Chapter 4. Influence of Invasive Species on Carbon Storage in Hawai'i's Ecosystems

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4.1. Highlights

- Invasive species are widely distributed among most of Hawai'i's forests, woodlands, shrublands, and grasslands.

- Primary groups of invasive nonnative species include nitrogen-fixing trees and shrubs, non-nitrogen-fixing trees and shrubs, and grasses. Each species within these groups may have a positive, negative, or neutral effect on carbon stocks, depending on the structural and functional characteristics of the invader as well as those of the native communities undergoing invasion. Common invasion scenarios and their ramifications for carbon storage and cycling are presented.

- Although there is worldwide interest to protect and even increase carbon storage in ecosystems to mitigate climate change (Intergovernmental Panel on Climate Change, 2006), and invasion of nonnative plants into Hawai'i's ecosystems may, in some cases, increase carbon stocks across landscapes of Hawai'i, invasive species are commonly the primary cause of profound, and in many cases irreparable, damage to Hawai'i's native ecosystems, degrading their compositional, structural, and functional integrity. In addition, it is not clear whether any carbon sequestration benefit of invasive species can be sustained on a long-term basis.

4.2. Introduction

    Nonnative invasive species have altered virtually all Hawaiian terrestrial ecosystems in a variety of ways, including substantial changes to the storage, production, and cycling of

carbon (Ehrenfeld, 2003). Globally, nonnative species have changed the composition, structure, and function of countless native ecosystems (Elton, 1958; Vitousek and others, 1996), and the extent and influence of nonnative species invasions are considered substantial components of global environmental change (Vitousek and others, 1997). In turn, other aspects of environmental change (for example, land-use change, nitrogen deposition, and increased atmospheric-CO_2 concentrations) have likely amplified the spread and influence of invasive species (Dukes and Mooney, 1999). Nonnative species may alter carbon storage and dynamics by invading open niches in plant communities or by displacing native species by virtue of greater competitive ability and (or) reproductive output. However, nonnative species that generate the largest changes in carbon storage and cycling in ecosystems are those with the capacity to alter ecosystem processes, in effect resetting the rules under which all other species in the system operate (Vitousek, Walker, and others, 1987). Such processes include hydrology, geomorphology, nutrient cycling, natural disturbance regimes, primary production, and decomposition (Vitousek and others, 1997). These latter two processes represent the most direct determinants of carbon storage and cycling in ecosystems.

    Isolated oceanic islands are generally more susceptible to, and more heavily impacted by, nonnative species invasions than are continental systems. Island species collectively tend to exhibit proportionally higher levels of endemism (species found only on said islands), lower levels of diversity, commonly disharmonic plant and animal communities (lacking important functional or structural components, such as ants or nitrogen-fixing plants), and lower tolerance to disturbance (Vitousek, Loope, and Stone, 1987; Vitousek, 1990). The native biota of the Hawaiian Islands, Earth's most isolated archipelago, strongly exhibits these characteristics. Over 90 percent of Hawai'i's native flora is endemic, and many plant growth forms and (or) functional types that are abundant in continental systems are underrepresented or entirely absent in Hawai'i (for example, palms, pyrophytic grasses, terrestrial mammals). These attributes, coupled with high rates of nonnative-species introductions following European contact 220 years ago, have resulted in an island flora comprising about 1,200 native plant species and a

roughly equal number of naturalized introduced nonnative species, approximately 10 percent of which are considered invasive (Vitousek, Loope, and Stone, 1987; Wagner and others, 1999).

Collectively, the Hawaiian Islands exhibit an impressive array of climatic and edaphic variation, where substrates range in age from days to millions of years, and where Hawai'i Island alone harbors 25 of the world's 35 Holdridge life zones (Holdridge, 1947; Asner and others, 2005). Unfortunately, nearly all of these varied ecological zones contain nonnative invasive species capable of displacing native counterparts or altering ecological processes. Although many nonnative species were introduced inadvertently during the past two centuries, many were purposefully introduced. Of the approximately 100 nonnative plant species considered invasive and detrimental to Hawai'i's native ecosystems, more than half of them were purposefully introduced by territorial and state foresters and planted extensively across the archipelago (Woodcock, 2003). The spread of both subsets of nonnative invasive species has been exacerbated by land conversion, altered disturbance regimes (for example, agriculture, logging, grazing, fire, and residential and urban development), and domestic and feral ungulate activity (cattle, sheep, goats, and pigs). These forces have resulted in profoundly altered landscapes where nonnative species commonly dominate (Cuddihy and Stone, 1990). In many instances, such as with ungulate grazing and fire, disturbance amplifies and entrenches dominance and relative influence of the respective nonnative invasive species (Hughes and others, 1991; D'Antonio and Vitousek, 1992; Hughes and Vitousek, 1993; Brooks and others, 2004; Hawbaker and others, this volume, chap. 5).

As a result of the historical and ecological interactions discussed above, each main Hawaiian Island today exists as a matrix of native and nonnative-dominated landscapes (table 4.1 adapted from Jacobi and others, this volume, chap. 2). Nonnative

invasive species are present on every main Hawaiian Island, but their areal extent and prevalence varies from island to island. Viewed as a proportion of total vegetated area of each Island occupied by nonnative species, Kaho'olawe exhibits the highest proportion (99 percent) and Hawai'i Island exhibits the lowest (42 percent). O'ahu, Lāna'i, and Moloka'i exhibit roughly similar proportions (81–86 percent), as do the islands of Maui and Kaua'i (63 and 70 percent, respectively). Clearly, the extent of nonnative occupancy is high by any measure, and relative proportions of nonnative vegetation highlight the widespread importance of nonnative invasive vegetation across much of the Hawaiian archipelago.

How do alien-dominated vegetation assemblages affect terrestrial carbon storage and dynamics relative to the remaining native-dominated areas or former native-dominated areas that they have replaced? The answer depends upon the ecosystem or ecological zone in question, the particular nonnative species or collection of nonnative species that have invaded, as well as the timeframe. For example, in moist-to-wet windward zones of the Hawaiian Islands, the "carbon effect" (in other words, whether the system experiences a net loss or gain of carbon) associated with shifts from native-dominated forest to nonnative forest or shrubland depends on the maturity and development of the native forest being displaced or altered and, perhaps more importantly, on the stature and growth characteristics of the nonnative species that ultimately dominate a given ecosystem following invasion.

The objectives of this chapter are to synthesize existing information and improve our understanding of the patterns and dynamics of carbon storage, particularly aboveground carbon storage, across a variety of common invasion scenarios found in the Hawaiian Islands (table 4.2). Here we draw upon published results to explore the dynamics of invasion and characterize their associated patterns of carbon storage. Specifically, we focus on three dominant nonnative functional guilds: nitrogen-fixing trees

Table 4.1.   Current extent of native-dominated and nonnative-invaded vegetation types on each of the main Hawaiian Islands.

Island	Total vegetated area (km²)	Native dominated		Nonnative invaded[1]	
		Area (km²)	Percent of total	Area (km²)	Percent of total
Hawai'i	6,937	4,021	58	2,915	42
Maui	1,311	489	37	822	63
Kaua'i	1,083	323	30	760	70
O'ahu	987	162	16	825	84
Moloka'i	606	115	19	491	81
Lāna'i	344	49	14	295	86
Kaho'olawe	90	1	1	90	99

[1]Denotes plant communities either dominated by nonnative species or where nonnative species are a significant component of the community.

Table 4.2.   General effects of invasion by three main nonnative functional guilds on carbon pools of three differing native-dominated community types.

[Arrows indicate changes (increase, ↑; decrease, ↓; or no change, ↔) on overall carbon pools following invasion. N, nitrogen]

Native-dominated community	Non-native functional guild		
	N-fixing woody	Non N-fixing woody	Grasses
N-fixing forest	↔	↓	↓
Non N-fixing forest	↑	↔ or ↑	↓
Grassland	↑	↑	↔

and shrubs, non-nitrogen-fixing trees and shrubs, and grasses. We also note that the effect of invasion on carbon storage is as much influenced by the carbon stocks of the pre-invasion native community as the particular characteristics of the respective invasive nonnative species and (or) guilds (table 4.2).

4.3. Input Data and Methods

Our area of interest encompasses the Hawaiian Islands, and includes the wide variety of invasive species and invaded communities present throughout the archipelago. We illustrate prominent examples of nonnative invasive plants and their impact on carbon cycling and storage—usually in relation to those of adjacent native-dominated plant communities—using data compiled from published literature.

4.4. Results and Discussion

4.4.1. Nitrogen-Fixing Trees and Shrubs

Invasive species that have the capacity to fix nitrogen through symbiotic associations with *Rhizobia*, in the case of legumes, or *Frankia*, in the case of actinorhizal plants, are capable of altering the function and composition of the native ecosystems. This has been documented in numerous settings around the world (Ehrenfeld, 2003), perhaps most notably in Hawai'i (Vitousek, Walker, and others, 1987) where native nitrogen-fixing species—particularly those exhibiting early-successional pioneer characteristics—are relatively uncommon, and where many native ecosystems are nitrogen-limited (Vitousek and Farrington, 1997). Many of Hawai'i's more problematic invasive alien species are those that fix nitrogen. Although invasive nitrogen-fixing plants generally increase net primary production of the ecosystems they invade, the sign and degree of carbon-storage change depends on the individual characteristics of the invasive species and the successional characteristics of the invaded system.

4.4.1.1. *Falcataria moluccana* and *Casuarina equisetifolia*

In extant native-dominated wet forests along Hawai'i Island's windward coastal lowlands (<900 m above sea level), two alien nitrogen-fixing tree species—*Falcataria moluccana* (also known as albizia) and *Casuarina equisetifolia*—can alter both nutrient cycling and carbon storage at the stand to ecosystem levels (Hughes and Denslow, 2005; Mascaro and others, 2012; Hughes and others, 2014). Prior to invasion of these tree species, primary succession by native vegetation in these areas typically manifests as colonization of young, barren pāhoehoe and 'a'ā lava substrates by a single cohort of *Metrosideros polymorpha*, which gradually develops as monotypic forest stand during the first 100–200 years (Mueller-Dombois and Fosberg, 1998), and which ultimately develops into more diverse and structurally complex native forests as species establish during subsequent centuries of succession (200–700 years) (Zimmerman and others, 2008). Early-successional native forests on young lava flows (<200 years) exhibit aboveground carbon densities (ACDs) averaging less than 60 megagrams of carbon per hectare (MgC/ha). On older lava flows (400–750 years), native forests, having had the time to gradually accumulate substantial amounts of biomass, exhibit ACD values of 130 MgC/ha (fig. 4.1).

Although native-dominated vegetation can still be found in lowland wet habitats of east Hawai'i Island, substantial portions are now occupied by nonnative tree and shrub species purposefully introduced as part of massive nonnative-tree-planting efforts that took place across Hawai'i throughout the 1900s. Over 10,000 nonnative species were introduced into Hawai'i and more than 13 million individuals were planted in what has been characterized as the largest environmental project ever conducted in Hawai'i (Woodcock, 2003). Of the approximately 100 species now considered invasive in Hawai'i, half were introduced during that period. In Forest Reserves of the Puna District of Hawai'i Island, in an area totaling about 2,000 ha, nearly 35,000 individuals of 114 different species, 74 distinct genera, and 38 plant families were planted between 1906 and 1960 (Skolmen, 1963; Nelson, 1965). Among the most commonly planted species were *C. equisetifolia* and *F. moluccana*. This latter species,

Figure 4.1. Plot of aboveground carbon density in native-dominated and nonnative-dominated forest stands along a gradient of increasing lava age in Hawai'i. MgC/ha, megagrams of carbon per hectare
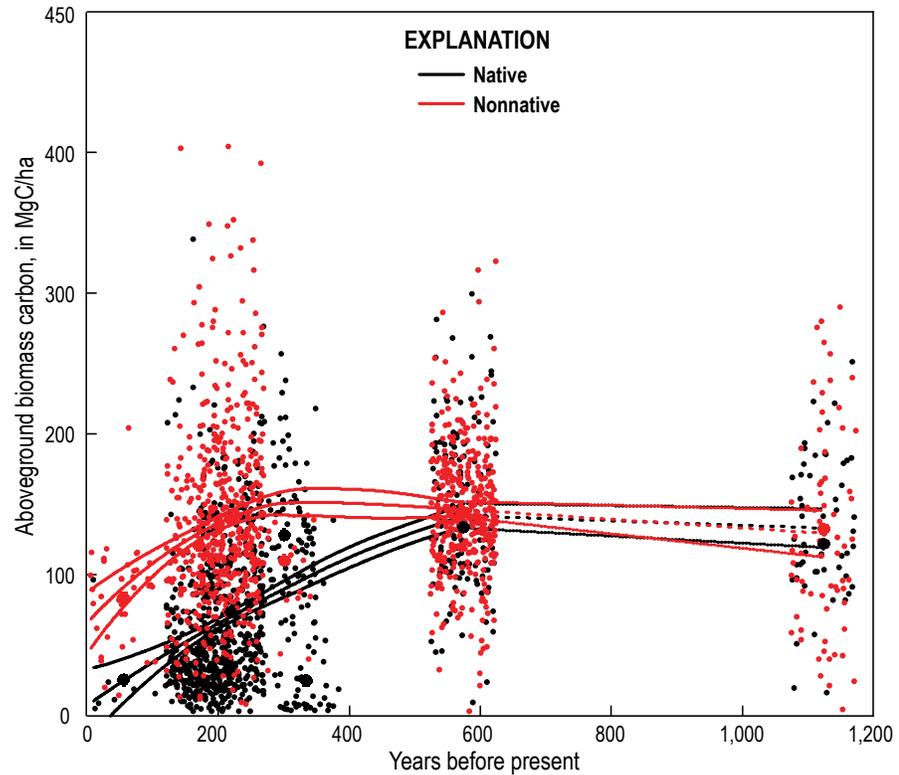
native to the Molucca Islands, New Guinea, New Britain, and the Solomon Islands and first introduced to Hawai'i in 1917, is a legume that fixes nitrogen through its symbiosis with *Rhizobia*. In contrast, *C. equisetifolia*, a tree native to Australia and introduced to Hawai'i in the 1890s, is an actinorhizal tree species that fixes nitrogen through its symbiosis with *Frankia*.

Although patterns of aboveground carbon accumulation among native forest stands were strongly controlled by lava substrate age and developed within century-scale timeframes, patterns of accumulation among *F. moluccana* and *C. equisetifolia* stands were decoupled from substrate age and developed within decadal-scale timeframes (fig. 4.1). Indeed, all nonnative forest stands inventoried by Hughes and others (2014) were established during the 1900s—some as late as 1955—and their ACD values were the result of no more than 90 years of succession. This attests to their capacity for comparatively rapid rates of ACD accumulation, particularly where such stands were dominated by tree species capable of symbiotic nitrogen fixation. On older lava substrates however, ACDs of native and nonnative stands were shown to be quite similar. Thus, comparisons between ACDs of native and nonnative nitrogen-fixing tree-dominated forests was highly dependent on lava substrate age and, hence, forest successional state. By virtue of their nitrogen-fixing capacities, the fast growing nitrogen-fixing trees *F. moluccana* and *C. equisetifolia* rapidly surpass ACDs of the slower growing dominant native tree *M. polymorpha* on young, nitrogen-limited lava flows. In contrast, although *F. moluccana* and *C. equisetifolia* attain ACD levels of about 130 MgC/ha in a matter of only a few decades on older lava substrate, those levels remain on a par with

native-dominated *M. polymorpha* forests that have experienced centuries of succession and carbon accumulation.

In addition to increasing ACD relative to that of native forests on young lava flows, Mascaro and others (2012) found that on lava flows aged 300 years before present and younger, both *F. moluccana*- and *C. equisetifolia*-dominated forest stands exhibited rates of litterfall, aboveground growth increment, and aboveground net primary production that were at least triple the same rates for native forest stands dominated by *M. polymorpha* on similarly aged lava flows. These authors also found that belowground carbon mass values of *F. moluccana*- and *C. equisetifolia*-dominated forests (~48 MgC/ha) were more than double those of *M. polymorpha*-dominated forest on young lava flows (20 MgC/ha). Again, the mechanism for such high rates of carbon cycling, accumulation, and storage is clear: newly formed lava substrates notably lack plant-available nitrogen (Vitousek and others, 1993), and inputs from sources other than higher plants (for example, precipitation and dry deposition, free-living cyanobacteria, and heterotrophic bacteria) are relatively low (Hughes and Denslow, 2005). The capacity of *F. moluccana* and *C. equisetifolia* to symbiotically fix nitrogen frees them from constraints posed by nitrogen limitation and allows for large increases in primary production, and increased nutrient acquisition (particularly phosphorus) (Binkley and others, 2004; Mascaro and others, 2012). In contrast, *M. polymorpha*, virtually the sole woody plant component of native-dominated primary succession on these lava flows, lacks the capacity to symbiotically fix nitrogen, and its productivity is highly constrained by nitrogen limitation (Hughes and Denslow, 2005; Mascaro and others, 2012).

4.4.1.2. *Morella faya*

In sub-montane and montane areas of Hawai'i Volcanoes National Park (HVNP) on the Island of Hawai'i, Vitousek and Walker (1989) showed that invasion by *Morella faya* (formerly *Myrica faya*) dramatically alters the functions of the formerly native-dominated community by quadrupling the amount of biologically available nitrogen entering these typically nitrogen-limited systems. Originally introduced to Hawai'i by Portuguese immigrants in the 19th century, *M. faya* is native to the Azores, Canary, and Madeira Islands; it is an actinorhizal nitrogen fixer that, like *F. moluccana* and *Casuarina* species, was planted widely throughout the main Hawaiian Islands during the early 20th century until its invasive potential was realized (Fosberg, 1937; Vitousek and Walker, 1989). First recorded in HVNP in 1961, *M. faya* occupied more than 12,000 ha of the Park by 1985 (Whiteaker and Gardner, 1985), and its distribution has increased dramatically during the last 30 years, particularly in seasonally dry portions of HVNP (D'Antonio and others, 2011). Numerous studies have demonstrated reinforcing effects of *M. faya* invasion on biogeochemical processes; these include increased trace gas emissions, litterfall, and soil organic carbon (Vitousek and Walker, 1989; Aplet, 1990; Hall and Asner, 2007).

Regarding the influence of *M. faya* invasion on aboveground carbon stocks, Asner and others (2010) compared native-dominated and *M. faya*-invaded communities along a shrubland–woodland–forest gradient (fig. 4.2). Although aboveground biomass (AGB) more than quadrupled from shrubland to forest
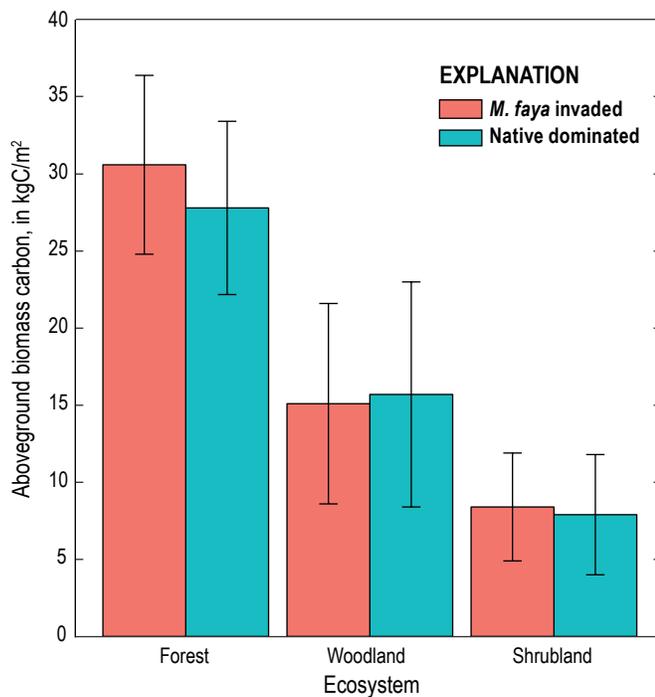

Figure 4.2. Plot of aboveground biomass carbon of native-dominated and *Morella faya*-invaded ecosystems in Hawai'i Volcanoes National Park (data from Asner and others, 2010). kgC/m², kilograms of carbon per square meter.

communities, *M. faya* AGB did not differ from that of native-dominated AGB in any of the three ecosystem types. As such, despite its capacity to substantially alter other ecosystem functions and characteristics, *M. faya* invasion failed to alter aboveground carbon stocks in any of the ecosystems it invaded in HVNP.

4.4.1.3. *Prosopis pallida* and *Leucaena leucocephala*

In arid ecosystems of Hawai'i, such as those on the leeward sides of the main Hawaiian Islands, the impact of invasive nitrogen fixers on carbon cycling and stocks is primarily controlled by water availability. Two widespread nitrogen-fixing trees exemplary of this are *Prosopis pallida* and *Leucaena leucocephala*; both are members of the Fabaceae family and as such fix nitrogen by symbiosis with *Rhizobia*. Both trees were introduced to Hawai'i in the early 1800s from their native range in the neotropics and naturalized rapidly across many of the arid zones of the main Hawaiian Islands (Wagner and others, 1999; Gallaher and Merlin, 2010); today they occupy a combined area of 59,000 ha, or 3.6 percent of the total land area of the Archipelago (Gon and others, 2006). Native species have been long extirpated from the vast majority of these areas, but native dry forests were likely composed of species such as *Erythrina sandwicensis*, *Reynoldsia sandwicensis*, and *Abutilon incanum* (Wagner and others, 1999).

In investigations into the effects of groundwater availability on plant–soil nitrogen cycling in areas invaded by *P. pallida* on the dry leeward coast of Hawai'i Island, Dudley and others (2014) compared nutrient acquisition and cycling as well as productivity of *P. pallida* trees growing in lowland areas where they could access shallow groundwater with *P. pallida* trees growing in upland areas where they had to rely solely on low volume, intermittent rainfall events. The authors found that *P. pallida* in upland environs experienced water stress, exhibited higher water-use efficiency, and exhibited lower predawn photosynthetic performance than did trees in lowland areas. Further, biologically available soil nitrogen pools and litter production were 10 and 17 times greater, respectively, in lowland *P. pallida* stands relative to upland stands. Differences in these functional attributes translated to large differences in ACD; lowland *P. pallida* stand-level carbon mass (20 MgC/ha) was more than six times greater than that of upland *P. pallida* stands (fig. 4.3). In the case of *P. pallida* invasion and growth across substantial portions of the main Hawaiian Islands, the degree to which these forests and woodlands store and cycle carbon is highly dependent on water availability.

In dry, leeward, lowland environments of the main Hawaiian Islands invaded and now occupied by *P. pallida* or *L. leucocephala* stands, associated herbaceous or grass biomass may contribute substantially to ecosystem carbon stocks and cycling. Ellsworth and others (2014) determined aboveground carbon mass in *L. leucocephala*-dominated woodlands; they found that although carbon mass in live biomass of the alien tree was generally greater than that in live grass biomass, the collective carbon mass of living and dead grass biomass was at least comparable, if not greater than, the
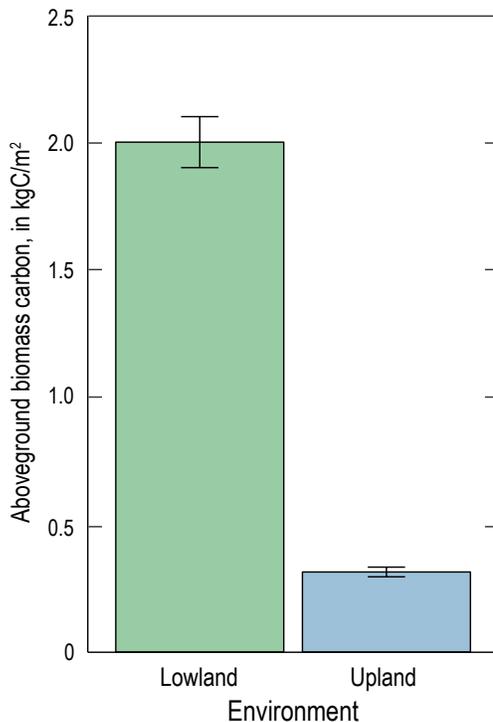
Figure 4.3.   Plot of aboveground biomass carbon of *Prosopis pallida* forest stands in upland and lowland environments along the dry leeward coast of Hawai'i Island (R. Flint Hughes, U.S. Department of Agriculture, Forest Service, unpublished data). Lowland stands have ample access to groundwater; upland stands do not have such access. kgC/m^2, kilograms of carbon per square meter.

Figure 4.4.   Plot of aboveground biomass carbon of *Leucaena leucocephala* stands and associated grass biomass in dry leeward lowland environments of O'ahu (modified from Ellsworth and others, 2014). kgC/m^2, kilograms of carbon per square meter.

combined living and dead mass of *L. leucocephala* (fig. 4.4). This is a common characteristic of many dry leeward systems invaded by *P. pallida* and *L. leucocephala*, and it likely results from increases in soil-nitrogen availability beneath these nitrogen-fixing tree species that facilitate the establishment and persistence of other plant species which, more commonly than not, tend to be introduced nonnatives (Dudley and others, 2014). In some cases, however, *P. pallida* and *L. leucocephala* stands lack herbaceous understories of any note, perhaps owing to heightened competition for scarce water resources.

Facilitation of other introduced alien plant species by virtue of increased nitrogen availability is a salient feature of invasive alien nitrogen-fixing tree species of Hawai'i, and this aspect commonly has a compounding effect on carbon stocks and cycling. Hughes and Denslow (2005) found that invasion of *F. moluccana* in lowland wet forests growing on young lava flows dramatically increased stem densities, basal area, and consequently ACD of the nonnative tree, *Psidium cattleianum*, relative to native-dominated forests on lava flows of comparable age and type. Asner and others (2008) documented similar changes in forest structure following invasion by alien nitrogen-fixing trees, and Vitousek and Walker (1989) noted establishment and rapid growth of *P. cattleianum* seedlings under canopies of *M. faya* on young
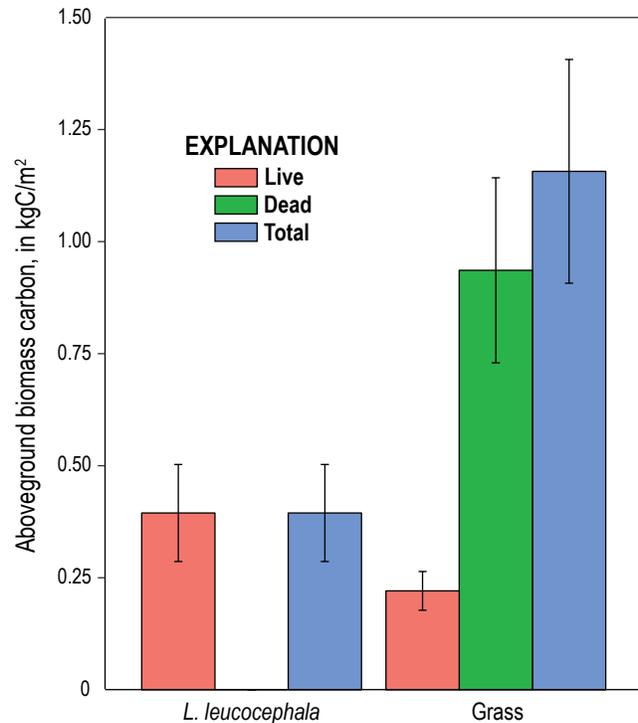
lava substrates that otherwise would be inhospitable to *P. cattleianum* invasion.

4.4.2. Non-Nitrogen-Fixing Trees and Shrubs

Many nonnative species that have successfully invaded a wide variety of Hawai'i's ecosystem do not have the capacity to fix nitrogen. Their effect on the balance of carbon stocks depends on their size and stature relative to native species and the degree to which they displace, rather than simply augment, ecosystem carbon stocks.

4.4.2.1. *Fraxinus uhdei*

Native to central and southern Mexico, *Fraxinus uhdei* trees were introduced to Hawai'i in the late 1800s and planted extensively across the archipelago; more than 700,000 individuals were planted on most of the main Hawaiian Islands (Wagner and others, 1999). This nonnative tree can attain heights up to 24 m and grow in relatively dense stands. *F. uhdei* can be fast growing in wet sub-montane or montane forests of Hawai'i and is responsive to increases in soil-nitrogen availability (Ares and Fownes, 2001), making it well suited to invading disturbed

sites during secondary succession. Rothstein and others (2004) found that *F. uhdei* increased nutrient cycling at the stand scale, though limited light availability in the understory apparently constrains subcanopy biomass. As such, establishment of this nonnative tree results in displacement of native species. However, because this tree is large, mature stands contain high amounts of carbon. In montane forests of the Laupahoehoe Unit of the Hawai'i Experimental Tropical Forest (HETF) on the windward side of Hawai'i Island, Asner and others (2009) found that, although native *M. polymorpha* and *Acacia koa* forests averaged 65 MgC/ha, *F. uhdei*-dominated stands averaged more than four times that amount (254 MgC/ha). Again these high values were not a function of *F. uhdei* augmenting native forests present in the locality. Rather, they reflect the displacement of native forests by alien tree species with a much higher capacity to acquire and store carbon.

4.4.2.2. *Psidium cattleianum*

In contrast to large trees such as *F. uhdei*, smaller stature non-nitrogen-fixing trees such as *P. cattleianum* typically decrease aboveground carbon storage in areas where it invades. Native to Brazil, *P. cattleianum* was introduced to Hawai'i in the early 1800s and has since become widespread across all the main Hawaiian Islands except Ni'ihau and Kaho'olawe (Wagner and others, 1999). It is considered one of the most serious weeds of Hawai'i (Smith, 1985). Its capacity to reproduce vegetatively (in other words, by rootsprouts or suckers), combined with its shade tolerance, enables it to invade otherwise undisturbed native forests, and it is currently the most widespread alien woody species in Hawai'i's mesic-, moist-, and wet-forest zones. Once established in a particular locality, *P. cattleianum* commonly forms dense, impenetrable thickets in understories of dominant canopy trees, whether native (for example, *M. polymorpha*) or nonnative (for example, *F. moluccana* or *C. equisetifolia*) (Hughes and Denslow, 2005; Asner and others, 2008). While not explicitly altering ecosystem function, *P. cattleianum* is a strong competitor for limiting resources such as light, water, and nutrients, and it represents a daunting obstacle to native-species recruitment; forest stands characterized by a native overstory canopy and a dense sub-canopy of *P. cattleianum* will most likely retrogress to monotypic thickets of this aggressive invader once the mature native trees senesce (Zimmerman and others, 2008; Hughes and others, 2014). Regarding carbon storage, Asner and others (2008) reported a general diminution in aboveground carbon across areas of *P. cattleianum* invasion; forest stands co-dominated by *P. cattleianum* and *Ficus rubiginosa*, another nonnative tree species, exhibited significantly lower aboveground carbon mass than their native-dominated counterparts on 5,000-, 20,000-, and 65,000-year-old lava substrates of the Laupahoehoe Unit of the HETF (fig. 4.5).

As a relatively small tree (typically 2–6 m tall, Wagner and others, 1999), *P. cattleianum* generally would be expected to harbor less carbon than the larger stature native forests they typically replace. However, in cases where stands of this species have matured to their fullest extent, it is possible for them to exhibit carbon mass roughly equivalent to that of native forests, although belowground carbon mass may be substantially greater in native-dominated stands (108 MgC/ha) relative to *P. cattleianum*-invaded stands (78 MgC/ha) (Mascaro and others, 2012). Regardless of whether *P. cattleianum* increases or decreases carbon stocks and cycling of the ecosystems it invades, its detrimental impacts on the diversity of Hawai'i's native biodiversity can neither be denied nor overstated.

4.4.2.3. *Grevillea robusta*

A member of the Proteaceae family and introduced from Australia in the late 1800s, *Grevillea robusta* is a common nonnative tree across dry leeward portions of the main Hawaiian Islands; more than 2.2 million individuals of this tree were planted across the archipelago by territorial foresters in the four decades between 1919 and 1959 (Wagner and others, 1999). Having spread to other areas from these initial plantings, *G. robusta*, along with *P. pallida*, constitutes most alien-dominated forests on drier, leeward parts of the Hawaiian Islands. *G. robusta* is a large tree, attaining heights of 10–25 m (Wagner and others, 1999); its inherent capacity to grow well even in dry, infertile soils makes it well suited to Hawai'i's leeward environments across which it has invaded (Lott and others, 2003; Shane and Lambers, 2005). Regarding
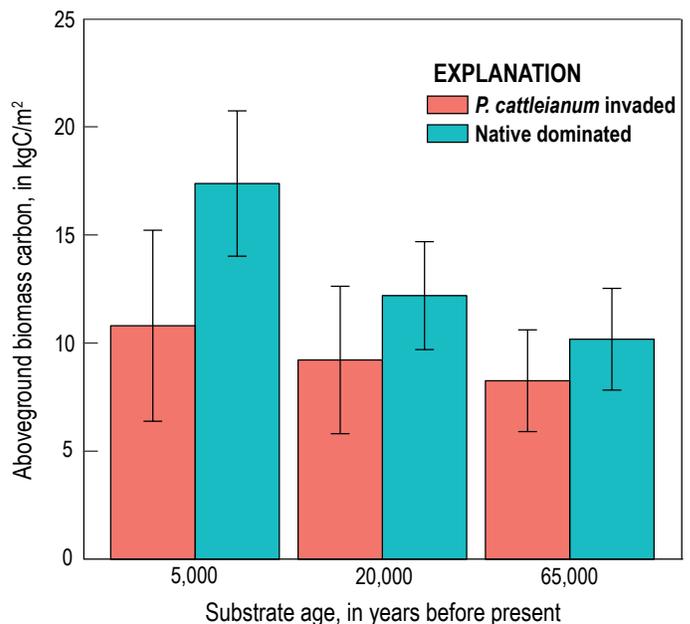

Figure 4.5. Plot of aboveground biomass carbon (mean +1 standard deviation) of native and *Psidium cattleianum*-invaded forest stands found on on lava substrates of three distinct age in the Laupahoehoe Unit of the Hawai'i Experimental Tropical Forest on the leeward side of Hawai'i Island (data from Asner and others, 2008). kgC/m^2, kilograms of carbon per square meter.

the degree to which *G. robusta* stores carbon (R. Flint Hughes, U.S. Department of Agriculture, Forest Service, unpublished data), found that mature stands of this species supported an average of 86 MgC/ha; this value was substantially higher than that of surrounding alien grasslands (<5 MgC/ha), but comparable to that of adjacent native forests co-dominated by *M. polymorpha* and *A. koa* (100 MgC/ha). Again, whereas stocks of carbon may be quite similar between native-dominated forests and alien invaded forests of these leeward portions, the most important difference between these forest types lies in the utter lack of native diversity in the latter relative to the former forests.

4.4.2.4. The Melastomes: *Clidemia hirta, Melastoma septemnervium*, and *Miconia calvescens*

Collectively, shrubby members of the Melastomataceae introduced to Hawai'i within the last 100 years, including *Clidemia hirta* (soap bush), *Melastoma septemnervium*, and *Miconia calvescens* (velvet tree), pose some of the most serious threats to both the native biodiversity of Hawai'i's forests and their capacity to store aboveground and belowground carbon. Native to lowlands of Central and South America and Caribbean Islands, *C. hirta* is a short stature shrub (0.5–3 m tall) first noted in Hawai'i in 1941; it has spread rapidly and extensively throughout mesic-to-wet forests at low to mid elevations and has been declared a noxious weed by the Hawai'i Department of Agriculture (Wagner and others, 1999; Dewalt and others, 2004). Smith (1992) reported that *C. hirta* had spread across more than 100,000 ha on the island of O'ahu alone. Somewhat taller than *C. hirta*, *M. septemnervium* (1.5–5 m tall) is native to Asia, Southeast Asia, and the Philippines; it was present in Hawai'i by 1928 and now occupies extensive areas on windward slopes, from sea level to 900 m (Wagner and others, 1999). The tallest of the three melastomes considered here, *M. calvescens* is native to South and Central America and was first introduced to Hawai'i in 1961. This species is considered among the worst invasive plant species in Pacific-island wet forests, and it has been designated by the IUCN Invasive Species Specialist Group as one of the 100 worst invasive species in the world (Lowe and others, 2000; Meyer, 1996). Because of the acknowledged ecological damage wrought by *M. calvescens* in Tahiti, limiting its expansion across Hawai'i's wet forests has been a management priority during the last two decades. For example, the State of Hawai'i spent $1.7 million to control *M. calvescens* across the islands in the year 2000 alone, and similar funding continues today. Previous studies have shown that these invasive species are better suited to capture and efficiently use available light resources than their native wet-forests counterparts (Baruch and Goldstein, 1999; Baruch and others, 2000). This is likely a key factor in their successful invasion of both disturbed and undisturbed mesic-to-wet Hawaiian forests.

Regarding the capacity of these three invasive melastomes to store and cycle carbon relative to the native

species they displace, *C. hirta* and *M. septemnervium* are both better characterized as shrubs than trees, and all three species are relatively low stature compared to the much taller native trees (for example, *M. polymorpha* and *A. koa*) they displace. As such, their invasion across landscapes formerly dominated by native forests has been typically accompanied by a substantial diminution in ecosystem carbon stocks. In addition, Allison and Vitousek (2004) noted that, unlike the leaf litter of native species of Hawai'i's wet forests which tends to decompose slowly, immobilizing nutrients and stabilizing soil carbon, litter of *C. hirta*, *M. septemnervium*, and *M. calvescens* decomposes quickly, releasing nutrients in the process. As such, we would expect soils supporting these invasive melastomes to accumulate and store substantially less carbon than their native-forest counterparts. Lastly, *M. calvescens* has the capacity to further inhibit soil-carbon accumulation by increasing erosion where it is established (Meyer, 1994); the large dark leaves of this species severely constrain subcanopy light availability and, consequently, understory plant cover. At the same time, these large leaves channel precipitation in such a way as to increase the energy of throughfall water drops, thereby increasing soil loss from erosion (Nanko and others, 2015).

4.4.3. Grasses

Across many regions of North and South America, Africa, and Australia, fire is an integral component of healthy, well-functioning native ecosystems. This is certainly not the case for the vast majority of Hawai'i's dry leeward ecosystems and wet windward ecosystems. During the 1,000 years prior to European contact, Hawaiians used fire extensively to clear native shrublands, woodlands, and forests for cultivation (Kirch, 1982). Fire was an effective tool for this purpose because, although some native species (for example, *A. koa* and *Deschampsia nubigena*) exhibit adaptations to fire, most native Hawaiian plant communities are best characterized as fire independent (Cuddihy and Stone, 1990); fires prior to human settlement of the Islands were likely irregular, infrequent, and short-term disturbances that exerted little evolutionary force (Smith and Tunison, 1992; Hawbaker and others, this volume, chap. 5).

Although, native-dominated grassland ecosystems were present in Hawai'i in coastal, lowland and montane areas, and were likely much more widespread than present day, most of these systems have been highly degraded and are now dominated by nonnative invasive species, including a suite of nonnative grasses. Hundreds of nonnative grass species were introduced to Hawai'i following the European contact in the late 1700s (Cuddihy and Stone, 1990), and today nonnative grasses currently dominate an area of 2,785 km^2, or some 25 percent of the total land area in the main Hawaiian Islands (Trauernicht and others, 2015; Jacobi and others, this volume, chap. 2), where their presence is primarily the result of either land clearing followed by grass establishment as pasture for grazing or abandonment of agricultural land followed

by invasion of pyrophytic, nonnative grasses. Dominant nonnative grass species in Hawai'i today include *Cenchrus setaceus* (fountain grass), *Cenchrus ciliaris* (buffel grass), and *Andropogon virginicus* (broomsedge) in drier environments and *Megathyrsus maximus* (guinea grass), *Cenchrus clandestinus* (kikuyu grass), *Ehrharta stipoides* (rice grass), and *Holcus lanatus* (velvet grass) in mesic-to-wet areas. *Melinis minutiflora* (molasses grass) can be locally prevalant in both dry and wet areas (Hawbaker and others, this volume, chap. 5).

At higher elevations and in more mesic conditions, many native forests were purposefully replaced by grass forage species for grazing purposes 100 or more years ago (Cuddihy and Stone, 1990). In addition, abandonment of agricultural land with the demise of the sugar cane industry has left many fallow agricultural fields that are now dominated by nonnative grasses (Trauernicht and others, 2015). Some of these areas are still actively grazed or farmed, particularly on the islands of Maui and Hawai'i. However, many of these areas have been abandoned during the past several decades and are, in some cases, being subsequently invaded by woody species, particularly where wildfires have not occurred and fences have been erected to exclude both domestic and feral ungulates. Native-dominated forests have also regenerated in some former pasture areas where nonnative grasses were temporarily controlled and scarification techniques allowed persistent seed banks of native, nitrogen-fixing *A. koa* to germinate and establish (Scowcroft and others, 2007).

Across many portions of dry leeward zones of the main Hawaiian Islands, replacement of native-dominated woody vegetation by nonnative invasive grasses typically involves a scenario where nonnative pyrophytic grasses invade the interstices of relatively open-canopy native woodlands and shrublands. Although it is unknown if these grasses were able to invade these areas in the absence of disturbance, it is most likely that many, if not all, of these grass invasions were facilitated by disturbance in the form of timber harvesting, grazing by domestic animals, and (or) invasion by nonnative feral ungulates (in other words, nonnative grass invasions as the passengers of ecological change) (MacDougall and Turkington, 2005). Once established, however, these nonnative grasses provide continuous flammable fuels that, when subject to frequent anthropogenic ignition sources (Trauernicht and others, 2015), facilitate frequent, widespread, and high-intensity fires that are likely far outside of the range of natural variability for native Hawaiian ecosystems (Trauernicht and others, 2015). Following fire, these grass species typically re-establish quickly and outcompete woody species in the post-fire environment, thereby facilitating a nonnative grass–wildfire cycle that is exceedingly difficult to break (D'Antonio and Vitousek, 1992). Consequently, a complete replacement of native woodlands and shrublands by nonnative grasslands often occurs, particularly when repeat fires occur in the same area over short time intervals (Hughes and others, 1991; Ainsworth and Kauffman, 2013; Hawbaker and others, this volume, chap. 5). Although generalized here, such grass invasion/wildfire scenarios are dynamic and complex, both spatially and temporally.

The consequences of nonnative grass invasions and the subsequent replacement of native, woody-dominated communities by nonnative grasslands for carbon storage are typically immediate and large (Hawbaker and others, this volume, chap. 5). Aboveground carbon storage in woody-dominated communities in Hawai'i ranged from 5 to 14 MgC/ha in dry ecosystems, 33 to 91 MgC/ha in mesic ecosystems, and 57 to 115 MgC/ha in wet forest ecosystems (Selmants and others, this volume, chap. 6). In contrast, average aboveground standing biomass (live and detrital) across several nonnative grassland types was found to be 3.5 MgC/ha in *C. clandestinus* stands, 4.8 MgC/ha in *C. setaceus* stands, 6.2 MgC/ha in *A. virginicus* stands, 8.7 MgC/ha in *M. maximus* stands, and 13.7 MgC/ha in *M. minutiflora* stands (Hawbaker and others, this volume, chap. 5). In turn, under suitable edaphic and climatic conditions and in the absence of wildfire, monotypic nonnative grasses can be subsequently invaded by nonnative woody species, some of which exhibit the capacity to fix nitrogen (for example, leguminous trees and shrubs), which increases aboveground carbon storage compared to that found in monotypic nonnative grasslands (Hawbaker and others, this volume, chap. 5).

4.5. Summary and Conclusions

Broadly, our results, as well as results presented elsewhere in this report (Jacobi and others, this volume, chap. 2; Selmants and others, this volume, chap. 6) show that the total extent of alien-dominated forest exceeds that of native-dominated forest in lower elevation zones on medium to older substrates in both dry and wet conditions. In contrast, most wetter, higher elevation and (or) older substrates remain dominated by native forest vegetation. Critically, we found greater ACD values in native-dominated forests at low-to-medium elevations across dry-to-mesic areas of the islands, whereas alien-dominated forests had slightly higher ACD values in wetter environments. At these broad multi-island scales, substrate age played only a small role in determining the relative difference in alien- and native-dominated forest ACD levels. This suggests strong limiting effects of nutrient-poor soils on growth and biomass accumulation for all species, independent of origin. In contrast, higher biomass of native forest canopies in drier zones on older substrates may reflect evolutionary adaptation to these environments, as well as a lack of analog tree taxa among the current alien species pool on the islands.

Overall our results suggest how native biological diversity intersects with carbon storage and how alien invasive species alter those relationships. For example, higher elevation, drier forests on older substrates may be dominated by alien forest cover, but native-dominated forests in similar environments can support twice the stored carbon on a per-area basis. Thus actions to conserve and restore high-elevation native ecosystems yield a co-benefit of increased carbon storage. On the other hand, areas characterized by young substrates in drier, high-elevation areas are currently dominated by native forest cover; alien species can double ACD levels in these environments. Forest managers and conservationists can use these landscape-scale relationships as

tradeoffs in planning efforts to increase carbon storage while managing for biological diversity.

Invasive species of one sort or another are ubiquitous across most of Hawai'i's forests, woodlands, shrublands, and grasslands, and introductions of these species continue to this day.

We acknowledge the worldwide interest to protect and even increase carbon storage in ecosystems in order to mitigate climate change (Intergovernmental Panel on Climate Change, 2006), and we have found that in some instances invasion of nonnative plants into Hawai'i's ecosystems can increase ACD across landscapes. However, invasive species are often the primary cause of profound, and in many cases irreparable, damage to Hawai'i's native ecosystems, degrading their compositional, structural, and functional integrity in myriad ways. Considering this, it is difficult to invoke a positive benefit of invasive species in terms of ecosystem services (increased carbon sequestration, for example) for Hawai'i's ecosystems, particularly when its citizens increasingly view nonnative species (for example, the tree *F. moluccana* or pyrophytic nonnative grasses) as financial burdens at best and threats to life and property at worst (Hughes and others, 2013).

Further, the Hawaiian archipelago as a whole has been identified as a prominent biodiversity hotspot (Myers and others, 2000), and Hawai'i is a prime example of how islands contain disproportionately high levels of Earth's biodiversity (Caujape-Castells and others, 2010). Although our discussion here indicates that continued invasion of native-dominated ecosystems by nonnative species may or may not increase carbon stocks at landscape scales, such transformations would further erode the important contributions of Hawai'i's native ecosystems to global biodiversity.

As such, although national and international programs that promote carbon sequestration (for example, HIREDD and California Carbon Program) provide useful mechanisms to encourage and enable landowners and land managers to reestablish and (or) protect native ecosystems of any sort, they should not be used to justify projects that lead to further establishment and persistence of invasive species. The idea that increased carbon sequestration by nonnative invasive species, where it actually occurs, could somehow justify the maintenance of invasive species across landscapes is a fallacy. Indeed, the degree to which invasive species are capable of invading native communities defines the degree that they themselves are "primary pathogens" to those ecosystems and such invasions cannot be considered compatible with the persistence of native-dominated ecosystems. The assertion Vitousek and others (1997) made two decades ago remains true today; that, "People and institutions working to understand, prevent, and control invasions [both in Hawai'i and globally] are carrying out some of the most important—and potentially most effective—work on global environmental change".

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