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RESEARCH ARTICLE

How invaded are Hawaiian forests? Non-native understory tree dominance signals potential canopy replacement

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Abstract
Context Non-native species invasions are altering the composition, structure, function, and dynamics of forests globally. The Hawaiian Islands are a global biodiversity hotspot for non-native invasive plant species. New spatial inventory data for forests of Hawai'i can provide insights into invasive species presence and dominance across complex landscapes.
Objectives We employed a network of 238 standardized plots spanning climate and soil gradients to conduct the first comprehensive assessment of non-native plant invasions in forests of Hawai'i. We examined non-native plant dominance from the forest floor to canopy to understand how invasion related to environmental and management-related factors.
Methods We tested whether significant differences in non-native dominance across forest strata existed based on ownership/management, fenced status, island group, and forest type. These analyses were conducted separately for each of six plot-level non-native dominance metrics, to assess the abundance and importance of non-native plants across forest strata. Biomass estimates for dominance were translated into carbon (C) units to assess invasive species impacts on C budgets.
Results Across forest types, non-native tree species accounted for 30% of large tree stems, 65% of sapling stems, and 67% of seedling stems. Distribution of C was very similar. Low-elevation forests were particularly degraded, but even montane forests were widely

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impacted and may become more so following forest disturbance. Forests on public lands, in conservation reserves, or in fenced areas were less impacted by non-native trees and shrubs, indicating possible benefits of conservation management.

Conclusions In all forest types, non-native trees constituted a larger proportion of the understory than the overstory tree component, which points to the potential eventual replacement of native canopy trees by non-native trees. The patterns and processes of plant invasion in Hawaiian forests provide data for the conservation of Hawaiʻi's unique flora and insights into how invasion trajectories may play out in other forests.

Keywords Invasive species · Ecosystem management · Invasion debt · Forest Inventory and Analysis (FIA) · Tropical islands · Hawaiʻi

Introduction

Movement of non-native species into new environments is changing the biogeography of the planet (Guo et al. 2017). Introduced species can impact ecosystem processes (Simberloff et al. 2013), cause landscape change (Fei et al. 2014), alter services provided by native ecosystems (Pejchar and Mooney 2009), alter functioning (Vitousek 1990), and homogenize plant and animal communities (La Sorte and McKinney 2007; McKinney and La Sorte 2007). Islands harbor many more naturalized and invasive non-native plant species relative to mainland regions (Essl et al. 2019), with tropical islands being particularly vulnerable to non-native species invasions because of historically high rates of species introductions and because their native species often compete poorly with introduced continental species for limiting resources (Loope et al. 1988; Denslow 2003). Understanding how naturalized non-native plants affect plant species endemic to oceanic islands is a high conservation priority (Caujape-Castells et al. 2010), particularly in habitats that are heavily invaded (Kueffer et al. 2010a).

The Hawaiian Islands, the world's most isolated archipelago (Mueller-Dombois and Fosberg 1998), are a global hotspot of non-native species richness (Dawson et al. 2017; Cordell 2021), where naturalized non-native plant taxa encompass between 49 and 54% of the archipelago's flora (Imada 2012). The introduction and large-scale naturalization of non-native plant and animal species has degraded Hawaiian ecosystems by altering disturbance regimes and ecological processes (Vitousek 1990); Richardson and Pyšek 2006; Gillespie et al. 2008; Cordell 2021). Hawaiian forests are among the most threatened in the world, largely because of the direct (competition, disease) and indirect (altered nutrient or disturbance regimes) effects of non-native species, which have led to the dominance of novel species assemblages and severe declines in native species (Barton et al. 2021). Given the presence of advanced invasion across all forest types, the Hawaiian archipelago may well represent a bioclimatic set of ecological endpoints for invasion, with important insights for local management but also potential future dynamics of plant invasions in forests elsewhere in the world, particularly on tropical islands. In particular, Hawaiʻi can provide insights into the transitions that are occurring from native dominance to non-native dominance, and how these transitions vary across forest type and management practice.

Recent decades have seen a wealth of valuable research on the impacts of naturalized species on Hawaiian forests, mostly focused on small-scale manipulative field studies. Recently, several have combined fine-scale airborne LiDAR and satellite data with field measurements on Hawaiʻi Island to identify and track the spread of certain non-native forest plant species (Asner et al. 2008) or to estimate forest carbon density accounting for naturalized tree species (Asner et al. 2011, 2016; Hughes et al. 2018). Work to classify vegetation cover across the state using remote sensing and other geospatial data estimated that approximately half of all Hawaiian land cover is either highly disturbed or consists of a mix of native and non-native species (Price et al. 2012; Jacobi et al. 2017). This characterization of native versus non-native canopy dominance, however, may lead to overly optimistic assessments of forest condition because the establishment of non-native woody species in the understory of these forests plays important roles in shaping stand composition, structure, and dynamics. For example, dense understories of non-native often invasive species can suppress the regeneration of native tree species whereby they alter succession and come to eventually replace native species in the canopy.

This has been a problem in forests around the world. For example, in Tahiti, dense monotypic stands of *Miconia calvescens* DC suppress the regeneration and growth of native plants to the point that this invader now covers two-thirds of the island of Tahiti Nui (Meyer and Florence 1996). Similarly, in Puerto Rico, *Syzygium jambos* L. (Alston) has altered the composition of native forests, with implications for landscape scale diversity patterns (Brown et al. 2006). In Europe, North American tree species now limit the regeneration of European native trees while homogenizing species composition (Dyderski and Jagodzinski 2020), while in eastern North America, invasive shrubs are causing large-scale alterations to understory forest composition and successional processes that determine structure and function (Fagan and Peart 2004; Hartman and McCarthy 2008; Link et al. 2018). Investigating composition and structure of lowland wet forests on Hawaiʻi Island, Zimmerman et al. (2008) showed that native species, particularly the widespread and shade-intolerant *Metrosideros polymorpha* Gaudich., exhibited very little recruitment in mature, closed canopy forests, and that non-native saplings and herbaceous species dominated the understory of these forests even while a native overstory canopy remained intact. Results suggested that where subcanopy invaders dominate, they effectively constrain native plant recruitment and have the capacity to profoundly alter successional trajectories of lowland forests. In these and possibly other Hawaiian forests, non-native seedling and sapling density may therefore serve as an important indicator of future forest composition and structure.

The Forest Inventory and Analysis (FIA) program of the USDA Forest Service has developed a national systematic plot sampling framework that enables comprehensive assessments of non-native plants, including for the state of Hawaiʻi. This includes how the degree of invasion varies across forest strata, and whether ongoing conservation efforts are effective in reducing the impacts of non-native plant species. The use of FIA data allows for meaningful evaluations of succession in Hawaiʻi's forests by incorporating the prevalence of non-native species throughout the vertical profile of forest stands, from forest floor to the overstory canopy. Previous inventory work found that native species continued to dominate the canopy of a third or more of Hawaiian vegetated land cover (Price et al. 2012; Jacobi et al. 2017), but such canopy assessments provide limited insights into the successional trends that are driven by mid-story and understory composition. At the same time, both broad-scale remote sensing (Asner et al. 2008) and small-scale stand studies (e.g., Gerrish and Mueller-Dombois 1980; Litton et al. 2006; Zimmerman et al. 2008; Minden et al. 2010) offer evidence that non-native invasive plants cause fundamental changes in the three-dimensional structure of Hawaiian forests, with the implications that (1) high levels of non-native plant invasion may occur under a native canopy, and (2) dominance by non-native species may occur in lower strata before moving to the canopy.

We rely on FIA data to assess the effectiveness of conservation efforts to manage non-native invasive species in Hawaiʻi (Smith 2016). Such information would be valuable for developing ways to prioritize actions and strategically guide the conservation of threatened native plant species on other oceanic islands (Caujape-Castells et al. 2010). Across the Hawaiian archipelago, many publicly administered forests are managed to maintain natural resource values and ecosystem services, but the degree and type of conservation protection vary. Different management missions and funding levels likely lead to differences in the degree of invasion of forests under different jurisdictions. A key management technique to maintain native biodiversity in forests, for example, is the construction of fences to exclude non-native ungulates, including pigs (*Sus scofa*) in wet habitats, and feral goats (*Capra hircus*) and mouflon sheep (*Ovis gmelini musimon*) in dry to mesic habitats. Feral pigs have significant environmental effects, including the reduction of native plant species abundance and the enhancement of conditions conducive for invasive plant establishment (Nogueira-Filho et al. 2009; Wehr et al. 2018). Fences may generally benefit native plants, though non-native plants have also increased in some fenced areas, including following wildfire, through the spread of seed by birds, and through expansion within sites where invasive plants were already established prior to fencing and ungulate removal (Loh and Tunison 1999; Cole et al. 2012; Cole and Litton 2014).

We analyzed forest composition and structure within 238 forest inventory plots across the Hawaiian FIA network to test the following hypotheses: (H_1) non-native dominance varies by forest strata (e.g., more invasive plant individuals in the understory than the canopy) and by forest type (e.g., more invasive plant individuals in wet montane versus lowland dry forests), and (H_2) conservation ownership and active management reduce or are associated with lower abundance of non-native plants (e.g., conservation actions translate into conservation outcomes).

Methods

Forest inventory data

The Forest Inventory and Analysis (FIA) program, administered by the United States Department of Agriculture Forest Service, provides the most comprehensive forest database currently available in the United States (Tinkham et al. 2018). It maintains a national sample intensity of approximately one plot per 2,428 ha (Bechtold and Patterson 2005), including in Hawaiʻi. Because the statistical design of the FIA plot network spans diverse ownerships and management strategies, FIA data can be used to compare the effectiveness of conservation ownership and management strategies in Hawaiʻi as elsewhere. Our analyses were based on data collected from 238 FIA plots visited by data-collection crews between 2010 and 2015 (Fig. 1). Each plot covered 0.067 hectares within four subplots arranged at the vertices and center of a triangle, and where inventory crews collect a wide variety of data using standardized protocols (Burrill et al. 2018). Plot locations were determined using a hexagonal sampling framework designed to be as spatially balanced as possible

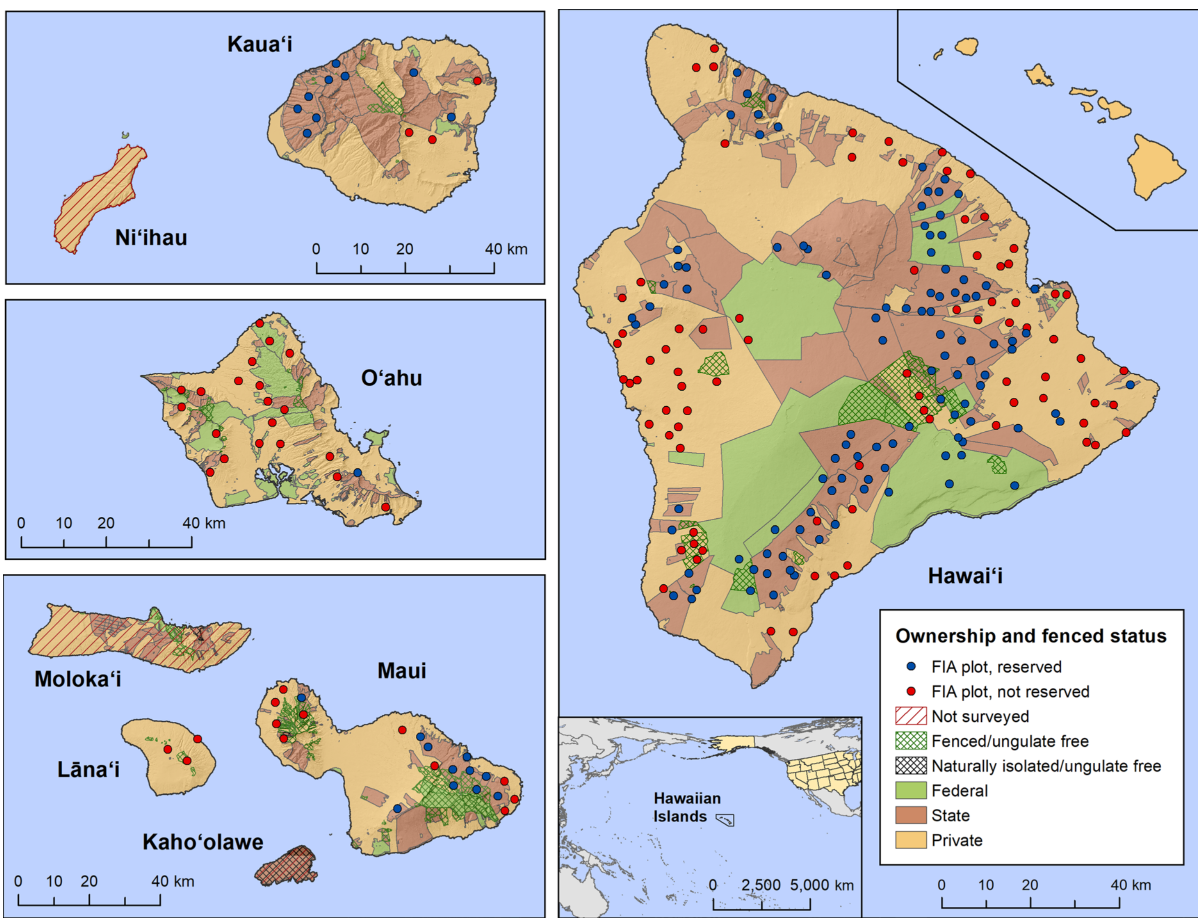

Fig. 1 Forest Inventory and Analysis (FIA) plots, by reserved status, across Hawaiʻi (approximate locations), superimposed over land ownership/management and fenced status

(Bechtold and Patterson 2005), with the plot location within each 2,428 ha hexagon visited by field crews if it is determined by remotely sensed data to be in forest land use. Some forested plots were not visited if private landowners denied access or if the location was hazardous (e.g., very steep slopes). This resulted in a lower sampling rate for some strata, including in private forest (Supplementary Table 1). Forests were defined as having ≥ 10% tree canopy cover (or having evidence of such cover) and being ≥ 0.4 ha in size and 37 m wide (Burrill et al. 2018). Plots were located on five of the major Hawaiian Islands: Hawai‘i, Maui, O‘ahu, Lāna‘i, and Kaua‘i. Access issues prevented plot establishment on the islands of Moloka‘i (difficult-to-access forests), Kaho‘olawe (restricted), and Ni‘ihau (privately owned). Our results may be affected by such under-sampling, particularly when comparing plot-level means between strata, although the FIA program includes a post-stratification adjustment (see "Plot-level analyses" below) to account for stratum under-sampling when making area and tree count estimates. This feature of the program design should minimize bias if non-sampled plots are missing at random within strata.

In each plot's four 7.31-m radius subplots, FIA field crews recorded diameter, height and species for every live tree with a diameter at breast height (DBH) ≥ 12.7 cm. Trees with DBH ≥ 2.54 cm but < 12.7 cm (saplings) were measured in a single 2.07-m-radius microplot located within each of the plot's four subplots. Tree densities were calculated by scaling plot-level data to per hectare estimates (Burrill et al. 2018). The FIA program estimates the aboveground dry biomass of each stem with DBH ≥ 2.54 cm in pounds using the component ratio method (Heath et al. 2009), which calculates the dry weight of individual tree components before summing them for the total aboveground biomass (Woodall et al. 2011). Tree measurements are used to calculate the volume of the tree bole, which is converted to biomass using a set of species wood gravities (Miles and Smith 2009) while the biomass of treetops, limbs, bark, and stump are based on the published component proportions for each (Jenkins et al. 2003). We converted pounds of biomass to metric tons of carbon (with C equivalent to 0.5 of biomass).

Field crews tallied seedlings by species within microplots; seedlings were defined as woody stems with a DBH < 2.54 cm and height ≥ 30.48 cm if a hardwood, or a height of ≥ 15.24 cm if a conifer (Burrill et al. 2018). Field crews recorded percent cover of the four most common species each of forbs, graminoids, and shrubs/subshrubs/woody vines within a subplot where an individual species' total canopy cover area was ≥ 3% of the subplot area (Burrill et al. 2018). Shrubs were defined as woody, multiple-stemmed plants of any size, with subshrubs those not exceeding 1 m height at maturity. Woody vines were defined as twining/climbing plants with relatively long, woody stems. Forbs were defined as herbaceous, broad-leaved plants, including non-woody vines and ferns. Graminoids were defined as grasses, sedges, and rushes. Within 205 of the 238 plots, field crews also recorded the cover of 40 non-native plant species of particular concern (Supplementary Table 2) regardless of growth habit and abundance. (The other 33 plots did not include this sampling protocol.) These are invasive species that were determined by local experts to most likely cause economic and environmental harm (USDA Forest Service 2004).

Our analyses differentiated between native and non-native plant species (both trees and understory plants) based on the Hawaiian Native and Naturalized Vascular Plants Checklist (Imada 2012) and the Hawaiian Naturalized Vascular Plants Checklist (Imada 2019). Plants were considered non-native if they had been introduced to Hawai‘i following European arrival in the eighteenth century and were subsequently able to maintain self-sustaining populations. In this study, we consider the presence of those invasive non-native species as contributing to the invasion of Hawaiian forests. We classified native species as endemic (i.e., occurring only in the Hawaiian Islands) or indigenous (i.e., occurring naturally in the Hawaiian Islands as well as elsewhere). A limited number of "canoe plants" were introduced by Polynesians who first settled the Hawaiian Islands starting some 1500 years ago (Whistler 2009). These species were classified as Polynesian Introductions. Pacific Island forest type (Mueller-Dombois and Fosberg 1998) was determined by the species exhibiting plurality of stocking or cover for all live trees that were not overtopped by other trees and the dominant tree species on each plot condition was determined based on the plurality of cover for all live trees that are not overtopped (USDA Forest Service 2013).

Plot-level analyses

We calculated several plot-level measures of non-native species dominance within different forest strata. Two metrics focused on importance value (IV) for large non-native trees (DBH ≥ 12.7 cm) and for saplings (DBH ≥ 2.54 cm but < 12.7 cm). IV is a measure of dominance within a community that incorporates number and size of trees of a given species or group of species within the community (Smith and Smith 2001). We calculated non-native IV as the mean percentage of non-native species' relative abundance and relative basal area on a plot compared to the total species plot abundance and basal area. Non-native dominance of tree seedlings was calculated as the percentage of total tree seedlings that were non-native. The relative covers of non-native shrubs/subshrubs/woody vines, forbs, and graminoids were calculated as the mean across each plot's four subplots. All plot-level non-native dominance measures were mapped using ArcGIS 10.7.1 (ESRI 2019).

The systematic FIA sample design allowed for statistical population-level estimates of various forest attributes, such as the area of a given forest type within a state, using an "expansion factor" assigned to each plot (Bechtold and Patterson 2005; Burrill et al. 2018). This factor is calculated as the area within the stratum of interest (e.g., private forest receiving more than 1000 mm of precipitation) divided by the number of plots within the area of that stratum. Expansion factors can be summed across plots in a population (e.g., a specific forest type or an island group) to provide an estimate of the total area within that population. When a plot was divided into different conditions (e.g., two forest types), the proportion of the plot in each condition was multiplied by the expansion factor to generate an estimate of area represented by that condition. Similarly, the FIA sample design allowed individual trees inventoried on plots to be scaled via an expansion factor to estimate the total number and C of trees within an area (e.g., Hawai‘i Island) or classification (e.g., trees with DBH ≥ 12.7 cm). Using this sample design, we estimated the number of trees by species and within general type classes (native, non-native, and Polynesian-introduced) and native classes (endemic and indigenous) for the three size classes (large trees, saplings, and seedlings). We also estimated metric tons of C by the type and nativity classes for large trees and saplings.

We used attributes of the FIA sample design to estimate the area of Hawaiian forest containing non-native tree species and the cover area of understory non-native plants of particular concern. A plot condition was considered to represent forest invaded by non-native trees if it contained one or more non-native tree and was considered dominated by non-native trees if the dominant tree species on the plot condition was naturalized. A plot's cover of non-native understory species of concern was calculated as the mean of such cover across the plot's four subplots. Area estimates were also generated separately for island groups (low elevation: O‘ahu/Kaua‘i/Lāna‘i, high elevation: Maui/Hawai‘i) and ownership/management groups (i.e., federal, state/local, and private) (Fig. 1) as well as for reserved status (i.e., publicly adminstered lands where timber management or harvest of wood products is prohibited by statute or agency mandate) and common Pacific Island forest types.

Statistical analyses

We tested the null hypotheses that there was no significant difference in non-native dominance based on ownership/management, reserved status, fenced status, island group, and common forest type. To do this, we used a set of multiple-sample, non-parametric Kruskal–Wallis tests using the NPAR1WAY procedure in SAS 9.4 (SAS Institute Inc. 2013) in which *p*-values were generated by 10,000 Monte Carlo runs. These analyses were conducted separately for each of the six plot-level non-native dominance metrics, described above, allowing us to assess the abundance and importance of non-native plants in different forest strata. Island groups, ownership/management, reserved status, and forest type were attributes available in the FIA data. The fenced status of plots was determined by intersecting plot locations with spatial data provided by the Hawai‘i Department of Land and Natural Resources that delimit areas fenced and free of feral ungulates in early 2020, or those that were naturally isolated and ungulate-free (Fig. 1). A large majority of fenced FIA plots are on Hawai‘i Island because this is where most fenced forest occurs. We also assessed differences in the six non-native dominance metrics within forest types within both of the island groups. We employed the MULTTEST procedure in SAS 9.4 (SAS Institute Inc. 2013) to calculate *q*-values (*p*-values adjusted for the false discovery rate associated with multiple comparisons) for the six plot-level non-native dominance metrics associated with each comparison (e.g., ownership).

Results

Tree counts and invaded forest area

The proportion of Hawaiian forest trees that were native varied considerably by size class. Approximately 70% of Hawai'i's estimated large trees (DBH ≥ 12.7 cm) within the study area were native, compared to 34% of the saplings (DBH ≥ 2.54 but < 12.7 cm) and 33% of the seedlings (Table 1). Tree carbon estimates followed a similar pattern by size class, with about 61% of large tree C in native trees compared to 36% for saplings. Most native trees across size classes were endemic to Hawai'i, encompassing 67% of large trees, 33% of saplings, and 31% of seedlings. Among endemic trees, *Metrosideros polymorpha* ('ōhi'a lehua) was the most common, representing 34% of all large trees (approximately 51% of endemics), 22% of all saplings (67% of endemics), and 12% of all seedlings (40% of endemics). Indigenous species were 3% of large trees, 2% of saplings, and 1% of seedlings. Polynesian-introduced species constituted about 1% of large trees, 2% of saplings, and less than 1% of seedlings. The three most abundant species in this category were *Morinda citrifolia* L. (noni), *Syzygium malaccense* (L.) Merr. & L.M. Perry ('ōhi 'a 'ai), and *Cordyline fruticosa* (L.) A.Chev. (ti) (Supplementary Table 3).

Overall, six of the 10 most abundant species were non-native, including *Psidium cattleyanum* Sabine (strawberry guava), which was the most abundant species in Hawai'i across size classes (441 million trees, 6 million large trees and 435 million saplings) and was recorded on 88 of the 238 FIA plots (Supplementary Table 3). Other abundant non-native species included *Schinus terebinthifolius* G. Raddi (Brazilian peppertree, 45 million trees; 28 plots), *Leucaena leucocepahala* (Lam.) de Wit (white leadtree, 43 million trees, 14 plots), *Ardisia elliptica* Thunb. (shoebutton, 33 million trees, 11 plots), *Psidium guajava*

Table 1 Estimated number and percent of tree stems and metric tons of carbon within nativity groups, by species and by size class, based on data collected from 238 Forest Inventory and Analysis (FIA) plots across Hawai'i between 2010 and 2015

	Large trees (≥ 12.7 cm)				Saplings (2.54–12.7 cm)				Seedlings	
	Stems	%	C (tons)	%	Stems	%	C (tons)	%	Stems	%
Native	109,964,699	69.8	14,817,812	60.7	355,975,979	34.4	1,956,593	36.4	891,657,119	32.5
Endemic	104,736,171	66.5	14,419,178	59.1	338,534,034	32.7	1,855,547	34.5	861,814,546	31.4
Indigenous	5,228,528	3.3	398,634	1.6	17,441,945	1.7	101,046	1.9	29,842,573	1.1
Non-native	44,938,298	28.5	9,351,418	38.3	654,972,027	63.2	3,340,508	62.2	1,813,345,630	66.0
Polynesian introduction	1,643,572	1.0	164,443	0.7	22,172,357	2.1	69,713	1.3	15,725,875	0.6
Unknown	1,002,910	0.6	83,525	0.3	2,444,480	0.2	7,446	0.1	25,013,808	0.9
Total	157,549,479	100.0	24,417,197	100.0	1,035,564,843	100.0	5,374,259	100.0	2,745,742,432	100.0

(Carbon was not estimated for seedlings)

L. (guava, 21 million trees, 32 plots), and *Acacia confusa* Merr. (small Philippine acacia, 15 million, 4 plots). The second most abundant tree species in Hawaiʻi (and most abundant large tree) was the endemic and ecologically important *Metrosideros polymorpha* (280 million trees, 163 plots). Other abundant native tree species included *Cheirodendron trigynum* (Gaudich.) Heller (ʻōlapa, 29 million trees, 56 plots), *Broussaisia arguta* Gaud. (kanawao, 26 million trees, 36 plots), *Cibotium glaucum* (Sm.) Hook. & Arn. (hāpuʻu, 26 million trees, 83 plots), *Acacia koa* A. Gray (koa, 14 million trees, 38 plots), and *Cibotium menziesii* Hook. & Arn. (hāpuʻu ʻiʻi, 12 million trees, 61 plots).

Eucalyptus grandis W. Hill (grand eucalyptus) was the most abundant large non-native tree, but its sapling and seedling estimates were low. *S. terebinthifolius* was the next most abundant non-native large tree, followed by *P. cattleyanum*, which had the most saplings. Its sapling abundance was nearly twice that of the native *Metrosideros polymorpha* and greater than ten times more abundant than the next most abundant non-native tree species, *L. leucocepahala. P. cattleyanum* also had the highest seedling estimate, followed by the non-native *A. elliptica* and by *M. polymorpha*. Nearly all of the 88 plots containing *P. cattleyanum* had seedlings and 61 had saplings, compared to only 28 with large trees. Conversely, nearly all the 163 M. *polymorpha* plots included large trees (152), but only about half (87) had seedlings.

We found that 56% of Hawaiʻi's 553,184 ha of forest land contained non-native tree species, with the remaining 44% being entirely native. Approximately 39% of these forests were dominated by non-native tree species, while 61% were dominated by natives (Table 2). Non-native invasive plants of particular concern were identified in 27% of surveyed forest understory. Of the different ownership/management categories examined here, federal lands supported the lowest percentages of forest containing, or dominated by, non-native trees (Table 2). Federal forests also exhibited the lowest cover percentages of non-native understory plants of concern. These were followed by state-administered and then private forests. A smaller percentage of reserved-status forests, where timber management or harvest of wood products is prohibited, were impacted by non-native plants than non-reserve-status forests. A smaller percentage of

Table 2 Total forest area, forest area with non-native trees and dominated by non-native trees (i.e., the tree species with the plurality of cover for all live trees that are not overtopped is non-native), and cover area of non-native understory plants of particular concern, in hectares, for Hawaiʻi and by ownership/management, reserved status, island group, and forest type

	Forest		Forest with non-native trees		Forest dominated by non-native trees		Forest non-native understory cover	
	Plots	Area (ha)	Area (ha)	%	Area (ha)	%	Area (ha)	%*
Total	238	553,183.7	308,033.8	55.7	218,129.4	39.4	127,863.7	26.5
Federal	25	53,494.2	14,097.2	26.4	9,461.4	17.7	2,378.3	6.4
State/local	118	278,003.4	140,883.0	50.7	82,886.0	29.8	69,475.6	27.4
Private	95	221,686.1	153,053.5	69.0	125,782.0	56.7	56,009.8	29.2
Reserved	122	281,782.3	115,883.7	41.1	64,795.8	23.0	60,332.8	22.9
Not reserved	116	271,401.3	192,150.1	70.8	153,333.6	56.5	67,530.9	30.8
Hawaiʻi/Maui	199	447,029.80	206,629.30	46.2	138,482.20	31.0	101,970.50	23.7
Oʻahu/Kauaʻi/Lānaʻi	39	106,153.90	101,404.50	95.5	79,647.20	75.0	25,893.20	50.0
Lowland tropical rainforest	53	133,699.7	112,489.6	84.1	83,742.6	62.6	63,159.4	59.3
Mesophytic or moist forest	65	137,423.9	74,457.4	54.2	53,949.6	39.3	25,641.4	22.3
Montane rainforest	71	172,693.0	67,604.0	39.1	29,193.5	16.9	27,859.9	17.0
Xerophytic forest	33	69,421.9	31,307.5	45.1	29,068.2	41.9	8,897.2	15.5

*Not all plots were inventoried for understory non-native plants

Hawai‘i Island/Maui forests were impacted by invasive species relative to those of O‘ahu, Kaua‘i and Lāna‘i (Table 2). A remarkable 96% of forests in lower-elevation areas of all islands contained non-native trees, with 75% dominated by non-native trees, compared to 46% in higher-elevation forests across islands, 31% of which were dominated by non-natives. The forest type with the highest percent of area invaded by non-native trees was lowland tropical rainforest, followed by mesophytic forests. The xerophytic forest type exhibited a greater percentage of area invaded than the montane rainforest type, but montane rainforest had a greater percent cover of understory non-native plants of concern.

Geographic patterns of non-native importance and abundance

The importance value (IV) of large non-native trees on Hawai‘i Island was highest in low-elevation areas, especially on the windward (eastern) side of the island (Fig. 2), but for other islands, IV for large non-native trees and saplings (Supplementary Fig. 1a) and percent of non-native seedlings (Supplementary Fig. 1b) were all high (≥ 60) across plots regardless of elevation. *Psidium cattleyanum* exhibited particularly high IVs in lowland wet forests of windward Hawai‘i Island and north coastal Maui, as well as in mesophytic forests across Kaua ‘i and central O‘ahu (Fig. 3a). *Schinus terebinthifolius* was

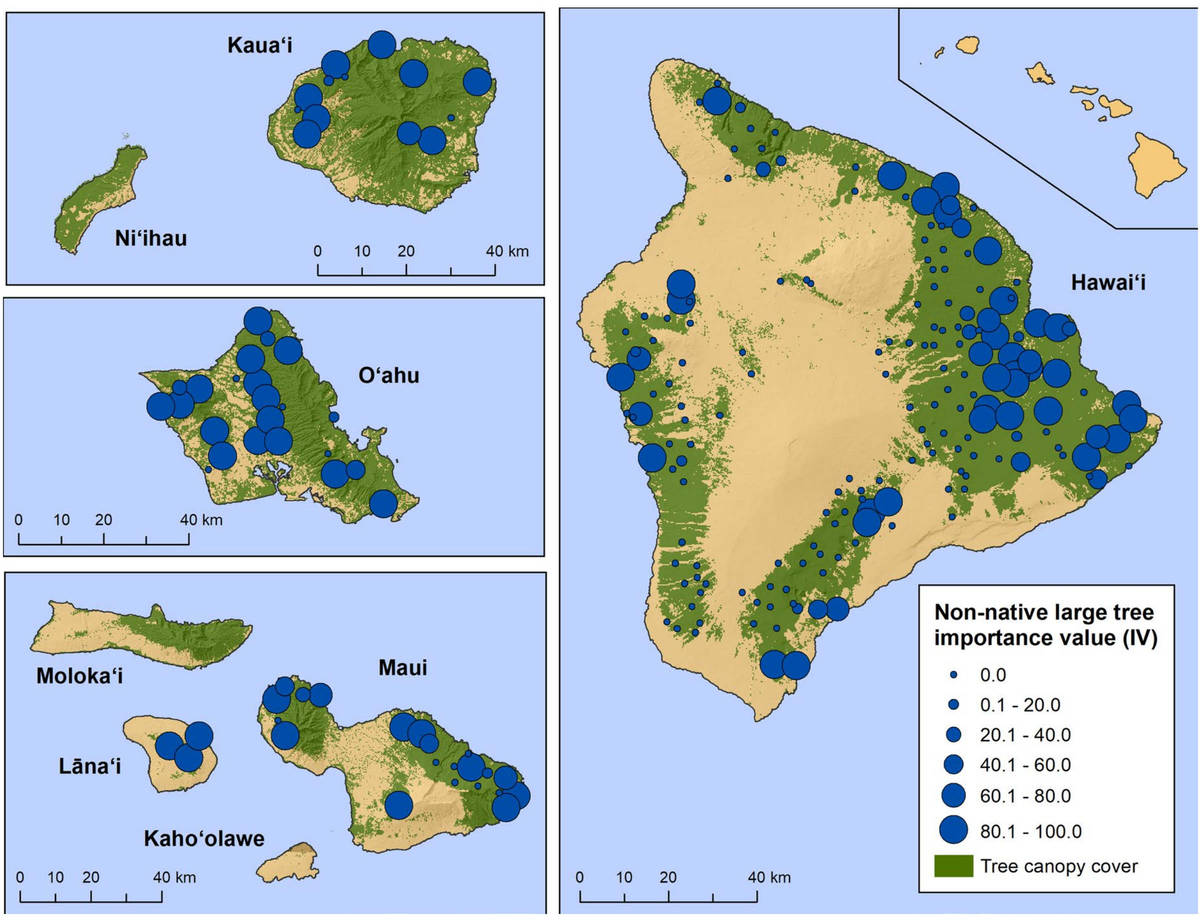

Fig. 2 Importance value (IV) of large non-native trees (≥ 12.7 cm diameter) on 238 Forest Inventory and Analysis (FIA) plots across Hawai‘i. Tree canopy cover (240 m) is based on data from a cooperative project between the Multi-Resolution Land Characteristics Consortium (Coulston et al. 2012) and the Forest Service Geospatial Technology and Applications Center using the 2011 National Land Cover Database. Plot locations are approximate

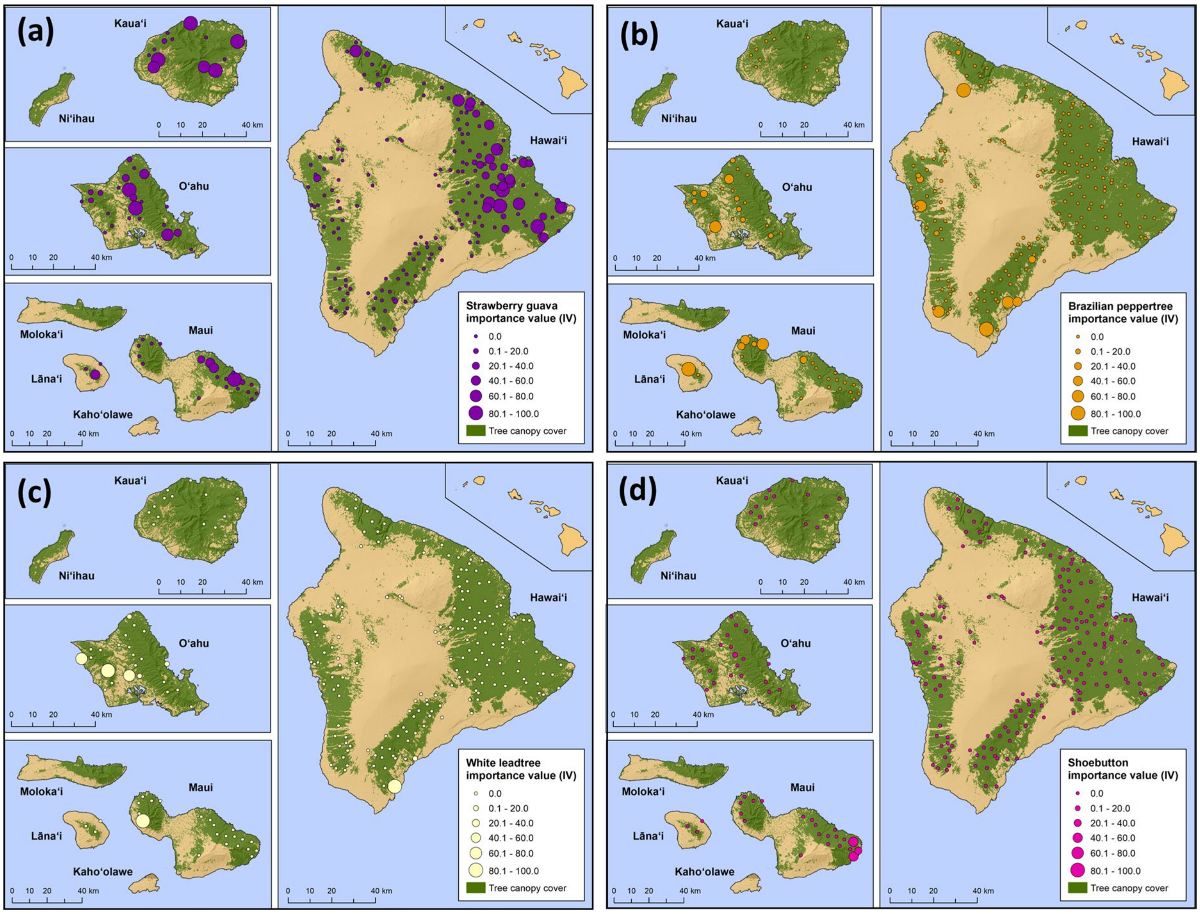

Fig. 3 Importance value (IV) of large non-native trees (≥ 12.7 cm diameter) for the four most commonly inventoried non-native tree species on 238 Forest Inventory and Analysis (FIA) plots across Hawai‘i, **a** *Psidium cattleyanum* (strawberry guava), **b** *Schinus terebinthifolius* (Brazilian peppertree), **c** *Leucaena leucocephala* (white leadtree), and **d** *Ardisia elliptica* (shoebutton). Plot locations are approximate

most common in mesophytic forests on windward Hawai‘i Island, northwest Maui, Lāna‘i, and O‘ahu (Fig. 3b). *Leucaena leucocephala* also dominated some mesophytic plots on Hawai‘i Island, Maui, and O‘ahu (Fig. 3c). *Ardisia elliptica* dominated wet plots at the eastern end of Maui (Fig. 3d).

Hawai‘i Island forests were associated with high percentages of non-native shrub/sub-shrub/woody vine cover at low elevations while on Kaua‘i, rates were high across elevations, respectively. There was only one plot on O‘ahu and a few plots in north coastal Maui with high percentages of non-native shrub cover (Supplementary Fig. 2a). Regarding forbs, plots on Hawai‘i Island exhibiting high percentages of invasive non-native cover were concentrated at low elevations on the windward (east) side and at all elevations on the leeward (west) side (Supplementary Fig. 2b). Plots of similar high forb cover were present across the other islands. Hawai‘i Island forests exhibited high percentages of invasive non-native graminoid cover, along with those along the northern and eastern Maui coasts, but high invasive graminoid cover was rare on Kaua‘i and O‘ahu (Supplementary Fig. 2c).

Comparisons across management, conservation status, island group, and forest type

Plots differed in degree of invasion across tree size class by ownership/management, reserved

Table 3 Mean and standard errors of Forest Inventory and Analysis (FIA) plot-level measures of non-native dominance by ownership/management, reserved status, island group, forest type, and fenced status, with *q*-values (*p*-values adjusted for the false discovery rate across the six non-native dominance measures for each comparison) from multiple-sample Kruskal–Wallis tests of group differences

		Large trees		Saplings		Seedlings		Shrubs/vines		Forbs		Graminoids	
		(IV)		(IV)		(% count)		(% cover)		(% cover)		(% cover)	
	Plots	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Ownership		**$q=0.0003$**		**$q=0.0038$**		**$q=0.0003$**		**$q=0.0443$**		$q=0.0612$		$q=0.4430$	
Federal	25	14.2	6.3	14.9	6.8	27.8	8.3	5.8	4.1	8.2	5.5	30.7	9.2
State/local	118	20.1	3.1	29.1	3.8	33.9	3.9	26.7	3.9	12.9	2.7	38.2	4.4
Private	95	48.3	4.7	45.3	4.8	58.3	4.6	33.0	4.7	22.8	3.8	42.4	5.0
Reserved status		**$q=0.0002$**		**$q=0.0002$**		**$q=0.0002$**		$q=0.2687$		$q=0.2687$		$q=0.9284$	
Reserved	122	14.0	2.6	23.0	3.5	27.8	3.6	23.8	3.7	12.7	2.7	39.1	4.3
Not reserved	116	48.4	4.2	45.7	4.3	58.9	4.1	30.5	4.2	20.3	3.3	39.0	4.5
Fenced status		**$q=0.0234$**		**$q=0.0234$**		**$q=0.0066$**		$q=0.0665$		$q=0.5975$		$q=0.6253$	
Fenced and ungulate free	16	8.5	6.5	7.9	6.4	7.8	5.1	6.3	6.3	11.0	7.3	32.5	11.8
Not fenced and ungulate free	222	32.3	2.8	36.0	3.0	45.5	3.0	28.5	2.9	16.8	2.2	39.5	3.2
Island group		**$q=0.0002$**		**$q=0.0002$**		**$q=0.0002$**		$q=0.0758$		$q=0.1138$		**$q=0.0002$**	
Hawai‘i/Maui	199	23.7	2.7	26.6	2.9	34.6	3.1	28.9	3.1	17.5	2.4	43.7	3.4
O‘ahu/Kaua‘i/Lāna‘i	39	66.8	6.0	72.0	6.8	85.9	4.0	17.7	6.0	10.8	4.2	15.4	5.9
Forest type		**$q=0.0002$**		**$q=0.0002$**		**$q=0.0002$**		**$q=0.0002$**		$q=0.1264$		$q=0.4878$	
Lowland tropical rainforest	53	45.2	5.6	62.0	6.2	69.4	5.7	55.3	6.6	23.6	4.8	30.8	6.3
Mesophytic or moist forest	65	33.5	5.4	36.4	5.6	40.6	5.5	22.5	5.1	11.7	3.6	39.1	5.9
Montane rainforest	71	9.8	2.9	16.6	3.8	28.8	4.6	21.5	4.8	14.0	3.8	35.2	5.6
Xerophytic forest	33	33.1	8.1	30.6	7.9	41.0	8.4	10.4	4.9	21.2	7.2	46.0	8.6

Non-native dominance of large trees (≥ 12.7 cm diameter) and saplings (2.54–12.7 cm diameter) was based on the importance value (IV) of non-native trees, encompassing stem density and basal area; *q*-values ≤ 0.05 are in bold status, fenced status, island grouping, and forest type (Table 3). The mean IV of non-native large trees and saplings and mean percent of non-native seedling stems were higher in plots on state-administered land compared to those on federal land, while those on private lands were higher than on state lands. Plots on non-reserved-status lands were more impacted across tree size classes compared to reserved public lands. Similarly, plots that were not fenced had higher non-native tree importance than those that were fenced and ungulate-free: 3.6 times higher large trees, 4.6 times by saplings, and 5.8 times for seedlings. Plots on Hawai‘i and Maui islands were less impacted by non-native trees than those on O‘ahu, Kaua‘i, and Lāna‘i (Table 3). In addition to having the largest area of non-native forests, lowland tropical rainforest also had the highest non-native importance values, followed by mesophytic forests and xerophytic forests. Montane rainforest plots were much less impacted by non-native trees.

All forest types were significantly more invaded on the lower elevation islands (O‘ahu/Kaua‘i/Lāna‘i) than on the higher elevation islands (Hawai‘i/Maui) across all three tree size classes (Table 4). For example, the mean IV of large non-native trees on lowland tropical rainforest plots was 70.4 for the lower-elevation islands and 35.5 for the higher-elevation islands, while the mean percent of non-native seedlings was 86.8 in mesophytic forests on the lower-elevation island plots compared to 30.1 on the higher-elevation islands. Additionally, non-native tree dominance metrics varied significantly by forest type for the higher-elevation islands but not the lower-elevation islands (Supplementary Table 4). In contrast, large tree IV, sapling IV, and percent seedlings for non-native trees were all highest in the lowland tropical rainforest for Hawai‘i/Maui (35.5, 60.9, and 61.9, respectively) and lowest in the montane rainforest (8.2, 14.9, and 25.9).

Plot-level means for non-native understory cover were less likely to exhibit differences by ownership/management, reserve status, fenced status, island grouping, or forest type (Table 3). Non-native shrub cover was higher on private than state lands, which in turn had higher non-native shrub cover than federal plots. Among forest types, non-native shrub cover was highest in lowland tropical rainforest and lowest in xerophytic forest. We found no significant differences for non-native forb cover, but graminoid cover was signficantly higher on Hawai‘i/Maui than on O‘ahu/Kaua‘i/Lāna‘i. Percent non-native graminoid cover ranged from 30 to 46% across forest types. Across non-native cover metrics, only shrub cover varied significantly by forest type on Hawai‘i/Maui, where it was by far highest in lowland tropical rainforest (Supplementary Table 4). No significant differences existed among forest types on O‘ahu/Kaua ‘i/Lāna‘i. When investigating differences in non-native cover within forest types across island groups, we found that graminoid cover was significantly higher on Hawai‘i/Maui than O ‘ahu/Kaua‘i/Lāna ‘i for all forest types (Table 4). There were no other significant differences in non-native plant cover.

Discussion

Our analyses of non-native plants from a network of 238 standardized plots in Hawaiian forests offer important new insights into how forest invasion varies across stratum and by forest type, management, or ownership. Our results are consistent with a statewide assessment of non-native vegetation cover derived from remote-sensing and ground-base inventories, which showed that invasions are widespread across a complex matrix of native and non-native dominated forests for each of the main Hawaiian Islands (Hughes et al. 2017; Jacobi et al. 2017). This study identified important new demographic patterns that provide additional evidence for greatly expanding dominance of non-native trees in Hawaiian forests. Invasive species already dominate multiple strata and across size classes across the forests of the lower-elevation islands, but the prevalence of non-native tree species in forest understories of the higher-elevation islands indicate eventual dominance shifts from native to non-native forest canopies there. These findings highlight the extensive and potentially rapid changes that are likley to occur in Hawai‘i's forests. They also provide insights for the future of island forests and for all forests that share similar non-native species compositional and structural attributes.

Plant invasion within forest strata and forest type

Our research confirms that fundamental and broad-scale ecological changes driven by non-native plants are well under way within the three-dimensional

Table 4 Mean and standard errors of Forest Inventory and Analysis (FIA) plot-level measures of non-native dominance by island groups within forest types, with q-values (p-values adjusted for the false discovery rate across the six non-native dominance measures for each comparison) from multiple-sample Kruskal–Wallis tests of group differences

		Large trees		Saplings		Seedlings		Shrubs/vines		Forbs		Graminoids	
		(IV)		(IV)		(% count)		(% cover)		(% cover)		(% cover)	
	Plots	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Lowland tropical rainforest		**$q = 0.0002$**		**$q = 0.0002$**		**$q = 0.0002$**		$q = 0.2214$		$q = 0.1380$		**$q = 0.0117$**	
Hawaiʻi/Maui	37	35.5	6.3	60.0	7.4	61.9	7.3	66.5	7.5	25.9	6.0	38.7	7.9
Oʻahu/Kauaʻi/Lānaʻi	16	70.4	9.4	66.4	11.5	86.5	7.2	29.4	11.4	18.2	7.6	12.5	8.5
Mesophytic or moist forest		**$q = 0.0004$**		**$q = 0.0003$**		**$q = 0.0003$**		$q = 0.4249$		$q = 0.4249$		**$q = 0.0048$**	
Hawaiʻi/Maui	53	22.2	5.3	24.9	5.5	30.1	5.8	25.8	5.9	12.5	4.0	44.2	6.6
Oʻahu/Kauaʻi/Lānaʻi	12	85.9	7.0	87.5	8.4	86.8	5.0	8.1	8.1	8.3	8.3	16.7	11.2
Montane rainforest		**$q = 0.0002$**		**$q = 0.0002$**		**$q = 0.0002$**		$q = 0.0511$		$q = 0.1855$		**$q = 0.0005$**	
Hawai ʻi/Maui	66	8.2	2.9	14.9	3.7	25.9	4.7	21.3	5.0	14.6	4.1	36.3	5.8
Oʻahu/Kauaʻi/Lānaʻi	5	44.6	13.5	39.2	21.0	66.1	16.6	24.8	19.4	6.1	6.1	20.0	20.0
Xerophytic forest		**$q = 0.0002$**		**$q = 0.0002$**		**$q = 0.0002$**		$q = 0.2602$		$q = 0.4923$		**$q = 0.0026$**	
Hawaiʻi/Maui	27	26.7	8.5	18.9	7.2	28.1	8.4	12.7	6.0	25.9	8.6	52.5	9.4
Oʻahu/Kauaʻi/Lānaʻi	6	98.9	20.1	83.3	16.7	98.9	1.1	0.0	0.0	0.0	0.0	16.7	16.7

Non-native dominance of large trees (≥ 12.7 cm diameter) and saplings (2.54–12.7 cm diameter) was based on the importance value (IV) of non-native trees, encompassing stem density and basal area; q-values ≤ 0.05 are in bold. Island group by forest type combinations with fewer than five plots were excluded from the analysis structure of Hawaiian forests, in line with remote sensing findings of Asner et al. (2008) for Hawai'i Island. Most forests in Hawai'i are now hybrid communities of native and non-native trees, with a large fraction being novel forests dominated by non-native species (Barton et al. 2021) and about half of Hawai'i's vegetated land cover being either highly disturbed or a mix of native and non-native species (Price et al. 2012; Jacobi et al. 2017). The data presented here highlight that with business-as-usual management, native-dominated but especially hybrid forests are likely to follow successional trajectories to novel, non-native dominated conditions. This trajectory appears to be modified by the factors assessed here, but our comprehensive analyses across forest layers signal a more dire future for native plants in Hawaiian forests than has been previously described. Critically, the finding that non-native trees across size classes and non-native shrubs are present in most forests and also dominate in many portends a considerable shift in Hawaiian forests from native to non-native dominance.

We found that the degree of invasion of forests by non-native trees throughout Hawai'i was manifested in three important trends. First, non-native trees in most landscapes constitute a much larger proportion of the understory (63% and 66% of saplings and seedlings, respectively) than the overstory tree component (29% of large trees), with important implications for successional trajectories. In such forests, high levels of non-native species regeneration indicate eventual and, in some places (e.g., disease-impacted *Metrosideros polymorpha* forests), rapid replacement of native canopy trees by non-native trees following canopy mortality events (Zimmerman et al. 2008), with non-natives effectively suppressing native tree recruitment. This invasion pathway represents a major concern in New Zealand where forest managers assess whether non-native invasive tree and shrub species are able to regenerate under forest canopies, enabling them to fundamentally alter succession (McAlpine et al. 2021). Second, while non-native species are present throughout all the main Hawaiian Islands, the lower-elevation islands of O'ahu, Kaua'i, and Lāna'i are more impacted by non-native trees than are the higher-elevation islands of Hawai'i and Maui. Finally, lower-elevation forests are generally more impacted than higher-elevation forests within island groups, consistent with research conducted in mountainous areas around the world (Seipel et al. 2012), including in Hawai'i (Ibanez et al. 2019).

These three trends represent a continuum of invasion intensity, spanning from the least-impacted high elevation refugia forests of Hawai'i Island and Maui to the highly impacted low elevation forests of O'ahu, Kaua'i, and Lāna'i. A major concern for conservation, then, is whether all Hawaiian forests along this continuum will follow an invasion trajectory that ends with extensive non-native species dominance. In other words, will all Hawaiian forests – including those at high elevations on Hawai'i Island and Maui—eventually become as invaded as the low elevation forests of O'ahu, Kaua'i, and Lāna'i? To answer this question will require detailed demogrpahic studies across a network of plots, such as those forming the basis of this study. However, preliminary evidence (albeit from a small sample size of plots) indicates that the high degree of invasion across size classes in the montane rainforests and mesophytic forests of O'ahu and Kaua'i (Table 4) certainly represents a possible outcome for those same forest types on Hawai'i Island and Maui. In mesophytic forests of O'ahu and Kaua'i, non-native species constitute more than 86% of large trees and saplings and 87% of seedlings. For montane rainforests on these islands, the non-native numbers are 45% for large trees and 66% for seedlings, with *Psidium cattleyanum* being the most abundant non-native species in these forests (Fig. 3A). If all Hawaiian forests are indeed following this invasion trajectory, non-native species could eventually constitute 75% or more of the forest tree stems and basal area on all islands and across forest types and elevations. This is in line with the idea that Hawaiian forests experience invasion debt, defined as the lag between the initiation of invasion and eventual ecological outcomes (Duncan 2021) as well as additional environmental and socio-economic impacts (Rouget et al. 2016). Understanding invasion debt and related lags is critical for managing non-native species because inaccurate assessment of invader spread and dominance can result in missed windows for effective management (Crooks 2005). Indeed, current Hawaiian forests with mostly native overstories and non-native understories are likely to transition to largely non-native dominated forests without management interventions, with the costs of non-native species management becoming exponentially larger (Povak et al. 2017).

The distribution and abundance of non-native species in Hawaiian forests, across islands and elevations, provides potential planning scenarios for management of invasion in other forests experiencing invasion debts, including those of oceanic islands (Kueffer et al. 2010a), Europe (Wagner et al. 2021), South Africa (Rouget et al. 2016), and the eastern United States (Allen and Bradley 2016). It is possible, however, that higher-elevation forests on Hawaiʻi and Maui islands and elsewhere may be more resistant to non-native tree invasion in part because of less intensive human land use at higher elevations (Seipel et al. 2012) and because of the environmental gradients associated with elevation (Alexander et al. 2011), but disease-related impacts (Fortini et al. 2019) and climate change (Kagawa-Viviani and Giambelluca 2020) may diminsh mechanisms of resistance. Repeat forest inventories will help to more precisely define invasion trajectories across Hawaiʻi.

A particular problem for Hawaiian forests, especially lowland tropical rainforests, is the lack of native species regeneration, which is typically replaced by a heavy subcanopy of non-native species—even where there is seed rain from native canopy trees and repeated removal of understory non-native competitors (Cordell et al. 2016). Native species, including the widely dominant *M. polymorpha*, typically grow more slowly than non-native competitors, which rapidly expand in size following disturbance (Friday et al. 2015). Meanwhile, the dominance of non-native plants in Hawaiian seed banks and their ability to germinate at higher percentages than native species makes them particularly well-positioned to increase in abundance following disturbance (Drake 1998; Cordell et al. 2009). Native seedlings and saplings, therefore, are likely to be displaced by non-native species, preventing them from replacing native trees in the canopy when these trees eventually die. Importantly, mortality of native species can be greatly accelerated, as with Rapid ʻŌhiʻa Death (ROD), a wilt disease caused by the aggressive fungal pathogen *Ceratocystis lukuohia* and the less aggressive *C. huliohia* (Barnes et al. 2018; Fortini et al. 2019; Hughes et al. 2020). This new disease poses an enormous threat to *M. polymorpha* forests because ROD-driven mortality events can cause dramatic shifts in dominance towards non-native trees, including important structural and compositional changes that are exacerbated by competition with non-native plants and disturbance by feral ungulates (Yelenik et al. 2020).

The results of our analyses offer some insights into the threat of non-native species on forest types, with implications for management specific to forest types and locations within different islands. For example, non-native tree species appear to pose less of a threat to Hawaiʻi Island mesophytic forests compared to the same forest type on the other islands or to lowland tropical rainforest on any island, where such species as *Psidium cattleyanum* and *Ardisia elliptica* can dominate. This may be the case because Hawaiʻi and Maui islands have mesophytic forests at both high and low elevations, while the forest type occurs only at low elevations elsewhere. Conservation efforts, such as the removal of non-native trees including *Schinus terebinthifolius*, *Leucaena leucocephala*, and *Acacia confusa*, may not be as highly resource-intensive on a per-unit-area basis for Hawaiʻi Island mesophytic forests as elsewhere. On the other hand, regeneration in Hawaiian lowland forests is likely to be almost entirely devoid of native species without control of aggressive invasive trees given their faster growth rates, dominance of seed banks, and higher germination rates (Cordell et al. 2009). Critically, even intensive efforts have not returned lowland wet forest stands to a native-dominated state, indicating that other approaches will be needed, such as outplantings of both native and non-invasive non-native species (Cordell et al. 2016) or the use of small artificial gaps that do not provide complete resistance to non-native species but may ensure cost-efficient recovery of native tree species (Kueffer et al. 2010b). At higher elevations, meanwhile, montane forests on Hawaiʻi Island and Maui (although not on Oʻahu/Kauaʻi/Lānaʻi) are relatively less impacted by either large or sapling sized non-native trees, but other costly-to-remedy species invasions are rapidly changing forest composition in these ecosystems (Povak et al. 2017). For example, understory plants such as *Hedychium gardnerianum* Sheppard ex Ker Gawl. (Kahili ginger) and *Clidemia hirta* (L.) D. Don (Koster's curse) are aggressively spreading in many montane forest stands, including the remote Kipahulu Valley in Haleakala National Park on Maui and in Hawaiʻi Volcanoes National Park (Loope et al. 2013);

these species are highly effective at suppressing native regeneration (Smith 1992; Minden et al. 2010). Consequently, these forests are prime candidates for early detection and rapid response efforts, particularly because native tree seedlings account for more than 70% of the seedlings in montane forests on Hawai'i Island and Maui. We caution that the percent understory cover of non-native invasive plants of concern in montane forests (17%), lowland tropical rainforests (59%), and mesophytic forests (22%) is likely underestimated because the FIA dataset is limited to an expert-defined list of the 40 non-native understory plants of the greatest concern.

The lower percent cover of non-native understory species of concern in xerophytic forests (16%), relative to lowland tropical rainforest, masks the actual vulnerability of these forests or the extent to which they have been damaged by naturalized species. Tropical dry forests are among the most endangered ecosystems in the world (Thaxton et al. 2010), with nearly all remnant dry forest being exposed to a variety of largely anthropogenic threats (Miles et al. 2006). In Hawai'i, introduced ungulates, and the interactive effects of invasive African and New World grass invasions, climate change, and changing fire regimes (Hughes et al. 1991; D'Antonio et al. 2011) have greatly reduced the extent of Hawaiian dry forests (Bruegmann 1996). Most of the lost xerophytic forestland has been replaced by fire-prone grasslands in which few trees can grow. FIA field crews visit plot locations on existing forest land, defined as at least 10% tree crown cover and at least 0.4 ha in size and 37 m wide (Burrill et al. 2018). Former xerophytic forest stands that have transitioned into non-native grassland are therefore not included in this study, resulting in an underestimation of the degradation of such forests and the amount of understory naturalized species cover they encompass. The management of remnant xerophytic forests remains a challenge, with natural regeneration of native plants strongly limited by invasive grasses (Cabin et al. 2002), the loss of native pollinators and seed dispersers, and the increasing frequency and intensity of droughts, which interact to require expanded approaches to management implemented for years, decades, or longer (Thaxton et al. 2010).

These results have conservation implications beyond the Hawaiian archipelago. Hawai'i is among the world's most invaded geographies (Pyšek et al. 2017), with more naturalized than native plant species (Essl et al. 2019) and the most naturalized plant species of all Pacific islands (Wohlwend et al. 2021). The pattern and process of plant invasion in Hawaiian forests therefore provide insights into how invasion trajectories and trends may play out on other islands, particularly as experts predict increased impacts of alien species on oceanic islands globally (Lenzner et al. 2020). This is particularly true in the Pacific, where islands are especially impacted by alien plant species, having the most naturalized species globally when accounting for their size and the highest biogeographic increases in species number with increasing land area (van Kleunen et al. 2015)—all despite their geographic isolation. Those islands without a high diversity of naturalized plants are vulnerable to human-mediated transport of non-natives from elsewhere (Denslow et al. 2009; Wohlwend et al. 2021). Research indicates that species-poor Pacific islands receive naturalized plant species from more species-rich and socioeconomically wealthy islands within the region rather than from beyond (Wohlwend et al. 2021). Hawai'i, which hosts many invaders not present elsewhere in the Pacific, may therefore act as a hub of naturalized plant introductions throughout the region, as well as an early warning site of the potential impacts of plant invasion (Traveset et al. 2014; Wohlwend et al. 2021).

Relationship between ownership/conservation management and non-native plants

Non-native invasive plants are an immense and growing problem in Hawaiian natural ecosystems, including forests, and the challenges of managing these species while conserving native biodiversity are correspondingly large (D'Antonio et al. 2017; Cordell 2021). Native Hawaiian tree species are a biota largely endemic to the archipelago (> 95%), so the extirpation of any of them is a global loss. Many of these species have important cultural and economic uses, as do the Polynesian-introduced trees that occur in relatively small numbers across Hawaiian forests (Abbott 1992). A key to successful conservation of native species is keeping the remaining relatively uninvaded native areas intact by preventing establishment of new naturalized species, limiting the impact of established non-native species, and restoring degraded areas necessary for imperiled species conservation (Smith 2016). Federal and state agencies with jurisdiction over 16% and 30% of Hawai‘i’s land area, respectively (Conservation Biology Institute 2016), generally aim to take these steps to varying degrees. For example, large-scale management of non-native plants in Hawai‘i Volcanoes National Park began in the 1980s and has expanded in the decades since (Loope et al. 2013). While the federal government spends a large amount of funding to remove non-native species from National Park Service, U.S. Fish and Wildlife Service, and Department of Defense lands, fewer resources have been available for state reserves to do the same (Gillespie et al. 2008), although federal funds have been directed to assist the conservation of state-managed lands. Fencing and removal of feral ungulates, a widely used management tool, has been shown to reduce impacts to high-value forests, especially on protected public lands (Loope et al. 2013), but results are not uniform. For example, fencing and ungulate removal can increase native plant species cover and density but sometimes fail to prevent invasive species spread (Loh and Tunison 1999; Cole et al. 2012; Cole and Litton 2014).

Our results confirm that plots in forest areas that are fenced and/or are managed by federal or state agencies were less impacted by non-native trees and shrubs than those in unfenced forests and/or on private land. Fenced plots, for example, were 75% less impacted by non-native plants than unfenced plots on average. Similarly, federal and state adminstered forests in some kind of reserve status (e.g., U.S. Fish and Wildlife Service Refuge or State Natural Area Reserve) were less impacted by non-native trees than other public lands. It is not possible to determine how much of this difference was the result of management or because protections were established for forests with the lowest presence of invasive species. Repeat inventories of the FIA plots will allow us to assess whether conservation management is effective at limiting the impacts of non-native plant species to native forests. Specifically, future FIA data collections will permit assessments of rates of change and of whether rates differ from forests with lower or no conservation investments. Notably, some private land ownerships invest heavily in native forest conservation while some public agencies may be constrained in their management because of inadequate funding for the control of non-native species. Ideally, future analyses will have access to per-unit-area resource investment with which to evaluate trends. While the patterns associated with fencing have several explanations, our results highlight that even where fenced, native forests often include a diversity of non-native species in various size classes that threaten the native condition of these forests. Other studies have suggested that management may slow the invasion of protected areas by many non-native plants in Hawai‘i, but that the most aggressive invasive plants remain intractable (Loope et al. 2013; Ibanez et al. 2020). The management of fenced areas, though expensive, would need to include the control of selected non-native understory plants and the outplanting of both rare and common native species that show inadequate recruitment (Cabin et al. 2002; Gillespie et al. 2008; Cole and Litton 2014). Further, fencing may provide the additional benefit of reducing ungulate wounding of trees that can facilitate infection of ‘ōhi‘a lehua trees by ROD (Fortini et al. 2019).

The lack of an effect of fencing or conservation status on non-native forb and grass importance (Table 3) may relate to the widespread distribution of such forb invaders as Kahili ginger and such graminoid invaders as fountain grass (*Pennisetum setaceum* (Forssk.) Morrone), broomsedge bluestem (*Andropogon virginicus* L.), and Columbian bluestem (*Schizachyrium condensatum* (Kunth) Nees), including within protected areas such as Hawai‘i Volcanoes and Haleakala National Parks (Loope et al. 2013). These understory plants interfere with establishment of native woody seedlings (Denslow et al. 2006; Litton et al. 2006; Minden et al. 2010) and, in the case of grass species, increase the risk of wildfire in woodland ecosystems (Hughes et al. 1991). Additionally, these invasive plants, especially grasses, can persist for decades in woodland systems even after the suppression of fires that benefit them (D’Antonio et al. 2011).

Conclusions

To our knowledge, this is first comprehensive, field-based assessment of non-native plant abundance and importance across the forests of an entire tropical island archipelago. The results were sobering: While 29% of the large trees across Hawai‘i were not native, that proportion more than doubles to

63% for saplings and 66% for seedlings, indicating the potential for accelerating change in the canopies of Hawai‘i's native forests. This finding provides strong evidence that Hawai‘i is operating with signficant invasion debt, a debt that is currently masking a more dire future for Hawai‘i's native forests, including those with native-species dominated canopies. Not suprisingly, low-elevation forests were particularly degraded with respect to species composition, but montane forests, widely viewed as native species refugia, supported non-native plant species across all geographies, indicating they are likely to become more degraded following the disturbances associated with ROD or climate change. These indications of a accelerating invasion trajectory for Hawai‘i highlight that its native-dominated forests are especially vulnerable to degradation by non-native invaders (Denslow 2003).

The results of this study may help improve the effectiveness of forest conservation in Hawai‘i and elsewhere. The degradation of low-elevation forests is likely to continue as remnant native overstory trees are replaced by non-natives. Attempts to return such forests to native-species dominance have been accomplished only at very small scales because costs are enormous (Cordell et al. 2016; Povak et al. 2017), requiring a rethinking of how to approach forest restoration such as using non-invasive naturalized or Polynesian introduced species on degraded sites where they can provide such ecosystem functions as soil and water quality protection, habitat for rare animals, and shelter for threatened and endangered plant species (Friday et al. 2015). While we found that the limited core conservation areas of high-native species dominance are relatively less impacted by non-native plants, this may reflect both effective management and differences in the starting conditions of those forests when initially fenced or designated. Ongoing re-inventory of the FIA plots will help to assess invasion trajectories for these gems of Hawai‘i's conservation system, as well as for more degraded forests.

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Data availability The data presented in this study are available on request from the corresponding author. FIA data are additionally available at https://www.fia.fs.fed.us

Declarations

Competing interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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