

**Insights on the distribution of the endemic Hawaiian fern
genus *Adenophorus* Gaudich. (Polypodiaceae) on the island
of O‘ahu, Hawai‘i.**

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Keywords: Epiphytes, Ferns, *Adenophorus*, Conservation, Hawai‘i

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Abstract:

Epiphytes, plants that grow on other plants, are conspicuous members of many ecosystems around the globe but are most pronounced in humid forests. In tropical regions such as Hawai‘i, upland wet forests sustain diverse communities of epiphytic vegetation, mainly consisting of bryophytes and ferns. Of the epiphytic ferns, the endemic genus *Adenophorus* Gaudich. (Polypodiaceae) is the most species- rich and represents a considerable amount of the biomass of Hawaiian epiphytic communities. However, little is known about the ecology and conservation status of this genus. This study assessed the distribution, abundance, and conservation status of *Adenophorus* species on the island of O‘ahu and identified some of the factors affecting it. I carried out surveys on transects along eight ridges of the Ko‘olau mountains as well as in the Ka‘ala Natural Area Reserve and sampled epiphytes on a total of 242 trees. *Adenophorus* abundance overall increased at higher elevations, although elevational patterns differed between species. *Adenophorus oahuensis* and *A. haalilioanus* distributions appear to be limited by elevation, the former at low elevations and the latter at higher elevations. *Adenophorus* abundance increased with bryophytes cover, and bryophytes appear to be important in the establishment of the gametophyte stage of these ferns. *Adenophorus haalilioanus* may exhibit host bias, but further studies are needed to confirm this. Several species of *Adenophorus* may be experiencing population declines (i.e., *A. oahuensis*, *A. tripinnatifidus*, and *A. haalilioanus*), a result of habitat degradation as well as shifts in precipitation likely due to climate change. *Adenophorus abietinus* shows great phenotypic variability and may warrant further investigation of two distinct varieties, one of which is mostly found at higher elevations near the Ko‘olau summit ridge and may also be susceptible to perturbation by climatic changes

in the near future if current trends of current climate change persist. These insights provide a strong foundation for the future conservation of these endemic ferns.

This paper is dedicated to my family and many others who have supported me throughout this endeavor. It is also dedicated to the people who work towards the conservation of the flora and fauna of Hawai‘i.

Acknowledgements:

I would like to acknowledge and thank my advisor, Dr. Tamara Ticktin, and my committee members Dr. Tom Ranker and Dr. Kasey Barton for their hard work in helping me to form this thesis as well as their expert guidance providing technical advice and support during my research. I would also like to acknowledge the Hau'oli Mau Loa Foundation for funding my research.

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Chapter 1: Introduction

1.1 Introduction to epiphytes and ferns

Across the world, plants play important roles in ecosystem function, especially in tropical settings, where rainforests and cloud forests support a wide array of plant diversity (Harrington & Watts 2021; Mehltreter et al., 2010). Within areas of adequate moisture, ferns comprise a large portion of the vegetation (Vernon & Ranker, 2013) and can be found growing on soil, and in crags of bare rock as well as upon other plants as epiphytes (Mehltreter et al., 2008; pers. obs.). Despite their rarity in geological time, vascular epiphytes are a major component of modern flora and add a significant amount of biodiversity to the habitats they live in. Approximately 10% of extant vascular plants are epiphytic (Nieder et al., 2001). Vascular epiphytes are not ubiquitous and are markedly absent in dry habitats. Epiphyte density and diversity are highest in mid-elevation, tropical forests (Gentry and Dodson 1987; Cardelus et al. 2006) and highest in the American tropics (Gentry & Dodson, 1987). Within forests, epiphytes grow at many levels. Some are restricted to the dark understory on trunks, exposed roots, or the exposed twigs of emergent trees (Watkins & Cardelus, 2012). A significant portion (up to 72%) of epiphytes in paleotropical areas like Australia and Micronesia are ferns and lycophytes (Dubuisson et al., 2009) that are either nest forming or grow via creeping rhizomes and clasping roots (Watkins & Cardelus, 2012). Ferns in general are found in many habitats across the globe, ranging from high alpine deserts to humid tropical forests but it is in these tropical settings where most of the fern diversity exists (Mehltreter et al., 2010; Mutke & Barthlott 2005). Data suggest that ferns may have low water use efficiency, indicating wetter forests may have facilitated fern diversification (Watkins & Cardelus, 2012).

Ecological studies of epiphytes have focused on vascular plants (i.e., bromeliads, orchids, and some ferns) with fewer studies on non-vascular flora such as bryophytes and lichens. Overall, epiphytic plants have been shown to facilitate cloud water irrigation, mineral cycling, reduce soil moisture loss below host plants, buffer temperature fluctuations beneath the canopy, and reduce throughfall volumes of precipitation (Stanton et al., 2014; Lee, 2015). In certain settings, epiphytic plants have been noted to hold up to 45 percent of the nutrient capital held in the foliage of their host trees (Lee, 2015). In addition, the canopy soils, from which epiphytes derive nutrients from, host a high diversity of invertebrates and potentially store significantly more amounts of cat/anions than their terrestrial counterparts (Lee, 2015; Benzing, 1998). Epiphytic plants must derive their nutrients directly from the atmosphere (precipitation or airborne dust particles) or from canopy soil provided by the breakdown of bark and leaf litter (Lee, 2015; Benzing, 1998; Stanton et al., 2014; Nadkarni, 1986), and therefore must survive a harsh environment, as compared to many terrestrial plants. In contrast to flowering plants, epiphytic ferns have a special challenge due to the poikilohydric qualities of the preliminary growth stage (the gametophyte) before the sporophyte emerges. For this reason, the habitats of many epiphytic ferns have to provide the correct moisture regimes to ensure that gametophytes can undergo fertilization and produce sporophytes. It should be noted, however, that a significant portion of taxa have gametophytes that have surprising thresholds of desiccation tolerance, sometimes surpassing that of conspecific sporophytes (Watkins et al., 2007). Despite this, much of the diversity of epiphytic ferns (especially Hygrophytes) are found in the wet tropics, especially on mountains (Dubuisson et al., 2009; Mehlreter et al., 2010). It should be noted that angiosperms similarly experience sensitivity to water stress in early growth stages (Barton et al., 2020; Corlett, 2016). Many of these species, especially those in drier forests, require sufficient

water during wet seasons at the seedling stage that do not typically occur on a consistent basis.

1.2 Tropical islands and Hawai'i

Tropical islands boast a diverse fern flora, especially islands with high elevations that support tropical montane cloud forests (Pouteau et al., 2016; Mehlreter, 2010). This is especially true for the Hawaiian Archipelago, which is composed of eight main islands with elevations reaching up to 13,000 ft on the largest island (Hawai'i) and a lower reach of 1,280 ft on the lowest main island (Ni'ihau). Hawai'i hosts a high endemism rate for ferns, roughly 76% of the native taxa, nearly on par with that of its flowering plant endemism which is roughly 90% (Ranker et al., 2003; Palmer et al., 2003; Wagner et al., 1990). Approximately one third of Hawaiian ferns are epiphytic (Ranker, 1992) and these often have small stature relative to the terrestrial flora (i.e., Hymenophyllaceae and some genera of the Polypodiaceae) (Palmer, 2003) although some attain large stature such as *Asplenium nidus* L., which can sometimes grow over 5 ft in diameter.

Taxonomically, the Hawaiian ferns have been well studied but more work needs to be done on other aspects, including their ecology (Ranker, 2016). As with many Hawaiian flowering plants, a portion of the native fern flora is threatened with extinction due to alteration of habitat by humans, invasive species, and climate change (Wagner et al., 1990; Gustafson et al., 2014; Zots & Bader, 2009). The list of endangered species includes 14 taxa of ferns and two species of lycophytes. In addition, four species of ferns and one species of lycophyte have been proposed for listing (Ranker, 2016) with more potentially to be added to the list. Although ferns that are subject to natural causes of disturbance may be able to persist over long-term periods

(Mehltreter et al., 2010; Pouteau et al., 2016; Zots & Bader, 2009), high levels of human disturbance have been documented to lead to massive species loss (Mehltreter et al., 2010).

1.3 Introduction to the genus *Adenophorus*

The aim of this study was to generate insight into the ecology, distribution, and conservation status of the endemic Hawaiian genus *Adenophorus* Gaudich. (Polypodiaceae) on O‘ahu, although this information may also apply to similar habitat types across the state. *Adenophorus* is one of two endemic Hawaiian genera of ferns (the other being *Sadleria* Kaulf.), first described by Charles Gaudichaud-Beaupré in his book “*Botanique du Voyage autour du monde*” (Gaudichaud, 1826) and is part of a larger subgroup within the Polypodiaceae known as the “grammitid” ferns (Sundue et al., 2014). This sub-group, once considered a separate family (Grammitidaceae) contains nearly 900 species, comprising roughly two thirds of the known taxa of the Polypodiaceae family (Ranker et al., 2003; Sundue et al., 2014). The genus *Adenophorus* went through several revisions, formerly placing members within the genus *Polypodium* L. (Dana & Wilkes *et al.*, 1852; Hillebrand, 1888; Robinson, 1913) and one species, formerly *Adenophorus tenellus* (Kaulf.) Ranker, within *Grammitis* Sw. (Bishop, 1974; Ranker 2008). *Adenophorus* comprises ten species, where two subgenera (*Adenophorus* and *Oligadenus*) were formerly proposed, differentiated based on frond dissection and rhizome structure (Bishop, 1974; Palmer, 2003; Ranker et al., 2003; Ranker 2004; Wilson, 1964). The subgenus *Adenophorus* was classified as having creeping rhizomes and mostly twice pinnate fronds whereas the subgenus *Oligadenus* contained simple to pinnate fronds that sometimes bear multicellular hairs and roots with adventitious buds (Bishop, 1974; Palmer, 2003; Wilson, 1964). Although these two subgenera contain morphologically similar species, a genetic study by Ranker et al. (2003) suggested that there was no strong evidence to support the classification of the subgenera as

described by Bishop (1974). However, three species that were classified under the subgenus *Oligadenus*; *Adenophorus oahuensis* (Copel.) Bishop, *Adenophorus haalilioanus* (Brack.) K.A. Wilson, and *Adenophorus pinnatifidus* Gaudich., were found to represent a clade. *Adenophorus periens* Brack. was found to be more closely related to a member of the former subgenus *Adenophorus*, *A. tripinnatifidus* Gaudich. (Ranker et al., 2003). Almost all members of this genus are associated with trees, exhibiting either epiphytic or sub-terrestrial growth (Palmer, 2003). One species, *Adenophorus pinnatifidus*, has been observed growing on rocks along stream beds (Palmer, 2003; pers. obs.).

Within the Hawaiian archipelago, the islands of Kaua‘i and O‘ahu hold the most species of *Adenophorus* (a total of nine each) (Table 1). Information from checklists and herbarium records show that some species have patchy distributions. For instance, *Adenophorus haalilioanus* (Brack.) K.A. Wilson is known from Kaua‘i and O‘ahu, but the distribution on O‘ahu is strictly confined to the Ko‘olau mountains near and on the summit ridge. In Kaua‘i, it is found in native wet forests in the northern section of the island. Although there are some voucher specimens [from the Consortium of Pacific Herbaria Database (PTBG 10865, PTBG 7307, PTBG 13083, BISH 715770)] that place this species on Maui, these are believed to be database errors (pers. comm. with Barbara Kennedy and Timothy Flynn, April 2, 2020). Another interesting species is *A. oahuensis* (Copel.) Bishop, which has only been collected from the Ko‘olau mountains of O‘ahu. Species such as these need to be studied and surveyed due to their narrow ranges and hence vulnerability of extirpation, eventually leading to extinction. A significant decline in population size would warrant a need to list these species as threatened or vulnerable under U.S Fish & Wildlife Service and/or International Union for the Conservation of Nature (IUCN) guidelines. On the opposite end of the spectrum, species like *Adenophorus*

tamariscinus (Kaulf.) Hook. & Grev., and *A. tenellus* have been reported to be common, with broad species ranges and can be found in almost every mesic to wet forest at elevations higher than 350 meters (Palmer et al., 2003; pers. obs.).

The above information provides insight into the habitats and the distributions of the species of *Adenophorus*. Herbaria at the University of Hawai‘i (Joseph Rock Herbarium-HAW) and the Bishop Museum (BISH) have specimens, often with labels that provide information of the collection locality as well as a description of the habitat. The book “Hawai‘i’s Fern & Fern Allies”, by Dr. Daniel D. Palmer, currently gives the best description of where these ferns are located, as does a paper on the revision of the genus *Adenophorus* (Bishop, 1974). Although various papers on phylogeny have been published (see Ranker et al., 1994 & Ranker et al., 2003), there is almost no ecological research on this genus. One exception is a study by Kettwich (2015), who examined the physiology of epiphytes (including *Adenophorus*) in relation to moisture acquisition and climate change sensitivity. This leaves major gaps in the knowledge of the genus, with very little understanding of what drives the differential distribution and abundance of the different species, especially for island endemics such as *Adenophorus epigeous* and *A. oahuensis*. This includes a lack of information on the variation in abundance across elevation, time, hosts (host bias) and microhabitats. Host associations are especially important to understand because specialist species are more likely to go extinct in altered habitats compared to generalists (Wagner et al., 2015). Herbarium vouchers along with peer and personal observations suggest that certain species of *Adenophorus* show some preference for certain trees but this has yet to be verified. The present study aims to address these gaps in knowledge and to contribute to a better understanding of the ecology and distribution of the genus. In Chapter 2, I assess the effects of elevation, host, microhabitat (bryophyte cover), and bryophyte community

on *Adenophorus* species presence and abundance. In Chapter 3, I complement the quantitative results in Chapter 2 with my observations on the natural history of this genus. Finally, I conclude with recommendations for conservation.

Table 1: Taxon list of the known species of *Adenophorus* per Ranker et al., 2019. Hybrids are not listed, nor are the varieties under *A. tamariscinus* and *A. pinnatifidus*. An “X” represents a species presence on island and “ex” represents extirpation from an island. Dark grey boxes represent absence or record from the island. Yellow boxes indicate a taxon is presumed extinct

Taxon	Conservation status	Island distribution					
		Kaua‘i	O‘ahu	Moloka‘i	Lāna‘i	Maui	Hawai‘i
<i>Adenophorus abietinus</i> (D.C. Eaton) K.A. Wilson	Secure	X	X		X	X	
<i>Adenophorus epigaeus</i> (L.E.Bishop) W.H. Wagner	Vulnerable	X					
<i>Adenophorus haalilioanus</i> (Brack.) K.A. Wilson	Vulnerable (candidate)	X	X				
<i>Adenophorus hymenophylloides</i> (Kaulf.) Hook. & Grev.	Secure	X	X	X	X	X	X
<i>Adenophorus oahuensis</i> (Copel.) L.E. Bishop	Vulnerable (candidate)		X				
<i>Adenophorus periens</i> L.E. Bishop	Endangered	X	X(ex)	X(ex)	X (ex)	X(ex)	X(ex)
<i>Adenophorus pinnatifidus</i> Gaudich.	Secure	X	X	X	X	X	X
<i>Adenophorus tamariscinus</i> (Kaulf.) Hook. & Grev.	Secure	X	X	X	X	X	X
<i>Adenophorus tenellus</i> (Kaulf.) Ranker	Secure	X	X	X	X	X	X

<i>Adenophorus tripinnatifidus</i> Gaudich.	Secure (Populations diverging ¹). Rare on O‘ahu	X	X	X	X	X	X
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1. In personal communication with Vithanage Nipuni Sirimalwatta

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Chapter 2: Distribution and abundance of Adenophorus on O‘ahu

2.1 Introduction:

Epiphytes are important components of tropical forest biodiversity where they play major roles in ecosystem function (Stanton et al, 2014; Hietz-Siefert et al., 1995). In Hawai‘i, epiphytes such as ferns have been shown to increase surface area and transpiration, increasing the efficiency of the water capturing ability of rainforests (Kettwich, 2015; Krömer et al., 2007). The distribution of most epiphytic ferns is limited by biotic and abiotic factors, particularly moisture regimes and substrate availability necessary for the recruitment and establishment of mature individuals (Mehltreter et al., 2013; Boelter et al., 2014; Kettwich, 2015). Even though gametophytes are poikilohydric (meaning they receive water by surface contact and not with roots), they can withstand desiccation in some species, sometimes more than the sporophytes they produce (Watkins, 2007). Nevertheless, the sheer abundance of sporophytes in wetter areas suggests that there is an affinity of both generations (sporophyte and gametophyte) to moisture and, therefore, also established bryophyte communities, which retain moisture. Bark water-holding capacity has also been shown to be the key factor influencing epiphyte presence in some forests (Tewari et al., 2009). While it is impossible to generalize, it is unlikely that a single aspect of bark influences epiphyte distribution, and a great deal more comparative data are needed. (Watkins & Cardelus 2012).

Hawai‘i receives the majority of its moisture from tradewinds that cause orographic rainfall and constant formation of clouds over the windward sides of the islands and high elevation leeward slopes such as ‘Auwahi on the island of Maui (Yeh et al., 1950; Scholl et al., 2007; pers. obs.). Cloud water interception by a forest canopy depends on many variables including wind speed, cloud liquid water content, and vegetation surface area (Scholl et al.,

2007). On O‘ahu, the Ko‘olau mountains catch the brunt of the force of orographic winds that form clouds over the summit of the Ko‘olau volcano (Yeh et al., 1950;). Some areas may receive more constant cloud or fog input rather than precipitation, and this is often overlooked when it comes to understanding how plants may retrieve water (Went, 1955). Fog, condensation, or dew formation may have the ability to quickly enter the tissues of plants with soft tissues or may collect on plants with trichomes or hairs (Kettwich, 2015; Watkins & Cardelus, 2012) and may be a more efficient means to quickly replenish moisture in plants. All *Adenophorus* species have trichomes but in varying densities, as well as having various frond shapes (Palmer, 2003) with different implications for the ability of the fern to capture and utilize the moisture. These differences in morphology can limit growth and/or distribution across microhabitats. For example, finely dissected plants like *Adenophorus tripinnatifidus* and *A. abietinus* are better adapted to collecting diffused water drops from cloud cover and may be limited to areas where such conditions occur (Kettwich 2015).

Areas that receive sufficient fog drip and/or cloud cover maintain a high humidity and have a high proportion of epiphytic bryophyte communities. These communities are dominated by leafy liverworts and mosses (as well as hornworts, lichen, and algae) and it is in these communities where *Adenophorus* species occur. Sporophytes of *Adenophorus* species as well as other epiphytes are often rooted in both cushion and mat forming colonies of bryophytes, especially those composed of *Acroporium fuscoflavum*, *Leucobryum gracile*, and *Pyrrhobryum spiniforme* (pers. obs.) as indicated on many of the herbarium vouchers at the Bishop Museum as well as the Joseph F. Rock Herbarium at the University of Hawai‘i Mānoa. *Adenophorus* interactions with bryophytes are not limited to trees, and sometimes these ferns may be found growing on bryophyte covered boulders. Since bryophyte communities have potential to serve as

a nutrient and moisture reservoir (Krömer et al., 2007; Harrington & Watts, 2021), it would be no surprise to find that cryptogamic species play a facilitative role for *Adenophorus*.

Nutrient acquisition of *Adenophorus* is largely unknown, although most epiphytic plants can absorb nutrients through leaves or from roots, depending on their architecture. The root systems on many epiphytic ferns are modified so as to not absorb nutrients directly from the soil (Mehltreter et al., 2013) and if this is the case with *Adenophorus*, these plants may be getting minerals from rain and water passing through bryophyte mats. However, from my experience collecting herbarium vouchers, *Adenophorus tamariscinus* and *A. abietinus* have well developed roots while more climbing species like *Adenophorus tenellus*, *A. tripinnatifidus*, and the *A. pinnatifidus-oahuensis-haalilioanus* type plants have thin, sprawling roots that cover significant surface area. Growth trials in lab settings have been done with these ferns using agar as well as field collected humus (Bishop, 1986; Stokey & Atkinson, 1958; Shayla Villanueva pers. com.) but both the gametophytes and sporophytes are slow growing. More research is needed in this area of study.

From a conservation perspective, the lack of ecological information on *Adenophorus* is problematic. The probable extinction of *Adenophorus periens* on most of the main islands, which declined very rapidly despite the presence of intact native forest habitats, demonstrates that native forest alone may not be enough to sustain a species. Without information on population distribution, status, or trends, similar downward trends in population size may be happening with other taxa, with local extirpations potentially going unnoticed. The epiphytic nature of *Adenophorus* also subjects these ferns to seasonal wet and drying trends that are experiencing significant shifts due to climate change. These shifts have been forecasted to be disastrous for cloud forests in Hawai‘i due to the abundance of steep microclimate shifts (Loope &

Giambelluca, 1998) Along with a change in climate, much of the forests of O‘ahu have been altered by logging and/or invasive species, and many of the populations remaining are relicts of once larger populations that became isolated and fragmented (Division of Forestry and Wildlife Pers. Comm.; Rehm et al., 2019).

Over the years of personal observations through hiking and working as a field technician with the Native Ecosystems Protection and Management (NEPM) branch of the Division of Forestry and Wildlife (DOFAW), I have noticed various ecological factors that appear to be important to the population status of *Adenophorus* and these are also consistent with the broader literature on epiphytes. In this study, I attempted to address the following questions: 1) What are the current distributions of the different species of *Adenophorus* in the Ko‘olau Mountains? 2) What is the effect of elevation on the distribution of *Adenophorus* species? 3) Do species of *Adenophorus* show different levels of occurrence on different tree species (host bias)? 4a) Is *Adenophorus* species abundance on host species correlated with the presence of bryophytes and/or filmy ferns? 4b) Do tree ferns such as *Cibotium* spp. provide a good substrate for *Adenophorus* species alone without the cover of bryophytes?

I hypothesized that (i) the proportion of trees with *Adenophorus* present, as well as the abundance of *Adenophorus* stands on trees, increases with elevation, since cloud cover is more frequent and moisture is greater at higher elevations (ii); *Adenophorus* abundance is lower on hosts with smooth bark but higher where bryophytes and/or filmy ferns are also present; (iii) when *Cibotium* species are hosts, there is a correlation between the presence and/or absence of *Adenophorus*, bryophytes, and filmy ferns due to the high water retention of the caudex, which is suitable substrate for a variety of epiphytes (Palmer, 2003; Wagner et al., 2015).

Study sites:

This study was focused on the island of O‘ahu, where I surveyed along ridge trails of the Ko‘olau mountains in the northern, central, and southern regions. A focus on the O‘ahu communities can be a proxy for a “typical” Hawaiian forest since the dominant genera for native mesic and wet forest canopy are very similar across the state for these habitats. The communities mainly consist of species of *Metrosideros*, *Acacia*, *Antidesma*, *Cheirodendron*, *Psychotria*, *Bobea*, *Polyscias*, *Kadua*, *Santalum*, *Melicope*, *Cibotium*, *Ilex*, and *Coprosma* genera (Wagner et al., 1999; pers. obs.). All *Adenophorus* species known to be on O‘ahu also are present in this mountain range. The Wai‘anae volcano lacks two species of known *Adenophorus* that occur on O‘ahu, *A. haalilioanus* and *A. oahuensis*. Surveys that I have done while working with DOFAW did not show any presence of these two species, which is why my surveys did not take place there. Nevertheless, I have included Ka‘ala bog as an added site of interest to examine epiphyte preference within the Native Ecosystems Protection and Management (NEPM) owned portion of the Natural Area Reserve. During typical trade wind conditions, clouds are intercepted in the western end over mount Ka‘ala, the highest peak on O‘ahu , roughly 4,025 ft. (or 1226.82 m) in elevation, forming an immature bog surrounded by stunted, bryophyte rich native forests.

The summit regions of the Ko‘olau have a relatively constant band of moisture but in the extreme northern and southern regions, precipitation noticeably decreases and the transition from wet to dry is rapid. The vicinities of Nu‘uanu, Mānoa, and Pālolo also intercept a considerable amount of moisture, especially at the high peaks of Kōnāhuanui, Lanihuli, and Āwawaloa (Hillebrand, 1880). These conditions provide relatively consistent moisture to support humid

forests at the heads of the valleys. Today, the central and northern regions of the Ko‘olau are considered to be the most “intact” in terms of contiguous native forest due to the rugged terrain of long, meandering ridges as well as little disturbance from agriculture and grazing by feral animals. The summit areas here form patches of swampy, dwarfed forests due to poor drainage and high winds that rush over the windward facing pali (cliff) of the ancient remnants of the Ko‘olau caldera.

2.2 Methodology:

Given the difficult terrain and access, the Ko‘olau sites were surveyed along known trails in the mountain range. A total of eight trails were chosen because they are spread across northern, central, and southern regions of the Ko‘olau mountain range (Table 1). Along each trail, I carried out surveys at three different elevational stations. Station 1 was the lowest elevation ranging from 400 m to 500 m. It was chosen because most communities of *Adenophorus* appear around this elevation in mesic to wet forests of the Ko‘olau, especially when hiking from leeward positions to the summit ridge. The next stations, 2 and 3, were at 501 m to 600 m, and 601 m to 700 m respectively. The last elevational site was from 701 m to 800 m which reaches the summit ridge of the Ko‘olau volcano. At the start of each station, I positioned a meter tape to run a 100 m transect with 2 m long perpendicular transects spaced every 10 m. The direction of each perpendicular transect (left or right side of trail) was decided with a coin toss (using a standard USA quarter dollar). For each tree alongside each transect, I looked at all trees along the transect with epiphytic communities that had a presence of *Adenophorus*. At each tree, I recorded the epiphytes present, from vascular plants to bryophytes, excluding lichens. All ferns were identified to species level and most bryophytes were identified to genus level, but for

some this was done to family. The identification of bryophytes was done by using keys from the “Manual of Hawaiian Mosses” by Edwin B. Bartram (1933), “Prodromus Florae Muscorum Polynesiae”, by H.A. Miller et al. (1978), and “Prodromus Florae Hepaticarum Polynesiae”, also by H.A. Miller et al. (1983). Due to the old age of these manuals, the current genera were referenced with the “Checklist of Hawaiian Anthocerotales and Hepatics” by Staples & Imada (2006)

I estimated canopy cover in categories of 0-25%, 26-50%, 51-75%, and 76-100%. Host trees were identified to species and were measured for diameter at breast height (DBH). Bark texture was recorded in four categories: Rough, Smooth, Peeling, Rugose (Boelter et al. 2014; Table 2). A category of “Spongy” was added for the tree fern genus *Cibotium* based on personal observation in the field. For trees that split close to the ground, DBH was calculated by taking the square root of the sum of the squares of the individual stem DBH’s (Truan, 2015). Due to difficulty of identification for some bryophytes and lack of current literature on species delineation, some individuals were only identified to family or genus level. Since most *Adenophorus* grow in clonal communities (i.e. creeping rhizomes and occasionally by root buds), true individual counts were difficult, so I counted individual “stands” (as defined in Mehltreter et al. 2005 & Sanford 1968) on trees. Individuals clearly separated from each other on the tree were counted as different individuals, due to apparent lack of connectivity. All surveys were carried out between the months of November 2020 to January 2021.

To increase sample sizes at the summit, where *Adenophorus* frequency and abundance is highest, I added an additional three transects each at four localities along the Ko‘olau summit ridge trail (known locally as the “KST”), I surveyed trees in the vicinity of Hawai‘i Loa, Kōnāhuanui, ‘Aiea, and Poamoho to represent the southern, central, and northern Ko‘olau

regions, respectively. Transects were 10 m wide by 2 m long and were placed in forest patches haphazardly chosen. All the trees within the transects were sampled as described above.

Table 1: List of trails surveyed in the Ko‘olau mountains, O‘ahu and their relative positions

<u>Trail</u>	<u>Region in Ko‘olau mountains</u>
Hawai‘i Loa ridge trail	Southeastern Ko‘olau
Wailupe trail	Southeastern Ko‘olau
Wiliwilinui ridge trail	Southeastern Ko‘olau
Ka‘au crater trail	Southern Ko‘olau
Kōnāhuanui trail	South/central Ko‘olau
‘Aiea ridge trail	Central Ko‘olau
Mānana ridge trail	Central Ko‘olau
Poamoho ridge trail	Northern Ko‘olau

Table 2: Bark Types (Boelter et al. 2014)

Tree spp.	Category
<i>Metrosideros</i> spp.	Peeling
<i>Kadua</i> spp.	Rugose
<i>Bobea</i> spp.	Rough
<i>Psychotria</i> spp.	Rough
<i>Acacia koa</i>	Rugose
<i>Syzygium sandwicense</i>	Rough
<i>Citharexylum caudatum</i>	Rough
<i>Araucaria columnaris</i>	Peeling
<i>Elaeocarpus angustifolius</i>	Rough
<i>Polyscias</i> spp.	Rough
<i>Cheirodendron</i> spp.	Rough
<i>Santalum freycinetianum</i>	Rugose
<i>Cibotium</i> spp.	Spongy
<i>Melicope</i> spp.	Rough

Data analysis:

To test if *Adenophorus* species frequency (presence or absence of a given species) varied as a function of elevation, DBH, bark texture, and/or bryophyte cover, I used a generalized linear model with a binomial error distribution. To test if *Adenophorus* species abundance (count per tree) varied as a function of the same variables, I used a general linear model with a Gaussian error distribution. I tested my model fit by visually examining model residuals for heteroskedasticity. I used Akaike's information criterion (AIC) to determine whether to drop or retain a given fixed effect term, retaining factors that reduced the AIC value of the model by 2 or more (Zuur et al., 2009). For both models, I used R Studio Version 3.6.1. To visualize associations among *Adenophorus* species, host trees and bryophyte community, I used Nonmetric Multidimensional Scaling (NMDS) with the packages "Vegan" 2.5-6 (R version 3.5.2) and "ggplot2" (R version 3.5.2). All analyses were performed in R studio Version 3.6.1 from data were inputted in Microsoft Excel for Mac Version 15.30.

Table 3: Results of best fit generalized linear model testing the effects of environmental variables on *Adenophorus* frequency (presence/absence per tree)

Binomial GLM (<i>Adenophorus</i> presence ~ Bryophyte cover + Canopy cover + Elevation + Bark texture)	Estimate	Std. Error	z value	Pr(> z)
Intercept	-1.685	0.5247	-3.212	0.00312**
Bryophyte cover (25%-50%)	1.818	0.184	9.808	<2e-16***
Bryophyte cover (50%-75%)	2.693	0.267	10.096	<2e-16***
Bryophyte cover (75%-100%)	4.446	0.295	15.051	<2e-16***
Elevation (m)	0.0026	0.001	3.26	0.0011**
Canopy cover (25%-50%)	-0.194	0.211	-0.918	0.35861
Canopy cover (50%-75%)	1.182	0.196	6.023	1.82e-07***
Canopy cover (75%-100%)	1.358	0.26	5.217	1.82e-07***
Bark texture (Rough)	-0.838	0.184	-4.565	5.00e-06***
Bark texture (Rugose)	-1.773	0.346	-5.124	3.00e-07***
Bark texture (Smooth) = <i>Psidium</i>	-2.543	0.334	-7.615	2.64e-14**
Bark texture (Spongy) = <i>Cibotium</i>	-2.726	0.467	-5.839	5.27e-09***

Table 4: Results of best fit generalized linear model testing the effects of environmental variables on *Adenophorus* abundance.

GLM (Count per tree ~ Bryophyte cover + Canopy cover + Elevation + Bark texture)	Estimate	Std. Error	t value	Pr(> t)
Intercept	-0.464	0.522	-0.889	0.376
Bryophyte cover (25%-50%)	0.562	0.281	1.999	0.049*
Bryophyte cover (50%-75%)	0.821	0.287	2.859	0.005**
Bryophyte cover (75%-100%)	1.056	0.235	4.49	2.17e-5***
Elevation (m)	0.0008	0.0007	1.101	0.273
Canopy cover (25%-50%)	0.309	0.246	1.253	0.213
Canopy cover (50%-75%)	0.385	0.209	1.846	0.068
Canopy cover (75%-100%)	0.859	0.261	3.29	0.001**
Bark texture (Rough)	-1.22	0.254	-4.818	6.08e-06***
Bark texture (Rugose)	-0.542	0.28	-1.935	0.056
Bark texture (Smooth) = <i>Psidium</i>	0.102	0.287	0.356	0.722
Bark texture (Spongy) = <i>Cibotium</i>	0.351	0.316	1.109	0.271

2.3 Quantitative results:

Results from general linear models show that *Adenophorus* spp. frequency increased significantly with elevation (Table 3; Fig. 1), occurring on 16% of trees at the lowest elevation to 95% at the summit. Although elevation was in the best-fit model for *Adenophorus* abundance (count per tree), the relationship was not significant (Table 4). *Adenophorus* abundance, as well as the frequency of trees with adenophorus both increased significantly with an increase in bryophyte cover category (Figs. 2 & 3). *Adenophorus* abundance also increased with canopy cover (Table 3). DBH was not a significant predictor of either frequency or abundance. For bark texture, trees with smooth and spongy (*Psidium* and *Cibotium*) bark had a significantly lower probability of *Adenophorus* spp. frequency, than those with other bark textures (especially *Kadua*). This effect was larger for *Adenophorus* spp. presence than it was for count. At the species level, the most common taxa were *Adenophorus tamariscinus*, *A. tenellus*, and *A. pinnatifidus* which were found across all elevations (Fig. 4). *Adenophorus oahuensis* and *A. haalilioanus* were found much less frequently and appeared to be separated by elevation, with *A. oahuensis* restricted to 400 m to 600 m and the *A. haalilioanus* above 650 m. *Adenophorus hymenophylloides* and *A. abietinus* were rare in my transects and these need more sampling to observe realistic elevational ranges.

As a genus, there was no indication of host bias (Figure 5). In terms of individual species, there were also no obvious host biases (Figure 6). One possible exception is *Adenophorus haalilioanus* which appeared on *Kadua* more so than any other species.

The NMDS analyses (Figure 7) using data from the ridge and summit transects illustrated some patterns in the composition of *Adenophorus* and bryophyte communities. Lower elevations

were associated with communities of *Leucobryum*, *Macromitrium*, *Jamesoniella*, *Frullania* and *Radula* and at mid elevations, bryophytes such as *Herbertus*, *Bazzania*, and *Acroporium* were more common. High elevations were associated with a much more diverse and species-rich community with more species of *Fissidens*, *Pseudosymblepharis*, *Pleurozia*, and *Homaliodendron*. *Adenophorus haalilioanus* was associated with communities of *Herbertus*, *Pleurozia*, *Fissidens*, and *Pseudosymblepharis* on *Kadua* trees. *Adenophorus tenellus* was associated with *Cibotium* spp. since they were found on *Cibotium* more commonly than other species of *Adenophorus*, but this needs to be investigated further.

2.4 Discussion:

2.4.1 Adenophorus Distribution:

On O‘ahu, ferns in the genus *Adenophorus* tend to inhabit mesic to wet forest habitat stretching from as low as 400 ft (~ 122 m) to cloud forest at roughly 4,000ft (~ 1,200 m) atop Mount Ka‘ala. In the Ko‘olau mountains where 8 of the 10 species occur, I found that the populations of the different taxa have striking differences in abundance and distribution. Populations of species such as *Adenophorus tamariscinus* and *Adenophorus tenellus* were relatively abundant throughout the study sites but plants such as *Adenophorus oahuensis*, *A. hymenophylloides*, *A. abietinus*, and *A. tripinnatifidus* were very patchy or rare.

Elevation appears to be important for at least three species: *Adenophorus oahuensis*, *A. tripinnatifidus*, and *A. haalilioanus*, although more research is needed to assess this trend for *A. tripinnatifidus* due to its rarity in my transects and general observations. Higher elevation cloud forests of 600m+ support the best colonies of *A. haalilioanus* whereas *A. oahuensis* usually inhabits forests around 550m and lower. These observations seem to be consistent with previous

notes about these related taxa being separated by elevational barriers (Bishop 1974, Palmer 2003). The more common species are often found across all elevations, but at the lower elevations they are in forests where humidity/moisture seems to be more constant. In these settings, there is a higher count per tree in large trees with more canopy cover which may reflect a need for moisture. In gulch bottoms and near streams, this is especially true and sometimes plants may be found at very low elevations (around 150 m). Precipitation, including fog interception would likely be better predictors of *Adenophorus* abundance and distribution, but the spatial distribution of these variables is not currently available at a fine scale. Although records do not exist, it would not be surprising if *Adenophorus* once inhabited intact lowland forests on windward slopes of all islands, possibly reaching some coastlines or sea cliffs. Some native ferns, such as *Dicranopteris linearis* and *Sadleria* spp. can reach coastal cliffs on Hawai'i Island in the districts of Hilo and Puna (pers. obs.). Unfortunately, the intact lowland wet forests were removed from nearly all islands where secondary stands of introduced species now grow.

2.4.3 Host trees:

My data suggests no strong host preference for any of the species of *Adenophorus*. This is consistent with findings elsewhere that many epiphytic ferns do not show strong host bias and may be affected by other effects such as growth rate of the host species (Wagner et al., 2015; Wagner & Zotz, 2020). Nevertheless, there are species that occur more often on some host taxa than others. For instance, *Adenophorus oahuensis* is often found on trees in the genus *Bohea*, even though it can be found on other species (Table 5). *Adenophorus haalilioanus* is often found on species of *Kadua* and *Antidesma* but is also found on *Metrosideros* and *Polyscias* (Figure 5).

Not surprisingly, smooth textured species (mainly *Psidium cattleianum*) were poor hosts for *Adenophorus*. This may be due to the young age of the trees, since most of the individuals sampled were relatively young vs. slower growing native counterparts. Contrary to expectations, trees with “Spongy” bark, which pertains to *Cibotium*, were also poor hosts for *Adenophorus*. This may be due to the relatively low number of plants sampled in general as well as the overall architecture of the ferns. Many of the *Cibotium* that were surveyed were low in stature as well as retaining a large crown of fronds. Those that had epiphytes had a smaller crown of fronds and much of the trunk exposed and were in wetter conditions versus plants on mesic ridges under heavy canopy. Aside from this study, I have observed *Cibotium* spp. to host various species of epiphytic ferns, mainly *Elaphoglossum*, *Hymenophyllum*, and *Adenophorus*. Higher elevation wet forests (especially at the Ko‘olau summit and on Mount Ka‘ala) have an abundance of *Cibotium* where congregations of *Adenophorus* can be seen in mixed bryophyte communities that shroud the trunks. So far, *A. tamariscinus*, *A. tenellus*, and *A. abietinus* have been recorded on *Cibotium menziesii* and *C. glaucum*, with *Adenophorus tenellus* being the most common. The only *Adenophorus* species I found on *Acacia koa* are *A. tamariscinus* and *A. tenellus*.

Table 5: Habitat and host tree of extant *Adenophorus* spp.

Taxon	Habitat	Known host trees (Pre-survey)	Known host trees (Post-survey)
<i>Adenophorus abietinus</i> (D.C. Eaton) K.A. Wilson	Epiphytic to sometimes terrestrial in bryophyte dominated groundcover	<i>Syzygium sandwicense</i>	<i>Cibotium menziesii</i>
		<i>Metrosideros polymorpha</i>	<i>Syzygium sandwicense</i>
			<i>Metrosideros polymorpha</i>
			<i>Melicope clusiifolia</i>

			<i>Polyscias oahuensis</i>
			<i>Cheirodendron trigynum</i>
			<i>Psychotria mariniana</i>
<i>Adenophorus hymenophylloides</i> (Kaulf.) Hook. & Grev.	Epiphytic	<i>Syzygium sandwicense</i>	<i>Syzygium sandwicense</i>
		<i>Metrosideros polymorpha</i>	<i>Metrosideros polymorpha</i>
<i>Adenophorus haalilioanus</i> (Brack.) K.A. Wilson	Epiphytic	<i>Kadua spp.</i>	<i>Kadua affinis</i>
		<i>Metrosideros spp.</i>	<i>Kadua fosbergii</i>
		<i>Psychotria spp.</i>	<i>Antidesma platyphyllum</i>
			<i>Metrosideros rugosa</i>
			<i>Metrosideros polymorpha</i>
			<i>Polyscias oahuensis</i>
<i>Adenophorus oahuensis</i> (Copel.) L.E. Bishop	Epiphytic to sometimes on rock faces (Degener specimen citation)	<i>Antidesma platyphyllum</i>	<i>Psychotria mariniana</i>
		<i>Bobea elatior</i>	<i>Bobea elatior</i>
		<i>Kadua fosbergii</i>	<i>Metrosideros polymorpha</i>
		<i>Cheirodendron trigynum</i>	<i>Metrosideros tremuloides</i>
		<i>Hibiscus arnottianus</i>	<i>Citharexylum caudatum</i>
		<i>Ilex anomala</i>	<i>Planchonella sandwicensis</i>
		<i>Myrsine lessertiana</i>	
		<i>Psychotria kaduana</i>	

		<i>Santalum freycinetianum</i>	
		<i>Scaevola gaudichaudiana</i>	
		<i>Tetraplasandra oahuensis</i>	
		<i>Metrosideros polymorpha</i>	
		<i>Psidium cattleianum</i>	
		All native trees and <i>Cibotium</i> <i>spp.</i>	<i>Metrosideros polymorpha</i>
		<i>Schinus terebinthifolius</i>	<i>Metrosideros tremuloides</i>
			<i>Metrosideros rugosa</i>
			<i>Metrosideros macropus</i>
			<i>Polyscias oahuensis</i>
			<i>Eucalyptus robusta</i>
			<i>Psidium cattleianum</i>
			<i>Acacia koa</i>
			<i>Syzygium sandwicense</i>
			<i>Cheirodendron trigynum</i>
			<i>Cheirodendron platyphyllum</i>
			<i>Kadua affinis</i>
			<i>Kadua fosbergii</i>
<i>Adenophorus tenellus</i> (Kaulf.) Ranker	Epiphytic to sometimes terrestrial in bryophyte dominated groundcover	All native trees and <i>Cibotium</i> <i>spp.</i>	All native trees & <i>Cibotium</i>
<i>Adenophorus tamariscinus</i> (Kaulf.) Hook. &	Epiphytic to sometimes epigeal/terrestrial	All native trees and <i>Cibotium</i> <i>spp.</i>	All native trees & <i>Cibotium</i>

Grev.	in Leucobryum dominated ground cover (Hawai'i loa), This was in mesic-dry forest at 1,400ft elevation.	<i>Roystonea regia</i>	<i>Archontophoenix spp.</i>
		<i>Schinus terebinthifolius</i>	<i>Eucalyptus spp.</i>
			<i>Psidium spp.</i>
			<i>Schinus terebinthifolius</i>
			<i>Cinnamomum</i>
			<i>Aleurites moluccana</i>
			Bryophyte covered rocks
			<i>Elaeocarpus angustifolius</i>
<i>Adenophorus tripinnatifidus</i> Gaudich.	Epigeal to terrestrial in bryophyte dominated groundcover	<i>Metrosideros polymorpha</i>	On trees in bryophytes.
		<i>Syzygium sandwicense</i>	Often on ground
		<i>Cheirodendron trigynum</i>	
		<i>Cheirodendron platyphyllum</i>	
		<i>Kadua fosbergii</i>	
<i>Adenophorus pinnatifidus</i>	Epiphytic, Epigeic, & Lithophytic	All native trees	All native trees and exotics
		<i>Psidium cattleianum</i>	Sometimes on stream banks

2.4.4 Bryophytes:

All *Adenophorus* seen were associated with bryophytes, or at least were rooted in them and both frequency and abundance increased with bryophyte cover. While I did not test for correlations between specific bryophyte species and *Adenophorus* presence/abundance, the

NMDS and my observations suggest that it may be more or less correlated to the physical attributes of bryophyte species (i.e., dense acrocarpus cushions of *Leucobryum* and *Syrrhopodon* vs. loosely congested taxa like *Bazzania* and *Herbertus*). The only species of *Adenophorus* that was noted to not grow in dense bryophyte communities (less than an inch thick) was *Adenophorus oahuensis*, which were always found in conspicuously thin mats of liverworts in the Jungermanniaceae and Lejeuneaceae as well as the moss *Macromitrium*.

The specific roles of bryophytes for *Adenophorus* are not known, but the gametophytes of these ferns are often found nested within epiphytic bryophyte communities, especially within *Odontoschisma*, *Bazzania*, and *Syrrhopodon* (pers. obs.). In a study by McCarthy (2007), she found that bryophytes may be positively selecting for epiphytic fern gametophytes by the accumulation of humus/canopy soil, the hindrance of bacteria and fungi, retention of water, and the physical matrix to which indeterminate epiphytic gametophytes use adhere themselves to. Her study also showed that epiphytic and terrestrial fern species grew similarly on epiphytic soils, but the addition of bryophytes selectively favored epiphytic fern species due to potential allelopathic effects. A study by Harrington & Watts (2021) in a Costa Rican Lowland Forest showed evidence that moss and other bryophytes facilitate epiphytic fern growth but as the moss becomes taller and more dense, the ferns become negatively impacted. By contrast, a study in Japan by Mizuno et al. (2015) on the fern *Lepisorus thunbergianus* showed that these epiphytic ferns favored areas of tall moss in desiccated urban areas due to retained moisture for the gametophytes, but fertilization seemed to be hindered possibly due to being outcompeted for resources by moss. The ferns were more or less successful in the tall moss patches if the gametophytes were able to mature. In the same study, it was noted that areas with mostly leafy liverworts were less favorable due to the higher desiccation tolerance of these plants. More

investigation needs to be done to determine the roles of different bryophytes and their effect on the gametophytes and sporophytes of *Adenophorus* species but based on my observations it seems that the gametophytes get established on the edges of thick bryophyte mats of species such as *Leucobryum* and *Herbertus* and infiltrate inward by indeterminate growth. Many epiphytic ferns in Hawai'i show proliferous mats of gametophytes that often have gemmae. These gemmae-producing mats help the ferns to compete with bryophytes in dense epiphytic bryophyte communities (Dassler, 1995).

On some of the ridgelines I monitored, such as Ka'au and Wiliwilinui, there were many dying trees with scarcely any bark left. These formerly bryophyte rich trees are not being replaced by native canopy and are being replaced by trees such as *Psidium cattleianum*, which seem to have a poor bark substrate for bryophyte colonization (unless from the ground up in wet forest). Bryophyte colonization on suitable habitats is still a relatively slow process and in areas where there is intact forest, these communities may take decades to recover (Rehm et al., 2019).

Bryophytes in general are good indicators of microclimates and an in-depth study of their relationships to *Adenophorus* and similar ferns would be important to gain insight on their conservation. As epiphytic studies in Hawai'i and other tropical forests become more common, the facilitative role of bryophytes and their ecological importance may be better understood in the field.

Figure 1: Percent of trees with *Adenophorus* versus total number of trees at each elevation category. The elevation categories are: 1 = 400 to 500m, 2 = 501m to 600m, 3 = 601m to 700m, & 4 = 701m to 800m.

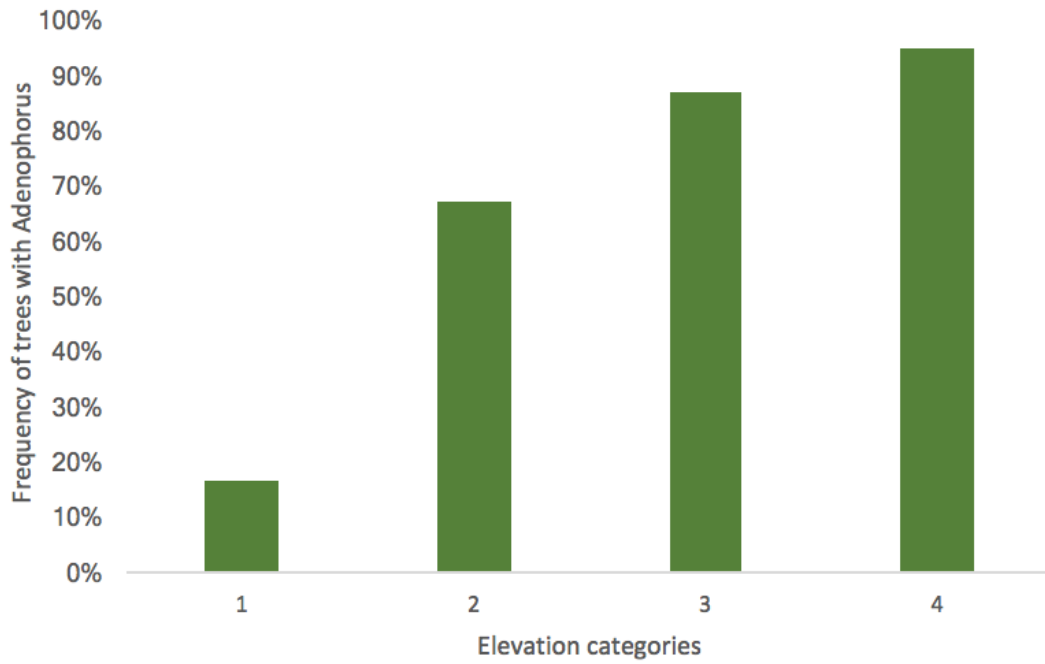


Figure 2: *Adenophorus* abundance (Count per tree) as a function of bryophyte cover

Adenophorus Count vs. Bryophyte % Cover

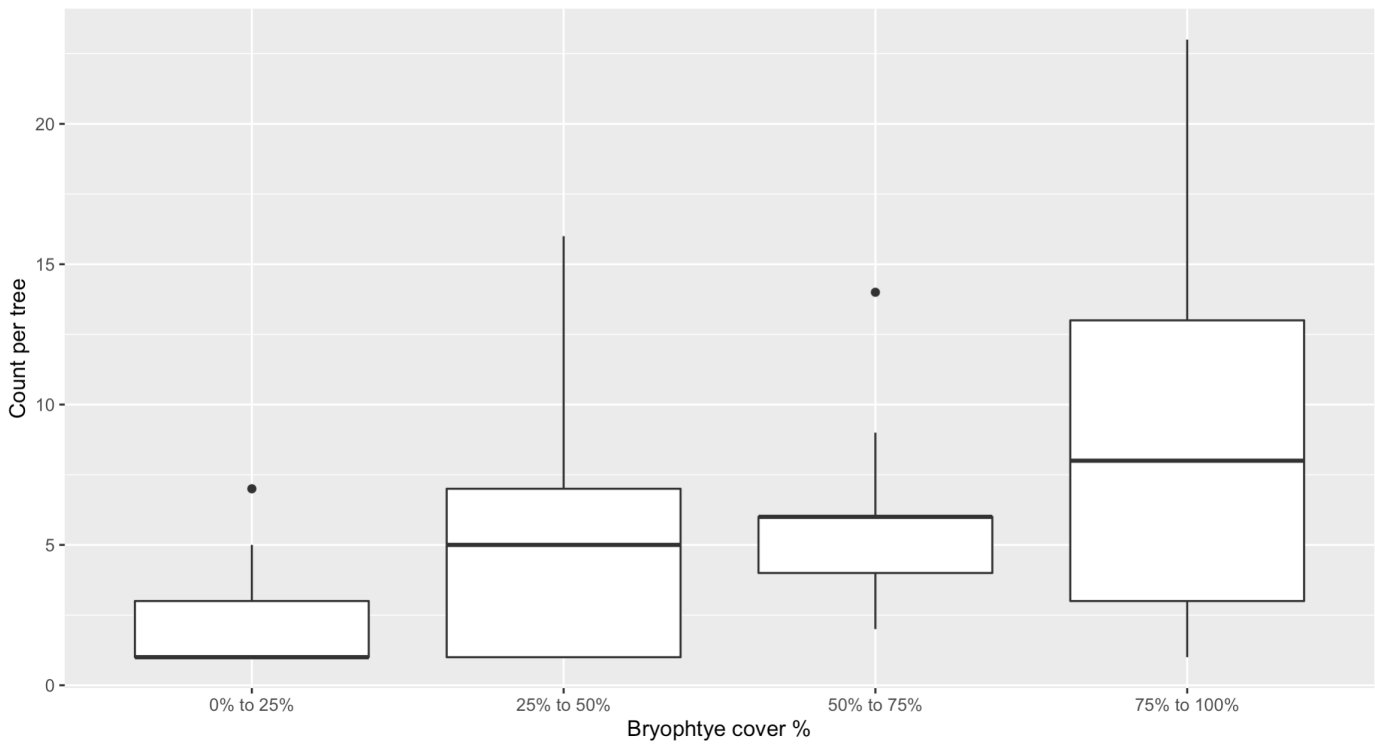


Figure 3: Frequency of *Adenophorus* presence as a function of bryophyte cover.

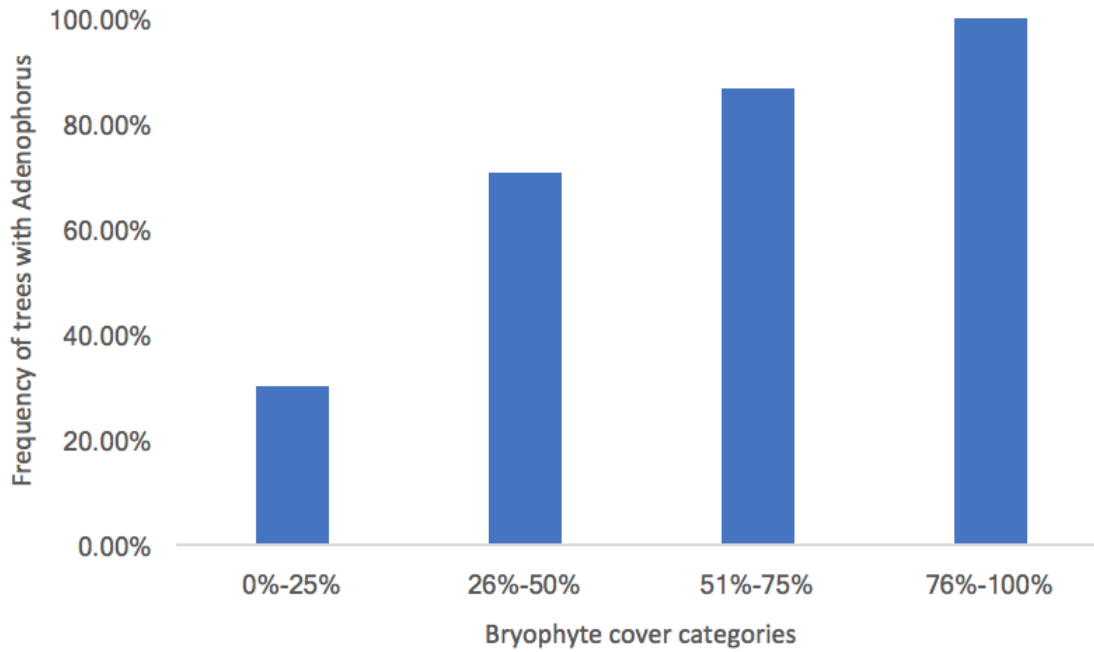


Fig. 4: Elevational distribution of *Adenophorus* species

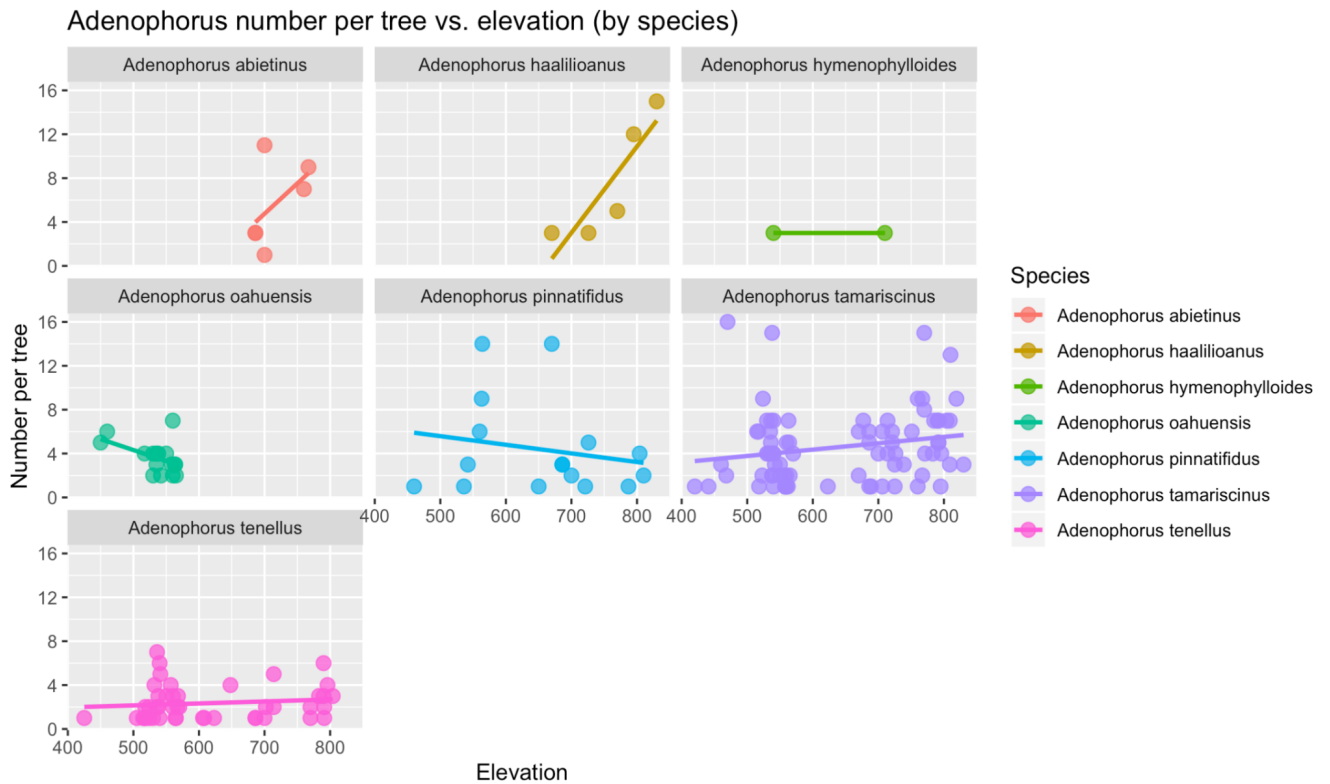
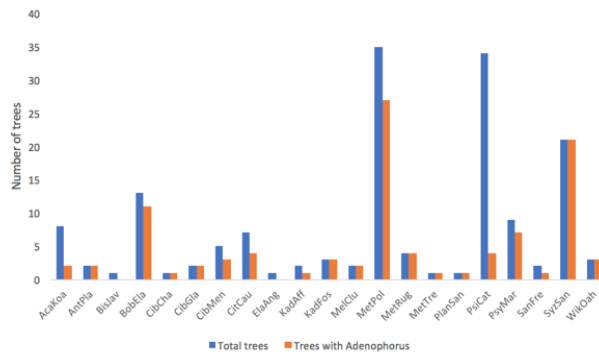


Fig. 5: *Adenophorus* Distribution along (a) ridge transects and (b) summit transects in the Ko‘olau mountains, O‘ahu. Blue bars represent the total number of trees sampled per host tree species. Orange represents the number of trees with *Adenophorus*. The abbreviations for the host taxa are as follows: AcaKoa = *Acacia koa*, AntPla = *Antidesma platyphyllum*, BisJav = *Bischofia javanica*, BobEla = *Bobea elatior*, CibCha = *Cibotium chamissoi*, CibGla = *Cibotium glaucum*, CibMen = *Cibotium menziesii*, CitCau = *Citharexylum caudatum*, ElaAng = *Elaeocarpus angustifolius*, KadAff = *Kadua affinis*, KadFos = *Kadua fosbergii*, MelClu = *Melicope clusiifolia*, MetPol = *Metrosideros polymorpha*, MetRug = *Metrosideros rugosa*, MetTre = *Metrosideros tremuloides*, PlanSan = *Planchonella sandwicensis*, PsiCat = *Psidium cattleianum*, PsyMar = *Psychotria mariniana*, SanFre = *Santalum freycinetianum*, SyzSan = *Syzygium sandwicense*, WikOah = *Wikstroemia oahuensis*.

a)



b)

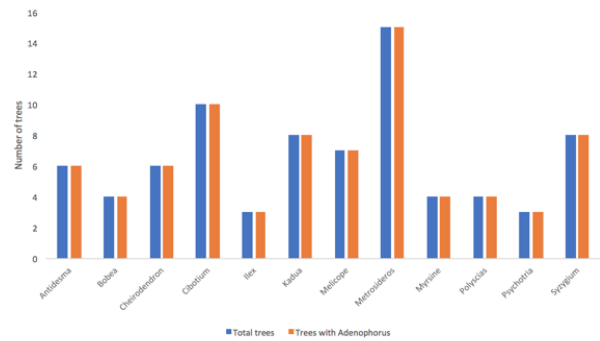


Figure 6: Distribution of *Adenophorus* species along (a) ridge transects and (b) summit transects (right) in the Ko‘olau mountains, O‘ahu. Blue bars represent the total number of trees sampled per host tree species. Orange represents the number of trees with *Adenophorus*. The abbreviations for the genera in column (a) are the same as in the preceding figure (Fig. 4)

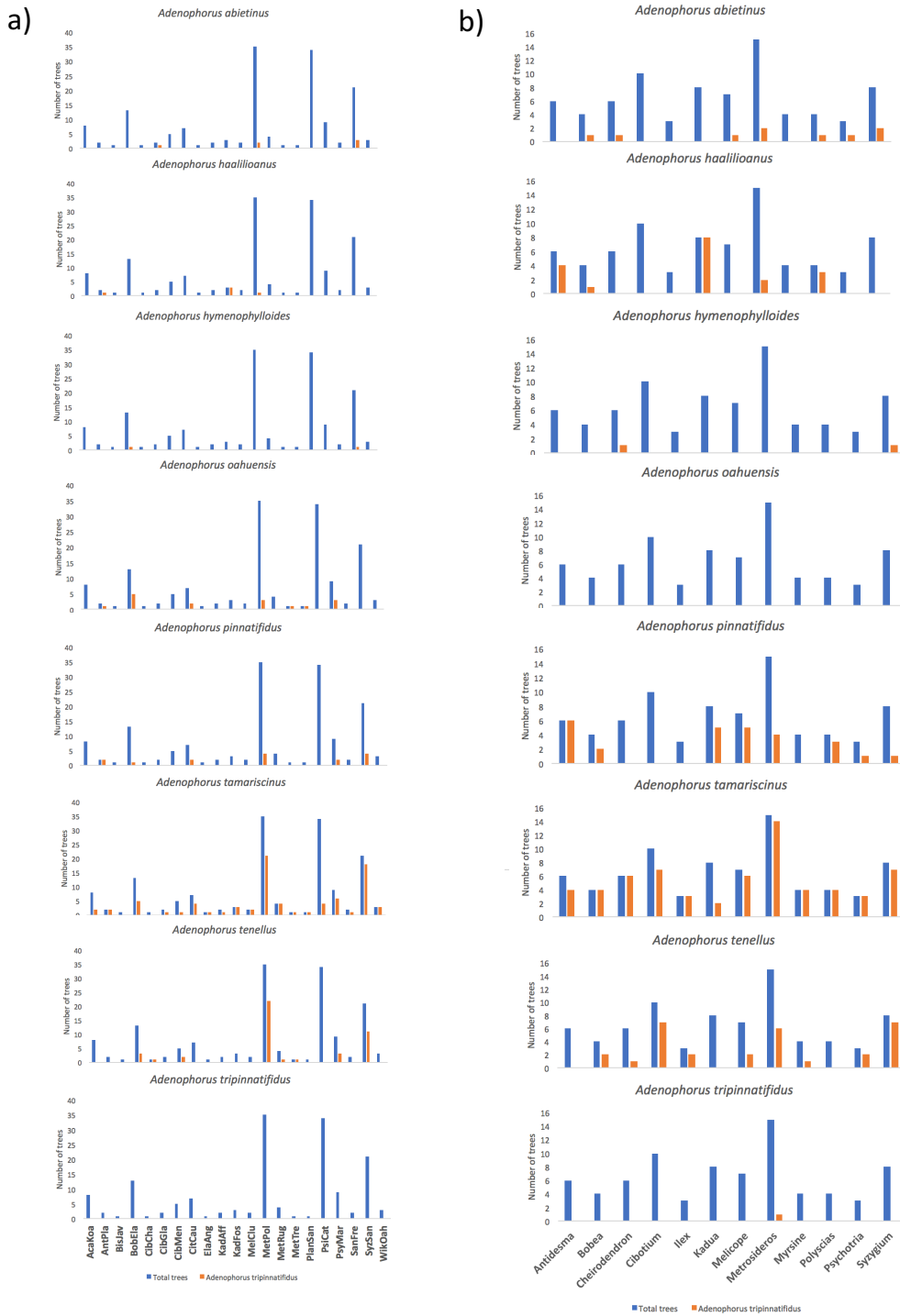
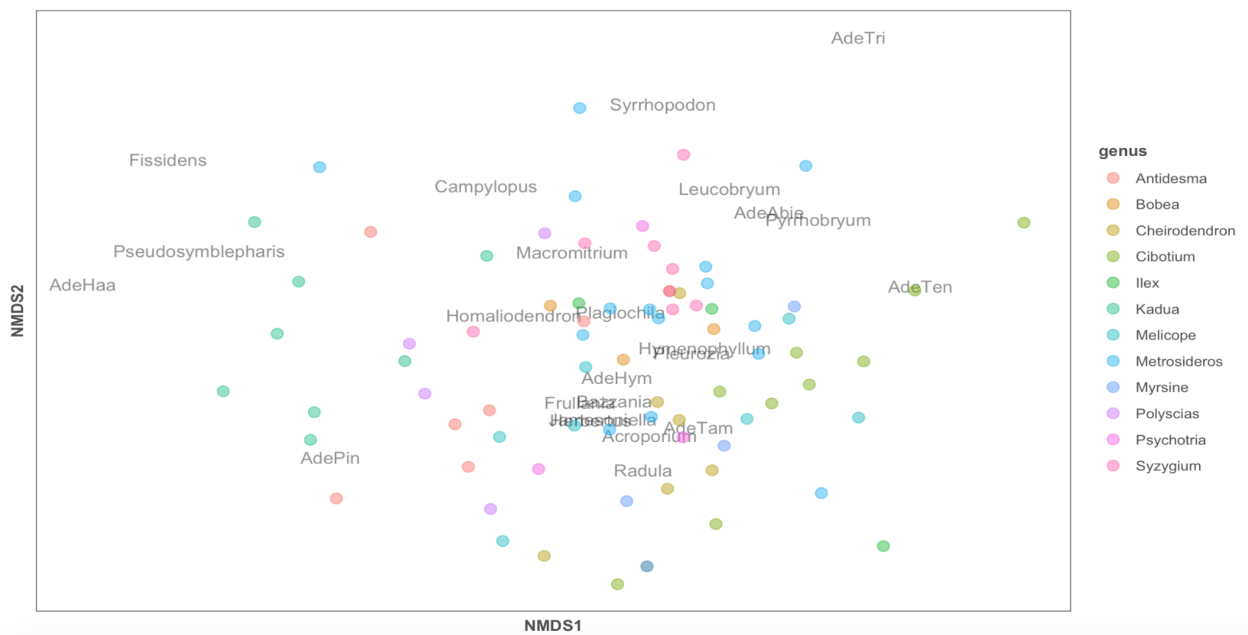


Figure 7: Nonmetric Multidimensional Scaling of epiphytes, their host trees and the presence of *Adenophorus* in a) ridge and b) summit transects on Oahu.

a)



b)



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Chapter 3: Observations, Natural History, and Conservation

3.1: Introduction

The data gathered from my survey serves as a snapshot of the distribution and some ecological aspects of the genus *Adenophorus*. However, the wider range of observations that I have collected over the years serves to fill in gaps that reveal important aspects about the distribution of various species that were not captured in my study. For instance, several species were rare along my transects but I have observed that they have much broader distribution and should not necessarily be viewed as rare or overlooked. In this chapter, I attempt to outline information for each species pertaining to the distribution and any relevant ecological interactions (habit of plant, community assembly, sympatry, etc.) that may serve useful to those seeking to better understand where to look for these taxa and how to best preserve them. A section dedicated to gametophytes is added here to illustrate information that is key to understanding the requirements of the genus as well as a section on conservation actions for those interested in the preservation of these ferns. A word of caution, these observations are based on surveys I have conducted in certain areas of the Ko‘olau and Wai‘anae mountains and do not reflect the full scope of what can be seen in the field. More studies and observations are required to better understand these taxa.

3.2.1 *Adenophorus abietinus*:



A very delicate and diminutive fern, this taxon has considerable variability that may be or may not be a result of habitat influence. In dark, shaded locations (such as in wooded areas or lower in valleys) the shape of the fronds is ovate with a very thin lamina. As one moves towards more exposed localities, plants appear elongated (i.e., more lanceolate) and slightly more coriaceous in frond texture with spatulate pinnules, but the general dimensions of the plants fit the concept of *Adenophorus abietinus* according to Bishop (1974). The distinct differences between the two phenotypes as well as the uniformity within populations suggest the possibility that two distinct varieties could be recognized, but further studies of genetic and population structure need to be done to test the validity of this hypothesis. Bishop also states in his monograph that the lanceolate variant of *Adenophorus abietinus* is especially common in the southern Ko‘olau mountains but makes no mention of it being on other islands. It is interesting that he made no attempt to separate the two forms at least to a varietal status. The differences of the two extreme forms caused me to reexamine my herbarium specimens, look at the lectotype of *A. abietinus*, and make more field observations in places I have not frequented. One particularly interesting area is the ridge known as the “Mānoa middle” which gains elevation very fast. This

region contains both variants of *A. abietinus* and it became clear along this trail that the two varieties show substantially uniform populations despite canopy cover and sun exposure. The “typical form” (D.C. Eaton no.18, BISH) seems to be found more commonly at slightly lower elevations (600m) in wet forest and the lanceolate form becomes relatively common above 700 m. Plants of the typical form maintained broad fronds and long stipes as well as relatively uniformly narrow pinnules that have very large sori. The lanceolate form, when exposed to sunlight shows a tendency to have more broadly spatulate pinnules, coriaceous fronds, and a distinct bottle brush appearance. When in shade, these plants had narrower pinnules but maintained the spatulate shape as well as having softer textured fronds. It seems that elevation, rather than habitat type, separates the two populations but this may not be true in other parts of the Ko‘olau. Consistent with observations by L.E. Bishop and Daniel D. Palmer, many of the populations I came across were on *Syzygium sandwicense* but there seems to be no indication of host specificity. Around the Poamoho summit, many populations cover species of *Metrosideros*, *Psychotria*, *Polyscias*, and *Cibotium*.

A. abietinus is often found rooted in fairly dense mats of *Leucobryum*, *Bazzania*, *Acroporium*, *Herbertus*, and *Pyrrhobryum*. Filmy ferns are also associated, and all three species of Hawaiian *Hymenophyllum*, as well as *Adenophorus tamariscinus* and *tenellus*, can be found growing sympatrically. I have not yet found this species growing on non-native trees, but I presume it has the ability to do so, since other closely related species like *A. tamariscinus* have been found on just about any bryophyte-covered tree in wet forests.

3.2.2 *Adenophorus haalilioanus*:



This species is nearly confined to the Ko‘olau summit on O‘ahu but is also occasionally found as low as 1,800 ft (Kōnāhuanui trail & ‘Aiea ridge trail, pers. obs.). The small propagula produced by lateral roots form distinctive patches of plants in more thin bryophyte mats than that of the *Adenophorus* species with creeping rhizomes but colonies can be found in relatively thicker colonies (i.e., *Herbertus*, *Bazzania*, *Campylopus*). Portions of the individual stands of this species may be found spreading into nearly bare sections of bark, though a significant portion remains amongst nonvascular cryptogams. As far as host species, my observations agree with Palmer (2003) that many of the plants seen are on species of *Kadua*, although I have seen them on trees including *Metrosideros* spp., *Cheirodendron* spp., *Pritchardia* spp., and *Antidesma platyphyllum* (See Table 1.). This taxon seems to be absent from Mount Ka‘ala but is recorded from the island of Kaua‘i, so more extensive and systematic surveys may reveal small populations in portions of the Wai‘anae mountains where wet/cloud forests exist.

3.2.3 *Adenophorus hymenophylloides*:



On O‘ahu, *A. hymenophylloides* is found mainly in wet forests that receive frequent rainfall and cloud cover. The populations on O‘ahu are infrequent in the southern region of the Ko‘olau and become more abundant as you move north. Populations of this species tend to be found primarily in native forest on a variety of trees, although most plants I have observed are on *Syzygium sandwicense*, *Metrosideros polymorpha*, and *Metrosideros rugosa*. They exist on overhangs of branches of living and sometimes dead/dying trees which gives insight to the inspiration behind the native name “Palai huna” which roughly translates to “fern that hides”, often intermixed with *Adenophorus tenellus* and various bryophytes. One specimen was observed on a large *Cibotium* above the western rim of Ka‘au crater in Pālolo valley, and another on *Citharexylum caudatum* near the Ko‘olau summit in Mānoa, O‘ahu.

In my experience, the regions of Poamoho to Kaluanui have dense populations with plants sometimes reaching 18cm in length. As in Pālolo, these plants are always pendent, growing out of the crevices and sides of branches and seem to benefit (or at least tolerate) thicker cushions of bryophytes. Observations of passing cloud cover and rain showed that these hanging ferns accumulate drops of water and may also be benefitted by the hygroscopic bryophyte

communities these ferns are usually nested in. Since the root stock is often guarded from direct moisture, the roots of this species may serve as a mechanical support and nutrients derived/utilized by foliar absorption. Many specimens of *A. hymenophylloides* are covered in glandular trichomes, which although are secretory, may serve another purpose as to facilitate nutrient exchange, collect moisture, and/or to increase the boundary layer of moist air around the stomata. This attribute needs further study.

3.2.4 *Adenophorus oahuensis*:



Adenophorus oahuensis seems to be able to exist on a variety of trees but is frequently found on *Metrosideros*, *Bobea*, and *Psychotria* (pers. obs.). Table 2 lists various other species it can be found on, but since populations were very localized, I was not able to see it growing on its full range of hosts. It seems to be limited by moisture and the many ridge top forests that have now become popular trails are not able to sustain the former epiphytic communities that once thrived at lower elevations in leeward aspects. Even in areas where it is present, it will form colonies on some trees and will be virtually absent for a significant distance until you find another tree. Poamoho trail, located near Wahiawā, O‘ahu, is where I saw the most extensive contiguous population within a band of *Metrosideros polymorpha*.

This species occurs with a very predictable community of bryophytes, mainly of the genera *Macromitrium*, *Holomotrium*, *Frullania*, *Anastrophyllum*, *Jamesoniella*, and *Odontoschisma*. These cryptogamic species produce thin mats of bryophytes that cover trees at lower elevation wet/mesic forest, rather than the larger acrocarpous species such as *Leucobryum* and *Acroporium*.

3.2.5 *Adenophorus pinnatifidus*:



This species exemplifies an interesting distribution as well. In some localities, it is just as abundant as the ever-present *A. tamariscinus* and *A. tenellus* but in many apparently similar areas, it is infrequent or absent. I found gametophytes within bryophyte mats that surround these colonies, but I could not confirm if these were of *Adenophorus pinnatifidus*. This species is also found abundantly on rocks in stream areas of the central Ko‘olau mountains. These semi lithophytic colonies are well rooted in built up humus collected by bryophyte mats. The varieties *pinnatifidus* and *rockii*, as well as intermediates, are often found growing together, which questions the validity of distinct varieties or just a hyper variable plant. I did not notice any strong correlations between habitat and variety type but there may be a reason for the expression of different leaf forms. Often, one may see a branch with the two varieties and a

range of intermediates mixed in the colonies. I agree with Palmer that the two extreme forms are so striking that they should be kept as separate varieties. More research in this area is needed, especially genetics to verify the relationship of these extreme forms.

3.2.6 *Adenophorus tamariscinus*:



By far the most common and variable species, this taxon showcases a wide array of phenotypes in various environments, often appearing as swarms of conspicuously different forms that form intermixing populations without clear delineations. Most plants are as pictured above, with a very uniform bipinnate frond, but other plants can look elongated in frond shape with conspicuously spaced pinnules and occasionally there are plants with broad fronds that have pinnae that rarely contract below. These forms often have nearly tripinnatifid pinnules that approach the overall appearance of *Adenophorus tripinnatifidus* but maintain clearly spatulate pinnules as well as a thick, short-creeping rhizome. These plants may represent a hybridization between the two species, but genetic and spore analyses need to be done to test this hypothesis. Such plants are often found in very humid forests, wet forests, and can exist near gulch bottoms at 1,400 ft (~ 430 m) to the summit ridge in cloud forest and are sympatric with the typical forms of *Adenophorus tamariscinus*. Plants are found in a wide array of environments, and part of its

success may be due to its variability as a species. Like other species of *Adenophorus*, these plants can be found on the ground or in trees with other epiphytes. An interesting observation on *Archontophoenix purpurea* at ‘Aihualama falls (Lyon Arboretum) showed a single patch of *Adenophorus tamariscinus* that was nested nearly 1m above ground on the bole of the trunk and within a patch of leafy liverworts (Lejeuneaceae, Frullaniaceae, and Lepidoziaceae).

In regions of sufficient humidity and moisture availability, this species often grows on the ground (a very common sight at the Ko‘olau summit and on mount Ka‘ala) and in one particular area on Hawai‘i Loa ridge, populations are growing on the side of a cliff in *Leucobryum*, *Macromitrium*, *Pyrrhobryum*, and *Crepidomanes* substrate. What is very interesting about this locality is that the surrounding forest is in a monoculture of *Psidium cattleianum* as well as within an area that receives low amounts of precipitation. The native name for the species, “Wahine noho mauna” translates to “Woman who lives in the mountain” and is testament to the montane, forested habit of these plants.

3.2.7 *Adenophorus tenellus*:



This is a very common species that is found from mesic to wet forests, usually growing in the vicinity of *Adenophorus tamariscinus*. As with *A. hymenophylloides*, this taxon is usually

found on the sides of trees or underhangs of branches, as well as crevices. It can be found growing as large, conspicuous colonies that sometimes cover large portions of trees. Typically, these plants are associated with *Leucobryum-Hymenophyllum* communities or within *Acroporium fuscoflavum*. A very interesting habit of this species is the tendency to grow deeply nested within bryophyte communities, with the distal half to third of the frond exposed. It seems that patches of *A. tenellus* are able to colonize trees and form extensive colonies. Other species such as *A. tamariscinus* and *A. hymenophylloides* are often seen growing intermixed within the patches, as well as other grammitid ferns (mainly *Oreogrammitis* and *Stenogrammitis*).

3.2.8 *Adenophorus tripinnatifidus*:



My work with the Division of Forestry and Wildlife on O‘ahu allowed me to work in and around transects of the Ka‘ala Natural Area Reserve to control invasive species such as *Hedychium gardnerianum*, *Psidium cattleianum*, and *Sphagnum palustre*. In these surveys, it became apparent that this locality contains several large contiguous populations of *Adenophorus tripinnatifidus*. Interestingly along the boardwalk, this taxon is not present although it has been noted from that immediate area (pers. comm. Susan Ching-Harbin). The summit of Kōnāhuanui is the only place I have seen an accessible population on my surveys in the Ko‘olau mountains. The plants in that locality are more often bipinnate than those of mount Ka‘ala and generally are

smaller in frond size, but both populations seem to be found in similar habitats: the understory of bryophyte covered trees as well as epiphytically. The rhizome of these plants creeps along the surface and will go fairly deep within hepatics such as (but not limited to) *Bazzania sandvicensis* (Gottsche ex Steph.) Steph. and *Plagiochila deflexa* Mont. (pers. obs.). Epiphytic populations have been observed to exist in communities mainly consisting of *Leucobryum*, *Bazzania*, and *Herbertus*.

3.3 Gametophytes:

Gametophytes, the initial growth form of ferns, are necessary for the long-term persistence of the sporophytes. The ecology of these organisms involves periods of desiccation due to the nature of the epiphytic environment. Desiccation tolerance seems to be relatively high in most epiphytic fern gametophytes, but the ability to recover from near total water loss is influenced by the rate of desiccation (Watkins et al., 2007). Another aspect of gametophyte establishment is the presence or absence of canopy soil. The canopy soil matrix, a histosol (>50% organic), is often shallow and concentrated in the interior of the crown (Watkins & Cardelus, 2012), but I have also observed that it can also accumulate within the root systems of vascular plants as well as in colonies of bryophytes.

Bryophytes are also important for the regeneration of woody trees that epiphytes utilize by facilitating recruitment on decaying logs and rocks, especially in areas that have high competition in soil substrates. (Rehm et al., 2019). On certain trails (i.e., Kōnāhuanui), Liverworts such as *Frullania hypoleuca*, *Herbertus gracilis*, and *Tropholejeunea sandvicensis* were seen essentially creeping up trunks of small *Psidium cattleianum* from the ground up and on trunk bases with these well developed communities, patches of *Adenophorus pinnatifidus* can

be seen colonizing these areas. The habitat of this area is wet forest at around 1,400 ft. elevation with many patches of *Adenophorus* found along the trail in trees as well on decaying logs covered in *Leucobryum*, *Pyrrhobryum*, and *Bazzania* communities.

Bryophytes seem to provide important substrates for plants that grow on rocks as well. The most common epipetric species is *Adenophorus pinnatifidus* (technically “pseudo-epipetric” due to plants not growing out of the rocky substrate, but rather are rooted in organic matter that collects on rocks). Where you do see species such as *A. tenellus*, *A. tamariscinus*, and *A. oahuensis* they are always growing amongst bryophytes or at least on the margins of bryophyte colonies.. The latter species is one I have not seen on rocks but there is a specimen from the herbarium of the Smithsonian institution of *A. oahuensis* that was collected by Otto Degener on “moss covered rocks in dry lantana region”, Waimalu, O‘ahu (Degener no. 10,165, US).

It would be worthwhile to test gametophyte growth amongst various species/communities of bryophytes, mimicking epiphytic substrate as best as possible. So far, my attempts to cultivate certain bryophytes such as *Leucobryum* reveal that standard potting mixes with slow release fertilizers can burn certain taxa but others seem to be enhanced by it. Climatic factors such as humidity and frequency of wet vs. dry are also important because certain species tend to decay and become chlorotic with overhead watering in hot, humid areas of greenhouses but do much better in cooler and misted settings. Terrariums make a great contribution to the study of how to cultivate these bryophytes but again, the greenhouse effect of closed terrariums facilitates rot and fungal explosions where certain species (i.e., *Pyrrhobryum*, *Distichophyllum*, *Leucobryum*, and *Pleurozia*) turn chlorotic and succumb to pathogens or they decay for no obvious reason. Terrariums in rooms with appropriate temperature have been observed to fare much better, so species adapted to high elevation show signs of requiring constant cool temperatures to persist.

When these bryophytes are better cultivated, it may provide a way to enhance the cultivation of the gametophyte stage of *Adenophorus* (especially wild collected ones) since the gametophytes are always found amongst bryophyte communities. What needs to be done for this to happen, however, is understanding nutrient input and cycling provided by these nonvascular plants and to replicate such aspects in sterile settings or in reproducible manners.

For many epiphytic ferns which live in the crowns of trees, leaf litter poses a problem by disrupting gametophyte establishment in canopy soil. Typically, *Adenophorus* species are found growing on limbs, axils of branches, and on vertical sections of branches as well as trunk. There are few species that can grow on or under leaf litter, and disturbance is necessary to expose the underlying mineral soil. Species in these habitats need to move through their life cycle quickly before litter deposition or competing plants replace them. The canopy, in contrast, may be less prone to disturbance (Watkins et al. 2007b), and such stability would facilitate long-lived gametophytes that can reach larger sizes (Watkins & Cardelus 2012). Some of the epiphytic gametophytes of *Lomariopsis vestita* and *Vittaria lineata*, initially marked in 2000, were found virtually unchanged roughly a decade later. (Watkins & Cardelus 2012). Walp (1951) also found that if fertilization was prevented, fern gametophytes can be quite long-lived; he reported that gametophyte longevity of 12 years has been reported under ideal lab culture conditions.

The establishment of *Adenophorus* gametophytes is limited by the fact that members of the genus possess green spores (Bishop, 1986). Green spores are associated with a suite of specialized functional traits, including rapid germination and short viability (Lloyd & Klekowski 1970); for these reasons, green spores may have facilitated the radiation of ancestors of *Adenophorus*, and related ferns, into epiphytic habitats. Data by Sundue et al. (2015) indicates this faster rate of diversification is not restricted to grammitids but instead a feature of green-

spored taxa. Gametophytes of *Adenophorus* and other epiphytic ferns often have gametophyte stages with indeterminate growth and are often strap-like in appearance (Bishop, 1986; Stokey & Atkinson, 1958; Tieman, 1981) and Successful epiphytic species would have required modifications in the gametophyte generation to include indeterminate growth, extreme stress tolerance, and an outcrossing breeding system during evolutionary processes (Watkins & Cardelus 2012). To assess how these ferns will fare in a changing environment, it is important to conduct research on the gametophyte stage.

3.4 Conservation recommendations

Conservation of epiphytic ferns is an understudied topic, and this is especially true of the grammitid group. One species, *Adenophorus periens*, has been extirpated from all main islands besides a single known population on Kauaʻi (pers. com. Scott Heintzman, Kauaʻi Plant Extinction Prevention Program). *Adenophorus oahuensis* appears to be experiencing a significant decline based on previous reports in the literature (Hillebrand, 1880), examination of herbarium specimens, my personal field observations, and personal communication with Daniel Palmer, as well as with other botanists. This species should also be listed as threatened due to the species being restricted to the Koʻolau mountains of Oʻahu. *Adenophorus haalilioanus* is another potential candidate to be listed as threatened due to the populations existing only along the Koʻolau summit region as well as in similar forest types on Kauaʻi. For Oʻahu, *Adenophorus tripinnatifidus* has been extirpated from much of the Koʻolau mountains based on a comparison of herbarium specimens, personal communication with Daniel Palmer, and from my observations in many parts of the Koʻolau mountains. This taxon is now mainly found on mount Kaʻala in bryophyte rich, undisturbed cloud forests. In the past it had been known from the entire length of

the Ko‘olau mountains and from several peaks in the Wai‘anae range. Based on this study and my long-term observations, I suggest several methods that may help with the conservation of *Adenophorus* and other epiphytic ferns. One is the need to establish a diverse canopy forest that can regenerate and provide substrate for epiphytic bryophytes to fill in. Along with these bryophytes, immigration and establishment of *Adenophorus* as well as other epiphytic ferns will likely take place, as long as they are proximal to existing populations. The existing populations of summit forest need special attention due to the lack of regeneration of trees and shrubs in many areas, and this lack of canopy has most likely affected remnant trees with epiphytic canopies. The importance of intact, closed canopy forests has been shown to be critical in the preservation of highly diverse epiphytic communities, especially for hygrophilous organisms such as fern gametophytes and bryophytes due to favorable microclimates (Dubuisson et al., 2009; Sporn et al., 2010) and such areas in Hawai‘i need to be protected and monitored, especially in areas of high diversity (Mehltreter et al., 2010). At the summit, even invasive species like *Citharexylum caudatum* and *Clidemia hirta* can have *Adenophorus* growing on them. Nevertheless, I have been visiting these areas year after year and have found a gradual decline of bryophytes and ferns. One factor that is very apparent is the invasion of grasses, such as *Axonopus compressus* which form mats along the summit ridges in areas forming “meadows”. These grasslands do not appear to be conducive to the regeneration of trees. In contrast, in areas of bryophytes, decaying wood, and soil, one can find that angiosperms and pteridophytes are able to take a hold and contribute to the development of wooded areas. This interaction of grass and the cloud forest zone was noted by Frank E. Egler (1939) in his paper “Vegetation zones of Hawai‘i”. He also discussed the utmost importance of these dwarf, hygrophilous forests as very important zones for the capture and conservation of water.

I found that *Metrosideros polymorpha*, *Bobea elatior* and *Syzygium sandwicense* support interestingly high diversity of *Adenophorus* and other epiphytes (Figure 5), especially at lower mesic-wet elevations. These species should be looked into as potential focal taxa to utilize in long term restoration projects to establish a diverse native epiphyte community. Along the cloud forest zone, almost every surface gets covered in bryophyte and epiphytic communities, and it is here that the diversity of epiphytes is highest.

Ex situ conservation is a tool used for many rare fern taxa across the world (Mehltreter et al., 2010), but the cultivation of *Adenophorus* is fairly difficult due to short lived spores, slow growing gametophytes, and gaps in knowledge on rearing sporophytes. Terraria and high elevation greenhouses, or climate-controlled greenhouses may be ways to at least culture plants if rare populations need to be relocated. The overall desiccation intolerance of the spores means that these ferns must germinate quickly and establish the gametophytes in a relatively short period of time (Bishop, 1986) which hinders the ability to collect and store spore packets for extended periods of time. Even when germination is successful, these plants are slow growing and growing from spores may take decades to create a viable population for reintroduction into the wild. Gametophytes have been successfully reared by Bishop (1986) and by researchers at Kaua‘i Community College via the National Tropical Botanical Garden under the supervision of Ruth Aguraijua. Gametophytes of other Grammitid ferns have been cultivated in the past and these gametophytes have persisted for over 4 years to reach the sexual stage (Stokey & Atkinson, 1958). The difficulty of cultivation highlights the importance of conserving remaining populations of *Adenophorus*.

In general, island ecosystems harbor a disproportionately large amount of species diversity when viewed on a global scale (Kier et al., 2009; Pouteau et al., 2016; Werden et al.,

2020). For fern species on islands, tropical montane cloud forests hold a higher proportion of species richness, whereas montane dry and lowland dry forests hold significantly fewer taxa (Pouteau et al., 2016). For most high islands, these tropical montane cloud forests extend from 2,000m to nearly 4,000m but in Hawai‘i these forests can exist from 800m to 1,000m due to microclimate effects (Loop & Giambelluca 1998). Loop & Giambelluca (1998) discuss various impacts that will likely affect these tropical montane cloud forests such as shifts in precipitation, changes in tradewind inversion layer, and species temperature tolerance zones (due to warmer average temperatures). The authors also highlight that invasive species will most likely be favored and such invasions into these highly diverse montane ecosystems will cause dramatic shifts in vegetation communities, often deleterious ones. These changes are not only found in island ecosystems, but in other tropical forests as well. Climate shifts to warmer and drier patterns have been noted to decrease species richness in communities as well as cause mortality in epiphytic vascular and non-vascular taxa (Gradstein, 2008). Communities of *Adenophorus*, as well as other epiphytic plants, may play a role in the water capturing ability of fog and cloud drip and the slowing down of rain via gravitation as it passes through the canopy (Stanton et al. 2014; Veneklaas, 1990). Biodiversity in itself is very important to ecosystem services as well as the longevity of species and their continued interaction and evolution (Brown, 1998; Godbold & Sloan, 2009). In the United States, Hawai‘i holds roughly 45% of the federally threatened and endangered species across all taxa, with roughly 25% of the federally listed plant species in Hawai‘i having less than 50 wild individuals, ranking Hawai‘i as one of the top biodiversity hotspots (Werden et al., 2020). Although only one species of *Adenophorus*, *Adenophorus periens*, is presumed extinct (with the exception of Kaua‘i), this study reveals that declining trends, especially for O‘ahu, of certain taxa are evident and these species may share the same fate

as the former species mentioned. If we do not pay attention to these declines, then we will undoubtedly continue to suffer species loss before we notice it.

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