesting interactions between plants and native invertebrate herbivores, which are highly diverse but taxonomically disharmonic in intriguing ways. For example, large leaf-chewing beetles are principally represented by a single possibly monophyletic group of weevils in the genus *Rhyncogonus* (Samuelson, 2003). Lepidoptera are a major member of the leaf-chewing guild in most tropical forests, and these too exhibit idiosyncratic representation; of the ~1000 known species in Hawai'i, only two are butterflies, and many groups of moths common in other tropical forests are absent (Nishida, 2002; Rubinoff, 2017). The piercing-sucking insect fauna is well developed in Hawai'i, and is similarly dominated by relatively few lineages that have diversified after arrival. As an example, the >80 species of delphacid planthoppers in the genus *Nesosydne* have evolved to utilize 28 plant families as hosts, but each species typically feeds on a single plant species (Bennett and O'Grady, 2012; Roderick and Percy, 2008). Conversely, all 35 species within a monophyletic radiation of gall-forming and free-living psyllids in the genus *Pariaconus* partition resource space within a single host plant species, *M. polymorpha* (Amada et al., 2019; Percy, 2017).

The community of endemic invertebrates that feeds on Hawai'i's forest plants also engages in a range of microbial symbioses. For example, the leaf- and sap-feeding insects (e.g., endemic planthoppers and leafhoppers) have intimate symbioses with bacteria and fungi that provide essential nutrients that may be missing in their phloem- and xylem-sourced diets (Baumann, 2005). A recent survey of several Hawaiian endemic insect species revealed that they maintained similar bacterial symbiotic interactions as their continental relatives (Poff et al., 2017), despite their long-term geographic and temporal isolation.

Despite declines in native insects, both *A. koa* and *M. polymorpha* currently experience high levels of native insect herbivory. The specialist koa moth, *Scotorythra paludicola* (Geometridae, Lepidoptera), undergoes periodic outbreaks that can defoliate tens of thousands of hectares of *A. koa* forest within a matter of months (Banko et al., 2014; Haines et al., 2009). With caterpillar abundances as high as 250,000 per tree during outbreaks, there is nonetheless variation in the intensity of defoliation among trees, and also variation among trees in their compensatory growth responses following defoliation (Banko et al., 2014). More research is needed to identify the factors that precipitate koa moth outbreaks and determine their severity and longevity, as well as the traits underlying variation in *A. koa* defenses. Like *A. koa*, *M. polymorpha* hosts abundant native arthropod communities, which are also species-rich (Gagne, 1979; Gruner, 2007). For example, Gruner (2007) collected 423 native arthropod species at five mesic forest sites across the archipelago chronosequence. Approximately 15–20 % of these species were herbivorous, and the abundance and biomass of herbivores were highest in intermediate-aged sites (5,000–150,000 years old), which were also the most productive, with the highest levels of foliar and litter nutrients. Considering that the greatest genetic diversity and taxonomic richness within the *Metrosideros* species complex is found on O'ahu (Stacy and Sakishima, 2019; Sur et al., 2018), the full diversity of arthropods associated with this landscape-dominant group remains unexplored. Arthropod diversity associated with other Hawaiian plants is even less well known.

Non-native insects are abundant in Hawaiian forests, are constantly being introduced through horticultural and agronomic activities, and cause severe damage to native plants. A wide range of common and rare trees are attacked by generalist herbivores, such as the black twig borer (*Xylosandrus compactus*) and lobate lac scale (*Paratachardina pseudolobata*). In addition, some native tree hosts have been decimated by highly specialized species, such as the Erythina gall wasp (*Quadrastichus erythrinae*) and Naio thrips (*Klambothrips myopori*) (Conant et al., 2009; Hara and Beardsley, 1979; Kaufman and Higashi, 2015; Rubinoff et al., 2010). The effects of these new herbivores range from stunting of trees to stand-level dieback. Non-native ants frequently increase abundances of phloem-feeding insects on plants by protecting them, but may also reduce densities of leaf-chewing herbivores (Krushelnycky, 2015).

Grazing by native birds was possibly an important source of herbivory on Hawaiian plants before these species went extinct. The endangered nene, *Branta sandwicensis*, currently feeds on native plants within its reduced distribution (Baldwin, 1947; Black et al., 1998). The now-extinct flightless moa-nalo and nene-nui likely caused even greater plant defoliation owing to their large size. It has been suggested that selection imposed by these extinct browsers led to the independent evolution of prickles in four lineages of the endemic genus *Cyanea* (Givnish et al., 1994). Even Hawaiian honeycreepers can act as herbivores in addition to their roles as pollinators and seed dispersers. For example, the endangered palila, *Loxioides bailleui* (Fringillidae, Drepanidinae) most commonly consumes immature seeds of *Sophora chrysophylla*, but also consumes leaves and flowers of six Hawaiian plant species from diverse families (Hess et al., 2014). Unfortunately, due to declines and extirpations, it is impossible to know the extent of native bird browsing or its effect on native plant fitness.

7.2. Pathogens

Effects of pathogens in Hawaiian forests are not well documented. It has been suggested that they may have played a role in the periodic forest diebacks that have been documented throughout the history of the islands (Anderson et al., 2002; Clarke, 1875; Forbes, 1918; Gardner, 1980; Hodges et al., 1986; Mortenson et al., 2016; Mueller-Dombois, 1987). The role of tree pathogens in these episodes is not clear, highlighting the inherent challenges of identifying the drivers of tree mortality, particularly when microbes may be involved. For example, *M. polymorpha* dieback observed in the 1960–70's was initially attributed to a widespread, soil-borne fungal pathogen (Burgan and Nelson, 1972), but it was later concluded that dieback was due to cyclical forest

Table 3

Tools and actions to promote conservation and restoration of Hawaiian forests, organized by focal outcome – enhance biodiversity, maintain suitable habitat, and protect ecosystem function. Some actions and tools have featured more commonly than others, and the ones marked with an asterisk have received relatively little attention and are fruitful areas for future research. Information about the natural history and biology of Hawaiian forest species from ecological and evolutionary research can enhance and improve conservation. Relevant theories and fields of study are identified for each conservation tool/action.

Theme	Classification	Tool/Action	Insights from Ecology & Evolution Research
Biodiversity	Conservation	Species discovery and taxonomy	Next-gen tools provide precision for recent lineages
		Living Collections: Seed banking	Seed storage behavior, longevity, and dormancy
		Living Collections: Tissue culture	
		Living Collections: seed orchards	Variation in phenology and seed production
		Living collections: nurseries, gardens	Seed and seedling ecology - germination and establishment behavior
		*Disease control	Novel diseases; evolution of defense of island plants
		*Predator/herbivore control	Novel predators and herbivores; evolution in defense of island plants
		*Mutualist protection (e.g. pollinators, seed dispersers)	Species networks and specificity of island plant-animal interactions
		Early detection of threats (non-native plants, enemies)	Invasion stages
		Protective designation: conservation priorities (e.g. endangered species, high biodiversity)	Ecosystem services, species network; diversity theory
	Restoration	*Cross breeding (e.g., between populations)	Inbreeding vs. outbreeding consequences (especially in low population sizes)
Habitat	Conservation	*In situ* outplanting (species scale)	Plant establishment; niche theory; priority effects
		Inter situ outplanting (species scale)	Plant establishment; niche theory; priority effects
		Ungulate control (fencing, hunting)	Ungulate behavior; population ecology
		*Outreach/service learning	Biocultural conservation
		Protective designation: habitat suitability	Niche theory
	Restoration	*In situ* outplanting (habitat scale)	Plant establishment; niche theory; priority effects
		Inter situ outplanting (habitat scale)	Plant establishment; niche theory; priority effects
		*Climate change mitigation: assisted migration	Plant stress tolerance; niche theory; intraspecific variation
		Non-native plant control (detection, removal, reduction)	Invasion stages; plant population dynamics and controls
Ecosystem function	Conservation	Protective designations (e.g., forest reserves)	Biodiversity; ecosystem services
		Biosecurity (early detection of threats)	Dispersal; invasion stages
		*Fire control (suppression, break establishment)	Disturbance ecology; plant fire tolerance
	Restoration	Conversion of fallow agriculture lands into novel forests (e.g., timber and agroforestry)	Succession
		*Hybrid forests (native and non-native)	Community assembly; ecosystem services; species interactions
		*Post-disturbance seed sowing	Plant recruitment; niche theory; priority effects

dynamics, possibly in combination with climatic conditions (Hodges et al., 1986; Jacobi, 1993; Mueller-Dombois, 1985). In contrast, recent declines of *A. koa* and *M. polymorpha* have more definitively been linked to introduced pathogenic fungi.

The disease Koa Wilt was first observed in 1980 in greenhouse *A. koa* saplings, which rapidly wilted and senesced (Gardner, 1980). Since then, stand-level diebacks have occurred across Hawai'i Island, particularly at elevations below 2500 feet, and sporadic tree mortality has been observed on the other main islands (Gardner, 1996). *Fusarium oxysporum* f. sp. *koae* was consistently isolated from infected trees, and it is now known to kill trees of all sizes and ages (Anderson et al., 2002; James et al., 2006). Mortality tends to radiate from a centrally infected tree, indicating transmission between root systems via soil and water (Anderson et al., 2002; Dudley et al., 2007). This epidemiological pattern has made it challenging to cultivate *A. koa* in plantations and to reestablish it in affected areas (Anderson et al., 2002; Gardner, 1980). Encouragingly, variation in mortality among trees suggests some natural resistance exists (Dudley et al., 2015).

Within the last 15 years, *M. polymorpha* trees have suffered two widespread outbreaks of fungal pathogens. In 2005, a seedling on O'ahu was observed to have fungal rust that was isolated and identified as *Austropuccinia psidii* (Beenken, 2017; Uchida et al., 2006); the disease has since spread throughout the archipelago. The *Austropuccinia* rust has had a relatively minor impact on *M. polymorpha* trees, infecting up to 5% of trees in areas where the disease is known to occur (Loope, 2010). However, *A. psidii* has also infected at least five other native trees and shrubs, with significant impact on the endangered *Eugenia koolauensis* (Zablan, 2007). Spores occur on the leaves of infected plants and can be spread via wind, or direct contact with humans, birds, and bees (Carnegie and Cooper, 2011).

Since 2010, rapid, stand-level mortality events commonly known as rapid 'ōhi'a death (ROD) have emerged as a serious threat to *M. polymorpha*, first on Hawai'i Island, and more recently, on Kaua'i, Maui, and O'ahu (Brill et al., 2019; Keith et al., 2015; Mortenson et al., 2016). Recently, ROD has been primarily attributed to a new fungal vascular pathogen, *Ceratocystis lukuohia* (Barnes et al., 2018) that leads to a swift decline in performance and mortality of trees within weeks following the onset of symptoms. The mechanisms of transmission for *C. lukuohia* likely involve a combination of local and long-range wind dispersal, non-native insects (Roy et al., 2019), humans, and ungulates, but further research in this area is needed. ROD is highly virulent, leading to >20 % annual mortality in infected stands, with several of the earliest impacted stands exhibiting almost 100 % mortality (Mortenson et al., 2016). Preliminary screening of young *M. polymorpha* plants on Hawai'i Island revealed variation in mortality rates and suggested the presence of some form of resistance in at least one variety (Luiz et al., 2021). At the time of this writing, ROD has spread throughout Hawai'i Island, impacting over 70,000 ha, and has dispersed to Kaua'i, Maui, and O'ahu as well. Given the role of *M. polymorpha* in shaping native forest structure, and the numerous rare understory species that are restricted to *M. polymorpha*-dominated forests, the further spread of the pathogen is likely to have wide ranging ecological effects beyond *M. polymorpha* mortality (Fortini et al., 2019).

8. Living in today's world – conservation challenges

Hawaiian forests are threatened by the same anthropogenic factors that are acting worldwide, including habitat loss, non-native species, and climate change. Island floras are particularly vulnerable to these threats due to their restricted species distributions, relatively low

genetic diversity, and high rates of endemism (Caujapé-Castells et al., 2010). As home to a unique endemic biodiversity, Hawai'i receives considerable attention with respect to managing these threats (Friday et al., 2015). There are many approaches to forest conservation and restoration around the world, and the same is true of Hawai'i (Gillespie et al., 2014; Jones, 2017; Kawelo et al., 2012). Forest restoration goals include, but are not limited to, increasing and restoring ecosystem services such as carbon sequestration and watershed function (Goldstein et al., 2008; Rayome et al., 2018; Strommer and Conant, 2018), increasing native species diversity, restoring habitat for native animals including birds, bats, snails, and insects (Pejchar et al., 2018), restoring resiliency and sustainability (Ostertag et al., 2015), restoring the Indigenous cultural landscapes (Box 3, Fig. 3) (Burnett et al., 2019; Pascua et al., 2017; Winter and Lucas, 2017; Winter et al., 2020b, c), educating the public about native forests, and benefiting from commercial timber operations (Harrington and Ewel, 1997; Ostertag et al., 2008) and integrated agroforestry (Friday et al., 2015). Meeting these goals depends on combined approaches to mitigate threats, proactively protect healthy forests, and restore lost functions or interactions, all of which benefit from an understanding of the complex ecological and evolutionary dynamics of Hawaiian forests.

8.1. New forest regime

Hawaiian forest assembly has been completely altered by non-native plants, animals, and microbes, and these non-native species have disrupted ecosystem dynamics (Box 5, Fig. 7). For example, in dry areas, fire-promoting C4 grasses from Africa now typically dominate the understory, resulting in the almost complete loss of native seedling recruitment, with cascading losses of forest structure (Litton et al., 2006). These changes in community structure and composition result in fuel and microclimate conditions that increase the likelihood of subsequent fires (D'Antonio and Vitousek, 1992; Freifelder et al., 1998). This cycle is now considered the primary agent in conversion of forest to grassland in dry and mesic ecosystems in Hawai'i and elsewhere in the tropics (Mack and D'Antonio, 1998). The transformation of a forest to a grassland yields a substantial loss of aboveground carbon and significantly alters nutrient cycling (Litton et al., 2006; Mack and D'Antonio, 2003). This is a radical shift from the pre-human contact period when grasslands were a small component of Hawaiian landscapes (Rollins, 2009).

Forest ecosystem dynamics have been profoundly altered by invasions as well. For example, in mesic and wet forest sites, dominance by nitrogen-fixing species, such as *Morella faya* and *Falcataria moluccana*, alters nutrient availability and reduces above-ground carbon stocks, facilitating further invasion by species that can take advantage of high soil nitrogen availability (Allison and Vitousek, 2004; Hughes et al., 2017; Hughes and Denslow, 2005; Vitousek and Walker, 1989). In dry forest sites, *Prosopis pallida* not only influences nitrogen-cycling, but also has deep roots that are able to tap into groundwater sources at the local (Dudley et al., 2014) and landscape levels (Dudley et al., 2020). *Morella faya* also alters the light environment, shading out light-dependent native under- and mid-story species (Asner et al., 2008). These altered biogeochemical cycles, coupled with reductions in light availability, ultimately shift these systems to entirely novel ecosystems (Mascaro et al., 2012). Among forest survey plots, *Psidium cattleyanum* is now the second most abundant tree (after *M. polymorpha*) across all islands (Table 1), and its continued spread is a major threat to Hawaiian forests. In addition to interactions with other non-native species, such as pigs that disperse their seeds, *P. cattleyanum* alters soil carbon and nutrient cycling (Barbosa et al., 2017; Enoki and Drake, 2017; Strauch et al., 2016).

Hawai'i's native trees and forests are at continued risk due to the arrival and spread of non-native microbial pathogens (DeNitto et al., 2015). The U.S. Department of Agriculture, Forest Service recently reported that given Hawai'i's central location in the Pacific and reliance on

an import economy, the regions that pose the greatest pathogen risk to the archipelago are the continental United States and Asia-Pacific (DeNitto et al., 2015). Unfortunately, awareness of pathogens in Hawai'i generally arises only after pathogen-plant-vector links are established and disease has occurred. Considerable time is then required to identify etiological agents and transmission mechanisms (Fletcher et al., 2010). Travelers leaving Hawai'i undergo strict inspections to prevent the spread of pests to mainland agriculture, but there are no inspections for travelers coming to Hawai'i, which could offer a beneficial strategy to protect native biodiversity in the islands. Given the limited screening of incoming biota and the lack of information on both the susceptibility of local plants to these threats and the importance of endemic and introduced animals as vectors, it is incredibly difficult to manage this threat. Unfortunately, this scenario leaves no opportunity for prevention, and limited knowledge to swiftly implement mitigation efforts (Fletcher et al., 2010).

Ongoing climate change may introduce yet further regime shifts in Hawaiian forests owing to differences between native and non-native trees in their ecohydrology. Differences in canopy structure and epiphyte abundance between native and non-native species cause differences in cloud water interception (Juvik and Nullet, 1995; Takahashi et al., 2011), further exacerbating drought effects. Several studies have shown lower water-use efficiency of non-native plants (see Section 5), with higher transpiration rates reducing local soil moisture (Michaud et al., 2015) and downstream watershed yields (Strauch et al., 2017). These complex threat interactions are challenging to explore, and may quickly become intractable as additional threats are considered (e.g., land-use and climate influencing fire risk, which in turn influences disturbance and consequently invasion risk).

The effects of climate change on non-native animals are important for the conservation of Hawai'i's forests and, in at least some cases, are being carefully monitored. There is perhaps no clearer global example than the warming-driven spread of avian malaria into high-elevation forests that threatens Hawaiian forest bird species (Benning et al., 2002). The high susceptibility of most native forest birds to avian malaria and the known temperature constraints to disease and vector development explain ongoing forest bird population declines and are expected to lead several species towards extinction with additional warming (Fortini et al., 2015; Liao et al., 2017; Paxton et al., 2016).

8.2. Conservation philosophies

There is a broad range of initiatives and entities involved in the conservation of Hawai'i's forests, including Federal and State agencies, watershed alliances that include both government and private lands, and non-profit organizations, each with their own missions that work independently or collaboratively with community groups towards forest conservation and restoration. Conflicts between hunters and conservationists and Indigenous cultural practitioners over natural resource management have been a major challenge since at least the 1990s (Adler, 1995; Kueffer and Kinney, 2017). In some cases, the conflicts arise due to different cultural priorities between conservation managers and natural resource users, as illustrated by demands to maintain non-native vertebrates for hunting. In other cases, the source of contention concerns approaches to conservation and how and where particular conservation tools (e.g., biocontrols versus chemical controls versus mechanical controls) should be used. Such challenges are not insurmountable, however, and more collaborative approaches to conservation are currently being pursued. A final major limitation concerns support for conservation efforts in terms of funding, personnel, and public perception, none of which are sufficient for conservation to be successful (Leonard, 2008).

There is a spectrum of philosophical foundations and goals to forest restoration projects in Hawai'i. Some aim to restore altered forests to a historical pre-contact state (Jones, 2017). However, the long history of non-native species in Hawai'i (since Polynesian arrival) makes it difficult

to identify the target "native" communities for this goal. Moreover, the loss of native species that performed key ecosystem services, such as pollination and seed dispersal, make many native forest species now dependent on non-native animals to fulfill those roles. As a consequence, conservation practitioners have increasingly developed strategies that combine native and non-native species into hybrid communities (Box 5, Fig. 7) for restoration in order to fulfill the goals of ecosystem services while maintaining at least some native biodiversity (Burnett et al., 2019; Cordell et al., 2016; Ewel and Putz, 2004; Ostertag et al., 2015; Ross et al., 2015). Often, the non-native species incorporated with this hybrid ecosystem approach are Polynesian introductions, thereby using this era as the target goal (Burney and Burney, 2016; Campbell and Campbell, 2017; Dietl et al., 2015). Although the hybrid ecosystem restoration approach is somewhat controversial (Murcia et al., 2014) and many restoration projects still focus exclusively on native species, this paradigm acknowledges that Hawaiian forests are in a new regime, one that cannot be feasibly returned to earlier states, at least not in all areas.

The human dimension is inextricably connected to conservation efforts. Humans may be the source of the problems—either directly or indirectly—but humanity is the solution. In efforts to restore biodiversity, ecological health, and ecosystem services, managers have a broad range of knowledge to draw upon from various scientific disciplines and cultural traditions, of ancient and modern tools and technologies to implement solutions, and of financial models to design sustainable programs that can last long into the future. Approaches that capitalize on shared cultural foundations of the intrinsic connection between humanity and nature are likely to be the most fruitful (Chang et al., 2019; Kueffer and Kinney, 2017; Pascua et al., 2017; Winter and Lucas, 2017). The efficacy of certain approaches has been studied (Burnett et al., 2019), but a comprehensive analysis of these approaches has yet to be undertaken in Hawai'i. New research could provide valuable insight in this area.

8.3. Common conservation practices

Based on the state of the ecosystem, management approaches can utilize restoration techniques that range from active to passive (Bechara et al., 2016; Burnett et al., 2019; Meli et al., 2017; Zahawi et al., 2014). Conservation and restoration of native forests benefits from a deep understanding of the ecology and evolution that underpins native forest dynamics, and thus practices that are guided by basic scientific principles are most likely to be successful (Table 3). Common conservation practices in Hawaiian forests include ungulate exclusion, non-native weed control, and out-planting, among others (Table 3).

Given the severe negative effects of non-native ungulates on Hawaiian plants, it is common management practice to exclude them from managed sites using fences, which in most cases results in positive gains for native vegetation, but in some cases may also increase abundances of non-native species. Removal of pigs leads to increases in cover and species richness of common native species in wet forest (Cole and Litton, 2014; Cole et al., 2012; Hughes et al., 2014; Loh and Tunison, 1999). Similarly, exclusion of goats (Scowcroft and Hobdy, 1987) and sheep (Scowcroft and Giffin, 1983) from dry forest sites results in greater establishment of common native woody species. Rare native species can also recover after ungulate removal, although this primarily depends on the presence of rare species at the time of ungulate removal (Cole and Litton, 2014). Recovery can be extremely slow or non-existent in some ecosystems as a consequence of dispersal limitation or habitat fragmentation, and a major concern surrounding non-native ungulate removal is the potential for rapid proliferation of non-native plants released from top-down control, as well as increased fire risk (Blackmore and Vitousek, 2000; Cole et al., 2012; Scowcroft and Conrad, 1992; Zavaleta et al., 2001). A nine-year study in dry forest sites on Hawai'i Island showed no change in the abundance of native vegetation following removal of a suite of non-native ungulates (Kellner et al.,

2011), and native woody species declined following exclusion of deer, pigs and goats from forests in mesic habitats on Kaua'i (Weller et al., 2011). Because ungulates are known to enhance non-native, but not native, plant dispersal (Diong, 1982; Nogueira-Filho et al., 2009; Warshauer et al., 1983), this result reveals the complexity of ungulate effects on native-non-native plant dynamics and highlights the need for additional research to refine predictions for how fencing can influence native diversity across the Hawaiian Islands.

Non-native plant control is a major focus of forest conservation and restoration in Hawai'i. In addition to manual removal and herbicide application, practitioners are experimenting with indirect control methods such as shading and biocontrol agents. As mentioned above with unintended positive effects of ungulate control on non-native plant proliferation, climate-related disturbances and change may also enhance the establishment and spread of non-native species. Of particular concern are shifts in native species ranges in high-priority management areas such as Hawai'i Volcanoes National Park, which are expected to experience substantial losses in native species of conservation interest (Camp et al., 2018). These examples of complexities involving non-native plants and climate change align with similar interactions observed elsewhere (Hellmann et al., 2008; Petitpierre et al., 2016; Ziska and Dukes, 2014).

9. Conclusions and future directions

Hawaiian forests are home to a unique endemic biota that has inspired people since the Polynesians first arrived. Due to its isolation and volcanic origin, the Hawaiian archipelago offers unparalleled opportunities to investigate adaptive radiations, the evolution of trait syndromes, and community assembly; as a result, Hawaiian forests are renowned among biologists worldwide. Our review of this extensive body of research has revealed several key generalities. First, despite the flora harboring considerable phenotypic variation and spanning wide distributions across extensive environmental gradients, only a few lineages have undergone explosive adaptive radiations. Second, among tropical forests of comparable mean annual rainfall and temperature, Hawai'i is relatively species-poor, and the dominance of forests by a few lineages is not well explained by morphological or physiological plant traits. Third, despite support for a few island syndrome predictions, there are exceptions to them all. Hawaiian plants on the whole are not less defended against herbivores, less dispersible, more conservative in their leaf economics, or more slow-growing than their continental relatives. Our synthesis suggests that despite the considerable body of work conducted across Hawaiian forests, greater synthesis is still needed to understand the complexities and subtleties that underlie the observed patterns. In particular, more work is needed to understand the drivers, sources, and constraints on phenotypic variation among Hawaiian species, and to understand the role of species interactions in mediating these patterns.

We still know remarkably little about interactions among forest plants, animals, and microbes, despite our deep understanding of the physical underpinnings that have created Hawai'i's forests (e.g., volcanic eruptions, tradewinds, orographic effects). Unfortunately, native species interactions are nearly impossible to characterize in Hawai'i's contemporary forests due to the dramatic regime shifts caused by human colonization and the spread of non-native species. Nearly all contemporary species interactions, among competing plants, between plant and herbivores, pollinators, seed dispersers, and diseases, now involve non-native species. Novel species interactions may provide hints regarding historical native community dynamics, but unraveling these mysteries may no longer be possible given the scale of disruption. As a consequence of the regime shifts, most Hawaiian forests are now hybrids of native and non-native species or novel communities completely dominated by non-native species. An increasing number of restoration efforts are leveraging hybrid communities for conservation of target native species and restoration of ecosystem services. Conservation and

restoration of Hawaiian forests depend on diverse tools and strategies grounded in basic ecological, evolutionary, and biocultural principles with the goals of mitigating the most pervasive threats (e.g., non-native ungulates, fire-prone grasses, and pathogens) to maximize native biodiversity and function. In turn, much can be learned regarding the ecology and evolution of Hawaiian forest species while simultaneously taking steps to conserve and restore native forests. The future of Hawaiian forests thus depends on explicit integration of ecological and evolutionary research with conservation and restoration activities.

Funding

Declaration of Competing Interest

The authors report no declarations of interest.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ppees.2021.125631.

References

Adler, P.S., 1995. Pig wars: mediating forest management conflicts in hawai'i. Negot. J. 11, 209–215.

Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol. Lett. 9, 968–980.

Aguraiuja, R., Zobel, M., Zobel, K., Moora, M., 2008. Conservation of the endemic fern lineage Diellia (aspleniaceae) on the Hawaiian Islands: Can population structure indicate regional dynamics and endangering factors? Folia Geobot. 43, 3–18.

Ainsworth, A., Drake, D.R., 2020. Classifying Hawaiian plant species along a habitat generalist-specialist continuum: implications for species conservation under climate change. PLoS One 15, 27.

Ainsworth, A., Kauffman, J.B., 2009. Response of native Hawaiian woody species to lava-ignited wildfires in tropical forests and shrublands. Plant Ecol. 201, 197–209.

Ainsworth, A., Kauffman, J.B., 2010. Interactions of fire and nonnative species across an Elevation/Plant community gradient in Hawaii Volcanoes National Park. Biotropica 42, 647–655.

Ali, J.G., Agrawal, A.A., 2012. Specialist versus generalist insect herbivores and plant defense. Trends Plant Sci. 17, 293–302.

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C., Salgado-Negret, B., Smith, C.M., Trierweiler, A., Van Bloem, S.J., Waring, B.G., Xu, X.T., Powers, J.S., 2017. Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? Environ. Res. Lett. 12, 15.

Allison, S.D., Vitousek, P.M., 2004. Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141, 612–619.

Allison, S.D., Nielsen, C., Hughes, R.F., 2006. Elevated enzyme activities in soils under the invasive nitrogen-fixing tree Falcataria moluccana. Soil Biol. Biochem. 38, 1537–1544.

Amada, G., Kobayashi, K., Izuno, A., Mukai, M., Ostertag, R., Kitayama, K., Onoda, Y., 2019. Leaf trichomes in *Metrosideros polymorpha* can contribute to avoiding extra water stress by impeding gall formation. Ann. Bot. 125, 533–542.

Anderson, R.C., Gardner, D.E., Daehler, C.C., Meinzer, F.C., 2002. Dieback of *Acacia koa* in Hawai'i: ecological and pathological characteristics of affected stands. For. Ecol. Manage. 162, 273–286.

Aplet, G.H., Vitousek, P.M., 1994. An age altitude matrix analysis of Hawaiian rain forest succession. J. Ecol. 82, 137–147.

Arndt, D., Zdrojewski, J., Chu, P.-S., 2018. National Record 24-Hour Precipitation at Waipa Garden, Hawai'i, National Climate Extremes Committee Report. National Oceanic and Atmospheric Administration, National Centers for Environmental Information.

Aslan, A., Hart, P., Wu, J., Aslan, C.E., 2014a. Evaluating the qualitative effectiveness of a novel pollinator: a case study of two endemic Hawaiian plants. Biotropica 46, 732–739.

Aslan, C.E., Zavaleta, E.S., Tershy, B., Croll, D., Robichaux, R.H., 2014b. Imperfect replacement of native species by non-native species as pollinators of endemic Hawaiian plants. Conserv. Biol. 28, 478–488.

Aslan, C.E., Shiels, A.B., Haines, W., Liang, C.T., 2019. Non-native insects dominate daytime pollination in a high-elevation Hawaiian dryland ecosystem. Am. J. Bot. 106, 313–324.

Asner, G.P., Goldstein, G., 1997. Correlating stem biomechanical properties of Hawaiian canopy trees with hurricane wind damage. Biotropica 29, 145–150.

Asner, G.P., Hughes, R.F., Vitousek, P.M., Knapp, D.E., Kennedy-Bowdoin, T., Boardman, J., Martin, R.E., Eastwood, M., Green, R.O., 2008. Invasive plants transform the three-dimensional structure of rain forests. Proc. Natl. Acad. Sci. U. S. A. 105, 4519–4523.

Asner, G.P., Martin, R.E., Knapp, D.E., Kennedy-Bowdoin, T., 2010. Effects of Morella faya tree invasion on aboveground carbon storage in Hawaii. Biol. Invasions 12, 477–494.

Asner, G.P., Hughes, R.F., Mascaro, J., Uowolo, A.L., Knapp, D.E., Jacobson, J., Kennedy-Bowdoin, T., Clark, J.K., 2011. High-resolution carbon mapping on the million-hectare Island of Hawai'i. Front. Ecol. Environ. 9, 434–439.

Asner, G.P., Sousan, S., Knapp, D.E., Selmants, P.C., Martin, R.E., Hughes, R.F., Giardina, C.P., 2016. Rapid forest carbon assessments of oceanic islands: a case study of the Hawaiian Archipelago. Carbon Balance Manag. 11, 1–13.

Athens, J.S., Tuggle, H.D., Ward, J.V., Welch, D.J., 2002. Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai'i. Archaeol. Oceania 37, 57–78.

Austin, A.T., Vitousek, P.M., 2000. Precipitation, decomposition and litter decomposability of Metrosideros polymorpha in native forests on Hawai'i. J. Ecol. 88, 129–138.

Bachelet, D., Rogers, B.M., Conklin, D.R., 2015. Challenges and limitations of using a DGVM for local to regional applications. In: Bachelet, D., Turner, D. (Eds.), Global Vegetation Dynamics: Concepts and Applications in the MC1 Model. John Wiley & Sons.

Baldwin, P.H., 1947. Foods of the Hawaiian goose. Condor 49, 108–120.

Baldwin, B.G., Sanderson, M.J., 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). Proc. Natl. Acad. Sci. U. S. A. 95, 9402–9406.

Banko, P.C., Banko, W.E., 2009. Evolution and ecology of food exploitation. In: Pratt, T. K., Atkinson, C.T., Banko, P.C., Jacobi, J.D., Woodworth, B.L. (Eds.), Conservation Biology of Hawaiian Forest Birds. Yale University Press, New Haven, pp. 159–193.

Banko, P.C., Peck, R.W., Yelenik, S.G., Paxton, E., Bonaccorso, F.J., Montoya-Aiona, K., Foote, D., 2014. Dynamics and Ecological Consequences of the 2013-2014 Koa Moth Outbreak at the Hakalau Forest National Wildlife Refuge. Hawaii Cooperative Studies Unit, University of Hawaii, Hilo, p. 89.

Barbosa, J.M., Asner, G.P., Hughes, R.F., Johnson, M.T., 2017. Landscape-scale GPP and carbon density inform patterns and impacts of an invasive tree across wet forests of Hawaii. Ecol. Appl. 27, 403–415.

Barnes, I., Wingfield, M.J., Harrington, T., Keith, L.M., 2018. Two new *Ceratocystis* species cause the serious and devastating rapid 'ohi' a death (ROD) on native *Metrosideros polymorpha* in Hawai'i. Phytopathology 108, 1.

Barton, K.E., 2014. Prickles, latex and tolerance in the endemic Hawaiian prickly poppy (*Argemone glauca*): variation between populations, across ontogeny and due to phenotypic plasticity. Oecologia 174, 1273–1281.

Barton, K.E., 2016. Low tolerance to simulated herbivory in Hawaiian seedlings despite induced changes in photosynthesis and biomass allocation. Ann. Bot. 117, 1053–1062.

Barton, K.E., Shiels, A.B., 2020. Additive and non-additive responses of seedlings to simulated herbivory and drought. Biotropica 52, 1217–1228.

Barton, K.E., Jones, C., Edwards, K.F., Shiels, A.B., Knight, T., 2020. Local adaptation constrains drought tolerance in a tropical foundation tree. J. Ecol. 108, 1540–1552.

Baruch, Z., Goldstein, G., 1999. Leaf construction cost, nutrient concentration, and net CO2 assimilation of native and invasive species in Hawai'i. Oecologia 121, 183–192.

Baskin, C.C., Baskin, J.M., 2014. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination, 2nd ed. Academic Press.

Baumann, P., 2005. Biology of bacteriocyte-associated endosymbionts of plant sap-sucking insects. Annu. Rev. Microbiol. 59, 155–189.

Bechara, F.C., Dickens, S.J., Farrer, E.C., Larios, L., Spotswood, E.N., Mariotte, P., Suding, K.N., 2016. Neotropical rainforest restoration: comparing passive, plantation and nucleation approaches. Biodivers. Conserv. 25, 2021–2034.

Beenken, L., 2017. *Austropuccinia*: a new genus name for the myrtle rust *Puccinia psidii* placed within the redefined family Sphaerophragmiaceae (Pucciniales). Phytotaxa 297, 9, 2017.

Bennett, G.M., O'Grady, P.M., 2012. Host-plants shape insect diversity: phylogeny, origin, and species diversity of native Hawaiian leafhoppers (Cicadellidae: *nesophrosyne*). Mol. Phylogenet. Evol. 65, 705–717.

Benning, T.L., LaPointe, D., Atkinson, C.T., Vitousek, P.M., 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. Proc. Natl. Acad. Sci. U. S. A. 99, 14246–14249.

Bialic-Murphy, L., Gaoue, O.G., 2018. Low interannual precipitation has a greater negative effect than seedling herbivory on the population dynamics of a short-lived shrub, Schiedea obovata. Ecol. Evol. 8, 176–184.

Bialic-Murphy, L., Gaoue, O.G., Kawelo, K., 2017. Microhabitat heterogeneity and a non-native avian frugivore drive the population dynamics of an island endemic shrub, *Cyrtandra dentata*. J. Appl. Ecol. 54, 1469–1477.

Bialic-Murphy, L., Gaoue, O.G., Knight, T., 2018. Using Transfer Function Analysis to develop biologically and economically efficient restoration strategies. Sci. Rep. 8, 6.

Black, J., Hunter, J., Woog, F., Marshall, A.P., Bowler, J., 1998. Foraging behavior and energetics of the Hawaiian Goose *Branta sandvicensis*. Wildfowl 45, 65–109.

Blackburn, T.M., Pysek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarosik, V., Wilson, J. R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333–339.

Blackmore, M., Vitousek, P.M., 2000. Cattle grazing, forest loss, and fuel loading in a dry forest ecosystem at Pu'u Wa'aWa'a ranch, Hawai'i. Biotropica 32, 625–632.

Borregaard, M.K., Amorim, I.R., Borges, P.A.V., Cabral, J.S., Fernadez-Palacios, J.M., Field, R., Heaney, L.R., Kreft, H., Matthews, T.J., Olesen, J.M., Price, J., Rigal, F., Steinbauer, M.J., Triantis, K.A., Valente, L., Weigelt, P., Whittaker, R.J., 2017. Oceanic island biogeography through the lens of the general dynamic model: assessment and prospect. Biol. Rev. 92, 830–853.

Bothwell, L.D., Selmants, P.C., Giardina, C.P., Litton, C.M., 2014. Leaf litter decomposition rates increase with rising mean annual temperature in Hawaiian tropical montane wet forests. Peerj 2.

Bowen, L., VanVuren, D., 1997. Insular endemic plants lack defenses against herbivores. Conserv. Biol. 11, 1249–1254.

Brill, E., Hughes, M.A., Heller, W.P., Keith, L.M., 2019. First report of *Ceratocystis lukuohia* on *Metrosideros polymorpha* on the island of Kaua'i, Hawai'i. Plant Dis. 103, 2961–2962.

Braje, T.J., Erlandson, J.M., 2013. Human acceleration of animal and plant extinctions: a Late Pleistocene, Holocene, and Anthropocene continuum. Anthropocene 4, 14–23.

Bruegmann, M.M., 1996. Hawai'i's dry forests. Endangered Species Bull. 21, 26–27.

Burgan, R.E., Nelson, R.E., 1972. Decline of the 'ōhi'a lehua forests in Hawai'i. General Technical Rep. PSW 3.

Burnett, K.M., Ticktin, T., Bremer, L.L., Quazi, S.A., Geslani, C., Wada, C.A., Kurashima, N., Mandle, L., Pascua, P., Depraetere, T., Wolkis, D., Edmonds, M., Giambelluca, T., Falinski, K., Winter, K.B., 2019. Restoring to the future: environmental, cultural, and management trade-offs in historical versus hybrid restoration of a highly modified ecosystem. Conserv. Lett. 12, 10.

Burney, D.A., Burney, L.P., 2016. Monitoring results from a decade of native plant translocations at Makauwahi Cave Reserve, Kaua'i. Plant Ecol. 217, 139–153.

Burney, D.A., Kikuchi, W.K.P., 2006. A millennium of human activity at Makauwahi Cave, Maha Ulepu, Kaua'i. Hum. Ecol. 34, 219–247.

Burney, D.A., Decandido, R.V., Burney, L.P., Kostelhughes, F.N., Stafford, T.W., James, H.F., 1995. A Holocene record of climate-change, fire ecology, and human activity from montane Flat Top Bog. Maui. J. Paleolimn. 13, 209–217.

Burney, D.A., James, H.F., Burney, L.P., Olson, S.L., Kikuchi, W., Wagner, W.L., Burney, M., McCloskey, D., Kikuchi, D., Grady, F.V., Gage, R., Nishek, R., 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. Ecol. Monogr. 71, 615–641.

Burns, K.C., 2014. Are there general patterns in plant defence against megaherbivores? Biol. J. Linn. Soc. 111, 38–48.

Burns, K.C., 2019. Evolution in Isolation: The Search for an Island Syndrome in Plants. Cambridge University Press.

Burton, P.J., 1982. The effect of temperature and light on *Metrosideros polymorpha* seed germination. Pac. Sci. 36, 229–240.

Burton, P.J., Mueller-Dombois, D., 1984. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. Ecology 65, 779–791.

Busby, P.E., Vitousek, P., Dirzo, R., 2010. Prevalence of tree regeneration by sprouting and seeding along a rainfall gradient in Hawai'i. Biotropica 42, 80–86.

Businger, S., Nogelmeier, M.P., Chinn, P.W.U., Schroeder, T., 2018. Hurricane with a history: hawaiian newspapers illuminate an 1871 storm. Bull. Amer. Meteorol. Soc. 99, 137–147.

Cabin, R.J., Weller, S.G., Lorence, D.H., Cordell, S., Hadway, L.J., Montgomery, R., Goo, D., Urakami, A., 2002. Effects of light, alien grass, and native species additions on Hawaiian dry forest restoration. Ecol. Appl. 12, 1595–1610.

Cadotte, M.W., Carboni, M., Si, X., Tatsumi, S., 2019. Do traits and phylogeny support congruent community diversity patterns and assembly inferences? J. Ecol. 107, 2065–2077.

Cai, W.J., Wang, G.J., Dewitte, B., Wu, L.X., Santoso, A., Takahashi, K., Yang, Y., Carreric, A., McPhaden, M.J., 2018. Increased variability of eastern Pacific El Niño under greenhouse warming. Nature 564, 201. +.

Camp, R.J., Berkowitz, S.P., Brink, K.W., Jacobi, J.D., Loh, R., Price, J., Fortini, L.B., 2018. Potential Impacts of Projected Climate Change on Vegetation-management Strategies in Hawai'i Volcanoes National Park, Scientific Investigations Report, Reston, VA, p. 164.

Campbell, H.V., Campbell, A.M., 2017. Community-based watershed restoration in He'eia (He'eia ahupua'a), O'ahu, Hawaiian Islands. Case Stud. Environ. 1, 8.

Cao, G.X., Giambelluca, T.W., Stevens, D.E., Schroeder, T.A., 2007. Inversion variability in the Hawaiian trade wind regime. J. Clim. 20, 1145–1160.

Carlquist, S.J., 1974. Island Biology. Columbia University Press, New York.

Carnegie, A.J., Cooper, K., 2011. Emergency response to the incursion of an exotic myrtaceous rust in Australia. Australas. Plant Pathol. 40, 346–359.

Carpenter, J.K., Wilmshurst, J.M., McConkey, K.R., Hume, J.P., Wotton, D.M., Shiels, A. B., Burge, O.R., Drake, D.R., 2020. The forgotten fauna: native vertebrate seed predators on islands. Funct. Ecol.

Carr, G.D., 1987. Beggars ticks and tarweeds - masters of adaptive radiations. Trends Ecol. Evol. 2, 192–195.

Case, S.B., Tarwater, C.E., 2020. Functional traits of avian frugivores have shifted following species extinction and introduction in the Hawaiian Islands. Funct. Ecol. n/a.

Caujapé-Castells, J., Tye, A., Crawford, D.J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, F.B.V., Moura, M., Jardim, R., Gómes, I., Kueffer, C., 2010. Conservation of oceanic island floras: present and future global challenges. Perspect. Plant Ecol. Evol. Syst. 12, 107–129.

Cavaleri, M.A., Ostertag, R., Cordell, S., Sack, L., 2014. Native trees show conservative water use relative to invasive trees: results from a removal experiment in a Hawaiian wet forest. Conserv. Physiol. 2, 14.

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J., Hedin, L.O., 1999. Changing sources of nutrients during four million years of ecosystem development. Nature 397, 491–497.

Chang, K., Winter, K.B., Lincoln, N.K., 2019. Hawai'i in focus: navigating pathways in global biocultural leadership. Sustainability 11, 9.

Chau, M.M., Chambers, T., Weisenberger, L., Keir, M., Kroessig, T.I., Wolkis, D., Kam, R., Yoshinaga, A.Y., 2019. Seed freeze sensitivity and ex situ longevity of 295 species in the native Hawaiian flora. Am. J. Bot. 106, 1248–1270.

Chazdon, R.L., 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspect. Plant Ecol. Evol. Syst. 6, 51–71.

Chazdon, R.L., Guariguata, M.R., 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48, 716–730.

Chimera, C.G., Drake, D.R., 2010. Patterns of seed dispersal and dispersal failure in a hawaiian dry forest having only introduced birds. Biotropica 42, 493–502.

Choi, J.Y., Purugganan, M., Stacy, E.A., 2020. Divergent selection and primary gene flow shape incipient speciation of a riparian tree on Hawai'i island. Mol. Biol. Evol. 37, 695–710.

Chu, P.S., Wang, J.X., 1998. Modeling return periods of tropical cyclone intensities in the vicinity of Hawaii. J. Appl. Meteorol. 37, 951–960.

Chu, P.S., Zhao, X., Ruan, Y., Grubbs, M., 2009. Extreme rainfall events in the Hawaiian Islands. J. Appl. Meteorol. Climatol. 48, 502–516.

Clague, D.A., 1996. The growth and subsidence of the hawaiian-emperor volcanic chain. In: Keast, A., Miller, S.E. (Eds.), The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes. Balogh Scientific Books, pp. 35–50.

Clark, J.D., Chu, P.S., 2002. Interannual variation of tropical cyclone activity over the Central North Pacific. J. Meteorol. Soc. Jpn. 80, 403–418.

Clarke, F.L., 1875. Decadence of Hawaiian forests. All About Hawai'i 1, 19–20.

Cole, R.J., Litton, C.M., 2014. Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. Biol. Invasions 16, 125–140.

Cole, R.J., Litton, C.M., Koontz, M.J., Loh, R.K., 2012. Vegetation recovery 16 years after feral pig removal from a wet Hawaiian forest. Biotropica 44, 463–471.

Cole, F.R., Loope, L.L., Medeiros, A.C., Raikes, J.A., Wood, C.S., 1995. Conservation implications of introduced game birds in high-elevation Hawaiian Shrubland. Conserv. Biol. 9, 306–313.

Comita, L.S., Uriarte, M., Forero-Montaña, J., Kress, W.J., Swenson, N.G., Thompson, J., Umaña, M.N., Zimmerman, J.K., 2018. Changes in phylogenetic community structure of the seedling layer following hurricane disturbance in a human-impacted tropical forest. Forests 9, 556.

Conant, P., Hirayama, C.K., Lee, M.I., Young, C.L., Heu, R.A., 2009. Naio Thrips, New Pest Advisory No. 09-02, Hawaii, p. 2.

Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. 70, 171–207.

Cooray, R.G., 1974. Stand Structure of a Montane Rain Forest on Mauna Loa, Hawai'i, US International Biological Program, Island Ecosystems Report. University of Hawaii, Honolulu, HI.

Cordell, S., Goldstein, G., Mueller-Dombois, D., Webb, D., Vitousek, P.M., 1998. Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. Oecologia 113, 188–196.

Cordell, S., Goldstein, G., Melcher, P.J., Meinzer, F.C., 2000. Photosynthesis and freezing avoidance in 'Ōhi'a (*Metrosideros polymorpha*) at treeline in Hawai'i. Arct. Antarct. Alp. Res. 32, 381–387.

Cordell, S., Cabin, R.J., Hadway, L.J., 2002. Physiological ecology of native and alien dry forest shrubs in Hawai'i. Biol. Invasions 4, 387–396.

Cordell, S., Ostertag, R., Rowe, B., Sweinhart, L., Vasquez-Radonic, L., Michaud, J., Cole, T.C., Schulten, J.R., 2009. Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. Biol. Conserv. 142, 2997–3004.

Cordell, S., Ostertag, R., Michaud, J., Warman, L., 2016. Quandaries of a decade-long restoration experiment trying to reduce invasive species: beat them, join them, give up, or start over? Restor. Ecol. 24, 139–144.

Cory, C., Pender, R., Jones, C.E., 2015. Can ornithophilous Hawaiian lobeliads produce seeds in the absence of pollinators? A test using Clermontia kakeana and Cyanea angustifolia (Campanulaceae). Pac. Sci. 69, 255–261.

Cowie, R.H., Holland, B.S., 2008. Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands. Philos. Trans. R. Soc. B-Biol. Sci. 363, 3363–3376.

Crausbay, S.D., Frazier, A.G., Giambelluca, T.W., Longman, R.J., Hotchkiss, S.C., 2014. Moisture status during a strong El Nio explains a tropical montane cloud forest's upper limit. Oecologia 175, 273–284.

Craven, D., Knight, T.M., Barton, K.E., Bialic-Murphy, L., Cordell, S., Giardina, C.P., Gillespie, T.W., Ostertag, R., Sack, L., Chase, J.M., 2018. OpenNahele: the open Hawaiian forest plot database. Biodiver. Data J. 6, 14.

Craven, D., Knight, T.M., Barton, K.E., Bialic-Murphy, L., Chase, J.M., 2019. Dissecting macroecological and macroevolutionary patterns of forest biodiversity across the Hawaiian archipelago. Proc. Natl. Acad. Sci. U. S. A. 116, 16436–16441.

Crews, T.E., Kitayama, K., Fownes, J.H., Riley, R.H., Herbert, D.A., Muellerdombois, D., Vitousek, P.M., 1995. Changes in soil-phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawai'i. Ecology 76, 1407–1424.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T., Mynsberge, A.R., 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science 331, 324–327.

Cronk, Q.C.B., Kiehn, M., Wagner, W.L., Smith, J.E., 2005. Evolution of *Cyrtandra* (Gesneriaceae) in the Pacific Ocean: the origin of a supertramp clade. Am. J. Bot. 92, 1017–1024.

Culliney, S., Pejchar, L., Switzer, R., Ruiz-Gutierrez, V., 2012. Seed dispersal by a captive corvid: the role of the' Alala (Corvus hawaiiensis) in shaping Hawai'i's plant communities. Ecol. Appl. 22, 1718–1732.

D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63–87.

D'Antonio, C.M., Hughes, R.F., Mack, M., Hitchcock, D., Vitousek, P.M., 1998. The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. J. Veg. Sci. 9, 699–712.

D'Antonio, C.M., Tunison, J.T., Loh, R.K., 2000. Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawai'i. Austral Ecol. 25, 507–522.

D'Antonio, C.M., Ostertag, R., Cordell, S., Yelenik, S., 2017. Interactions among invasive plants: lessons from Hawai'i. In: Futuyma, D.J. (Ed.), Annual Review of Ecology, Evolution, and Systematics, vol 48. Annual Reviews, Palo Alto, pp. 521–541.

Daly, H.V., Magnacca, K.N., 2003. Hawaiian *Hylaeus* (Nesoprosopis) Bees (Hymenoptera: Apoidea). University of Hawaii Press, Honolulu.

Darcy, J.L., Swift, S.O.I., Cobian, G.M., Zahn, G.L., Perry, B.A., Amend, A.S., 2020. Fungal communities living within leaves of native Hawaiian dicots are structured by landscape-scale variables as well as by host plants. Mol. Ecol. 29, 3102–3115.

Datlof, E.M., Amend, A.S., Earl, K., Hayward, J., Morden, C.W., Wade, R., Zahn, G., Hynson, N.A., 2017. Uncovering unseen fungal diversity from plant DNA banks. Peerj 5, 18.

Davies, S.J., Abiem, I., Abu Salim, K., Aguilar, S., Allen, D., Alonso, A., Anderson-Teixeira, K., Andrade, A., Arellano, G., Ashton, P.S., Baker, P.J., Baker, M.E., Baltzer, J.L., Basset, Y., Bissiengou, P., Bohlman, S., Bourg, N.A., Brockelman, W.Y., Bunyavejchewin, S., Burslem, D.F.R.P., Cao, M., Cárdenas, D., Chang, L.-W., Chang-Yang, C.-H., Chao, K.-J., Chao, W.-C., Chapman, H., Chen, Y.-Y., Chisholm, R.A., Chu, C., Chuyong, G., Clay, K., Comita, L.S., Condit, R., Cordell, S., Dattaraja, H.S., de Oliveira, A.A., den Ouden, J., Detto, M., Dick, C., Du, X., Duque, Á., Ediriweera, S., Ellis, E.C., Obiang, N.L.E., Esufali, S., Ewango, C.E.N., Fernando, E.S., Filip, J., Fischer, G.A., Foster, R., Giambelluca, T., Giardina, C., Gilbert, G.S., Gonzalez-Akre, E., Gunatilleke, I.A.U.N., Gunatilleke, C.V.S., Hao, Z., Hau, B.C.H., He, F., Ni, H., Howe, R.W., Hubbell, S.P., Huth, A., Inman-Narahari, F., Itoh, A., Janík, D., Jansen, P.A., Jiang, M., Johnson, D.J., Jones, F.A., Kanzaki, M., Kenfack, D., Kiratiprayoon, S., Král, K., Krizel, L., Lao, S., Larson, A.J., Li, Y., Li, X., Litton, C.M., Liu, Y., Liu, S., Lum, S.K.Y., Luskin, M.S., Lutz, J.A., Luu, H.T., Ma, K., Makana, J.-R., Malhi, Y., Martin, A., McCarthy, C., McMahon, S.M., McShea, W.J., Memiaghe, H., Mi, X., Mitre, D., Mohamad, M., Monks, L., Muller-Landau, H.C., Musili, P.M., Myers, J.A., Nathalang, A., Ngo, K.M., Norden, N., Novotny, V., O'Brien, M.J., Orwig, D., Ostertag, R., Papathanassiou, K., Parker, G.G., Pérez, R., Perfecto, I., Phillips, R.P., Pongpattananurak, N., Pretzsch, H., Ren, H., Reynolds, G., Rodriguez, L.J., Russo, S.E., Sack, L., Sang, W., Shue, J., Singh, A., Song, G.-Z.M., Sukumar, R., Sun, I.F., Suresh, H.S., Swenson, N.G., Tan, S., Thomas, S.C., Thomas, D., Thompson, J., Turner, B.L., Uowolo, A., Uriarte, M., Valencia, R., Vandermeer, J., Vicentini, A., Visser, M., Vrska, T., Wang, X., Wang, X., Weiblen, G. D., Whitfeld, T.J.S., Wolf, A., Wright, S.J., Xu, H., Yao, T.L., Yap, S.L., Ye, W., Yu, M., Zhang, M., Zhu, D., Zhu, L., Zimmerman, J.K., Zuleta, D., 2021. ForestGEO: understanding forest diversity and dynamics through a global observatory network. Biol. Conserv. 253, 108907.

Dawson, J.W., 1992. Myrtaceae - leptospermoidea. In: Morat, P., MacKee, H.S. (Eds.), Flore De La Nouvelle-Calédonie Et Dépendances. Muséum National d'Histoire Naturelle, Paris, pp. 1–251.

Dawson, J., Stemmermann, L., 1990. *Metrosideros* (gaud). In: Wagner, W., Herbst, D.R., Sohmer, S.H. (Eds.), Manual of the Flowering Plants of Hawaíi. University of Hawai'i Press, Honolulu, HI.

DeBoer, N., Stacy, E.A., 2013. Divergence within and among 3 Varieties of the Endemic Tree,' Ohi'a Lehua (Metrosideros polymorpha) on the Eastern Slope of Hawai'i Island. J. Hered. 104, 449–458.

Deenik, J., McClellan, A.T., 2007. Soils of Hawai'i, Cooperative Extension Service Soil and Crop Management. University of Hawaii at Manoa, Hawaii, pp. 1–12.

DeNitto, G.A., Cannon, P., Eglitis, A., Glaeser, A., Maffei, J.A., Smith, S., 2015. Risk and Pathway Assessment for the Introduction of Exotic Insects and Pathogens That Could Affect Hawai'i's Native Forests, Gen. Tech. Rep. PSW-GTR-250. U.S. Department of Agriculture, Forest Service. Pacific Southwest Research Station, Albany, CA, p. 171.

Denslow, J.S., Uowolo, A.L., Hughes, R.F., 2006. Limitations to seedling establishment in a mesic Hawaiian forest. Oecologia 148, 118–128.

Dietl, G.P., Kidwell, S.M., Brenner, M., Burney, D.A., Flessa, K.W., Jackson, S.T., Koch, P. L., 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. In: Jeanloz, R., Freeman, K.H. (Eds.), Annual Review of Earth and Planetary Sciences, vol 43. Annual Reviews, Palo Alto, pp. 79–103.

Diong, C.H., 1982. Population Biology and Management of the Feral Pig (*Sus Scrofa*) in Kipahulu Valley. Maui. University of Hawai'i at Mānoa, Honolulu, HI.

Drake, D.R., 1992. Seed dispersal of *Metrosideros polymorpha* (Myrtaceae) - a pioneer tree of Hawaiian lava flows. Am. J. Bot. 79, 1224–1228.

Drake, D.R., 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. J. Veg. Sci. 9, 103–112.

Drake, D.R., Hunt, T.L., 2009. Invasive rodents on islands: integrating historical and contemporary ecology. Biol. Invasions 11, 1483–1487.

Drake, D.R., Mueller-Dombois, D., 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. Ecology 74, 1012–1019.

Drake, D.R., Pratt, L.W., 2001. Seedling mortality in Hawaiian rain forest: the role of small-scale physical disturbance. Biotropica 33, 319–323.

Driscoll, H.E., Barrington, D.S., 2007. Origin of Hawaiian *Polystichum* (Dryopteridaceae) in the context of a world phylogeny. Am. J. Bot. 94, 1413–1424.

Dudley, N.S., James, R.L., Sniezko, R.A., Yeh, A., 2007. Investigating Koa Wilt and dieback in Hawai'i pathogenicity of *fusarium* species on *Acacia koa* seedlings. Nativ. Plants J. 8, 259–266.

Dudley, B.D., Hughes, R.F., Ostertag, R., 2014. Groundwater availability mediates the ecosystem effects of an invasion of *Prosopis pallida*. Ecol. Appl. 24, 1954–1971.

Dudley, N.S., Jones, T.C., James, R.L., Sniezko, R.A., Cannon, P., Borthakur, D., 2015. Applied disease screening and selection program for resistance to vascular wilt in Hawaiian *Acacia koa*. South. For. 77, 65–73.

Dudley, B.D., Hughes, R.F., Asner, G.P., Baldwin, J.A., Miyazawa, Y., Dulai, H., Waters, C., Bishop, J., Vaughn, N.R., Yeh, J., Kettwich, S., MacKenzie, R.A., Ostertag, R., Giambelluca, T., 2020. Hydrological effects of tree invasion on a dry coastal Hawaiian ecosystem. For. Ecol. Manage. 458, 117653.

Dunbar-Co, S., Wieczorek, A.M., Morden, C.W., 2008. Molecular phylogeny and adaptive radiation of the endemic Hawaiian *Plantago* species (Plantaginaceae). Am. J. Bot. 95, 1177–1188.

Dupuis, J.R., Pillon, Y., Sakishima, T., Gemmill, C.E.C., Chamala, S., Barbazuk, W.B., Geib, S.M., Stacy, E.A., 2019. Targeted amplicon sequencing of 40 nuclear genes supports a single introduction and rapid radiation of Hawaiian *Metrosideros* (Myrtaceae). Plant Syst. Evol. 305, 961–974.

Durand, L.Z., Goldstein, G., 2001. Growth, leaf characteristics, and spore production in native and invasive tree ferns in Hawai'i. Am. Fern J. 91, 25–35.

Eakins, B.W., Robinson, J.E., Kanamatsu, T., Jiro, N., Smith, J.R., Takahashi, E., Clague, D.A., 2003. Hawai'i's Volcanoes Revealed, U.S Geological Survey Geologic Invetigations Series Map I-2809.

Ekar, J.M., Price, D.K., Johnson, M.A., Stacy, E.A., 2019. Varieties of the highly dispersible and hypervariable tree, *Metrosideros polymorpha*, differ in response to mechanical stress and light across a sharp ecotone. Am. J. Bot. 106, 1106–1115.

Eldridge, L.G., Miller, S.E., 1995. How many species are there in Hawai 'i. Bishop Museum Occasional Papers 41, 3–18.

Ellsworth, L.M., Litton, C.M., Dale, A.P., Miura, T., 2014. Invasive grasses change landscape structure and fire behaviour in Hawai'i. Appl. Veg. Sci. 17, 680–689.

Ellsworth, L.M., Litton, C.M., Leary, J.J.K., 2015. Restoration impacts on fuels and fire potential in a dryland tropical ecosystem dominated by the invasive grass Megathyrsus maximus. Restor. Ecol. 23, 955–963.

Emerson, B.C., Gillespie, R.G., 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol. Evol. 23, 619–630.

Engelbrecht, B.M.J., Kursar, T.A., 2003. Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136, 383–393.

Enoki, T., Drake, D.R., 2017. Alteration of soil properties by the invasive tree Psidium cattleianum along a precipitation gradient on O'ahu Island, Hawai'i. Plant Ecol. 218, 947–955.

Ewel, J.J., Putz, F.E., 2004. A place for alien species in ecosystem restoration. Front. Ecol. Environ. 2, 354–360.

Flaspohler, D.J., Giardina, C.P., Asner, G.P., Hart, P., Price, J., Lyons, C.K., Castaneda, X., 2010. Long-term effects of fragmentation and fragment properties on bird species richness in Hawaiian forests. Biol. Conserv. 143, 280–288.

Fleischer, R.C., James, H.F., Olson, S.L., 2008. Convergent evolution of hawaiian and australo-pacific honeyeaters from distant songbird ancestors. Curr. Biol. 18, 1927–1931.

Fleming, T.H., Kress, W.J., 2013. The Ornaments of Life. University of Chicago Press, Chicago.

Fletcher, J., Luster, D., Bostock, R., Burans, J., Cardwell, K., Gottwald, T., McDaniel, L., Royer, M., Smith, K., 2010. Emerging infections plant diseases. In: Scheld, W.M., Grayson, L., Hughes, J.M. (Eds.), Emerging Infections 9. ASM Press, Washington D.C, p. 337.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C. S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581.

Forbes, D., 1918. Report of committee on forestry. Hawaiian Planters' Record 18, 202–205.

Fortini, L.B., Jacobi, J.D., 2018. Identifying opportunities for long-lasting habitat conservation and restoration in Hawai'i's shifting climate. Reg. Environ. Change 18, 2391–2402.

Fortini, L., Price, J., Jacobi, J., Vorsino, A., Burgett, J., Brinck, K., Amidon, F., Miller, S., Gon, S.O., Koob, G., Paxton, E., 2013. A landscape-based assessment of climate change vulnerability for all native Hawaiian plants. USGS Tech. Rep. 141.

Fortini, L.B., Vorsino, A.E., Amidon, F.A., Paxton, E.H., Jacobi, J.D., 2015. Large-scale range collapse of Hawaiian forest birds under climate change and the need 21st century conservation options. PLoS One 10, 22.

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

Fosberg, F.R., 1949. Derivation of the Flora of the Hawaiian Islands. University of Hawaii Press, Honolulu, HI.

Foster, J.T., 2009. The history and impact of introduced birds. In: Pratt, T.K., Atkinson, C.T., Banko, P.C., Jacobi, J.D., Woodworth, B.L. (Eds.), Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna. Yale UNiversity Press, New Haven, pp. 312–330.

Foster, J.T., Robinson, S.K., 2007. Introduced birds and the fate of Hawaiian rainforests. Conserv. Biol. 21, 1248–1257.

Frazier, A.G., Giambelluca, T.W., 2017. Spatial trend analysis of Hawaiian rainfall from 1920 to 2012. Int. J. Climatol. 37, 2522–2531.

Frazier, A.G., Elison Timm, O., Giambelluca, T.W., Diaz, H.F., 2018. The influence of ENSO, PDO and PNA on secular rainfall variations in Hawai'i. Clim. Dyn. 51, 2127–2140.

Freifelder, R.R., Vitousek, P.M., D'Antonio, C.M., 1998. Microclimate change and effect on fire following forest-grass conversion in seasonally dry tropical woodland. Biotropica 30, 286–297.

Freund, M.B., Henley, B.J., Karoly, D.J., McGregor, H.V., Abram, N.J., Dommenget, D., 2019. Higher frequency of Central Pacific El Niño events in recent decades relative to past centuries. Nat. Geosci. 12, 450. -+.

Friday, J.B., Cordell, S., Giardina, C.P., Inman-Narahari, F., Koch, N., Leary, J.J.K., Litton, C.M., Trauernicht, C., 2015. Future directions for forest restoration in Hawai'i. New For. 46, 733–746.

Funk, J.L., McDaniel, S., 2010. Altering light availability to restore invaded forest: the predictive role of plant traits. Restor. Ecol. 18, 865–872.

Funk, J.L., Throop, H.L., 2010. Enemy release and plant invasion: patterns of defensive traits and leaf damage in Hawai'i. Oecologia 162, 815–823.

Funk, J.L., Vitousek, P.M., 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446, 1079–1081.

Funk, V.A., Wagner, W.L., 1995. Biogeography of seven ancient hawaiian plant lineages. In: Wagner, W.L., Funk, V.A. (Eds.), Hawaiian Biogeography: Evolution on a Hotspot Archipelago. Smithsonian Institution Press, Washington D.C., USA, pp. 160–194.

Funk, J.L., Glenwinkel, L.A., Sack, L., 2013. Differential allocation to photosynthetic and non-photosynthetic nitrogen fractions among native and invasive species. PLoS One 8, 10.

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

Gagne, W.C., Cuddihy, L.W., 1990. Vegetation. In: L., W.W, Herbst, D.R., Sohmer, S.H. (Eds.), Manual of the Flowering Plants of Hawaii. University of Hawaii Press, Honolulu, pp. 45–114.

Ganders, F.R., Nagata, K.M., 1983. Relationships and floral biology of *Bidens cosmoides* (Asteraceae). Lyonia 2, 23–32.

Ganders, F.R., Nagata, K.M., 1984. The role of hybridization in the evolution of *Bidens* in the Hawaiian Islands. In: Grant, W.F. (Ed.), Plant Biosystematics. Chapman and Hall, New York, pp. 179–194.

Gardner, D.E., 1980. *Acacia koa* seedling wilt caused by *Fusarium oxysporum* f. Sp. *koae*, f. Sp. *Nov*. Phytopathology 70, 594–597.

Gardner, D.E., 1996. Notes on the decline problem of koa. Newslett. Hawaiian Botanical Soc. 35, 27–31.

Gemma, J.N., Koske, R.E., Habte, M., 2002. Mycorrhizal dependency of some endemic and endangered Hawaiian plant species. Am. J. Bot. 89, 337–345.

Giambelluca, T.W., Chen, Q., Frazier, A.G., Price, J.P., Chen, L.-L., Chu, P.-S., Eischeid, J. K., Delparte, D.M., 2013. Online rainfall atlas of Hawaii. Bull. Am. Meteorol. Soc. 94, 313–316.

Giardina, C.P., Litton, C.M., Crow, S.E., Asner, G.P., 2014. Warming-related increases in soil CO2 efflux are explained by increased below-ground carbon flux. Nat. Clim. Chang. 4, 822–827.

Gibson-Reinemer, D.K., Rahel, F.J., 2015. Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. PLoS One 10, 15.

Gillespie, R., 2004. Community assembly through adaptive radiation in hawaiian spiders. Science 303, 356–359.

Gillespie, R.G., 2016. Island time and the interplay between ecology and evolution in species diversification. Evol. Appl. 9, 53–73.

Gillespie, R., Baldwin, B., 2009. Island biogeography of remote archipelagoes. In: Losos, J.B., Ricklefs, R.E. (Eds.), The Theory of Island Biogeography Revisited. Princeton University Press, pp. 358–387.

Gillespie, R.G., Roderick, G.K., 2002. Arthropods on islands: colonization, speciation, and conservation. Annu. Rev. Entomol. 47, 595–632.

Gillespie, T.W., Keppel, G., Pau, S., Price, J.P., Jaffre, T., O'Neill, K., 2013. Scaling species richness and endemism of tropical dry forests on oceanic islands. Divers. Distrib. 19, 896–906.

Gillespie, T.W., O'Neill, K., Keppel, G., Pau, S., Meyer, J.Y., Price, J.P., Jaffre, T., 2014. Prioritizing conservation of tropical dry forests in the Pacific. Oryx 48, 337–344.

Givnish, T.J., Sytsma, K.J., Smith, J.F., Hahn, W.J., 1994. Thorn-like prickles and heterophylly in *Cyanea* - adaptations to extinct avian browsers on Hawai'i. Proc. Natl. Acad. Sci. U. S. A. 91, 2810–2814.

Givnish, T.J., Montgomery, R.A., Goldstein, G., 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. Am. J. Bot. 91, 228–246.

Givnish, T.J., Millam, K.C., Mast, A.R., Paterson, T.B., Theim, T.J., Hipp, A.L., Henss, J. M., Smith, J.F., Wood, K.R., Sytsma, K.J., 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: campanulaceae). Proc. R. Soc. B-Biol. Sciences 276, 407–416.

Givnish, T.J., Bean, G.J., Ames, M., Lyon, S.P., Sytsma, K.J., 2013. Phylogeny, floral evolution, and inter-island dispersal in Hawaiian *Clermontia* (Campanulaceae) based on ISSR variation and plastid spacer sequences. PLoS One 8, 15.

Gleason, S.M., Ares, A., 2004. Photosynthesis, carbohydrate storage and survival of a native and an introduced tree species in relation to light and defoliation. Tree Physiol. 24, 1087–1097.

Goldstein, J.H., Pejchar, L., Daily, G.C., 2008. Using return-on-investment to guide restoration: a case study from Hawai'i. Conserv. Lett. 1, 236–243.

Gon, S.M., Winter, K.B., 2019. A Hawaiian renaissance that could save the world. Am. Sci. 107, 232–239.

Gon, S.M., Tom, S.L., Woodside, U., 2018. 'Aina Momona, Honua Au Loli-Productive Lands, changing world: using the hawaiian footprint to inform biocultural restoration and future sustainability in Hawai'i. Sustainability 10, 21.

Gorresen, P.M., Brinck, K.W., DeLisle, M.A., Montoya-Aiona, K., Pinzari, C.A., Bonaccorso, F.J., 2018. Multi-state occupancy models of foraging habitat use by the Hawaiian hoary bat (Lasiurus cinereus semotus). PLoS One 13, 14.

Green, P.S., 1990. Norfolk Island and Lord Howe Island, Flora of Australia. Australian Government Publishing Service, Canberra.

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

Gruner, D.S., 2007. Geological age, ecosystem development, and local resource constraints on arthropod community structure in the Hawaiian Islands. Biol. J. Linn. Soc. 90, 551–570.

Haines, W.P., Heddle, M.L., Welton, P., Rubinoff, D., 2009. A Recent Outbreak of the Hawaiian Koa Moth, *Scotorythra paludicola* (Lepidoptera: geometridae), and a Review of Outbreaks between 1892 and 2003. Pac. Sci. 63, 349–369.

Hanna, C., Foote, D., Kremen, C., 2013. Invasive species management restores a plant-pollinator mutualism in Hawai'i. J. Appl. Ecol. 50, 147–155.

Hara, A.H., Beardsley, J.W., 1979. The biology of the black twig borer, *Xylosandrus compactus* (Eichhoff), in Hawai'i. Proc. Hawaiian Entomol. Soc. 23, 55–70.

Harrington, R.A., Ewel, J.J., 1997. Invasibility of tree plantations by native and non-indigenous plant species in Hawai'i. For. Ecol. Manage. 99, 153–162.

Harrington, R.A., Fownes, J.H., Scowcroft, P.G., Vann, C.S., 1997. Impact of Hurricane Iniki on native Hawaiian *Acacia koa* forests: damage and two-year recovery. J. Trop. Ecol. 13, 539–558.

Hart, P.J., 2010. Tree growth and age in an ancient Hawaiian wet forest: vegetation dynamics at two spatial scales. J. Trop. Ecol. 26, 1–11.

Hart, P., 2012. Patterns of tree mortality in a monodominant tropical forest. In: Sudarshana, P. (Ed.), Tropical Forests. InTech, Shanghai, pp. 349–358.

Harter, D.E.V., Irl, S.D.H., Seo, B., Steinbauer, M.J., Gillespie, R., Triantis, K.A., Fernandez-Palacios, J.M., Beierkuhnlein, C., 2015. Impacts of global climate change on the floras of oceanic islands - Projections, implications and current knowledge. Perspect. Plant Ecol. Evol. Syst. 17, 160–183.

Hayward, J., Hynson, N.A., 2014. New evidence of ectomycorrhizal fungi in the Hawaiian Islands associated with the endemic host Pisonia sandwicensis (Nyctaginaceae). Fungal Ecol. 12, 62–69.

Helfenstein, J., Tamburini, F., von Sperber, C., Massey, M.S., Pistocchi, C., Chadwick, O. A., Vitousek, P.M., Kretzschmar, R., Frossard, E., 2018. Combining spectroscopic and isotopic techniques gives a dynamic view of phosphorus cycling in soil. Nat. Commun. 9, 3226.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conserv. Biol. 22, 534–543.

Henn, J.J., Yelenik, S., Damschen, E.I., 2019. Environmental gradients influence differences in leaf functional traits between native and non-native plants. Oecologia 191, 397–409.

Herbert, D.A., Fownes, J.H., 1999. Forest productivity and efficiency of resource use across a chronosequence of tropical montane soils. Ecosystems 2, 242–254.

Herbert, D.A., Fownes, J.H., Vitousek, P.M., 1999. Hurricane damage to a Hawaiian forest: nutrient supply rate affects resistance and resilience. Ecology 80, 908–920.

Hess, S.C., Banko, P.C., Brenner, G.J., Jacobi, J.D., 1999. Factors related to the recovery of subalpine woodland on Mauna kea. Hawaii. Biotropica 31, 212–219.

Hess, S.C., Banko, P.C., Miller, L.J., Laniawe, L.P., 2014. Habitat and food preferences of the endangered palila (*Loxioides bailleui*) on Mauna kea, Hawai'i. Wilson J. Ornithol. 126, 728–738.

Higgs, E., 2017. Novel and designed ecosystems. Restor. Ecol. 25, 8–13.

Hoan, R., Ormond, R., Barton, K.E., 2014. Prickly poppies can get pricklier: ontogenetic patterns in the induction of physical defense traits. PLoS One 9, E96796.

Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation of decomposition in Hawaiian forests. Ecology 81, 1867–1877.

Hobbs, R.J., Higgs, E., Hall, C.M., Bridgewater, P., Chapin III, F.S., Ellis, E.C., Ewel, J.J., Hallett, L.M., Harris, J., Hulvey, K.B., Jackson, S.T., Kennedy, P.L., Kueffer, C., Lach, L., Lantz, T.C., Lugo, A.E., Mascaro, J., Murphy, S.D., Nelson, C.R., Perring, M. P., Richardson, D.M., Seastedt, T.R., Standish, R.J., Starzomski, B.M., Suding, K.N., Tognetti, P.M., Yakob, L., Yung, L., 2014. Managing the whole landscape: historical, hybrid, and novel ecosystems. Front. Ecol. Environ. 12, 557–564.

Hodges, C.S., Adee, K.T., Stein, J.D., Wood, H.B., Doty, R.D., 1986. Decline of 'Ōhi'a (*Metrosideros polymorpha*) in Hawai'i: a Review. Gen. Tech. Rep. PSW- 86. Berkeley, CA.

Holdridge, L.R., 1947. Determination of world plant formations from simple climatic data. Science 105, 367–368.

Holland, B.S., Cowie, R.H., 2009. Land snail models in island biogeography: a tale of two snails. Am. Malacol. Bull. 27, 59–68.

Hotchkiss, S., Juvik, J.O., 1999. A late-quaternary pollen record from Ka'au crater, O'ahu, Hawai'i. Quat. Res. 52, 115–128.

Howarth, D.G., Baum, D.A., 2005. Genealogical evidence of homoploid hybrid speciation in an adaptive radiation of *Scaevola* (Goodeniaceae) in the Hawaiian Islands. Evolution 59, 948–961.

Howarth, F.G., Mull, W.P., 1992. Hawaiian Insects and Their Kin. University of Hawaii Press, Honolulu, HI.

Hubbell, S.P., 2006. Neutral theory and the evolution of ecological equivalence. Ecology 87, 1387–1398.

Hughes, R.F., Denslow, J.S., 2005. Invasion by a N-2-fixing tree alters function and structure in wet lowland forests of Hawai'i. Ecol. Appl. 15, 1615–1628.

Hughes, F., Vitousek, P.M., 1993. Barriers to shrub reestablishment following fire in the seasonal submontane zone of Hawai'i. Oecologia 93, 557–563.

Hughes, F., Vitousek, P.M., Tunison, T., 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. Ecology 72, 743–746.

Hughes, R.F., Asner, G.P., Mascaro, J., Uowolo, A., Baldwin, J., 2014. Carbon storage landscapes of lowland Hawai'i: the role of native and invasive species through space and time. Ecol. Appl. 24, 716–731.

Hughes, R.F., Asner, G.P., Litton, C.M., Selmants, P.C., Hawbaker, T.J., Jacobi, J.D., Giardina, C.P., Sleeter, B.M., 2017. Influence of invasive species on carbon storage in hawai'i's ecosystems. In: Selmants, P.C., Giardina, C., Jacobi, J.D., Zhu, Z. (Eds.), Baseline and Projected Future Carbon Storage and Carbon Fluxes in Ecosystems of Hawai'i. U.S. Department of the Interior. U.S. Geological Survey, Reston, VA, pp. 43–55.

Hynson, N.A., Merckx, V., Perry, B.A., Treseder, K.K., 2013. Identities and distributions of the co-invading ectomycorrhizal fungal symbionts of exotic pines in the Hawaiian Islands. Biol. Invasions 15, 2373–2385.

Imhoff, M.L., 1995. Radar backscatter and biomass saturation - ramifications for global biomass inventory. Ieee Trans. Geosci. Remote. Sens. 33, 511–518.

Inman-Narahari, F., Ostertag, R., Cordell, S., Giardina, C.P., Nelson-Kaula, K., Sack, L., 2013. Seedling recruitment factors in low-diversity Hawaiian wet forest: towards global comparisons among tropical forests. Ecosphere 4, 19.

Inman-Narahari, F., Ostertag, R., Hubbell, S.P., Giardina, C.P., Cordell, S., Sack, L., 2016. Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests. J. Ecol. 104, 773–780.

Iwashita, D.K., Litton, C.M., Giardina, C.P., 2013. Coarse woody debris carbon storage across a mean annual temperature gradient in tropical montane wet forest. For. Ecol. Manage. 291, 336–343.

Izuno, A., Kitayama, K., Onoda, Y., Tsujii, Y., Hatakeyama, M., Nagano, A.J., Honjo, M. N., Shimizu-Inatsugi, R., Kudoh, H., Shimizu, K.K., Isagi, Y., 2017. The population genomic signature of environmental association and gene flow in an ecologically divergent tree species Metrosideros polymorpha (Myrtaceae). Mol. Ecol. 26, 1515–1532.

Jacobi, J.D., 1993. In: Huettl, R., Mueller-Dombois, D. (Eds.), Distribution and Dynamics of *Metrosideros* Dieback on the Island of Hawai'I: Implications for Management Programs. Forest Decline in the Atlantic and Pacific Region Springer, Berlin, Heidelberg, pp. 236–242.

Jacobi, J.D., Price, J.P., Fortini, L.B., Gon, S.M.I., Berkowitz, P., 2017. Chapter 2. Baseline Land cover. In: Selmants, P.C., Giardina, C.P., Jacobi, J.D., Zhu, Z. (Eds.), Baseline and Projected Future Carbon Storage and Carbon Fluxes in Ecosystems of Hawaii. U.S. Geological Survey Professional Paper, pp. 9–20.

James, H.F., Burney, D.A., 1997. The diet and ecology of Hawaii's extinct flightless waterfowl: evidence from coprolites. Biol. J. Linn. Soc. 62, 279–297.

James, H.F., Stafford Jr, T.W., Steadman, D.W., Olson, S.L., Martin, P.S., Jull, A.J., McCoy, P.C., 1987. Radiocarbon dates on bones of extinct birds from Hawaii. Proc. Natl. Acad. Sci. U. S. A 84, 2350–2354.

James, R.L., Dudley, N.L., Yeh, A., 2006. Investigating koa wilt in Hawai'i: examining *Acacia koa* seeds and seedpods for *Fusarium* species. Nativ. Plants J. 7, 315–323.

Joe, S.M., Daehler, C.C., 2008. Invasive slugs as under-appreciated obstacles to rare plant restoration: evidence from the Hawaiian Islands. Biol. Invasions 10, 245–255.

Johnson, M.A., Price, D.K., Price, J.P., Stacy, E.A., 2015. Postzygotic barriers isolate sympatric species of Cyrtandra (Gesneriaceae) in Hawaiian montane forest understories. Am. J. Bot. 102, 1870–1882.

Johnson, M.A., Clark, J.R., Wagner, W.L., McDade, L.A., 2017. A molecular phylogeny of the Pacific Glade of Cyrtandra (Gesneriaceae) reveals a Fijian origin, recent diversification, and the importance of founder events. Mol. Phylogenet. Evol. 116, 30–48.

Johnson, M.A., Pillon, Y., Sakishima, T., Price, D.K., Stacy, E.A., 2019. Multiple colonizations, hybridization and uneven diversification in *Cyrtandra* (Gesneriaceae) lineages on Hawai'i Island. J. Biogeogr. 46, 1178–1196.

Jones, T.A., 2017. Ecosystem restoration: recent advances in theory and practice. Rangel. J. 39, 417–430.

Juvik, J.O., Nullet, D., 1995. Relationships between rainfall, cloud-water interception, and canopy throughfall in a hawaiian montane forest. In: Hamilton, L.S., Juvik, J.O., Scatena, F.N. (Eds.), Tropical Montane Cloud Forests. Springer, New York, NY.

Kagawa, A., Sack, L., Duarte, K., James, S., 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., Giambelluca, T.W., 2020. Spatial patterns and trends in surface air temperatures and implied changes in atmospheric moisture across the Hawaiian Islands, 1905-2017. J. Geophys. Res.-Atmos. 125, 17.

Kaiser, L., 2014. Assessing the Impacts of Kona Lows on Rainfall: Variability and Spatial Patterns in the Hawaiian Islands, Geography and Environment. University of Hawaii at Manoa, Honolulu, Hawaii, p. 48.

Karpa, D.M., Vitousek, P.M., 1994. Successional development of a Hawaiian montane grassland. Biotropica 26, 2–11.

Kaufman, L.V., Higashi, C.H.V., 2015. Expansion of lobate lac scale distribution into O'ahu forest systems. Proc. Hawaiian Entomol. Soc. 47, 83–92.

Kawelo, H.K., Harbin, S.C., Joe, S.M., Keir, M.J., Weisenberger, L., 2012. Unique reintroduction considerations in hawai'i: case studies from a decade of rare plant restoration at the o'ahu army natural Resource rare plant program. In: Maschinski, J., Haskins, K.E. (Eds.), Plant Reintroduction in a Changing Climate. Island Press, Washington D.C, pp. 209–226.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 16, 406–411.

Keith, L.M., Hughes, R.F., 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, 1276–1277.

Kellner, J.R., Asner, G.P., Vitousek, P.M., Tweiten, M.A., Hotchkiss, S., Chadwick, O.A., 2011. Dependence of forest structure and dynamics on substrate age and ecosystem development. Ecosystems 14, 1156–1167.

Kinney, K.M., Asner, G.P., Cordell, S., Chadwick, O.A., Heckman, K., Hotchkiss, S., Jeraj, M., Kennedy-Bowdoin, T., Knapp, D.E., Questad, E.J., Thaxton, J.M., Trusdell, F., Kellner, J.R., 2015. Primary succession on a Hawaiian dryland chronosequence. PLoS One 10, 13.

Kitayama, K., Mueller-Dombois, D., 1994. An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian island mountain: (2) vegetation zonation. Phytocoenologia 24, 135–154.

Kitayama, K., Mueller-Dombois, D., 1995. Vegetation changes along gradients of long-term soil development in the Hawaiian montane rainforest zone. Vegetatio 120, 1–20.

Kitayama, K., Mueller-Dombois, D., Vitousek, P.M., 1995. Primary succession of Hawaiian montane rain forest on a chronosequence of 8 lava flows. J. Veg. Sci. 6, 211–222.

Kitayama, K., Pattison, R., Cordell, S., Webb, D., MuellerDombois, D., 1997a. Ecological and genetic implications of foliar polymorphism in *Metrosideros polymorpha* Gaud. (Myrtaceae) in a habitat matrix on Mauna Loa, Hawai'i. Ann. Bot. 80, 491–497.

Kitayama, K., Schuur, E.A.G., Drake, D.R., MuellerDombois, D., 1997b. Fate of a wet montane forest during soil ageing in Hawai'i. J. Ecol. 85, 669–679.

Knope, M.L., Bellinger, M.R., Datlof, E.M., Gallaher, T.J., Johnson, M.A., 2020. Insights into the evolutionary history of the Hawaiian *Bidens* (Asteraceae) adaptive radiation revealed through phylogenomics. J. Hered. 111, 119–137.

Koch, J.B., Sahli, H.F., 2013. Patterns of flower visitation across elevation and successional gradients in Hawai'i. Pac. Sci. 67, 253–266.

Kodama, K., Barnes, G.M., 1997. Heavy rain events over the south-facing slopes of Hawai'i: attendant conditions. Weather Forecast. 12, 347–367.

Koide, D., Yoshida, K., Daehler, C.C., Mueller-Dombois, D., 2017. An upward elevation shift of native and non-native vascular plants over 40 years on the island of Hawai'i. J. Veg. Sci. 28, 939–950.

Koske, R.E., Gemma, J.N., 1990. VA-Mycorrhizae in strand vegetation of Hawaii - evidence for long-distance codispersal of plants and fungi. Am. J. Bot. 77, 466–474.

Koske, R.E., Gemma, J.N., 2006. Arbuscular mycorrhizae effects on growth of two Hawaiian species: indigenous Osteomeles anthyllidifolia (Rosaceae) and invasive Psidium cattleianum (Myrtaceae). Pac. Sci. 60, 471–482.

Koske, R.E., Gemma, J.N., Flynn, T., 1992. Mycorrhizae in Hawaiian angiosperms - a survey with implications for the origin of the native flora. Am. J. Bot. 79, 853–862.

Koutnik, D.L., 1990. *Chamaesyce* (native species). In: Wagner, W.L., Herbst, D.R., Sohmer, S.H. (Eds.), Manual of Flowering Plants of Hawai'i. University of Hawaii Press and Bishop Museum Press, Honolulu, HI, pp. 602–615.

Kraft, N.J.B., Valencia, R., Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an amazonian forest. Science 322, 580–582.

Krushelnycky, P.D., 2015. Ecology of some lesser-studied introduced ant species in Hawaiian forests. J. Insect Conserv. 19, 659–667.

Krushelnycky, P.D., Starr, F., Starr, K., Longman, R.J., Frazier, A.G., Loope, L.L., Giambelluca, T.W., 2016. Change in trade wind inversion frequency implicated in the decline of an alpine plant. Clim. Chang. Responses 3, 1.

Kueffer, C., Kinney, K., 2017. What is the importance of islands to environmental conservation? Environ. Conserv. 44, 311–322.

Kuppler, J., Hofers, M.K., Trutschnig, W., Bathke, A.C., Eiben, J.A., Daehler, C.C., Junker, R.R., 2017. Exotic flower visitors exploit large floral trait spaces resulting in asymmetric resource partitioning with native visitors. Funct. Ecol. 31, 2244–2254.

Kurashima, N., Fortini, L., Ticktin, T., 2019. The potential of indigenous agricultural food production under climate change in Hawai'i. Nat. Sustain. 2, 191–199.

Lach, L., 2008. Floral visitation patterns of two invasive ant species and their effects on other hymenopteran visitors. Ecol. Entomol. 33, 155–160.

Lammers, T.G., Freeman, C.E., 1986. Ornithophily among the Hawaiian LOBELIOIDEAE (CAMPANULACEAE) - evidence from floral nectar sugar compositions. Am. J. Bot. 73, 1613–1619.

LaRosa, A.M., Tunison, J.T., Ainsworth, A., Kauffman, J.B., Hughes, R.F., 2008. Fire and nonnative invasive plants in the hawaiian Islands bioregion. In: Zouhar, K., Smith, J. K., Sutherland, S., Brooks, M.L. (Eds.), Wildland Fire in Ecosystems: Fire and Nonnative Invasive Plants. USDA Forest Service Rocky Mountain Research Station, Ogden, UT, pp. 225–242.

Laurance, W.F., 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biol. Conserv. 141, 1731–1744.

Leibold, M.A., McPeek, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87, 1399–1410.

Leonard, D.L., 2008. Recovery expenditures for birds listed under the US Endangered Species Act: the disparity between mainland and Hawaiian taxa. Biol. Conserv. 141, 2054–2061.

Leopold, C.R., Hess, S.C., 2019. Facilitating adaptation to climate change while restoring a montane plant community. PLoS One 14, 17.

Lewontin, R.C., Birch, L.C., 1966. Hybridization as a source of variation for adaptation to new environments. Evolution 20, 315–336.

Liao, W., Atkinson, C.T., LaPointe, D.A., Samuel, M.D., 2017. Mitigating future avian malaria threats to Hawaiian forest birds from climate change. PLoS One 12.

Lieberman, D., Lieberman, M., Hartshorn, G., Peralta, R., 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa rica. J. Trop. Ecol. 1, 97–109.

Lim, J.Y., Marshall, C.R., 2017. The true tempo of evolutionary radiation and decline revealed on the Hawaiian archipelago. Nature 543, 710. -+.

Lindqvist, C., Motley, T.J., Jeffrey, J.J., Albert, V.A., 2003. Cladogenesis and reticulation in the Hawaiian endemic mints (Lamiaceae). Cladistics-Int. J. Willi Hennig Soc. 19, 480–495.

Litton, C.M., Sandquist, D.R., Cordell, S., 2006. Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawai'i. For. Ecol. Manage. 231, 105–113.

Litton, C.M., Giardina, C.P., Albano, J.K., Long, M.S., Asner, G.P., 2011. The magnitude and variability of soil-surface CO2 efflux increase with mean annual temperature in Hawaiian tropical montane wet forests. Soil Biol. Biochem. 43, 2315–2323.

Loh, R.K., Tunison, J.T., 1999. Vegetation Recovery Following Pig Removal in' Ola'a-Koa Rainforest Unit, Hawaii Volcanoes National Park, Pacific Cooperative Studies Unit Technical Report 123. University of Hawaii Press, Mānoa, Honolulu, HI.

Loh, R., Ainsworth, A., Tunison, T., D'Antonio, C.M., 2009. Testing Native Species Response to Fire – a First Step towards Building Fire Resilient Native Plant Communities at Hawai'i Volcanoes National Park, Technical Report. Pacific Cooperative Studies Unit. University of Hawaii Press, p. 30.

Lohse, K.A., Nullet, D., Vitousek, P., 1995. Effects of extreme drought on vegetation of a lava flow on Mauna Loa, Hawai'i. Pac. Sci. 49, 212–220.

Loope, L., 2010. A Summary of Information on the Rust *Puccinia psidii* Winter (guava Rust) With Emphasis on Means to Prevent Introduction of Additional Strains to Hawai'i, Technical Report No. 2010-1082, p. 31.

Loope, L.L., Giambelluca, T.W., 1998. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui. Hawaii. Clim. Change 39, 503–517.

Lu, B.-Y., Chu, P.-S., Kim, S.-H., Karamperidou, C., 2020. Hawaiian regional climate variability during two types of el niño. J. Clim. 33, 9929–9943.

Lugo, A.E., 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. Austral Ecol. 33, 368–398.

Lugo, A.E., Wang, D., Bormann, F.H., 1990. A comparative analysis of biomass production in five tropical tree species. For. Ecol. Manage. 31, 153–166.

Luiz, B., Stacy, E.A., Keith, L.M., 2021. Screening of *Metrosideros polymorpha* ('ōhi'a) varieties for resistance to *Ceratocystis lukuohia*. Eur. J. Forest Pathol. 51, e12656.

Lurie, M.H., Barton, K.E., Daehler, C.C., 2017. Pre-damage biomass allocation and not invasiveness predicts tolerance to damage in seedlings of woody species in Hawai'i. Ecology 98, 3011–3021.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

MacDonald, G.A., Abbott, A.T., Peterson, F.L., 1983. Volcanoes in the Sea: the Geology of Hawaii. University of Hawaii Press, Honolulu.

Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. Trends Ecol. Evol. 13, 195–198.

Mack, M.C., D'Antonio, C.M., 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. Ecol. Appl. 13, 154–166.

Magnacca, K.N., 2007. Conservation status of the endemic bees of Hawai'i, *Hylaeus* (nesoprosopis) (Hymenoptera: colletidae). Pac. Sci. 61, 173–190.

Maguire, K.C., Nieto-Lugilde, D., Fitzpatrick, M.C., Williams, J.W., Blois, J.L., 2015. Modeling species and Community responses to past, present, and future episodes of climatic and ecological change. In: Futuyma, D.J. (Ed.), Annual Review of Ecology, Evolution, and Systematics, vol 46. Annual Reviews, Palo Alto, p. 343. -+.

Malhi, Y., Wright, J., 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. Philos. Trans. R. Soc. B-Biol. Sci. 359, 311–329.

Mascaro, J., Becklund, K.K., Hughes, R.F., Schnitzer, S.A., 2008. Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i. For. Ecol. Manage. 256, 593–606.

Mascaro, J., Hughes, R.F., Schnitzer, S.A., 2012. Novel forests maintain ecosystem processes after the decline of native tree species. Ecol. Monogr. 82, 221–238.

Matsuoka, K., 2020. Seed Dispersal and Germination by Native and Exotic Avian Frugivores of Hawai'i Island, Tropical Conservation Biology and Environmental Science. University of Hawaii at Hilo, Hilo, Hawaii.

McDaniel, S., Ostertag, R., 2010. Strategic light manipulation as a restoration strategy to reduce alien grasses and encourage native regeneration in Hawaiian mesic forests. Appl. Veg. Sci. 13, 280–290.

McDowell, N., Allen, C.D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher, R., Fontes, C.G., Galbraith, D., Goodsman, D., Grossiord, C., Hartmann, H., Holm, J., Johnson, D.J., Kassim, A., Keller, M., Koven, C., Kueppers, L., Kumagai, T., Malhi, Y., McMahon, S.M., Mencuccini, M., Meir, P., Moorcroft, P., Muller-Landau, H.C., Phillips, O.L., Powell, T., Sierra, C.A., Sperry, J., Warren, J., Xu, C.G., Xu, X.T., 2018. Drivers and mechanisms of tree mortality in moist tropical forests. New Phytol. 219, 851–869.

Medeiros, C.D., Scoffoni, C., John, G.P., Bartlett, M.K., Inman-Narahari, F., Ostertag, R., Cordell, S., Giardina, C., Sack, L., 2019. An extensive suite of functional traits distinguishes Hawaiian wet and dry forests and enables prediction of species vital rates. Funct. Ecol. 33, 712–734.

Meier, J.I., Marques, D.A., Mwaiko, S., Wagner, C.E., Excoffier, L., Seehausen, O., 2017. Ancient hybridization fuels rapid cichlid fish adaptive radiations. Nat. Commun. 8, 14363.

Meli, P., Holl, K.D., Benayas, J.M.R., Jones, H.P., Jones, P.C., Montoya, D., Mateos, D.M., 2017. A global review of past land use, climate, and active vs. Passive restoration effects on forest recovery. PLoS One 12, 17.

Meredith, F.L., Tindall, M.L., Hemmings, F.A., Moles, A.T., 2019. Prickly pairs: the proportion of spinescent species does not differ between islands and mainlands. J. Plant Ecol. 12, 941–948.

Michaud, J., Cordell, S., Cole, T.C., Ostertag, R., 2015. Drought in an invaded hawaiian lowland wet forest. Pac. Sci. 69, 367–383.

Miller, A.E., Brosi, B.J., Magnacca, K.N., daily, G.C., Pejchar, L., 2015. Pollen carried by native and nonnative bees in the large-scale reforestation of pastureland in Hawai'i: implications for pollination. Pac. Sci. 69, 67–79.

Miyasaka, S.C., Habte, M., Matsuyama, D.T., 1993. Mycorrhizal dependency of 2 Hawaiian endemic trees - koa and mamane. J. Plant Nutr. 16, 1339–1356.

Mooney, H.A., Bullock, S.H., Medina, E., 1995. Introduction. In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.), Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, pp. 1–8.

Moreira, X., Castagneyrol, B., García-Verdugo, C., Abdala-Roberts, L., 2021. A meta-analysis of insularity effects on herbivory and plant defences. J. Biogeogr. n/a.

Morrison, K.R., Stacy, E.A., 2014. Intraspecific divergence and evolution of a life-history trade-off along a successional gradient in Hawaii's *Metrosideros polymorpha*. J. Evol. Biol. 27, 1192–1204.

Mortenson, L.A., Hughes, R.F., Friday, J.B., Keith, L.M., Barbosa, J.M., Friday, N.J., Liu, Z.F., Sowards, T.G., 2016. Assessing spatial distribution, stand impacts and rate of Ceratocystis fimbriata induced' ohi'a (*Metrosideros polymorpha*) mortality in a tropical wet forest, Hawai'i Island. USA. Forest Ecol. Manag. 377, 83–92.

Mueller-Dombois, D., 1981. Fire in tropical ecosystems. In: Mooney, H.A., Bonnicksen, T. M., Christensen, N.L., Lotan, J.E., Reiners, W.A. (Eds.), Fire Regimes and Ecosystem Properties Conference. USDA Forest Service, Honolulu, HI,, pp. 137–176.

Mueller-Dombois, D., 1985. 'Ōhi'a dieback in Hawai'i: 1984 synthesis and evaluation. Pac. Sci. 39, 150–170.

Mueller-Dombois, D., 1987. Forest dynamics in Hawai'i. Trends Ecol. Evol. 2, 216–220.

Mueller-Dombois, D., 2000. Rain forest establishment and succession in the Hawaiian Islands. Landsc. Urban Plan. 51, 147–157.

Mueller-Dombois, D., Fosberg, F.R., 1998. Northern Polynesia: the Hawaiian Islands. Vegetation of the Tropical Pacific Islands. Springer, New York, pp. 461–577.

Mueller-Dombois, D., Jacobi, J.D., Cooray, R.G., Balakrishan, N., 1977. 'Ōhi'a Rainforest Study: Ecological Investigations of 'Ōhi'a Dieback Problems in Hawai'i, Cooperative National Park Studies Unit, 20th ed. Honolulu, HI.

Mueller-Dombois, D., Jacobi, J.D., Boehmer, H.J., Price, J.P., 2013. 'Ōhi'a Lehua Rainforest. Friends of the Joseph Rock Herbarium.

Mulder, C.P.H., Anderson, W.B., Towns, D.R., Bellingham, P.J., 2011. Seabird Islands: Ecology, Invasions, and Restoration. Oxford University Press, New York.

Murakami, H., Wang, B., Li, T., Kitoh, A., 2013. Projected increase in tropical cyclones near Hawai'i. Nat. Clim. Chang. 3, 749–754.

Murcia, C., Aronson, J., Kattan, G.H., Moreno-Mateos, D., Dixon, K., Simberloff, D., 2014. A critique of the' novel ecosystem' concept. Trends Ecol. Evol. 29, 548–553.

Nadkarni, N.M., Matelson, T.J., 1992. Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a Neotropical montane forest, Costa rica. Biotropica 24, 113–120.

Nepokroeff, M., Sytsma, K.J., Wagner, W.L., Zimmer, E.A., 2003. Reconstructing ancestral patterns of colonization and dispersal in the Hawaiian understory tree genus *Psychotria* (Rubiaceae): a comparison of parsimony and likelihood approaches. Syst. Biol. 52, 820–838.

Nishida, G., 2002. Hawaiian Terrestrial Arthrodod Checklist, 4th ed. Honolulu, HI.

Nogueira-Filho, S.L.G., Nogueira, S.S.C., Fragoso, J.M.V., 2009. Ecological impacts of feral pigs in the Hawaiian islands. Biodivers. Conserv. 18, 3677–3683.

O'Rorke, R., Cobian, G.M., Holland, B.S., Price, M.R., Costello, V., Amend, A.S., 2015. Dining local: the microbial diet of a snail that grazes microbial communities is geographically structured. Environ. Microbiol. 17, 1753–1764.

Olson, A.C., 2014. A hard nut to crack: rapid evolution in the Kona grosbeak of Hawai'i for a locally abundant food source (Drepanidini: chloridops kona). Wilson J. Ornithol. 126, 1–8.

Ostertag, R., 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. Ecology 82, 485–499.

Ostertag, R., Verville, J.H., 2002. Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. Plant Ecol. 162, 77–90.

Ostertag, R., Giardina, C.P., Cordell, S., 2008. Understory colonization of Eucalyptus plantations in Hawai'i in relation to light and nutrient levels. Restor. Ecol. 16, 475–485.

Ostertag, R., Inman-Narahari, F., Cordell, S., Giardina, C.P., Sack, L., 2014. Forest structure in Low-Diversity tropical forests: a study of Hawaiian wet and dry forests. PLoS One 9.

Ostertag, R., Warman, L., Cordell, S., Vitousek, P.M., 2015. Using plant functional traits to restore Hawaiian rainforest. J. Appl. Ecol. 52, 805–809.

Ostertag, R., Cordell, S., Michaud, J., Cole, T.C., Schulten, J.R., Publico, K.M., Enoka, J. H., 2009. Ecosystem and restoration consequences of invasive woody species removal in hawaiian lowland wet forest. Ecosystems 12, 503–515.

Ostertag, R., Sebastián-González, E., Peck, R., Hall, T., Kim, J., DiManno, N., Rayome, D., Cordell, S., Banko, P., Uowolo, A., 2020. Linking plant and animal functional diversity with an experimental community restoration in a Hawaiian lowland wet forest. Food Webs 25, e00171.

Palmer, D.D., 2003. Hawai'i's Ferns and Fern Allies. University of Hawaii Press, Honolulu, HI.

Pascua, P., McMillen, H., Ticktin, T., Vaughan, M., Winter, K.B., 2017. Beyond services: a process and framework to incorporate cultural, genealogical, place-based, and indigenous relationships in ecosystem service assessments. Ecosyst. Serv. 26, 465–475.

Patiño, J., Whittaker, R.J., Borges, P.A.V., Fernandez-Palacios, J.M., Ah-Peng, C., Araujo, M.B., Avila, S.P., Cardoso, P., Cornuault, J., de Boer, E.J., de Nascimento, L., Gil, A., Gonzalez-Castro, A., Gruner, D.S., Heleno, R., Hortal, J., Illera, J.C., Kaiser-Bunbury, C.N., Matthews, T.J., Papadopoulou, A., Pettorelli, N., Price, J.P., Santos, A.M.C., Steinbauer, M.J., Triantis, K.A., Valente, L., Vargas, P., Weigelt, P., Emerson, B.C., 2017. A roadmap for island biology: 50 fundamental questions after 50 years of the Theory of Island Biogeography. J. Biogeogr. 44, 963–983.

Pattison, R.R., Goldstein, G., Ares, A., 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117, 449–459.

Paxinos, E.E., James, H.F., Olson, S.L., Sorenson, M.D., Jackson, J., Fleischer, R.C., 2002. mtDNA from fossils reveals a radiation of Hawaiian geese recently derived from the Canada goose (Brantacanadensis). Proc. Natl. Acad. Sci. 99, 1399–1404.

Paxton, E.H., Camp, R.J., Gorresen, P.M., Crampton, L.H., Leonard, D.L., VanderWerf, E. A., 2016. Collapsing avian community on a Hawaiian island. Sci. Adv. 2, e1600029.

Pearson, H.L., Vitousek, P.M., 2001. Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. Ecol. Appl. 11, 1381–1394.

Peay, K.G., von Sperber, C., Cardarelli, E., Toju, H., Francis, C.A., Chadwick, O.A., Vitousek, P.M., 2017. Convergence and contrast in the community structure of Bacteria, Fungi and Archaea along a tropical elevation-climate gradient. FEMS Microbiol. Ecol. 93, 12.

Pejchar, L., 2015. Introduced birds incompletely replace seed dispersal by a native frugivore. AoB Plants 7 plv072.

Pejchar, L., Gallo, T., Hooten, M.B., Daily, G.C., 2018. Predicting effects of large-scale reforestation on native and exotic birds. Divers. Distrib. 24, 811–819.

Pender, R.J., Shiels, A.B., Bialic-Murphy, L., Mosher, S.M., 2013. Large-scale rodent control reduces pre- and post-dispersal seed predation of the endangered Hawaiian lobeliad, *Cyanea superba* subsp *superba* (Campanulaceae). Biol. Invasions 15, 213–223.

Pender, R.J., Morden, C.W., Paull, R.E., 2014. Investigating the pollination syndrome of the Hawaiian lobeliad genus *Clermontia* (Campanulaceae) using floral nectar traits. Am. J. Bot. 101, 201–205.

Peñuelas, J., Sardans, J., Llusia, J., Owen, S.M., Silva, J., Niinemets, U., 2010. Higher allocation to low cost chemical defenses in invasive species of Hawai'i. J. Chem. Ecol. 36, 1255–1270.

Percy, D.M., 2017. Making the most of your host: the *Metrosideros*-feeding psyllids (Hemiptera, Psylloidea) of the Hawaiian Islands. ZooKeys 1–163.

Percy, D.M., Garver, A.M., Wagner, W.L., James, H.F., Cunningham, C.W., Miller, S.E., Fleischer, R.C., 2008. Progressive island colonization and ancient origin of Hawaiian *Metrosideros* (Myrtaceae). Proc. R. Soc. B-Biol. Sci. 275, 1479–1490.

Peterson, D.M., Ellen, S.D., Knifong, D.L., 1993. Distribution of Past Debris Flows and Other Rapid Slope Movements from Natural Hillslopes in the Honolulu District of Oahu. US Geological Survey, Hawaii.

Petillon, J., Privet, K., Roderick, G.K., Gillespie, R.G., Price, D., 2020. Non-native spiders change assemblages of Hawaiian forest fragment kipuka over space and time. Neobiota 1–9.

Petitpierre, B., McDougall, K., Seipel, T., Broennimann, O., Guisan, A., Kueffer, C., 2016. Will climate change increase the risk of plant invasions into mountains? Ecol. Appl. 26, 530–544.

Pierre, S., Hewson, I., Sparks, J.P., Litton, C.M., Giardina, C., Groffman, P.M., Fahey, T.J., 2017. Ammonia oxidizer populations vary with nitrogen cycling across a tropical montane mean annual temperature gradient. Ecology 98, 1896–1907.

Poff, K.E., Stever, H., Reil, J.B., Seabourn, P., Ching, A.J., Aoki, S., Logan, M., Michalski, J.R., Santamaria, J., Adams, J.W., Eiben, J.A., Yew, J.Y., Ewing, C.P., Magnacca, K.N., Bennett, G.M., 2017. The native Hawaiian insect microbiome initiative: a critical perspective for Hawaiian insect evolution. Insects 8, 14.

Poorter, L., van der Sande, M.T., Arets, E., Ascarrunz, N., Enquist, B., Finegan, B., Licona, J.C., Martinez-Ramos, M., Mazzei, L., Meave, J.A., Munoz, R., Nytch, C.J., de Oliveira, A.A., Perez-Garcia, E.A., Prado, J., Rodriguez-Velazques, J., Ruschel, A.R., Salgado-Negret, B., Schiavini, I., Swenson, N.G., Tenorio, E.A., Thompson, J., Toledo, M., Uriarte, M., van der Hout, P., Zimmerman, J.K., Pena-Claros, M., 2017. Biodiversity and climate determine the functioning of Neotropical forests. Glob. Ecol. Biogeogr. 26, 1423–1434.

Pratt, H.D., 2005. The Hawaiian Honeycreepers. Oxford UNiversity Press, Oxford, UK.

Pratt, T.K., 2009. Origins and evolution. In: Pratt, T.K., Atkinson, C.T., Banko, P.C., Jacobi, J.D., Woodworth, B.L. (Eds.), Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna. Yale University Press, New Haven, pp. 3–24.

Price, J.P., 2004. Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. J. Biogeogr. 31, 487–500.

Price, J.P., Clague, D.A., 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. Proc. R. Soc. B-Biol. Sci. 269, 2429–2435.

Price, J.P., Elliott-Fisk, D., 2004. Topographic history of the Maui Nui complex, Hawai'i, and its implications for biogeography. Pac. Sci. 58, 27–45.

Price, J.P., Wagner, W.L., 2004. Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. Evolution 58, 2185–2200.

Price, J.P., Wagner, W.L., 2018. Origins of the Hawaiian flora: phylogenies and biogeography reveal patterns of long-distance dispersal. J. Syst. Evol. 56, 600–620.

Price, J.P., Jacobi, J.D., Gon III, S.M., Matsuwaki, D., Mehrhoff, L., Wagner, W., Lucas, M., Rowe, B., 2012. Mapping Plant Species Ranges in the Hawaiian Islands - Developing a Methodology and Associated GIS Layers. U.S. Geological Survey Open-File Report.

Price, M.R., O'Rorke, R., Amend, A.S., Hadfield, M.G., 2017. Diet selection at three spatial scales: implications for conservation of an endangered Hawaiian tree snail. Biotropica 49, 130–136.

Ramsey, J., Bradshaw, H.D., Schemske, D.W., 2003. Components of reproductive isolation between the monkeyflowers *Mimulus lewisii* and *M. Cardinalis* (Phrymaceae). Evolution 57, 1520–1534.

Ranker, T.A., Imada, C.T., Lynch, K., Palmer, D.D., Vernon, A.L., Thomas, M.K., 2019. Taxonomic and nomenclatural updates to the fern and Lycophyte Flora of the Hawaiian Islands. Am. Fern J. 109, 54–72.

Rayome, D.D., Ostertag, R., Cordell, S., 2018. Enhancing aboveground carbon storage and invasion resistance through restoration: early results from a functional trait-based experiment. Pac. Sci. 72, 149–164.

Restrepo, C., Vitousek, P., 2001. Landslides, alien species, and the diversity of a Hawaiian montane mesic ecosystem. Biotropica 33, 409–420.

Restrepo, C., Vitousek, P., Neville, P., 2003. Landslides significantly alter land cover and the distribution of biomass: an example from the Ninole ridges of Hawai'i. Plant Ecol. 166, 131–143.

Rhoades, A., 2012. The Evolution of Reproductive Isolation within an Endemic Hawaiian Tree Species (*Metrosideros Polymorpha*) Across Environmental Extremes. University of Hawai'i at Hilo, Hilo, Hawai'i.

Roderick, G.K., Gillespie, R.G., 1998. Speciation and phylogeography of Hawaiian terrestrial arthropods. Mol. Ecol. 7, 519–531.

Roderick, G.K., Percy, D.M., 2008. Host plant use, diversification, and coevolution: insights from remote oceanic islands. In: Tilmon, K.J (Ed.), Specialization, Speciation, and Radiation: the Evolutionary Biology of Herbivorous Insects. University of California Press, Berkeley, CA, pp. 151–161.

Rollins, M.G., 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. Int. J. Wildland Fire 18, 235–249.

Rominger, A.J., Goodman, K.R., Lim, J.Y., Armstrong, E.E., Becking, L.E., Bennett, G.M., Brewer, M.S., Cotoras, D.D., Ewing, C.P., Harte, J., Martinez, N.D., O'Grady, P.M., Percy, D.M., Price, D.K., Roderick, G.K., Shaw, K.L., Valdovinos, F.S., Gruner, D.S., Gillespie, R.G., 2016. Community assembly on isolated islands: macroecology meets evolution. Glob. Ecol. Biogeogr. 25, 769–780.

Ross, M.R.V., Bernhardt, E.S., Doyle, M.W., Heffernan, J.B., 2015. designer ecosystems: incorporating design approaches into applied ecology. In: Gadgil, A., Tomich, T.P. (Eds.), Annual Review of Environment and Resources, vol 40. Annual Reviews, Palo Alto, pp. 419–443.

Roy, K., Ewing, C.P., Hughes, M.A., Keith, L., Bennett, G.M., 2019. Presence and viability of *Ceratocystis lukuohia* in ambrosia beetle frass from Rapid 'Ōhi'a Death-affected *Metrosideros polymorpha* trees on Hawai'i Island. Eur. J. Forest Pathol. 49, 4.

Rubinoff, D., 2017. Hawaiian Lepidoptera represent remarkable diversity that is disappearing before it can be discovered. News of the Lepidopterists' Soc. 59, 202–204.

Rubinoff, D., Holland, B.S., Shibata, A., Messing, R.H., Wright, M.G., 2010. Rapid invasion despite lack of genetic variation in the Erythrina gall Wasp (*Quadrastichus erythrinae* kim). Pac. Sci. 64, 23–31.

Rankin, E.E.W., Knowlton, J.L., Gruner, D.S., Flaspohler, D.J., Giardina, C.P., Leopold, D. R., Buckardt, A., Pitt, W.C., Fukami, T., 2018. Vertical foraging shifts in Hawaiian forest birds in response to invasive rat removal. PLoS One 13, 19.

Russell, A.E., Raich, J.W., Vitousek, P.M., 1998. The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawai'i. J. Ecol. 86, 765–779.

Sakai, A.K., Wagner, W.L., Ferguson, D.M., Herbst, D.R., 1995. Origins of dioecy in the Hawaiian flora. Ecology 76, 2517–2529.

Sakai, A.K., Wagner, W.L., Mehrhoff, L.A., 2002. Patterns of endangerment in the Hawaiian flora. Syst. Biol. 51, 276–302.

Samuelson, G.A., 2003. Review of *Rhyncogonus* of the Hawaiian Islands (Coleoptera: Curculionidae). Bishop Museum Bulletin in Entomology, Honolulu.

Sandquist, D.R., Cordell, S., 2007. Functional diversity of carbon-gain, water-use, and leaf-allocation traits in trees of a threatened lowland dry forest in Hawai'i. Am. J. Bot. 94, 1459–1469.

Santiago, L.S., 2000. Use of coarse woody debris by the plant community of a Hawaiian montane cloud forest. Biotropica 32, 633–641.

Santiago, L.S., Goldstein, G., Meinzer, F.C., Fownes, J.H., Mueller-Dombois, D., 2000. Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. Tree Physiol. 20, 673–681.

Sardans, J., Llusia, J., Niinemets, U., Owen, S., Peñuelas, J., 2010. Foliar mono- and sesquiterpene contents in relation to leaf economic spectrum in native and alien species in O'ahu (Hawai'i). J. Chem. Ecol. 36, 210–226.

Schmidt, J.P., Drake, J.M., 2011. Time since introduction, seed mass, and genome size predict successful invaders among the cultivated vascular plants of Hawai'i. PLoS One 6, 7.

Schulten, J.R., Cole, T.C., Cordell, S., Publico, K.M., Ostertag, R., Enoka, J.E., Michaud, J. D., 2014. Persistence of native trees in an invaded Hawaiian lowland wet forest: experimental evaluation of light and water constraints. Pac. Sci. 68, 267–285.

Schuur, E.A.G., 2001. The effect of water on decomposition dynamics in mesic to wet Hawaiian montane forests. Ecosystems 4, 259–273.

Schuur, E.A.G., Chadwick, O.A., Matson, P.A., 2001. Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests. Ecology 82, 3182–3196.

Scoffoni, C., Kunkle, J., Pasquet-Kok, J., Vuong, C., Patel, A.J., Montgomery, R.A., Givnish, T.J., Sack, L., 2015. Light-induced plasticity in leaf hydraulics, venation, anatomy, and gas exchange in ecologically diverse Hawaiian lobeliads. New Phytol. 207, 43–58.

Scowcroft, P.G., Conrad, C.E., 1992. Alien and native plant response to release from feral sheep browsing on mauna kea. In: Stone, C.P., Smith, S.W., Tunison, J.T. (Eds.), Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. Alien and native plant response to release from feral sheep browsing on Mauna Kea, Honolulu, HI, pp. 394–408.

Scowcroft, P.G., Giffin, J.G., 1983. Feral herbivores suppress mamane and other browse speices on Mauna kea, Hawai'i. J. Range Manage. 36, 638–645.

Scowcroft, P.G., Hobdy, R., 1987. Recovery of goat-damaged vegetation in an insular tropical montane forest. Biotropica 19, 208–215.

Seehausen, O., 2013. Conditions when hybridization might predispose populations for adaptive radiation. J. Evol. Biol. 26, 279–281.

Selmants, P.C., Hart, S.C., 2010. Phosphorus and soil development: Does the Walker and Syers model apply to semiarid ecosystems? Ecology 91, 474–484.

Selmants, P.C., Litton, C.M., Giardina, C.P., Asner, G.P., 2014. Ecosystem carbon storage does not vary with mean annual temperature in Hawaiian tropical montane wet forests. Glob. Chang. Biol. 20, 2927–2937.

Selmants, P.C., Giardina, C., Jacobi, J.D., Zhu, C.D., 2017. Baseline and projected future carbon storage and carbon fluxes in ecosystems of Hawaiʻi. U.S. Geol. Survey Professional Paper 1834, 134.

Shaw, K.L., Gillespie, R.G., 2016. Comparative phylogeography of oceanic archipelagos: hotspots for inferences of evolutionary process. Proc. Natl. Acad. Sci. U. S. A. 113, 7986–7993.

Shay, K., Drake, D.R., Taylor, A.D., Sahli, H.F., Euaparadorn, M., Akamine, M., Imamura, J., Powless, D., Aldrich, P., 2016. Alien insects dominate the plant-pollinator network of a Hawaiian coastal ecosystem. Pac. Sci. 70, 409–429.

Sherrod, D., Sinton, J.M., Watkins, S.E., Brunt, K.M., 2007. Geologic Map of the State of Hawaiʻi, US Geological Survey Open-file Report, p. 83.

Shiels, A.B., Drake, D.R., 2011. Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaiʻi? Biol. Invasions 13, 883–894.

Shiels, A.B., Ennis, M.K., Shiels, L., 2014. Trait-based plant mortality and preference for native versus non-native seedlings by invasive slug and snail herbivores in Hawaiʻi. Biol. Invasions 16, 1929–1940.

Simberloff, D., 1995. Why do introduced species appear to devastate islands more than mainland areas? Pac. Sci. 49, 87–97.

Smith, C.W., Tunison, J.T., 1992. Fire and alien plants in hawaiʻi: research and management. In: Stone, C.P., Smith, S.W., Tunison, J.T. (Eds.), Alien Plant Invasions in Native Ecosystems of Hawaiʻi: Management and Research. University of Hawaii Press, Honolulu, HI, pp. 394–408.

Smith, J.M., Kennedy, A.B., Westerink, J.J., Taflanidis, A.A., Cheung, K.F., 2012. Hawaiʻi hurricane wave and surge modeling and fast forecasting. Coast. Eng. Proc. 1, 8.

Sorenson, J.C., 1979. Fire, Lightening and ʻŌhiʻa Dieback. Newsletter of the Hawaiian Botany Society, Honolulu, HI, pp. 9–23.

Sperry, J.H., OʻHearn, D., Drake, D.R., Hruska, A.M., Case, S.B., Vizentin-Bugoni, J., Arnett, C., Chambers, T., Tarwater, C.E., 2021. Fruit and seed traits of native and invasive plant species in Hawaiʻi: implications for seed dispersal by non-native birds. Biol. Invasions.

St. John, H., 1946. Proceedings of the California academy of sciences. Series 4 (25), 377–419.

Stacy, E.A., Johnson, M.A., 2021. Floral variation across three varieties of the landscape-dominant tree Metrosideros polymorpha (Myrtaceae): insights from a Hawaii Island Common Garden. Int. J. Plant Sci. 182, 46–58.

Stacy, E.A., Sakishima, T., 2019. Phylogeography of the highly dispersible landscape-dominant woody species complex, *Metrosideros*, in Hawaiʻi. J. Biogeogr. 46, 2215–2231.

Stacy, E.A., Johansen, J.B., Sakishima, T., Price, D.K., Pillon, Y., 2014. Incipient radiation within the dominant Hawaiian tree *Metrosideros polymorpha*. Heredity 113, 334–342.

Stacy, E.A., Johansen, J.B., Sakishima, T., Price, D.K., 2016. Genetic analysis of an ephemeral intraspecific hybrid zone in the hypervariable tree, *Metrosideros polymorpha*, on Hawaiʻi Island. Heredity 117, 173–183.

Stacy, E.A., Paritosh, B., Johnson, M.A., Price, D.K., 2017. Incipient ecological speciation between successional varieties of a dominant tree involves intrinsic postzygotic isolating barriers. Ecol. Evol. 7, 2501–2512.

Stacy, E.A., Sakishima, T., Tharp, H., Snow, N., 2020. Strong isolation within *Metrosideros* (ʻŌhiʻa) on Oʻahu correlates with extreme environments. J. Hered. 111, 103–118.

Staples, G.W., Imada, C.T., Hoe, W.J., Smith, C.W., 2004. A revised checklist of Hawaiian mosses. Trop. Bryol. 25, 35–69.

Stemmermann, L., 1983. Ecological studies of Hawaiian *Metrosideros* in a successional context. Pac. Sci. 37, 361–373.

Stratton, L.C., Goldstein, G., 2001. Carbon uptake, growth and resource-use efficiency in one invasive and six native Hawaiian dry forest tree species. Tree Physiol. 21, 1327–1334.

Stratton, L.C., Goldstein, G., Meinzer, F.C., 2000. Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. Oecologia 124, 309–317.

Strauch, A.M., Bruland, G.L., MacKenzie, R.A., Giardina, C.P., 2016. Soil and hydrological responses to wild pig (Sus scofa) exclusion from native and strawberry guava (Psidium cattleianum)-invaded tropical montane wet forests. Geoderma 279, 53–60.

Strauch, A.M., Giardina, C.P., MacKenzie, R.A., Heider, C., Giambelluca, T.W., Salminen, E., Bruland, G.L., 2017. Modeled effects of climate change and plant invasion on watershed function across a steep tropical rainfall gradient. Ecosystems 20, 583–600.

Strommer, L., Conant, S., 2018. Conservation value of koa (*Acacia koa*) reforestation areas on Hawaiʻi Island. Pacific Conserv. Biol. 24, 35–43.

Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. Trends Ecol. Evol. 19, 46–53.

Sugi, M., Murakami, H., Yoshida, K., 2017. Projection of future changes in the frequency of intense tropical cyclones. Clim. Dyn. 49, 619–632.

Sur, G.L., Keating, R., Snow, N., Stacy, E.A., 2018. Leaf micromorphology aids taxonomic delineation within the hypervariable genus *Metrosideros* (Myrtaceae) on Oʻahu. Pac. Sci. 72, 345–361.

Takahashi, M., Giambelluca, T.W., Mudd, R.G., Delay, J.K., Nullet, M.A., Asner, G.P., 2011. Rainfall partitioning and cloud water interception in native forest and invaded forest in Hawaiʻi Volcanoes National Park. Hydrol. Process. 25, 448–464.

Tamarin-Brodsky, T., Kaspi, Y., 2017. Enhanced poleward propagation of storms under climate change. Nat. Geosci. 10, 908. -+.

Tanentzap, A.J., Lee, W.G., Dugdale, J.S., Patrick, B.P., Fenner, M., Walker, S., Coomes, D.A., 2011. Differential responses of vertebrate and invertebrate herbivores to traits of New Zealand subalpine shrubs. Ecology 92, 994–999.

Thaxton, J.M., Cole, T.C., Cordell, S., Cabin, R.J., Sandquist, D.R., Litton, C.M., 2010. Native species regeneration following ungulate exclusion and nonnative grass removal in a remnant Hawaiian dry forest. Pac. Sci. 64, 533–544.

Thaxton, J.M., Cordell, S., Cabin, R.J., Sandquist, D.R., 2012. Non-native grass removal and shade increase soil moisture and seedling performance during hawaiian dry forest restoration. Restor. Ecol. 20, 475–482.

Timm, O.E., Giambelluca, T.W., Diaz, H.F., 2015. Statistical downscaling of rainfall changes in Hawaiʻi based on the CMIP5 global model projections. J. Geophys. Res.-Atmos. 120, 92–112.

Trauernicht, C., 2019. Vegetation—rainfall interactions reveal how climate variability and climate change alter spatial patterns of wildland fire probability on Big Island. Hawaii. Sci. Total Environ. 650, 459–469.

Trauernicht, C., Pickett, E., Giardina, C.P., Litton, C.M., Cordell, S., Beavers, A., 2015. The contemporary scale and context of wildfire in Hawaiʻi. Pac. Sci. 69, 427–444.

Treseder, K.K., Vitousek, P.M., 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. Ecology 82, 946–954.

Tunison, J.T., Loh, R., DʼAntonio, C.M., 2000. Fire and Invasive Plants in Hawaiʻi Volcanoes National Park, National Congress on Fire Ecology. Prevention, and Management, Tallahassee, FL.

Uchida, J., Zhong, S., Killgore, L., 2006. First report of a rust disease on ohia caused by *Puccinia psidii* in Hawaii. Plant Dis. 90, 524-524.

Vandergast, A.G., Gillespie, R.G., 2004. Effects of natural forest fragmentation on a Hawaiian spider community. Environ. Entomol. 33, 1296–1305.

Vannette, R.L., Leopold, D.R., Fukami, T., 2016. Forest area and connectivity influence root-associated fungal communities in a fragmented landscape. Ecology 97, 2374–2383.

Van Steenis, C.G.G.J., 1981. Rheophytes of the World: an Account of the Flood-resistant Flowering Plants and Ferns and the Theory of Autonomous Evolution. Springer Netherlands, The Netherlands.

Vaughn, N.R., Asner, G.P., Giardina, C.P., 2014. Centennial impacts of fragmentation on the canopy structure of tropical montane forest. Ecol. Appl. 24, 1638–1650.

Vega, F.E., Simpkins, A., Aime, M.C., Posada, F., Peterson, S.W., Rehner, S.A., Infante, F., Castillo, A., Arnold, A.E., 2010. Fungal endophyte diversity in coffee plants from Colombia, Hawaiʻi, Mexico and Puerto Rico. Fungal Ecol. 3, 122–138.

Via, S., Bouck, A.C., Skillman, S., 2000. Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. Evolution 54, 1626–1637.

Vitousek, P., 2004. Nutrient Cycling and Limitation: Hawaiʻi as a Model System. Princeton University Press, Princeton, New Jersey.

Vitousek, P.M., Walker, L.R., 1989. Biological invasion by *Myrica faya* in Hawaiʻi - plant demography, nitrogen-fixation, ecosystem effects. Ecol. Monogr. 59, 247–265.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., Matson, P.A., 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaiʻi. Science 238, 802–804.

Vitousek, P.M., Matson, P.A., Turner, D.R., 1988. Elevational and age gradients in Hawaiian montane rainforest - foliar and soil nutrients. Oecologia 77, 565–570.

Vizentin-Bugoni, J., Tarwater, C.E., Foster, J.T., Drake, D.R., Gleditsch, J.M., Hruska, A. M., Kelley, J.P., Sperry, J.H., 2019. Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawaiʻi. Science 364, 78–82.

Vizentin-Bugoni, J., Sperry, J.H., Kelley, J.P., Gleditsch, J.M., Foster, J.T., Drake, D.R., Hruska, A.M., Wilcox, R.C., Case, S.B., Tarwater, C.E., 2021. Ecological correlates of species' roles in highly invaded seed dispersal networks. Proc. Natl. Acad. Sci. 118 e2009532118.

Vogel, C., Helfenstein, J., Massey, M.S., Sekine, R., Kretzschmar, R., Beiping, L., Peter, T., Chadwick, O.A., Tamburini, F., Rivard, C., Herzel, H., Adam, C., Pradas del Real, A. E., Castillo-Michel, H., Zuin, L., Wang, D., Félix, R., Lassalle-Kaiser, B., Frossard, E., 2021. Microspectroscopy reveals dust-derived apatite grains in acidic, highly-weathered Hawaiian soils. Geoderma 381, 114681.

Vogl, R.J., 1969. The role of fire in the evolution of the hawaiian flora and vegetation. Annual Tall Timbers Fire Ecology Conference, Tallahassee, FL 5–60.

Wagner, W.L., Weller, S.G., Sakai, A.K., 1995. Phylogeny and biogeography in *Schiedea* and *Alsinidendron* (caryophyllaceae). In: Warren, W.L. (Ed.), Hawaiian Biogeography. Smithsonian Institution Press, pp. 221–258.

Wagner, W., Herbst, D., Sohmer, S., 1999. Manual of the Flowering Plants of Hawaiʻi, Revision Ed. University of Hawaii Press, Honolulu.

Wagner, W.L., Herbst, D.R., Lorence, D.H., 2005. Flora of the Hawaiian Islands Website. http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/index.htm [accessed August 2021].

Waite, M., Sack, L., 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. New Phytol. 185, 156–172.

Waite, M., Sack, L., 2011. Shifts in bryophyte carbon isotope ratio across an elevation x soil age matrix on Mauna Loa, Hawaii: do bryophytes behave like vascular plants? Oecologia 166, 11–22.

Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98, 725–736.

Walsh, S.K., Pender, R.J., Junker, R.R., Daehler, C.C., Morden, C.W., Lorence, D.H., 2019. Pollination biology reveals challenges to restoring populations of *Brighamia insignis* (Campanulaceae), a critically endangered plant species from Hawaiʻi. Flora 259, 10.

Walther, M., Hume, J.P., 2016. Extinct Birds of Hawaiʻi. Mutual Publishing, Honolulu.

Wardle, D.A., Walker, L.R., Bardgett, R.D., 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305, 509–513.

Warshauer, F.R., Jacobi, J.D., La Rosa, A.M., Scott, J.M., Smith, C.W., 1983. The Distribution, Impact and Potential Management of the Introduced Vine *Passiflora*

mollissima (Passifloraceae) in Hawai'i. Cooperative National Park Resources Study Unit, Honolulu, HI.

Weisenberger, L.A., Weller, S.G., Sakai, A.K., 2014. Remnants of populations provide effective source material for reintroduction of an endangered Hawaiian plant, *Schiedea kaalae* (Caryophyllaceae). Am. J. Bot. 101, 1954–1962.

Weller, S.G., Cabin, R.J., Lorence, D.H., Perlman, S., Wood, K., Flynn, T., Sakai, A.K., 2011. Alien plant invasions, introduced ungulates, and alternative states in a mesic forest in Hawaii. Restor. Ecol. 19, 671–680.

Weller, S.G., Sakai, A.K., Campbell, D.R., Powers, J.M., Pena, S.R., Keir, M.J., Loomis, A. K., Heintzman, S.M., Weisenberger, L., 2017. An enigmatic Hawaiian moth is a missing link in the adaptive radiation of *Schiedea*. New Phytol. 213, 1533–1542.

Westerband Knight, T., Barton, K.E., 2021. Intraspecific trait variation and reversals of trait strategies across key climate gradients in native Hawaiian plants and non-native invaders. Ann. Bot. 127, 553–564.

Westerband, A., Kagawa-Viviani, A.K., Bogner, K.K., Beilman, D.W., Knight, T.K., Barton, K.E., 2019. Seedling drought tolerance and functional traits vary in response to the timing of water availability in a keystone Hawaiian tree species. Plant Ecol. 220, 321–344.

Westerband, A., Bialic-Murphy, L., Weisenberger, L.A., Barton, K.E., 2020. Intraspecific variation in seedling drought tolerance and associated traits in a critically endangered, endemic Hawaiian shrub. Plant Ecol. Divers. 13, 159–174.

Whittaker, R.J., Triantis, K.A., Ladle, R.J., 2008. A general dynamic theory of oceanic island biogeography. J. Biogeogr. 35, 977–994.

Whittaker, R.J., Fernandez-Palacios, J.M., Matthews, T.J., Borregaard, M.K., Triantis, K. A., 2017. Island biogeography: taking the long view of nature's laboratories. Science 357, 885. ·+.

Wilmshurst, J.M., Hunt, T.L., Lipo, C.P., Anderson, A.J., 2011. High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. Proc. Natl. Acad. Sci. U. S. A. 108, 1815–1820.

Wilson, E.E., Holway, D.A., 2010. Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp. Ecology 91, 3294–3302.

Wilson, E.E., Sidhu, C.S., LeVan, K.E., Holway, D.A., 2010. Pollen foraging behaviour of solitary Hawaiian bees revealed through molecular pollen analysis. Mol. Ecol. 19, 4823–4829.

Winter, K.B., Lucas, M., 2017. Spatial modeling of social-ecological management zones of the Ali'i era on the island of Kaua'i with implications for large-scale biocultural conservation and forest restoration efforts in Hawai'i. Pac. Sci. 71, 457–477.

Winter, K.B., Beamer, K., Vaughan, M.B., Friedlander, A.M., Kido, M.H., Whitehead, A. N., Akutagawa, M.K.H., Kurashima, N., Lucas, M.P., Nyberg, B., 2018. The moku system: managing biocultural resources for abundance within social-ecological regions in Hawai'i. Sustainability 10, 19.

Winter, K.B., Lincoln, N.K., Berkes, F., Alegado, R.A., Kurashima, N., Frank, K.L., Pascua, P., Rii, Y.M., Reppun, F., Knapp, I.S.S., McClatchey, W.C., Ticktin, T., Smith, C., Franklin, E.C., Oleson, K., Price, M.R., McManus, M.A., Donahue, M.J., Rodgers, K.S., Bowen, B.W., Nelson, C.E., Thomas, B., Leong, J.-A., Madin, E.M.P., Rivera, M.A.J., Falinski, K.A., Bremer, L.L., Deenik, J.L., Gon I.I.I., S.M., Neilson, B., Okano, R., Olegario, A., Nyberg, B., Kawelo, A.H., Kotubetey, K., Kukea-Shultz, J.K., Toonen, R.J., 2020a. Ecomimicry in Indigenous resource management: optimizing ecosystem services to achieve resource abundance, with examples from Hawai'i. Ecol. Soc. 25.

Winter, K.B., Rii, Y.M., Reppun, F.A.W.L., Hintzen, K.D., Alegado, R.A., Bowen, B.W., Bremer, L.L., Coffman, M., Deenik, J.L., Donahue, M.J., Falinski, K.A., Frank, K., Franklin, E.C., Kurashima, N., Lincoln, N.K., Madin, E.M.P., McManus, M.A., Nelson, C.E., Okano, R., Olegario, A., Pascua, Pa., Oleson, K.L.L., Price, M.R., Rivera, M.A.J., Rodgers, K.S., Ticktin, T., Sabine, C.L., Smith, C.M., Hewett, A., Kaluhiwa, R., Cypher, M., healani Thomas, B., Leong, J.-A., Kekuewa, K., Tanimoto, J., Kukea-Shultz, K., nekoa Kawelo, A.H., ilei Kotubetey, K., Neilson, B.J.,

Lee, T.S., Toonen, R.J., 2020b. Collaborative research to inform adaptive comanagement: a framework for the He'eia National Estuarine Research Reserve. Ecol. Soc. 25.

Winter, K.B., Ticktin, T., Quazi, S.A., 2020c. Biocultural restoration in Hawai'i also achieves core conservation goals. Ecol. Soc. 25, 18.

Wong, T.M., Ticktin, T., 2015. Using population dynamics modelling to evaluate potential success of restoration: a case study of a Hawaiian vine in a changing climate. Environ. Conserv. 42, 20–30.

Wood, J.R., Alcover, J.A., Blackburn, T.M., Bover, P., Duncan, R.P., Hume, J.P., Louys, J., Meijer, H.J.M., Rando, J.C., Wilmshurst, J.M., 2017. Island extinctions: processes, patterns, and potential for ecosystem restoration. Environ. Conserv. 44, 348–358.

Worbes, M., 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. J. Ecol. 87, 391–403.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.

Wu, J.X., Delparte, D.M., Hart, P.J., 2014. Movement patterns of a native and non-native frugivore in Hawaii and implications for seed dispersal. Biotropica 46, 175–182.

Yang, Y., Berry, P.E., 2011. Phylogenetics of the *Chamaesyce* clade (*Euphorbia*, Euphorbiaceae): reticulate evolution and long-distance dispersal in a prominent C-4 lineage. Am. J. Bot. 98, 1486–1503.

Zablan, M., 2007. *Eugenia Koolauensis* (Nioi)—5-year Review Summary and Evaluation. Honolulu, HI.

Zahawi, R.A., Reid, J.L., Holl, K.D., 2014. Hidden costs of passive restoration. Restor. Ecol. 22, 284–287.

Zahn, G., Amend, A.S., 2017. Foliar microbiome transplants confer disease resistance in a critically-endangered plant. Peerj 5, 16.

Zavaleta, E.S., Hobbs, R.J., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. Trends Ecol. Evol. 16, 454–459.

Zhang, C.X., Wang, Y.Q., Hamilton, K., Lauer, A., 2016. Dynamical Downscaling of the Climate for the Hawaiian Islands. Part II: Projection for the Late Twenty-First Century. J. Clim. 29, 8333–8354.

Ziegler, A.C., 2002. Hawaiian Natural History, Ecology, and Evolution. University of Hawai'i Press, Honolulu.

Zimmerman, E.C., 1948. Introduction, Insects of Hawaii. University of Hawaii Press, Honolulu.

Zimmerman, N.B., Vitousek, P.M., 2012. Fungal endophyte communities reflect environmental structuring across a Hawaiian landscape. Proc. Natl. Acad. Sci. U. S. A. 109, 13022–13027.

Ziska, L.H., Dukes, J.S., 2014. Invasive Species and Global Climate Change, CABI Invasives Series. CABI, Oxfordshire, United Kingdom, p. 368.

Further reading

Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pysek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T.M., Dyer, E.E., Cassey, P., Scrivens, S.L., Economo, E.P., Guenard, B., Capinha, C., Seebens, H., Garcia-Diaz, P., Nentwig, W., Garcia-Berthou, E., Casal, C., Mandrak, N.E., Fuller, P., Meyer, C., Essl, F., 2017. Global hotspots and correlates of alien species richness across taxonomic groups. Nat. Ecol. Evol. 1, 7.