Hawaiian Subalpine Plant Communities: Implications of Climate Change[1]

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Abstract: Globally, subalpine and alpine plant communities are receiving increasing attention owing to disproportionately rapid warming at high altitudes, and the resultant habitat shrinkage leaving high-altitude specialists with nowhere to migrate. The Hawaiian subalpine zone (1,700–3,000 m) is an interesting example of this potential phenomenon because of the high endemism. We analyzed plant species richness, cover, and density from 89 plots (1,000 m^2) sampled in 2010–2018 across two volcanic mountains, Haleakalā on Maui, and Mauna Loa on Hawai'i. Most of the 139 plant species recorded were non-native (55%), with the remainder endemic (31%) and indigenous (14%). Plot-level richness differed from gamma diversity, with endemic species more abundant than non-native species. Non-native species richness was higher on Haleakalā than Mauna Loa. These communities are patchy with low-lying (<1 m) vegetation, and lower cover on younger drier Mauna Loa (36%) than Haleakalā (54%). Density was largely consistent with the understory cover data, with endemic *Vaccinium reticulatum* (>3,500/ha) and indigenous *Leptecophylla tameiameiae* (>2,430/ha) shrubs dominant on both volcanoes. Woodland communities were encountered only on Mauna Loa, with endemic trees *Metrosideros polymorpha* on wetter, south aspects, and *Sophora chrysophylla* on the drier, leeward side. Hawaiian subalpine vegetation varies among islands, volcanoes, and aspects, yet remains largely native-dominated, though with increasing threats from climate change, invasive non-native species, and wildfire. We recommend continued monitoring of biotic communities and climate in this sensitive zone, in situ physiological studies for the native matrix species, stricter non-native species biosecurity and sanitation protocols, wildfire prevention, and improved documentation of the effects of feral ungulates.

Keywords: biodiversity, endemic plants, plant community, high elevation, Hawai'i Volcanoes National Park, Haleakalā National Park, island

GLOBALLY, SUBALPINE AND ALPINE plant communities are receiving increasing attention owing to disproportionate rapid warming at high altitudes (MRI 2015), upward shifts in species' optimum elevations (Lenoir et al. 2008), and the potential shrinkage of habitat for subalpine and alpine specialists (e.g., cold-adapted, with low nutrient demands) (Rumpf

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et al. 2018). These communities tend to be relatively low in diversity and simple in structural complexity, consist of species near their physiological limits, and are currently experiencing disproportionate warming (and for some regions, drying). High elevation communities exist in habitat islands, which, like true islands, are geographically isolated from each other by dispersal barriers, and may therefore differ despite having similar climatic conditions. Theoretically, according to the tolerance–dominance tradeoff, species specialized to persist and/or thrive in environmentally harsh conditions, such as alpine environments, are not strong competitors, because traits associated with competitive ability were less evolutionarily advantageous there (Boulangeat et al. 2012). Similarly, high elevation endemism hotspots were thought to be resistant to non-native species invasions owing to the extreme environmental conditions and necessity of specialized adaptations (M.A. 2003), as was found along elevation gradient roadside surveys in Tenerife, Canary Islands (Bacaro et al. 2015). Today, invasive species are present—at least along anthropogenic corridors—in nearly all high elevation communities examined worldwide, presumably owing to globalization (= increased propagule pressure) and climate change (Pauchard et al. 2009). With ongoing climate change, high elevation native plant communities will likely face even greater threats, particularly on islands (Fernández-Palacios et al. 2021).

The Hawaiian Islands have served as a model system for many ecological studies, resulting in advancements in numerous fields, including speciation, competition, facilitation, ecosystem processes, soil development, erosion, and species invasions (Vitousek 2004, Barton et al. 2021). Similarly, the Hawaiian subalpine zone can serve as a model for other mountain systems, providing an early warning of the effects of climatic warming, drought, and extreme climatic events on relatively intact plant communities with high endemism (e.g., Berio Fortini et al. 2022). The Hawaiian subalpine zone supports montane xerophytic vegetation and occurs primarily between 1,700 and 3,000 m on Haleakalā on Maui

Island and Hualālai, Mauna Kea, and Mauna Loa on Hawaiʻi Island (Gagné and Cuddihy 1990). The subalpine zone is a good model system because each volcano represents a different primary successional sere or substrate type along the chronosequence of Hawaiian Islands age gradients. Haleakalā is the oldest of the four and has better developed soils and greater botanical diversity than Mauna Loa, which is the youngest (Wagner et al. 1999, Vitousek 2004). Each subalpine zone has a relatively stable, well-defined lower boundary at the trade wind temperature inversion (TWI), where cloud development is capped, resulting in much higher irradiance and lower precipitation and relative humidity above (Cao et al. 2007). The TWI produces a similar sharp boundary on a number of other tropical, oceanic, high islands as well (Leuschner 1996). This boundary has been identified as an important floristic break (Kitayama and Mueller-Dombois 1992, Mueller-Dombois and Fosberg 1998, Crausbay et al. 2014), where the onset of global climate change may be easily detected (Loope and Giambelluca 1998). Strong altitudinal plant community boundaries associated with climatic stability have been postulated in the Hawaiian Islands because this tight correlation allowed plant life form alone to serve as a strong indicator of local climatic condition (Mueller-Dombois 1992). However, it is worth noting that many decades ago the same author also stated that "global warming or cooling may change that (relationship)" (Mueller-Dombois 1992).

In addition to climatically defined altitudinal boundaries (i.e., lower boundary–TWI, upper boundary–frost), the Hawaiian subalpine zone is characterized by a range of moisture conditions owing to orographic effects of the northeast trade winds, which create dry shrublands and woodlands, mesic grasslands, and a mixed wet bog community with increasing precipitation (Gagné and Cuddihy 1990). These subalpine communities, like other Hawaiian plant communities, have high endemism and low species richness compared to other tropical systems (Ostertag et al. 2014). Additionally, low species turnover along elevational gradients has been highlighted relative to other island mountain

systems of similar age and type because the Hawaiian flora is depauperate resulting in many plants with broad altitudinal ranges (Kitayama and Mueller-Dombois 1992, Ainsworth and Drake 2020). It should be straightforward to detect change between communities—and theoretically over time—because these low-diversity communities are each dominated by only a few species: *Deschampsia nubigena* grasslands, *Leptecophylla tameiameiae* / *Vaccinium reticulatum* shrublands, and *Metrosideros polymorpha* woodlands and *Sophora chrysophylla* woodlands.

The Hawaiian subalpine and alpine zones have less history of anthropogenic land use impacts than those in the lowlands (Gagné and Cuddihy 1990; but see effects of grazing below). They are still dominated by native plant species, but recent studies of temperate versus tropical invaders and models of habitat invasibility under changing climate scenarios have predicted future increases in invasion pressure at upper elevations (Angelo and Daehler 2013, Vorsino et al. 2014). There have already been documented increases in presence for many non-native species (Ibanez et al. 2020). Up until the 1990s, these communities were highlighted for their lack of non-native plant invasion, with the notable exception of invasive *Verbascum thapsus* (Gagné and Cuddihy 1990). However, the number of non-native plant species has been increasing rapidly, with 151 species identified as naturalized above 2,000 m (Daehler 2005). Despite the increasing presence of non-native plant species at higher elevation, their cover and abundance thus far remain low (Ibanez et al. 2019). Additionally, all subalpine communities have been impacted to varying extents by non-native ungulates (goats, sheep, mouflon, pigs) (Gagné and Cuddihy 1990). Despite dramatic recovery of subalpine vegetation following fencing and ungulate removal in some managed sites, the legacy of past disturbance persists in many of these protected ecosystems (Jacobi 1981, Hughes et al. 2014, Krushelnycky et al. 2019).

The objective of this study was to describe and compare plant community composition and structure within the subalpine zone of two Hawaiian volcanoes, Haleakalā (3,055 m) on

Maui and Mauna Loa (4,169 m) on Hawaiʻi. We predicted that: (1) endemic and indigenous species diversity would be higher on Haleakalā than Mauna Loa because Haleakalā is older, having had greater time for soil development, plant colonization, adaptation, and speciation; (2) non-native species diversity would be similar between volcanoes, because while Haleakalā has more developed soils, Mauna Loa has a more recent history of ungulate disturbance, potentially facilitating species invasions; and (3) community structure would be similar between volcanoes, with dominant endemic and indigenous shrubs and few woody non-native species.

MATERIALS AND METHODS

Study Area

This study was conducted in the Hawaiian Islands (19–22° N, 155–160° W; Figure 1). Sampling occurred on two volcanic mountains, Haleakalā and Mauna Loa, on the islands of Maui and Hawaiʻi, respectively. The lower limit of the subalpine zone is defined by the top of the trade wind inversion layer; below this boundary, moisture brought by the north-easterly trade winds is deposited along the volcanic slopes. The TWI is a temperature inversion that persists through most of the year (>80%) and places an altitudinal cap on cloud development, creating the significantly drier subalpine zone above it (Cao et al. 2007). The upper limit of the subalpine zone is the alpine zone, above approximately 3,000 m, where conditions are extremely dry and cold with sparse to absent vegetation (Gagné and Cuddihy 1990). The Hawaiian Islands are volcanic in origin, and sampled substrates range from less than 400 years old on Hawaiʻi to over one million years old on Maui. Sample sites are located on andisol and aridisol soil orders (Deenik and McClellan 2007) including more than 20 different soil series (Soil Survey Staff 2015).

Vegetation Data

Vegetation data (89 plots, including 139 plant species) were collected by the National Park Service Pacific Island Inventory and
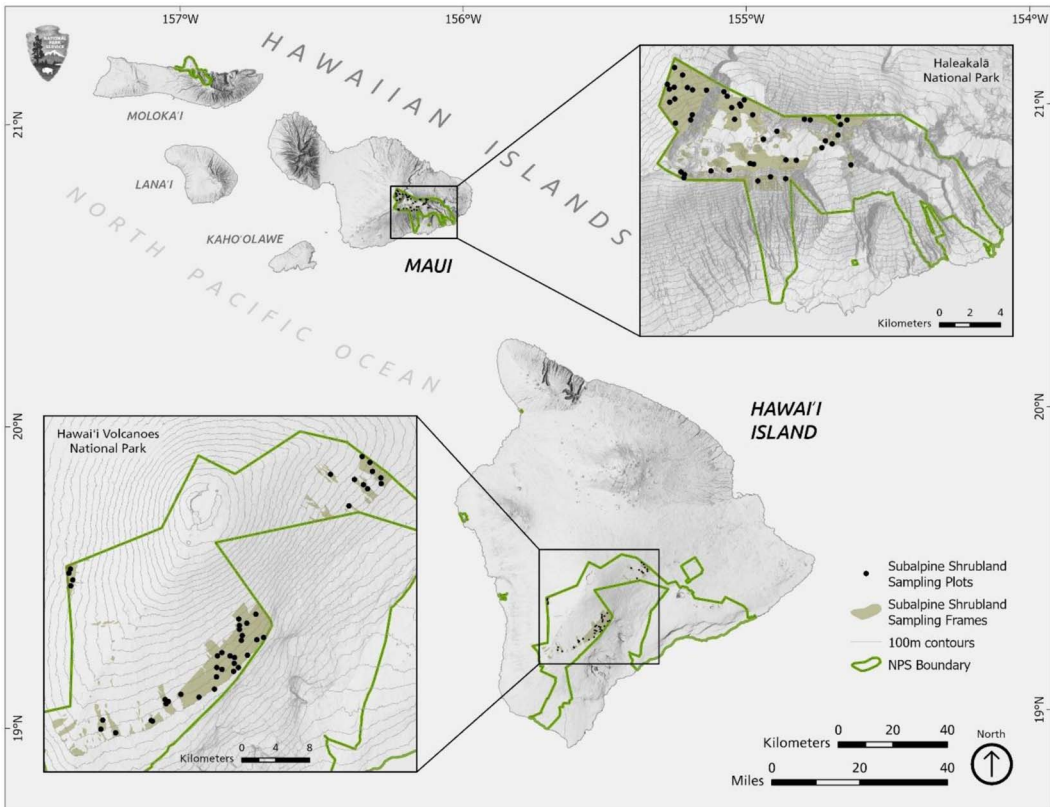
FIGURE 1. The sampled subalpine plant communities (light green shaded regions) on Haleakalā volcano in Haleakalā National Park on Maui Island and on Mauna Loa volcano in Hawai'i Volcanoes National Park on Hawai'i Island.

Monitoring Program on Mauna Loa within Hawai'i Volcanoes National Park (HAVO) and on Haleakalā within Haleakalā National Park (HALE) on Hawai'i and Maui between 2010 and 2018 (Pacific Island Network Focal Terrestrial Plant Communities Monitoring Dataset available online https://irma.nps.gov/DataStore/Reference/Profile/2294244).

These data include 89 rectangular plots (1,000 m²) installed to assess status and detect long-term trends within the subalpine plant communities of Haleakalā (43 plots) and Mauna Loa (46 plots). All plots included in this analysis were within the subalpine zone sampling frames (Ainsworth et al. 2011) except two plots that were initially in the wet forest frame and reclassified as subalpine shrublands (Ainsworth 2021). Later, two Haleakalā and one Mauna Loa subalpine plots were excluded from analysis owing to low (<5%) total vegetation cover. Subalpine plots range from 1,530 m to 2,500 m. Mean annual precipitation in the plots ranges from 695 mm to 3,745 mm and mean annual temperature ranges from 8.4°C to 11.7°C (Giambelluca et al. 2013, Giambelluca et al. 2014).

Vegetation sampling was conducted using a modified Whittaker nested plot design (Mueller-Dombois and Ellenberg 1974, Ainsworth et al. 2011). Vascular plant species presence and tree density (≥1 cm at ~1.3 m above the base (dbh, diameter at breast height)) were recorded within the entire plot (20 × 50 m), shrub and tree seedling density (≥50 cm height or length) were recorded in a nested subplot (2 × 50 m), and understory cover (<2 m tall) and substrate type (litter,

rock, cinder/gravel, soil, bryophyte, lichen, tree trunk) were recorded every 0.5 m along three 50 m transects (300 points/plot) using pole-intercept (Ainsworth et al. 2011). Live and dead tree and shrub densities were recorded. Plant nomenclature was standardized using Wagner et al. (1999, 2012) and Palmer (2003).

Analysis

Measures of plant diversity were calculated from the species presence data within each plot as gamma = total number of species encountered per study and per volcano, alpha = species richness per plot, and relative frequency = percent of plots occupied by each species. Species richness was analyzed as a two-factor analysis of variance (ANOVA) with biogeographic origin (endemic, indigenous, non-native), volcano, and their interaction as fixed effects. Non-native species richness was further analyzed by life form (herbaceous, woody), volcano, and their interaction.

Shrub, seedling, and tree counts were reported as density (number per hectare). Tree ferns were counted as trees. To assess differences between volcanoes for many vegetation parameters (total vegetation cover, substrate types, shrub species densities) two sample *t*-tests were used. All frequentist statistical analyses were carried out using R 3.6.3 software (R Core Team 2020).

Multivariate statistical analysis of vegetation data was based on cover values generated from understory pole-intercept transects (300 points/plot) for all species (McCune and Mefford 2011). We applied cluster analysis using the Sorensen (Bray-Curtis) distance measure with a group average linkage method to divide the 89 plots into four distinct clusters. Multi-response permutation procedure (MRPP) was used to test the null hypothesis of no difference between cluster groups and to test the null hypothesis of no difference between volcanoes. Indicator species analysis (ISA) was used to examine the relationships of individual species to (1) cluster groups and (2) volcano (Dufrêne and Legendre 1997). Nonmetric multidimensional scaling (NMS) ordination was used to delineate patterns between clusters, volcanoes, and species (Kruskal 1964, Mather 1976). Multivariate analyses were carried out using PC-ORD (McCune and Mefford 2011).

Plant Community Composition

A total of 139 vascular plant species were recorded in the subalpine zone on Haleakalā and Mauna Loa between 2010 and 2018 (Table 1). Over half of these species were non-native (55%), with the remainder being endemic (31%) and indigenous (14%). The distribution of species differed between volcanoes, with approximately one-third found only on Haleakalā (40), one-third only on Mauna Loa (53), and one-third shared (46). Interestingly, less than 20% of the non-native species recorded were found on both volcanoes. In contrast, most endemic and indigenous species were shared between volcanoes. The general distribution of species by biogeographic origin was similar between volcanoes (Figure 2A). Most non-native species were herbs and grasses (Figure 2B), whereas native species were more evenly distributed among life forms.

Alpha diversity (species richness per plot) differed from gamma diversity in that endemic species richness was greater than that of non-native species for both volcanoes (F (2) = 67.10, $p < 0.001$, Figure 3A). Alpha diversity differs by the origin-volcano interaction ($F(2) = 3.99$, $p = 0.02$) due to the high number of non-native species on Haleakalā. All five life forms are represented in each biogeographic origin category, with endemic species primarily graminoids and shrubs and non-native species primarily herbs and graminoids (Figure 3B). While alpha diversity for all species did not differ by volcano ($F(2) = 67.10$, $p < 0.001$, Figure 3A), when non-native species were isolated, the number of species per plot did differ by life form ($F(1) = 94.49$, $p < 0.001$) and volcano ($F(1) = 4.71$, $p = 0.03$), with more herbaceous and woody non-native species on Haleakalā than on Mauna Loa (Figure 3C). The interaction between non-native species life

TABLE 1

Species Recorded in the Subalpine Communities on Haleakalā (HALE) and Mauna Loa (HAVO) Volcanoes

Family	Species	BO	Life Form	Frequency (%)		
				HALE	HAVO	ALL
Amaranthaceae	*Dysphania ambrosioides* (L.) Mosyakin & Clemants	non	herb	0	4	2
Apiaceae	*Daucus carota* L.	non	herb	0	2	1
Apiaceae	*Daucus pusillus* Michx.	non	herb	0	2	1
Aquifoliaceae	*Ilex anomala* Hook. & Arnott	ind	tree	0	4	2
Araliaceae	*Cheirodendron trigynum* ssp. *trigynum* (Gaudich) A. Heller	end	tree	0	4	2
Aspleniaceae	*Asplenium adiantum-nigrum* L.	ind	fern	40	33	36
Aspleniaceae	*Asplenium trichomanes* L. subsp. *densum* (Brack.) W. H. Wagner	end	fern	44	17	30
Asteliaceae	*Astelia menziesiana* Sm.	end	herb	0	2	1
Asteraceae	*Ageratina adenophora* (Spreng.) R. King & H. Robinson	non	herb	30	0+	15
Asteraceae	*Ageratina riparia* (Regel) R. King & H. Robinson	non	herb	5	0	2
Asteraceae	*Argyroxiphium kauense* (Rock & Neal) O. Deg. & I. Deg.	end	herb	0	4	2
Asteraceae	*Argyroxiphium sandwicense* subsp. *macrocephalum* (A. Gray) Mérat	end	herb	2	0	1
Asteraceae	*Cirsium vulgare* (Savi) Ten.	non	herb	0	4	2
Asteraceae	*Conyza bonariensis* (L.) Cronq.	non	herb	9	2	6
Asteraceae	*Conyza canadensis* (L.) Cronq.	non	herb	5	0	2
Asteraceae	*Dubautia ciliolata* (DC) D. Keck subsp. *ciliolata*	end	shrub	0	39	20
Asteraceae	*Dubautia menziesii* (A. Gray) D. Keck	end	shrub	**51**	0	25
Asteraceae	*Dubautia waianapanapaensis* G. D. Carr	end	shrub	2	0	1
Asteraceae	*Emilia fosbergii* Nicolson	non	herb	0	2	1
Asteraceae	*Euchiton japonicus* (Thunb.) A. Anderb.	non	herb	2	13	8
Asteraceae	*Euchiton sphaericus* (Willd.) A. Anderb.	non	herb	0	13	7
Asteraceae	*Gamochaeta purpurea* (L.) Cabrera	non	herb	0	2	1
Asteraceae	*Helichrysum foetidum* (L.) Cass.	non	herb	0	2	1
Asteraceae	*Hypochaeris radicata* L.	non	herb	**95**	41	67
Asteraceae	*Pluchea carolinensis* (Jacq.) G. Don	non	shrub	0	2	1
Asteraceae	*Pseudognaphalium sandwicensium* (Gaudich.) A. Anderb.	end	herb	7	26	17
Asteraceae	*Senecio madagascariensis* Poir.	non	herb	16	20	18
Asteraceae	*Senecio sylvaticus* L.	non	herb	0	13	7
Asteraceae	*Sonchus oleraceus* L.	non	herb	2	4	3
Asteraceae	*Taraxacum officinale* W. W. Weber ex Wigg.	non	herb	5	0	2
Asteraceae	*Tetramolopium humile* (A. Gray) Hillebr.	end	shrub	26	20	22
Blechnaceae	*Sadleria cyatheoides* Kaulf.	end	tree fern	5	0	2
Blechnaceae	*Sadleria pallida* Hook. & Arn.	end	tree fern	0	7	3
Brassicaceae	*Cardamine flexuosa* With.	non	herb	0	4	2
Brassicaceae	*Coronopus didymus* (L.) Sm.	non	herb	0	2	1
Campanulaceae	*Wahlenbergia gracilis* (G. Forster) A. DC	non	herb	0	7	3
Caryophyllaceae	*Arenaria serpyllifolia* L.	non	herb	2	0	1
Caryophyllaceae	*Cerastium fontanum* Baumg. *subsp. vulgare*	non	herb	7	0	3
Caryophyllaceae	*Petrorhagia dubia* (Raf.) G. López & Romo	non	herb	2	0	1
Caryophyllaceae	*Polycarpon tetraphyllum* (L.) L.	non	herb	2	9	6
Caryophyllaceae	*Silene gallica* L.	non	herb	5	0	2

TABLE 1

Family	Species	BO	Life Form	Frequency (%)		
				HALE	HAVO	ALL
Cibotiaceae	*Cibotium glaucum* (Sm.) Hook. & Arn.	end	tree fern	0	2	1
Cyperaceae	*Carex alligata* Boott	end	sedge	0	7	3
Cyperaceae	*Carex macloviana* Dum. D'Urv. subsp. *subfusca*	ind	sedge	14	2	8
Cyperaceae	*Carex wahuensis* C. A. Mey.	end	sedge	37	13	25
Cyperaceae	*Morelotia gahniiformis* Gaudich.	end	sedge	42	**83**	63
Cyperaceae	*Oreobolus furcatus* H. Mann	end	sedge	2	0	1
Cyperaceae	*Uncinia brevicaulis* Thouars	ind	sedge	2	0	1
Cyperaceae	*Uncinia uncinata* (L. f.) Kük.	ind	sedge	2	4	3
Dennstaedtiaceae	*Pteridium aquilinum* subsp. *decompositum* (Gaudich) Lamoureux ex J. A. Thomson	end	fern	**70**	15	42
Dryopteridaceae	*Dryopteris hawaiiensis* (Hillebr.) W. J. Rob.	end	fern	0	2	1
Dryopteridaceae	*Dryopteris subbipinnata* W. H. Wagner & Hobdy	end	fern	0	2	1
Dryopteridaceae	*Dryopteris wallichiana* (Spreng.) Hyl.	ind	fern	7	17	12
Elaphoglossaceae	*Elaphoglossum paleaceum* (Hook. & Grev.) Sledge	ind	fern	5	9	7
Elaphoglossaceae	*Elaphoglossum wawrae* (Luerss.) C. Chr.	end	fern	0	7	3
Ericaceae	*Leptecophylla tameiameiae* (Cham. & Schltdl.) C. M. Weiller	ind	shrub	88	100	94
Ericaceae	*Vaccinium calycinum* Sm.	end	shrub	2	4	3
Ericaceae	*Vaccinium reticulatum* Sm.	end	shrub	84	89	87
Euphorbiaceae	*Euphorbia peplus* L.	non	herb	0	4	2
Fabaceae	*Lotus subbiflorus* Lag.	non	herb	2	0	1
Fabaceae	*Medicago lupulina* L.	non	herb	2	0	1
Fabaceae	*Sophora chrysophylla* (Salisb.) Seem.	end	shrub	**37**	11	24
Fabaceae	*Trifolium repens* L. var. *repens*	non	herb	2	0	1
Gentianaceae	*Centaurium erythraea* subsp. *erythraea* Raf.	non	herb	0	7	3
Geraniaceae	*Erodium cicutarium* (L.) L'Hér.	non	herb	2	0	1
Geraniaceae	*Geranium cuneatum* Hook.	end	shrub	19	33	26
Geraniaceae	*Geranium homeanum* Turcz.	non	herb	0	15	8
Geraniaceae	*Geranium multiflorum* A. Gray	end	shrub	2	0	1
Gleicheniaceae	*Dicranopteris linearis* (Burm. f.) Underw.	ind	fern	2	2	2
Iridaceae	*Sisyrinchium acre* H. Mann	end	herb	0	4	2
Juncaceae	*Juncus bufonius* L.	non	rush	2	0	1
Juncaceae	*Juncus effusus* L.	non	rush	0	4	2
Juncaceae	*Juncus planifolius* R. Br.	non	rush	0	2	1
Juncaceae	*Luzula hawaiiensis* Buchenau	end	rush	**67**	65	66
Lamiaceae	*Marrubium vulgare* L.	non	herb	0	7	3
Lamiaceae	*Prunella vulgaris* L.	non	herb	2	13	8
Liliaceae	*Dianella sandwicensis* Hook. & Arnott	ind	herb	5	0	2
Lycopodiaceae	*Lycopodiella cernua* (L.) Pic. Serm.	end	fern	2	4	3
Lycopodiaceae	*Lycopodium venustulum* Gaudich.	ind	fern	2	22	12
Lythraceae	*Lythrum maritimum* Kunth	non	shrub	21	0	10
Myoporaceae	*Myoporum sandwicense* A. Gray	ind	shrub	0	2	1
Myrsinaceae	*Myrsine lessertiana* A. DC.	end	tree	0	4	2
Myrtaceae	*Metrosideros polymorpha* Gaudich.	end	tree	2	**65**	35
Onagraceae	*Epilobium billardierianum* Ser. subsp. *cinereum* (A. Rich) P. H. Raven & Engelhorn	non	herb	9	0	4

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Onagraceae	*Oenothera stricta* Ledeb. Ex Link subsp. *stricta*	non	herb	23	0	11
Oxalidaceae	*Oxalis corniculata* L.	non	herb	2	9	6
Pinaceae	*Pinus patula* Schiede ex Schltdl. & Cham.	non	tree	2	0	1
Pinaceae	*Pinus radiata* D. Don	non	tree	2	0	1
Plantaginaceae	*Plantago lanceolata* L.	non	herb	19	0	9
Plantaginaceae	*Veronica peregrina* L. subsp. *xalapensis*	non	herb	0	4	2
Plantaginaceae	*Veronica plebeia* R. Br.	non	herb	0	7	3
Plantaginaceae	*Veronica serpyllifolia* L.	non	herb	0	7	3
Poaceae	*Agrostis sandwicensis* Hillebr.	end	grass	21	17	19
Poaceae	*Aira caryophyllea* L.	non	grass	19	0	9
Poaceae	*Andropogon virginicus* L.	non	grass	0	2	1
Poaceae	*Anthoxanthum odoratum* L.	non	grass	42	39	40
Poaceae	*Bromus tectorum* L.	non	grass	5	0	2
Poaceae	*Cenchrus clandestinus* Hochst. Ex Chiov.	non	grass	0	9	4
Poaceae	*Cenchrus polystachios* (L.) Morrone	non	grass	0	4	2
Poaceae	*Dactylis glomerata* L.	non	grass	7	0	3
Poaceae	*Deschampsia nubigena* Hillebr.	end	grass	86	67	76
Poaceae	*Ehrharta stipoides* Labill.	non	grass	0	13	7
Poaceae	*Eragrostis brownei* (Kunth) Nees ex Steud.	non	grass	19	20	19
Poaceae	*Festuca bromoides* L.	non	grass	0	9	4
Poaceae	*Festuca myuros* L.	non	grass	19	0	9
Poaceae	*Festuca rubra* L.	non	grass	**26**	0	12
Poaceae	*Gastridium ventricosum* (Gouan) Schinz & Thell.	non	grass	2	0	1
Poaceae	*Holcus lanatus* L.	non	grass	**84**	33	57
Poaceae	*Lachnagrostis filiformis* (G. Forst.) Trin.	ind	grass	0	7	3
Poaceae	*Melinis minutiflora* P. Beauv.	non	grass	0	4	2
Poaceae	*Panicum tenuifolium* Hook. & Arn.	end	grass	0	2	1
Poaceae	*Poa annua* L.	non	grass	0	2	1
Poaceae	*Poa pratensis* L.	non	grass	2	0	1
Poaceae	*Polypogon interruptus* Kunth	non	grass	0	2	1
Poaceae	*Rytidosperma penicillatum* (Labill.) Connor & Edgar	non	grass	9	0	4
Poaceae	*Rytidosperma pilosum* (R. Br.) Connor & Edgar	non	grass	14	2	8
Poaceae	*Schizachyrium condensatum* (Kunth) Nees	non	grass	0	13	7
Poaceae	*Sporobolus africanus* (Poir.) Robyns & Tournay	non	grass	5	15	10
Poaceae	*Trisetum glomeratum* (Kunth) Trin.	end	grass	**67**	50	58
Polygonaceae	*Rumex acetosella* L.	non	herb	56	9	31
Polypodiaceae	*Lepisorus thunbergianus* (Kaulf.) Ching	ind	fern	5	9	7
Polypodiaceae	*Polypodium pellucidum* Kaulf.	end	fern	30	28	29
Primulaceae	*Anagallis arvensis* L.	non	herb	26	0	12
Pteridaceae	*Pellaea ternifolia* (Cav.) Link	ind	fern	**67**	50	58
Pteridaceae	*Pityrogramma austroamericana* Domin	non	fern	2	0	1
Pteridaceae	*Pteris cretica* L.	ind	fern	0	2	1
Rosaceae	*Fragaria chiloensis* (L.) Duchesne subsp. *sandwicensis*	ind	herb	5	2	3
Rosaceae	*Fragaria vesca* L.	non	herb	0	7	3

Family	Species	BO	Life Form	Frequency (%)		
				HALE	HAVO	ALL
Rosaceae	*Osteomeles anthyllidifolia* (Sm.) Lindl.	ind	shrub	9	0	4
Rosaceae	*Rubus argutus* Link	non	shrub	2	0	1
Rosaceae	*Rubus hawaiensis* A. Gray	end	shrub	7	7	7
Rubiaceae	*Coprosma ernodeoides* A. Gray	end	shrub	47	89	69
Rubiaceae	*Coprosma montana* Hillebr.	end	shrub	**63**	39	51
Santalaceae	*Santalum haleakalae* Hillebr. var. *haleakalae*	end	tree	2	0	1
Sapindaceae	*Dodonaea viscosa* Jacq.	ind	shrub	35	54	45
Scrophulariaceae	*Verbascum thapsus* L.	non	herb	0	7	3
Thelypteridaceae	*Thelypteris globulifera* (Brack.) C. F. Reed	end	fern	0	4	2
Thymelaeaceae	*Wikstroemia phillyreifolia* A. Gray	end	shrub	0	2	1
Urticaceae	*Hesperocnide sandwicensis* (Wedd.) Wedd.	end	herb	0	2	1

Biogeographic origin (BO; end = endemic, ind = indigenous, non = non-native), life form, and frequency (% of 1,000 m^2 plots occupied). Bold frequency values identify significant indicator species of the site.

form and volcano was not significant ($F(1) = 0.95$, $p = 0.33$).

The Hawaiian subalpine zone is characterized by patchy vegetation, mostly <1 m tall, and substantial open space. Understory cover was lower on Mauna Loa (36%) than Haleakalā (54%) ($t = 3.00$, $df = 78.19$, $p < 0.01$). The substrate (top surface layer) encountered along pole-intercept transects had less litter on Mauna Loa (36%) than on Haleakalā (50%) reflecting the lower vegetation cover. Cinder and gravel were also less common on Mauna Loa than Haleakalā. In contrast, the exposed soil and larger rock categories were more common on Mauna Loa than Haleakalā.

Cluster analysis of the 89 sample plots, based on understory percent cover, resulted in two community groups and two outlier groups. Most of the plots (82) grouped together and are characterized as the "Subalpine Shrubland" community and the four other group-clustered plots are the "Subalpine Woodland" community (Figure 4A). The MRPP analysis revealed significant differences between the shrubland and woodland cluster groups (chance-corrected within-group agreement $A = 0.043$, $p < 0.001$), further supporting that they are distinct species assemblages. The outlier plots are

outliers owing to very sparse total vegetation (two plots, 8–9%) and high non-native species richness (>83%, one plot), including invasive grass *Bromus tectorum*. The NMS ordination showed no overlap of community cluster groups in species space (Figure 4A). The 2-D solution represented 80% of the variance in the data set (Axis 1 $r^2 = 0.53$, Axis 2 $r^2 = 0.27$) with relatively low final stress (14.62) and instability (<0.001) after 47 iterations. Owing to their relatively high abundance and frequency in the shrubland community, endemic *Vaccinium reticulatum* and indigenous *Leptecophylla tameiameiae* shrubs were strong indicator species there as compared to the woodland community (Figure 4B,C).

To examine differences in composition between volcanoes, the plots within the NMS ordination were grouped/color-coded by volcano (Figure 5A) as opposed to community cluster group (Figure 4A). MRPP analysis revealed significant differences between volcanoes (chance-corrected within-group agreement $A = 0.053$, $p < 0.001$) and multiple indicator species were identified for each volcano (Table 1). The strongest indicator species for Haleakalā included two non-native species, *Holcus lanatus* and *Hypochaeris radicata*, and an endemic subspecies of one fern, *Pteridium*
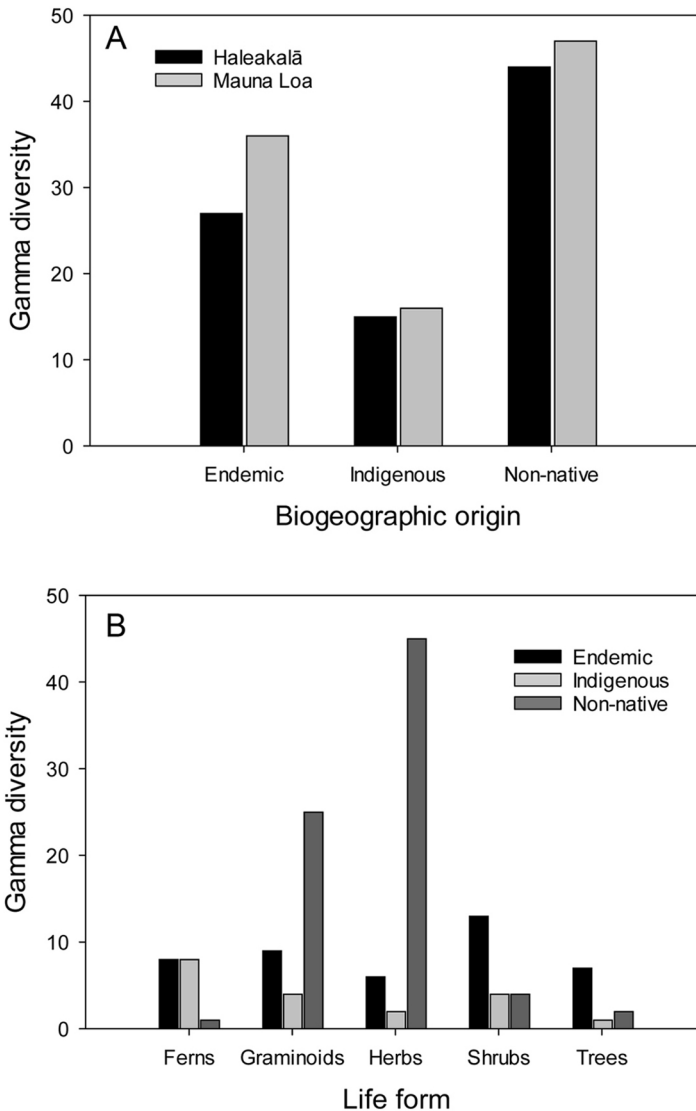
FIGURE 2. Gamma diversity of species' biogeographic origin by (*A*) volcano and (*B*) life form based on 89 1,000 m^2 sample plots. Non-native species, primarily herbs and grasses, constitute 55% of the 139 species encountered within the subalpine vegetation on Haleakalā and Mauna Loa.

aquilinum subsp. *decompositum* (Figure 5*B–D*). All three species were also present on Mauna Loa but were far less frequent and abundant there. In contrast, Haleakalā indicator species *Dubautia menziesii*, is a single-island endemic shrub (Figure 5*E*; Wagner et al. 1999).

Coprosma montana and *Sophora chrysophylla*, are endemic shrubs found on both volcanoes, but designated as Haleakalā indicators (Figure 5*F,G*) owing to higher abundance there (but see *Sophora chrysophylla* shrub and tree densities below). Only two species were identified
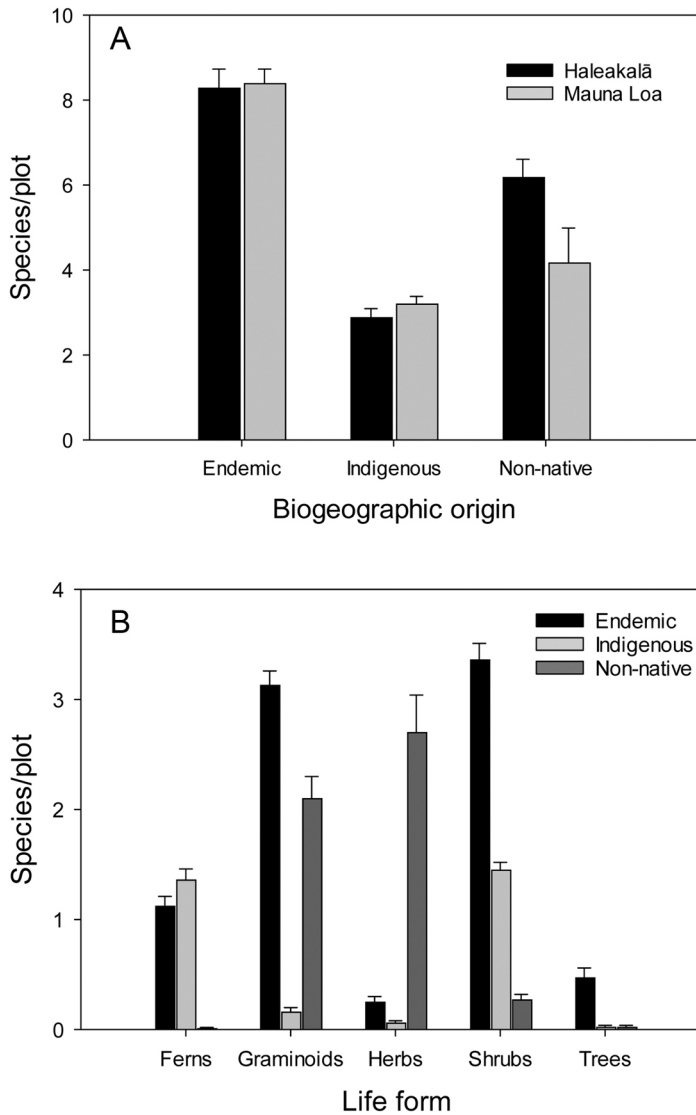
FIGURE 3. Mean (±SE) alpha diversity (species richness) per 1,000 m² plot (*A*) differs by the origin-volcano interaction. All five life forms (*B*) are represented in each biogeographic origin category, with endemic species being primarily graminoids and shrubs and non-native species primarily herbs and graminoids. The number of non-native species per plot (*C*) differs by life form and volcano.

as indicators of Mauna Loa plots: the endemic tree, *Metrosideros polymorpha*, and the endemic sedge, *Morelotia gahniiformis*, both of which were also present on Haleakalā (Figure 5H,I).

Plant Community Structure

Twelve of the 21 shrub species encountered in the subalpine vegetation (Table 1) were abundant enough to be captured within the
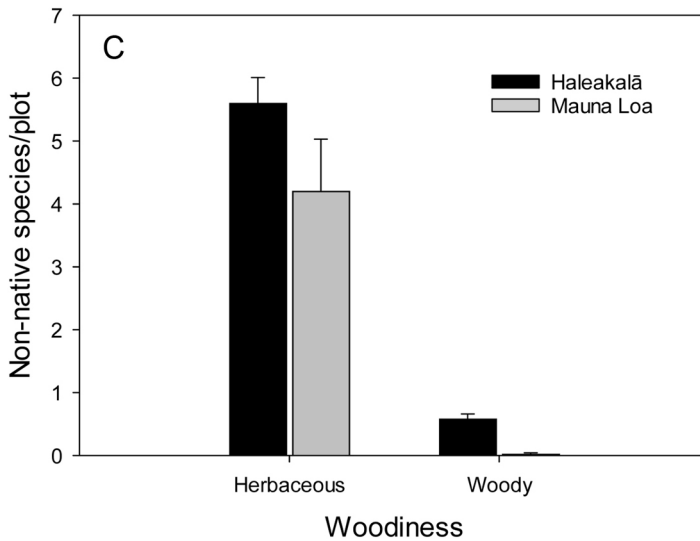
FIGURE 3. (*Continued*)

nested plot density belts and were all endemic (9 species) or indigenous (3 species) (Figure 6). Consistent with the understory cover data, *Vaccinium reticulatum* (>3,500/ha) and *Leptecophylla tameiameiae* (>2,430/ha) were dominant, did not differ in density between volcanoes, and had densities at least 3-fold greater than any other shrub species. For both species, most live individuals recorded were in the smallest size class. Standing dead *Leptecophylla tameiameiae* shrubs were 6-fold more abundant on Mauna Loa than on Haleakalā ($F(1) = 0.65, p = 0.01$) and accounted for nearly 15% of all *Leptecophylla tameiameiae* encountered on Mauna Loa.

Three shrub species' densities did differ between volcanoes (Figure 6). *Coprosma ernodeoides* ($t = -2.08$, $df = 86.89$, $p = 0.04$) and *Dodonaea viscosa* ($t = -3.22$, $df = 68.32$, $p = 0.002$) were more abundant on Mauna Loa than Haleakalā, whereas shrub-sized *Sophora chrysophylla* ($t = 2.88$, $df = 42.00$, $p = 0.006$) was more abundant on Haleakalā. Small *Sophora chrysophylla* individuals (shrubs and/or seedlings dbh < 1 cm) were documented only within plots on Haleakalā and had more live than dead shrubs with most individuals in the smaller size classes.

Some species can span multiple life forms. For instance, while no tree life form *Sophora chrysophylla* individuals (>1 cm dbh) were documented on Haleakalā, they were common in five plots on Mauna Loa. Four of these plots are in the Kahuku region of Hawai'i Volcanoes National Park (NW aspect) and clustered as the four woodland plots (Figure 4*A*). The other plot with *Sophora chrysophylla* trees is further east on the Mauna Loa Road (S aspect) and in species space of the ordination was the closest plot to the woodland cluster (Figure 4*A*).

The vast majority (95%) of *Metrosideros polymorpha* recorded in this study were on Mauna Loa, primarily in the shrubland–wet forest treeline ecotone above the Ka'ū Forest Reserve on Mauna Loa (S-SE aspect) or on the Mauna Loa Road (S aspect). The live and dead size class distribution of *Metrosideros polymorpha* trees within the 32 Mauna Loa plots where densities were recorded is generally a reverse-J shaped curve as expected for a regenerating forest.

The only trees recorded on Haleakalā (four *Metrosideros polymorpha*, seven small and 65 large *Sadleria cyatheoides* tree ferns) were in the same plot located within the shrubland–wet forest treeline ecotone (Ainsworth 2021) of upper Kīpahulu Valley (E aspect).
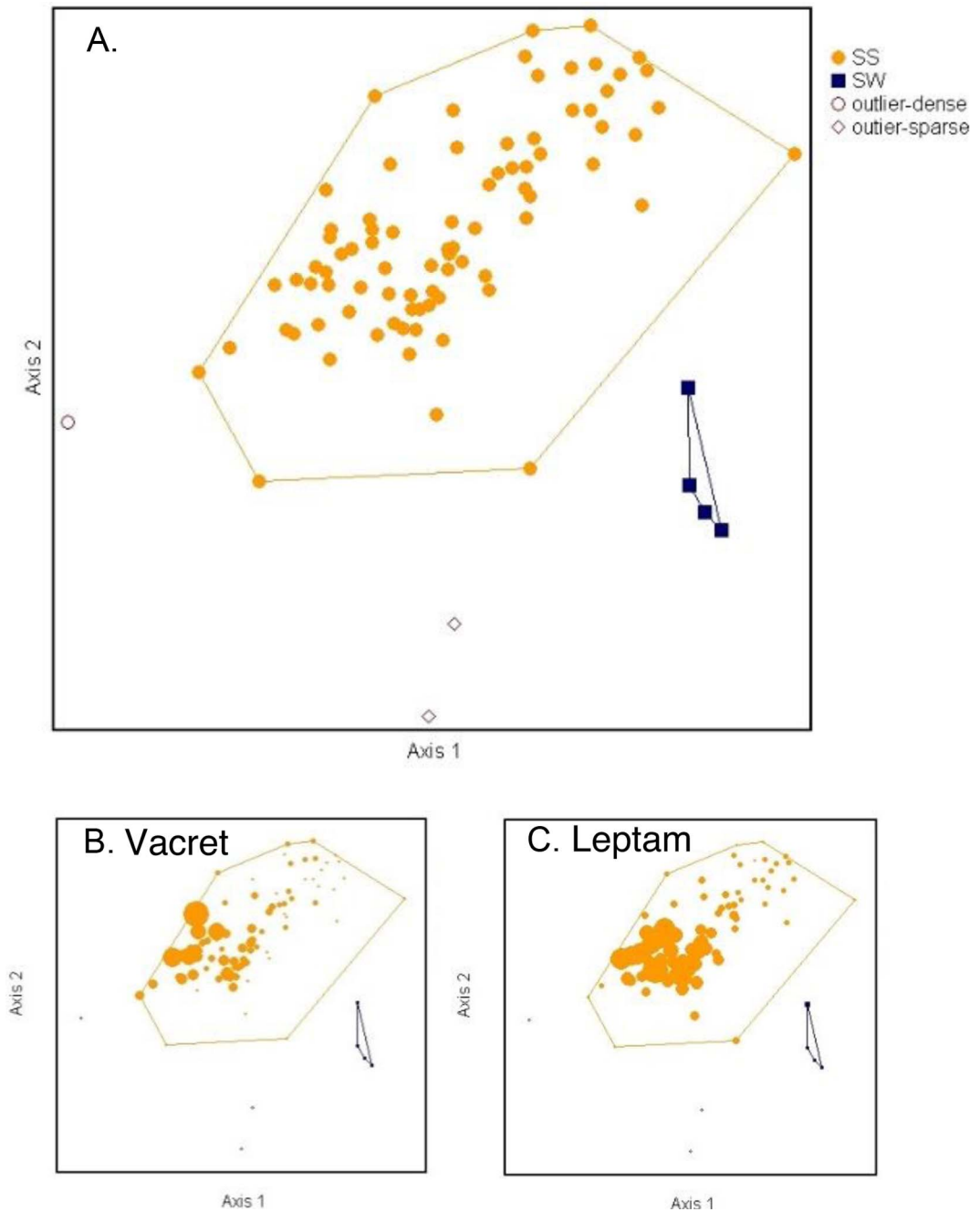
FIGURE 4. Diagrams of NMS ordination analysis, showing the positions of separated cluster community groups (SS = subalpine shrubland, SW = subalpine woodland) and outlier plots (*A*). Two strong SS indicator species *Vaccinium reticulatum* (*B*) and *Leptecophylla tameiameiae* (*C*) are overlaid on ordination diagrams with larger plot symbols representing higher species abundance.
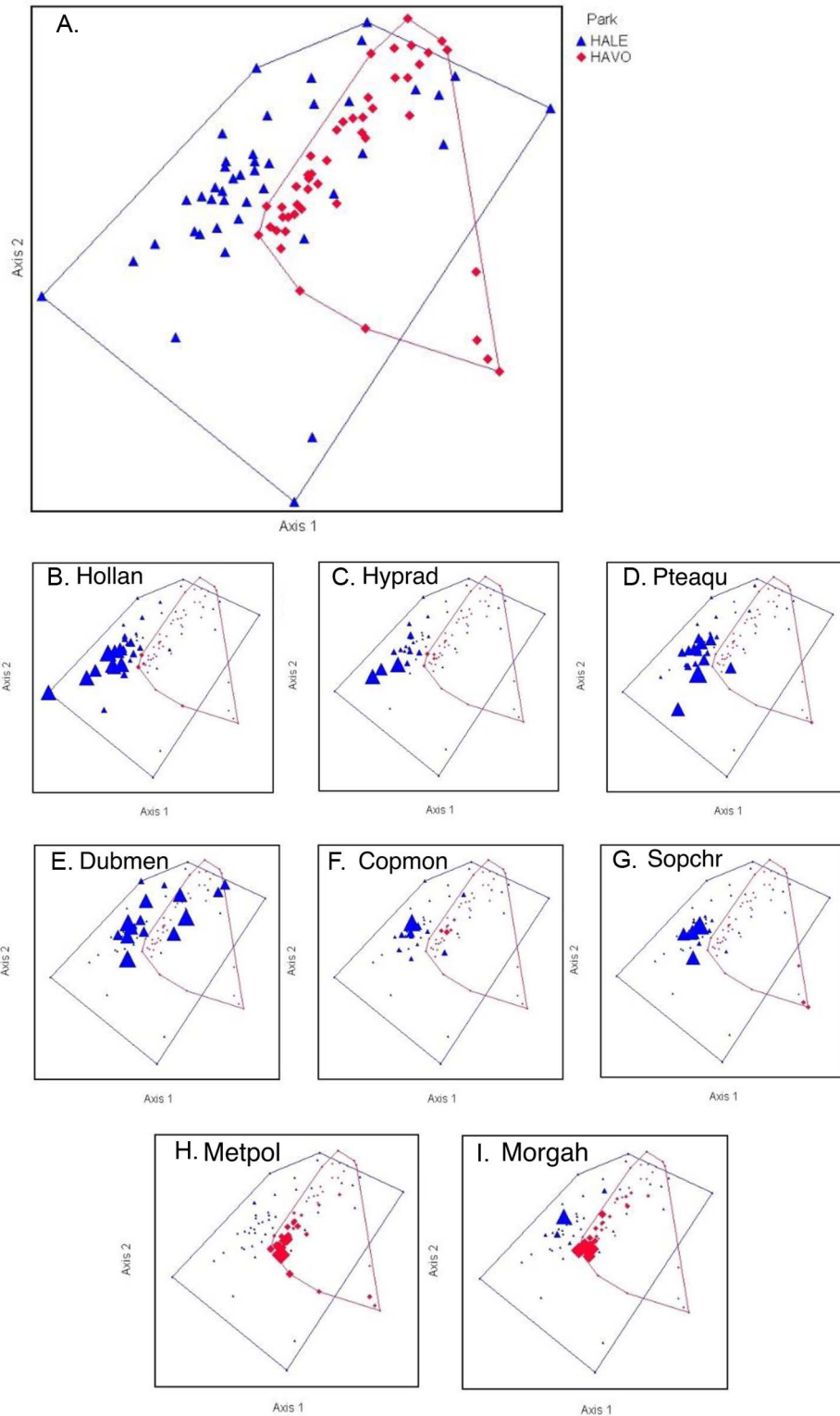
FIGURE 5. Diagrams of NMS ordination analysis, showing the overlap in composition of plots (*A*) on Haleakalā (HALE, blue triangles) and Mauna Loa (HAVO, red squares) particularly in the SS community (see Figure 4). Haleakalā indicator species include non-native *Holcus lanatus* (*B*) and *Hypochaeris radicata* (*C*) and endemic subspecies *Pteridium Aquilinum* subsp. *decompositum* (*D*), *Dubautia menziesii* (*E*), *Coprosma montana* (*F*), and *Sophora chrysophylla* (*G*) (see Table 1 for full list of 10 Haleakalā indicator species). Two endemic species were identified as indicators of Mauna Loa, *Metrosideros polymorpha* (*H*) and *Morelotia gahniiformis* (*I*). To increase interpretability the ordination was rotated to maximize the correlation of volcano identity with Axis 1.
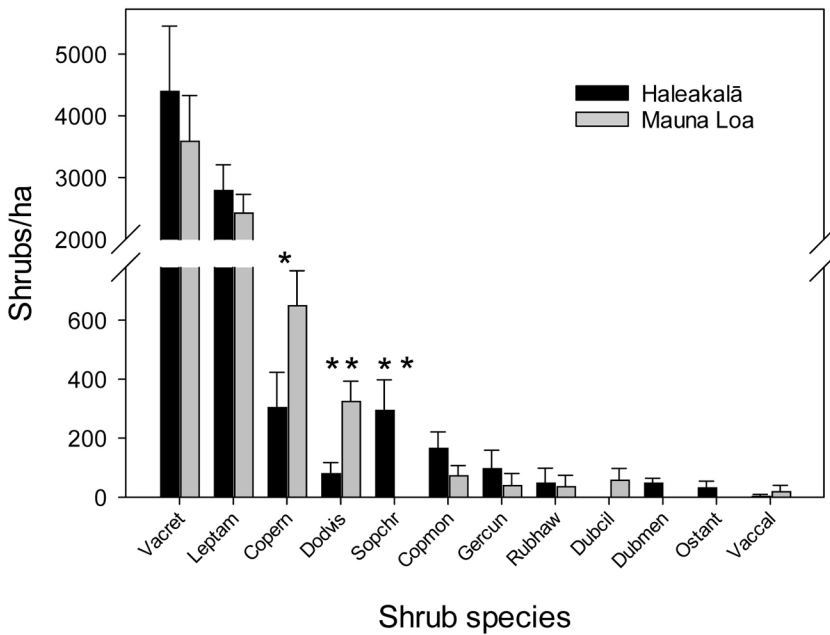
FIGURE 6. Mean density (individuals/ha ± SE) of shrubs in the subalpine zone. Two native species, *Vaccinium reticulatum* and *Leptecophylla tameiameiae*, were dominant on both volcanoes and did not significantly differ in density. Three species' densities differed by volcano. *Coprosma ernodeoides* and *Dodonaea viscosa* were more abundant on Mauna Loa, whereas *Sophora chrysophylla*, in shrub form, was more abundant on Haleakalā. Asterisks indicate significant differences between volcanoes (*<0.05, **<0.01). Full species names are available in Table 1 with the first three letters of the code the first three letters of the *Genus* and the second three letters of the code the first three letters of the species.

DISCUSSION

Plant Community Structure

The primary subalpine community type on both volcanoes, the subalpine shrubland, had community structures largely consistent with the understory data, with endemic *Vaccinium reticulatum* (>3,500/ha) and indigenous *Leptecophylla tameiameiae* (>2,430/ha) shrubs dominating. Despite being dominated by similar native shrubs and there being few non-native shrubs or trees, there were significant differences in community structure between volcanoes. Specifically, on Mauna Loa we found (1) an additional subalpine community type, the subalpine woodland composed of *Sophora chrysophylla* canopy trees, (2) significantly more *Metrosideros polymorpha* trees, and (3) high *Leptecophylla tameiameiae* shrub mortality.

The subalpine woodland with *Sophora chrysophylla* trees common in the overstory on Mauna Loa (Figure 4*A*) is consistent with the woodland community (Ainsworth 2021) and the description of the "Subalpine Dry Forest–*Sophora* Forest" in Gagné and Cuddihy (1990). While this community type is known to occur at Haleakalā, it is more common on Hawai'i Island—particularly on Mauna Kea. In this very dry community type, *Sophora chrysophylla* trees have been identified as critical facilitators for understory species, which benefit from their capture of fog drip (Gagné and Cuddihy 1990). This high elevation dry forest type has been threatened across the islands for decades by invasive ungulates (Gagné and Cuddihy 1990). Consistent with the impact of ungulates (Hart et al. 2020), we found in this study very little regeneration of *Sophora chrysophylla* under the

canopy, presumably owing to invasive mouflon, sheep, and goats within this limited woodland, and very high non-native herbaceous species richness (Simon et al. 2016).

The *Metrosideros polymorpha* subalpine forest (Gagné and Cuddihy 1990), unlike the *Sophora chrysophylla* forest, is not known from Maui Island, and primarily occurs on the upper slopes of Mauna Loa and Hualālai. Feral goats, sheep, and mouflon have impacted these forests; however, large portions of these subalpine forests have been and are currently being fenced to exclude feral ungulates. Most of our sample plots for this type fell within the treeline ecotone zone above the Kaʻū Forest Reserve, where, encouragingly, *Metrosideros polymorpha* appears to be regenerating with a clear reverse j-shaped demographic curve.

In the shrub layer, the proportion of the *Leptecophylla tameiameiae* population that was dead was greater on Mauna Loa than Haleakalā, which may be an indicator of greater drought stress. Following a strong drought event in 1992, high mortality rates were documented above 2,000 m on Mauna Loa for smaller size classes of *Leptecophylla tameiameiae*, *Vaccinium reticulatum*, and *Coprosma ernodeoides* shrubs (Lohse et al. 1995). Direct comparisons were made of six shrub species' water relations at Haleakalā, and *Leptecophylla tameiameiae* had the lowest mean ratio of turgid to dry weight, and was highlighted as the strongest example of drought tolerance, whereas all other species had mechanisms to enable drought avoidance (Meinzer et al. 1994). Similarly, in a recent study, Krushelnycky et al. (2020) found extremely low transpiration rates of *Leptecophylla tameiameiae* in comparison to *Dubautia menziesii* and *Argyroxiphium sandwicense*. The possession of a highly specialized drought tolerant hydraulic strategy relative to other sympatric shrub species may explain the higher mortality rate of *Leptecophylla tameiameiae* under extreme water stress conditions. Interestingly, unlike Lohse and colleagues (1995) we did not find differences in *Leptecophylla tameiameiae* mortality among size classes, nor did we find comparable mortality of *Vaccinium reticulatum* or *Coprosma*

ernodeoides. The lack of consistent drought response across these species could reflect the arrival of a new pathogen or pest specific to *Leptecophylla tameiameiae*. However, there have recently (2021) been several additional drought-related mortality events on Haleakalā that involved both *Leptecophylla tameiameiae* and *Vaccinium reticulatum* (Krushelnycky pers. com). Shrub browning (presumed mortality) was noticeably higher on younger substrates (i.e., recent flows) producing an obvious mosaic pattern of differential mortality on adjacent substrates for multiple species. It is unlikely that a pathogen alone could be responsible for this multi-species mosaic mortality pattern. A better understanding of the current and future effects of climatic stress on these critical matrix species is urgently needed.

To what extent *Leptecophylla tameiameiae* facilitates additional native species' establishment and succession into these extreme dry mountain environments has been debated. This species has been called a critical component needed to promote soil development (Mueller-Dombois 1967), highlighted for a lack of interdependence with other species (Fosberg 1959) and even considered as having the most individualistic distribution of all species encountered across Hawaiian mountain environments (Kitayama and Mueller-Dombois 1992). More research is needed to understand how sensitive this matrix species is to shifting climatic conditions in Hawaiʻi, but regardless of how interconnected it may be, its sheer dominant density within these communities suggests that if climate change causes its decline, significant changes in community structure and composition would result.

Diversity

Our summarized data (Figures 2*A* and 3*A*) did not support the hypothesis that the subalpine zone on Haleakalā had more native (endemic and indigenous) species than Mauna Loa. In fact, native gamma diversity on Mauna Loa was 24% higher than on Haleakalā. However, this finding is likely a spurious artifact of the sample design and an example of the potential

risk of using existing data to explore hypotheses as opposed to designing the field study around a priori hypotheses. More native species have been documented within the subalpine of Haleakalā than the subalpine of Mauna Loa (Wagner et al. 1999). In our data, five of the nine native plant species found only on Mauna Loa (Table 1) are obligate wet forest species that were observed in sample plots within the shrubland–wet forest treeline ecotone above the Kaʻū Forest Reserve (see Ainsworth 2021). Conversely, only one plot on Haleakalā was in this treeline ecotone type at the top of the Kīpahulu Biological Reserve and therefore fewer wet forest species were captured in the diversity measures on Haleakalā. Despite the higher gamma diversity on Mauna Loa, no difference was found in endemic or indigenous species richness per plot between volcanoes and these values were comparable to other high elevation (>2,000 m) sites in Hawaiʻi (Kitayama and Mueller-Dombois 1992).

When we exclude the wet forest species (e.g., most ferns and trees) from the Mauna Loa treeline ecotone plots, the resultant diversity patterns for this study are more in line with our hypothesis. Seven subalpine species were found only on Haleakalā. Five of these species are Maui-island endemics, including the threatened iconic herb *Argyroxiphium sandwicense* subsp. *macrocephalum*, three large shrubs *Dubautia menziesii*, *Dubautia waianapanapaensis*, the endangered *Geranium multiflorum*, and the tree *Santalum haleakalae* (Wagner et al. 1999). The endemic sedge, *Oreobolus furcatus*, is found on Maui and the older islands but not known from Hawaiʻi island (Wagner et al. 1999). The final subalpine species only found on Haleakalā in our data (*Sadleria cyatheoides*) is a co-dominant with *Vaccinium calycinum* of the subalpine mesic shrubland community occurring between 1,950 and 2,300 m elevation only on the windward slopes of east Maui (Gagné and Cuddihy 1990). In comparison, only three Hawaiʻi-island endemic species were encountered in this study, endangered *Argyroxiphium kauense*—a congener of *Argyroxiphium sandwicense* on Maui, *Dubautia ciliolata*—a shrub congener of *Dubautia menziesii* on Maui, and *Hesperocnide sandwicensis*—a rare endemic herb

(Wagner et al. 1999). The other two native species encountered only on Mauna Loa were the endemic herb *Sisyrinchium acre* and endemic grass *Panicum tenuifolium*, both of which are also known from Haleakalā.

Accurate consistent identification of subspecies would likely have affected the results of this study, specifically, we would have detected bigger differences between volcanoes because of single-mountain and/or single-island endemics. For example, some endemic species in this study were tallied as "shared" between volcanoes but differ at the subspecies level. *Geranium cuneatum* was found on both volcanoes, but only subspecies *tridens* is known from Maui whereas the Mauna Loa subspecies was likely either *hypoleucum* or *hololeucum*. Similarly, *Tetramolopium humile* was considered shared when the Haleakalā individuals were likely subspecies *haleakalae* and the Mauna Loa individuals were subspecies *humile*. *Polypodium pellucidum* and *Luzula hawaiiensis* were inconsistently identified at the subspecies level and have a number of possible subspecies for each island (Wagner et al. 1999, Palmer 2003).

Non-Native Species

More non-native species were encountered than endemic or indigenous species on both volcanoes, with no measurable difference in gamma diversity between volcanoes (Figure 2A). However, when we isolated non-native alpha richness, we found more herbaceous and woody species per plot on Haleakalā than Mauna Loa (Figure 3C). Similarly, a model of non-native species richness across multiple Pacific islands found island identity more important in explaining variance than elevation, precipitation, or native species richness (Ibanez et al. 2019). Although younger sites, such as Mauna Loa, may have lower species diversity and theoretically more open niche opportunities for invaders (Kueffer et al. 2010), in Hawaiʻi, soil nutrients have been documented as limiting invasions by non-native species on younger lava flows (Turner and Vitousek 1987, Vitousek 2004, Ibanez et al. 2019). Compared to Mauna Loa, Haleakalā subalpine sites had higher total vegetation cover, as found in a previous study

for older (>3,000 yr vs. 135–1,300 yr) lava flows on Mauna Loa (Karpa and Vitousek 1994). Greater vegetation cover supports the idea that soils are less limiting on older (Haleakalā) substrates than on younger ones (Mauna Loa); however, it is unlikely in the subalpine (even on Haleakalā) that competition with natives is preventing non-native species invasions, because the total above ground cover remained relatively low (<70%). It is important to note that this study did not measure or account for below ground competition in this water-limited environment. Additionally, in high elevation sites, climatic constraints may filter species assembly more than competition (Michalet et al. 2014). Measures of water exchange (i.e., actual evapotranspiration) have been found to be better predictors of non-native richness than temperature (Jakobs et al. 2010) and on Haleakalā the subalpine zone had greater moisture availability than this zone on Mauna Loa (Ainsworth 2021).

While many non-native species have been documented in these high elevation sites, population growth (range expansion) is likely still occurring. Other authors have suggested that high elevation climatic conditions are more limiting to the spread of non-native species (abundance or coverage) than to richness (Ibanez et al. 2019). Alternatively, low cover of non-native species despite high richness may be an artifact of the time since invasion required for range expansion, population growth, or both. Two of the strongest indicator species of the Haleakalā subalpine plots were invasive *Holcus lanatus* grass and *Hypochaeris radicata* herbs, both of which have occurred on Haleakalā for decades. These species were recorded in Kīpahulu in 1967 (Lamoureux 1968) and highlighted as threats to native species diversity in the 1980s (Anderson et al. 1992), and *Hypochaeris radicata* was the only non-native recorded above 2,700 m in the early 1990s (Kitayama and Mueller-Dombois 1992). Both invaders were assigned high weed risk assessment scores (i.e., more invasive potential; Daehler et al. 2004), were the most frequently encountered non-natives along 1,000 m subalpine transects in 2012 (51% and 73%, respectively) (Gross et al. 2017), and were the highest elevation (1,100 m to > 2,000 m) non-native

species in a recent Kīpahulu study (Ibanez et al. 2020). Despite high frequency for these species on Haleakalā, cover remains low (< 5%) (Gross et al. 2017). On Mauna Loa, both species are also present in the subalpine, with *Hypochaeris radicata* presence on Mauna Loa dating back to the 1950s (Fosberg 1959) with sightings above 3,050 m in the 1960s (Mueller-Dombois 1967). Both species have expanded upward on Mauna Loa since the 1970s (Koide et al. 2017) but were still found in this and other recent studies on Mauna Loa at lower frequencies (10% and 39%, respectively) and cover (<1%) than on Haleakalā (Simon et al. 2016).

It is important to determine what is currently limiting invasive species establishment and spread within the Hawaiian subalpine zone, especially considering that climate change models are predicting increases in invasion in these areas (Vorsino et al. 2014). Upward movement of non-native species along roadways on Mauna Loa has been suggested to be climate change related (Juvik et al. 2011, Angelo and Daehler 2013, Koide at al. 2017). A recent review of Hawaiian forests emphasized that expecting upslope movement of native and non-native plant species with warming alone is naïve in these complex systems having trade wind inversions (Barton et al. 2021). With increasing globalization, invasive plant species adapted to similar climatic conditions elsewhere may arrive via multiple pathways of introduction, therefore climate alone is unlikely to predict future invasions (Alexander et al. 2011). The subalpine shrubland on Haleakalā experiences less drought stress than the equivalent zone on Mauna Loa (Ainsworth 2021), has greater visitor access because the main visitor infrastructure is located within the subalpine zone (Krushelnycky et al. 2019), and has greater human population density and economic activity at the island scale (Jakobs et al. 2010), all of which likely result in greater invasive species propagule pressure (Lonsdale 1999).

Conclusion

The Hawaiian subalpine zone varies among islands, volcanoes, and aspects, yet remains largely native dominated despite increasing threats from climate change, non-native

species, and wildfire. Within these National Parks, the subalpine shrubland is dominated by native species with recruiting populations and intact island endemism. The subalpine woodlands (*Sophora chrysophylla* and *Metrosideros polymorpha*) are less common than the shrublands and have suffered greater impacts from feral ungulates. Critically, these sparsely vegetated, environmentally extreme communities may represent the last habitat for many of Hawai'i's disappearing endemic plants, insects, and birds. To what extent climatic conditions will continue to change in these high elevation sites is unknown; however, we can predict loss of native species and potentially of community types if the current threats of invasive ungulates, expanding populations of non-native plants, continuous new species introductions, and anthropogenic wildfires are not actively managed. We recommend continued monitoring of community composition and climate in this sensitive indicator zone, additional in situ physiological studies for the few native matrix subalpine plant species, stricter non-native species biosecurity and sanitation protocols, wildfire prevention and studies on species resistance to fire, and improved documentation of the effects of feral ungulates at high elevation including ongoing removal.

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