NAVIGATING NOVEL ECOSYSTEMS: FERAL PIGS AND THE TRANSFORMATION OF HAWAIIAN FORESTS

By

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ABSTRACT

We live in an era of global change. Human activities have significantly reshaped ecosystems, driving biodiversity loss and altering fundamental ecological processes. Invasive species are a major component of anthropogenic change, altering the composition, structure, and function of ecosystems worldwide. The impacts of invasion are particularly severe on islands due to their geographic isolation, small size, and high endemism. Ungulates, such as feral pigs (*Sus scrofa*), are among the most destructive invaders globally, and have been found to disproportionately impact island systems. Hawai‘i Island serves as an ideal model system to investigate the ecological mechanisms driving invasion and the effects of non-native plant encroachment. This dissertation investigates the interaction of feral pig activity and non-native plant invasions within Kohala, in an invaded but relatively intact, montane forest-peatland complex at risk of further encroachment. Across four chapters, I explore how feral pigs drive ecosystem change through direct disturbance and trophic interactions. Chapter 1 uses field surveys to map understory vegetation composition and link feral pig activity and habitat characteristics to patterns of invasion. Chapter 2 investigates how feral pig disturbance facilitates non-native plant establishment, leveraging plant functional traits to understand species’ responses. Chapter 3 explores functional and phylogenetic diversity through the lens of niche theory to assess community assembly processes. Chapter 4 reconstructs feral pig trophic dynamics using stable isotopes to understand their dietary ecology and functional role in their introduced range. Together, these studies advance our understanding of the mechanisms behind the spread of non-native species, the interactions among ungulates and invasive plants, and the unique challenges to island biota in the face of global change.

INTRODUCTION

Human activities have profoundly transformed ecosystems worldwide, ushering in an era of unprecedented global change (Steffen et al., 2007, 2011). The impacts of human action extend to even the most remote regions, altering fundamental ecological processes that regulate ecosystem structure and function (Ellis, 2011; Vitousek et al., 1996). Land-use change, climate change, and biotic exchange continue to intensify, resulting in extinctions, rapid shifts in species distributions, and changes to trophic dynamics (Hobbs et al., 2006; Rockström et al., 2009). These changes pose significant challenges to conserving biodiversity and promoting ecosystem resilience (Zalasiewicz et al., 2008), which are crucial to maintaining ecosystem services (Oliver et al., 2015). Understanding how ecosystems and their governing processes shift in response to human activity and global change is critical to preserving biodiversity.

Invasive species represent one of the most persistent and pervasive threats facing ecosystems worldwide (Pyšek & Richardson, 2010). Globalization has accelerated the introduction and spread of non-native species across biogeographical barriers (Hulme, 2009). Displacement of native species due to competition, predation, herbivory, and pathogen transmission by invasive species is a significant driver of ecosystem change (Walker & Smith, 1997). Invasive species are often found to possess traits differing from those of the native community where they invade, sometimes conferring a competitive advantage in novel environments (Simberloff et al., 2013). Release from natural enemies in their native range frequently provides an advantage over native competitors in their introduced range (Keane & Crawley, 2002; Liu & Stiling, 2006). Invasion accelerates the process of biotic homogenization, promoting the loss of unique species assemblages and a shift toward dominance by generalist and invasive taxa sharing similar functional strategies, often reducing diversity and resulting in a depauperate ecological community (Olden et al., 2004). Furthermore, invasive species can alter disturbance regimes, nutrient cycling, and other processes, leading to long-term changes in ecosystem dynamics (Vitousek et al., 1987; Walker & Smith, 1997).

Ungulates are among the most influential invasive species globally, exerting profound effects on ecosystems through grazing, trampling, soil disturbance, and nutrient redistribution (Côté et al., 2004; Siemann et al., 2009). Invasive ungulates frequently reach densities far exceeding those of their native counterparts, often due to a lack of sufficient top-down pressure (Hess & Jacobi, 2011; Scowcroft & Giffin, 1983). Heightened grazing and browsing pressure from large population sizes frequently results in significant vegetation loss, particularly among native plant species without adaptations to ungulate herbivory (Mack & D'Antonio, 1998). Furthermore, the effects of introduced ungulates can extend to other ecosystem processes, with invasion often resulting in soil compaction, heightened erosion, and the introduction of novel disturbances in the form of digging and trampling behavior (Kotanen, 1995; Krull et al., 2013). These disturbances drive shifts in plant community composition, often facilitating the establishment of invasive plant species, further influencing ecosystem dynamics and reducing native biodiversity (Cushman et al., 2004; Relva et al., 2010).

Feral pigs (*Sus scrofa*) are among the most widespread and ecologically disruptive invasive ungulates, with global impacts rivaled only by humans (*Homo sapiens*) in extent and destructive capacity (Barrios-Garcia & Ballari, 2012). Originating from swine domesticated from several subspecies of wild boar in Europe and Asia (Giuffra et al., 2000), feral pigs have been introduced to and become established on every major continent except Antarctica (Wehr, 2021). Feral pig populations are characterized by high reproductive rates, with female pigs often reaching reproductive maturity within one year and producing litters of 5-6 offspring on average (Wehr et al., 2018). In the tropics where non-native pigs can breed year-round, females are commonly found to rear two litters per year, with a high percentage (between 20% - 40%) of females becoming pregnant each year (Diong, 1982). Dietary generalism and behavioral plasticity enable pigs to thrive in diverse environments, exhibiting remarkable trophic flexibility across their introduced range (Ballari & Barrios-García, 2014). Their rooting and wallowing behavior disturbs soil structure, promotes erosion, and disrupts seedling establishment (Murphy et al., 2014; Nogueira-Filho et al., 2009). Additionally, feral pigs facilitate the spread of invasive plants by dispersing seeds via endo- and epizoochory, and by creating disturbed habitats conducive to colonization by ruderal, fast-growing species (Baltzinger et al., 2019; Tierney & Cushman, 2006). Consequently, invasion by feral pigs is among the greatest drivers of ecosystem change and non-native plant invasion worldwide (Risch et al., 2021).

Islands are disproportionately vulnerable to the impacts of biological invasion due to their biogeographic isolation, small size, and high levels of endemism (Fernández-Palacios et al., 2021; Kueffer et al., 2010). Island plants are thought to lack key defenses due to evolution under relatively benign conditions (i.e. lacking substantial herbivory or competition), making them particularly susceptible to invasion (Bowen & Van Vuren, 1997; Simberloff, 1995). Moreover, the small size of islands compared to their continental counterparts amplifies the impacts of habitat modification and species loss following invasion, with cascading effects on ecological networks and functional stability (Whittaker & Fernandez-Palacios, 2007). Ungulates, lacking natural predators and introducing a suite of novel disruptive behaviors, are especially problematic on island systems where floras often evolved in the absence of large herbivores (Loope et al., 1988; Nogueira-Filho et al., 2009). Islands, being on the front lines of biological invasion, provide valuable model systems for studying invasion ecology. Their low species richness relative to continental systems makes quantifying community dynamics more tractable, enabling focused investigations into the mechanisms facilitating invasion and the effects of native species displacement on ecosystem processes (Vitousek, 2002). Furthermore, islands offer insights into how community assembly processes shift in response to disruption by novel drivers, providing lessons applicable to invasion impacts on a global scale.

This dissertation explores the impacts of non-native species invasions on Hawaiʻi Island, a well-studied model system for understanding ecosystem processes such as soil development (Crews et al., 1995; Vitousek & Farrington, 1997), successional dynamics (Vitousek et al., 2009; Zimmerman et al., 2008), nutrient cycling (Austin, 2002; Vitousek et al., 1995), paleoclimate history (Hotchkiss et al., 2000; Barrett et al., 2021), and biological invasion (Ainsworth & Kauffman, 2010; Loope et al., 1992). The central focus of this investigation is the interaction of invasive ungulate activity and non-native plant invasion. Feral pigs, the most destructive ungulate on Hawaiʻi Island (Diong, 1982; Nogueira-Filho et al., 2009), serve as the focal driver of ecosystem change in this investigation, with an emphasis on their impacts on community dynamics and the factors influencing their behavior in introduced ranges. Here I present a series of studies conducted in a montane forest on Kohala Mountain. The forest understory is undergoing non-native species encroachment yet currently retains a relatively intact native plant assemblage that is at risk of further displacement. I also explore feral pig trophic dynamics across the island to identify the factors modulating the impacts of pigs in Hawaiʻi.

This dissertation is structured into four chapters. In Chapter 1, I conduct a comprehensive field survey to characterize understory vegetation and estimate pig population density across Kohala. Using these data, I investigate the environmental drivers of compositional change in understory communities and identify key factors promoting non-native species invasion. Chapter 2 focuses on the mechanisms of non-native species facilitation by feral pig soil disturbance, employing plant functional traits to characterize ecological strategies and understand species' responses to disturbance. In Chapter 3, I analyze patterns of functional and phylogenetic diversity across Kohala, applying niche theory to explore how abiotic and biotic drivers shape assembly processes. Finally, Chapter 4 presents a reconstruction of feral pig trophic dynamics using stable isotopes to provide insights into habitat constraints on the dietary ecology of pigs on Hawaiʻi Island.

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CHAPTER 1

Invasive species and feral ungulate disturbance: lessons from a Hawaiian montane forest understory

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Abstract

Biological invasion poses a significant threat to biodiversity, particularly for island ecosystems with high rates of endemism. While lowland forests in Hawaiʻi have been largely replaced by non-native vegetation, many high-elevation montane forests remain in earlier stages of invasion, primarily via their understories. Invasive ungulates may accelerate this transition through soil disturbance, altering establishment conditions and facilitating the spread of non-native plants. Here we investigated understory community composition and invasion dynamics within the relatively intact Puʻu O Umi Natural Area Reserve on Kohala mountain, Hawaiʻi. We identified six distinct community assemblages that varied in their degree of non-native dominance. Non-native species co-occurred along a single compositional axis using non-metric multidimensional scaling (NMDS), with evidence suggesting soil disturbance by feral pigs was a critical driver of non-native establishment. Largely intact, native-dominated communities were compositionally distinct from those either dominated by non-native vegetation or in the process of encroachment. Overstory canopy coverage and nurse log substrate drove differences among native assemblages, suggesting native communities are largely structured by local microhabitat factors influencing light and water supply. Variation in *Entolasia marginata* abundance occurred largely independently from other exotic species, and likely captures an incipient invasion from adjacent pasturelands. Our findings highlight the importance of feral pig control and targeted interventions to conserve Hawaiian montane forest understories, focusing on preventing transitions to non-native dominance.

Keywords: invasive species, community dynamics, understory vegetation, Hawaii, feral pigs, disturbance

Introduction

In an age of ecological upheaval and rapid change, biological invasions are among the most pressing threats to biodiversity worldwide (McGeoch et al., 2010; Pyšek et al., 2012). Increased trade, transportation, and human land use have resulted in record rates of biological exchange among regions, resulting in significant biodiversity losses (Hulme, 2009; Seebens et al., 2017). Non-native invasive species frequently alter ecosystem composition, structure, and function (Pyšek & Richardson, 2010), often by displacing native species through direct (e.g. competition, predation) and indirect (e.g. disrupting species interactions, altering disturbance regimes) mechanisms (Gaertner et al., 2014). Local extinctions, loss of specialized interactions, and ongoing changes to climate and land use have resulted in cascading impacts on ecosystem resilience (Scheffer et al., 2001; Spake et al., 2022). The impacts of invasive species are disproportionately felt in systems characterized by high endemism, where species losses have an outsized effect on ecosystem function (Walsh et al., 2012).

Biological invasion and the associated losses of native biodiversity are particularly pronounced in island systems (Caujapé-Castells et al., 2010; Fernández-Palacios et al., 2021), which cover a small proportion of global land area but hold a disproportionate extent of global biodiversity (Kreft et al., 2008). Isolated island floras largely originate from the diversification of lineages established by long-distance dispersal and harbor substantial endemism (Price & Wagner, 2018). Islands are thought to be at heightened risk of invasion by non-native plants due to several factors (D’Antonio & Dudley, 1995). First, remote geographic distances from continental sources have led to comparatively low species richness and depauperate floras, which may enable higher invasion success due to reduced niche overlap of invaders with residents

(Barton & Fortunel, 2023; Henn et al., 2019). Second, evolution under reduced antagonistic interactions (i.e. competition, herbivory) may have led to convergence toward adaptations promoting slow growth and weak defenses (Burns, 2019). Third, invasive plants may possess faster growth rates, fewer enemies in their introduced range, and rare or novel adaptations compared to the island flora (e.g. nitrogen fixation), which can enable rapid establishment and population growth (Van Kleunen et al., 2010; Vitousek & Walker, 1989). Consequently, islands have become flashpoints for biological invasion, resulting in significant biodiversity losses (Kueffer et al., 2010).

The Hawaiian Islands harbor a vast array of endemic species (Werden et al., 2020). Extreme isolation and dispersal limitation, together with steep environmental gradients, have resulted in spectacular radiations and unique assemblages of plants and animals (Price & Wagner, 2018). Species richness is low (Barton et al., 2021); for example, forest overstories across a wide range of climate conditions are dominated by a single genus, *Metrosideros* (ʻōhiʻa; Seeley et al., 2023). Like other tropical and subtropical systems, a substantial portion of biodiversity in Hawaiʻi's forests is held in the understory (Gentry et al., 1987). Ferns are abundant and widespread across the archipelago (Palmer, 2002), often dominating in mesic and wet forest understories (Ranker, 2016). Forest canopies in Hawai'i are relatively open compared to other tropical systems, leading to comparatively higher light levels in the understory with significant heterogeneity (Funk & McDaniel, 2010; Inman-Narahari et al., 2016). Understory light conditions influence distributional patterns among species through performance trade-offs and adaptation to different light regimes (Givnish & Montgomery, 2014; Inman-Narahari et al., 2013). Elevation, substrate, and local microtopography also play major roles in structuring understory communities through differential establishment success and habitat associations

(Inman-Narahari et al., 2014; Kandert et al., 2021; Tweiten et al., 2014). Local microstructure and substrate type greatly influence seedling recruitment, with many common understory species showing a preference for establishing on nurse logs and tree fern stems, likely due to trapped organic matter and substrate moisture retention (Inman-Narahari et al., 2013; Santiago, 2000).

Hawaiʻi is emblematic of the heighted threat faced by oceanic island floras. Non-native vegetation has largely displaced native flora at lower elevations (Barton et al., 2021). Many lineages famous for their widespread radiations, such as the Hawaiian lobeliads (*Campanulaceae*; Givnish et al., 2009) and endemic mints (*Lamiaceae*; Tomlin et al., 2024), have experienced numerous extinctions, and remaining extant members are rare. While higher elevation montane forests tend to remain less invaded, non-native species are progressively encroaching into these systems via their understories (Potter et al., 2023). Noxious weeds such as Kahili ginger (*Hedychium gardnerianum*), Koster's curse (*Clidemia hirta*), and banana poka (*Passiflora tarminiana*) are particularly problematic in mesic to wet forests, forming monotypic stands and quickly displacing native understory vegetation where they invade (Huenneke & Vitousek, 1990; Loope et al., 1992). Land conversion and encroachment by introduced pasture grasses has led to an almost complete suppression of native recruitment where they establish, leading to significant shifts in trajectories of forest development (Denslow et al., 2006; Thaxton et al., 2012). Non-native dominated grasslands experience carbon losses, changes to biogeochemical cycling, and altered disturbance regimes (Ainsworth & Kauffman, 2010; D'Antonio & Vitousek, 1992; Litton et al., 2006). Vegetation communities in Hawaiʻi that shift to non-native dominance have been found to be highly resilient to change, maintaining non-native species assemblages in the face of disturbance (Yelenik et al., 2024).

Invasive ungulate disturbance constitutes a major factor facilitating the spread of exotic plants in Hawaiʻi (Aplet et al., 1991). Feral pigs (*Sus scrofa*), in particular, have been introduced to many island systems and are among the most destructive invasive species globally (Barrios-Garcia & Ballari, 2012). Their disruptive foraging behaviors – uprooting vegetation, trampling seedlings, and disturbing soil – displace native vegetation and create favorable conditions for non-native species establishment (Wehr et al., 2018). Pigs were introduced to Hawai'i multiple times, beginning with Polynesian settlers between 400 – 1000 CE and later by Europeans in the late 18th century (Linderholm et al., 2016; Wilmshurst et al., 2011). While historical pig population densities remain uncertain, contemporary estimates are high; the upper bounds of modern estimates often fall between 12 and 17 pigs km^{-2}, but sometimes exceed these numbers (Hess & Jacobi, 2014; Peyton et al., 2023; Scheffler et al., 2012). High populations are likely sustained by the availability of non-native earthworms as supplemental protein (Loope et al., 1988) and by the lack of top-down pressure beyond human hunting, which is insufficient to limit population growth (Hess & Jacobi, 2014). Feral pigs have been implicated in the spread of non-native plants primarily through soil disturbance (Peyton et al., 2023) and seed dispersal (Huenneke & Vitousek, 1990). Biotic soil disturbance, resulting from foraging, rooting, and wallowing activity, has the potential to significantly alter understory communities by imposing novel pressures on native plants (Aplet et al., 1991; Gray et al., 2020; Webber et al., 2010). Recurrent disruption to soil structure can alter conditions for seedling establishment and induce significant mortality for native plants lacking adaptations to persist under frequent disturbance (Leopold & Hess, 2017). The removal of native species through soil disturbance and herbivory provides opportunities for invasive species to capitalize on space and resources, leading to further encroachment (Cushman et al., 2004). On islands, ungulate disturbance has sometimes shifted vegetation into alternative stable states that resist restoration efforts once thresholds are surpassed (Bastille-Rousseau et al., 2017).

Understanding how communities transition from native to non-native dominance is critical for conserving biodiversity in island systems and minimizing the disproportionate threats native species face from invasion. In this study, we investigate understory vegetation dynamics within a montane wet forest on Hawaiʻi Island, targeting a relatively intact system experiencing ongoing invasion to assess the factors driving transitions in community composition. We assess compositional differences in understory variation along a gradient of pig population density quantified via camera trap surveys across four distinct study zones. By identifying distinct community assemblages and isolating the environmental and biotic factors shaping these transitions, we examine the roles of climate, local microhabitat features, and ungulate activity in driving shifts in community composition. Specifically, we test the hypothesis that non-native plant species encroachment and soil disturbance caused by feral pigs – a novel disturbance in this ecosystem – are primary drivers of variation among communities. We predict that the extent of non-native dominance will vary across assemblages, with disturbance-mediated shifts representing a key mechanism underlying transitions in vegetation structure and composition. Such shifts toward non-native dominance may ultimately represent an alternative stable state, whereby community composition is reinforced by ungulate disturbance, potentially limiting opportunities for restoration.

Methods

Study site

This study was conducted at the Puʻu O Umi Natural Area Reserve, situated on Kohala mountain on Hawaiʻi Island (Fig. 1). The site lies on the slopes of Kohala, the oldest shield volcano on the island, on substrates formed approximately 150 ka (Sherrod et al., 2021; Spengler & Garcia, 1988). The study area experiences minimal variation in temperature near the summit, with a mean annual temperature of 13–14°C, and receives > 2000 mm of annual rainfall, supplemented by significant cloud water interception (Giambelluca et al., 2013). This creates a wet forest dominated by native species with a canopy predominantly composed of ʻōhiʻa (*Metrosideros polymorpha*), while the understory consists largely of native ferns and shrubs such as ʻōhelo (*Vaccinium calycinum*), ʻōlapa (*Cheirodendron trigynum*), and hāpuʻu (*Cibotium spp.*). *Sphagnum palustre* forms the ground cover on a significant portion of the Kohala summit region (Schomaker, 2017), differing from other wet forests on Hawaiʻi Island. Despite the dominance of native overstory vegetation, some non-native species pose ongoing management concerns in the understory, including Kāhili ginger (*Hedychium gardnerianum*), water smartweed (*Persicaria punctata*), carpet grass (*Axonopus fissifolius*), and bordered panic grass (*Entolasia marginata*). Feral pigs have been excluded northeast of the summit region for decades but remain abundant in other areas of the reserve.

Data collection

We conducted this study across a gradient of feral pig density, with sites located within four 1-km radius zones (A-D) approximating the minimum home-range size of pigs in Hawaiian forests (Diong, 1982). Selection of zone locations was guided by expert opinion from land managers at the Hawaiʻi Department of Land and Natural Resources (DLNR) to capture a broad range of pig population density across the Puʻu O Umi Natural Area Reserve. To quantitatively estimate pig density, we carried out a camera trap survey in 2019 using methods based on Rowcliffe et al. (2008). To our knowledge, this was the first survey of pig population density conducted in Kohala. Trapping locations were generated using a stratified random design within each zone, and a subset of 4 to 6 cameras were randomly selected and deployed per zone over three 10- to 14-day periods. To confirm pig absence in the fenced Zone D in the northeastern summit region, 7 additional deployments were conducted during the final two periods. Camera traps were set to capture three images per activation with a 1-second delay between triggers. Cameras were placed ~50 cm above the ground on trees within 20 m of sampling points in areas with visible pig activity (e.g., trails, rooting, scat) to avoid underestimating density (Rowcliffe et al., 2008). Traps were positioned to cover a 5 m range at a ~45-degree angle. Pig density was estimated using the random encounter model (REM), which relates trapping rate to population density while accounting for covariates affecting detection probabilities (Rowcliffe et al., 2008, 2014). Site variability and model uncertainty was addressed using a bootstrapping approach (Appendix S1).

Understory vegetation, pig disturbance, and site characteristics

We surveyed 30 sites in each pig density zone using a stratified-random design, resulting in 120 total survey sites (one additional site was mistakenly included in Zone A, bringing the total to 121). Areas with > 50% canopy coverage were selected to target closed-canopy conditions. At each site, we established a 20-m transect along a random azimuth to survey understory vegetation and habitat characteristics. We used a point-intercept approach to estimate the abundance of vascular plant species between 0 and 2 m in height intercepted at each point located at 0.5-m intervals along each transect, totaling 41 points per site. *Sphagnum palustre* was also recorded at ground level. Flowering plant taxonomy was based on Wagner et al. (1991) with updated nomenclature by Smith and Brown (2018) and pteridophyte taxonomy was based on Palmer (2002). As key identifying characteristics were often missing for *Peperomia*, *Coprosma*, and *Adenophorus*, members of those lineages were identified to the genus level. To minimize the influence of rare species, which can disproportionally influence analyses and obscure broader compositional patterns, we excluded those that occurred in fewer than 3% of sites.

Feral pig disturbance, defined as soil visibly disturbed by rooting, wallowing, or trampling, was measured and recorded in 5-cm increments where intersected by each transect, as were nurse logs (defined as woody stems at less than a 45° angle from the ground). Measurements were summed to estimate the cover of these features at each site. As no other ungulates (e.g. goats, sheep) were detected during the camera trap survey, all ungulate soil disturbance was assumed to be by feral pigs. We also assessed light availability by capturing hemispherical photographs at three equally spaced points along each transect using a fisheye lens. The photographs were analyzed using Gap Light Analyzer software (Frazer et al., 1999) to calculate canopy openness, which was averaged across each site to represent light availability.

Climate

We characterized climatic variation across the study area using eight climate variables sourced from the Hawaiʻi Evapotranspiration Atlas and the Rainfall Atlas of Hawaiʻi

(Giambelluca et al., 2013). While these climate datasets are based on relatively few weather stations, they effectively capture the major gradients relevant to this study. The variables included mean annual temperature (Tmean), maximum annual temperature (Tmax), minimum annual temperature (Tmin), mean annual precipitation (MAP), mean annual vapor pressure deficit (VPD), total solar irradiance (TSI), mean annual transpiration (E), and cloud frequency. Elevation was measured at each site using a Garmin 64S GPS unit.

To summarize the climatic variation across the sites, we conducted a principal component analysis (PCA) on the eight climate variables along with elevation (Appendix Fig S3). The first two principal components accounted for over 98% of the variance, with PC1 (59.9%) reflecting moisture availability and PC2 (38.2%) associated with temperature differences (Appendix S2). We proceeded by using PC1 (positive = wetter) and PC2 (positive = warmer) scores to capture climatic variation across sites.

Data analysis

We used hierarchical agglomerative clustering to identify understory vegetation community types. First, we calculated a pairwise Bray-Curtis dissimilarity matrix across sites using point-intercept estimates of species abundance. We then employed an unconstrained cluster algorithm using Ward’s method (Ward, 1963) to detect distinct vegetation clusters. To determine the optimal number of clusters, we assessed the reduction in total within-cluster sum of squares across increasing cluster numbers. The point of diminishing returns – where additional clusters yielded minimal improvement in reducing within-cluster variability – was determined where the slope of the relationship between within-cluster sum of squares and the number of clusters departed from the initial trend and became substantially less negative (see Appendix S3, Fig S4), yielding six distinct vegetation community types.

We ran non-metric multidimensional scaling (NMDS) on the Bray-Curtis dissimilarity matrix to explore patterns in understory composition across community types. NMDS is non-parametric and uses rank-order distances or dissimilarities, which makes it robust to non-linear and zero-inflated species composition data. To determine the optimal dimensionality of the NMDS solution, we explored solutions with 1 to 5 dimensions and evaluated the corresponding stress values. Stress decreased substantially between one (stress = 0.38) and two (stress = 0.25) dimensions, further dropping to 0.18 with the addition of a third dimension, below the acceptable stress threshold of < 0.2 (Kruskal, 1964). We selected the three-dimensional solution given that the inclusion of further dimensions provided only modest improvements, with stress values of 0.15 and 0.12 for 4 and 5 dimensions, respectively. NMDS was calculated using the *metaMDS* function in the package *vegan* (Oksanen et al., 2008) in R statistical software (v4.3.0).

Species associations with ordination axes were quantified using Pearson's correlation coefficients (r), calculated for each species with respect to individual NMDS axes. Simple linear regressions between species abundances and NMDS scores were used to derive r from R^2 (Table 1), with significance established at $p < 0.05$. Estimates for habitat characteristics – pig population density, soil disturbance, *Sphagnum* coverage, canopy openness, nurse log coverage, temperature, and moisture (hereafter collectively referred to as 'environmental' variables) – were passively overlain onto the NMDS ordination. Environmental vectors were fit using the *envfit* function in the *vegan* package, with vector lengths scaled by R^2. Statistical significance was evaluated using permutation tests (n = 999).

To assess variation in growth form composition across communities, we classified each species into one of six categories (herb, shrub, tree, fern, tree fern, and vine) based on Wagner et al. (1991) and Palmer (2002). The abundance of each growth form at each site was calculated as the proportional cover of each respective form relative to total species cover. Linear relationships of these growth-form proportions and NMDS axes were then passively fit to the ordination and visualized as vectors scaled by the strength of association (R^2; as with environmental variables).

To investigate the primary environmental drivers contributing to differences among understory community types, we first conducted permutational multivariate analysis of variance (PERMANOVA) to identify community types differing in their habitat characteristics. PERMANOVA was performed on a matrix of scaled environmental variables using Euclidean distance with pairwise comparisons using Bonferroni correction. P-values were obtained through permutations (n = 10,000). Subsequently, we applied similarity percentage analysis (SIMPER) to pairs of community types found to differ significantly to identify environmental variables contributing most to the observed variation. SIMPER decomposes pairwise group dissimilarities into individual component contributions, using permutations (n = 10,000) to assess significance. Environmental variables differing significantly between community types likely play an outsized role in shaping compositional differences. PERMANOVA was performed using the *pairwiseAdonis* package (Martinez Aribizu, 2020), while SIMPER was conducted using the *vegan* package (Oksanen et al., 2008).

Results

Pig population density estimates varied considerably across the study zones, ranging from a complete absence of individuals in Zone D to a maximum density of 17.5 ± 7.5 (mean ± sd) individuals per km² in Zone A (Fig 1b; the zones were classified from A to D in order of decreasing pig density). Median soil disturbance was greatest at Zone A and decreased with falling pig density (Fig 1c), indicating density estimates closely tracked pig activity and impacts across the study area.

Vegetation community types

Hierarchical clustering revealed six understory community types, which we categorized based on species composition (Fig. 2). We found marked differences in the relative abundance of native to non-native species across community types. Two community types were dominated by native species, which we classified as "Native *Vaccinium/Metrosideros*" and "*Native Myrsine/Metrosideros*" communities based on the most abundant species found summed across all sites in those communities (Fig. 3c) The remaining four communities demonstrated varying degrees of non-native dominance. Two communities, classified as "Non-native/*Vaccinium*" and "Non-native dominant," exhibited < 50% and > 50% non-native cover across all sites, respectively. Non-native/*Vaccinium* communities supported abundant native *Vaccinium calycinum*, but also contained high abundance of non-native species, including *Persicaria punctata, Hedychium gardnerianum, Juncus effusus*, and *Axonopus fissifolius*. Communities classified as Non-native dominant were chiefly composed of *Persicaria punctata* and *Hedychium gardnerianum*, while other species – both native and non-native – were found at relatively low abundance. The remaining two community types also varied in non-native dominance, but this was almost entirely due to a single species: *Entolasia marginata*. These communities were classified as "*Entolasia* encroachment" and "*Entolasia* dominance" based on the relative proportion of *Entolasia* coverage.

NMDS revealed that three axes captured the key dimensions of understory species composition across the study site (Fig 3). The first axis (NMDS1) primarily distinguished communities dominated by non-native species from those dominated by native species (e.g. placing the Native *Myrsine/Metrosideros* and non-native dominant communities at opposite ends of the spectrum). Negative NMDS1 values indicated increased abundance of non-native species, including *Persicaria punctata* and *Hedychium gardnerianum*, while native taxa such as *Myrsine sandwicensis* and *Adenophorus* ferns were associated with positive values (Table 1). Pig density and soil disturbance decreased with NMDS1, whereas *Sphagnum* cover and moisture increased (Fig 3; Appendix S4). NMDS1 also tracked variation in the proportional cover of herbaceous vs tree species, where lower values were associated with greater herbaceous cover and higher values with greater understory tree cover. The second axis (NMDS2) largely captured variability among native-dominated communities, although some variation in non-native species was captured (see *Axonopus fissifolius*; Table 1). Higher NMDS2 values corresponded to the presence of species such as *Vaccinium calycinum*, *Styphelia tameiameiae*, and *Metrosideros polymorpha*. In contrast, lower values reflected species such as *Cibotium glaucum* and *Broussaisia arguta,* and closely tracked increases in the proportional abundance of tree ferns. Canopy openness showed a positive correlation with NMDS2, while soil disturbance exhibited a weak negative relationship. The third axis (NMDS3) tracked variation in the abundance of vines (i.e. *Alyxia stellata*) and ferns, and was closely associated with variation in temperature and elevation. NMDS3 varied with both native and non-native species, including *Entolasia* *marginata*, which increased with positive NMDS values. Other non-native (e.g. *Hedychium gardnerianum*, *Persicaria punctata*) and native (e.g. *Carex alligata*, *Melicope clusiifolia*, *Peperomia* spp.) were also associated with positive and negative values of NMDS3.

Drivers of variation

PERMANOVA and SIMPER analysis identified significant environmental variables contributing to dissimilarity across understory community types (Fig 4). The *Entolasia* encroachment and *Entolasia* dominant communities –the only communities that did not differ significantly from each other in the PERMANOVA analysis – were omitted from this analysis as *Entolasia marginata* was confined to a single zone (Zone B). *Entolasia* communities were localized to the middle of the pig density gradient and located near the forest-pasture edge.

Pig density and soil disturbance emerged as the dominant contributors in most comparisons, particularly between non-native dominant communities and other community types. Pig density was also the primary differentiator between Non-native/*Vaccinium* communities and those dominated by native species. Canopy openness and nurse log coverage drove variation between Native *Vaccinium*/*Metrosideros* communities and Native *Myrsine*/*Metrosideros* communities, with Native *Vaccinium*/*Metrosideros* communities exhibiting greater canopy openness and reduced nurse log coverage (Fig 5), albeit with considerable variation between sites. The effects of *Sphagnum* and climate variables were typically small across comparisons.

Discussion

Feral pig activity emerged as a dominant driver of non-native occurrence and the primary contributor to structuring plant community composition. Disturbances such as land clearing, fire, and livestock grazing often facilitate invasion when those disturbances are historically novel and native species lack adaptations to persist under the new regime (D’Antonio & Vitousek, 1992; Hierro et al., 2006; Hobbs, 2001). Our results suggest feral pigs create a novel disturbance type in Hawai‘i by suppressing native recruitment and promoting non-native establishment. Prior to their extinction from human hunting, endemic flightless waterfowl (e.g. moa-nalos) occupied a similar functional role to pigs as large herbivores, but any biotic disturbances by herbivorous waterfowl likely differed considerably in type, severity, and spatial extent to those by contemporary feral pigs (James & Burney, 1997). Contemporary forests support high feral pig population densities due to a lack of top-down control beyond human hunting (Hess & Jacobi, 2014; Luat-Hū‘eu et al., 2023), and most native Hawaiian plants likely lack adaptations to quickly establish and grow post-disturbance (Baruch & Goldstein, 1999). Hawaiian plants generally exhibit slow rates of growth compared to many of their non-native counterparts (Pattison et al., 1998), which could limit establishment and recovery under frequently disturbed conditions. Many non-native species are herbaceous and can achieve higher rates of growth due to greater foliar nitrogen (N), high photosynthetic rates, and lower allocation to structural support, permitting rapid establishment in disturbed patches and the suppression of native seedling recruitment through competition for light and resources (Díaz et al., 2016; Leishman et al., 2007; Poorter et al., 2012). Indeed, greater pig population density and soil disturbance were strongly associated with a shift from woody (i.e. understory trees) to herbaceous species in the understory (Fig. 3a), likely due to the growth advantages of the herbaceous habit. Notably, disturbance was pivotal in pushing communities exhibiting partial non-native encroachment into full non-native dominance (Fig 4), suggesting displacement of native species and altered soil conditions play crucial roles in this transition. Understory communities exposed to ungulate-induced soil disturbance likely approach a critical threshold, beyond which disturbances could accelerate the shift to non-native dominance.

The partial encroachment of non-native species, seen in the transition from native-dominated communities (i.e. Native *Vaccinium/Metrosideros,* Native *Myrsine/Metrosideros*) to the Non-native/*Vaccinium* community, was linked to pig population density rather than soil disturbance (Fig. 4). Greater feral pig abundance in the Non-native/*Vaccinium* community suggests other mechanisms of pig activity apart from disturbance, such as seed dispersal or herbivory, might also facilitate invasion. Coarse pig density metrics across zones likely obscure localized variation in impacts; however, this aggregate measure nonetheless captures the cumulative effects of pig activity, integrating differences in population size. Pigs are known to disperse invasive species like strawberry guava (*Psidium cattleianum*) and Koster's curse (*Clidemia hirta*) at lower elevation (Loope et al., 1988). Although these species were absent from the study area, pigs may act as dispersal agents for other invasive taxa similarly dispersed through epi- and endozoochory. Herbivory is highly selective; tree ferns in the genus *Cibotium* are frequently targeted for their starchy pith, and rare taxa such as the endemic lobeliads and mints often experience intense browsing pressure, leading to considerable mortality (Loope et al., 1988). The facilitation of specific non-native taxa through dispersal and the selective herbivory of native taxa likely contributed to the observed patterns of non-native encroachment in areas with elevated feral pig abundance. Although we did not directly quantify soil nutrient variation across sites, increased N deposition through urine and fecal inputs may also facilitate non-native species establishment by favoring fast-growing herbaceous plants with elevated foliar N demands (Mackay et al., 2021). While our observations are insufficient to conclusively test these mechanisms, they suggest that alternative features of pig activity may act synergistically to facilitate encroachment by non-native species, even in the absence of disturbance.

The *Native Vaccinium/Metrosideros* and *Native Myrsine/Metrosideros* communities likely reflect vegetation more typical of Hawaiian understories in the absence of invasion. As expected, these communities experienced minimal pig activity (Appendix S5; Fig. S5). Differences in these native assemblages – chiefly captured along NMDS 2 – occurred largely independently of non-native invasion (Fig 3, Table 1). Tree ferns, particularly those in the *Cibotium* genus, drove a significant component of the variation along NMDS2, with Native *Myrsine*/*Metrosideros* communities supporting a greater abundance of *Cibotium menziesii*. *Cibotium* tree ferns make up a significant component of Hawaiian forest under- and mid-story vegetation and play an outsized role in ecosystem function, contributing disproportionately to nutrient cycling and producing nurse logs for native seedling establishment (Ranker, 2016; Vitousek, Turner, Walker, et al., 1995). Studies suggest *Cibotium* prefers wetter conditions, occurring most prevalently in mesic to wet forests (Wagner et al., 1991). While it has been found to increase in abundance following canopy dieback, *Cibotium* also exhibits significant shade tolerance and typically persists under closed-canopy conditions (Mueller-Dombois & Boehmer, 2013). Shade tolerance in *Cibotium* is supported by our findings demonstrating a negative association between tree ferns – a category predominantly composed of *Cibotium glaucum* and *Cibotium menziesii* – and canopy openness along NMDS2 (Fig. 3a). Additional compositional differences observed between these communities also appear to reflect differences in moisture conditions, as well as light infiltration. For example, species such as *Carex alligata*, *Vaccinium* *calycinum*, and *Styphelia tameiameia* – found at greater abundance in Native *Vaccinium/Metrosideros* communities – are tolerant of drier, more open canopy conditions, and can occupy shrubland habitats in addition to closed-canopy forest (Kitayama & Mueller-Dombois, 1992). In contrast, Native *Myrsine/Metrosideros* communities supported greater abundance of species typical of moist, closed-canopy environments (e.g. *Myrsine sandwicensis*, *Peperomia spp.*, *Adenophorus spp.*; Kitayama & Mueller-Dombois, 1992).

Growing conditions in tropical mesic and wet forests are often strongly influenced by moisture variability (Tan et al., 2013) and light conditions (Brenes-Arguedas et al., 2011). In the understory, these may be shaped primarily by small-scale structural factors, such as canopy openness, substrate type, and microtopography (Denslow et al., 1998, 2019). Indeed, recruitment success for native understory species in Hawaiian forests has been found be strongly influenced by microsite preferences (Kandert et al., 2021). Our results similarly identified microsite conditions – namely, canopy openness and nurse log substrate – as major drivers of variation across native-dominated communities, while climate did not have an appreciable effect (Fig. 4). This may be due to the small range of climate conditions captured by this study, but nonetheless highlights the relative importance of local conditions in structuring native understory communities under forested conditions. In agreement with other studies of Hawaiian forests (Denslow et al., 2006; Funk & McDaniel, 2010; Givnish & Montgomery, 2014; Inman-Narahari et al., 2014, 2016), we found light conditions play an important role in the dynamics of understory vegetation communities. Unlike canopy trees, which may be less strongly influenced by small-scale environmental variation, smaller understory plants typically do not have access to deeper water reserves and are subject to fluctuating soil moisture as a result of solar radiation through the canopy (Ghimire et al., 2018). Accordingly, Native *Vaccinium/Metrosideros* assemblages were typically found under more open canopies and comprised assemblages with a greater abundance of species adapted to drier conditions. Local recruitment conditions are influenced strongly by nurse logs in Hawai'i (Inman-Narahari et al., 2013; Tweiten et al., 2014), which we also found to be an important factor shaping native community structure. Nurse logs modify local microhabitat conditions and significantly influence community composition (Sanchez et al., 2009), possibly by increasing local moisture retention and nutrient availability (Pichlerová et al., 2013). A greater abundance of nurse logs likely influenced species composition in the Native *Myrsine/Metrosideros* community, promoting the establishment of native species adapted to wetter conditions. Our results indicate native Hawaiian understory communities are, similarly to other tropical wet forests, strongly influenced by local factors affecting light and moisture conditions.

The encroachment of *Entolasia* in Zone B likely represents an early stage of invasion distinct from other non-native species, localized primarily near the forest-pasture edge. This pattern suggests that *Entolasia* is actively in the process of invading the Kohala forest understory. Notably, in addition to clustering geographically, communities characterized by *Entolasia* encroachment and *Entolasia* dominance did not differ significantly in their habitat characteristics (PERMANOVA; Table 2), indicating that the transition to dominance occurs intrinsically once *Entolasia* establishes. A marked decline in native species (e.g. *Cibotium glaucum*) observed under *Entolasia* dominance suggests some degree of displacement (Appendix S5; Fig. S7). While direct evidence of competitive exclusion is lacking, and this may reflect a loss of native species due to unrelated factors and subsequent competitive release for *Entolasia*, the observed patterns nevertheless remain consistent with those of other highly competitive invasive species. Encouragingly, only a small number of sites were dominated by *Entolasia*, and its encroachment remained largely confined to a single zone, presenting an opportunity for targeted management interventions to control its spread and mitigate further impacts within the Pu'u O Umi Natural Area Reserve.

Our study had several limitations that warrant consideration. First, while our observational approach identified strong correlations between non-native species invasion and feral pig activity, a stronger establishment of causality requires further study through experimental validation. Nevertheless, the observed patterns align with prior research showing that feral pigs disrupt understory communities through soil disturbance, fostering conditions favorable for invasive species establishment (Aplet et al., 1991; Cushman et al., 2004; Wehr et al., 2018). Second, our ability to identify drivers of community composition was contingent on the environmental variables measured. While we included key variables known to shape community dynamics, some variables were not accounted for. For example, biologically available soil nutrients – often a key determinant of community dynamics in tropical systems (Vitousek, 1985; Vitousek, Turner, & Kitayama, 1995), were not assessed, potentially limiting the detection of additional environmental variation across communities. The resilience of native and non-native understory assemblages remains an open question, but studies have demonstrated that some non-native dominated communities in Hawaiʻi resist invasion and remain stable in the face of disturbance (D’Antonio et al., 2017; Yelenik et al., 2024). Targeted interventions to maintain communities below invasion thresholds present a promising conservation strategy in forest understories experiencing the early stages of invasion. Effective management should integrate feral pig control with proactive measures to prevent tipping points, emphasizing the importance of long-term ecological monitoring and adaptive strategies.

Conclusion

Our findings highlight the threat posed by non-native species invasion in Hawaiian forest understories, even within relatively intact, high-elevation montane forests. With the exception of *Entolasia*, invasion was primarily structured along a single dimension, with most non-native species exhibiting a tendency to co-occur. Feral pig activity was implicated as a key driver variation in community composition, particularly by facilitating the establishment and spread of non-native species through soil disturbance. Local microsite factors, including canopy openness and nurse log abundance, were identified as important determinants of native understory community structure, likely through their influence on moisture availability The distribution of *Entolasia marginata* suggests that it is in the early stages of invasion and may continue to spread. Our findings underscore the need for management strategies focused on feral pig control and targeted interventions to curtail invasive species spread, ideally before a shift to non-native-dominance occurs. Long-term ecological monitoring and adaptive management will be essential for mitigating further transitions towards non-native dominance in Hawaiian understory ecosystems.

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Figures

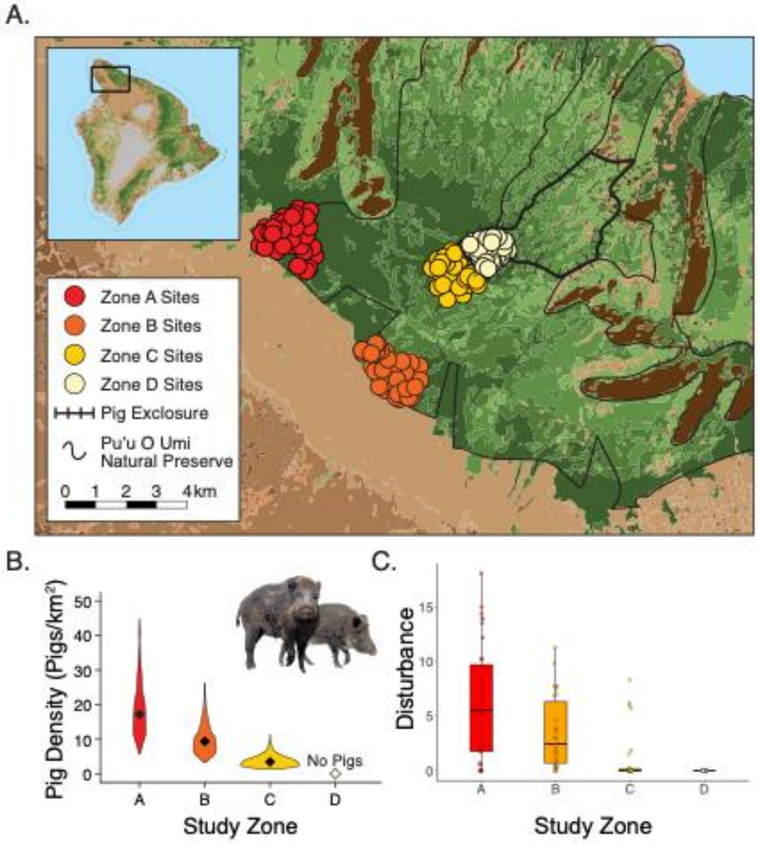

Figure 1. (A.) Map of the study area. Outline of the Pu'u O Umi Natural Area Reserve given in grey polygon, with hatched polygon marking the pig exclosure near the Kohala summit. Colors indicate positioning of sites within pig-density Zones. (B) Violin plots show estimates of pig density from REM on camera trap data. Black dots mark median estimates for each Zone. (C) Boxplots show soil disturbance extent within sites across pig density Zones. Horizontal line represents median values for disturbance within each Zone.

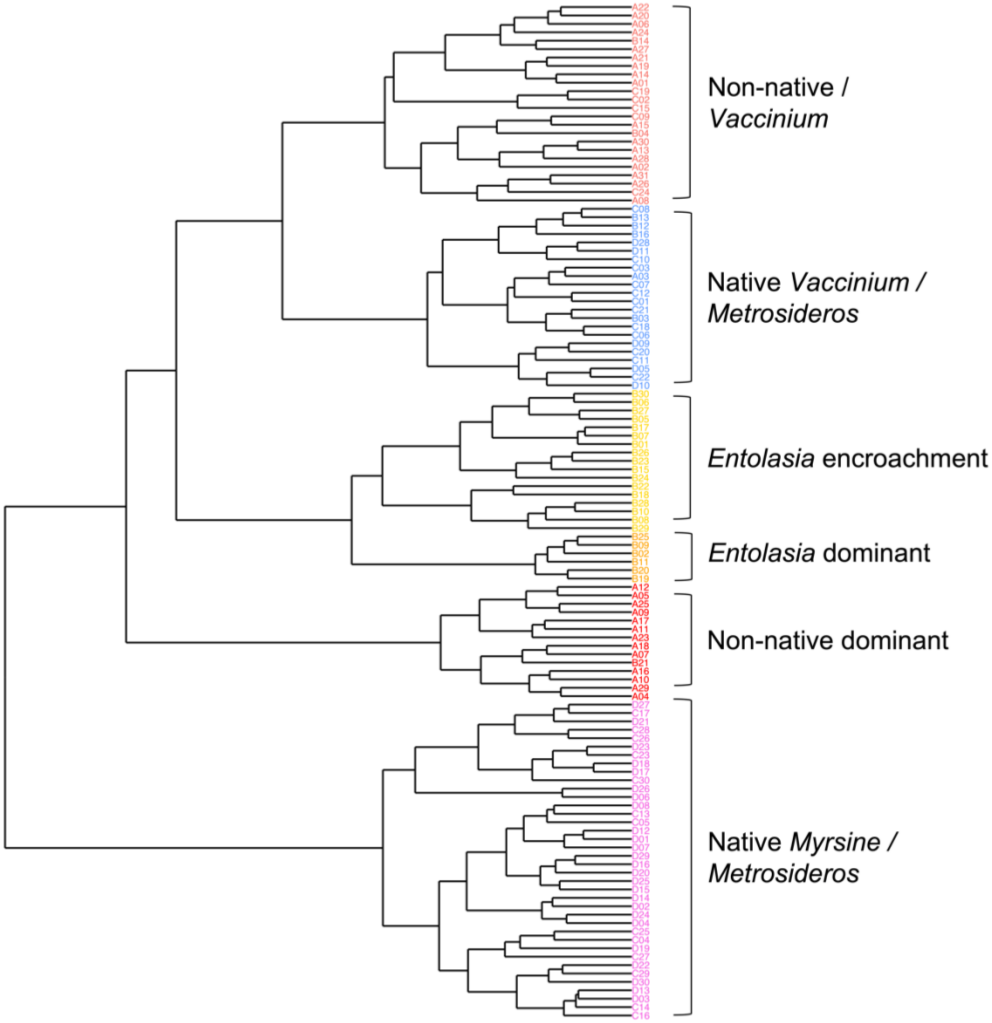

Figure 2. Hierarchical clustering dendrogram of vegetation community types using Ward's clustering method based on Bray-Curtis dissimilarity. Clusters represent distinct vegetation community types: Non-native/*Vaccinium*, Native *Vaccinium*/*Metrosideros, Entolasia* encroachment, *Entolasia* dominant, Non-native dominant, and Native *Myrsine*/*Metrosideros*.

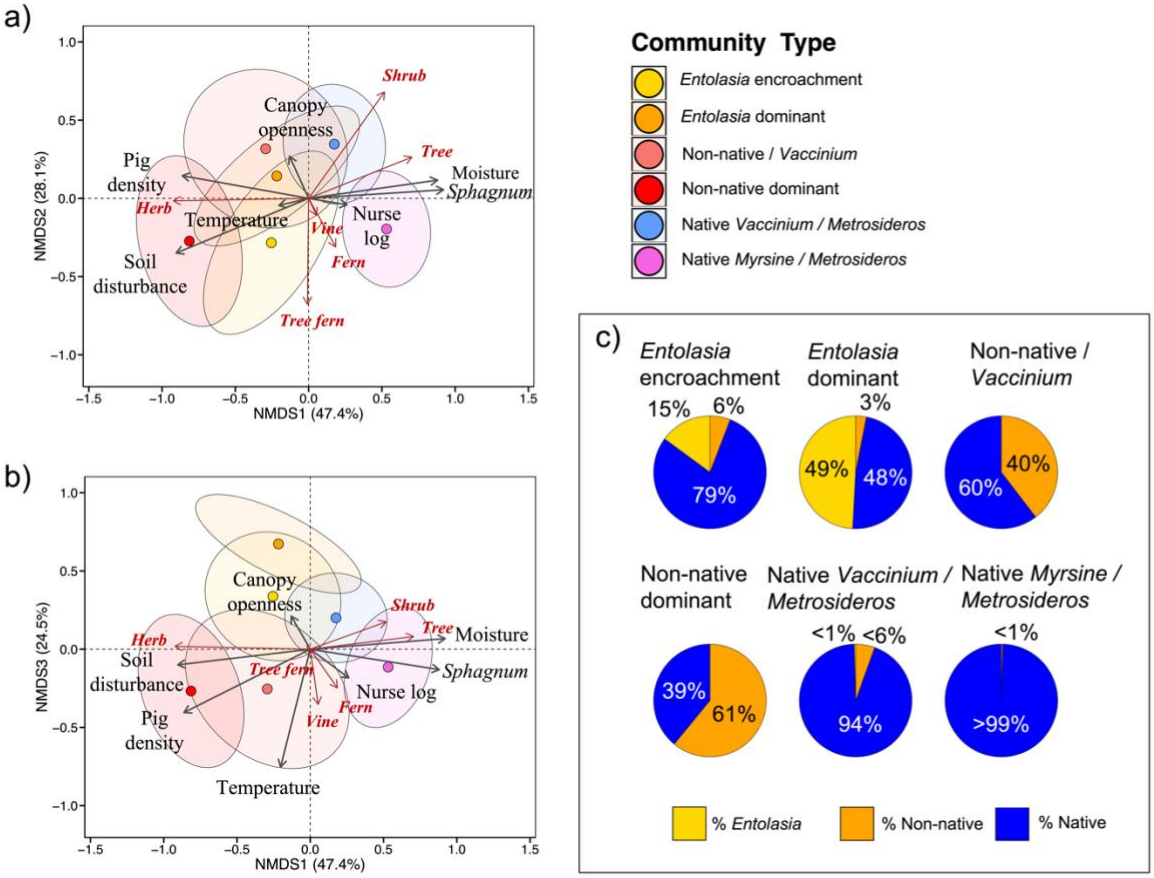

Figure 3. Multivariate analysis of community composition. (a) NMDS plot (axes 1 and 2) based on species composition across sites. Points represent community type centroids, with ellipses indicating one standard deviation. Black vectors represent environmental variables, while red vectors represent the proportion of each growth form (herb, shrub, tree, tree fern, fern, and vine) found at each site. Vectors are scaled by R^2 for NMDS1 and NMDS2. (b) NMDS plot (axes 1 and 3), with figure symbology following panel (a). (c) Proportional composition of native and non-native species in each community type, with *Entolasia* distinguished from other non-native species. Proportions area derived from site sums of each community type.

Table 1. Linear relationships of individual species to axis scores NMDS1, NMDS2, and NMDS3. All taxa shown are significant to $p < 0.001$, and have correlation of $r > 0.3$ (equivalent to $R^2 < 0.09$). Negative *r* values indicate a negative relationship with axis scores, positive *r* values indicate positive relationship with axis scores. Non-native species indicated in bold.

NMDS axis 1		NMDS axis 2		NMDS axis 3	
Species	*r*	Species	*r*	Species	*r*
Myrsine sandwicensis	0.64	*Vaccinium calycinum*	0.73	***Entolasia marginata***	**0.52**
Adenophorus spp	0.57	*Styphelia tameiameiae*	0.48	*Melicope clusiifolia*	-0.46
Persicaria punctata	**-0.56**	*Cibotium glaucum*	-0.43	*Carex alligata*	0.43
Peperomia spp	0.51	***Axonopus fissifolius***	**0.39**	***Hedychium gardnerianum***	**-0.40**
Geniostoma hedyosmifolium	0.46	*Metrosideros polymorpha*	0.35	*Peperomia spp*	-0.37
Hedychium gardnerianum	**-0.46**	*Broussaisia arguta*	-0.35	*Cibotium menziesii*	-0.32
Metrosideros polymorpha	0.45			*Asplenium polyodon*	-0.31
Broussaisia arguta	0.42				
Myrsine lessertiana	0.42				
Coprosma spp	-0.40				
Asplenium polyodon	-0.40				
Juncus effusus	**-0.38**				
Melicope clusiifolia	0.35				
Cibotium glaucum	-0.35				
Melicope pseudoanisata	0.34				
Rhynchospora chinensis	-0.33				
Rubus hawaiensis	-0.31				
Axonopus fissifolius	**-0.30**				

Table 2. Results of PERMANOVA assessing differences in environmental variables among community types. Pairwise comparisons were assessed using Bonferroni correction. R^2 indicates the proportion of total variance in the environmental variables for each comparison explained by community type. Significance is indicated by: · *p.adj* < 0.1 ; * *p.adj* < 0.05; ** *p.adj* < 0.01; *** *p.adj* < 0.001

Comparisons	*F*	*R^2*	*p.adj*
Non-native/*Vaccinium* vs Native *Vaccinium/Metrosideros*	18.91	0.30	**
Non-native/*Vaccinium* vs Non-native dominated	7.11	0.17	**
Non-native/*Vaccinium* vs *Entolasia* encroachment	11.79	0.23	**
Non-native/*Vaccinium* vs *Entolasia* dominated	7.32	0.21	**
Non-native/*Vaccinium* vs Native *Myrsine/Metrosideros*	52.60	0.47	**
Native *Vaccinium/Metrosideros* vs Non-native dominated	30.07	0.47	**
Native *Vaccinium/Metrosideros* vs *Entolasia* encroachment	16.55	0.31	**
Native *Vaccinium/Metrosideros* vs *Entolasia* dominated	4.99	0.16	·
Native *Vaccinium/Metrosideros* vs Native *Myrsine/Metrosideros*	8.14	0.12	**
Non-native dominated vs *Entolasia* encroachment	16.03	0.36	**
Non-native dominated vs *Entolasia* dominated	17.34	0.49	**
Non-native dominated vs Native *Myrsine/Metrosideros*	85.86	0.63	**
Entolasia encroachment vs *Entolasia* dominated	1.41	0.06	
Entolasia encroachment vs Native *Myrsine/Metrosideros*	54.39	0.51	**
Entolasia dominated vs Native *Myrsine/Metrosideros*	21.60	0.34	**

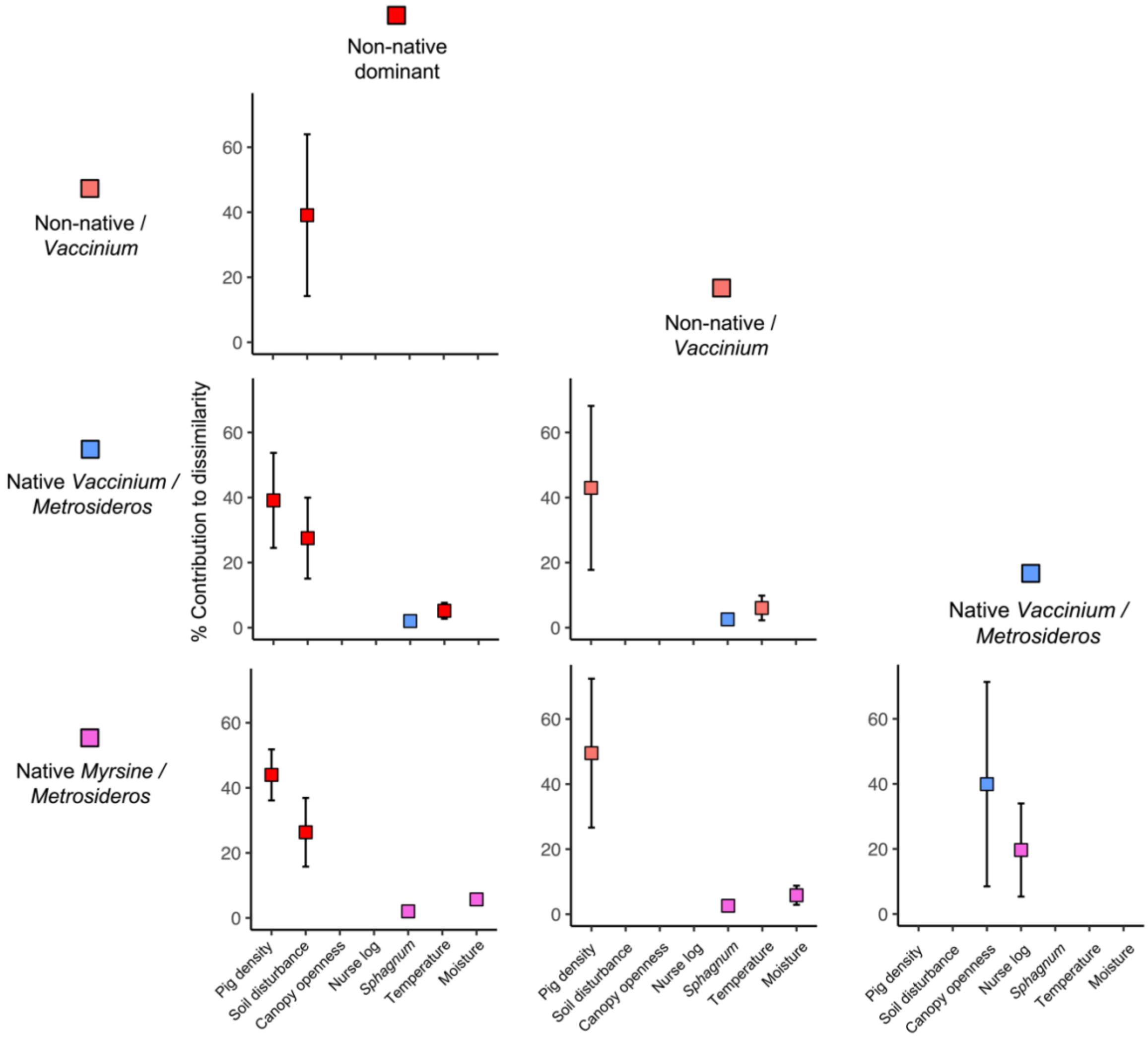

Figure 4. Results of SIMPER for pairwise comparisons of environmental variables across community types. Points correspond to the percentage contribution to overall dissimilarity between communities with bars representing one standard deviation. Only statistically significant variables are shown, with significance assessed using permutations (n = 10,000). Each panel shows a different pairwise comparison given by the names of the community types shown in the row and column labels, with environmental variables displayed along the x-axis. Points are

colored by the community type exhibiting higher median values for a given environmental variable in each pairwise comparison.

SUPPORTING INFORMATION

Appendix S1

Pig density model description and parameterization

Photos were processed and tagged (Adobe Bridge Adobe Systems, San Jose, CA), and metadata created with the R package *camtrapR* (Niedballa et al. 2016). The detection frequency of a species at randomly placed motion-triggered cameras (i.e., camera traps) is a function of abundance, movement rate, and detectability (Jennelle et al. 2002, Parsons et al. 2017). We developed an approach that relies on the random encounter model by Rowcliffe et al (2008), considering the variability of detection within sites and species-specific variability of each known parameter. First, we estimated the site-level trap rate (T) using the optimized average trap rate from independent camera traps at each site (R). We estimated (T) from the exponential likelihood function by integrating over the upper tail of the probability density function. The full likelihood for T given the trap rate of individual cameras R_i (over i = 1, 2, …, M sites) is (Eqn. 1):

$$\mathcal{L}(T|R_i) = \prod_{i=1}^{M} T e^{-TR_i} \tag{1}$$

Yielding $\hat{T}$, the average trap rate of the site. Using $\hat{T}$, we estimated density using the following formula (Eqn. 2):

$$\hat{D} = \hat{T} * \frac{pi}{vr(2+\theta)} * g$$

, where $\hat{D}$ is the estimated density, $\hat{T}$ is the site-level trap rate, *v* is the average moving velocity of pigs, *r* and θ are the average radius and the angle of the detection zone, respectively, and *g* is the average group size of pigs in the study area. This method enabled us to estimate density from trapping rate data, in combination with unbiased independent estimates of the other parameters derived from previous literature. We estimated the average and variance of $\hat{D}$ by using a non-parametric bootstrap approach using n = 10,000 density estimates, resampling $\hat{T}$ and each known parameter (v, r, θ, and g) with replacement. Within each run, we included a random draw from the minimum, maximum, average, and standard deviation of independently known parameters (*v*, *r*, *θ*, and *g*) using a truncated normal distribution using the R package *truncnorm v1.0-8* (Mersmann et al., 2018). Our estimates of *v* were min. = 1.0, max. = 2.0, and 1.5 ± 0.5 km/hr (mean ± SD; Spitz and Janeau 1990, Allwin et al. 2016). We used estimates from Rowcliffe et al. (2011) and Apps and McNutt (2018) for Bushnell cameras to for *r* and θ. We randomly selected 100 photographs from each site and used the average number of individuals to estimate *g* (min. = 1.0, max. = 6.0, 1.81±1.03 individuals/photo). Lastly, to account for potentially unaccounted bias in our estimate of $\hat{D}$, we included a residual error term using the delta method (Seber 1982) for the estimates using the R package *msm v1.7* (Jackson, 2011).

We explicitly tested the impact of (i) capture independence (the time between photographs to consider a photo independent) and (ii) activity time on our estimates of density ($\hat{D}$). First, we extracted photos from our raw data using four separate independence windows (2, 5, 10, and 30 minutes) and reran our density estimates (Fig S2A). Using 10 minutes as independent events, we used five buffered windows of the peak activity times of feral pigs at each site (Figure S2), using the peak activity time ± 1, 2, 4, 6 (half-day), and 12 (the entire day) hours (Figure S2B).

Appendix S1 Figures

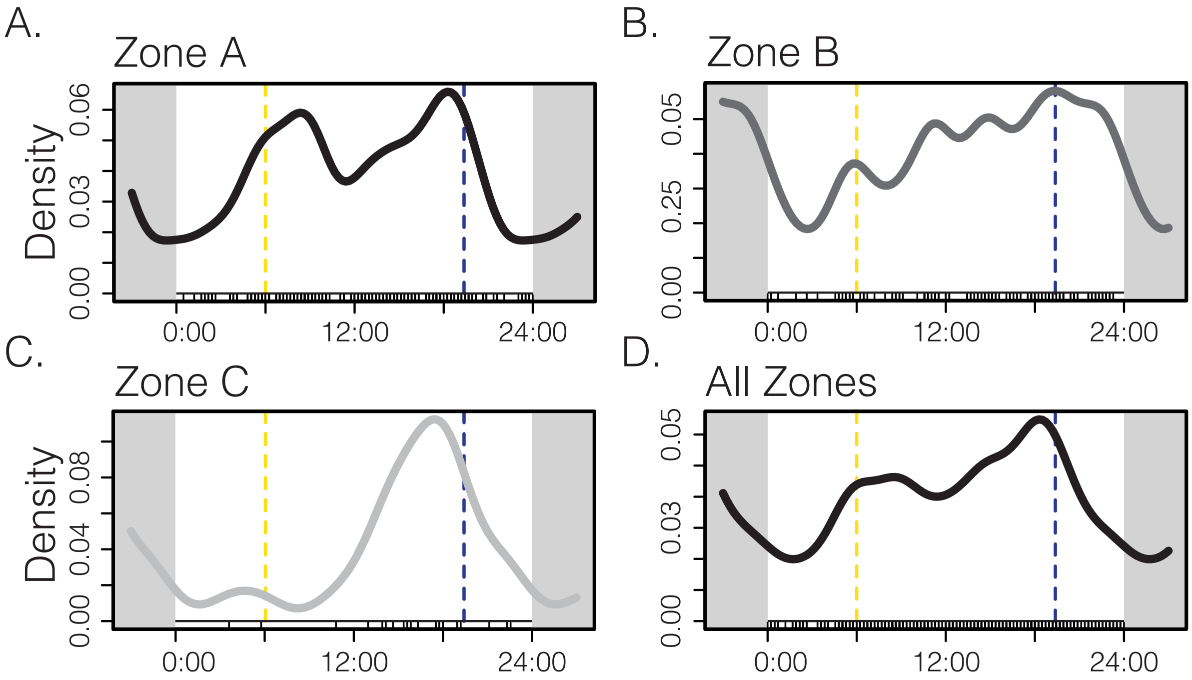

Figure S1. Activity times of feral pigs (*Sus scrofa*) at each Zone of our study (A, B, and C) and the activity times of all zones (D). Each panel shows the average sunrise (6:00 AM) and sunset (7:00 PM) time during our study period. Gray shaded regions in each panel are continuations of the previous (left) and next (right) day.

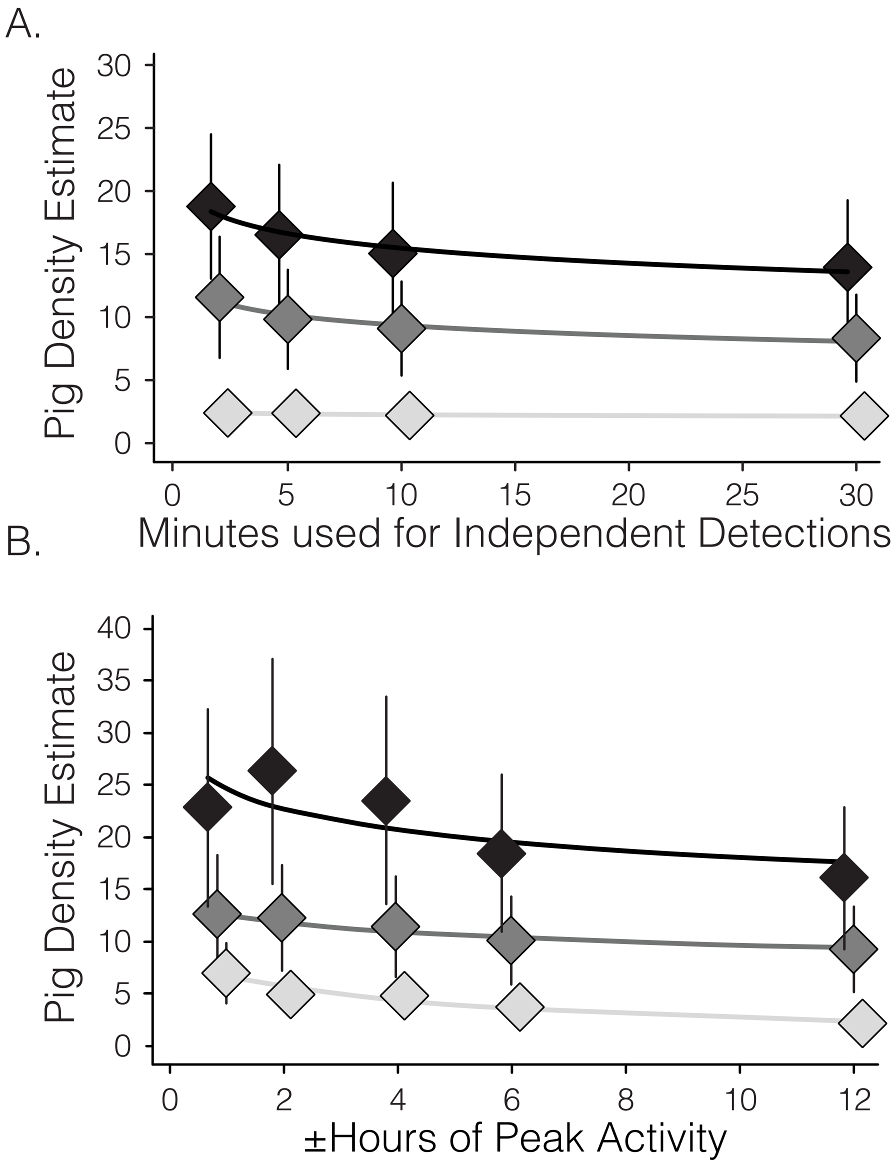

Figure S2. Capture independence of feral pigs (*Sus scrofa*; A) using four windows, 2, 5, 10, and 30 minutes between detections. Black diamonds represent estimates from Zone A, grey from Zone B, and light grey from Zone C. We deemed 10 minutes as independent events and used five buffered windows of the peak activity times at each site, using the peak activity time ± 1, 2, 4, 6 (half-day), and 12 (the entire day) hours. Notice that each estimate and SD is centered around the value used but jittered to allow seeing the variability estimate. Population density estimates of pigs (B) using five windows for peak activity. As the length of the activity window had a large qualitative effect on estimates from Zone A, we conservatively used the entire 24-hour window for our estimates.

Appendix S2

Climate parameterization

Estimates of climate variables were obtained from the Hawaiʻi Evapotranspiration Atlas and the Rainfall Atlas of Hawaiʻi (Giambelluca et al., 2013). Variables included mean annual temperature (Tmean), maximum annual temperature (Tmax), minimum annual temperature (Tmin), mean annual precipitation (MAP), mean annual vapor pressure deficit (VPD), total solar irradiance (TSI), mean annual transpiration (E), cloud frequency, and elevation (m). Variable estimates were calculated from relatively few weather stations and strongly covary, raising issues of multicollinearity. We applied dimension reduction by means of Principal Component Analysis (PCA) to extract the dominant axes of variation in climate.

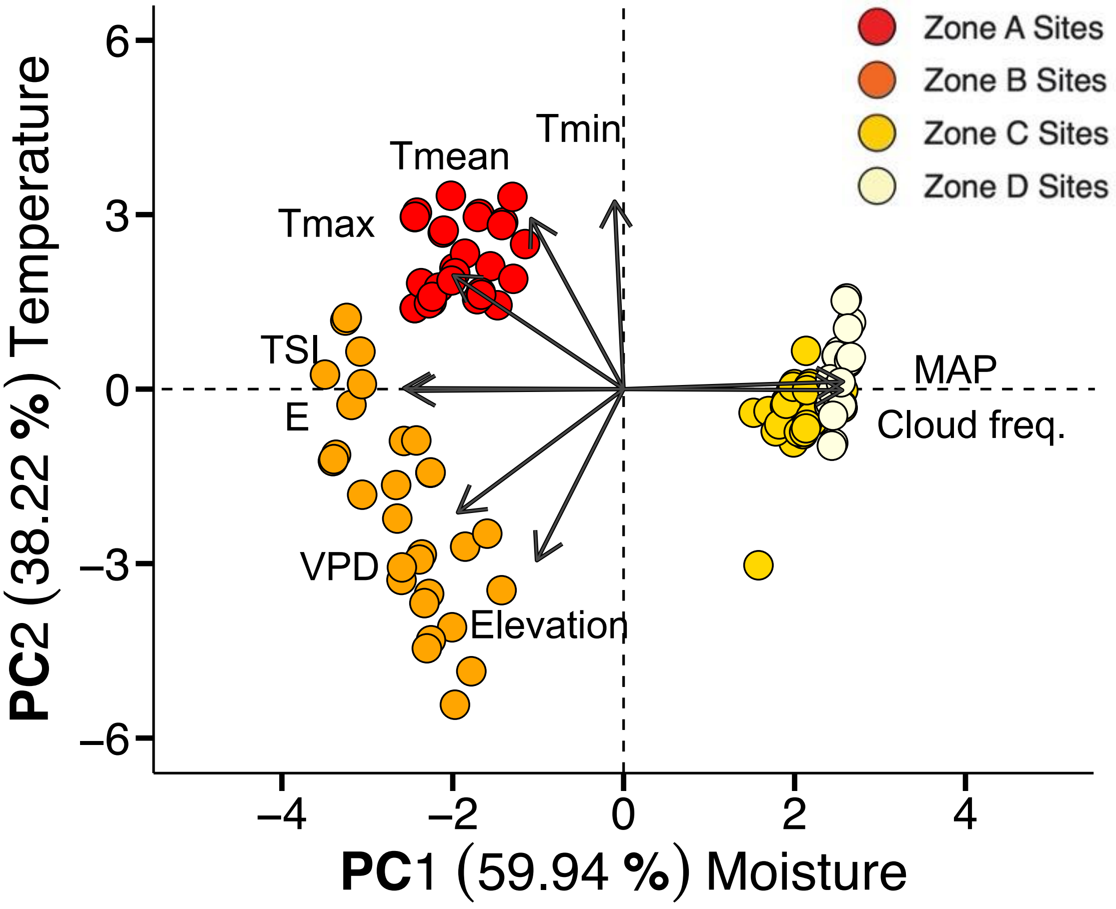

Fig S3. Principal component analysis of climate variables across the study area. Points represents sites and are color coded by pig density Zone. PC1 and PC2 capture > 98% of total variance. PC1 captures a gradient of moisture availability, with strong loadings from MAP, cloud frequency, TSI, and E. Negative values indicate drier conditions, while positive values indicate wetter conditions. PC2 tracks variation in Tmin and elevation, indicating PC2 largely captures a gradient of temperature, with negative values for colder, high elevation sites and positive values for warmer, low elevation sites.

Appendix S3

Optimal vegetation clusters

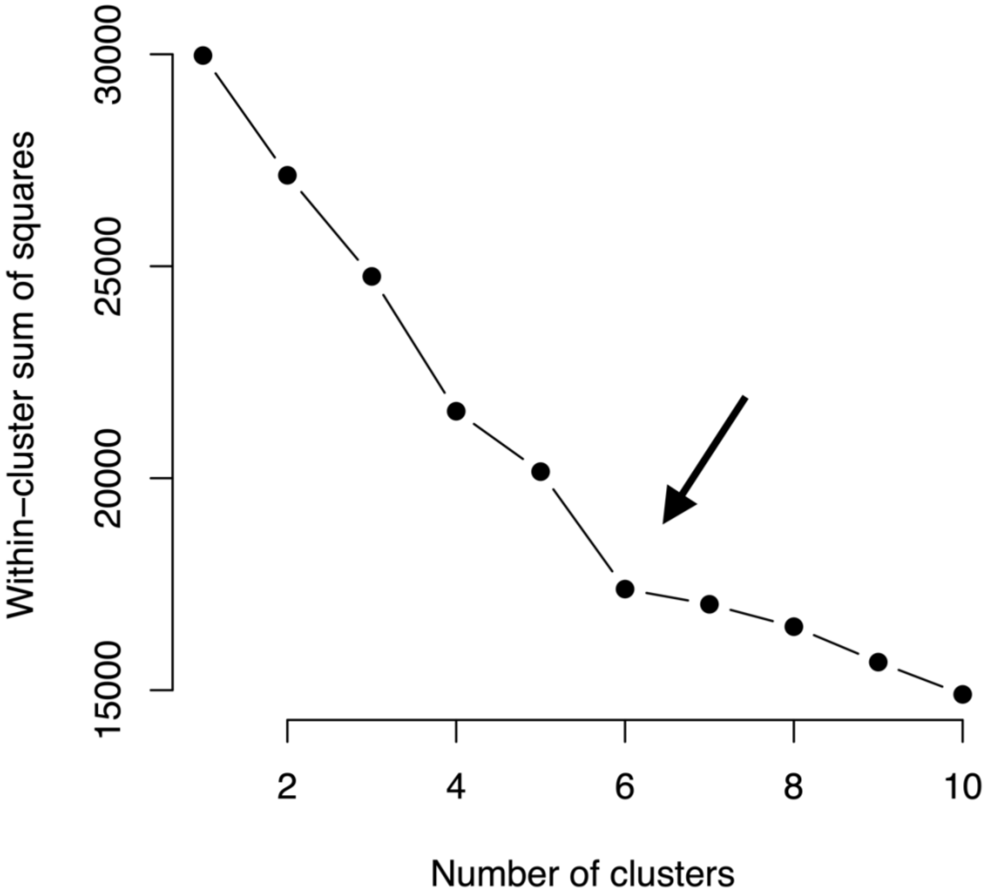

Figure S4. The optimal number of clusters for hierarchical agglomerative clustering of vegetation data was determined by assessing the reduction in within-cluster sum of squares (SS) as the total number of clusters was increased. The black arrow indicates the point where the relationship between within-cluster SS and number of clusters becomes less negative, indicating increasing cluster number past six clusters yielded diminishing returns (i.e. less reduction in within cluster variability with increasing number of clusters).

Appendix S4

Relationships between environment and species composition

Table S1. Linear relationships of environmental variables with NMDS axis scores. All variables shown are significant to $p < 0.05$. Correlation r calculated from regression R^2, with negative values indicating negative relationship to axis scores and positive values indicating positive relationship.

NMDS axis 1			**NMDS axis 2**			**NMDS axis 3**		
Variable	*r*	*p*	Variable	*r*	*p*	Variable	*r*	*p*
Soil disturbance	-0.78	***	Soil disturbance	-0.23	*	Temperature	-0.61	***
Sphagnum	0.77	***	Canopy openness	0.22	*	Pig density	-0.25	**
Pig density	-0.76	***						
Moisture	0.74	***						
Nurse log	0.24	**						
Temperature	-0.23	*						

Appendix S5

Community types

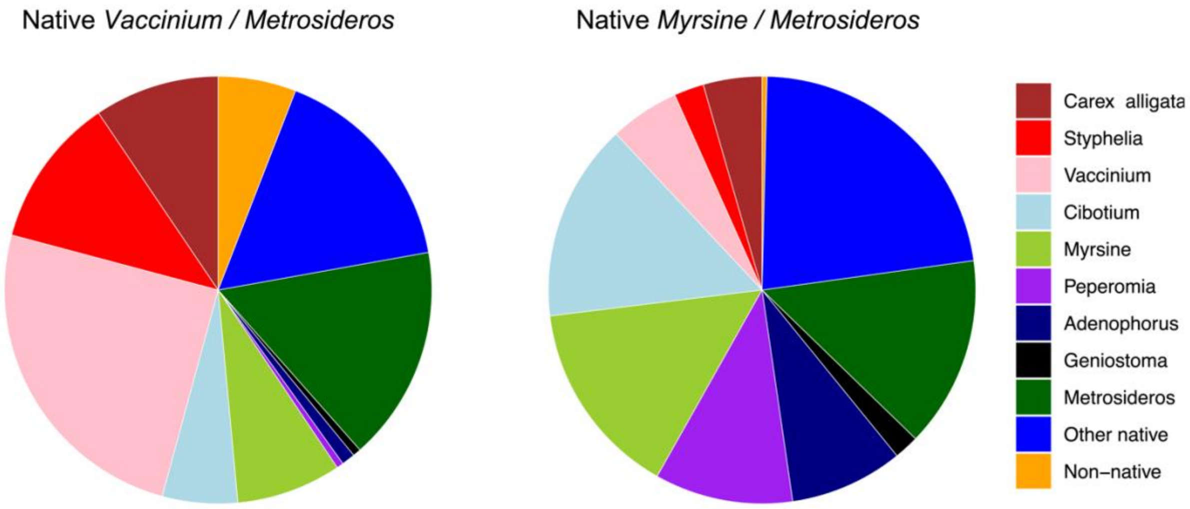

Figure S5. Species composition of Native *Vaccinium/Metrosideros* and Native *Myrsine/Metrosideros* communities. *Cibotium glaucum* and *Cibotium menziesii* combined into a single *Cibotium* category. Proportions correspond to the summed cover of each species across all sites within each community type, relative to total species cover for that community type.

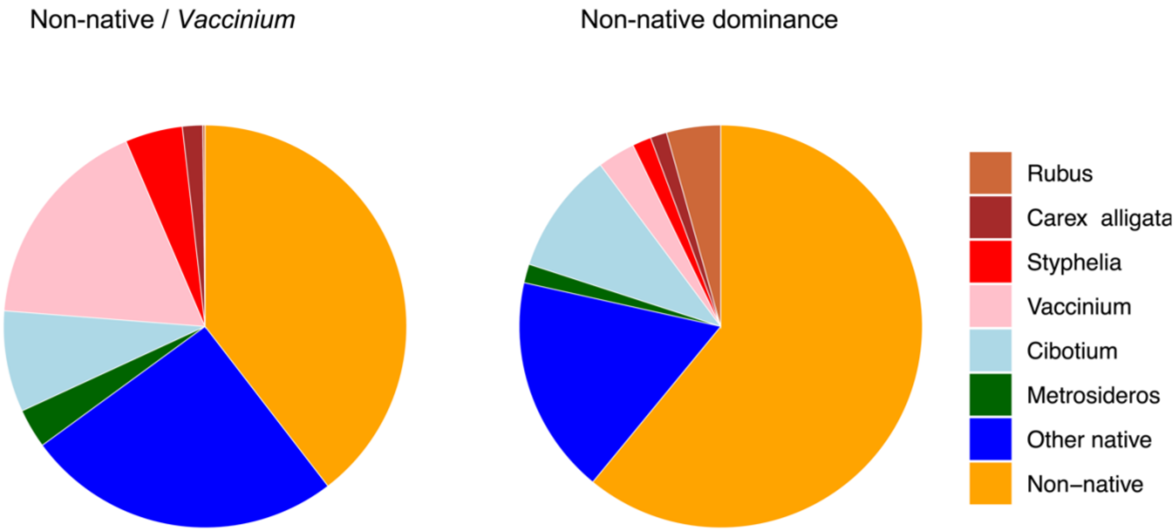

Figure S6. Species composition of Non-native/*Vaccinium* and Non-native dominance communities. *Cibotium glaucum* and *Cibotium menziesii* combined into a single *Cibotium* category. Proportions correspond to the summed cover of each species across all sites within each community type, relative to total species cover for that community type.

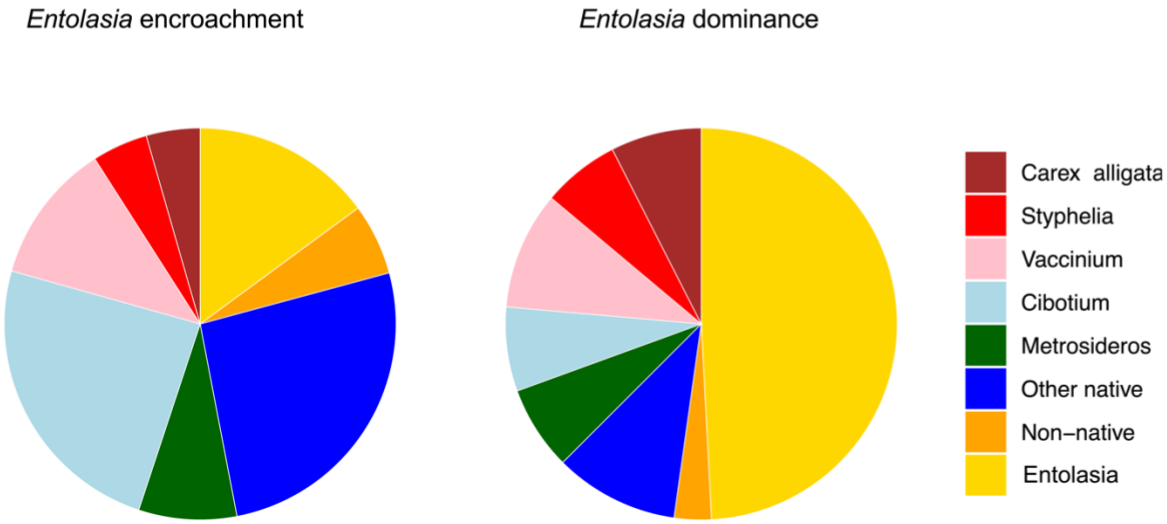

Figure S7. Species composition of *Entolasia* encroachment and *Entolasia* dominance communities. *Cibotium glaucum* and *Cibotium menziesii* combined into a single *Cibotium* category. Proportions correspond to the summed cover of each species across all sites within each community type, relative to total species cover for that community type.

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CHAPTER 2

Feral pig (*Sus scrofa*) disturbance facilitates establishment of resource-acquisitive species in Hawaiian forest understories

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Abstract

1. Invasive mammals exert pervasive effects on vegetation communities in island systems through several pathways, including by introducing novel disturbances. In Hawaiʻi, feral pigs pose a particular threat to endemic species that evolved in the absence of native ungulates. The effects of pig soil disturbance on understory vegetation are contingent on the distribution and density of disturbed patches and subsequent species responses influenced by traits conferring growth and reproductive strategies. However, little is known about how these traits influence native- non-native species turnover in response to pig disturbance, or how such disturbances affect trait-mediated responses to other environmental variables.

2. Here we quantify the effects of leaf traits and dispersal attributes on species responses to pig soil disturbance at two spatial grains – 0.5 m^2 *patches* embedded along 20 m transects within

sites – across a gradient of pig density in a Hawaiian montane wet forest using Bayesian mixed models.

3. Native and non-native species demonstrated divergent responses, with increasing presence and abundance of non-native species in the understory as soil disturbance within patches and sites increased. Dominant patterns in measured traits tracked the leaf economic spectrum (LES), with non-native species tending toward resource-acquisitive traits. Species with resource-acquisitive traits, regardless of identity, were favored by disturbance and responded positively to light availability in disturbed sites. Models showed species primarily dispersed by wind were more prevalent in disturbed patches and sites than those dispersed by endozoochory, while seed mass had no effect.

4. Our results suggest pig activity influences community composition and favors non-native species establishment, and these effects are mediated in part by traits conferring rapid resource acquisition. We also show that the extent of disturbance at the site-grain is relevant for the influence of leaf architecture on understory responses to light availability, demonstrating how the effects of disturbance are scale-dependent and can influence species sorting along independent environmental gradients.

Keywords: disturbance, invasive species, feral pigs, Hawaii, functional traits, community dynamics

Data available through the Dryad Digital Repository: https://doi.org/10.5061/dryad.3bk3j9ks5

Introduction

Ecosystems are increasingly shifting toward dominance by non-native species (Hulme, 2009; McGeoch et al., 2010; Pyšek & Richardson, 2010). This is a growing concern to conservation and management, especially in areas with high levels of endemism (Foster, Huenneke & Vitousek, 1990), where pressure on native species often leads to their local extinction (Leopold & Hess, 2017). Invasive mammalian herbivores can accelerate these shifts through numerous pathways, including by introducing novel disturbances, such as mechanical soil disturbance, which can favor non-native species establishment (Cushman et al., 2004; Huntly, 1991; Vavra et al., 2007; Wisdom et al., 2009). These impacts are particularly pronounced on remote islands with no history of mammalian herbivores (Risch et al., 2021), where they can dramatically transform vegetation communities (Webber et al., 2010). Digging, rooting, and trampling activity directly damages or removes established vegetation (Busby et al., 2010), indirectly alters nutrient dynamics (Aplet et al., 1991, Long et al., 2017), and creates a mosaic of patches in varying stages of regrowth with distinctly different soil properties from the surrounding habitat (Krull et al., 2013). The resulting changes to vegetation communities depend largely on plant species' responses to such disturbances, which are shaped by life-history characteristics and traits reflecting the conditions under which a particular lineage evolved (Cushman et al., 2004; Donovan et al., 2011; Gray et al., 2020) through effects on growth, defense, and reproduction (Sack & Buckley, 2020).

Advances in trait-based ecology have highlighted how physiological trade-offs and selective pressures constrain possible trait combinations across species and within communities (Agrawal, 2020; Díaz et al., 2016; Funk et al., 2017; Givnish, 1988; Shipley et al., 2006;

Westoby et al., 2002). These tradeoffs (e.g. leaf investment strategies in plants) have implications for competitive success under dynamic conditions (Dybzinski & Tilman, 2007; Laliberté et al., 2012; Suding et al., 2005). Accordingly, traits constraining rates of resource use and acquisition are important for community dynamics across resource gradients (Fajardo & Siefert, 2016) or where shifts in the strength of competition affect the importance of growth rates for competitive success (Webb et al., 2010). The leaf economic spectrum (LES) – describing return-on-investment in leaf construction, ranging from resource-acquisitive (fast) to resource-conservative (slow) strategies (Reich, 2014; Wright et al., 2004) – may be particularly important in shaping community structure when small-scale, patchy disturbance events modify the availability of space and resources (Anke & Michael, 2008; Lehsten & Kleyer, 2007). By altering competitive dynamics and selecting for particular trait combinations, biotic disturbances affect how LES traits influence responses to environmental variation (Colville et al., 2002; Douma et al., 2012; Fontana et al., 2017), which can fundamentally alter community structure and function (Lienin & Kleyer, 2012).

Success for resource-acquisitive or resource-conservative strategies depends on how the competitive benefits of fast growth rates compare to the costs of investment in photosynthetic tissue given the availability of water, nutrients, and light (Reich, 2014). Disturbance-adapted ecological strategies – characteristic of invasive species – are often associated with rapid resource acquisition and high dispersal ability, the latter typically conferred by small seeds and wind dispersal (Brown & Boutin, 2009; Mcintyre et al., 1995). Patch-grain biotic disturbance, then, can operate as a proximate mechanism for non-native species to persist (Hierro et al., 2006), and may facilitate their expansion by establishing source populations in disturbed patches. Disturbance-mediated native–non-native species turnover therefore likely varies across spatial scale, possibly leading to different patterns of non-native spread across scales. A comprehensive understanding of the mechanisms of disturbance-mediated species turnover must account for the functional traits of individual species, while also accounting for disturbance patterns across spatial scales.

Arguably the most consequential mammalian invader globally is the feral pig (*Sus scrofa*), which is now found on every continent except Antarctica (Nogueira-Filho et al., 2009; Wehr et al., 2018). Feral pigs significantly influence plant communities through several pathways, including by herbivory (Risch et al., 2021), altering nutrient dynamics (Gray et al., 2020), and acting as dispersal agents for native and non-native species (Diong, 1982), ultimately contributing to shifts in community composition and structure (Aplet et al., 1991). Critically, pigs also play a distinct role as biotic disturbance agents, significantly modifying surface soil conditions through activities such as rooting and wallowing, which dramatically alter establishment conditions for native plant species (Long et al., 2017). Understanding the effects of pig disturbance as a driver of ecological change involves identifying the mechanisms by which traits shape species outcomes in response to the influence of disturbance on the physical environment, and understanding how those effects interact with other environmental variables influencing trait expression. Linking plant functional traits to changes in occurrence and abundance (hereafter condensed to *species responses*) as a result of disturbance from exotic mammalian herbivores can help generate predictions to aid in understanding native–non-native species turnover.

Hawaiʻi is the most geographically isolated archipelago globally; as such, native species are predominantly endemic (Price & Wagner, 2018; Stone, 1967). Over the past millennium Hawaiʻi has been subjected to substantial invasion by exotic species, including many invasive plants that have already pushed a large number of endemic species to the brink of extinction (Stone et al., 1992; Vitousek & Walker, 1989). Pigs (*Sus scrofa*) were introduced between 400 – 1100 CE by Polynesian settlers, and again with European contact beginning in 1778 CE (Linderholm et al., 2016; Wilmshurst et al., 2011). Population densities of feral pigs in most sites are unknown due to difficulties in estimating population size in dense forests (Anderson & Stone, 1993). While flightless waterfowl (e.g., moa-nalos) were the dominant herbivores prior to human settlement (James & Burney, 1997), their effects likely differed from those of modern pigs due to divergent patterns of herbivory and soil disturbance, as well as a novel modern understory assemblage that includes non-native plants. The contemporary impacts of this novel top-down pressure on vegetation are dramatic, with significant effects on vegetation spatial structure (Webber et al., 2010), composition (Leopold & Hess, 2017), and productivity (Cole et al., 2012; Murphy et al., 2014). Pig soil disturbance has been shown to increase non-native species abundance and diversity in some systems (Cushman et al., 2004; Krull et al., 2013) but not others (Gawel et al., 2018; Gray et al., 2020); in Hawai‘i, pig removal sometimes results in substantial increases in the abundance of non-native plant species at the expense of native species, which are outcompeted following this release from top-down pressure (Cole et al., 2012). Exclosures are typically employed to study these effects, and while powerful, this approach overlooks processes influencing community dynamics at other points along the continuum of pig population density where most contemporary Hawaiian forests are likely positioned. Studying how vegetation dynamics are influenced by biotic disturbance along this continuum can inform our understanding of the resilience of Hawaiian forests to novel biotic disturbance and non-native invasion.

Here we explore the influence of feral pig activity on community dynamics in a Hawaiian montane wet forest understory by investigating patterns in community composition along a gradient of pig population density and disturbance, using plant functional traits to identify mechanisms behind divergent responses among species. We target closed-canopy conditions where light is limiting to examine how relevant traits shape community dynamics in the presence of pig disturbance, utilizing local spatial scales where establishment success among individuals and populations is unlikely to be constrained by dispersal distances. While we recognize the importance of seed dispersal by pigs in structuring Hawaiian understory communities, we here focus primarily on the effects of soil disturbance and the ecological strategies influencing those responses. Specifically, we ask: (i) do differences in pig density and disturbance extent influence variation in plant community composition and outcomes for native and non-native species, (ii) what are the primary differences among native and non-native plant species in traits relevant for adaptations toward frequent disturbance, and (iii) can plant functional traits explain species-specific responses to pig disturbance by identifying shared ecological strategies? We hypothesize that biotic disturbances, via mechanical soil disruption, promote particular ecological strategies by altering the physical environment and abundance of native individuals, facilitating non-native species. Specifically, we predict that species with traits conferring rapid establishment and resource acquisition – which we predict are more likely to be non-native – would be associated with high levels of pig disturbance. Ultimately, these interactions could accelerate exotic species colonization or native-non-native species turnover.

Methods

Study System

We conducted this study at the Pu‘u O Umi Natural Area Reserve, located on Kohala mountain on Hawai‘i Island (Fig. 1). All work was done in accordance with Hawaii Natural Area Reserve special use permits (I1314, I2643). Kohala is a shield volcano, formed roughly 1000 kya with subsequent eruptions forming the dominant substrate layer in the study area roughly 150 kya (Sherrod et al., 2021; Spengler & Garcia, 1988). Kohala is the oldest volcano on Hawai‘i Island and hosts significant topographic relief due to thousands of years of erosion. Variation in climate in the study area near the summit of Kohala is limited, with mean annual temperature ranging from 13 – 14° C and precipitation exceeding 2000 mm annually with additional inputs from cloud water interception (Giambelluca et al., 2013), resulting primarily in a closed-canopy wet forest community (Wagner et al., 1991). The canopy is dominated by ‘ōhi‘a (*Metrosideros polymorpha*), and the understory supports abundant ferns including tree-ferns in the *Cibotium* and *Sadleria* genera as well as several common understory trees and shrubs such as ‘ōhelo (*Vaccinium calycinum*) and ‘ōlapa (*Cheirodendron trigynum*). Higher-elevation wet forests in Hawai‘i retain a higher diversity of native flora than do the more heavily invaded lowland areas (Ainsworth & Kauffman, 2010). Aggressive invasive species known to be dispersed by pigs through endozoochory, such as strawberry guava (*Psidium cattleyanum*) (Diong, 1982), are absent from the study area in Kohala. However, encroachment by other non-native species, such as Kāhili ginger (*Hedychium gardinarium*), water smartweed (*Persicaria punctata*), and carpet grass (*Axonopus fissifolius*) is of management concern in these forests. Pig exclusion fences have been used in Kohala to control feral pig populations for several decades, including northeast of the summit, where fencing was erected ~ 20 years ago. The relatively low-diversity assemblage of native and non-native understory plant species, along with the existence of the fenced area, provides a rare opportunity to explore how novel communities respond to introduced biotic disturbance, and how traits conferring adaptations that arose under markedly different conditions structure those responses.

Data Collection

The impacts of pig activity and disturbance vary by spatial grain, and effects on community composition are mediated in part by differences in establishment success due to disturbance within habitat patches. To capture these effects, we used a hierarchical design incorporating pig density at the zone-level, our broadest spatial grain, and pig soil disturbance (i.e. physically overturned soil as a result of pig activity) at two consecutively smaller grains: (i) within sites nested within zones (hereafter, D_{site}), and (ii) within habitat patches nested within sites (hereafter, D_{patch}). Four zones with 1-km radii, roughly equal to conservative estimates of pig home-range size in Hawaiian forests, were established within the study site (Fig. 1A; Diong, 1982). To capture patterns in understory composition and soil disturbance at the site- and patch-grain, we surveyed 30 sites within each zone using a stratified-random design (1 additional site was accidentally surveyed in Zone A, leading to a total of 121 sites). Sites with < 50% canopy coverage were excluded to target the understory under forested conditions. At each site, we established a 20-m transect oriented along a random azimuth from 0 – 360 degrees to capture site-grain community composition and disturbance. We then uniformly distributed 0.5 m x 0.5 m quadrats (hereafter, *patches*) at 3-m intervals along the transect starting from the 2-meter mark, for a total of six patches per site representing individual habitat patches where plant species establishment might occur. 14 patches were discarded from the analysis due to trees or other obstructions preventing quadrat establishment at locations along the transect, resulting in a total of 712 patch-grain measurements. This nested, hierarchical approach allowed us to untangle the effects of pig disturbance across multiple spatial grains and to test the underlying impacts of disturbance on vegetation community dynamics.

Disturbance and Vegetation Characterization

To quantify pig density within zones, we conducted a camera trap survey during Summer 2019 designed to estimate density following Rowcliffe et al. (2014). No animals were handled during this study; therefore, United States Federal Institutional Animal Care and Use Committee approval was not required. We randomly generated 20 potential trapping locations within each zone and deployed cameras at a random subset of 4-6 locations over three 10-14 day trapping periods. The absence of pigs at the fenced zone D was confirmed by camera traps at seven locations over the final two trapping periods. Camera traps were programmed to collect a set of three pictures for every trigger with a 1-second delay between triggers. Cameras were attached to trees within a 20-m radius from each sampling location in an area where pig activity was evident from signs of trails, rooting activity, and scat to avoid underestimation of population size (Rowcliffe et al., 2008). Cameras were attached ~50 cm above the base of a tree and were oriented to have a capture distance of 5 m and to capture images within an angle of ~45 degrees. To calculate pig density estimates, we fit a random encounter model (REM), which assumes the trapping rate (number of photographs taken per unit time) provides quantitative information about the density of a species (Rowcliffe et al., 2008, 2014). This model estimates population density from random encounters with camera traps while parameterizing covariates that affect trapping rate. We used a bootstrapping approach to integrate sampling (location-specific variability) and non-sampling (i.e., model dependencies) error in our final density estimates (see Chapter 1 Appendix S1).

To capture site- and patch-specific patterns of pig disturbance, we conservatively defined disturbed area as that with visible signs of mechanical disturbance to surface soil structure from digging, wallowing, and trampling activity. Other ungulates (e.g. goats, sheep) that could be associated with these disturbances were not detected in the camera trap survey and are presumed to be absent. Pig trails, defined here as patches and pathways with clear evidence of pig use but without overturned soil, were excluded. To calculate disturbance extent within patches (D_{patch}), we estimated percent disturbed area within each patch and assigned estimates to cover categories of 0%, 0-10%, 10-25%, 25-50%, 50-75%, and 75-100%. Estimates are presented as the median value for each category to reduce measurement bias. To capture disturbance at the site grain (D_{site}), we independently measured disturbance along each 20-m transect at each site by summing the length (within 0.05 m) of transect segments intersecting disturbed soil as defined above. As nurse logs are important for native woody species establishment in Hawaiian wet forests (Rehm et al., 2021; Santiago, 2000), we quantified nurse log area using the same methods as disturbance (NL_{patch} in patches, NL_{site} in sites).

We estimated light availability using hemispherical photographs taken with a 180° fisheye camera lens at three points along each transect, each located between quadrat pairs. Using the Gap Light Analyzer software (Frazer et al., 1999), we calculated canopy openness for each photograph, which we used as a metric for light availability. For patch-grain measurement, we assigned light availability values (hereafter, $Light_{patch}$) to pairs of patches located most closely to where each photograph was taken, and averaged all three measurements for site-grain estimates (hereafter, $Light_{site}$).

Finally, we assessed the composition of understory vascular plants at both the patch- and site-grain. At the patch-grain we identified individuals < 2 m tall and rooted within each quadrat to assess species occurrence (i.e. presence/absence) within habitat patches. At the site-grain we evaluated patterns of community composition by estimating understory species cover using a point-intercept approach. Vascular plant species intercepted between 0 – 2 m in height were recorded at intervals of 0.5 m for a total of 41 points per site. Individuals were identified to the species level except for *Peperomia*, *Coprosma*, and *Adenophorus*, which were identified to the genus level because characteristics for species-level identification were typically missing. Flowering plant taxonomy was based on Wagner (1991) with updated nomenclature according to Smith and Brown (2018), and pteridophyte taxonomy was based on Palmer (2002).

Trait data collection

To understand how plant responses to pig activity and disturbance are influenced by differences in plant ecological function, we measured functional traits associated with leaf construction and dispersal. Leaf investment strategies can be identified by covariance in leaf traits linked to maximum photosynthetic rate and growth, such as specific leaf area (SLA), leaf carbon to nitrogen ratio (C:N), leaf thickness, and leaf dry matter content (LDMC) (Díaz et al., 2016; Reich, 2014; Wright et al., 2004). To measure these characteristics, we sampled fully expanded leaves (≥5 per individual) from 6 haphazardly selected individuals of each species where possible, distributed across at least 3 pig-activity zones. Due to the presence of *Sphagnum* in Kohala (Schomaker, 2017), 3 individuals of each species were selected to be rooted in *Sphagnum* where possible to account for differences in N concentrations in *Sphagnum* and non-*Sphagnum* areas. All leaves were collected, weighed, placed in moist plastic bags, and leaf area and thickness were measured within 48 hours of collection. Leaf area was measured using a LI-COR area meter. Leaves were weighed for fresh mass, dried at 60°C for at least 48 hours or until fully dry, weighed again for dry mass, ground using a Wiley mill, and sent to the University of New Mexico Center for Stable Isotopes (Albuquerque, NM) for %C and %N content using accelerator mass spectrometry. SLA was calculated by dividing leaf area by dry mass, and LDMC was calculated by dividing dry mass by fresh mass. Lycophytes were removed from the analysis due to incongruencies in comparing lycophyte microphylls to megaphylls of other species. Average seed mass for angiosperms was extracted from Yoshinaga et al. (*unpub*) and published sources from the TRY Plant Traits Database (Kattge et al., 2020) (Appendix S5). For species for which data were not available, we averaged available seed mass values among the most closely related species in the genus. Analyses involving seed mass and dispersal were conducted with pteridophytes removed.

Data Analysis

Patterns of community composition

To evaluate whether pig density and disturbance are associated with compositional differences among sites, we first explored patterns in site-level community cover estimates using non-metric multidimensional scaling (NMDS). NMDS is unconstrained and non-parametric, lacking assumptions about how species distribute along gradients. Rare taxa (those occurring at <5% of sites) were removed to reduce overweighting. We fit the ordination to 2 dimensions using Bray-Curtis distance with the *metaMDS* function in the *vegan* package (Philip, 2003) in the statistical software R (v4.1.2; R Core Team 2021). Measured drivers (D_{site}, $Light_{site}$, NL_{area}, and pig density) were passively overlaid to visualize linear relationships between community composition and the measured drivers using the *envfit* function in the *vegan* package.

Traits of native and non-native species

To define our functional leaf trait space, we conducted a principal components analysis (PCA) on leaf traits using mean values for the species included above. We identified the LES along the first axis of the ordination (see results) and proceeded by extracting values of PC1 as a composite latent variable describing species' relative position on the LES for subsequent analyses.

Plant functional responses

Multi-level generalized linear mixed models (GLMMs) are a powerful tool for testing trait-environment relationships while retaining location-level information, accounting for non-independence among species responses to environmental variables within locations, and describing the full hierarchical structure of the data (Jamil et al., 2013; Li & Ives, 2017; Miller et al., 2019; Pollock et al., 2012). The approach fits a single model to predict the occurrence of *n* species at *m* locations simultaneously (Miller et al., 2019; ter Braak, 2019). Species are allowed to vary in their intercepts and slopes to account for species-specific responses to environmental variables. Here we used a Bayesian generalized linear mixed model for binomial data with the form:

$$Y_i = \text{binomial}(n,p)$$

$$\text{logit}(p) = \text{env} * \text{trait} + (1|\text{location}) + (1|\text{spp}) + (\text{env}|\text{spp}) + (\text{trait}|\text{location}),$$

where Y_i gives the occurrence (i.e. presence/absence) of each species in each patch. The interaction (env * trait) tests the trait-environment relationship and is our focus of evaluation. (1|location) provides the random effect for location, and the random effect (1|species) accounts for differences in occurrence probabilities among species. (env|spp) gives random effects for species-specific responses to environmental variable env and follows a multivariate Gaussian distribution. This assumes species-specific slopes in response to env are variable but independent among species. The random effect (trait|location) accounts for variation in trait values attributed to unobserved environmental variables that can vary by location, and can lead to inflated Type-I errors if left unaccounted for (ter Braak, 2019).

Closely related species tend to share traits more often than distantly related species, which can lead to inflated type-I errors (Li & Ives, 2017; Miller et al., 2019). Thus, we performed our analyses while accounting for phylogenetic relatedness using Bayesian phylogenetically structured versions of generalized linear mixed-effects models (PGLMM’s). Specifically, we included a separate (env|spp) random variable containing variation among species in response to environment, with this variation assumed to be correlated among species, where phylogenetically related species show similar responses to env. The model fitting process weights phylogenetic and non-phylogenetic (env|spp) according to the data, and if, for example, phylogenetically related species are not more likely to share the same response to env, the variance of the corresponding random variable is estimated as zero. We obtained a phylogeny of all vascular plant species in our study using the V.Phylomaker package (Jin & Qian, 2019). V.Phylomaker incorporates an angiosperm phylogeny generated from molecular data from GenBank and the Open Tree of Life project (Smith & Brown, 2018) and Zanne et al.'s (2014) pteridophyte phylogeny to construct a larger vascular plant mega-tree. We pruned this larger phylogeny to include only species found in our dataset. While this tree has low taxonomic resolution at the species level and can be considered inappropriate for addressing evolutionary questions, the information it contains should be more than adequate to account for community-scale phylogenetic patterns (Li et al., 2019). PGLMM's were conducted using the *pglmm* function in the package *phyr* (Li et al., 2020).

We fit different models at the patch- and site-grain to assess occurrence in habitat patches and abundance in sites, using phylogenetic linear mixed-effects models (PLMM's) for the site-grain with a similar structure to the PGLMM's used for the patch-grain. For each spatial grain, we fit separate models for each trait of interest and evaluated the strength of the interaction of the chosen trait variable with patch-, site-, or zone-level drivers. Specifically, we assessed interactions with D_{patch}, D_{site}, pig density, $Light_{patch}$, and NL_{patch} as fixed effects for patch-grain models, and D_{site}, pig density, $Light_{site}$, and NL_{site} for site-grain models. Each of these covariates were also included in separate random effects (env|spp). We used the patch and site as the random effect for location in the patch-grain and site-grain models, respectively, after confirming no qualitative differences in fixed effects when including higher levels of hierarchical organization. Both categorical traits (species native or non-native status) and continuous traits (species PC1 values identifying relative position along the LES) were tested using this model structure. Specifically for models using LES traits (PC1 values), we also tested interactions among traits, light availability ($\mathrm{Light}_{\mathrm{patch}}$ for patch-grain models, $\mathrm{Light}_{\mathrm{site}}$ for site-grain models), and disturbance at each spatial grain (D_{patch} and D_{site} for patch-grain models, D_{site} for site-grain models) separately with three-way interactions within the same model structure to explore whether disturbance at each spatial grain influenced how LES traits structure responses (i.e. occurrence within patches or abundance within sites) along the independent light availability gradient. All continuous predictors were scaled prior to inclusion in models.

We isolated flowering plants to test the effects of dispersal mechanism and seed mass separately using the same model structure as above, excluding ferns due to differences in reproductive and early life-history characteristics (Gómez-Noguez et al., 2016). We tested the effect of dispersal mechanism using a binary categorical variable to conservatively characterize species by the two primary modes of dispersal (wind vs animal dispersal) obtained from Wagner et al., (1991), with the understanding that some wind-dispersed species may also be dispersed through epizoochory, albeit less often (Sorensen, 1986).

Results

Pig disturbance and community composition

The estimated population density of pigs was highly variable across zones, ranging from 0 individuals at Zone D to 17.5±7.5 (mean ± SD) individuals per km^2 in Zone A (Fig 1B). Sites demonstrated some segregation in understory community composition across pig density zones along the first axis of the NMDS, with considerable overlap along the second axis (Fig 1C). Zone A (high pig density Zone) exhibited the highest variation among sites, while Zone D (pig exclusion Zone) showed the lowest. Pig density and site-grain disturbance (D_{site}) demonstrated strong correlation with NMDS site scores, principally along axis 1 (positive), while nurse logs (NL_{site}) showed a weak and opposite (negative) correlation along axis 1. $Light_{site}$ was primarily correlated with axis 2 (Table 1). All non-native species exhibited positive species scores along axis 1 (i.e. in the same direction as pig density and soil disturbance), while native species exhibited both positive and negative scores (Appendix S2). The average ratio of non-native vs native cover by site decreased from Zones A – D (A: 1.38±1.43, B: 0.53±0.72, C: 0.11±0.22, D: 0±0.01; mean ± SD), tracking declines in pig density (Appendix S1).

Trait characterization

Our PCA captured >80% of leaf trait variation within the first two axes. The first axis (PC1, 52.59% variance explained) closely tracked the LES, primarily describing variation in C:N, SLA, and LDMC, with positive values representing low C:N, high SLA, low LDMC leaves (Fig. 2). Species with higher PC1 values possessed traits associated with resource-acquisitive leaf investment while negative PC1 values were associated with resource-conservative leaf investment. The second axis (PC2, 28.49% variance explained) primarily encompassed variation in leaf thickness, with positive values for species with thicker leaves and negative values for species with thinner leaves. Leaf dry matter content (LDMC) was also associated with this dimension and increased with more negative values of PC2 (Appendix S3). Native and non-native species overlapped along both PCA axes but demonstrated more separation along the first axis of the ordination, with native species generally possessing lower PC1 values and non-native species exhibiting higher PC1 values. These results suggest trade-offs in carbon economics underlie the primary differences among these taxa in the measured traits, and the principal separation between native and non-native species occurs along this dimension. We proceeded by using PC1 axis scores as a metric quantifying the relative position of species along the LES.

Phylogenetically structured models

Our PGLMM's and PLMM's depict the extent to which traits influenced species responses to pig activity and other drivers. Our patch-grain model showed non-native species were associated with greater D_{patch} and zones with higher pig density. Our site-grain model similarly demonstrated that non-native species increased with D_{site} and pig density, while native species also increased with NL_{site}, supporting prior research demonstrating the importance of nurse-logs for native species (Santiago 2000). Our PC1 trait models showed that resource-acquisitive species (those with higher PC1 values) occurred with higher probability in more fully disturbed patches and at higher abundances in more disturbed sites than did resource-conservative species (Fig. 3), although D_{site} did not favor resource-acquisitive species in the patch-grain model. Light availability did not influence resource-acquisitive species occurrence or abundance in either model, but both models supported a positive interaction with light and D_{site}, indicating higher light availability favored resource-acquisitive species in disturbed sites, and the slope of this relationship increased with higher values of D_{site} (Fig 3A, 3C). Our patch-grain dispersal model supported dispersal mechanism as an important trait predicting angiosperm species responses (i.e. occurrence) to D_{patch} and D_{site} – favoring wind-dispersed species – but our site-grain model found no effect (Fig. 4). Surprisingly, seed mass had no effect on angiosperm species responses at either spatial grain.

Discussion

Novel disturbances can accelerate the spread of non-native species by introducing dynamic conditions favoring adaptations shared among invading species (Fenesi et al., 2015; Marvier et al., 2004). Our findings support predictions that invasive feral pigs, as biotic disturbance agents, can propagate these effects to influence native–non-native turnover. Indeed, compositional differences among sites along NMDS axis 1 indicated sites exposed to higher pig density and soil disturbance host understory assemblages that differ from those with low pig density and disturbance (Fig 1C) and supported a higher abundance of non-native species. Furthermore, we detected (i) divergent responses to pig activity by native and non-native species in both patches and sites (Fig 3B, 3D), (ii) qualitative differences in our measured functional traits, demonstrating well-established differences along the LES (Fig 2), and (iii) differences in species responses to soil disturbance associated with their relative position along the LES (Fig 3A, 3C). Generally, native and non-native species were positioned toward opposite ends of the LES, reflecting findings from other invaded systems with non-native species largely possessing resource-acquisitive traits (Baruch & Goldstein, 1999; Escobedo et al., 2021; Gallagher et al., 2015; Leishman et al., 2007). Resource-conservative leaf investment was more frequently observed in the absence of disturbance, likely due to higher resource-use efficiency facilitating persistence and growth under more stable conditions (Grime, 1973). Conversely, we found resource-acquisitive species were more frequently observed in disturbed patches and sites (Fig

3). Periodic disturbance has been shown to limit competitive dominance by resource-conservative, slower-growing species (Carreño-Rocabado et al., 2012; McCoy-Sulentic et al., 2017), providing conditions for faster-growing resource-acquisitive species to establish and grow to maturity between disturbance events (Anke & Michael, 2008; Douma et al., 2012). Our findings demonstrate pig soil disturbance likely functions similarly to other small-scale, periodic disturbances by creating gaps where established individuals – particularly those of native origin – are removed (Appendix S4), thus promoting species with faster rates of resource acquisition and utilization and establishing patches within the habitat mosaic more suitable for non-native species.

Position along the resource-acquisitive to resource-conservative spectrum did not directly influence species responses to light availability within the bounds of our low- to moderate-understory light gradient, but did so in interaction with D_{site}, demonstrating how disturbance can alter trait-mediated responses to environmental variables. Research on LES traits has repeatedly demonstrated that species with resource-acquisitive strategies generally exhibit higher rates of carbon capture and growth in higher light conditions (Marino et al., 2010); however, under the range of light conditions we sampled (63 – 93% canopy cover), we found evidence for this pattern only in more abundantly disturbed sites, as shown by a positive D_{site} x light interaction and no support for a main effect of light at both spatial grains (Fig 3A, 3C). This suggests that *site-grain disturbance* creates conditions favorable for resource-acquisitive species to exploit higher understory light conditions and was observed in both patch-grain occurrence and independently measured site-grain abundance of resource-acquisitive species. A lack of evidence for a similar positive effect of light with patch-grain disturbance (D_{patch} x $Light_{patch}$) indicates that resource-acquisitive species establishment in response to patch-grain disturbance occurs largely independently of understory light availability. These findings collectively demonstrate how trait-mediated species responses to local light availability, under relatively closed-canopy conditions, qualitatively differ with the spatial grain of disturbance.

These divergent trait-mediated light responses suggest a role for LES traits in structuring responses to light in disturbed sites but not in disturbed patches. The observed patterns may be expected if localized disturbance within a patch operates more strongly to promote resource-acquisitive species establishment than does disturbance diffusely distributed within a site, obscuring any differences influenced by light availability within disturbed patches. The spatial grain of disturbance may also affect its influence on competitive dynamics: for example, if patch-grain disturbance acts more strongly to remove established residents and limit belowground competition than does site-grain disturbance, patch-grain disturbance may release nutrient constraints from belowground competition for resource acquisitive species establishment under low-light conditions. This can result in resource-acquisitive establishment in disturbed *patches* independently of light availability while supporting an effect of light on establishment in disturbed *sites*. Alternatively, higher rates of N mineralization in disturbed patches may locally increase biologically available N in the short term (Kristensen et al. 2000), expanding the range of light conditions that can sustain resource-acquisitive investment (Goldberg & Miller, 1990; Harpole et al., 2016). Testing these and other hypotheses falls outside the limits of our approach, but our findings nevertheless suggest the effects of disturbance vary by spatial grain to influence how carbon economics shape community dynamics along environmental gradients.

Dispersal unmistakably plays a major role in influencing a species' ability to colonize and establish within recently disturbed patches (Canham & Marks, 1985). Wind dispersal is often accompanied by the production of large numbers of seeds, which can increase the likelihood of arriving at a disturbed patch (Howe & Smallwood, 1982). Wind dispersal is also more effective in open sites where higher wind speeds increase the efficacy of transport (Lorts et al., 2008). Results from our patch-grain model testing the effect of wind vs animal dispersal in flowering plants partially aligned with these observations, with wind dispersal favoring occurrence in disturbed patches and sites, but with no effect of canopy openness, likely due to the limited range of canopy coverage included in this study (Fig 4.) However, we found no effect of dispersal mechanism in structuring responses at the site-level, suggesting that while patch-grain establishment in disturbed sites is mediated by the mode of dispersal, overall abundance within a local understory community is primarily driven by other factors such as resource use and carbon capture. However, our designation of dispersal mechanism was coarse and therefore did not capture the full spectrum of complexity encompassed by dispersal syndromes; for example, primarily wind-dispersed species may be dispersed through fur-epizoochory or by adhesion to hooves (Baltzinger et al., 2019), which may also explain the higher occurrence of wind-dispersed species in disturbed patches. Epi-and-endozoochory by pigs undoubtably influences species distributions (Pedrosa et al., 2019), particularly in other forests with invasive species (e.g. strawberry guava) known to be dispersed by pigs (Diong, 1982), but we did not find support for an effect of pig density in our models at either spatial grain. More careful designation of dispersal syndromes, including the characterization of traits facilitating epi-and-endozoochory, is necessary to determine the role pig dispersal plays in structuring this community. Nevertheless, even with a binary characterization of dispersal mechanisms, our results still suggest soil disturbance influences how dispersal affects establishment success.

In summary, our findings demonstrate pig soil disturbance in Hawaiian wet forest understories alters conditions to favor non-native species through shared traits involved in resource acquisition and dispersal. We see a shift from conditions rewarding efficiency to those favoring rapid establishment and resource acquisition, as expected when frequent disturbances disrupt otherwise stable conditions and alter trajectories of understory development – favoring the spread of non-native species and furthering native-non-native species turnover. We also show that the effects of disturbance vary by spatial grain to alter the influence of leaf architecture on species sorting along the understory light availability gradient, demonstrating how disturbance can influence species responses to independent environmental variables. Hawai‘i island varies enormously in climate over larger spatial scales (Giambelluca et al., 2013), and further study on how disturbance interacts to influence trait expression and species responses along climatic gradients will provide important context for current species distributions and future dynamics. While some impacts of pigs on vegetation – such as herbivory – were not directly captured in this study, our measurements of pig density roughly captured the effect of these factors in the aggregate. These collectively demonstrated positive effects for non-native plant species unexplained by traits involved in carbon economics and should warrant further study. Finally, we show that applying trait-based techniques and hierarchical statistical modelling can provide useful insights into the drivers behind shifts in community dynamics. Applying similar frameworks to questions of biotic invasions and disturbance offers the opportunity to obtain deeper insights into the mechanisms driving ecological change, particularly where management and conservation goals require a sophisticated understanding of system dynamics.

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Figures

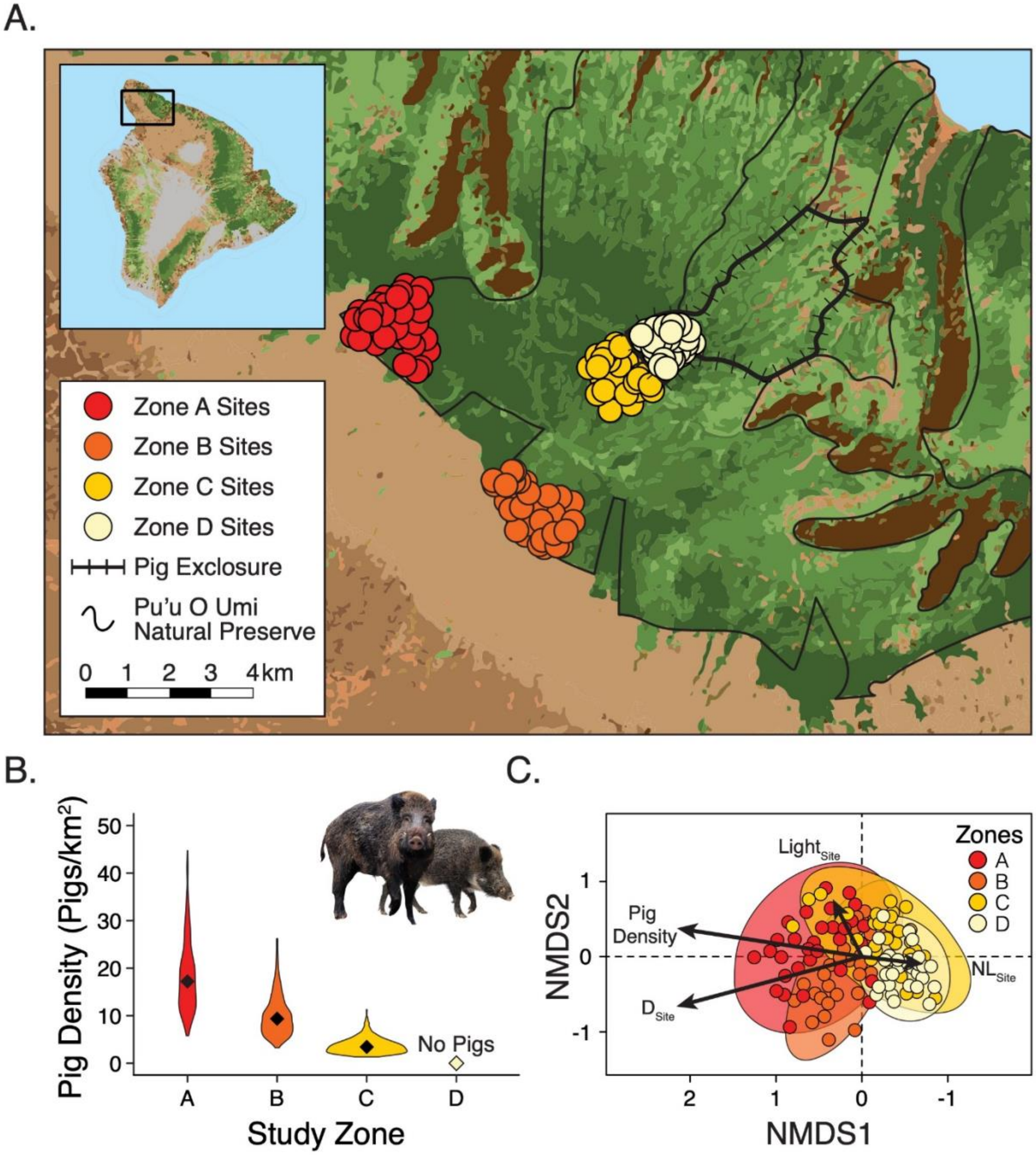
A.
Zone A Sites
Zone B Sites
Zone C Sites
Zone D Sites
Pig Exclosure
Pu'u O Umi Natural Preserve
0 1 2 3 4km
B.
Pig Density (Pigs/km²)
50
40
30
20
10
0
No Pigs
A
B
C
D
Study Zone
C.
Zones
A
B
C
D
Light_Site
Pig Density
D_Site
NL_Site
NMDS2
1
0
-1
2
1
0
-1
NMDS1

Figure 1. A: Locations of the vegetation survey sites color coded by position within pig-density zones in Kohala on Hawaiʻi island. Green shading marks the extent of forest cover and solid grey-outlined polygons delineate the Pu’u O Umi Natural Area Reserve. The hatched polygon marks the extent of the pig exclosure. B: Pig density estimates for each zone from the camera trap REM. C: Results from the unconstrained NMDS visualizing differences in species composition among sites in species-space using Bray-Curtis distance. Ellipses mark the 95% confidence interval for each pig-density zone. Vectors show linear relationships between species composition and measured drivers, and their lengths are scaled by their correlation (R^2) to NMDS1 and NMDS2.

Table 1. Table showing linear relationships between passively overlaied environmental drivers and species compositional scores in the NMDS (Fig. 1C). NMDS1 and NMDS2 show normalized coefficients representing the slopes of drivers with each NMDS axis. R^2 shows the proportion of variance in each driver explained by association with NMDS scores, and p-values were obtained using permutation tests (n = 999).

Environmental drivers	NMDS1	NMDS2	R^2	p
D_{site}	0.9626	-0.2710	0.6423	< 0.0001
Pig Density	0.9873	0.1589	0.6073	< 0.0001
NL_{site}	-0.9923	-0.1237	0.0669	0.0139
$Light_{site}$	0.4363	0.8998	0.0779	0.0074

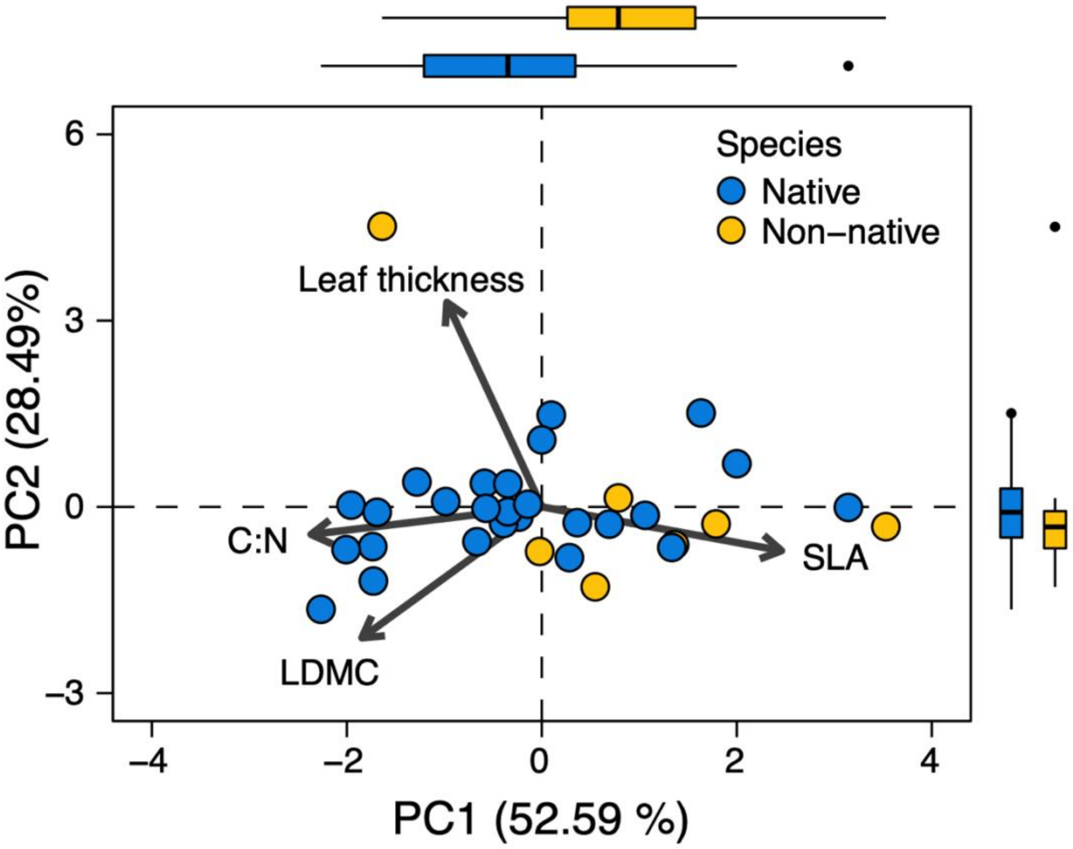

Figure 2. Principal component analysis of traits for the species occurring at >5% of sites. Blue dots signify native species, yellow dots signify non-native species. Vectors for each trait are proportional to PC1 and PC2 loading. PC1 can be described by the LES and explains 52.59% of the variance in measured traits, with higher values indicating resource-acquisitive leaf investment and lower values indicating resource-conservative leaf investment. Boxplots indicate separation between native and non-native species occurs primarily along PC1.

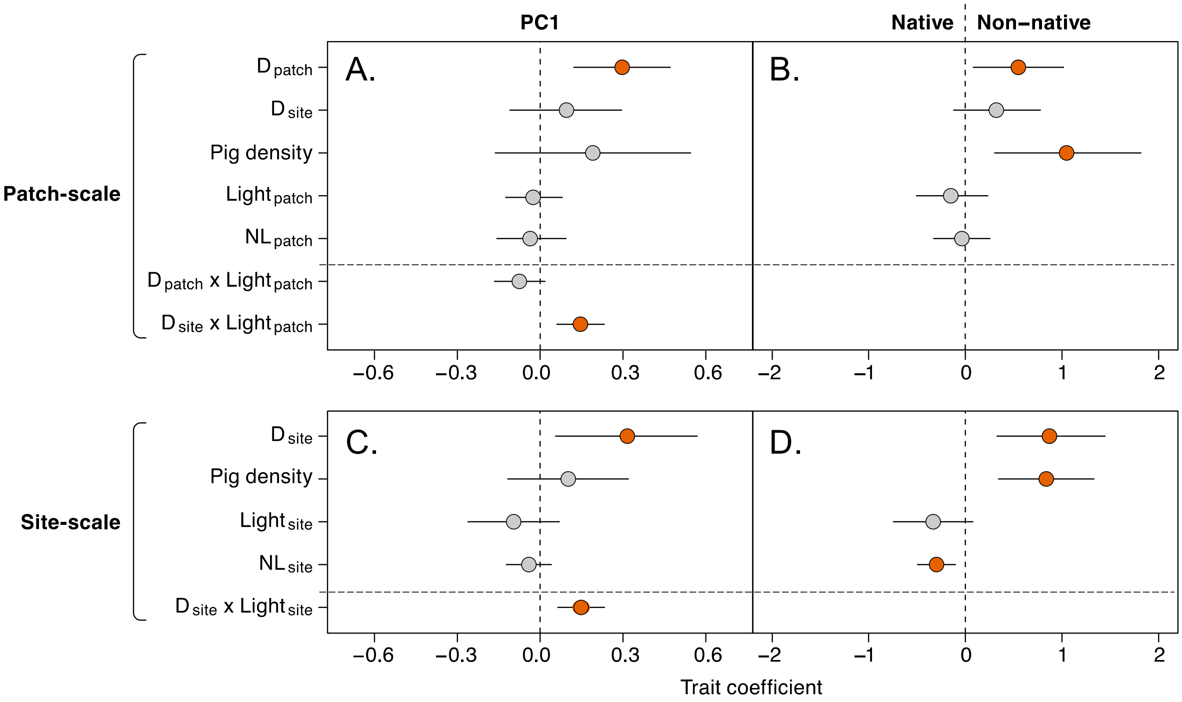

Figure 3. Coefficients of Bayesian PGLMM's and PLMM's testing the effects of species traits on occurrence (in patches) and abundance (in sites) with lines providing approximate 95% credible intervals. Red dots indicate strongly supported effects, grey dots indicate unsupported effects. PC1 represents species position along the LES, with positive values indicating resource-acquisitive investment and negative values indicating resource-conservative investment (Fig 2). Effects on native and non-native species were tested using binary categorization. A. Patch-scale PGLMM results showing the effect of PC1 on structuring differences in species occurrence with environmental drivers. D_{patch} x $Light_{patch}$ and D_{site} x $Light_{patch}$ demonstrate the interaction of disturbance at each scale with local light availability. B. Patch-scale PGLMM results showing how native vs non-native identity influences differences in species occurrence with

environmental drivers. C. Site-scale PLMM results showing the effect of PC1 on structuring differences in species abundance with environmental drivers. D_{site} x $Light_{site}$ demonstrates the interaction of disturbance with local light availability. D. Site-scale PLMM results showing how native vs non-native identity influences differences in species abundance with environmental drivers.

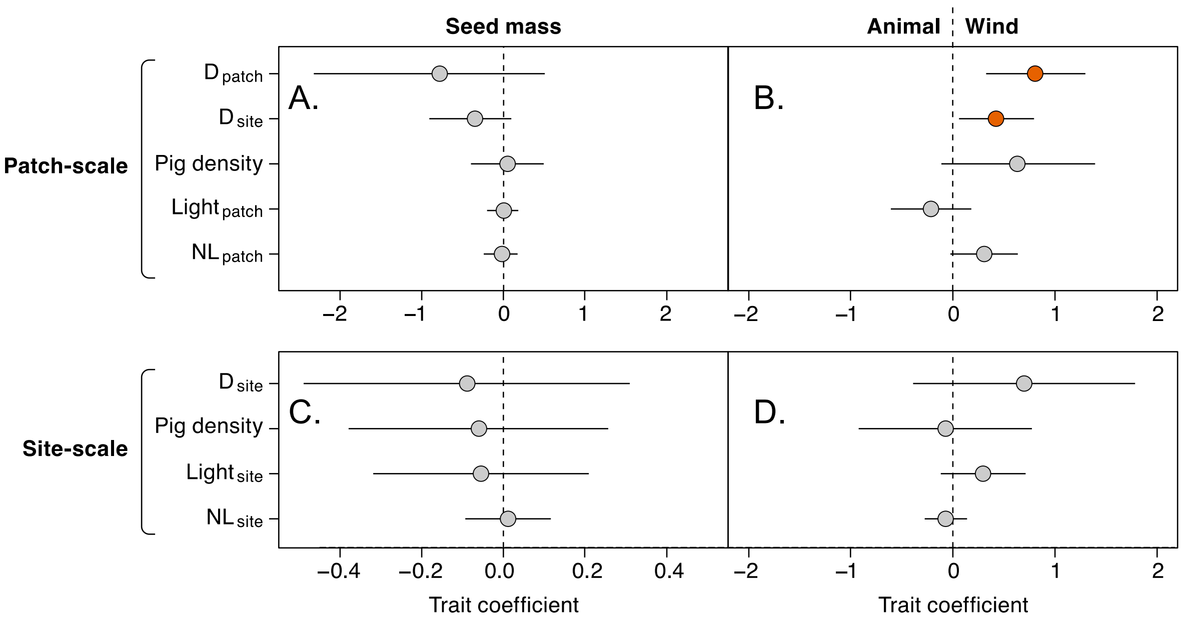

Figure 4. Coefficients of Bayesian PGLMM's and PLMM's testing the effects of dispersal traits on occurrence (in patches) and abundance (in sites) with lines providing approximate 95% credible intervals. Red dots indicate strongly supported effects, grey dots indicate unsupported effects. Effects on dispersal mechanism were tested using binary categorization (animal vs wind dispersal). A. Patch-scale PGLMM results showing the effect of seed mass on structuring differences in species occurrence with environmental drivers. B. Patch-scale PGLMM results showing the effect of dispersal mechanism on differences in species occurrence with environmental drivers. C. Site-scale PGLMM results showing the effect of seed mass on structuring differences in species abundance with environmental drivers. D. Site-scale PGLMM

results showing the effect of dispersal mechanism on differences in species abundance with environmental drivers.

SUPPORTING INFORMATION

Appendix S1

Table S1: Top: mean and sd for the ratio of site-scale non-native:native species cover by zone. Bottom: mean site-scale % cover estimates (number of 'hits' or detections by point-intercept / total number of points) by zone given for individual native and non-native species. Non-native species marked with *.

	Zone A	Zone B	Zone C	Zone D
Mean non-native:native cover ratio	1.38	0.53	0.11	0.00
SD non-native:native cover ratio	1.43	0.72	0.22	0.01
Mean species cover				
Non-native species				
*Axonopus_fissifolius	4.8	0.0	3.3	0.0
*Persicaria_punctata	18.0	2.3	0.2	0.0
*Hedychium_gardnerianum	13.5	3.7	0.8	0.1
*Ehrharta_stipoides	0.9	0.3	0.9	0.0
*Carex_longii	6.2	0.0	0.0	0.0
*Juncus_effusus	9.0	0.0	2.9	0.0
*Entolasia_marginata	0.0	22.2	0.2	0.0
Native species				
Carex_alligata	1.3	7.8	5.2	4.5
Cibotium_glaucum	3.0	11.4	1.4	1.5
Styphelia_tameiameiae	4.9	6.3	7.2	2.0
Metrosideros_polymorpha	3.6	9.5	12.8	12.3
Myrsine_sandwicensis	2.4	5.8	8.9	12.8
Rhynchospora_chinensis	3.0	7.1	1.5	0.1
Vaccinium_calycinum	13.8	13.2	18.0	5.8
Cheirodendron_trigynum	1.7	1.7	0.4	0.4
Cibotium_menziesii	5.9	6.3	4.7	12.3

Coprosma_spp	1.6	1.0	0.6	0.8
Dryopteris_glabra	0.8	0.9	0.4	0.2
Melicope_clusiifolia	2.7	0.7	2.7	4.1
Polypodium_pellucidum	0.3	0.4	0.0	0.0
Asplenium_polyodon	2.4	0.7	0.2	0.0
Peperomia_spp	1.2	1.0	3.1	8.9
Athyrium_microphyllum	1.4	1.7	0.3	1.4
Ilex_anomala	0.6	0.3	0.5	0.5
Broussaisia_arguta	0.1	0.7	2.0	2.4
Adenophorus_spp	0.2	0.2	3.3	6.7
Dryopteris_wallichiana	0.1	1.1	1.4	0.1
Alyxia_oliviformis	1.3	0.1	0.6	0.4
Sadleria_pallida	0.0	0.1	2.0	2.2
Rubus_hawaiensis	1.8	0.0	0.2	0.0
Myrsine_lessertiana	0.0	0.0	2.0	1.4
Melicope_pseudoanisata	0.0	0.0	1.9	1.9
Geniostoma_hedyosmifolium	0.0	0.0	0.5	2.0

Appendix S2

Table S2: NMDS species scores for each species, provided with native vs. non-native status. Note that all non-native species exhibit positive NMDS1 scores, while native species show a mix of both positive and negative NMDS1 values.

Species	NMDS1	NMDS2	Native/Non-native
Rubus_hawaiensis	1.2131	-0.8691	Native
Persicaria_punctata	1.1011	0.0030	Non-native
Hedychium_gardnerianum	0.8095	-0.2049	Non-native
Asplenium_polyodon	0.8012	0.0725	Native
Dryopteris_wallichiana	0.7904	0.1485	Native
Carex_longii	0.7566	0.4550	Non-native
Juncus_effusus	0.7146	0.4552	Non-native
Ehrharta_stipoides	0.6982	0.9193	Non-native
Coprosma_spp	0.6946	-0.3462	Native
Axonopus_fissifolius	0.6361	1.0073	Non-native
Rhynchospora_chinensis	0.4843	-0.0506	Native
Cibotium_glaucum	0.4223	-0.7570	Native
Dryopteris_glabra	0.4188	-0.1478	Native
Cheirodendron_trigynum	0.3771	0.0949	Native
Entolasia_marginata	0.3415	-0.4200	Non-native
Athyrium_microphyllum	0.3189	-0.4850	Native
Polypodium_pellucidum	0.2296	0.3744	Native
Ilex_anomala	0.0080	0.2485	Native
Vaccinium_calycinum	0.0003	0.5557	Native
Carex_alligata	-0.0534	0.1071	Native
Styphelia_tameiameiae	-0.0890	0.6471	Native
Alyxia_oliviformis	-0.1037	-0.5296	Native
Cibotium_menziesii	-0.1833	-0.1685	Native
Sadleria_pallida	-0.2343	0.0899	Native
Melicope_clusiifolia	-0.3002	-0.0282	Native
Metrosideros_polymorpha	-0.3144	0.3328	Native
Myrsine_sandwicensis	-0.4128	-0.0383	Native
Broussaisia_arguta	-0.5087	-0.5777	Native

Peperomia_spp	-0.6137	-0.1838	Native
Adenophorus_spp	-0.6868	-0.2398	Native
Myrsine_lessertiana	-0.7001	0.1293	Native
Geniostoma_hedyosmifolium	-0.8658	-0.2238	Native
Melicope_pseudoanisata	-0.8765	-0.0458	Native

Appendix S3

Trait PCA results

Table S3. PC loadings for each trait along four PC axes.

Traits	PC1	PC2	PC3	PC4
SLA	0.6144	-0.1767	0.0940	0.7631
C:N	-0.5918	-0.1110	-0.6017	0.5248
LDMC	-0.4615	-0.5275	0.6942	0.1640
Leaf thickness	-0.2435	0.8236	0.3837	0.3395

Table S4. PC scores along four PC axes for each species. Values of PC1 indicate relative position along the leaf economic spectrum, with positive values signifying resource-acquisitive leaf construction, while negative values signify resource-conservative leaf construction.

Species	PC1	PC2	PC3	PC4	Native/Non-native
Persicaria_punctata	2.4332	-0.2997	0.0294	2.3193	Non-native
Athyrium_microphyllum	2.1679	-0.0092	-0.4582	1.8324	Native
Rhynchospora_chinensis	1.3787	0.6511	-0.4177	0.0362	Native
Axonopus_fissifolius	1.2320	-0.2581	0.1177	0.0615	Non-native
Geniostoma_hedyosmifolium	1.1258	1.4167	0.3261	-2.6139	Native

Entolasia_marginata	0.9385	-0.5722	1.1952	0.1345	Non-native
Dryopteris_glabra	0.9195	-0.6139	-0.0081	1.2727	Native
Asplenium_polyodon	0.7302	-0.1279	0.0901	-0.8197	Native
Hedychium_gardnerianum	0.5416	0.1351	-0.4855	-1.2208	Non-native
Dryopteris_wallichiana	0.4767	-0.2610	0.1536	-0.3265	Native
Ehrharta_stipoides	0.3776	-1.2073	1.9682	-0.4830	Non-native
Adenophorus_spp	0.2506	-0.2390	-0.8622	-0.1606	Native
Rubus_hawaiensis	0.1944	-0.7660	1.1857	-0.0437	Native
Peperomia_spp	0.0664	1.3842	-2.0610	0.4286	Native
Broussaisia_arguta	-0.0009	1.0101	-1.3144	-0.6782	Native
Carex_longii	-0.0156	0.6734	-1.0359	-1.1080	Non-native
Alyxia_oliviformis	-0.0988	0.0385	0.0098	-0.8610	Native
Cheirodendron_trigynum	-0.1638	-0.1560	-0.5102	-0.5181	Native
Coprosma_spp	-0.2396	-0.0752	0.0023	-0.6001	Native
Sadleria_pallida	-0.2401	0.3473	0.5992	-0.1402	Native
Cibotium_menziesii	-0.2706	-0.2517	0.4116	-0.4967	Native
Polypodium_pellucidum	-0.3951	-0.0224	0.8159	-0.2319	Native
Melicope_clusiifolia	-0.4059	0.3551	0.3267	-0.9306	Native
Cibotium_glaucum	-0.4587	-0.5259	0.9399	-0.6948	Native
Melicope_pseudoanisata	-0.6798	0.0801	-0.0789	-0.7745	Native
Myrsine_sandwicensis	-0.8842	0.3750	-0.7631	0.3684	Native
Juncus_effusus	-1.1298	4.2333	2.7896	1.6096	Non-native
Myrsine_lessertiana	-1.1651	-0.0820	-1.1618	0.5612	Native

Vaccinium_calycinum	-1.1919	-1.1196	0.4447	1.0294	Native
Carex_alligata	-1.1967	-0.6002	-0.1460	0.3727	Native
Ilex_anomala	-1.3496	0.0253	-1.6350	1.1463	Native
Metrosideros_polymorpha	-1.3844	-0.6451	-0.3102	0.6548	Native
Styphelia_tameiameiae	-1.5624	-1.5460	1.2544	0.8748	Native

Appendix S4

PGLMM model results

Table S5. Phylogenetic generalized mixed model (PGLMM) results for patch-scale multi-level models (MLMs). Results shown for PC1 model, identity model, dispersal mechanism model, and seed mass model, respectively. PC1 and seed mass model test continuous responses, while identity and dispersal mechanism models test binary categorizations. 'Pvalue' column for fixed effects represents whether 95% credible interval does (0.6) or does not (0.04) overlap with 0.

PC1 (LES traits) model

Random Effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Patch	5.20E-05	0.00721382	1.92E-05	0.00024829
1|species	1.88024717	1.37122105	1.23161435	3.19151305
1|species(phylo)	6.08E-05	0.00779553	2.03E-05	0.00037301
Dpatch|species	0.15301554	0.39117201	0.08172737	0.33953096
Dpatch|species(phylo)	5.43E-05	0.00736708	1.94E-05	0.00028237
Dsite|species	0.21880346	0.46776432	0.10816552	0.52122582
Dsite|species(phylo)	4.01E-05	0.00633434	1.05E-05	0.00041344
Lightpatch|species	3.57E-05	0.00597906	1.05E-05	0.00018766
Lightpatch|species(phylo)	0.03584717	0.18933349	0.01969131	0.08003138
pig.density|species	0.86592345	0.93055008	0.50992434	1.619627
pig.density|species(phylo)	5.23E-05	0.0072321	1.86E-05	0.0002835
NLpatch|species	5.02E-05	0.00708398	1.90E-05	0.00023453
NLpatch|species(phylo)	0.05477674	0.23404431	0.02616843	0.13518116
PC1|Patch	3.99E-05	0.0063157	1.35E-05	0.00023183

Fixed Effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	-3.7594926	-3.9067363	-3.6262897	0.04

Dpatch	-0.2605843	-0.3906672	-0.1391268	0.04
Lightpatch	-0.0085424	-0.082987	0.06415682	0.6
PC1	-0.1958153	-0.6951041	0.30653539	0.6
Dsite	-0.0265628	-0.1486439	0.09218888	0.6
NLpatch	0.08353419	-0.0001569	0.16229896	0.6
pig.density	0.11120324	-0.0115659	0.22968216	0.6
Dpatch:Lightpatch	-0.1206781	-0.2421333	-0.0020766	0.04
Dpatch:PC1	0.29770136	0.12166923	0.47407118	0.04
Lightpatch:PC1	-0.0239783	-0.1248878	0.082098	0.6
Lightpatch:Dsite	-0.0699073	-0.1725635	0.03078675	0.6
PC1:Dsite	0.09682696	-0.1084716	0.29831633	0.6
PC1:NLpatch	-0.0354051	-0.1570844	0.09676781	0.6
PC1:pig.density	0.19162925	-0.1625053	0.54639365	0.6
Dpatch:Lightpatch:PC1	-0.0736737	-0.1661416	0.01990732	0.6
Lightpatch:PC1:Dsite	0.14721236	0.06097536	0.23447493	0.04

Identity (Native vs Non-native) model

Random Effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Patch	3.41E-05	0.00584064	9.34E-06	0.00032699
1|species	1.87371755	1.36883803	1.13414531	3.33439616
1|species(phylo)	4.33E-05	0.00657962	1.11E-05	0.00043726
Dpatch|species	0.20938588	0.45758702	0.10687334	0.44955318
Dpatch|species(phylo)	6.19E-05	0.00786693	1.60E-05	0.00070535
Dsite|species	0.17439097	0.41760145	0.08248107	0.42763401
Dsite|species(phylo)	3.08E-05	0.00555	7.56E-06	0.00027059
Lightpatch|species	3.23E-05	0.00568738	8.21E-06	0.0003077
Lightpatch|species(phylo)	0.03119919	0.17663291	0.01436702	0.08752639
pig.density|species	0.64073452	0.80045895	0.35656307	1.25219999
pig.density|species(phylo)	3.26E-05	0.00571079	8.09E-06	0.00029776
NLpatch|species	3.31E-05	0.00575381	9.05E-06	0.00026756
NLpatch|species__	0.05100717	0.22584767	0.02294929	0.13831536
Identity|Patch	2.99E-05	0.00546749	7.84E-06	0.00025562

Fixed Effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	-3.6930578	-3.9973334	-3.4074367	0.04

Dpatch	-0.3912711	-0.5862626	-0.2110318	0.04
IdentityNon-native	-0.2689897	-1.4985103	0.96012194	0.6
Dsite	-0.1055122	-0.2748597	0.05797372	0.6
NLpatch	0.1108783	-0.0103029	0.21519931	0.6
Lightpatch	0.0512895	-0.0366869	0.13568509	0.6
pig.density	-0.1217563	-0.3309956	0.07664854	0.6
Dpatch:IdentityNon-native	0.54175818	0.07808249	1.01982478	0.04
IdentityNon-native:Dsite	0.32181162	-0.1242368	0.78168979	0.6
IdentityNon-native:NLpatch	-0.1479375	-0.5084589	0.2411716	0.6
IdentityNon-native:Lightpatch	-0.0368061	-0.3312865	0.26128227	0.6
IdentityNon-native:pig.density	1.04953742	0.29889763	1.82052942	0.04

Dispersal mechanism (animal vs wind dispersed) model

Random Effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Patch	3.13E-05	0.00559101	7.44E-06	0.00033488
1|species	2.30641667	1.51868913	1.33700251	4.64584527
1|species(phylo)	3.30E-05	0.00574059	7.77E-06	0.00038303
Dpatch|species	0.15918543	0.39898049	0.07646775	0.44919111
Dpatch|species(phylo)	3.67E-05	0.00606197	7.58E-06	0.00050093
Dsite|species	0.08049662	0.28371926	0.02617539	0.32251461
Dsite|species(phylo)	3.84E-05	0.00619909	9.41E-06	0.0004712
Lightpatch|species	3.27E-05	0.00572226	7.47E-06	0.00038312
Lightpatch|species(phylo)	0.03039933	0.17435403	0.01207084	0.09777305
pig.density|species	0.6351022	0.796933	0.33383243	1.45776231
pig.density|species(phylo)	3.06E-05	0.00553417	7.69E-06	0.00032733
NLpatch|species	4.34E-05	0.0065878	9.95E-06	0.00059135
NLpatch|species(phylo)	0.04250775	0.20617408	0.01654172	0.13759418
dispersal|Patch	3.40E-05	0.0058287	8.36E-06	0.00035327

Fixed Effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	-3.799124	-4.3482612	-3.2764057	0.04
Dpatch	-0.669822	-0.9854574	-0.3763193	0.04
dispersalWind	0.24314411	-1.0860598	1.58323637	0.6
Dsite	-0.2359353	-0.4530386	-0.0242843	0.04
NLpatch	0.10032339	-0.0854784	0.2640303	0.6

Lightpatch	-0.0391542	-0.1923096	0.10817912	0.6
pig.density	-0.1312124	-0.468854	0.18708864	0.6
Dpatch:dispersalWind	0.80642402	0.32433658	1.2971052	0.04
dispersalWind:Dsite	0.4216806	0.05917886	0.79645424	0.04
dispersalWind:NLpatch	-0.2180891	-0.6065221	0.18143833	0.6
dispersalWind:Lightpatch	0.3060827	-0.0240557	0.63593326	0.6
dispersalWind:pig.density	0.62480944	-0.1119037	1.39211743	0.6

Seed mass model

Random Effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Patch	3.44E-05	0.00586288	9.24E-06	0.00024172
1|species	2.05507275	1.43355249	1.16651755	4.07804269
1|species(phylo)	3.30E-05	0.00574687	8.71E-06	0.00023889
Dpatch|species	3.61E-05	0.0060108	9.12E-06	0.00035236
Dpatch|species(phylo)	0.19783816	0.44479001	0.09824427	0.47989962
Dsite|species	0.14290918	0.37803331	0.06149005	0.41366345
Dsite|species(phylo)	3.55E-05	0.00595626	9.18E-06	0.00030936
Lightpatch|species	4.10E-05	0.00640423	1.28E-05	0.00026045
Lightpatch|species(phylo)	0.03733581	0.19322475	0.01644008	0.10394052
pig.density|species	0.70859994	0.84178379	0.36582735	1.60580467
pig.density|species(phylo)	3.41E-05	0.00584249	9.74E-06	0.00021574
NLpatch|species	3.71E-05	0.00608703	9.35E-06	0.00032992
NLpatch|species(phylo)	0.04460969	0.21121007	0.01994561	0.12082341
propagule_mass|Patch	3.65E-05	0.00604471	9.35E-06	0.0003335

Fixed Effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	-3.8315744	-4.0916833	-3.6057087	0.04
Dpatch	-0.5415488	-1.000844	-0.1659783	0.04
propagule_mass	-0.9516164	-1.8308805	-0.1406774	0.04
Dsite	-0.1216419	-0.3132748	0.04380484	0.6
NLpatch	0.0197874	-0.0860429	0.11579004	0.6
Lightpatch	0.07016279	-0.0186885	0.15392253	0.6
pig.density	0.10342107	-0.0441075	0.24317776	0.6
Dpatch:propagule_mass	-0.7229826	-2.1349061	0.46393748	0.6
propagule_mass:Dsite	-0.3201857	-0.8329869	0.08767102	0.6

propagule_mass:Nlsite	0.0029864	-0.1833678	0.16578278	0.6
propagule_mass:Lightsite	-0.0171713	-0.2197738	0.16227381	0.6
propagule_mass:pig.density	0.04686339	-0.3673493	0.45265244	0.6

Table S6. Phylogenetic generalized mixed model (PGLMM) results for site-scale multi-level models (MLMs). Results shown for PC1 model, identity model, dispersal mechanism model, and seed mass model, respectively. PC1 and seed mass model test continuous responses, while identity and dispersal mechanism models test binary categorizations. 'Pvalue' column for fixed effects represents whether 95% credible interval does (0.6) or does not (0.04) overlap with 0.

PC1 (LES traits) model

Random Effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Site	2.88E-05	0.00536444	6.32E-06	0.00035711
1|species	1.20908475	1.0995839	0.75398784	2.16027773
1|species(phylo)	0	0	0	Inf
Dsite|species	0	0	0	Inf
Dsite|species(phylo)	0.32706628	0.57189709	0.16851501	0.74461534
Lightsite|species	0.09850861	0.31386082	0.0436293	0.24994989
Lightsite|species(phylo)	0	0	0	Inf
Pig_Density|species	0.29221173	0.54056612	0.11667006	0.86813756
Pig_Density|species(phylo)	0.00029039	0.01704091	7.68E-05	0.00758772
NLsite|species	0.00038766	0.01968896	6.73E-05	0.04080352
NLsite|species(phylo)	0.0001557	0.01247801	2.36E-05	0.01036384
PC1|Site	0.00016222	0.01273643	3.35E-05	0.00648064
residual	6.11030427	2.47190297	5.84281886	6.39039864

Fixed Effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	1.19981635	1.12240943	1.27715714	0.04
Dsite	0.02000747	-0.0795791	0.11950889	0.6
Lightsite	0.10467292	0.02458707	0.1846903	0.04
PC1	-0.3317958	-0.7194197	0.05598901	0.6

NLsite	0.0277687	-0.0518471	0.10731642	0.6
Pig_Density	0.08009767	-0.0168158	0.17692823	0.6
Dsite:Lightsite	0.05730688	-0.027747	0.14228805	0.6
Dsite:PC1	0.31575254	0.05425239	0.57049493	0.04
Lightsite:PC1	-0.0956141	-0.2630895	0.07098765	0.6
PC1:NLsite	-0.0409254	-0.1242613	0.04226222	0.6
PC1:Pig_Density	0.10175365	-0.1182883	0.32128024	0.6
Dsite:Lightsite:PC1	0.14848368	0.06210152	0.23479331	0.04

Identity (Native vs Non-native) model

Random Effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Site	1.07E-31	3.27E-16	3.77E-50	0.00642546
1|species	0.57042391	0.75526414	0.3485327	1.10190611
1|species(phylo)	0.40508047	0.63645932	0.14619651	2.73282048
Dsite|species	0.19137617	0.43746563	0.08953972	0.46226162
Dsite|species(phylo)	0.00072627	0.02694939	6.83E-05	0.40165436
Lightsite|species	9.46E-06	0.00307525	5.59E-06	0.07825935
Lightsite|species(phylo)	0.05675818	0.23823976	0.01778039	0.20482451
Pig_Density|species	0.17293951	0.41585996	0.0758085	0.43885189
Pig_Density|species(phylo)	0	0	0	Inf
NLsite|species	3.84E-05	0.00619398	9.34E-06	0.01843328
NLsite|species(phylo)	0.00083453	0.02888823	0.00013776	0.01454606
Identity|Site	1.74E-27	4.17E-14	3.86E-06	0.01033989
residual	6.12098094	2.47406163	5.84831933	6.3993607

Fixed Effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	1.21813464	0.96234108	1.48869238	0.04
Dsite	-0.1635054	-0.3497664	0.00609112	0.6
IdentityNon-native	-0.070853	-1.2976762	1.08083506	0.6
NLsite	0.09360916	0.00313585	0.18406172	0.04
Lightsite	0.16345272	0.04462182	0.28537484	0.04
Pig_Density	-0.0952862	-0.2319136	0.04130117	0.6
Dsite:IdentityNon-native	0.91956258	0.27291459	1.6850739	0.04
IdentityNon-native:NLsite	-0.29944	-0.5035883	-0.0961748	0.04
IdentityNon-native:Lightsite	-0.335856	-0.7828105	0.08349037	0.6

IdentityNon-native:Pig_Density	0.84555507	0.38739826	1.30179752	0.04

Dispersal mechanism (animal vs wind dispersed) model

Random effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Site	0	0	0	Inf
1|species	0.26431815	0.51411881	0.14510133	0.59353893
1|species(phylo)	0.7957718	0.89206042	0.3557493	2.42625351
Dsite|species	0	0	0	Inf
Dsite|species(phylo)	0.43486259	0.65944112	0.10952268	2.9755565
Lightsite|species	0	0	0	Inf
Lightsite|species__	0.11063703	0.33262145	0.03732	0.37287042
Pig_Density|species	0.00885813	0.09411763	0.00137921	0.37682366
Pig_Density|species(phylo)	0.00065346	0.02556281	6.84E-05	0.59983802
NLsite|species	0.00041608	0.02039813	3.61E-06	0.00227445
NLsite|species__	0.00046043	0.02145765	0.00010944	0.00265438
dispersal|Site	0.00011714	0.0108233	7.08E-05	0.00037056
residual	7.21580308	2.68622469	6.86033989	7.64944339

Fixed effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	0.99485391	0.39088271	1.58644412	0.04
Dsite	-0.2450401	-0.7835895	0.29090913	0.6
dispersalWind	0.90812063	-0.6507619	2.49923493	0.6
NLsite	0.02133701	-0.1068523	0.14942044	0.6
Lightsite	-0.0188597	-0.2483213	0.20548718	0.6
Pig_Density	0.13268051	-0.1256816	0.43882025	0.6
Dsite:dispersalWind	0.68090612	-0.717575	2.08517884	0.6
dispersalWind:NLsite	-0.0679428	-0.2786474	0.14258994	0.6
dispersalWind:Lightsite	0.55657297	0.01967789	1.11013566	0.04
dispersalWind:Pig_Density	0.07910974	-0.6850311	0.68073652	0.6

Seed mass model

Random Effects

	Variance	Std.Dev	lower.CI	upper.CI
1|Site	9.37E-05	0.00968181	4.37E-05	0.00039659

1|species	1.45110308	1.2046174	0.83994568	2.80724211
1|species(phylo)	0	0	0	Inf
Dsite|species	0	0	0	Inf
Dsite|species(phylo)	0.57202064	0.75632046	0.29008443	1.34220043
Lightsite|species	0	0	0	Inf
Lightsite|species__	0.05837148	0.24160191	0.02200464	0.23482294
Pig_Density|species	0.30523853	0.55248397	0.15090616	0.79772475
Pig_Density|species(phylo)	8.94E-05	0.00945725	2.92E-05	0.00344898
NLsite|species	0.00203303	0.04508912	0.00071185	0.01316906
NLsite|species(phylo)	0.00190794	0.04367992	0.00065164	0.01039455
propagule_mass|Site	0.00012233	0.01106025	6.23E-05	0.00050979
residual	7.24652537	2.6919371	6.85933162	7.63114194

Fixed Effects

	Value	lower.CI	upper.CI	Pvalue
(Intercept)	1.33539915	1.23719061	1.43352547	0.04
Dsite	0.0102989	-0.1143928	0.13488619	0.6
propagule_mass	-0.2803401	-0.7877504	0.22650193	0.6
NLsite	-0.0041416	-0.1052422	0.09687447	0.6
Lightsite	0.18985437	0.09081334	0.28881249	0.04
Pig_Density	0.16234711	0.03939393	0.28519736	0.04
Dsite:propagule_mass	-0.0134292	-0.3450133	0.31904668	0.6
propagule_mass:NLsite	0.01289935	-0.0916155	0.11731848	0.6
propagule_mass:Lightsite	-0.0246592	-0.1806039	0.13324022	0.6
propagule_mass:Pig_Density	-0.0619827	-0.3311202	0.20686124	0.6

Appendix S5

Data sources for seed mass

Adenophorus_spp:

1. Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Asplenium polyodon:

1. Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Athyrium microphyllum:

1. Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Axonopus fissifolius: Avereage of 3 measurements from TRY:

1. 2. 3. Odgers, B. M., & Rogers, R. W. (1993). Contrasting diaspore and vegetation attributes of grasses from natural and disturbed habitats in an urban eucalypt forest reserve. *Australian journal of botany*, *41*(6), 637-648.

Broussaisia arguta:

1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Carex alligata:

1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Carex longii: Taken from the most closely related species on TRY [*C. suberecta*, Hipp, A. L., Reznicek, A. A., Rothrock, P. E., & Weber, J. A. (2006). Phylogeny and classification of Carex section Ovales (Cyperaceae). International Journal of Plant Sciences, 167(5), 1029-1048.]

1. Royal Botanical Gardens KEW. 2008. Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/.

Cheirodendron trigynum:

1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Cibotium glaucum:

1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Cibotium menziesii:

1. Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Coprosma ochracea:

1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Dryopteris glabra:

2. Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Dryopteris wallichiana:

1. Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Ehrharta stipoides: Averaged two measurements on TRY

1. Royal Botanical Gardens KEW. 2008. Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/.

Geniostoma hedyosmifolium:

1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Hedychium gardnerianum: Taken from most closely related species on TRY [*Hedychium spicatum*, Wood, T. H., Whitten, W. M., & Williams, N. H. (2000). Phylogeny of Hedychium and related genera (Zingiberaceae) based on ITS sequence data. *Edinburgh Journal of Botany*, *57*(2), 261-270.]

2. Royal Botanical Gardens KEW. 2008. Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/.

Juncus effusus: Averaged 10 measurements from TRY, 5 of which from LEDA traitbase [citation #6]:

1. Jones, Q., & Earle, F. R. (1966). Chemical analyses of seeds II: oil and protein content of 759 species. *Economic Botany*, 127-155.

2. Thompson, K. B. S. R., Band, S. R., & Hodgson, J. G. (1993). Seed size and shape predict persistence in soil. *Functional ecology*, 236-241.
3. Shipley, B., & Parent, M. (1991). Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seedling relative growth rate. *Functional ecology*, 111-118.
4. Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., ... & Whitehouse, J. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos*, 259-281.
5. Royal Botanical Gardens KEW. Seed Information Database (SID), http://data.kew.org/sid/ accessed May 2014
6. Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., ... & Peco, B. (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of ecology*, *96*(6), 1266-1274.

Styphelia tameiameiae:
1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Melicope clusiifolia:
1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Metrosideros polymorpha:
1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Myrsine sandwicensis:
1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Peperomia spp: Averaged 4 species occurring on Hawaii island
1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Persicaria punctata: Averaged 2 measurements from TRY:
1. Moles, A. T., D. S. Falster, M. R. Leishman, and M. Westoby. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. Journal of Ecology 92:384-396.
2. Royal Botanical Gardens KEW. Seed Information Database (SID), http://data.kew.org/sid/.

Polypodium pellucidum:
1. Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Rhynchospora chinensis:

1. Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

Sacciolepis indica: Averaged 4 species in the same genus [all from KEW]:

1. Royal Botanical Gardens KEW. 2008. Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/.

Sadleria pallida:
Gómez-Noguez, F., Pérez-García, B., Mehltreter, K., Orozco-Segovia, A., & Rosas-Pérez, I. (2016). Spore mass and morphometry of some fern species. *Flora*, *223*, 99-105.

Vaccinium calycinum:
Yoshinaga A, Chau M, Sack L. unpublished Hawaii Seed Mass Database

CHAPTER 3

Feral pigs and *Sphagnum* influence assembly processes in Hawaiian montane wet forest understories

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Abstract

Biodiversity loss in tropical forest understories, particularly in island ecosystems like the Hawaiian archipelago, is exacerbated by novel pressures resulting from species invasions. Forests on Kohala volcano on Hawaiʻi Island, home to significant numbers of endemic species, face threats from feral pigs, *Sphagnum* encroachment, and invasive vascular plants, which alter nutrient dynamics, habitat conditions, and species interactions. We applied niche theory to patterns of taxonomic, functional, and phylogenetic diversity to explore the effects of these novel drivers on assembly processes in forest understory communities varying along a gradient of pig population density. We measured 10 traits to characterize ecological function and estimated phylogenetic relationships using a pruned vascular plant phylogeny, using both to estimate functional and phylogenetic dispersion by calculating the standardized effect size of mean pairwise distance (SES.MPD) and mean nearest taxon distance (SES.MNTD). Selection of top performing models and weighted averaging of coefficients was implemented using AICc to identify the key factors influencing diversity across sites. Our findings demonstrate that species invasions, particularly by *Sphagnum* and feral pigs, have significant impacts on plant community assembly in Hawaiian wet forest understories. *Sphagnum* likely acts primarily as an environmental filter, reducing both functional and phylogenetic diversity by limiting niche space, particularly for non-native species. In contrast, feral pig activity had context-dependent effects, likely expanding niche space through soil disturbance but ultimately facilitating non-native species and reducing native diversity. These results underscore the importance of managing invasive species even in relatively intact ecosystems, where the impacts of invasion can nevertheless profoundly alter community structure and function.

Keywords: community assembly, functional diversity, phylogenetic diversity, *Sphagnum*, feral pigs, invasive species, niche

Introduction

Biodiversity loss in the face of global change is a significant challenge facing many ecosystems (Pyšek et al., 2012). Tropical forest understories serve as reservoirs for much of this diversity (Gentry et al., 1987) and contribute to nutrient cycling, soil stabilization, and habitat provisioning for various organisms (Gilliam, 2007; Silver et al., 1996; Zhang et al., 2022). Island ecosystems, characterized by high rates of endemism and unique species assemblages (Whittaker et al., 2017), are especially vulnerable to biodiversity loss (Burns, 2019; Simberloff, 1995). Invasive species encroachment in these systems can lead to dramatic shifts in community dynamics, altering the functional make-up of understory assemblages (Drenovsky et al., 2012; Funk et al., 2008).

These challenges are especially prominent in the Hawaiian archipelago, where extreme isolation, steep environmental gradients, and diverse microhabitats have driven remarkable speciation events and radiations, resulting in a high degree of endemism (Carlquist, 1980). Dispersal limitation from mainland sources has resulted in a relatively depauperate flora and fauna, leading to an increased risk from disturbance, invasion, and disruption of established interactions among native species (Barton et al., 2021). Hawaiian forest overstories are dominated by a single genus, *Meterosideros* – and, on Hawaiʻi island, the single species *Meterosideros polymorpha* (Seeley et al., 2023) – and native forest diversity is largely contained within the understory (Friday et al., 2015; Mueller-Dombois & Fosberg, 2013). These communities are particularly vulnerable to the effects of novel threats from invasive species, which tend to proliferate in the understory in the initial stages of invasion (Potter et al., 2023; Zimmerman et al., 2008).

Among the primary novel pressures impacting these understory communities are feral pigs, *Sphagnum* encroachment, and invasive vascular plants, which jointly present a challenge for species unaccustomed to the conditions imposed by these threats. Feral pigs (*Sus scrofa*), introduced by Polynesian settlers 400 – 1100 CE and again by Europeans from 1778 CE onward (Linderholm et al., 2016; Wilmshurst et al., 2011), disrupt soil surfaces through rooting, wallowing, and digging, which facilitates the establishment of non-native species in these disturbed areas (Peyton et al., 2023). Pigs have been documented dispersing aggressive invasive species like strawberry guava (*Psidium cattleianum*) and Koster's Curse (*Miconia crenata*), and selectively foraging on species ranging from tree ferns in the *Cibotium* genus to endangered lobeliads and mints (Loope et al., 1988; Murphy et al., 2014; Nogueira-Filho et al., 2009). *Sphagnum palustre*, arriving in Kohala between 51 and 49 ka. BP (Karlin et al., 2012), spreads vegetatively on upland soils and exhibits rapid growth (Hoe, 1971; Kelman Wieder, 2001; Ohlson & Økland, 1998). In fact, growth patterns closely resemble those of its invasive counterpart in Oʻahu, where *Sphagnum palustre* has established a rapidly spreading population in the Kaʻala Natural Area Reserve (Joe, 2015). *Sphagnum* alters nutrient dynamics by forming acidic peat layers low in available nitrogen with slow decomposition rates, drastically altering the establishment and survival of native understory species (Malmer et al., 2003; Schomaker, 2017). In addition, the introduction of invasive vascular plants, including aggressive ornamentals such as Kahili ginger (*Hedychium gardinarium*) and pasture grasses like carpet grass (*Axonopus fissifolius*) have displaced native flora. > 50 % of forests in Hawaiʻi are now dominated by non-native species (Barton et al., 2021), and while higher-elevation wet forests appear more resistant to invasion, encroachment by non-native vascular plants remains a continual challenge. These novel threats have significant impacts on native understory biodiversity and profoundly alter community dynamics by changing habitat conditions, disrupting species interactions, and displacing native taxa (Vitousek et al., 1996; Walker & Smith, 1997).

Integrating taxonomic, functional, and phylogenetic metrics into investigations of biodiversity change have yielded powerful insights into the processes and mechanisms structuring ecological communities (Baraloto et al., 2012; Cadotte, 2011; Devictor et al., 2008; Galván-Cisneros et al., 2023; Gerhold et al., 2013; Pellissier et al., 2013). Taxonomic diversity, represented by diversity metrics such as the Shannon-Wiener index (Shannon, 1948) or Simpson's reciprocal index (Simpson, 1949), quantifies the number and relative abundance of species to provide a foundational measure of biodiversity. Functional diversity, characterizing the range of functional traits within a community, offers insights into the roles that species play in ecosystem processes and their responses to environmental changes (Cadotte et al., 2011). Resource use strategies are particularly important in shaping plant performance and competitive outcomes and are characterized by trade-offs in leaf construction and function (Shipley et al., 2006; Wright et al., 2004). Phylogenetic diversity, reflecting the evolutionary relationships among species, can reveal patterns of shared ancestry that influence ecological function, especially if traits are phylogenetically constrained (Cavender-Bares et al., 2009; Faith, 1992).

Linking patterns in functional and phylogenetic diversity to niche theory has led to significant advances in the identification of ecological processes shaping how species assemble into ecological communities (Flynn et al., 2011; Kraft et al., 2007). Niche theory predicts that abiotic or environmental filtering will lead to trait and phylogenetic clustering due to shared adaptations, while strong competition (i.e. biotic filtering) leads to overdispersion due to competitive exclusion and limiting similarity (Webb et al., 2002). However, competitive hierarchies may also lead to clustering, resulting from shared adaptations due to competition for a single resource (Herben & Goldberg, 2014), while divergent ecological strategies under harsh abiotic conditions (e.g. drought tolerance, avoidance, or escape) may lead to overdispersion in stressful environments (Kozlowski & Pallardy, 2002). While niche theory provides a powerful tool to understand mechanisms of community assembly, challenges to using this framework remain, including the violation of equilibrium assumptions and the difficulty of using a single dimension (i.e. dispersion) to untangle processes functioning simultaneously but working antagonistically. Nevertheless, functional and phylogenetic diversity patterns can provide useful information about how external drivers shape community dynamics and help to understand biodiversity and ecosystem function in threatened communities facing rapid change.

Here we investigate understory taxonomic, functional, and phylogenetic diversity in a montane wet forest on Hawai‘i Island. We focus on the impacts of invasive pig activity, *Sphagnum* encroachment, and non-native species to identify their influence on ecological processes and community dynamics. Specifically, we ask (i) which ecological drivers are most important in structuring diversity patterns, (ii) whether there are notable convergences or divergences in how drivers influence taxonomic, functional, and phylogenetic diversity, and (iii) what these patterns reveal about how novel drivers influence assembly processes. We predict *Sphagnum* encroachment will lead to functional and phylogenetic clustering due to site homogenization and environmental filtering under the stressful conditions imposed by *Sphagnum*. We also expect that feral pig activity will increase site heterogeneity, thereby increasing functional and phylogenetic diversity by providing habitat for non-native species with traits dissimilar to those of native species to invade. By altering conditions influencing establishment and survival, we predict these drivers will significantly shape how plant communities assemble in the forest understory.

Methods

Study site

We conducted this study at the Puʻu O Umi Natural Area Reserve located on Kohala mountain on Hawaiʻi Island (Fig. 1). Kohala is the oldest of the five shield volcanoes comprising Hawaii Island, formed roughly 1000 kya, with substrates derived from tephra deposits and underlying lava flows of ʻaʻa and pāhoehoe morphology (Chadwick et al., 2007; Wolfe & Morris, 1990). The climate at the study site remains relatively stable, with mean annual temperatures ranging from 13 - 14 °C. Annual precipitation exceeds 2000 mm, with additional moisture contributed by cloud water interception (Giambelluca et al., 2013). These conditions support a closed-canopy forest dominated by ʻōhiʻa (*Metrosideros polymorpha*) and have led to the formation of persistent montane peatlands interspersed within the wet forest mosaic (Barrett et al., 2021). *Sphagnum palustre* grows in both lowland and upland conditions, often forming a thick layer of ground cover on the forest floor. While fencing excludes feral pigs from a section northeast of the Kohala summit, they remain widespread in other areas of the reserve.

Data collection

We designed this study across a gradient of pig density represented by four 1-km radius pig-density zones (A-D), roughly equal to conservative estimates of minimum pig home-range size in Hawaiian forests (Diong, 1982). We quantified pig population density following

Rowcliffe et al. (2008) with a camera trap survey conducted during Summer 2019 (Peyton, et al. 2023). The camera trap survey involved deployment to 4 – 6 random locations per zone over three separate 10 – 14 day trapping periods, with confirmation of pig absence at fenced zone D with 7 deployments during the final two trapping periods. We estimated pig population density with a random encounter model (REM), which uses encounters between animals and cameras to estimate density while parameterizing covariates that influence the trapping rate (see Chapter 1 Appendix).

Vegetation and habitat characterization

To capture relevant habitat characteristics and understory vegetation composition, we randomly generated 30 points within each pig density zone for a total of 120 sites (1 additional site was accidentally surveyed in Zone A, leading to a total of 121 sites). We excluded peatlands and other sites with < 50% canopy coverage to target sampling on closed-canopy wet forest understories. Within each site, a 20-m transect was established along a random azimuth direction and used to survey vegetation and habitat characteristics (i.e. disturbance and nurse log extent). A point-intercept approach was used along the transect at intervals of 0.5 m for a total of 41 points per site, where vascular plant species intercepted between 0 – 2 m in height were recorded. *Sphagnum palustre* intercepted at the ground level was also included in this manner. We proceeded by removing species occurring in < 3% of sites to avoid overweighting by rare species. The length of transect segments intercepting disturbed soil (here defined conservatively as soil visibly overturned by rooting, wallowing, and trampling activity) and nurse logs (here defined as woody stems at < 45° from ground level) were measured in 5-cm increments and summed to estimate the relative coverage of these habitat features. We estimated light availability using hemispherical photographs taken with a 180° fisheye camera lens at three points equally spaced along each transect. Using the Gap Light Analyzer software (Frazer et al., 1999), we calculated canopy openness for each photograph, which we averaged across the site as a metric of light availability.

Eight climate variables were obtained from the Hawaiʻi Evapotranspiration Atlas and the Rainfall Atlas of Hawaiʻi (Giambelluca et al., 2013) to describe spatial variation in climate across the 121 study sites. These climate data are interpolated from relatively few weather stations across the Kohala study area and may introduce errors at finer spatial scales, but the estimates are effective in capturing and controlling for major climatic variations, thereby more accurately isolating the impacts of our focal drivers. Variables included average annual temperature (Tmean), maximum annual temperature (Tmax), minimum annual temperature (Tmin), mean annual precipitation (MAP), vapor pressure deficit (VPD), total solar irradiance (TSI), mean annual transpiration rate (E), and cloud frequency (cloud freq). To identify the dominant climatic differences among sites, we conducted a principal components analysis (PCA) using these eight variables and elevation (measured using a Garmin GPS unit at each site). The first two principal components explained over 98% of the variance, with PC1 (59.9%) corresponding to differences in moisture and PC2 (38.2%) corresponding to differences in temperature (Chapter 1 Appendix S2). Thus, we used PC1 (positive = wetter) and PC2 (positive = hotter) scores to represent relative differences in moisture and temperature across sites. Accounting for variation due to moisture and temperature, which was relatively small compared to that of our focal drivers, ensured that the main effects of our target variables were not confounded by climate.

Trait data collection

We measured functional traits from haphazardly selected mature individuals of each species in the < 2 m height class within at least three pig-density zones, where possible. Replicate sizes ranged from 2 – 13 individuals per species (median = 6), and replicate sizes of n < 3 for only 3 out of 42 species. To account for potential differences in leaf nitrogen in *Sphagnum* versus non-*Sphagnum* sites, at least three individuals were selected from *Sphagnum*-dominated areas when available. While some species that did not co-occur with *Sphagnum* were only measured in sites without *Sphagnum,* all species sampled in *Sphagnum* sites were also sampled in non-*Sphagnum* sites.

We measured 9 traits using standard methods (Cornelissen et al., 2003): specific leaf area (SLA, $cm^2\ g^{-1}$), leaf dry matter content (LDMC), leaf thickness (mm), leaf area (LA, cm^2), foliar %N, foliar C:N, foliar $\delta^{13}C$ (‰), stem specific density (SSD, $g\ cm^{-3}$), and stem water content (SWC). Leaves were collected and stored in moist bags; leaf thickness, area (measured using a LI-COR area meter), and fresh mass were measured within 48 hours. Leaves were then dried at 60°C for at least 48 hours, weighed for dry mass, ground, and packaged for %C, %N, and $\delta^{13}C$ analysis using accelerator mass spectrometry at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM). Small, cylindrical stem samples were selected for stem trait measurements. Fresh mass, length (L), and mean diameter (D; n = 3 measurements along section) were collected within 48 hours. Volume (V) was calculated using $V = (0.5D)2 \times \pi \times L$. Stems were dried at 60°C for at least 72 hours and weighed for dry mass. Leaf $\delta^{13}C$ is used as a proxy for intrinsic water use efficiency (iWUE), and has been shown to be tightly coupled to carbon acquisition strategies (Li et al., 2022; Prieto et al., 2018). We were unable to collect entire tree fern fronds for leaf area measurements, so estimates for *Cibotium glaucum* and *C. menziziana* were taken from Arcand et al., (2008). We used measurements of leaf area for *Sadleria pallida* for closely related *S. souleyetiana*, which has comparable frond lengths (Wagner et al., 1991).

Seed mass measurements were compiled from the TRY trait database, the Hawaiian seed mass database, and the Flora of the Hawaiian Islands web repository (Kattge et al., 2020; Wagner et al., 2005; Yoshinaga et al., unpublished). For species lacking seed mass data at the species level, seed mass values were averaged among the most closely related species within the genus. Diaspore mass for pteridophytes was excluded due to differences between angiosperms and pteridophytes in reproductive and life-history traits.

Data analysis

To quantify taxonomic diversity, we calculated three classical diversity metrics for each site: (i) species richness, (ii) the Shannon-Wiener diversity index (H), and (iii) Simpson's reciprocal index (1/D). We also calculated (iv) the ratio of non-native species cover to total species cover to use as an index of non-native dominance for each site. Functional composition was quantified using community-weighted mean (CWM) trait values, which weight species trait values by relative abundance. While CWMs may obscure within-site variability (Miller et al., 2019), they nonetheless capture the dominant patterns of trait expression for species persisting under particular environmental conditions (Lepš & de Bello, 2023). To explore patterns of community composition across sites, we ran non-metric multidimensional scaling (NMDS) on species relative abundances using Bray-Curtis distance. NMDS was computed using the *metaMDS* function in the *vegan* package (Oksanen et al., 2008) in the statistical software R (v4.1.2; R Core Team 2021). We passively overlaid both the focal drivers and the CWM trait values to visualize linear relationships with species composition using the *envfit* function in *vegan*.

We assessed functional diversity by calculating trait distance matrices constructed with Gower distance, which is a flexible metric robust to missing values (Gower, 1971). Traits associated with resource acquisition and the LES (hereafter, *resource traits*) were analyzed separately to assess variation in resource strategies. These included SLA, LDMC, LT, foliar %N, and C:N (Shipley et al., 2006; Wright et al., 2004). Analyses were conducted with the full species set and with non-native species removed (i.e. native species only) to investigate the effects of non-native vascular plants on functional diversity. The resulting four categories were as follows: (i) all traits for all species, (ii) all traits for native species, (iii) resource traits for all species, and (iv) resource traits for native species.

We measured phylogenetic diversity using a phylogeny of vascular plant species generated with the V.Phylomaker package (Jin & Qian, 2019). This phylogeny integrates molecular data from GenBank and the Open Tree of Life Project (Smith & Brown, 2018) for angiosperms and a pteridophyte phylogeny from Zanne et al. (2014). The resulting phylogeny, while coarse at the species level, provides a robust community-scale topology suitable for analyzing phylogenetic community structure. Using this phylogeny, we constructed a distance matrix to calculate phylogenetic diversity metrics for: (i) the full community assemblage, (ii) all native species, (iii) all angiosperms, and (iv) native angiosperms, excluding pteridophytes and lycophytes from (iii) and (iv) due to the effects of long evolutionary distances in those lineages.

We used the distance matrices and species relative abundance estimates from each site to calculate abundance-weighted mean pairwise distance (MPD) and mean nearest-taxon distance (MNTD) metrics. MPD calculates the mean of functional or phylogenetic distances among species in a site, while MNTD calculates the mean pairwise distances among nearest neighbors for each species. Weighting by abundance incorporates species evenness by focusing on individuals detected at each site, rather than species presence/absence. To assess deviation from random expectations, we compared MPD and MNTD to distributions generated by 1000 iterations of a null model using the "independent-swap" method (Gotelli & Entsminger, 2003), which randomizes community composition while preserving species abundance across sites and species richness within each site. Standardized effect scores (SES) were calculated for each metric, approximating a z-score using the null distribution mean and standard deviation (SES.MPD and SES.MNTD). These metrics quantify deviations in functional or phylogenetic diversity from expectations of null assembly where communities consist of random species assemblages. SES.MPD and SES.MNTD were computed using the *ses.mpd* and *ses.mntd* functions, respectively, in the R package *picante* (Kembel et al., 2010).

Model selection

We identified the habitat characteristics most strongly influencing taxonomic, functional, and phylogenetic diversity by fitting global models with feral pig density (pigs km^{-2}), pig soil disturbance (m), *Sphagnum* coverage (%), nurse log extent (m), and canopy openness (%) as covariates, along with moisture (climate PC1 scores) and temperature (climate PC2 scores) to control for climate variation. All variables were rescaled using mean and sd (mean = 0) prior to analysis. Model performance was ranked using AICc via the *dredge* function in the *MuMIn* package (Barton, 2009), with better-fitting models indicated by lower AICc values. We conducted conditional model averaging among the top models (within ΔAICc < 10 of the best-fitting model), weighted by ΔAICc (Anderson & Burnham, Kenneth, 2002; Grueber et al., 2011). Variance inflation factors (VIFs) were calculated to assess multicollinearity; all global models had VIFs < 10, indicating no multicollinearity issues, and thus, all covariates were included in each analysis.

Assessing phylogenetic signal in trait syndromes

To evaluate the phylogenetic signal in measured traits, we calculated Blomberg's K and Pagel's λ as independent measurements of phylogenetic signal for each trait (Blomberg et al., 2003; M. Pagel, 1999) using the *picante* package in the statistical software R. Values of Blomberg's K greater than 1 indicate stronger phylogenetic signal (i.e. greater variance among clades) than expected under Brownian motion, while values smaller than 1 suggest weaker signal (i.e. greater variance within clades). Values of Pagel's λ are scaled between 0 and 1, where λ = 1 indicates trait evolution is fully captured by phylogenetic relationships, while λ = 0 indicates traits are independent of phylogeny (Meireles et al., 2020). These calculations were performed across the four phylogenetic groups: (i) the full phylogeny, (ii) all native species, (iii) all angiosperms, and (iv) native angiosperms (Table 2). P-values were calculated using permutation tests (n = 1000).

Results

Pig population estimates fell along a gradient ranging from 0 to 17.5±7.5 (mean ±SD) individuals km^{-2}. Zones were ordered from A – D following this gradient with the highest values assigned to Zone A and 0 individuals km^{-2} at Zone D (Peyton et al., 2023). NMDS revealed patterns of compositional turnover across pig density zones along the first axis of the ordination (Fig. 2). NMDS1 correlated positively with pig density and soil disturbance, and increased with greater community-weighted mean values for SLA, foliar %N, and δ13C. Negative NMDS1 values aligned with high moisture and *Sphagnum* cover, with higher CWM seed mass and foliar C:N. NMDS2 was negatively associated with canopy openness, with lower values indicating more open canopy conditions and supporting greater CWM LDMC, SSD, and smaller leaves. Lower values of NMDS3 were associated with warmer temperatures and more closed-canopy conditions, favoring higher LDMC and thinner leaves.

Taxonomic, functional, and phylogenetic diversity

Model averaging indicated that species richness, Shannon index (H), and Simpson's diversity index (1/D) exhibited similar relationships to environmental factors, though the effect magnitudes of certain parameters differed among biodiversity indices (Fig. 3). No parameters significantly influenced species richness for all species (i.e. native and non-native), but nurse log coverage, moisture, and temperature showed significant patterns in native species. Other taxonomic diversity metrics (H, 1/D) mirrored trends in species richness, but with some significant patterns when non-native species were included. H and 1/D consistently decreased with *Sphagnum* coverage for all species, whereas a slight positive effect was observed in native species with nurse log coverage, significant only for H. While pig population density was non-significant, it qualitatively suggested sites with a higher density of pigs experienced an increase in total plant diversity. Non-native dominance increased with both feral pig abundance and soil disturbance and showed minor declines with nurse log coverage. Soil disturbance and canopy openness had negligible effects across all taxonomic diversity metrics.

Habitat characteristics influenced functional diversity metrics differently across trait categories (Fig. 4). The inclusion or exclusion of non-native species led to notable divergences, particularly for resource traits. Differences between SES.MPD and SES.MNTD – capturing the degree of dispersion in functional traits relative to null assembly – were primarily in effect size and significance. Functional diversity, particularly for resource traits, increased with soil disturbance for both SES.MPD and SES.MNTD. Patterns at sites differing in pig density were varied, with native species tending to experience greater declines in functional diversity than when non-native species were included. Resource trait SES.MPD notably increased with greater pig population density when non-native species were included. Functional SES.MPD and SES.MNTD significantly fell with *Sphagnum* coverage for all categories except for native species full trait SES.MNTD. Nurse log coverage and canopy openness saw no significant effects for any functional diversity metrics. Moisture and temperature were included to account for variation in climate across the study site, which was small. Moisture increased resource trait SES.MPD and SES.MNTD when non-native species were excluded, and decreased SES.MNTD for native species. SES.MNTD increased with temperature across all categories, and for all trait SES.MPD.

Phylogenetic diversity metrics, covering all species, native species, angiosperms, and native angiosperms, generally aligned in their response to habitat characteristics (Fig. 5). Although the magnitude of effects varied, the direction of effects was largely consistent, with some exceptions. Phylogenetic SES.MPD significantly decreased with *Sphagnum* coverage, albeit with weak significance for angiosperms, but *Sphagnum* coverage did not affect SES.MNTD. Soil disturbance saw a minor positive effect for native angiosperms for both SES.MPD and SES.MNTD. Nurse logs were associated with a minor increase in angiosperm diversity for both SES.MPD and SES.MNTD. SES.MPD declined with canopy openness for phylogenies including pteridophytes and lycophytes, but did not impact phylogenies including only angiosperms. Moisture effects generally trended negative, except for SES.MPD in angiosperms, while temperature trended positive across all phylogenies and metrics.

Permutation tests showed little evidence for a phylogenetic signal in traits, with weak phylogenetic signal found in SLA using Blomberg's K with the full phylogeny, and for seed mass in native angiosperms using Pagel's λ (Table 1). Likewise, the topology of the community phylogeny showed little similarity with trait dendrograms representing multivariate trait relationships among species (Fig. 6), indicating functional distances among species in Kohala were largely independent of their phylogenetic relatedness.

Discussion

Our findings suggest that in Hawai‘i, novel drivers, including *Sphagnum*, feral pigs, and non-native vascular plants, influence assembly processes even in relatively intact montane wet forest understories. Overall, patterns in functional and phylogenetic dispersion provide evidence that while *Sphagnum* operated largely as an environmental filter by constraining niche space, the effects of feral pig activity were context-dependent, with contrasting effects on different dimensions of diversity and function. Non-native species appeared to be facilitated by feral pig activity and weakly suppressed by *Sphagnum*. Nurse logs had small positive effects on native species (Fig 3) and increased phylogenetic diversity (Fig 4) among angiosperms, supporting prior research showing nurse logs are important for native species establishment (Kandert et al., 2021; Santiago, 2000). We found little evidence of phylogenetic signal in traits, even among native Hawaiian species, indicating plant functional strategies were not strongly phylogenetically conserved (Table 1). This is perhaps unsurprising given the short climatic gradients in this study and the extensive radiations that have occurred in Hawaiian plant lineages (Price & Wagner, 2018). Patterns in functional and phylogenetic diversity, then, likely do not capture the same axes of adaptation or niche differentiation given the lack of trait conservatism. Non-native species tended to be overrepresented in the monocot clade (Fig 4), and many exhibited resource-acquisitive traits (see Chapter 2). This functional and phylogenetic clustering among many non-native species likely contributed to the weak phylogenetic signal found in SLA across the full phylogeny.

As predicted, S*phagnum* encroachment appeared to limit establishment of other plant species, likely by decreasing pH in the rhizosphere and reducing the uptake of critical nutrients (Malmer et al., 2003). In Kohala, *Sphagnum palustre* grows rapidly, carpeting the forest floor and creating a homogenous bryophyte layer that can reduce microsite heterogeneity (Schomaker, 2017). *Sphagnum* decreased both functional and phylogenetic diversity across most metrics (Fig. 4, 5), demonstrating that communities became more functionally similar and contained more closely related species when *Sphagnum* was abundant. *Sphagnum* encroachment, thus, likely acts as an abiotic filter, inhibiting the establishment of species lacking the appropriate traits or trait syndromes, including those involved in resource acquisition. Resource use strategies appeared to be heavily constrained by *Sphagnum*, which is consistent with the expected reduction in nutrients and pH associated with *Sphagnum* establishment. The resulting conditions should promote conservative resource use (Agrawal, 2020). Indeed, community-weighted means for resource traits (SLA, %N, foliar C:N) demonstrated shifts toward resource-conservative values with greater *Sphagnum* coverage. Both native and non-native species were affected, though with some suggestion that non-native species incurred greater losses, as would be expected of species with resource-acquisitive traits under conditions of limited resource availability (Schumacher et al., 2009). The notable exception to the observed clustering pattern was found in the phylogenetic distances among nearest relatives (phylogenetic SES.MNTD) which remained unchanged, even as *Sphagnum* induced clustering across the phylogeny (phylogenetic SES.MPD). This may be due to the restriction of whole lineages rather than individual taxa, which suggests, if true, that adaptations influencing persistence under *Sphagnum* establishment are relatively conserved. In the aggregate, these patterns indicate *Sphagnum* largely constrains niche space, restricting establishment and favoring taxa with adaptations favored under stressful conditions.

The effects of feral pigs were varied, reflecting their multiple roles as introduced herbivores, biotic disturbance agents, and seed dispersers. Soil disturbance was generally associated with modest increases in functional diversity, suggesting feral pigs expanded niche space by introducing greater environmental heterogeneity through the creation of disturbed patches in varying stages of succession (Fig. 4). This was consistently true for resource traits, likely reflecting the establishment of more resource-acquisitive species in an otherwise resource-conservative community (Fig. 2). Notably, this overdispersion pattern was found regardless of the exclusion of non-native species (Fig. 4), suggesting soil disturbance expanded niche space and supported a greater diversity of resource strategies for both native and non-native species. Both pig soil disturbance and population density increased non-native dominance (Fig. 3), indicating that multiple dimensions of pig activity facilitate the spread of non-native species. However, we see that the effects of soil disturbance on functional and phylogenetic dispersion diverged from those of pig density, indicating that the effects of soil disturbance differed from the overall impact of large population sizes, which could aggregate the effects of seed dispersal, herbivory, nutrient redistribution, and other processes (Barrios-Garcia & Ballari, 2012; Wehr et al., 2018).

Understory communities in areas of high pig density largely saw reductions in overall niche space, as reflected by functional and phylogenetic clustering, particularly for native species (but see below for resource trait SES.MPD; Fig. 4, 5;). This may be due to environmental filtering, whereby establishment is limited for species lacking adaptations to novel pressures introduced by feral pigs. The effects of activities such as herbivory and repeated trampling may interact to constrain niche space for understory vegetation. Conversely, clustering may be a result of a competitive hierarchy, whereby novel conditions restructure competition to a single or limited number of dimensions, favoring adaptations that promote strong competitive ability under those conditions (Gross et al., 2015; Kraft et al., 2014). For example, under asymmetric competition for light, fitness differences select for greater height and result in trait clustering (Mayfield & Levine, 2010). Similarly, some effects of pig activity, such as seed dispersal and nutrient redistribution, may introduce strong benefits to those taxa with favorable adaptations and induce greater functional and phylogenetic clustering. Areas supporting high pig density – whether by environmental filtering or shifting competitive dynamics – experienced a significant loss of phylogenetic diversity, particularly for native species, while shifting to a more non-native dominated community.

Sites supporting large feral pig population sizes saw significant declines in functional diversity among native species, but these effects diminished significantly when non-native species were included (Fig. 4). Resource trait diversity, in particular, demonstrated a considerable departure, exhibiting a significant increase at sites supporting high pig population density when non-native species were considered. These notable differences indicate that greater non-native establishment and the loss of native species played a substantial role in these patterns. The consistent decline of native phylogenetic diversity at high pig population density suggests native biodiversity loss is a primary effect of large pig population sizes. Unlike with soil disturbance, greater resource trait SES.MPD where pigs were abundant likely does not reflect niche expansion. If so, sites supporting greater pig density would have similarly demonstrated increased resource trait dispersion for native species, reflecting enhanced establishment of native species with resource acquisitive traits as seen with soil disturbance. Rather, it is possible that multiple mechanisms of feral pig activity, such as selective herbivory and seed dispersal, act to collectively favor non-native species at the expense of native species. While large feral pig populations appear to support a greater diversity of plant resource strategies, this results from the establishment of non-native species and the loss of phylogenetic diversity through the displacement of native flora.

Conclusions

Hawaiian montane wet forest understories serve as an important reservoir of biodiversity but continue to experience novel threats from species introductions, even in remote, relatively intact areas. We found evidence that the impacts of *Sphagnum*, feral pigs, and non-native vascular plants are significant and shape community assembly and function. *Sphagnum* and feral pig activity both appeared to constrain niche space but did so by different means, with patterns in functional and phylogenetic diversity suggesting *Sphagnum* acted as an environmental filter for both native and non-native species. Sites supporting high pig densities largely experienced functional and phylogenetic clustering; however, soil disturbance expanded the resource trait niche, likely by increasing site heterogeneity. While pig activity appeared to facilitate non-native dominance, the effects of *Sphagnum*, while reducing diversity for both native and non-native species, were likely stronger for non-native species. We show that applying niche theory to studies of biodiversity can uncover important processes influencing the dynamics of ecological communities and is important for developing a comprehensive understanding of imperiled systems. Our work highlights the importance of managing the impacts of species invasions in areas of high conservation concern, and we urge continued vigilance in areas that are comparatively intact, many of which may be experiencing effects that are not easily visible.

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Figures

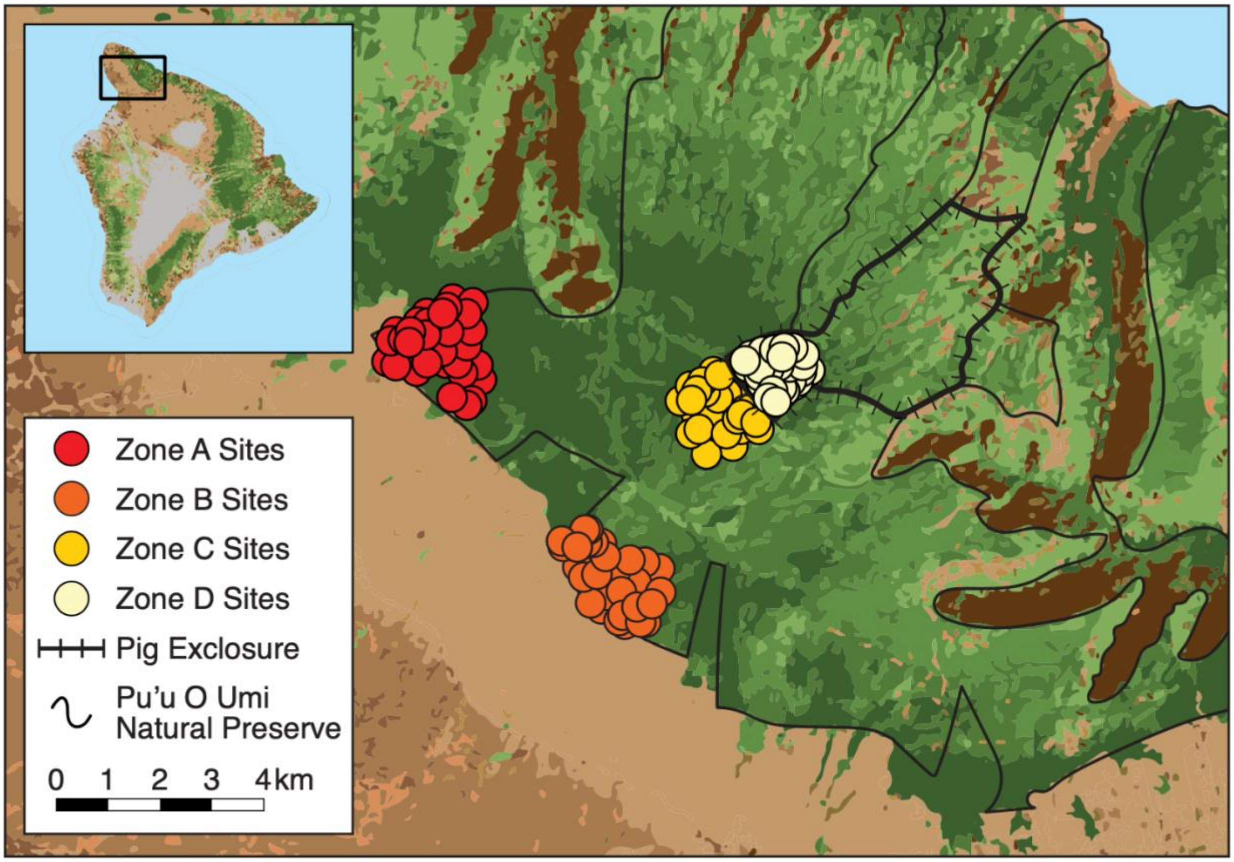


Figure 1. Map of the study area in Kohala. Points represent sampling sites and are color coded by position within pig-density Zones varying from high (Zone A) to pig exclusion (Zone D). The grey, solid-line polygon marks the boundary of the Puʻu O Umi Natural Area Reserve, while the hatched polygon marks the pig exclosure area. Green shading indicates the extent of forest cover.

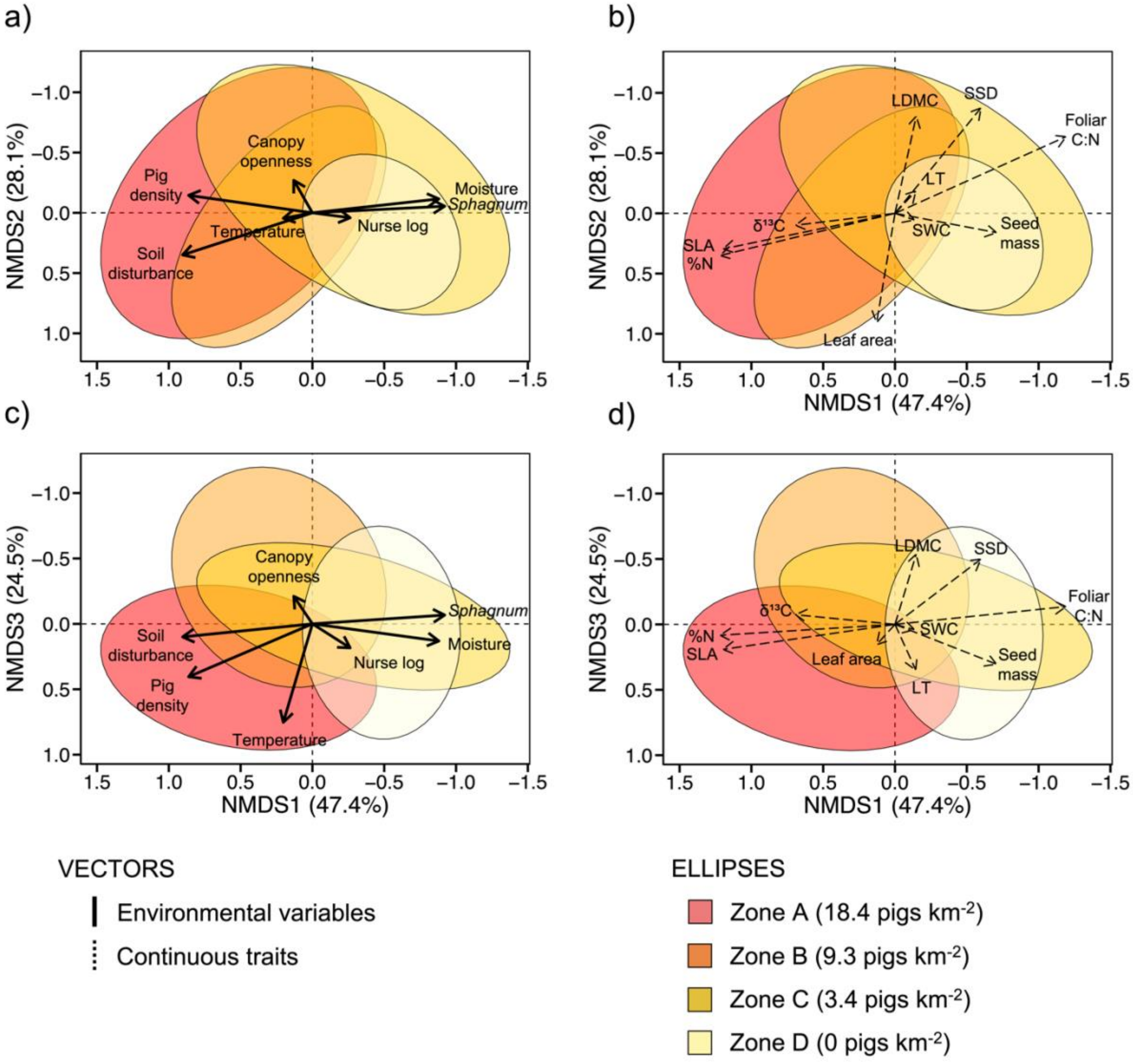


Figure 2. Non-metric multidimensional scaling (NMDS) ordination of community composition across four pig-density Zones. Ellipses represent 95% CI's for each Zone. Panels (a) and (b) show NMDS1 and NMDS2, while panels (c) and (d) show NMDS1 and NMDS3. Vectors in panels (a) and (c) show linear relationships with habitat drivers, while (b) and (d) depict linear relationships with community weighted mean (CWM) trait values. Vector lengths are scaled by

R^2 to capture to strength of relationships with ordination axes. Note axis numbers are flipped to match orientation in Chapter 2 (Peyton, et al. 2023).

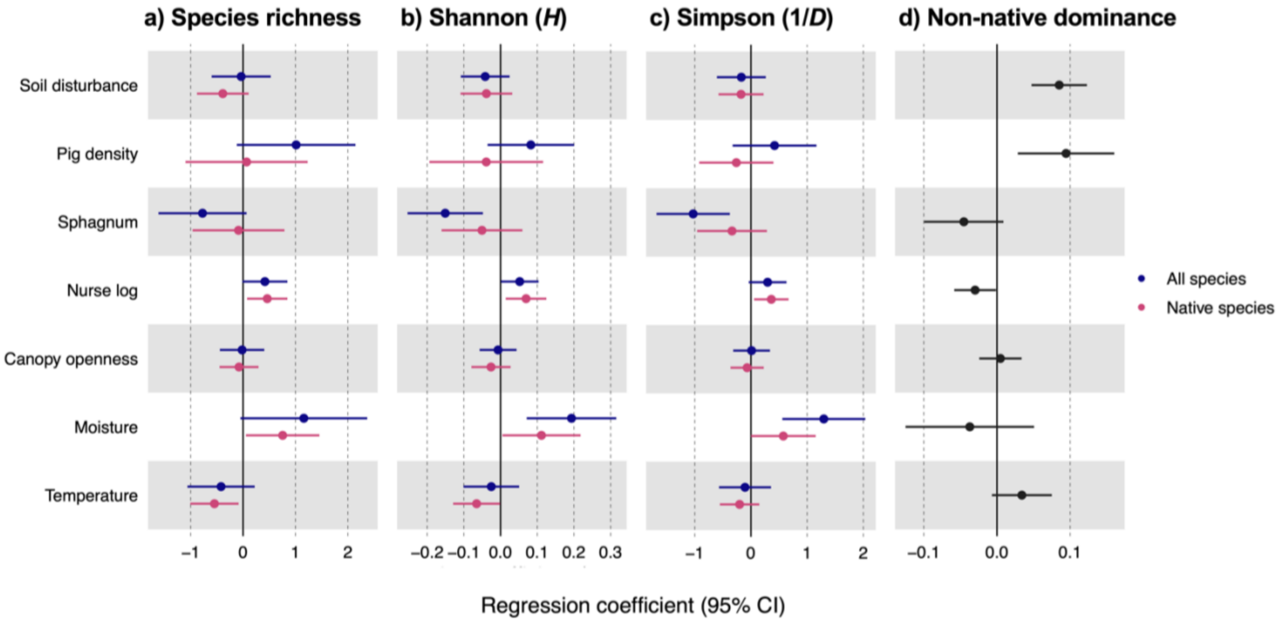


Figure 3. Coefficients of weighted model averaging for top models with AIC < 10 for a) species richness, b) Shannon diversity (*H*), c) reciprocal Simpson index (1/*D*), and d) non-native dominance (non-native cover/native cover). Bars show 95% CI for coefficient estimates, with the black vertical line marking 0 for each model. Models showing results for all species in blue, models showing results for native species (i.e. non-native species removed) in red.

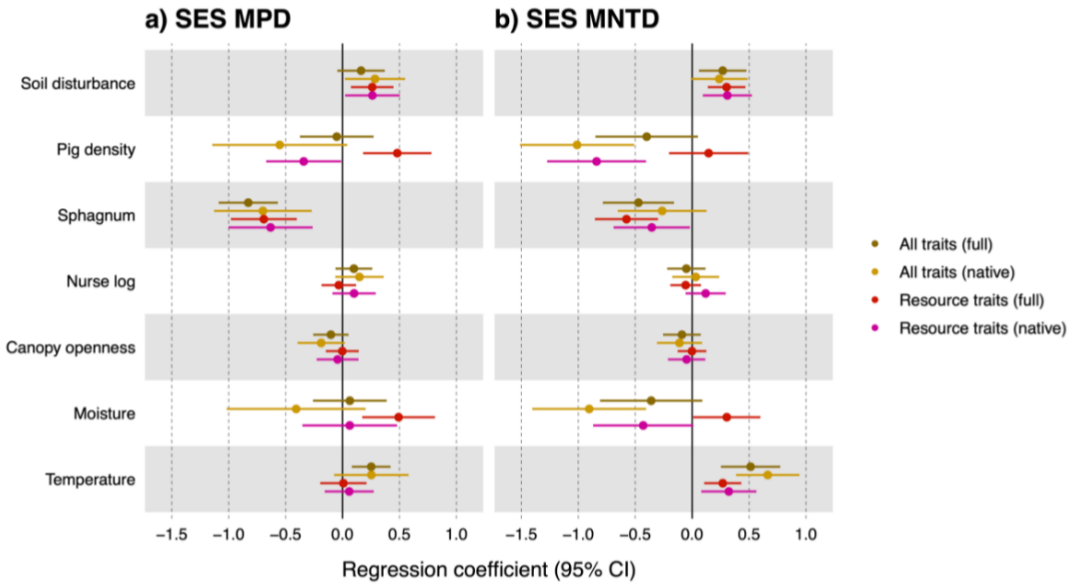


Figure 4. Coefficients of weighted model averaging for top models with AIC < 10 for functional (trait) diversity metrics a) SES.MPD and b) SES.MNTD. Bars show 95% CI for coefficient estimates, with the black vertical line marking 0 for each model. Results shown for (i) all species with all traits (brown), (ii) native species with all traits (orange), (iii) all species with resource traits (red), and (iv) native species with resource traits (maroon). All variables were rescaled (mean 0, ±1 SD) prior to inclusion in models. Moisture and temperature were included to account for any confounding effects of climate on target parameters.

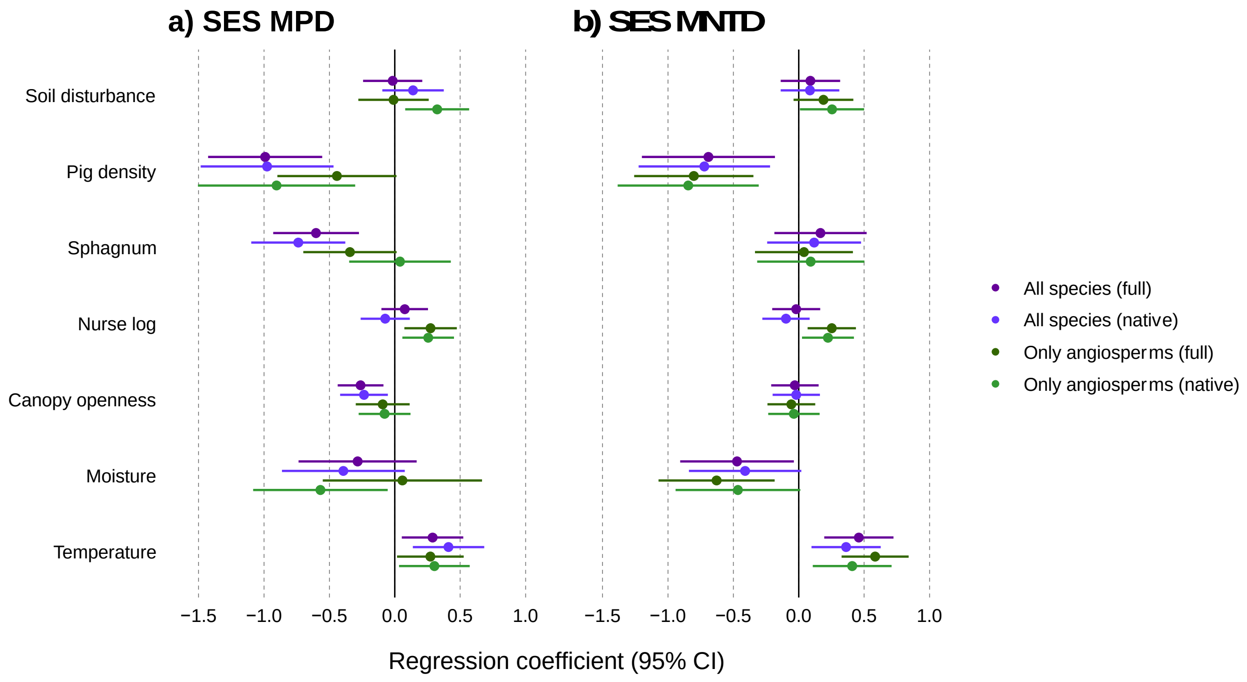
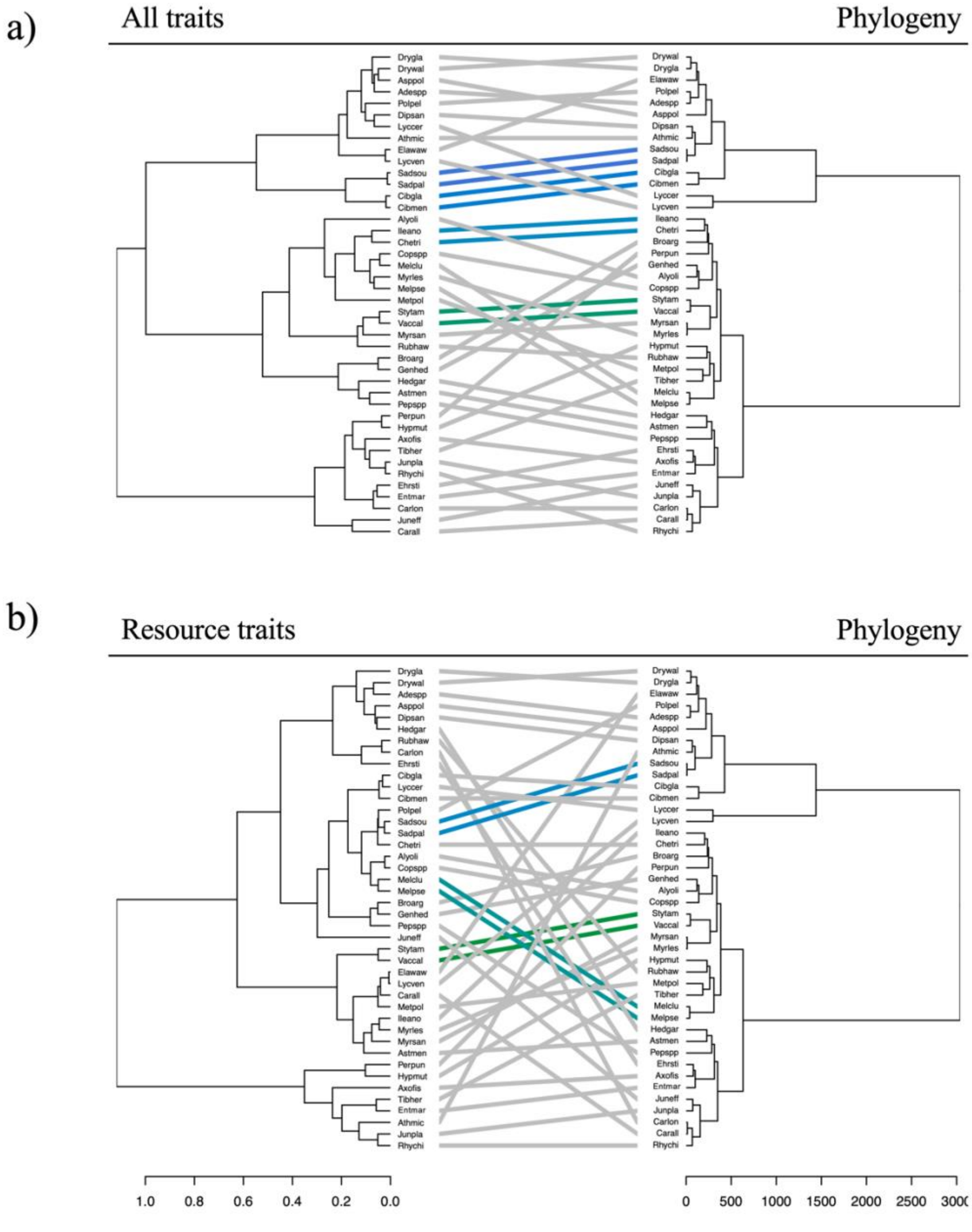


Figure 5. Coefficients of weighted model averaging for top models with AIC < 10 for phylogenetic diversity metrics a) SES.MPD and b) SES.MNTD. Bars show 95% CI for coefficient estimates, with the black vertical line marking 0 for each model. Results shown for (i) all species (native and non-native; black), (ii) native species (purple), (iii) all angiosperms (native and non-native; dark green), and (iv) only native angiosperms (green). All variables were rescaled prior to inclusion in models. Moisture and temperature were included to account for any confounding effects of climate on target parameters.

Table 1. Results for tests of phylogenetic signal in traits. K and λ values listed for Blomberg's K and Pagel's λ. Values of Blomberg's K > 1 indicate strong phylogenetic signal, while values < 1 indicate weak or no signal. Values of Pagel's λ near 1 indicate phylogeny strongly structures trait values, while λ near 0 indicates traits are independent of phylogeny. Blomberg's K and Pagel's λ calculated for (i) the full phylogeny with all species, (ii) a reduced phylogeny with only native species, (iii) a reduced phylogeny with only angiosperms, and (iv) a reduced phylogeny with only native angiosperms. P-values derived from permutation tests (n = 1000). Values significant at p < 0.05 are highlighted in bold.

Continuous traits		Pagel's λ	p	Blomberg's K	p
Full phylogeny					
	SLA	0.107	0.430	**0.29**	**0.038**
	LDMC	0.000	1.000	0.14	0.444
	LA	0.000	1.000	0.23	0.254
	LT	0.000	1.000	0.04	0.950
	C:N	0.064	0.598	0.21	0.192
	%N	0.064	0.625	0.26	0.118
	d13C	0.000	1.000	0.15	0.710
	Seed_mass	0.000	1.000	0.24	0.391
	SWC	0.000	1.000	0.11	0.801
	SSD	0.000	1.000	0.09	0.895
	Max height	0.000	1.000	0.15	0.551
Native species					
	SLA	0.000	1.000	0.12	0.712
	LDMC	0.000	1.000	0.20	0.442
	LA	0.000	1.000	0.07	0.906
	LT	0.000	1.000	0.23	0.294
	C:N	0.000	1.000	0.10	0.780
	%N	0.000	1.000	0.11	0.698
	d13C	0.000	1.000	0.08	0.838
	Seed_mass	0.006	0.972	0.21	0.842
	SWC	0.000	1.000	0.18	0.883
	SSD	0.000	1.000	0.16	0.970

	Max height	0.000	1.000	0.15	0.521
All angiosperms					
	SLA	0.000	1.000	0.38	0.533
	LDMC	0.000	1.000	0.42	0.366
	LA	0.809	0.163	0.56	0.358
	LT	0.000	1.000	0.10	0.957
	C:N	0.000	1.000	0.35	0.759
	%N	0.000	1.000	0.45	0.568
	d13C	0.000	1.000	0.40	0.726
	Seed_mass	0.000	1.000	0.61	0.514
	SWC	0.344	0.631	0.79	0.302
	SSD	0.000	1.000	0.60	0.750
	Max height	0.000	1.000	0.20	0.861
Native angiosperms					
	SLA	0.000	1.000	0.54	0.370
	LDMC	0.000	1.000	0.71	0.095
	LA	0.000	1.000	0.53	0.317
	LT	0.785	0.486	0.62	0.157
	C:N	0.000	1.000	0.62	0.157
	%N	0.000	1.000	0.55	0.349
	d13C	0.000	1.000	0.33	0.662
	Seed_mass	**1.013**	**0.049**	0.91	0.124
	SWC	0.000	1.000	0.67	0.108
	SSD	0.000	1.000	0.54	0.248
	Max height	0.000	1.000	0.55	0.265


a)
All traits
Phylogeny
Drygla
Drywal
Asppol
Adespp
Polpel
Dipsan
Lyccer
Athmic
Elawaw
Lycven
Sadsou
Sadpal
Cibgla
Cibmen
Alyoli
Ileano
Chetri
Copspp
Melclu
Myrles
Melpse
Metpol
Stytam
Vaccal
Myrsan
Rubhaw
Broarg
Genhed
Hedgar
Astmen
Pepspp
Perpun
Hypmut
Axofis
Tibher
Junpla
Rhychi
Ehrsti
Entmar
Carlon
Juneff
Carall
Drywal
Drygla
Elawaw
Polpel
Adespp
Asppol
Dipsan
Athmic
Sadsou
Sadpal
Cibgla
Cibmen
Lyccer
Lycven
Ileano
Chetri
Broarg
Perpun
Genhed
Alyoli
Copspp
Stytam
Vaccal
Myrsan
Myrles
Hypmut
Rubhaw
Metpol
Tibher
Melclu
Melpse
Hedgar
Astmen
Pepspp
Ehrsti
Axofis
Entmar
Juneff
Junpla
Carlon
Carall
Rhychi
b)
Resource traits
Phylogeny
Drygla
Drywal
Adespp
Asppol
Dipsan
Hedgar
Rubhaw
Carlon
Ehrsti
Cibgla
Lyccer
Cibmen
Polpel
Sadsou
Sadpal
Chetri
Alyoli
Copspp
Melclu
Melpse
Broarg
Genhed
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Juneff
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Vaccal
Elawaw
Lycven
Carall
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Myrles
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Hypmut
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Melclu
Melpse
Hedgar
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Ehrsti
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Entmar
Juneff
Junpla
Carlon
Carall
Rhychi
1.0
0.8
0.6
0.4
0.2
0.0
0
500
1000
1500
2000
2500
300

Figure 6. Comparisons between the topology of dendrograms depicting multivariate trait relationships among species (left side) and trees depicting phylogenetic relationships (right side). Both phylogenies show all species and have the same topology, while trait dendrograms differ and show relationships resulting from cluster analysis of a) all traits, and b) resource traits. Grey lines highlight the position of each species in the trait dendrogram and the phylogeny, while colored lines show species pairs that remain as nearest neighbors for both the dendrogram and the phylogeny. Four species pairs are conserved for a), while only three are conserved for b). Two pairs, the *Sadleria pallida* and *Sadleria souleytiana* pair (Blechnaeae) and the *Styphelia tameiameiae* and *Vaccinium calycinum* pair (Ericaceae), remain clustered across both comparisons.

SUPPORTING INFORMATION

Appendix S1

Table S1. List of four-letter species codes and corresponding scientific names.

SIX-LETTER CODE	SCIENTIFIC NAME
Native species	
CARALL	Carex_alligata
CIBGLA	Cibotium_glaucum
STYTAM	Styphelia_tameiameiae
METPOL	Metrosideros_polymorpha
MYRSAN	Myrsine_sandwicensis
RHYCHI	Rhynchospora_chinensis
VACCAL	Vaccinium_calycinum
CHETRI	Cheirodendron_trigynum
CIBMEN	Cibotium_menziesii
COPSPP	Coprosma_spp
DRYGLA	Dryopteris_glabra
MELCLU	Melicope_clusiifolia
POLPEL	Polypodium_pellucidum
ASPPOL	Asplenium_polyodon
PEPSPP	Peperomia_spp
ATHMIC	Athyrium_microphyllum
ILEANO	Ilex_anomala
BROARG	Broussaisia_arguta
ADESPP	Adenophorus_spp
DRYWALL	Dryopteris_wallichiana
ALYOLI	Alyxia_oliviformis
SADPAL	Sadleria_pallida
RUBHAW	Rubus_hawaiensis
MYRLES	Myrsine_lessertiana
MELPSE	Melicope_pseudoanisata
GENHED	Geniostoma_hedyosmifolium
ELAWAW	Elaphoglossum_wawrae
DIPSAN	Diplazium_sandwicensanium

SADSOU	Sadleria_souleyetiana
LYCVEN	Lycopodium_venustulum
LYCCER	Lycopodiella_cernua

Non-native Species

AXOFIS	Axonopus_fissifolius
PERPUN	Persicaria_punctata
HEDGAR	Hedychium_gardnerianum
EHRSTI	Ehrharta_stipoides
CARLON	Carex_longii
JUNEFF	Juncus_effusus
ENTMAR	Entolasia_marginata
JUNPLA	Juncus_planifolius
HYPMUT	Hypochaeris_muticum
TIBHER	Tibouchina_herbacea

CHAPTER 4

Dietary niche variation in an invasive omnivore: the effects of habitat on feral pig resource use in Hawai‘i

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Abstract

Invasive omnivores may have profound impacts on ecological communities through diet selection, particularly when their functional roles differ from those in their native range. While the threat of feral pigs (*Sus scrofa*) to native plant communities in Hawai‘i is well known, their trophic dynamics and the drivers of variation in their diet remain understudied. We investigated the feral pig trophic niche on Hawai‘i Island using stable isotopes (^{13}C and ^{15}N) and Bayesian mixing models to identify drivers of variation in resource use. We also reconstructed intra-individual variability for six subsampled individuals to understand temporal variation in resource use and individual diet specialization. Our results revealed feral pigs on Hawai‘i Island exhibit a broad trophic niche characterized by diverse diets, with substantial overlap in resource use across districts and habitats. Differences in dietary composition in the transition from forest to open habitat were driven primarily by a decline in invertebrates and an increasing reliance on resources enriched in ^{15}N, which may reflect a shift in protein sources with habitat. Pigs in forested areas exhibited a smaller trophic niche than those in open habitats, largely driven by differences in feeding strategies and resource availability. Diets for subsampled individuals varied little, suggesting feral pig resource-use strategies in Hawai‘i tend to be relatively stable through time. Individual niche-width was relatively narrow compared to that of feral pigs in Hawai‘i at large, indicating the relatively wide feral pig dietary niche is characterized by substantial intraspecific diet specialization, likely as a result of strong intraspecific competition. Understanding the drivers of feral pig resource use offers key information for management strategies aimed at mitigating their ecological impacts in imperiled systems like Hawai‘i.

Keywords

dietary niche, omnivore, feral pig, stable isotope, diet, specialization, Hawaii, *Sus scrofa*

Data available through the Dryad Digital Repository: https://doi.org/10.5061/dryad.w6m90 5qx5.

Introduction

Despite the role of omnivores in shaping ecosystems worldwide, their trophic dynamics are relatively understudied (Hamalainen et al., 2022). Omnivory is generally associated with a broad dietary niche (Rozin, 1976), but variation in occupied niche space can be considerable, even within a species (Layman & Allgeier, 2012; Newsome et al., 2009; Paolini et al., 2018). Resource quality and availability (Hamalainen et al., 2022; Manlick & Pauli, 2020), intra- and inter-specific competition (Galetti et al., 2015; Milinski, 1982; Morse, 1974), and individual past experience (Garcia et al., 1974; Rogers & Blundell, 1991; Rozin, 1976) can all significantly influence a consumer's dietary niche by affecting resource selection and subsequently altering trophic interactions. Even when omnivores and other generalist consumers occupy a broad niche at the population level, how niche space is partitioned among individuals can differ substantially (Bolnick et al., 2003). Recent work has highlighted the importance of variation within and across individuals to understand the dietary ecology of generalist consumers (e.g. Larson et al., 2020; McEachern et al., 2006; Scholz et al., 2020), and it is becoming increasingly evident that effects driven by intraspecific variation in resource use can propagate through food webs to fundamentally influence community structure (Newsome et al., 2009; Scholz et al., 2020; Svanbäck & Persson, 2004) and function (Benkendorf & Whiteman, 2021; Křivan & Diehl, 2005). Filling these gaps is especially important in the case of invasive omnivores in ecosystems where their functional roles are poorly understood.

Feral pigs (*Sus scrofa*) are among the most destructive and widely introduced invasive species globally (McClure et al., 2018) and have dramatically altered ecosystems worldwide (Wehr et al., 2018). As omnivores and diet generalists, feral pigs exploit a large variety of resources, which not only supports their establishment and spread in a wide range of climate and habitats (Ballari & Barrios-García, 2014), but also allows pigs to shift their diets temporally based on seasonal resource availability (Loggins et al., 2002; Wilcox & Van Vuren, 2009; Wurster et al., 2012). Seasonal variation in pig diet can lead to a dynamic restructuring of trophic impacts through time (McMeans et al., 2019). For example, feral pigs have directly led to widespread declines and, in some cases, extinction of native plant and animal species due to herbivory (Murphy et al., 2014), predation (Whytlaw et al., 2013), and competition (Galetti et al., 2015), and have indirectly contributed to the spread of other non-native species through biotic disturbance and dispersal (Peyton et al., 2023). When available, human food subsidies constitute a significant portion of feral pig diet, often resulting in the destruction of agricultural and residential property (Herrero et al., 2004).

In Hawaiʻi, like other island systems with no history of large mammalian herbivores, feral pigs are largely unconstrained by competition and predation. Under these conditions, pigs have created novel top-down forcing for native communities with naïve species lacking adaptations to such conditions (Cordell et al., 2009; Scheffler et al., 2012), which has resulted in significant changes to species composition in forests where pigs encroach (Cole et al., 2012; Murphy et al., 2014). The lack of interspecific competition for pigs in these systems may promote higher inter-individual variation and the expansion of their trophic niche (Bolnick et al., 2003; Van Valen, 1965). This variation and diet expansion often results in trophic impacts distributed heterogeneously across individuals and populations (Bolnick et al., 2010; Lunghi et al., 2020).

While substantial effort has focused on the dramatic effects of pigs on Hawaiian flora and fauna, there are relatively few investigations on the feeding ecology of pigs or the drivers of variation in diet. Exploring pig trophic dynamics is especially important on an ecologically diverse island like Hawaiʻi Island (the ʻBig Island'), where steep gradients in climate and vegetation generate significant variation in habitat type (Mueller-Dombois, 1988). Feral pigs have invaded the majority of Hawaiʻi Island, and the ecological diversity of the island has likely led to differences in resource use and home-range size among populations (Diong, 1982). Generalists can persist in otherwise unsuitable habitats with sufficient subsidies from anthropogenic resources (Larson et al., 2020; Pedrosa et al., 2021), which may allow them to overcome constraints associated with macronutrient availability (Cervo & Guadagnin, 2020; Stillfried et al., 2017). Utilization of human food resources is commonly documented (Wehr et al., 2018) and is likely driven by risk-reward trade-offs (Houston et al., 1993) and the availability of other resources. Seasonality may also influence resource availability and dietary niche breadth; in Hawaiʻi, seasonality is characterized by wet (November through April) and dry (May through October) periods, with the greatest seasonal moisture variation in areas where mean annual precipitation is low (Giambelluca et al., 2013). Indicators of spatial and temporal patterns in resource use can provide valuable context to identify the functional role that feral pigs occupy under conditions far removed from their native range.

Here we quantify the feral pig trophic niche on Hawaiʻi Island using stable isotopes of carbon and nitrogen from tail hairs collected by hunters across the island. Stable isotope analysis has led to significant advances in dietary ecology in recent years (Bicknell et al., 2020; El-Sabaawi et al., 2009; Happel et al., 2015; Layman & Post, 2008; Shiels et al., 2013; Vaudo & Heithaus, 2011). Stable isotopes allow us to quantify dietary composition via the isotopic distinction of resources in a consumer's diet that have become assimilated into inert tissues (Moore & Semmens, 2008; S. Newsome et al., 2007; Phillips & Gregg, 2003). Ratios of stable carbon, reflecting ^{13}C vs ^{12}C discrimination based on biochemical differences in carbon fixation during C3 and C4 photosynthesis, and stable nitrogen isotopes, tracking trophic position with ^{15}N enrichment at higher trophic levels, are especially useful in dietary analysis due to their direct links to trophic processes and their high abundance in biological tissues (Peterson & Fry, 1987). We estimated dietary composition of individuals captured in different districts and habitats using Bayesian mixing models and identified factors influencing resource use. Furthermore, we reconstructed intra-individual resource-use patterns for a subset of six sequentially subsampled individuals to quantify resource niche heterogeneity and individual diet specialization. We predicted that isotopic signatures and dietary composition differ across habitats and districts due to differences in resource availability. Furthermore, we expected that the feral pig dietary niche space in drier areas with open vegetation would be larger than that of wetter districts and forested habitats due to greater spatial and temporal heterogeneity in the availability of resources in drier areas.

Methods

Study system

We obtained pig hair samples from hunters across the island in partnership with the United States Forest Service (USFS) and the Keiki of Da ʻĀina nonprofit organization on Hawaiʻi Island. Feral pigs were captured from 5 of 6 districts representing *moku*, or traditional Hawaiian land divisions (Puna, Hāmākua, Kohala, Kona, and Hilo; no pigs were captured in Kaʻū district). Each district aggregates adjacent watersheds, spans a wide elevational gradient, and contains considerable heterogeneity in land cover (Fig 1). The Kona, Puna, and Hilo districts are characterized by approximately 50% forest cover, whereas Hāmākua and Kohala have notably less (23% and 10%, respectively; Hawaiʻi Land Cover and Habitat Status CAH 2017). The Kohala district features a substantially greater percentage of open habitat than other districts due to the presence of pasture and ranchland, along with converted forest and shrubland, both of which are largely dominated by non-native C4 grasses (Chadwick et al., 2007). Agriculture and agroforestry practices are present to varying degrees in each district but cover the greatest area in Puna (> ¼ of land cover). Dramatic agricultural shifts in the past 40 years have led to significant declines in sugar and pineapple production, with a concurrent rise in coffee, macadamia nuts, and local crop cultivation (taro, tropical fruits, etc.), along with the expansion of commercial eucalyptus plantations in former sugarcane fields along the northeast coast in the Hāmākua and Hilo districts (Perroy et al., 2016). Hilo and Kona are the most populous districts as of 2020, with populations of 53,600 and 53,100 respectively (US Census Bureau, 2023). These human populations are largely centered around the city and town of Hilo and Kailua-Kona, respectively. Pigs are found in all districts and occupy a variety of habitats. These include low elevation mesic and wet forest dominated by non-native C3 vegetation, high elevation montane forest with varying degrees of intact native C3 vegetation, and open shrub and grassland with abundant non-native C4 grasses (Barton et al., 2021).

Sample collection and preparation

Feral pig hair samples were collected on April 1st 2023 during the 10th annual Keiki of Da ʻĀina pig hunting tournament, in which teams from across the island tracked and captured pigs within a 12-hour window. We collected samples from the tail hair of 48 feral pigs, and information on sex, age (by dentition), weight, and body length were recorded. We distinguished between castrated males (Laho‘ole; castrated and released as piglets) and non-castrated males. Due to time constraints, we were unable to collect age and size data for all individuals. Hunters provided information about the district where pigs were collected, as well as the habitat where they were found (forest, open, and mixed – i.e., intermediate habitats between forest and open). Only 2 individuals were captured in Hilo; thus, they were removed from analyses among districts. While the spatial resolution and habitat information were coarse and we cannot guarantee they reflect the long-term conditions experienced by each individual, recent resource use likely reflects local conditions. Home range estimates for pigs vary widely based on habitat and resource availability, ranging from 0.62 – 48.3 km^2 globally (Garza et al., 2018). Direct estimates from radio-collared individuals in Hawai‘i are smaller than average global estimates, ranging from 0.62 – 2.01 km^2 under forested conditions (Anderson & Stone, 1993; Diong, 1982) and from 5.18 – 10.36 km^2 in open habitats (Griffin, 1978). Maximum home-range estimates do not exceed the minimum area encompassed by districts (1,255 km^2 for Kohala; Fig. 1), though habitat type varies within districts. Although more recent direct estimates are, to our knowledge, lacking in Hawai‘i, Risch et al. (2022) found significant seasonal shifts in abundance across ecotones in Maui, suggesting pigs may migrate longer distances seasonally due to changes in resource availability and hunting pressure. Nevertheless, it is reasonable to assume recent (i.e. 5 – 7 days) sources of C and N assimilated into inert tissues were derived from resources near the capture location for most individuals (Wurster et al., 2012).

Pigs consume a wide range of food resources, many of which cannot be distinguished isotopically. To determine the isotopic signatures of potential resources, we opportunistically collected samples of common resource categories known to be consumed by feral pigs on Hawaiʻi Island, including native C3 plant tissues (fruits, leaves, roots; n = 20), non-native C4 pasture grasses (leaves, roots; n = 12), and invertebrates (i.e. earthworms and other detritivores; n = 7) from across the island (Appendix Table S1), while recognizing that some native C4 plants and non-native C3 plants may contribute to pig diet. We ran separate MANOVAs for C3 and C4 plants to identify differences in isotopic signatures among tissue types (i.e. leaves, roots, fruits), and tissues did not differ significantly within either C3 or C4 plants. We proceeded by using C3 plants, C4 plants, and invertebrates as resource categories in our analyses. Samples were collected primarily in the Kohala and Hilo districts, which differ considerably in climate and substrate age (Giambelluca et al., 2013). However, MANOVA showed that isotopic signatures did not differ significantly between sampling locations within resource categories (Appendix Table S2), indicating differences due to climate and substrate age are far exceeded by those due to resource category. To include estimates for possible anthropogenic resource consumption, we used values of δ^{13}C and δ^{15}N for United States residents from Hülsemann et al. (2015) corrected for trophic enrichment. Feral pigs encounter a wide range of anthropogenic resources in the form of food refuse, agricultural crops, and intentional supplementation by hunters to promote growth (Ballari & Barrios-García, 2014). While using corrected human isotopic values does not permit discrimination among these specific categories, it does provide a method of incorporating broad estimates of anthropogenic inputs. While human consumption of marine resources is likely higher in Hawaiʻi than in the continental United States, using values from Asian countries with higher fish consumption – and thus slightly higher δ^{15}N and lower δ^{13}C values – provided no qualitative differences in our results. In addition to anthropogenic resources, feral pigs are known to consume a wide range of other resources typically found at higher trophic position (Wehr et al., 2018) and with a similarly elevated δ^{15}N signature. These include ground-nesting seabirds, eggs (Nogueira-Filho et al., 2009) and scavenged inter- and intraspecific animal material (Cukor et al., 2020). We note here that feral pig consumption of these trophically elevated resources contributes largely to estimates of human food resource use in our models, and thus should be considered as a possible contributor to the human food resource category.

Pig hair samples were cleaned using a 2:1 chloroform:methanol solution, sectioned, and ^{13}C and ^{15}N were quantified using accelerator mass spectrometry at the University of New Mexico's Stable Isotope Laboratory (Albuquerque, NM). We used 3-mm sections of the most recently grown hair (i.e. closest to the skin) for analyses exploring how resource use varied with spatial location. We also sequentially sampled hair from six individuals representative of a range of conditions (i.e. sex, capture district, habitat type) to explore temporal variation in dietary composition within individuals. 3-mm segments were taken at each 9-mm interval except for one individual (i.e. the boar captured in the Puna district), where the last four segments were taken contiguously to sufficiently sample across a shorter total length. 12 – 16 subsamples were taken from each individual for a total of 85 subsamples. As all individuals were captured and harvested on the same day, we assumed 3-mm sections of hair represented assimilation across a similar interval among individuals, with the understanding that hair growth rates may vary.

Statistical analyses

Spatial variation

Bayesian versions of mixing models provide a method of estimating the contributions of resources to a consumer's diet while incorporating the inherent variability in isotopic values, C and N concentration, and trophic discrimination factors (Parnell et al., 2013). We applied separate Bayesian mixing models to samples of recently grown hair for each individual using the *simmr* package (Govan & Parnell, 2018) in R (R Core Team 2023), using trophic discrimination factors (TDFs) of -2.3 ± 0.5 and 3.5 ± 0.5 (mean ± sd) for $\delta^{13}C$ and $\delta^{15}N$, respectively. The models were run using three chains with 100,000 iterations with 20,000 removed for burn-in and sample thinning by a factor of 100 to reduce autocorrelation. One individual with an abnormally high $\delta^{15}N$ value (12.9 before applying TDFs) was outside of the mixing space and was removed from the analysis. Median resource contribution values from the resulting posterior distributions were extracted to estimate average dietary composition for each individual.

As resource availability and behavioral differences influence variation among individuals in dietary composition (Rogers & Blundell, 1991), we tested for differences in both isotopic signatures and estimated dietary composition among sexes, capture districts, and capture habitats. To do this, we used PERMANOVA with pairwise comparisons using Bonferroni correction in the *vegan* (Oksanen et al., 2008; Philip, 2003) and *pairwiseAdonis* packages in R (Martinez Aribizu, 2020). Age, weight, and body length were not sufficiently sampled to confidently analyze differences across age and size classes. Among groups identified as dissimilar, we used Similarity Percentage (SIMPER) analysis from the *simper* function in the *vegan* package to identify which resources primarily contributed to those differences. Resources driving differences between groups play a disproportionate role in determining differences in diet preferences and trophic impacts across populations. To characterize the dietary niche in resource space, we ordinated resource estimates for individuals using non-metric multidimensional scaling (NMDS) with Bray-Curtis distance. Next, we quantified dietary niche width using estimated Bayesian standard ellipse areas (SEA; a measure of niche breadth) corrected for small sample size (SEAc) using the R package *SIBER* (Jackson et al., 2011) and calculated niche width among sexes, capture districts, and capture habitats in both isotopic (i.e. δ^{13}C and δ^{15}N) and resource (i.e. NMDS) space. Models were run using three chains for 100,000 iterations, with 2000 removed for burn-in and thinning by a factor of 100.

Individual diet specialization

To understand diet flexibility within individuals, we ran Bayesian mixing models on the six sequentially subsampled individuals, with individual models for each 3-mm hair segment. Hair growth rates are, to our knowledge, unknown for pigs in Hawaiʻi, and very few estimates have been calculated for feral pigs in general. Applying a hair growth rate estimate of 0.4 mm day^{-1} from Wurster et al. (2012) and Cerling and Viehl (2004), each 3-mm segment represents 7.5 days. While this growth rate estimate is not sufficiently calibrated for our study site to reconstruct precise temporal trends, we can reasonably assume each segment represents a relatively short (~ 1 week) period of assimilation, and comparisons of same-length segments at different positions can be used to quantify temporal diet variability within individuals.

To quantify the degree of individual diet specialization, we estimated niche breadth and overlap of the six subsampled individuals in relation to total, population-wide niche space in both isotopic and resource space following Bolnick et al. (2002). In this formulation, individual diet specialization can be quantified by the ratio of the within-individual component (WIC) of niche width to the total niche width (TNW) of the population, expressed as WIC/TNW. Individuals with low WIC/TNW occupy a small portion of niche space in relation to the total niche breadth. It is important to recognize that this measurement of diet specialization, sensu Bolnick et al. 2002, differs from the designation of diet specialists vs diet generalists related to the evenness in the distribution of resource contributions, sensu Newsome et al. (2012), and provides an index of individual diet variability relative to the population. We calculated WIC/TNW from Bayesian standardized ellipse areas corrected for small sample size (SEAc's) in both isotopic- and resource-space using the R package *SIBER* (Jackson et al., 2011). Models were run using similar parameters as those above to quantify SEAc's for populations delineated by district and habitat. We compared SEAc's for each of the six subsampled individuals to (i) the total feral pig dietary niche, (ii) the dietary niche of pigs found in the same district, and (iii) the dietary niche of pigs found in the same habitat.

Results

Spatial variation

Individual pigs varied considerably in isotopic space, ranging from -26.1 to -15.8 ‰ and 2.0 to 9.8 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (Fig. 2). We observed substantial overlap among pigs from different districts and habitats, each exhibiting a broad range of isotopic values. Pigs found in the Kohala district and in open habitats appear to exhibit higher $\delta^{13}C$ and $\delta^{15}N$ values than in other districts and habitats, potentially indicating a higher reliance on C4 grasses and resources of higher trophic position such as scavenged animal material or human food subsidies. PERMANOVA showed separation across both district and habitat distinctions in isotopic space, but no differences among sexes (Table 1). Pigs from Kohala differed in their isotopic composition from those in Kona and Puna, while pigs found in forests differed from those in open habitat. SEAc values across habitat distinctions showed that pigs in forests occupied the smallest isotopic niche width, followed by those in mixed habitat, and those in open habitat occupy the broadest isotopic space (Table S3).

Mixing models revealed high variability in estimated resource consumption patterns, supporting our expectation of diverse diets and a broad niche for feral pigs across Hawai‘i Island (Fig. 2). Similarly to metrics derived from raw isotopic values above, SEAc values from resource estimates increased across habitat distinctions from forest to open habitat (Table S3). Estimates from mixing models and PERMANOVA showed somewhat similar patterns to those in isotopic space across capture districts and habitats (Table 1). Differences were again found between pigs in open and forested habitats, but only pigs in the Kohala and Kona districts were found to differ significantly, with weakly significant differences between Kohala and Puna (Table 1). SIMPER showed all resources contributed to differences in dietary composition between pigs found in the Kohala and Kona districts (Table S4). Human foods (hereafter designated with asterisks when highlighting the possible inclusion of other resources enriched in ^{15}N, i.e. *human foods*; 0.18 ± 0.11, $p < 0.001$) and invertebrates (0.09 ± 0.05, $p < 0.001$) primarily drove differences in resource use in open and forested habitats (Fig. 3; Table S4). Median values for invertebrate consumption were greater in forest habitat than in open habitat, while *human foods* were greater in open habitat than in forest (Fig. 4). Furthermore, NMDS suggests resource use for pigs in Kohala tend toward higher values of *human food* than in other districts (Fig. 2c, e), although findings may be confounded by differences in sample sizes.

Individual diet specialization

Sequentially sampled individuals demonstrated minor changes in isotopic values and resource use estimates over time (Fig. 5). We observed qualitative differences in dietary composition among districts and habitats that mirrored results at the population level, except for the individual captured in forested habitat in Kohala. The two individuals captured in the Puna forest habitat and the individual captured in the South Kona mixed habitat exhibited isotopic values and resource use estimates similar to others captured in forest and mixed habitat, respectively. The two individuals found in the Kona open habitat expressed elevated $\delta^{13}C$ and $\delta^{15}N$ values, with mixing models estimating large contributions from possible animal tissues and human food, contrasted by relatively low proportions of other resources. The individual captured in the Kohala forest exhibited patterns indicating a high reliance on C4 grasses, differing from most individuals captured in forest habitat but resembling others captured in the Kohala district. The dietary niche width of individuals – measured by both raw isotopic values and by resource estimates – was small compared to that of the total feral pig niche width and that of all pigs captured in the same district or habitat (Fig. 5, Table S5). WIC/TNW values were slightly larger on average in isotopic space than in resource space, and while minor differences were present among individuals in the two metrics, the overall trend indicated high individual specialization. Median WIC/TNW estimates ranged from 0.01 to 0.13 in isotopic space and 0.01 to 0.06 in resource space when TNW was estimated from the total population niche width, and values were similar when TNW was estimated as that of the capture district or habitat (Table S5), although with some rank-reversals.

Discussion

Feral pigs are notorious for their dietary flexibility, which contributes to their invasion of a wide range of habitats globally (Barrios-Garcia & Ballari, 2012). Our findings show populations in Hawaiʻi are no exception, with feral pigs collectively inhabiting a broad dietary niche (Fig. 2). Notably, $\delta^{15}N$ values from individuals indicated that these pigs occupy a wide range of different trophic positions, with some individuals exhibiting values typically expressed by terrestrial scavengers and carnivores (Rodriguez Curras et al., 2022). High values are likely driven by a reliance on animal tissues and human food subsidies with $\delta^{15}N$ values exceeding those typically found in other commonly utilized resources (Hülsemann et al., 2009). Resource estimates from mixing models support these initial observations, with feral pigs exhibiting a wide range of resource combinations and demonstrating several distinct foraging strategies across populations. We recognize that these estimates are subject to varying degrees of uncertainty, and we acknowledge that estimate precision for C3 plants and invertebrates is limited for some individuals due to their linear configuration with both resources in isotope space (Newsome et al. 2012). Given that pigs typically prefer vegetative material over animal material (Senior et al., 2016), model underestimation of C3 consumption may explain why our results show a lower reliance on C3 plant material than we expected in forest habitats. However, studies show that compared to their native range, animal material constitutes a larger portion of the feral pig diet in their introduced range (Ballari & Barrios-García, 2014), and individual diets can vary widely. Nevertheless, both model estimates and raw isotopic values support a wide range of resource-use patterns and demonstrate the considerable intraspecific variability in diet selection among pigs across Hawaiʻi Island.

Spatial variation in resource use

We found substantial overlap in resource use across capture districts and habitats (Fig 2). This is certainly due, in part, to our coarse spatial resolution for capture location, which is intentionally imprecise so hunters can protect their choice hunting grounds. Our spatial resolution is therefore limited to districts, which are often highly heterogeneous and include multiple habitat types. In addition, accuracy in habitat designation was difficult to determine even with relatively broad classifications since hunters may lack a shared definition of habitat distinctions. We nevertheless observed distinct patterns in resource use among pig populations separated by district and habitat, indicating site use and diets were sufficiently spatially constrained that distinctions can be detected even with such coarse designations. We observed that habitat classification was particularly informative in shaping resource use, suggesting recent assimilation of C and N likely occurred largely within the boundaries of the habitat type where individuals were captured. Habitat differentiates resource use patterns more strongly than does capture district, which is undoubtably attributable, in part, to the high degree of habitat heterogeneity in districts. The exception to this pattern is Kohala, which differs from other districts in the abundance of open habitat conditions characterized by pastureland at higher elevation (Maly & Maly, 2004) and dry grass- and shrubland at lower elevation. This pattern is due to a history of forest clearance and ranching, along with an extraordinarily steep moisture gradient ranging from 150 mm to > 3000 mm mean annual precipitation over a distance of < 15 km (Giambelluca et al., 2013). These conditions make Kohala unusual in supporting a substantially higher proportion of open habitat than other districts (Fig 1) and significant habitat heterogeneity over small spatial scales, which increases the likelihood of differential habitat use and subsistence in open habitat.

Feral pig isotopic and dietary composition followed a distinct pattern along the gradient from forest to open habitat, whereby pigs inhabiting mixed habitat occupied an intermediate position between pigs in forest and open habitats. Our findings suggest that the feral pig dietary niche increases from wetter (forest) to drier (open) habitats as pigs shift toward reliance on resources enriched in both ^{13}C and ^{15}N (Fig. 2). This appears to be due to pigs in forests generally consuming more uniform proportions of each resource category and overlapping in their resource use strategies, while pigs in mixed and open habitats exhibit less uniformity in resource use (Fig. 4) and greater variability among individuals (Fig 2,3). This leads to divergent patterns characterized by increasing reliance on C4 grasses or on animal tissues and human food subsidies as habitats become more open, as evidenced by enrichment in ^{13}C and ^{15}N, respectively. While several factors may contribute to these patterns, they are likely driven, in part, by differences in resource availability between habitats. Forests, which typically host a higher abundance of available resources – particularly invertebrates and C3 plants – may support a smaller resource niche as individuals capitalize on preferred resources (Lesser et al., 2020). Current commercial agricultural production occurs primarily in wetter regions on Hawaiʻi Island, and consists largely of C3 crops such as macadamia, coffee, and tropical fruits (Perroy et al., 2016), which almost certainly play a role in C3 contribution under forested and mixed conditions. Drier sites on Hawaiʻi Island, often in the lee of mountains or other orographic barriers (Giambelluca et al., 2013), are typically characterized by a much more dramatic loss of native vegetation historically than forested areas due to past agriculture and livestock grazing, which has largely replaced native vegetation with non-native C4 pasture grasses. Indeed, a sizeable proportion of individuals in open and mixed habitat exhibited a high proportion of C4 grass in their diet; however, SIMPER revealed that C4 grass proportion was not a significant driver of resource-use differences between forest and open habitat (Table S4).

^{15}N enrichment from forest to open habitat appears to have been driven primarily by lower invertebrate consumption in conjunction with increased reliance on trophically elevated resources in open habitat, such as human food and animal tissues (Table 1; Fig 3). These findings are consistent with patterns we would expect if resource quality – particularly protein content – were a significant driver shaping diet in these populations. Protein content in forage can act as a metabolic constraint (Barrett, 1978; Bowen et al., 1995; Parker et al., 2009), shaping preferences toward maximizing protein intake given the available resources on the landscape. Protein limitation has been suggested to shape feral pig diet selection in other systems (Baubet et al., 2004; Belden & Frankenberger, 1990; Wilcox & Van Vuren, 2009) and has even been offered as a mechanism to explain suspicions that pig population density in Hawaiian forests was low until the introduction of non-native European earthworms (Loope et al., 1988). Animal tissues and human foods may satisfy protein requirements for pigs in open habitats in place of invertebrates under forested conditions, supporting this observed trade-off in open vs forest habitats (Table 1, Fig. 3). Conversely, we did see a small number of individuals in all habitats that relied more heavily on C4 grasses with minimal consumption (< 10 %) of other resource categories, which ostensibly contradicts this hypothesis. However, our results indicate N concentrations are higher in C4 grasses than the sampled native C3 plants (Table S1), which, along with supplementation by small quantities of ^{15}N enriched protein sources as indicated by mixing models, is possibly sufficient to fulfill metabolic requirements. These requirements seemingly cannot be fully met on a specialized diet of C3 plants, as evidenced by the lack of individuals clustering near the δ-values for C3 plants in the isotopic mixing space (Fig 2) and estimates of greater invertebrate consumption in forests (Wehr et al., 2020). While the configuration of the mixing space introduces some difficultly in precisely estimating the proportion of invertebrates vs C3 plants for some individuals, widespread accounts of native plant consumption (Loope et al., 1988; Nogueira-Filho et al., 2009; Wehr et al., 2018) suggest it is highly unlikely that forest pigs clustering near invertebrate N and C δ-values do not consume C3 plants as a significant portion of their diet. Even in their introduced range, where they feed more heavily on animal material than in their native range (Ballari & Barrios-García, 2014), feral pigs typically prefer vegetative material (Senior et al., 2016).

It is unclear whether reliance on trophically elevated protein sources in place of invertebrates is driven by the scarcity of invertebrates in open habitats (i.e. animal tissue and/or human food as a fallback) or if alternative protein sources are more available in open habitats relative to forests (i.e. animal tissue and/or human food as a preferred resource). The former is suggested by generally lower aboveground net primary productivity and associated resource availability in drier sites in Hawai‘i, which exceeds the marginal decline in productivity in the wettest sites > 2000 mm yr^{-1} (Austin, 2002). In other systems, human food waste specifically has been observed to serve as a backup when natural resources are unavailable rather than as a preferred resource (Stillfried et al., 2017). The minimal differences in diet found among districts also support this hypothesis, as we would expect higher consumption of anthropogenic resources in districts with high human population density if anthropogenic food subsidies are preferred (Fig 4). Pigs in open habitat may also exhibit larger home-range sizes (Diong, 1982), which would increase the likelihood of exposure to alternative protein sources. Whatever the mechanism, our findings indicate there exist distinct and divergent foraging strategies for pigs on

Hawaiʻi Island shaped by habitat type. Moreover, we find evidence to suggest contemporary pig populations in open, drier habitats may be sustained by alternative protein sources from those found in wetter, forested habitats.

Individual specialization in resource use

Isotopic signatures and resource use estimates for individuals remained relatively stable through time, with some variability in within-individual niche breadth. Resource use among individuals across habitat types was consistent with patterns observed above, except for the individual captured in forest in Kohala. Due to the high degree of habitat heterogeneity in Kohala, it is possible that this individual – while captured in forest habitat – primarily foraged in open grassland, which would explain the high estimates of C4 grasses in its diet. Collectively, these patterns among individuals corroborate findings that pigs employ distinct patterns of resource use and indicate that feral pig feeding strategies, broadly defined by patterns of consumption, do not vary considerably through time. This may be due to the relatively minor changes in resource availability across time in Hawaiʻi compared to regions with greater seasonal variation. Diong (1982) likewise found that pig home-range sizes in Hawaiʻi, which were expected to shift with seasonal changes in resource availability, varied little seasonally in both wet and dry forest habitats. However, seasonal shifts in their distribution and abundance have since been found (Risch et al., 2022), and other systems at similar latitudes have detected patterns of resource use linked to seasonality, particularly in drier habitats (Wilcox & Van Vuren, 2009; Wurster et al., 2012). It also may be that temporal differences in consumption are characterized by variation within, not among, resource categories (e.g. shifting among different sources of C3 plants). Alternatively, pig diets may be relatively stable through time as a result of learned behavior, whereby patterns of resource use remain consistent over time even as conditions shift (Rogers & Blundell, 1991; Rozin, 1976). On Hawaiʻi Island, significant spatial variation occurs over short distances, so individuals may also compensate for changing conditions by moving to access resources. Regardless of the mechanisms, feral pigs in Hawaiʻi appear to establish a broadly consistent resource-use strategy and deviate little through time.

This narrow resource-use strategy hypothesis is further supported by our finding that individual niche width was relatively small compared to that of the total niche width for feral pigs in Hawaiʻi. Raw isotopic values and mixing model estimates both demonstrated that while pigs as a species occupy a wide dietary niche, there is substantial intraspecific diet specialization (sensu Bolnick). While our study is limited to a small number of subsampled individuals, every individual sampled occupied only a small portion of available niche space compared to both the overall feral pig niche (Fig 5) and to that of pigs found in different districts and habitats (Table S5). Low within-individual niche width is indicative of conditions under which strong intraspecific competition can drive individuals to specialize on a narrow range of resources or resource proportions (Araújo et al., 2011). This may occur either in resource-poor environments or under high population densities (Kobler et al., 2009; Svanbäck & Persson, 2004). Feral pig population density in Hawaiʻi is likely high in most areas as they lack any top-down control aside from human hunting, which is below the levels required to control population growth (Hess & Jacobi, 2014). Intraspecific competition is thought to increase in the absence of interspecific competition (Grant & Price, 1981; Van Valen, 1965), as is likely for pigs in many of the areas where they are found. While feral pigs do overlap with other invasive ungulates (i.e. goats, sheep) in some, primarily drier, sites, they are often the sole invasive ungulate where they establish – particularly in wetter forested areas (Ikagawa, 2013; Stone & Anderson, 1988). Our findings suggest a high degree of inter-individual variation and considerable diet specialization in individuals across habitat types, likely driven by high population densities. This may result in variable ecological impacts across individuals and populations, possibly influencing the nature of their effects on communities and ecosystems.

We acknowledge some limitations within our dataset and approach. First, we reiterate that our data come from a non-random sample of individuals captured by hunters and are unlikely to be fully representative of the population at large. In particular, the full range of demographic and body-size parameters is unlikely to be adequately represented due to the preferential take of larger individuals. Second, while stable isotope mixing models are powerful tools for inferring dietary composition, they should be interpreted with caution (see: Shipley & Matich, 2020). In some cases, results may diverge from other methods such as scat or stomach content analysis. Importantly, isotopic signatures incorporate signals from abiotic processes as well as from diet, which may lead to erroneous interpretations if not carefully accounted for. Additionally, while our isotopic endmembers represent the primary resources known to constitute the feral pig diet in Hawai‘i, some individuals may rely on other resources not included in our mixing models. Combining more traditional approaches – or others such as DNA metabarcoding – with stable isotope analysis to provide informative priors offers a method of overcoming some of the limitations of our approach. These approaches will become more available as we continue to partner with local hunters. Our results demonstrate the utility of using stable isotope analysis in collaboration with local hunting communities to investigate the trophic ecology of one of the most problematic invasive omnivores in Hawai‘i.

Conclusions

The feral pig dietary niche on Hawai‘i Island is wide, though intraspecific variation and resource availability have led to several distinct feeding strategies. Differences in resource use were broadly shaped by habitat conditions along a gradient from forest to open habitat, with pigs found in forests occupying a narrower resource niche while pigs in open habitats exhibited greater variation, resulting in a broader niche. Dietary choice is likely constrained by protein content, which may explain trophic elevation in pigs as they switch from invertebrate consumption in forests to human food and animal tissues in open habitats. Furthermore, we found considerable individual diet specialization among subsampled individuals, consistent with strong intraspecific competition driven by high population densities. Despite the challenges associated with reconstructing wild animal diets, we were able to identify important drivers of variation in resource use among feral pigs in Hawai‘i by partnering with local hunting organizations.

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Figures

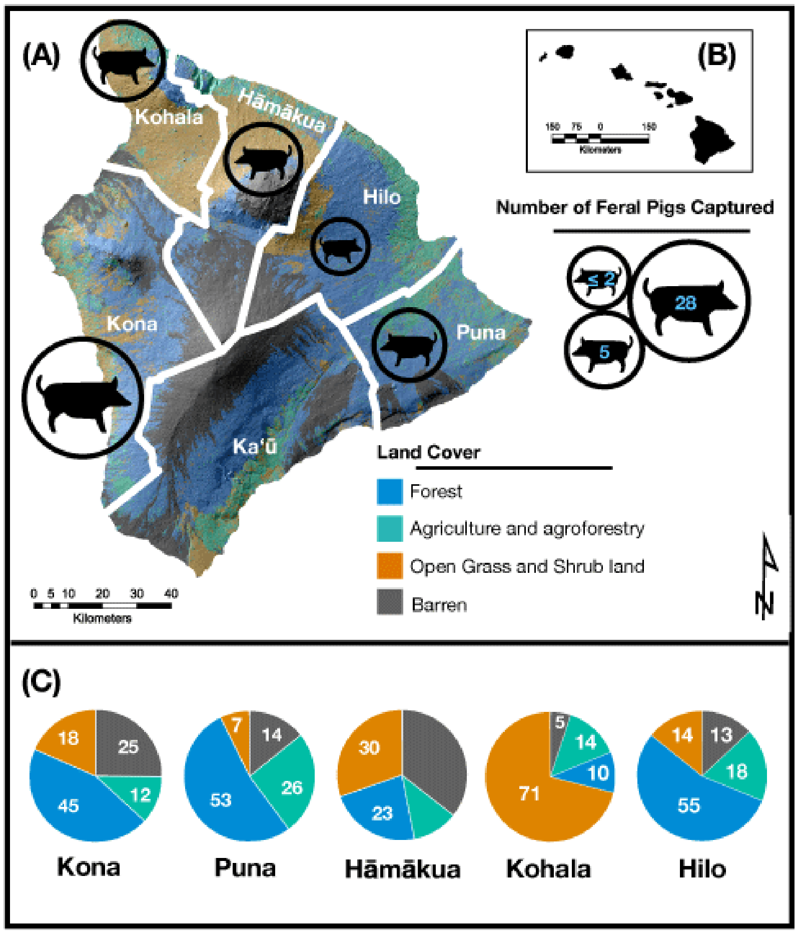


Figure 1. Study area: (A) Map of captures by district, (B) inset of Hawaiian islands, (C) relative percentage of vegetation in each district (Hawai'i Land Cover and Habitat Status CAH 2017) *No pigs were captured in Ka'ū .

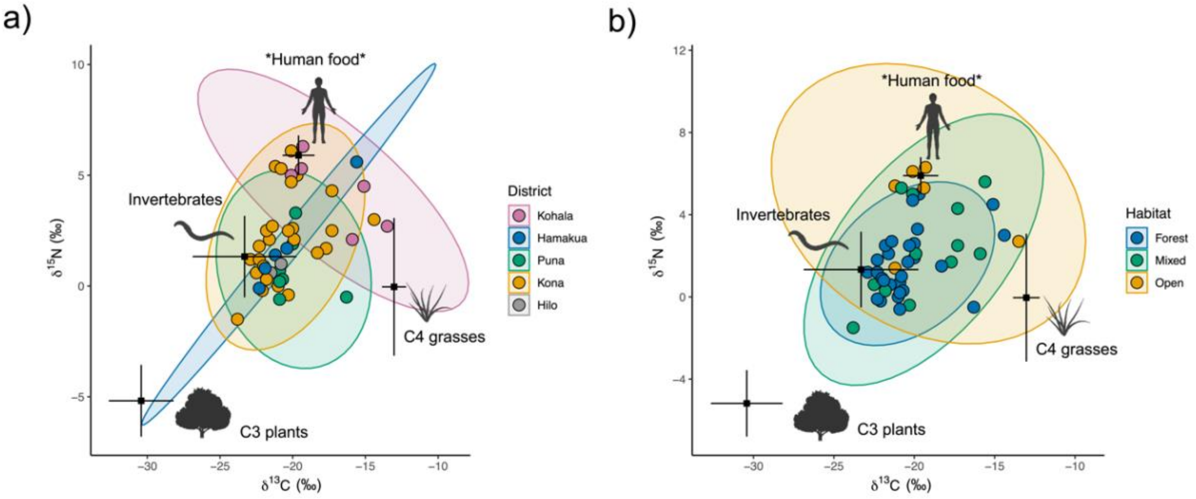


Figure 2. Isotope plots for raw $\delta^{13}C$ and $\delta^{15}N$ values of sampled individuals. Ellipses represent 95% confidence intervals for populations delineated by a) capture district and b) capture habitat. Black dots show the means and 95% confidence intervals for resource categories (C3 plants, C4 grasses, invertebrates, *human food*) after applying trophic discrimination factors. *Human food* may also represent inclusion of other resources found at higher trophic position.

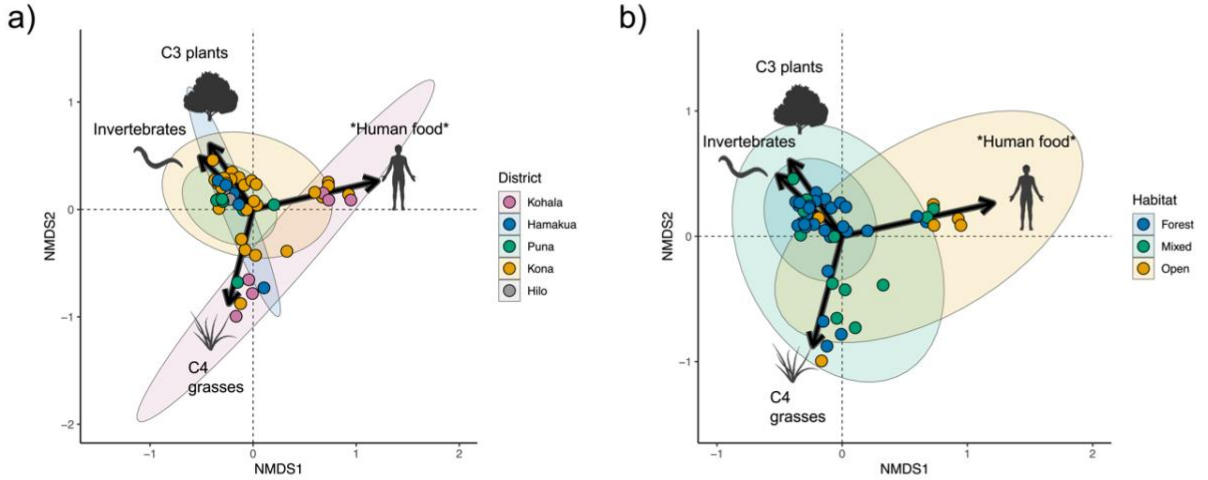


Figure 3. Results of NMDS quantifying relationships among individuals in resource-space using Bray-Curtis distance. Vectors signify resources, with length scaled to vector loadings on NMDS1 and NMDS2. Ellipses represent 95% confidence intervals for populations delineated by a) capture district and b) capture habitat.

Table 1. Results of PERMANOVA with pairwise comparisons between districts, habitats, and sexes (*laho'ole* signifies castrated males). Bolded values are significant at α < 0.05 with p values adjusted using Bonferroni correction, bolded values marked with an asterisk are weakly significant at α < 0.10.

	Isotopic space		**Resource space**	
	R2	**p (adjusted)**	**R2**	**p (adjusted)**
District				
Kohala vs Kona	**0.226**	**0.005**	**0.153**	**0.026**
Kohala vs Puna	**0.451**	**0.005**	***0.311**	***0.088**
Kohala vs Hāmākua	0.297	0.358	0.262	0.406
Kona vs Puna	0.048	0.905	0.042	1.000
Kona vs Hāmākua	0.002	1.000	0.023	1.000
Puna vs Hāmākua	0.050	1.000	0.015	1.000
Habitat				
Forest vs Open	**0.176**	**0.013**	**0.220**	**0.003**
Mixed vs Open	0.093	0.609	0.137	0.308
Forest vs Mixed	0.043	0.538	0.046	0.450
Sex				
Male vs Female	0.012	1.000	0.007	1.000
Female vs Laho'ole	0.014	1.000	0.019	1.000
Laho'ole vs Male	0.003	1.000	0.009	1.000

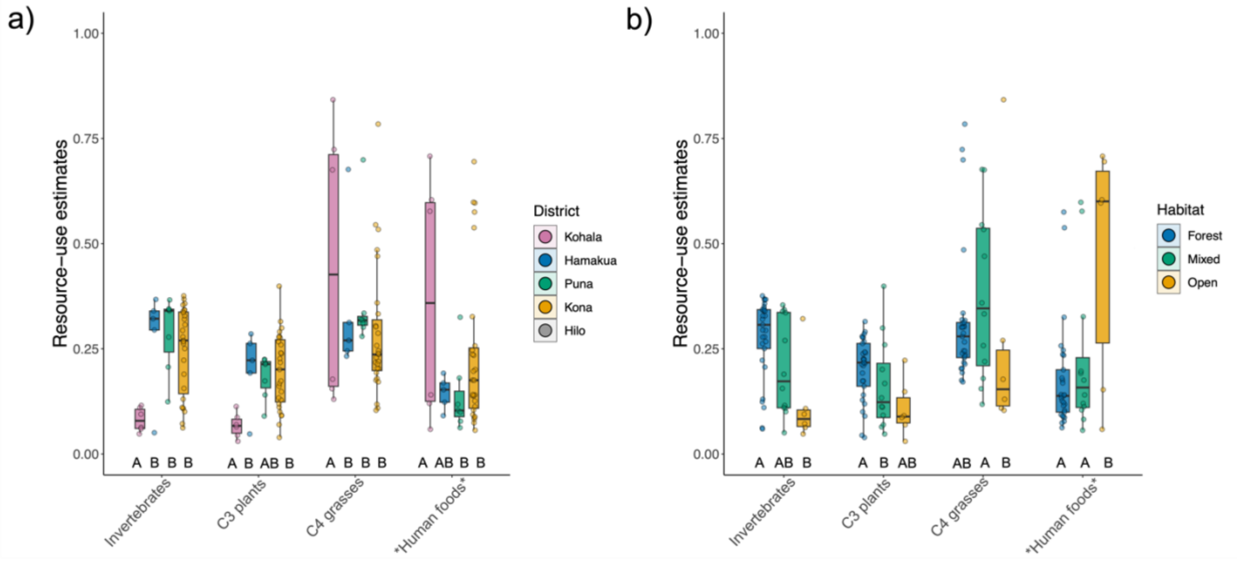
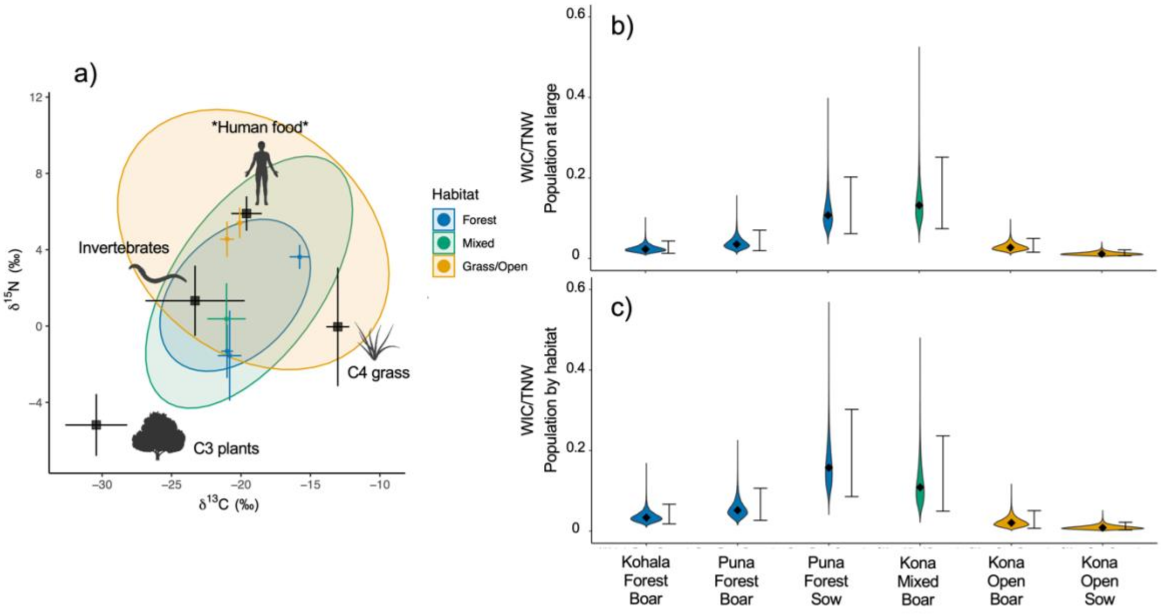


Figure 4. Median resource-use estimates from Bayesian mixing models separated by a) district and b) habitat. Letters signify differences between habitats from SIMPER permutation tests – habitats with no shared letters are significantly different.

Isotopic space



Resource space

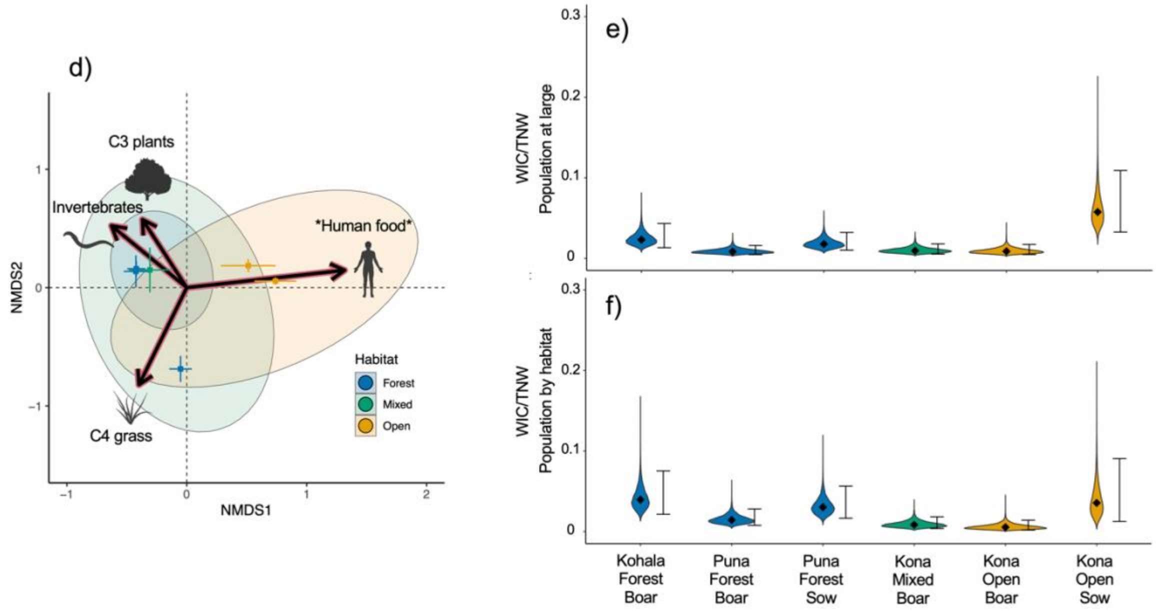


Figure 5. Individual niche width for the 6 chronologically subsampled individuals colored by capture habitat. Error bars show 95% confidence intervals in a) isotopic space and d) resource space for each individual. WIC/TNW given in plots b) (in isotopic space) and e) (in resource space), with TWN defined as the niche width for the population at large (i.e. all sampled individuals). WIC/TNW given in plots c) (in isotopic space) and e) (in resource space), with TWN defined as the niche width of the population associated with the habitat where that individual was captured. Violin plots show the posterior distributions for Bayesian SEAc ratios (SEAc for individual / SEAc for population), error bars represent 95% confidence intervals.

SUPPORTING INFORMATION

Table S1: δ^{13}C and δ^{15}N values (top) and C and N concentrations (bottom) for resource endmembers used in Bayesian stable isotope mixing models

	δ13C		**δ15N**		**n**
Resource	**mean**	**sd**	**mean**	**sd**	
Invertebrates	-23.31	3.57	1.33	1.84	7
C3 (native)	-30.42	2.23	-5.18	1.62	20
C4 (non-native)	-13.03	0.83	-0.037	3.11	12
Human foods	-19.16	1.10	5.90	0.90	1000

	C concentration (%)		**N concentration (%)**		**n**
Resource	**mean**	**sd**	**mean**	**sd**	
Invertebrates	41.31	10.19	8.93	3.21	7
C3 (native)	47.18	3.45	0.94	0.49	20
C4 (non-native)	46.08	1.36	1.59	0.83	12
Human foods	52.80	0.45	6.90	0.06	1000

Table S2: Results of MANOVA testing differences in δ^{13}C and δ^{15}N values in resource endmembers across districts (top) and across different tissue types (bottom). Districts sampled include Hilo and Kohala. Tissues for C3 plants include leaves, roots, and fruits, while tissues for C4 plants include leaves and roots. Asterisk marking invertebrates signifies the lower sample size (n = 7).

	Pillai's trace	**F**	**df (resid)**	**Pr(>F)**
Districts				
*Invertebrates	0.50	2	5	*0.25
C3 plants	0.05	0.48	18	0.63
C4 plants	0.13	0.68	10	0.53
Tissues				
C3 plants	0.09	0.39	17	0.82
C4 plants	0.13	0.69	10	0.53

Table S3: Dietary niche space quantified by SEAc in isotopic space (left) and resource space (right) for populations defined by capture district (top) and habitat (bottom). Median values and standard deviations given for each ellipse.

SEAc	**Isotopic space**		**Resource space**	
District	median	sd	median	sd
Kohala	11.2	6.19	0.47	0.26
Hāmākua	12.0	7.97	0.11	0.07
Puna	7.6	3.74	0.17	0.08
Kona	15.1	3.00	0.37	0.08
Habitat	median	sd	median	sd
Forest	9.7	1.88	0.25	0.05
Mixed	17.1	5.67	0.48	0.16
Open	18.7	10.5	0.69	0.38

Table S4: Results of SIMPER showing contribution to dietary differences among populations characterized by district (top) and habitat (bottom). Bolded district and habitat combinations on the left-hand column are shown by PERMANOVA to be significantly different at α < 0.10. Bolded values with asterisk are shown by permutation tests to be significant at α < 0.05.

SIMPER	**Invertebrates**	**C3 plants**	**C4 grass**	**Human foods**
District				
Kohala vs Kona	***0.087**	***0.069**	***0.157**	***0.141**
Kohala vs Puna	***0.105**	0.060	***0.153**	***0.144**
Kohala vs Hāmākua	***0.106**	***0.074**	***0.153**	0.138
Kona vs Puna	0.055	0.043	0.084	0.084
Kona vs Hāmākua	0.062	0.050	0.086	0.075
Puna vs Hāmākua	0.053	0.051	0.087	0.080
Habitat				
Forest vs Open	***0.093**	0.059	0.117	***0.181**
Mixed vs Open	0.069	0.051	***0.141**	***0.172**
Forest vs Mixed	0.067	***0.057**	0.104	0.078

Table S5: Median WIC/TWN for each individual in both isotopic space (left) and resource space (right). Values given with TWN defined as (i) total feral pig niche space, (ii) population niche space defined by capture habitat, and (iii) population niche space defined by capture district.

	In isotopic space			**In resource space**		
	Total	Habitat	District	Total	Habitat	District
Kohala.Forest.Boar	0.02	0.03	0.03	0.02	0.04	0.02
Puna.Forest.Boar	0.04	0.05	0.07	0.01	0.01	0.02
Puna.Forest.Sow	0.11	0.16	0.20	0.02	0.01	0.04
Kona.Mixed.Boar	0.13	0.11	0.13	0.01	0.01	0.01
Kona.Open.Boar	0.03	0.02	0.03	0.01	0.01	0.01
Kona.Open.Sow	0.01	0.01	0.01	0.06	0.04	0.07

CONCLUSIONS

Island ecosystems are particularly vulnerable to invasion by non-native species, which threaten to displace native species and introduce novel, disruptive processes. This dissertation used Hawaiʻi Island as a case study to explore the interaction of ungulate activity and non-native plants, with a focus on their combined influence on community dynamics. Using Kohala's montane forest understories as a study system, I explored how feral pig activity shapes plant communities, facilitates non-native species encroachment, and influences the assembly of ecological communities. Additionally, I investigated the trophic ecology of feral pigs as invasive generalist consumers, providing a window into the factors influencing variation in their impacts. By integrating functional traits, phylogenetic relationships, trophic dynamics, and community assembly, this research contributes to a broader understanding of invasion ecology in the context of global change.

The findings presented here demonstrate the myriad impacts of feral pigs on vegetation communities, not only as agents of disturbance but also as facilitators of biological invasion. Chapter 1 revealed how **feral pig populations influence shifts in understory vegetation composition**, with pig density strongly correlated with the dominance of non-native plant species. Ungulate soil disturbance was found to act as a catalyst, pushing communities past a tipping point toward non-native dominance. Chapter 2 identified several key mechanisms underlying these shifts, showing how **traits associated with rapid resource acquisition facilitate establishment post-disturbance, leading to disturbance-mediated shifts in the functional composition of the community**. The spatial scale of disturbance was important in structuring responses to light, demonstrating how disturbance can influence species responses to independent abiotic factors. Chapter 3 extended these insights by examining functional and phylogenetic diversity, finding that ***Sphagnum* and feral pig activity significantly influence plant community assembly**. *Sphagnum* largely constrained niche space and induced functional and phylogenetic clustering, while feral pig activity has contrasting impacts on native and non-native species. Finally, Chapter 4 provided a reconstruction of feral pig trophic dynamics using stable isotopes, revealing how **habitat constrains resource use, with open habitat characterized by higher trophic position and a broader dietary niche**. Individual diet specialization was high regardless of habitat, likely due to high intraspecific competition from large population sizes.

Collectively, these studies advance our understanding of how invasive ungulates and non-native plants interact to drive ecosystem change in island ecosystems. They also highlight several areas in need of further study. Notably, the long-term impacts of pig activity on forest resilience and trajectories of vegetation change remain poorly understood, including during their past > 1 ka of establishment in Hawaiʻi. Similarly, the interactive effects of feral pigs and other ungulates with other drivers of global change, such as climate change and human land-use, warrant further investigation. Addressing these gaps will require an integrative approach that combines long-term ecological monitoring, paleoecological records of past ungulate populations, manipulative experimental studies, and predictive modeling to better inform conservation and management strategies.

This dissertation highlights the importance of managing invasive species in Hawaiʻi and beyond. Particularly important will be the effective management of feral pigs to mitigate their impacts on soil integrity and the spread of invasive plants. Targeting the early stages of invasion will likely find greater success than managing areas already dominated by non-native species.

Integrating functional traits into management provides a framework for understanding the mechanisms driving invasion, allowing managers to diagnose issues and design evidence-based interventions. Furthermore, building a deeper understanding of the behavioral and trophic ecology of invasive ungulates will clarify how their impacts vary through space and time. As islands remain at the forefront of biological invasion, they remain vital laboratories for understanding ecological processes and informing conservation strategies.