SEED DISPERSAL BY WILD PIGS IN HAWAIIAN FORESTS

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I dedicate this research to my late hānai grandma, Ellen Gray, who took me in when I came to Hilo and there was nowhere else to go. She showed me unconditional love and was the absolute catalyst and support for finishing school. She also gave me my hānai dad, Troy Castro, and my best friend til the end, Torylee Castro. I love you guys, always.

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Abstract

The introduction of novel species around the world can lead to dramatic shifts in native ecosystems. In Hawaiʻi, invasive species have drastically altered the composition and function of native systems. It is important to understand the effects that these species have in order to anticipate and mitigate any detrimental impacts. Pigs (*Suidae*) are a prevalent invasive species in many parts of the world and occur on all continents except Antarctica. Within their native range, pigs perform a variety of ecosystem services, especially in forests where they increase soil nutrients through rooting and act as seed dispersers. Pig introduction outside of their native range, however, has proven to be detrimental to native species across the globe. In Hawaiʻi, wild pigs decrease native plant regeneration and abundance, prey on native ground-nesting birds, alter soil composition, and disperse non-native seeds. Studies done on other islands in Oceania have shown that pigs disperse native seeds in addition to non-native seeds. To determine if pigs are dispersing native seeds in Hawaiʻi, my thesis focused on the question: How do the species richness and total abundance of germinants in the scat compare to the fruiting species at low and high elevation sites over time? To examine this question, three high and three low elevation forests on the east side of the Island of Hawaiʻi were chosen based on elevation, precipitation, and dominant vegetation type. Elevation and precipitation were consistent amongst the two sets of sites, while native vs. non-native vegetation dominance was the determining selection factor. Scat was collected and germinated during four time points over the course of 19 months from December 2022 to July 2024 to understand seasonal variability. A total of 346 scat samples were collected and of those 173 germinated with a total of 33,508 seedlings. No native seedlings germinated from any of these samples during any time points. There was a greater species richness in the forest compared to the scat, with some germinants that were completely absent in

the vegetation and available fruit. Total abundance of seedlings was greater at low elevation sites, but did not differ over time points. The two dominant species that germinated from the samples, *P. cattleyanum* and *C. obtusifolia*, were present in low elevation scat from all time points. Overall, this study highlights the fact that pigs are not dispersing native seeds and are facilitating colonization of non-native plants in areas where these plant species were not present.

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Introduction

In an increasingly connected world, the introduction of species to new spaces far exceeds
historical rates (Strauss et al. 2006). As introduced species intermingle and sometimes overtake
natives, novel ecosystems emerge with compositions and functions that may be drastically
different than those in the past (Aslan et al. 2014; Case and Tarwater 2020). Island systems in
particular are more sensitive to invasion due to their isolation (Wallace 1887; Elton 1958).
Beginning with early settlers from across Oceania to modern day travelers, a variety of plant and
animal species have settled in Hawaiʻi and further changed the cultural and ecological landscape
of the islands (Aslan et al. 2014). A major consequence of these introductions is the loss of
native species, some of which are found nowhere else in the world, that serve important
ecological functions (Aslan et al. 2014). With the decrease in native species and associated loss
of ecosystem services, their ecological roles are left unfulfilled and may or may not be replaced
by introduced species (Pejchar 2015; Kaushik et al. 2018).

One major ecological function that can be altered by the loss of native species is seed
dispersal. In the tropics specifically, seed dispersal by animals plays a major role in forest
regeneration, whereas in more temperate areas dispersal by wind is more prevalent (Wunderle
1997). Animals differ in their behavior and physiology, which directly affect their ability to
disperse seeds, implying that changes in diversity and density would alter the efficacy of
dispersal mechanisms and could have major consequences for the plants that depend on animal-
mediated seed dispersal (McConkey et al. 2011; Selwyn et al. 2023). This dependence is
especially true for plants that require dispersal some distance from the parent plant to be
successful (La Rosa 1984; Wenny 2001; Jones 2011). While many animals disperse seeds, large-

bodied mammalian seed dispersers are particularly important facilitators of forest regeneration in most tropical systems (Pedrosa et al. 2019).

Ecosystems in Hawaiʻi, however, experience different challenges related to seed dispersal than elsewhere in the tropics. With the absence of mammals before human colonization, animal-mediated dispersal occurred by birds. However, the extinction of native frugivore species and the introduction of non-native species has led to considerable changes in seed dispersal functions (Cole et al. 1995; Case and Tarwater 2020). The largest native frugivorous passerine that still exists today is the ʻAlalā (*Corvus hawaiiensis*); however, this species was extinct in the wild until recent reintroduction to Kīpahulu, Maui (Culliney et al. 2011, Hawaiʻi Division of Forestry and Wildlife 2024). The ʻAlalā most likely served as a key disperser of large seeds that smaller birds are unable to consume (Culliney et al. 2011). Culliney et al. (2011) showed that native plant species like ʻōhā kēpau (*Clermontia hawaiiensis*) and hōʻawa (*Pittosporum hosmeri*) benefitted from passing through the gut of ʻAlalā and experienced improved germination rates. Unfortunately, the current situation is dire; only three native seed dispersers remain in the wild—the Puaiohi (*Myadestes palmeri*), found only on Kauaʻi, the ʻŌmaʻo (*Myadestes obscurus*) that inhabits the island of Hawaiʻi (Kaushik et al. 2018, Matsuoka 2020) and Nēnē (*Branta sandvicensis*) an endemic Hawaiian goose found on Kauaʻi, Maui, and the island of Hawaiʻi (Woog 1999). The Puaiohi is critically endangered with about 500 birds remaining in the wild (Kaushik et al. 2018). The ʻŌmaʻo on the other hand still exists in sufficient enough numbers to be ecologically functional as a seed disperser (Pejchar et al. 1995, Matsuoka 2020). While also a seed disperser, the nature of Nēnē dispersal varies from the the other three and is more focused on species inhabiting lava flows like ʻōhelo (*Vaccinium* spp.) and ʻūlei (*Osteomeles anthyllidifolia*) (Woog 1999). While there are non-native seed-dispersing birds, they only

partially fill the role because of differences in various factors such as body size and type of seeds that they can ingest (Kaushik et al. 2018). Overall, the ʻŌmaʻo spreads a more diverse set of seeds compared to the non-native birds, with some seeds being completely absent in the seed rain where they are not found (Pejchar et al. 1995).

The introduction of wild pigs (*Sus* scrofa) in Hawaiʻi has greatly influenced seed dispersal of some species (Diong et al. 1982, La Rosa 1984, Jones 2011 but the relative contribution of pigs in dispersing native vs. non-native seeds is unknown. As a large-bodied mammal, pigs within their native range offer dispersal benefits for the plants there (Ickes, 2001; Yong et al. 2010). However, pigs are also invasive in many locations and are one of the leading causes of diminished native species presence around the world (McCann et al. 2014). Pigs are found on all continents except Antarctica (McCann et al. 2014) so exploring how their roles differ globally is crucial in understanding their effects ecosystems. This research addresses understanding the role that pigs in Hawaiʻi play in the spread of native and non-native species. Studying the dietary preferences and nature of wild pig seed dispersal will give important insight into how this species may be affecting the overall composition of Hawaiian forests and indicate whether they are filling the niche of spreading native species.

History of S. scrofa *in Hawaiʻi*

The predecessors of wild pigs (*Sus scrofa*) in Hawaiʻi were brought to the islands by early Polynesian settlers as a source of food, with later introductions of European breeds contributing to feral populations as well (Diong 1982). These first pigs that were brought to Hawaiʻi were an extremely valuable and culturally important resource that served as the basis for many aspects of Hawaiian society (Maly et al. 2013). For instance, the process of preparing a

heiau could command the need for over a thousand pigs to be prepared for consumption (Ziegler 2002). Acquiring this number of pigs would not be possible had they been free-living in forests where they would have to be tracked down and hunted. There is a lack of evidence to support the idea that these early pigs existed in forests as they were a highly important protein source that was probably carefully managed by Hawaiians (Anderson and Stone 1993), unlike the wild pigs that roam free today.

These Polynesian pigs were raised as domestic animals with the existence of pens used to confine them signaling their importance as a maintained resource (Maly et al. 2013). Although they were mostly confined, there were some free-roaming populations; however, they were small and still closely associated with and dependent on humans (Maly et al. 2013). The lack of available food sources such as large non-native fruit and earthworms prevented pigs from becoming established and expanding to what we see today. Pigs that may have entered the forests would be restricted to eating species like hāpuʻu (*Cibotium* spp.) in addition to ground nesting birds and their eggs (Ziegler 2002) which were probably not as available as the many different non-native fruits we have today.

The pigs utilized by Hawaiians had more ancestral features such as longer snouts, small perky ears, and long legs suggesting that these animals were in the early stages of domestication compared to the heavily modified domestic European and Asian pigs (Baker 1975; Diong 1982). When visiting the island of Hawaiʻi, Cook mentioned that it was uncommon to receive a pig over 50 pounds (Baker 1975; Diong 1982). The first domestic breed brought to Hawaiʼi after contact was introduced by Cook himself, who brough a male and female pair of English pigs to Niʻihau in 1778 (Baker 1975). Many introductions occurred after this, however, most of them were not documented (Baker 1975). After the introduction of these more artificially selected pigs, the

features of the Polynesian pigs underwent major changes because of hybridization (Diong 1982). Many of the pigs in Hawaiʻi now resemble their highly domesticated ancestors as opposed to the more ancestral type of Polynesian pigs (Baker 1975). Aside from physical appearances, genetic analysis shows an admixture of ancestry from both Pacific, European, and Asian lineages, the latter two a result of more recent introductions (Linderholm 2016).

Environmental changes that took place after European contact such as the introduction of earthworms also facilitated the dispersal of pigs into forested areas that were previously uninhabited (Nogueira-Filho et al. 2009). After moving into forests, *S. scrofa* began to degrade those habitats by preying upon native plants, dispersing seeds from non-native species, and negatively affecting soil quality (Diong, 1982; Nogueira-Filho et al. 2009; Wehr et al. 2018). The sheer amount of *S. scrofa* in combination with their destructive behaviors is damaging native Hawaiian forests (Diong 1982; Jones 2011).

Negative impacts on forests

Feral pig colonization both within and outside of their native range has detrimental effects on species throughout the world (Graves 1984; Cole et al. 2012). Two characteristics of pigs, their foraging behavior (rooting) and their omnivorous diet, contribute to their detrimental effects on ecosystems (Graves 1984). Currently, feral pigs in Hawaiʻi have been shown to have negative effects on native forests by consuming native plant species, altering soil composition, and dispersing non-native seeds, and (Diong 1982; Nogueira-Filho et al. 2009; Cole et al. 2012; Gawel et al. 2018; Wehr et al. 2018). After pig removal native plant species increase significantly in both presence and density, with some species that were originally extant even returning following control (Cole et al. 2010). The same was true for herbaceous non-native

plants in areas where pigs were not excluded (Cole et al. 2010), suggesting that some non-native species increase following pig disturbance.

In addition to these direct interactions with plants, pig activity also affects soil composition and biota which are also tied to plants. In one study performed by Wehr et al. (2020) the exclusion of pigs was used to determine the effects of their activity on soil macroinvertebrate communities. The presence of feral pigs was recorded based on activities such as trampling and rooting (Wehr et al. 2020). It was found that trampling compacted the soil and had a negative effect on macroinvertebrate abundance, whereas rooting was shown to have no significant impact on macroinvertebrate abundance (Wehr et al. 2020). A slight increase in earthworms was observed but could not be attributed to the activity of rooting itself (Wehr et al. 2020).

Aside from impacts on soil, feral pigs can also disperse non-native seeds such as strawberry guava (*Psidium cattleyanum*) (Diong 1982). Dispersal of *P. cattleyanum* by feral pigs was corroborated by Jones (2011) who collected scat along an elevational gradient in Laupāhoehoe forest, then dried them and measured seed weights. It was found that feral pigs were actively dispersing strawberry guava farther distances from parent trees and into areas where the species was not currently present (Jones 2011). Another study conducted in Laupāhoehoe demonstrated that wild pigs at that site dispersed banana poka (*Passiflora tarminiana*) seeds (La Rosa 1984), contributing to the spread of this non-native species. The ability of pigs to disperse non-native seeds is important when considering the changes in the composition of forests in Hawai'i, signaling a possible shift to non-native dominated forest systems. The limited understanding of wild pig seed dispersal in Hawai'i requires more research

to understand the potential role of feral pigs in dispersing native seeds. If wild pigs disperse native seeds as well, they may be maintaining some level of native plant regeneration.

A comprehensive study examining the biology of *S. scrofa* in Kīpahulu, Maui, was conducted by Diong (1982) as a doctoral thesis and provides the basis for papers arguing the negative effects of feral pigs on Hawaiian forests by dispersal of invasive seed species and alteration of soil composition. The study contains important findings regarding population ecology, diet, habitat usage and more. This information has guided many other studies that cover the management of feral pigs in Hawai'i as well as their impact on Hawaiian ecosystems (Anderson and Stone 1993; Nogueira-Filho et al. 2009). Diong's proposition that feral pigs are actively manipulating habitats in ways that facilitate invasion has been used to argue that management is necessary. His analysis of methods of capture and removal provide insight for future management goals (Diong 1982). Overall, his work covers many important characteristics of feral pigs in Hawai'i, but the information on diet and effects on ecosystems are the most used.

Dispersal of native seeds outside of Hawai'i

Since the pigs brought by early Polynesians were most likely in the early stages of domestication as evidenced by the retention of ancestral traits (Diong 1982), their dispersal abilities may mimic their ancestral species within their native range more so than their more domesticated European and Asiatic counterparts. Although they do play important roles in areas where they are native to, even these places can experience negative effects if densities are high enough (Ickes 2001). For instance, dipterocarps in Borneo had no regeneration because of increased pig density and greater seed predation (Ickes 2001). Another study done in the Pasoh Forest Reserve in Malaysia explored the effect of pig exclusion on the plant community and

found increased regeneration and density as well as a greater number of species within the enclosures (Ickes et al. 2001). These studies show that differences in pig density have profound effects on plant communities around the world. The presence of negative consequences when densities are increased represent their major influence on the ecosystems they reside in, which may be more intense in oceanic island ecosystems where they attain much higher densities than in continental areas (Sweitzer 1998).

In Aotearoa, feral pig scat was collected and sifted for seeds of the native mataī tree (*Prumnopitys taxifolia*) and compared to those found in the scat of captive pigs that were fed the seeds directly (O'Connor and Kelly 2012). Seeds other than the native mataī were not considered in this study, so the dispersal of non-native seeds was not investigated (O'Connor and Kelly 2012). The seeds collected from the scat were germinated in a greenhouse (O'Connor and Kelly 2012). The study showed that seeds collected from feral pig scat had a 68.4% germination rate compared to 57.1% and 63.5% for captive-fed and hand-cleaned, respectively (O'Connor and Kelly 2012). These results strongly suggest that feral pigs have potential to disperse native seeds as well, which could have implications for forest regeneration and composition especially in areas like Hawai'i where native many native frugivores are absent or declining (Pejchar 2015; Matsuoka 2020).

A similar study was performed in Guam where the native frugivorous birds have gone extinct because of brown treesnakes (*Boiga irregularis*), so examining how non-native species may fill those ecological niches is highly important (Gawel et al. 2023). In this study scat was collected and, unlike O'Connor and Kelly (2023), germinated directly on media without being sifted (Gawel et al. 2018). The scat was allowed to germinate until the seedlings could be properly identified (Gawel et al. 2018). Counts of adult trees of each species in the study were

divided by the total number of adult trees at each site to determine abundance, which was compared to the abundance of each seedling species germinated (Gawel et al., 2018). It was found that there were differences in abundance between the seedlings and trees, which means that pigs could be actively selecting certain species over others (Gawel et al. 2018). Although the pigs were found to disperse non-native seeds, they also dispersed native seeds (Gawel et al. 2018). The findings also showed that they preferred fleshy fruit that had many seeds (Gawel et al., 2018). These studies show that feral pigs have the potential to disperse native seeds, but additional work needs to be done in Hawai'i for more location specific information on their role in native seed dispersal.

Methodology limitations

Studies of diet and seed dispersal capabilities of pigs often involve the collection and germination of scat (O'Connor and Kelly 2012; Gawel et al. 2018); however, for examining species-specific dispersal, seeds are sometimes sifted out of the scat (Diong 1982; O'Connor and Kelly 2012). These differences in methods make comparison amongst studies difficult since some are sorting out species (Diong 1982; O'Connor and Kelly 2012) while others allow the entire collected scat to germinate (Gawel et al. 2018). The scat is then germinated in a greenhouse setting (O'Connor and Kelly 2012; Gawel et al. 2018), but unless the facility is enclosed there is a possibility that seeds from external sources could contaminate the samples. While these tactics involving the collection of scats can be simple, sometimes more invasive approaches are taken to examine diet.

In one study, pigs were shot and had their stomach contents analyzed to determine dietary composition (Diong 1982), which is difficult to do as it requires tracking down pigs in

potentially dangerous terrain and dispatching them. Comparing stomach contents to scat presents challenges since materials may be at different rates of digestion depending upon the timeframe of which they were ingested to when the animal was dispatched. Remnants in scat may present a different diversity and abundance of food materials than those observed directly from stomach contents, but scat is more easily collected and manageable. The identification of stomach contents was performed visually (Diong 1982), which is tedious and could be difficult to identify depending on how digested the food materials are. Diong (1982) found remnants of both native and non-native, however their stomach contents comprised of mostly native herbaceous plants. Difficulties associated with physical data collection could be offset by more hands-off methods.

Another method for determining seed dispersal capabilities is by utilizing cameras to detect presence of seed dispersers and predators (Sanguinetti and Kitzberger 2009; Lindsell et al. 2015). The camera trap method is widely utilized in tracking and recording animal behavior and presence (Price Tack et al. 2016). These cameras are used in place of invasive techniques that may require more labor and come at a greater cost (Price Tack et al. 2016). The processing of these images is where the difficulty lies as adequate technology to examine the photos is lacking (Price Tack et al. 2016). Issues regarding data and equipment management can arise as well as inconsistencies in processing by humans and differences in capture methods (Price Tack et al. 2016). While there are challenges and benefits associated with all methods, a key determining factor in the feasibility of understanding pig seed dispersal is accessing the areas where they are found. Places that are difficult to reach or traverse are less studied than areas with easier accessibility (Anderson and Stone 1993). These factors associated with monitoring seed dispersal can be limiting when designing a study, so methods should be chosen depending on what works best for the specific area being studied.

Control and exclusion

Many of the areas where pigs are controlled tend to be places that are easily accessed, so the more remote, native-dominant spaces are often left unmanaged (Anderson and Stone 1993). Public hunting is not a proven way to control pigs because in places where hunting is permitted, there are fluctuations in hunting pressure depending on game availability (Nogueira et al. 2007). When pigs are plentiful there is appeal from hunters; however, as populations decrease so does the hunters' interest in pursuing game which in turn allows for a population boom until enough interest returns to have an effect (Nogueira et al. 2007). Consistent, long-term control is necessary to prevent the negative effects that pigs have on Hawai'i's ecosystems and hunting is not an effective mechanism for achieving this.

Experimental approach

The overarching research question guiding this study is: How does species richness and total abundance of germinants in scat compare to the fruiting species at low and high elevation sites over time? The scope of this study is on seed dispersal to examine how pigs may be influencing the spread and regeneration of native and non-native plants species. The approach used is to compare initial vegetation surveys to determine whether the composition was native or non-native dominant, and to compare the relative proportions of seeds germinating from scat to existing vegetation. Three low and three high elevation sites were selected, to encompass areas with high dominance of mostly non-native species and mostly native species. In addition, sampling of scat was collected at four different time points throughout the year to encompass seasonal fruit availability. The two variables that were considered for this study to examine how

elevation, timepoint, and fruit availability might influence dispersal. Five specific hypotheses

were tested to examine the response variables of richness and proportional abundance:

H_1: The <u>species richness,</u> as indicated by the number of each fruiting plant species in the

forest, will be greater than the <u>species richness</u> of fruiting species able to germinate from

the scat at each site.

> **Rationale**: Feral pigs in Hawai'i prefer sweet non-native fruit, which could skew
>
> the results to favor non-native fruiting species in the scat (Anderson 1994;
>
> Nogueira et al. 2007). This may be especially true for lower, non-native dominant
>
> sites (Ostertag et al. 2009; Schulten et al. 2014) that have higher densities of pigs'
>
> preferred food sources.

H_2: There is a correlation between the proportion of avail fruit in the forest vs prop of

germinants in the scat by species, and that relationship varies by elevation.

> **Rationale**: Since pigs prefer non-native sweet fruit (Anderson 1994; Nogueira et
>
> al. 2007), the abundance of these seeds in the scat may be higher than the relative
>
> abundances found in the forests. Location also helps determine which fruit are
>
> available to be dispersed, affecting the interaction between pigs and the plant
>
> species that they disperse (Graves 1984).

H_3: The species richness in scat found at low elevation non-native dominant sites will be

different from the species richness in scat found at native dominant high elevation sites.

> **Rationale**: The location of a pig's home range plays a role in which kind of seeds
>
> are dispersed across the landscape (Graves 1984). Hawaiian lowland wet forests
>
> tend to be highly invaded and feature a greater number of non-native species

(Ostertag et al. 2009; Schulten et al. 2014) which could lead to an overall increase in species richness.

H$_4$: The total abundance of seedlings germinated from the scat will be different between the low and high elevation sites.

> **Rationale**: Non-native dominance at lower elevations (Ostertag et al. 2009; Schulten et al. 2014) combined with pigs' preference for non-native fruit (Diong 1982) implies that lower elevation sites would have more seedlings given the greater availability of preferred fruit as opposed to high sites.

H$_5$: The total abundance of germinants will vary over time.

> **Rationale**: Pigs are known to shift their diet based on food availability (Diong 1982), so tracking changes in total abundance of germinants over time will determine if they are consuming the same amount of fruit and how much of their diet is comprised by certain species.

H$_6$: The species richness found in the scat will vary by collection time point.

> **Rationale**: Across the world, season is an important aspect of pig behavior and dispersal potential (Graves 1984), making this a key focus of this study. From around August to December when strawberry guava is fruiting, which is a preferred food source of pigs (Diong 1982) suggesting that there will be more strawberry guava germinating from the scat than other species.

Methods

Six forests were selected on the east side of Hawaiʻi Island with the focus being on elevation, precipitation, and dominant vegetion type (1). Elevation and precipitation were similar amongst both types of elevation, to control for the influence of vegetation type. All three of the high elevation sites were chosen for their native-dominant vegetation composition, mostly consisting of ʻōhiʻa (*Metrosideros polymorpha*) and koa (*Acacia koa*) (Table 1). These same factors were used to decide the low sites as well which were all non-native dominant.

Table 1. List of the three low and high elevation study sites and their environmental characteristics. Precipitation values from Giambelluca et al. (2014).

Site	Location	Group	Elevation (m)	Precipitation (mm)	Dominant Vegetation
Keaukaha Military Reservation	N 19°42.623' W 155°02.355'	Low	30	3300	*Psidium cattleyanum, Clusia rosea*
Keauʻohana Forest Reserve	N 19°25.047' W 154°57.063'	Low	255	2500	*Psychotria hawaiianesis, Trema orientalis*
Waiākea Forest Reserve	N 19°37.517' W 155°06.033'	Low	300	3000	*Psidium cattleyanum, Trema orientalis*
Hilo Watershed Reserve	N 19°41.433' W 155°16.133'	High	1200	4200	*Metrosideros polymorpha, Cibotium glaucum*
Laupāhoehoe HETF	N 19°55.875' W 155°17.262'	High	1200	2500	*Metrosideros polymorpha, Cibotium glaucum*
Hakalau Forest National Wildlife Refuge	N 19°47.453' W 155°20.216'	High	1500	2500	*Acacia koa*

Vegetation surveys

Vegetation surveys were used to assess the relative abundance and species richness, which was determined using count data, of woody species with fleshy fruits at the six sites. The transect designated at each site was 2-m wide (Gawel et al. 2018) and 1-km long. Pig home ranges have been found to span from around 1.65 to 2 km in Hawaiʻi (Salbosa and Lepczyk 2009). A combination of point-intercept and Braun-Blanquet was used to understand the relative abundance of species at each site. Points were selected randomly along the 1-km transect using a random number table and recorded using a Garmin GPSMAP 64sx until additional points were

no longer necessary. At each point, a circular plot with a 5 m radius was created. Within each

plot, the Braun-Blanquet method was used to estimate the percent cover of all woody shrubs and

trees (Wikum and Shanholtzer 1978). A percent cover scale was designated as follows: 100-95,

95-75, 75-50, 50-25, 25-10, 10-5, 5-1, <1. The midpoint for each range was used for abundance

calculations (Wikum and Shanholtzer 1978). Plots were examined until no new species were

found in two consecutive plots signaling that most of the major species have been recorded. At

each site, surveys were completed after 3-5 plots. The vegetation surveys were completed at the

start of the study in October and November of 2022 before any collection of scats occurred.

Phenology

Phenology data were collected to examine the relative abundance of fruit by time point at

each low and high elevation site. Phenology data were taken quarterly throughout the year in

conjunction with scat collection. The same transect used in the vegetation survey was examined

to determine the relative abundances of available fruit for each plant species. Trees and shrubs

were examined visually with estimates of cover recorded as a percentage of branch tips with fruit

using the same classes and midpoints as the vegetation surveys: 100-95, 95-75, 75-50, 50-25, 25-

10, 10-5, 5-1, <1. Only ripe, mature fruit were considered as these have the potential to fall and

be dispersed by pigs. Five random points were designated along the transect using an online

random number generator, with points being selected from a range of 0-1000 meters. There was

no minimum distance set between points. A Garmin GPSMAP 64sx was used to measure the

distances of each random point from the beginning of the transect. At each point the closest

individual of each species with fruit was observed and estimated while those without fruit were

not recorded. A new set of five random points was selected each collection time point for a total of 20 at each site to incorporate as many individuals as possible.

Scat collection

Pig scat was collected at each of the forest sites at four different times (Table 2). Each collection time point lasted about two months to complete all six sites since multiple trips were required to collect enough scat as well as permitting and key reservation processes. Intervals between time points were approximately a month long; however, the interval between the second and third collections was four months during the process of locating and transitioning to a new greenhouse. The same transects that were used for the initial vegetation surveys were followed for the collections. The scat was gathered opportunistically along the entire transect to maximize the number of samples collected. All scat the size of a palm or larger was collected regardless of the state of decomposition to represent a wider range of germination possibilities. Fresher samples had a solid shape, visibly more moisture, and intact seeds. Older samples were lighter in color, more dried out, and had decaying seeds. Samples that were completely flattened and unable to be picked up were not collected. Any scat that had already germinated was also not collected. Individual scat pieces that were within a 15-cm radius of each other were collected as one sample. Plastic dog bags were used to collect the samples which were sorted and stored in gallon sized plastic bags until they were able to be taken to the greenhouse.

Table 2. List of months when each collection took place.

1	December 2022 - January 2023
2	March 2023 - May 2023
3	October 2023 - November 2023
4	January 2024 - February 2024

Germination

For germination trials, the general design was based on the methods of Gawel et al. (2018). Germination trays were filled with a media mixture consisting of 1:1 perlite and peat moss (Gawel et al. 2018). For every ten scat trays, a control tray without any scat was made to identify anything that germinated from the greenhouse itself. Gawel et al. (2018) placed the trays outdoors, but for this study the initial greenhouse, located at the USDA-APHIS facility in Wainaku, Hilo (N 19.7275°, W -155.09695°), was selected so that irrigation could be closely controlled to prevent influence from rainfall. Samples from the first two collections were grown out for a 6-month period in the USDA greenhouse, located in Hilo, HI, while the final two collections were grown for 6 months at the UH Hilo Farm which is also located in Hilo (N 19.65305°, W -155.04945°) following the decommissioning of the USDA greenhouse. Both greenhouses were at similar elevations; however, the USDA greenhouse was more enclosed whereas the UH Farm was more open which may have allowed for slightly more exposure to light and moisture. Both greenhouses had automatic irrigation systems that followed the same timing schedule.

Plastic 25.5 cm x 61 cm seed trays were used for germination. Six compartments were created by stapling five 1.3 cm thick cedar wood inserts into the trays, making each compartment section approximately 90 cm^2. A 1:1 mixture of perlite and peat moss was used as the germination media Trays were watered with automatic timers once a day in the morning at 9 AM. Depending on the season and need for water, the timer was set for anywhere from 3-5 minutes a day with adjustments made as necessary to maintain moisture. Samples were not

allowed to dry out completely between waterings. Once seedlings were large enough to be identified by species, they were counted and removed from the media. Seedlings were checked every 2-4 weeks depending on the observed rates of germination and the need for removing seedlings to provide space for others to germinate. Each germination period lasted 6 months.

Statistical analysis

All statistical analysis was performed using Minitab v. 21.2. A two-way ANOVA was used to determine if there were differences in species richness between the forest versus scat as well as between the low and high elevation sites. An interaction between the two independent variables was also included in this model. The species richness of each individual scat sample was considered its own data point, while the number of species in each forest plot along the transect was used in the other set of points. Another two-way ANOVA was created to examine any differences in species richness withing the individual the scat samples found at the high versus low elevations as well as between the four collection dates (Figure 2). The interaction between elevation and collection time point was also added. The relationship between the proportion of germinants in the scat and the proportion of available fruit for each species was evaluated through a Pearson correlation to determine if pigs were eating what was available or if they are exhibited preference for certain species. Aside from species richness, the total abundances of seedlings in each scat sample were also used in the analysis. A two-way ANOVA was performed to examine if there was a difference in scat collected at low vs. high elevations along with the different collection timepoints.

Results

Species richness of fruiting species in vegetation vs. scat

There was a range in percent cover for the native and non-native species across sites (Figure 1). The top three species with the highest proportional cover were *M. polymorpha*, *P. cattleyanum*, and *C. glaucum*, signaling a more native-dominant community with *P. cattleyanum* standing out as a particularly prevalent non-native species. Three non-native species had the greatest cover were *P. cattleyanum*, *T. orientalis*, and *C. rosea*. Three natives with the greatest cover were *M. polymorpha*, *C. glaucum*, and *A. koa*, all of which are non-fruiting species that were not included in the analysis.

Comparing species richness between the fruiting vegetation and scat (H_1) showed that there was greater species richness in the forest ($F_{1,192} = 14.24$, $p < 0.001$, $t = 3.77$, $p < 0.001$) (Figure 2). Forests and scat at high elevations had fewer species than the lower elevations sites ($F_{1,192} = 6.78$, $p = 0.01$, $t = -2.60$, $p = 0.01$). The interaction between location and elevation did not influence species richness in the forest and scat ($F_{1,192} = 0.39$, $p = 0.531$).

Low elevation sites had both native and non-native fruit available during all collections (Figure 3). However, the high elevation sites only had native fruit available. High sites had available fruit during the second and third collections which consisted of *C. trigynum* and *V. calycinum*, respectively. The species that had fruit during all collections at the low sites were *C. obtusifolia*, *P. cattleyanum*, and *T. orientalis*. (H_2) There was no correlation between the proportion of available fruit in the forest and the proportion of that species' germinants in scat at low and high elevations (Figure 4).
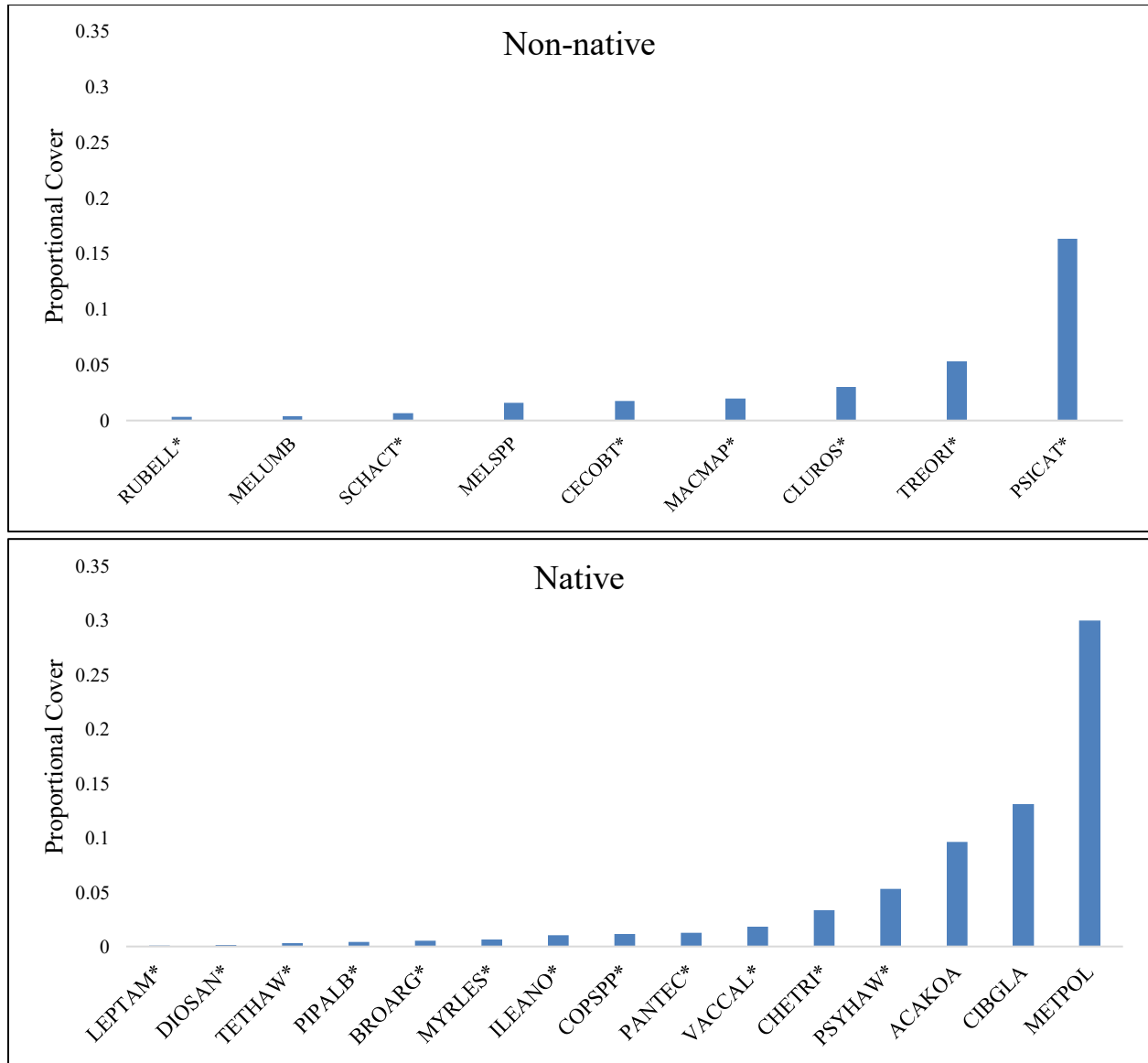
Figure 1. Percent cover of non-native and native species in the vegetation across the low and high sites. Species codes as in Appendix 1. *Indicates fruiting species used in analysis.
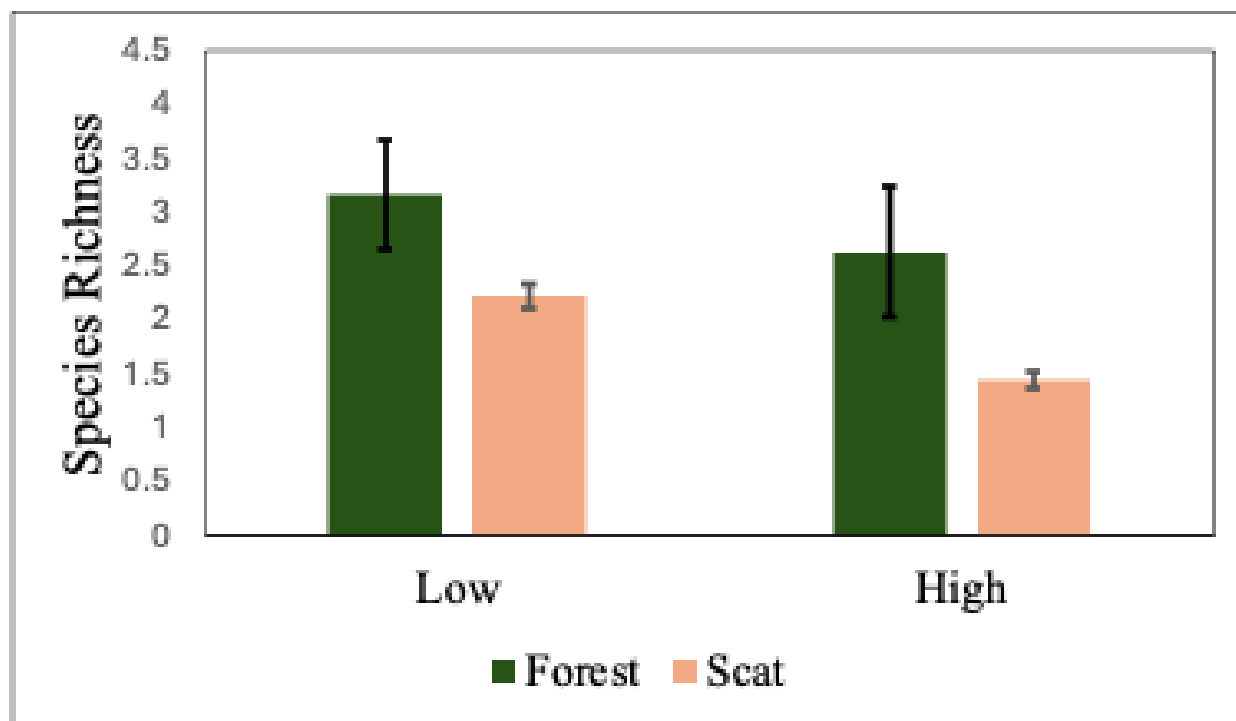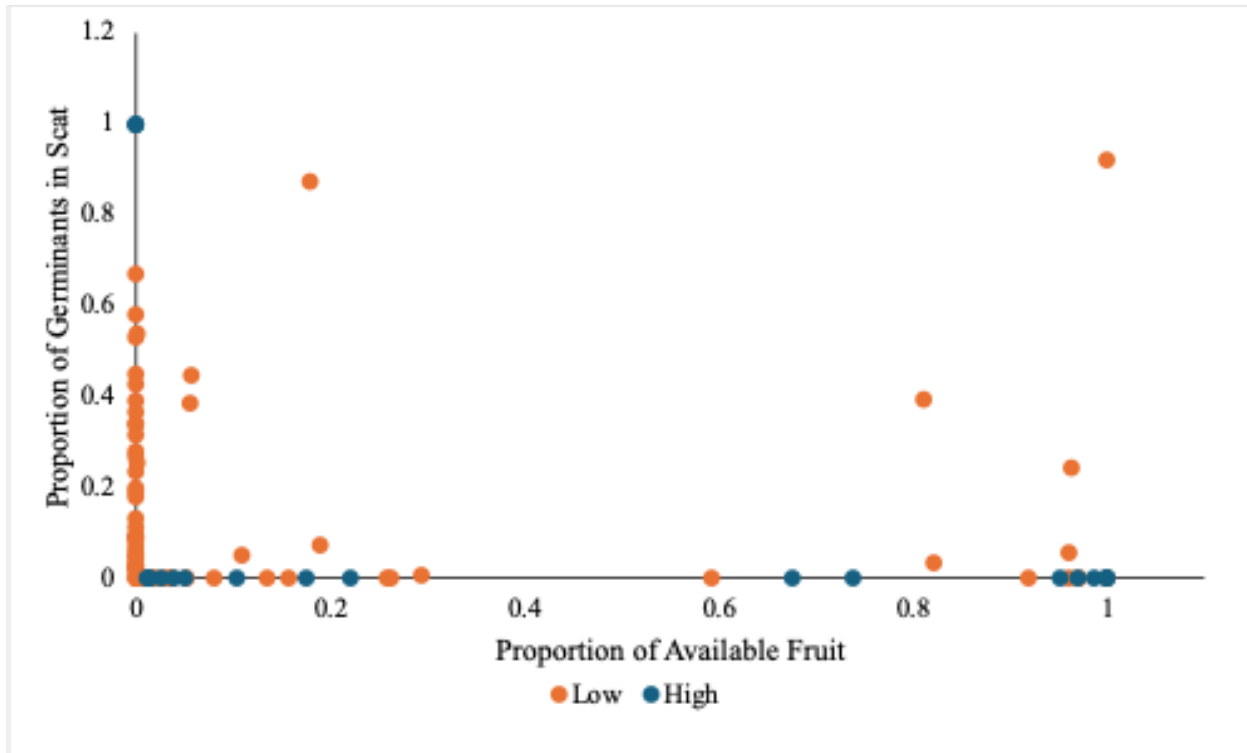
Figure 2. Average (and standard error) number of fruiting plant species in the forest plots from three low elevation and three high elevation sites.
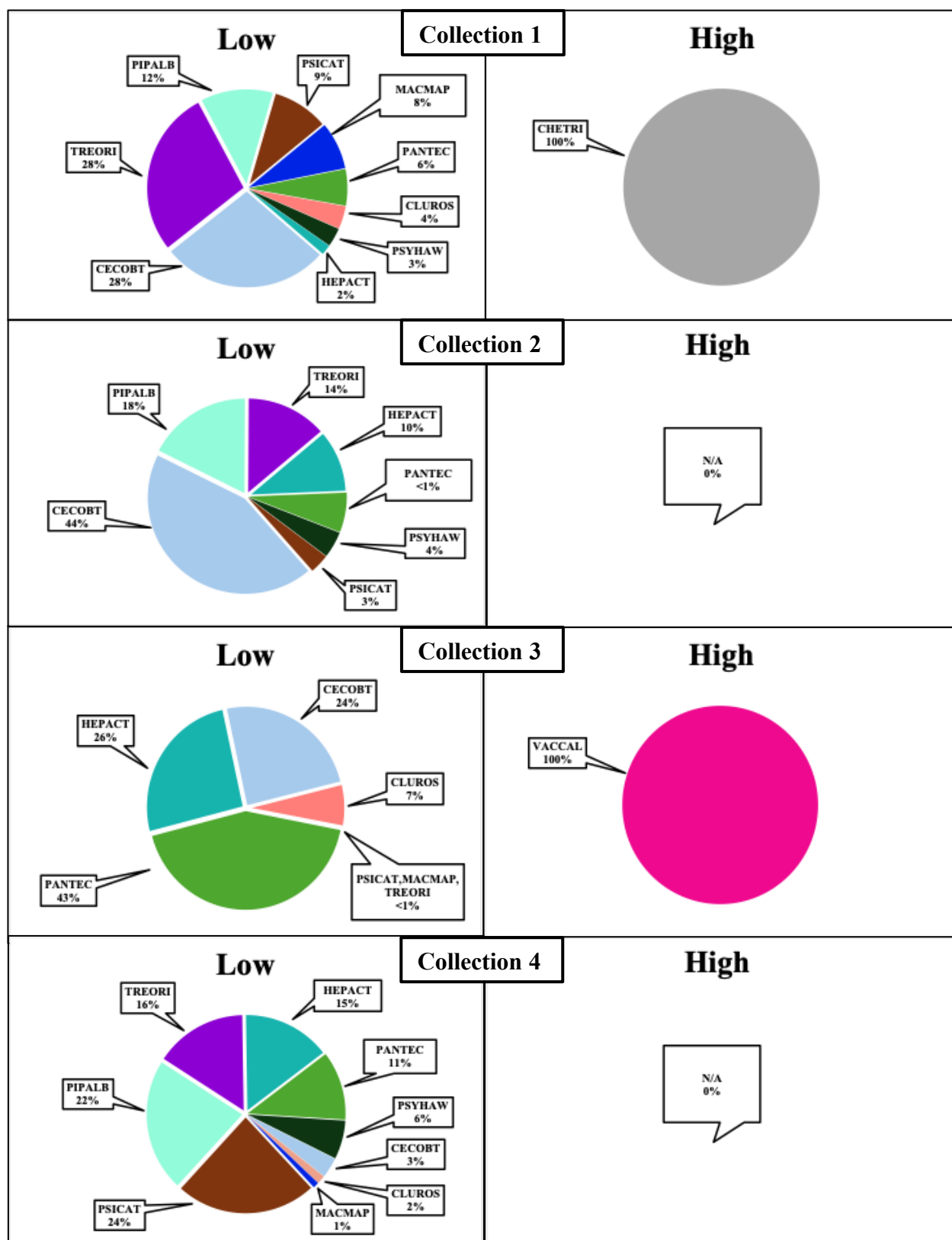
Figure 3. Composition of available fruit at the low and high elevation sites across four timepoints.

Figure 4. Proportion of germinants in scat vs proportion of available fruit at low and high elevation sites.

Effects of elevation and time on species richness and abundance of germinants in the scat.

A total of 346 samples were collected and 173 germinated (Table 3). No native species germinated from the scat (Appendix 1). Although each grow-out period was six months, seedlings stopped germinating from the scat after about 4 months. There were initial influxes of certain species like *P. cattleyanum* and *C. obtusifolia*, with the number of seedlings tapering off over time. Some species were slower to germinate and did not show up initially but were present weeks later such as *M. citrifolia* and *H. actinophylla*. The composition of germinants varied over time, with certain species like *P. cattleyanum*, *C. obtusifolia,* and *R. ellipticus* making up the bulk of the seedlings.

The frequency of germinants in the scat varied amongst species and elevations (Appendix 2). For the low elevation sites, *P. cattleyanum* was present in more than half of the scat, whereas *C. obtusifolia* and *P. guajava* germinated from about a third of the samples. Lastly, *P. edulis* germinated from around a quarter of the scat. High elevation sites had three species that were found in approximately a tenth of the samples: *P. cattleyanum*, *P. guajava*, *P. edulis*. All the species that germinated from both the low and high elevations were in the top five for total abundance, as opposed to species found in scat from only one of the elevations.

Scat between elevations varied in their species richness ($F_{1,\ 165} = 18.06$, $p < 0.001$), (Figure 5) and seedling abundance ($F_{1,165} = 10.42$, $p = 0.002$) (H3 and H4). The low elevation sites had greater species richness than the higher elevation sites ($t = -4.25$, $p < 0.001$) (Figure 5). Samples collected from the low elevation sites also had more seedlings than those from the high forests ($t = -3.23$, $p = 0.002$), (Figure 6).

Time had a significant effect on species richness $F_{3,165} = 4.62$, $p = 0.004$) (Figure 5), but no effect on total abundance of germinants ($F_{1,165} = 0.94$, $p = 0.425$) (Figure 6) (H5 and H6). Samples gathered during the second collection had lower species richness than those collected during the other time points ($t = -3.65$, $p < 0.001$). The interaction between elevation and collection was significant ($F_{3,165} = 2.68$, $p = 0.049$), with the lowest species richness found at high elevation sites during the second collection ($t = 2.01$, $p = 0.046$).

Table 3. Total number of scat collected and germinated from the low and high elevations for all time points.

Germination Interval	Elevation	Collected	Germinated	Germination Proportion
1	Low	53	47	0.89
[Jan – June 2023]	High	68	15	0.22
2	Low	25	25	1.00
[March 2023 – Sep 2023]	High	47	21	0.45
3	Low	31	21	0.68
[Oct 2023 – March 2024]	High	44	11	0.25
4	Low	34	25	0.74
[Jan 2024 – June 2024]	High	44	8	0.18
	Totals	*346*	*173*	*0.48*
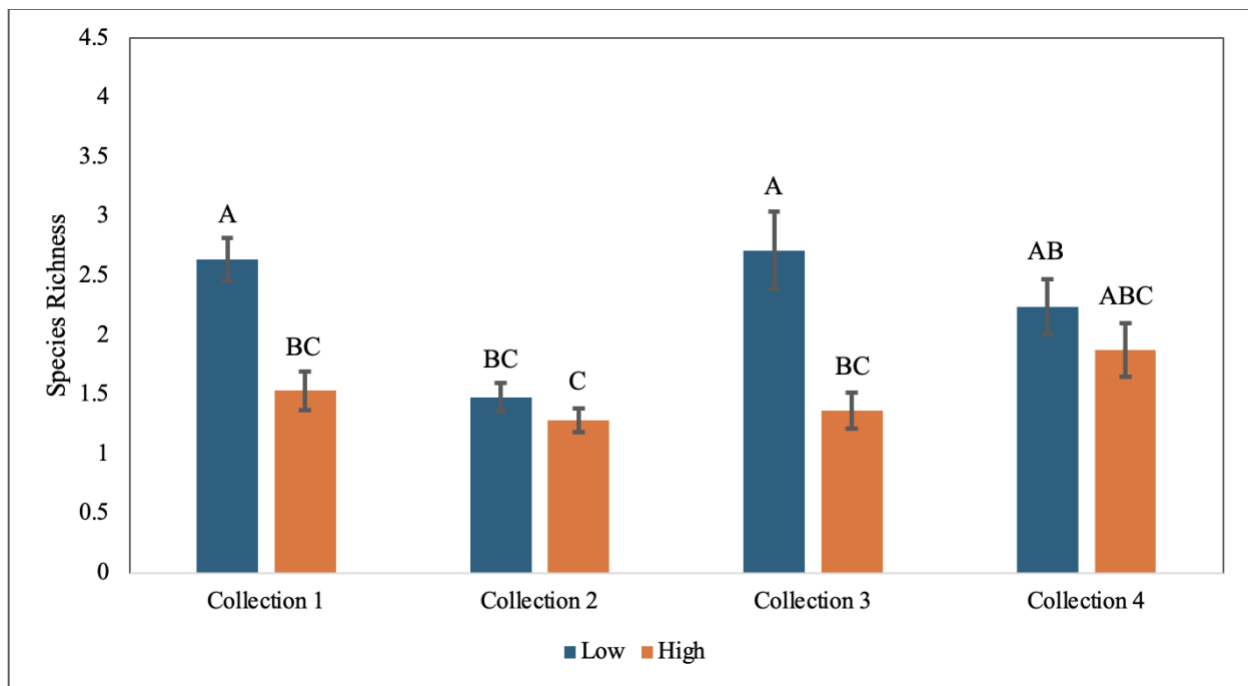
Figure 5. Average (and standard error) number of fruiting plant species in the scat from three low elevation and three high elevation sites across four different time points.
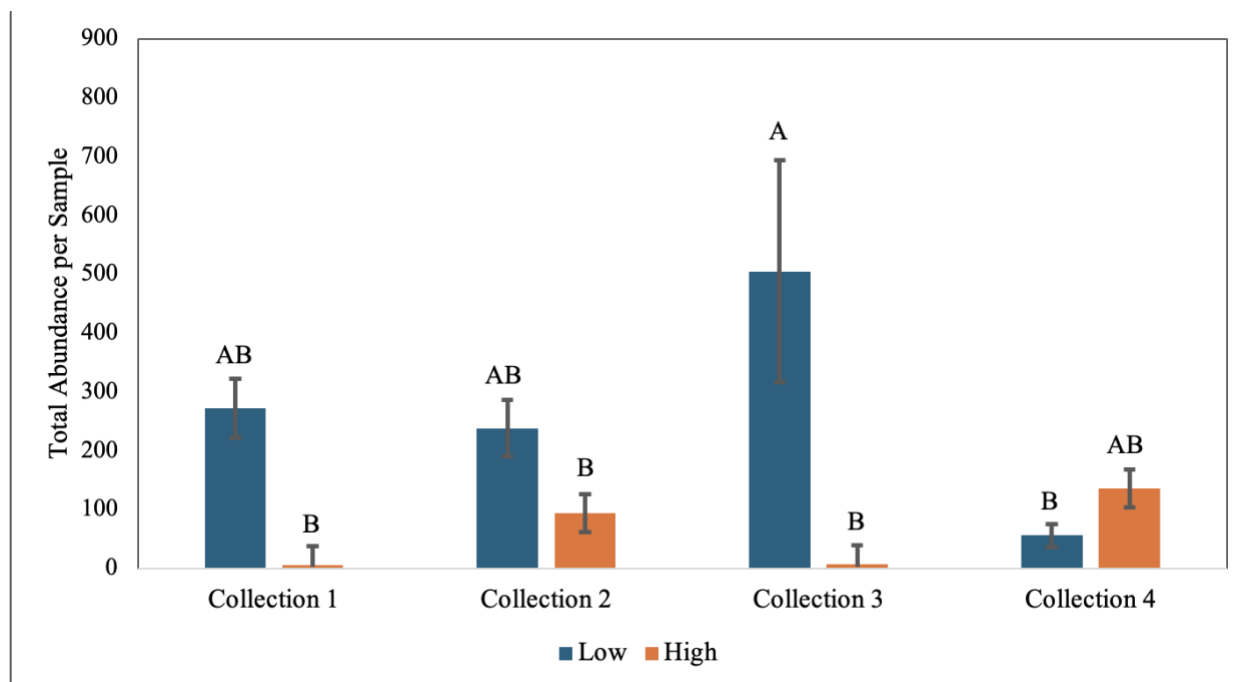
Figure 6. Average (and standard error) total abundance of germinants in the scat from three low elevation and three high elevation sites across four different time points.
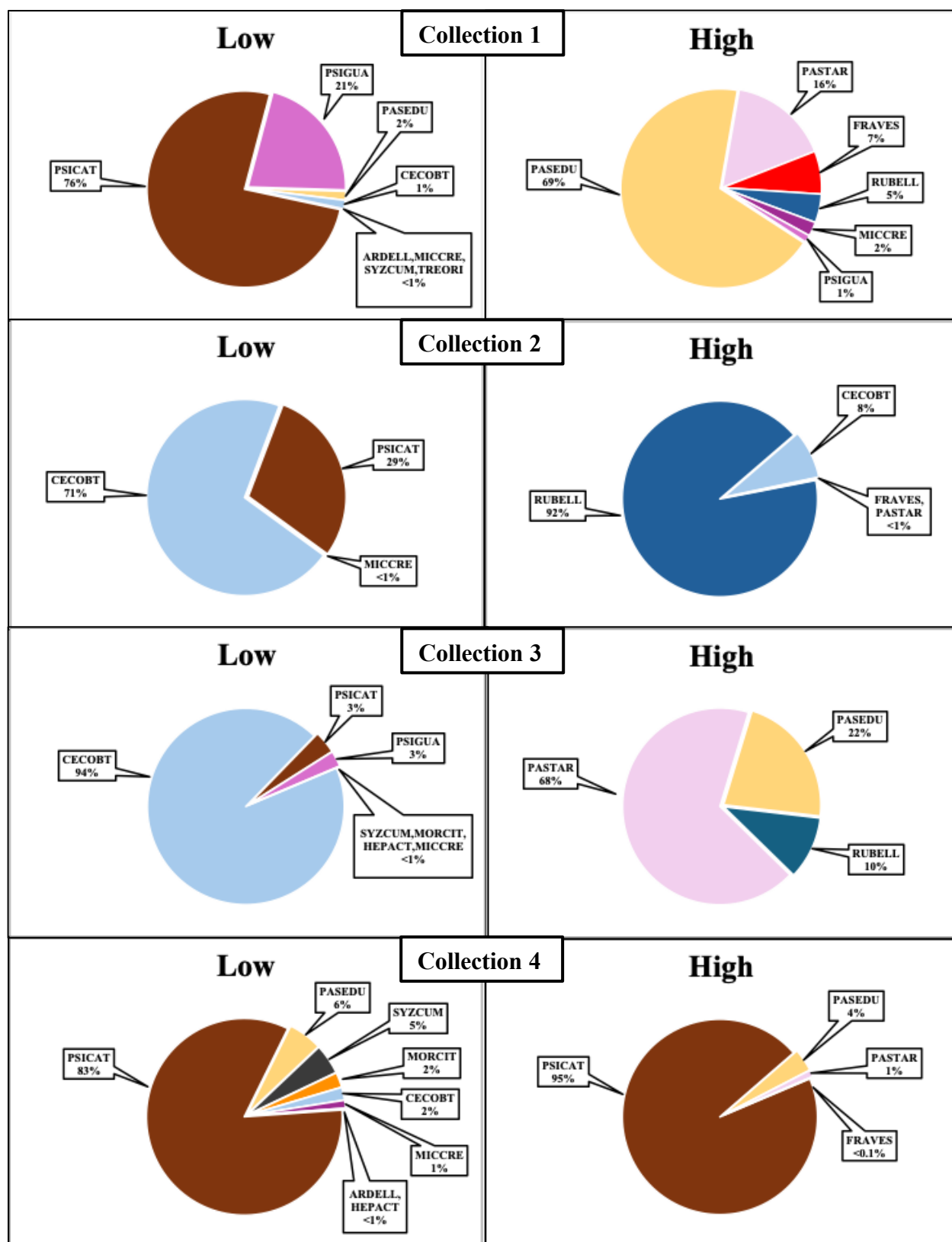
Figure 7. Composition of germinants in scat at low and high elevations across four time points.

Discussion

Although the species richness and abundance of germinants varied between elevations over time, none of the seedlings identified were native. When examining preference, H_1 was supported by the difference in species richness between elevations with a greater number of species found in the forest compared to the scat, however, H_2 was not supported due to the lack of correlation between the proportion of available fruit in the forest and the proportion of germinants in the scat. The acceptance of H_1 and rejection of H_2 show that wild pigs exhibit dietary preference is not based solely on which species are available. The seeds dispersed by pigs represent a subset of all the fruiting species and indicate which ones they prefer. Regarding elevation, both H_3 and H_4 were supported by the data that showed higher species richness and a greater number of seedlings at the lower elevation sites, which coincides with the trend of non-native dominance at low elevations found in this study and supports the premise that pigs prefer non-native fruit. In relation to seasonality, H_5 was not supported since there was no difference in total abundance of seedlings by time point, but there were differences in species richness allowing the acceptance of H_6. The findings of H_5 and H_6 indicate that although the species that are being dispersed shift throughout the year, the total number of seeds that were spread remained the same, which shows a consistent level of dispersal over time regardless of which species are available. This study shows that pigs are not fulfilling the role of native seed dispersal, which has been severely diminished due to the extinction of numerous native birds (Pejchar 2015; Case and Tarwater 2020) and are instead facilitating the spread of non-native seeds. Ultimately, wild pigs are not dispersing native seeds in these areas despite evidence on other islands in Oceania (O'Connor and Kelly 2011; Gawel et al. 2018). As a result of these findings in conjunction with known ecological effects of pigs (Sweitzer 1998; Nogueira-Filho et

al. 2009; Wehr et al. 2018) control and management of wild pig populations would be beneficial for protection of native forests. Future research elucidating the complex picture of wild pig interaction with the landscape as well as ecology on the species itself is vital to build our understanding and shape management approaches to effectively work towards conservation goals.

Patterns with elevation and season

Despite having less species to select from, germinants from high elevations were dominated by a more diverse set of species compared to the low sites. This result contrasts the lower elevation sites, which had greater species richness in the scat and a higher abundance of seeds germinated. The restriction and absence of the lower elevation dominants—*P. cattleyanum* and *C. obtusifolia*—respectively, at high elevations indicates that these fruits are not as easily accessible. *P. cattleyanum* decreases in abundance and density as elevation increases (Jones 2011). The decrease in *P. cattleyanum* at higher elevation forests might push pigs to seek out other options that may not be as desirable or available in large enough quantities. At high elevation sites, the increased abundance of seedlings of *R. ellipticus* and *P. cattleyanum* coincide with their known fruiting periods (Mercado-Silva et al. 1998; Ding et al. 2021), showing that pigs are consuming the fruit themselves rather than ingesting them inadvertently from the seed bank. Lower species richness at high elevations when *R. ellipticus* becomes available indicates a strong preference for these fruit.

Changes in frequency throughout show a seasonal shift, but the effect of elevation and time on species richness and total abundance paints a more complex relationship between the environment and dispersal throughout the year. There is a short window of fruiting when the fruit

are ripe and when they show up in the scat, shown by the lag in species over the course of several months. Scat collected from March to May of 2023 had lower species richness compared to the other three collections. Despite lower species richness during this this time, total abundance remained the same. This contrast shows that pigs are consistent dispersers, but the species they spread varies throughout the year. Diong (1982) found that in seasons where *P. cattleyanum* was less abundant there was increased predation on hāpuʻu, so pigs may be affecting forests in different ways depending on the availability of certain food sources. Wherever *P. cattleyanum* was present in the vegetation it was also found in the scat suggesting a strong preference for this fruit. Trends in *P. cattleyanum* abundance might be associated with pig density and could be an important consideration for future research.

The time point at which the scat was collected did not affect the total abundance of seedlings, so throughout the year they are spreading generally the same number of seeds; and because the number of seedlings was relatively similar across all timepoints but the composition of species changed, pigs were most likely shifting their diets based on seasonal changes in fruit availability. The data showed that pigs' diet focused in on preferred species when they became available, then generalized to include fewer desirable species during other times of the year. This trend followed Diong's (1982) observation of dietary shifts at different times of the year in Kīpahulu, Maui. He discovered that in the fall and winter when *P. cattleyanum* was available it was a major part of wild pigs' diet, whereas in the spring and summer they reverted to eating mostly the native tree fern *C. glaucum*. This food source is present throughout the year, but a shift in pig diet to *P. cattleyanum* when it becomes available suggests that *P. cattleyanum* is a preferred food source (Baker 1975). Although it is unlikely, in years where non-native fruit availability is poor, pigs may be pressured into eating more native seeds with the increased

potential for dispersal. Non-native plants also fruit for longer periods of time than natives

(Sperry 2021), increasing the potential for consumption and subsequent dispersal.

Characteristics of pig-mediated dispersal

As evidenced by the germination of seedlings from their scat, pigs are taking on the role

of dispersal in Hawaiian forests; however, the composition and type of species that they spread

differ greatly from birds. In birds, the size of their body and gape determines what kinds of seeds

they can consume and disperse (Pejchar et al. 1995). In addition to body size, the amount of time

it takes for seeds to pass through their gut also affects dispersal (Wu et al. 2014). ʻŌmaʻo are

estimated to have a gut passage time of around 30 minutes, whereas pigs can continue dispersing

seeds for longer time periods (La Rosa 1984), allowing pigs to spread seeds much farther

distances than birds, increasing the rate at which non-native plants colonize new areas.

Many of the species that germinated from the scat were not found in vegetation surveys

nor did they have any available fruit, which shows that pigs were dispersing seeds away from

parent plants and into areas where they were absent. A study focusing on *P. cattleyanum* in

Laupāhoehoe, Hawaiʻi also found that pigs were spreading this species into areas where it was

not present (Jones 2011). Since *P. cattleyanum* is now the most abundant tree species in Hawaiʻi

(Potter et al. 2023), its potential for dispersal is even greater. It should be noted, however, that

while some species were not present in the vegetation or phenology surveys, they were present

nearby in places such as roads and access trails.

In addition to dispersing seeds, pig gut passage may increase germination rates.

Preliminary research in Laupāhoehoe, Hawaiʻi indicated that the invasive vine *Passiflora*

tarminiana germinated at a higher rate than fresh seeds following wild pig gut passage (La Rosa

1984). There is conflicting evidence as to how guava (*Psidium* spp.) germination is affected by gut passage (Somarriba 1986; Motta et al. 2008; Azevedo 2013), so more studies should be done on pigs in Hawaiʻi to elucidate how their digestive tract may influence *Psidium* germination rates. Other seeds may also benefit from gut passage; however, research focusing on germination of the less prevalent species is lacking. *Psidium guajava* germination rate in particular were not shown to be affected by gut passage in cows (Somarriba 1986) and rheas (Azevedo 2013), so these seeds may only require movement away from the parent plants as opposed to gut passage conditions.

Dispersal can also occur externally through movement itself without ingestion. Pigs are known to spit out large seeds after depulping (Pedrosa 2019), which does move them some distance. Much like pigs, rats may disperse seeds through including ingestion and external movement such as caching and hoarding seeds in new areas where they later germinate and contribute to regeneration. (Shiels and Drake 2011). Understanding how these introduced species interact with seeds as both predators and dispersers can help inform management decisions seeking to prevent the destruction of native seeds and the dispersal of invasive species.

The influence of habitat on pig dispersal

Seed dispersal in this study was only observed in rainforests, so the role of pigs as dispersers may be different depending on habitat. For example, in Hawaiʻi Volcanoes National Park, the diet of pigs found in open grassland habitats consisted of almost fifty percent grasses, whereas rainforest pigs consumed mostly *Cibotium* spp. At sites across Hawaiʻi Island, pigs' observed habitat preference was rainforests at mid-elevation areas where there was an ample supply of food sources, cover, and water available (Giffin 1978). All of the forests in this study

receive generally similar amounts of precipitation; however, Waiākea, Hakalau, and Hilo Watershed featured more open areas in relation to the other sites, which may explain the low number of scats collected there and the lack of seedlings that germinated. The vegetation at KMR, Keauʻohana, and Laupāhoehoe was much denser and comprised of more non-native fruit. There was more scat collected from the latter sites as well as seedlings that germinated, aligning with the preferred habitat type observed by Baker (1975).

Based on Salbosa and Lepczyck's (2009) and La Rosa's (1984) results, an individual pig could potentially move seeds up to 1 km away from the parent plant. If those seeds are able to germinate, mature, and succesfully reproduce, then a secondary resource center might form that could act as a dispersal pathway into other overlapping home ranges. Both Salbosa and Lepczyck (2009) and Diong (1982) used radiotelemetry, yet Baker's (1975) study using the capture-recapture method yielded similar results with an average movement distance of 1-2 km. Pigs in open pasture habitat traveled approximately twice as far as their rainforest counterparts, most likely due to a lack of resources (Baker 1975). Open areas are also easier to navigate, so pigs may travel farther and can act as connectivity between forest stands separated by land that has been cleared as was observed by Baker (1975) in Laupāhoehoe where pigs travelled as far as 2 km between forests. Diong (1982) found extensive overlap in home ranges, so there could be a piggyback effect that allows seeds to be dispersed at a much greater distance, especially between forests, than of what an individual pig is incapable of.

Pigs in these dense rainforest settings grow much larger and more quickly compared to their open grassland and pasture counterparts, which are slow growing because of inferior food sources (Giffin 1978). In some cases, pigs in pasture habitats lose weight (Giffin 1978). There was an observed weight difference of approximately 10-20 kg between rainforest and open

habitat pigs (Giffin 1978). One boar harvested from rainforest habitat in Kohala had an estimated weight of 260 kg based on carcass size and known proportions of a smaller boar, while in pasture habitat the largest pig found in the study was 68 kg (Baker 1975). Considering that body size is directly tied to dispersal (Pejchar et al. 1995; Kaushik et al. 2018), these larger rainforest pigs would be able to consume more fruit, exaggerating the effects of their seed dispersal. Major differences in body size between the original Polynesian pigs, which ranged from 22-27 kg pounds (Baker 1975; Diong 1982), and the wild pigs in Hawai'i today suggest that if these early pigs were in fact living in forests, their role in shaping the community would have been much less pronounced.

Differences in reproductive behavior in relation to fruit availability may also affect the number of seeds dispersed and the distance traveled during different times of the year. For instance, sows in rainforest habitat on Hawai'i Island were noted to breed in peaks during January and March as well as September and October (Giffin 1978). On Maui, Diong (1982) observed similar peaks, and both studies acknowledged that the fall farrowing period from around November to March was associated with greater fruit availability because of increased precipitation (Giffin 1978). The correspondence of reproductive timelines with fruiting seasons suggests that breeding is highly affected by resource availability as opposed to seasonality.

In this study, scat from lower elevation sites had more seedlings than the high elevation sites, suggesting that pigs in this area could be breeding more than high elevation pigs as a result of increased food availability. There was also greater species richness at low sites, which might allow pigs to breed more frequently due to differences in fruiting periods between multiple plant species (Mercado-Silva et al. 1998; Ding et al. 2021) rather than one large fruiting even by a single species. Observations of reproductive behavior show that bigger sows produce larger

litters at a much faster rate than smaller females (Larger pigs that breed often and produce more offspring would create a population that could have higher seed dispersal potential. In their native range, pigs' invasiveness is directly tied to density (Ickes 2001), so it is logical to assume that pigs in rainforest habitat have a greater effect on the surrounding community than in open pasture habitat. Because the data showed that *P. cattleyanum* is a highly preferred food source that pigs seem to depend on, the incursion of this species at higher sites should be compared to pig size and growth rates to determine how the spread of its seeds could be influencing body size and density of pigs, and therefore their invasiveness.

Tropical seed dispersal patterns in Hawaiʻi and elsewhere

In tropical systems, many woody plant species are dispersed by vertebrates including birds and mammals (Donatti 2007). The evolutionary history between plants and birds in Hawaiʻi has led to relationships that are unlike those around the world. Seeds brought to Hawaiʻi by birds would need to be small enough to be swallowed or attached externally, selecting for species with smaller fruit. As evidenced in this study, the larger and sweeter non-native fruit are a highly desired food source that would have been lacking in native forests. The complete lack of native seeds and high number of non-native seedlings present in the scat from these forests signal that wild pigs are not fulfilling the role of seed dispersal that native Hawaiian birds do. This disconnect between wild pigs and native fruit suggests that island systems that lack large mammalian native seed dispersers may not benefit from the introduction of large mammals, but further studies are needed examining fruit and seed traits in relation to their dispersers to support this claim.

In Aotearoa, where the native *P. taxifolia* is dispersed by wild pigs, there were Moa (Dinornithiformes), large flightless birds that are now extinct that may have dispersed seeds like this (Clout and Hay 1989), however, evidence shows that may not be the case (Carpenter et al. 2018 and 2020). It would be logical to assume that these large-bodied birds would have consumed and dispersed larger seeds, but our current understanding of this relationship is that Moa may have acted more as seed predators rather than dispersers since most seeds would be destroyed by their gizzards that could contain several kilograms of stones that grind and crush (Carpenter et al. 2018 and 2020). Hawai'i did have Moa Nalo, another group of large extinct flightless birds, but analysis of fossilized scat, known as coprolites, suggests they were herbivorous and mostly folivores feeding on ferns and leaf material (James and Burney 1997). Although seeds do not preserve as well as spores and pollen, there were small concavities in the coprolites that could have possibly been places where seeds were present, however, the evidence is lacking and there are other reasonable explanations as well (James and Burney 1997). The lack of evidence for effective seed dispersal by Moa and Moa nalo are evidence that body size is not enough to assume dispersal abilities. Research on the diets and ecology of these extinct large island birds can form a better understanding of the evolution of seed dispersal in island systems and how that historical development may affect future associations with large, introduced dispersers like pigs.

Research Needs

This study was conducted on the east side of Hawai'i island and represented a relatively narrow precipitation and elevation range. Because pig diet and behavior are known to be influenced by habitat type and resource availability (Baker 1975, Diong 1982), seed dispersal

research needs to be conducted in other habitat types such as pasture and dry forest to form a clearer picture of dispersal in Hawaiʻi overall. Pigs prefer habitat at mid-elevations (Risch et al. 2025), but this study focused on low and high sites to tease apart differences in native vs. non-native dominance. Future studies focusing on this middle range may allow for a greater number of samples that might reflect the dispersal of pigs at a greater magnitude. This elevation preference in habitat suggests that pigs may be acting as an intermediary between low and high sites and could be further facilitate the spread of non-native seeds because of preferred habitat use. Since resource availability is linked to animal movement patterns (Delciellos 2017), years with low fruit productivity in this mid-range may encourage pigs to move out of this preferred habitat in search of food at the lower or higher elevations. These seasonal movement patterns could be altering forest composition at a much larger scale than we already know.

The distance that a pig can travel is also an important factor to consider along with body size and gut passage time. While it was not considered in this study, lava flow age at the sites may also affect dispersal. Shifts in vegetation and resource availability are known to affect behavior and movement of species across matrix habitats (Delciellos 2017) and in Hawaiʻi substrate age plays a key role in forest growth (Kellner 2011). Baker (1975) observed that pigs in Hawaiʻi can traverse rigorous terrain with ease, but ʻaʻā lava flows are particularly difficult for them to navigate. So, dispersal studies centered around substrate may uncover how pigs spread seeds across lava flows of different ages. Because pigs are also known to travel across pasture with relative ease (Baker 1975), germination trials comparing scat between unconnected adjacent forests may be an interesting way to further our understanding of dispersal potential in these matrix habitats. This information may also prove useful in forecasting how the ingress of pigs

into new areas could affect the composition of forests and shape future competition with invasive species.

While this study focused solely on seed dispersal, the results are inextricably connected to a multitude of conservation issues both directly and indirectly caused by wild pigs. Further research on pig ecology, dispersal dynamics, and changes in forest composition are necessary to better inform management practices and determine the effectiveness of various control strategies to achieve conservation goals across Hawaiʻi.

Management of Pig Populations

Because pigs have not been shown to disperse native seeds and are contributing to substantial spread of non-native plants, population control is necessary to conserve native forests. In dense rainforests where pigs are most abundant, hunting generally occurs on the periphery of the habitat (Giffin 1978), so these areas experience less hunting pressure than open pasture. Consequently, forested areas with lower hunting pressure may receive greater amounts of pig-dispersed non-native seeds. Place-specific dietary preference and its influence on behavior and growth allude to wild pigs' highly adaptable nature and stresses the importance of control in all habitat types; however, if the goal is to prevent the spread of non-native seeds, control efforts should prioritize rainforest areas.

Because pigs are particularly fond of strawberry guava and have exhibited preference for this food source over hāpuʻu (Diong 1982), the removal and control of *P. cattleyanum* may increase predation on hāpuʻu. Because of this predation pressure in the absence of non-native fruit, forests where *P. cattleyanum* is being controlled should also incorporate control of wild pigs to mitigate any possible indirect impacts on native forests. Both native and non-native

vegetation benefit from pig exclusion; however, pig activity often results in optimal conditions for non-native recruitment (Potter et al. 2023). The dispersal relationship between *P. cattleyanum* and wild pigs could be a feedback loop that may afford both species success invading native forests at upper elevations. The abundance of *P. edulis, R. ellipticus, P. tarminiana* in the absence of *P. cattleyanum* at higher elevation sites suggests that other species may require control as well to remove secondary food sources that may also be supporting pig populations. Control efforts may be more effective if management strategies target both wild pigs and their mutualist plants. In addition to dismantling this relationship, the information in this study could be used to determine areas of focus for pig research based on known food sources. Areas with high abundance of these non-native fruit may prove to be the most beneficial for research given the appearance of high numbers of these species' seedlings in the scat.

The need for localized control can utilize the information in this study to prioritize and target specific areas depending on conservation goals. One example of these data being applied is the targeted use of specific fruits as bait following the patterns associated with species richness and abundance of germinants. At Keaukaha Military Reserve, land managers have adapted their trapping technique to include seasonally available fruit such as *M. citrifolia* and *S. cumini* as bait, which has proven effective in capturing pigs. The use of locally available, seasonal fruit should be further researched to determine its effectiveness in different situations in comparison to traditional bait such as macadamia nuts and corn. If shown to be effective, using non-native fruit in specific instances could reduce costs associated with acquiring traditional bait or act as a temporary solution if more common bait types are unavailable.

Overall, wild pigs have proven to be a major threat to Hawaiian forests, presenting various problems that work in conjunction to degrade native systems. Pig presence has now been

correlated with higher instances of Rapid ʻŌhiʻa Death (ROD), which continues to decimate ʻōhiʻa across Hawaiʻi (Perroy et al. 2021). Since ʻōhiʻa serve as important keystone species across the archipelago providing critical habitat and maintaining conditions for native species to thrive (Fortini et al. 2019; Perroy et al. 2021) protecting this species is highly important. Drastic differences in mortality densities were observed between fenced and unfenced areas on the windward side of Hawaiʻi island, where mortality in some unfenced areas is up to 69 times greater than nearby areas where ungluates are excluded (Perroy et al. 2021), This association strongly suggests that pigs may be responsible for spreading ROD and further strengthens the need for control and exclusion from intact forests, which will also mitigate dispersal of invasive plants. The initial canopy loss casued by ROD (Perroy et al. 2021), followed by wild pigs trampling vegetation and altering soil composition throg rooting (Long et al. 2017) creates optimal conditions for non-native plants to take hold (Nogueira et al. 2007; Wehr et al. 2018). In addition to their direct effects on plants, other behaviors exhibited by pigs including rooting and wallowing have also been shown to negatively impact forest health (Anderson 1994; Nogueira et al. 2007; Wehr et al. 2018). These wallows provide breeding grounds for mosquitoes that spread avian malaria which has decimated native bird populations (Aslan et al. 2014; Atkinson et al. 2014; Stierhoff 2024). Given the complexity of the effects of pigs controlling and managing this species may offer more benefits than we currently understand.

Aside from general dispersal, pigs may also facilitate gene flow between different groups within a species by transporting genetic material to new areas (Fenster 1991; Dick et al. 2008). In some instances, seed dispersal spreads genetic material farther than pollen dispersal (Fenster 1991), highlighting the importance of examining the effects of wild pig seed dispersal on gene flow in Hawaiʻi. The loss of native pollinators (Aslan et al. 2014) and seed dispersers (Pejchar

1995) in Hawaiʻi and the subsequent transfer of those roles to non-native species makes it even more important to explore how wild pig seed dispseral affects various aspects of community composition. While it was not the focus of this study, the transfer of genes along with dispersal of thousands of seeds means that pigs may be drastically changing the landscapes they interact with. Ultimately, wild pigs most likely expedites the spread of non-native plant species in multiple ways.

Considering the combined effects of wild pigs, population control and management is vital to protect and conserve Hawaiian forests. The inadequacy of hunting as an effective means of reducing populations suggests that, although labor and materials are expensive, fencing may be the most effective method to prevent and minimize the damaging effects of wild pigs. Not only can exclusion prevent dispersal of invasive seeds, but investments in these management techniques may also prove useful in mitigating a wider array of negative effects associated with pig ingress. This precautionary approach necessitates further research on pig ecology and the effectiveness of management techniques for achieving conservation goals.

Appendix 1. List of species that germinated from the scat and their elevational presence.

Species Code	Family	Species	Common Name	Low	High	Abundance
CECOBT	*Urticaceae*	*Cecropia obtusifolia*	Trumpet Tree	X		14438
PSICAT	*Myrtaceae*	*Psidium cattleyanum*	Waiawī, Strawberry Guava			13996
PSIGUA	*Myrtaceae*	*Psidium guajava*	Kuawa, Common Guava			2523
RUBELL	*Rosaceae*	*Rubus ellipticus*	Golden Himalayan Raspberry		X	1805
PASEDU	*Passifloraceae*	*Passiflora edulis*	Liliko'i, Passion Fruit			378
SYZCUM	*Myrtaceae*	*Syzygium cumini*	Java Plum	X		118
PASTAR	*Passifloraceae*	*Passiflora tarminiana*	Banana Poka	X		103
MORCIT	*Rubiaceae*	*Morinda citrifolia*	Noni, Indian Mulberry	X		61
MICCRE	*Melastomataceae*	*Miconia crenata*	Clidemia, Soapbush	X		45
HEPACT	*Araliaceae*	*Heptapleurum actinophyllum*	Octopus Tree	X		25
FRAVES	*Rosaceae*	*Fragaria vesca*	Strawberry		X	12
ARDELL	*Primulaceae*	*Ardisia elliptica*	Shoebutton Ardisia	X		3
TREORI	*Cannabaceae*	*Trema orientalis*	Gunpowder Tree	X		1

***Appendix 2. List of species that germinated from the scat and their frequency in the scat.
(Put another column with the proportion)***

Species	Elevation	Present	Total Scats
Ardisia elliptica	Low	3	143
	High	0	203
Cecropia obtusifolia	Low	53	143
	High	2	203
Fragaria vesca	Low	0	143
	High	4	203
Morinda citrifolia	Low	12	143
	High	0	203
Miconia crenata	Low	17	143
	High	1	203
Passiflora edulis	Low	38	143
	High	21	203
Passiflora tarminiana	Low	0	143
	High	24	203
Psidium cattleyanum	Low	75	143
	High	5	203
Psidium guajava	Low	43	143
	High	1	203
Rubus ellipticus	Low	0	143
	High	22	203
Heptapleurum actinophylla	Low	11	143
	High	0	203
Syzygium cumini	Low	23	143
	High	0	203
Trema orientalis	Low	1	143
	High	0	203

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