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ORIGINAL PAPER

# Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest

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**Abstract** Invasive mammals can fundamentally alter native plant communities, especially on isolated islands where plants evolved without them. The globally invasive feral pig (*Sus scrofa*) can be particularly destructive to native plant communities. Tree ferns are an important understory component in many forests facilitating the establishment of a variety of species. However, the extent and effects of feral pig damage to tree ferns, and associated impacts on plant community regeneration, are largely unknown. We quantified the effect that feral pig damage has on tree fern growth, survival, and epiphytic woody seedling abundance over 1 year on 438 randomly selected tree ferns of three endemic species (*Cibotium chamissoi*, *Cibotium glaucum*, and *Cibotium menziesii*) in a Hawaiian montane wet forest with high tree fern and feral pig densities. Across all tree fern species, feral pigs damaged 13 % of individuals over 1 year. Compared with undamaged tree ferns, moderately- to heavily-damaged individuals had decreases of 4 to 27 % in trunk length increment and lost tenfold more fronds. Tree fern angle (standing, leaning, prone, or semi-prone) and woody seedling abundance co-varied with feral pig damage. Specifically, damaged tree ferns were more often prone or semi-prone and supported more seedlings, but also had annual mortality up to 34 % higher than undamaged tree ferns. Overall, feral pig damage had substantial negative effects on tree ferns by reducing growth and survival. Given the importance of tree ferns as regeneration sites for a variety of native plants, feral pig damage to tree ferns will likely alter future forest composition and structure. Specifically, feral pig damage to tree ferns reduces potential establishment sites for species that either regenerate preferentially as epiphytes or are currently restricted to epiphytic establishment due to ground rooting by feral pigs.

**Keywords** *Cibotium* spp. · Habitat disturbance · Pacific Islands · Permanent plots · Tropical forest invasions · Feral pigs (*Sus scrofa* L.) · Woody seedling abundance

## Introduction

Invasive species can fundamentally alter ecosystems in three ways: using resources differently than native

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biota, affecting trophic interactions, and modifying disturbance regimes (Vitousek 1990). Invasive mammals can do all three of these simultaneously, and thus have the potential to strongly impact ecological processes at population, community, and ecosystem levels (Spear and Chown 2009; Nuñez et al. 2010). Island ecosystems that evolved without native mammalian herbivores may suffer particularly severe impacts (Spear and Chown 2009), and some of these ecosystems do not recover even after nonnative ungulate removal (Coomes et al. 2003; Nuñez et al. 2010). Thus, research on the influences of invasive mammals in ecosystems globally, but particularly on islands, is essential to ensure land managers have adequate, science-based information to develop effective management prescriptions for the long-term maintenance of biodiversity and ecosystem function.

Feral pigs (*Sus scrofa* L.; wild boar in their native ranges) are one of the most widespread and potentially destructive invasive mammals, threatening native ecosystems globally by altering community structure and ecosystem function throughout their introduced ranges (Spear and Chown 2009; Barrios-Garcia and Ballari 2012). Rooting, trampling, and browsing by feral pigs affect plant and animal diversity, soil properties, and water quality and can facilitate the spread of other invasive species (Hone 2002; Spear and Chown 2009; Barrios-Garcia and Ballari 2012). Even within their native ranges, wild boars may substantially damage vegetation when their densities become high due to lack of predators (Ickes et al. 2005). Despite increasing recognition of the destructive potential of feral pigs (Nuñez et al. 2010), critical knowledge gaps remain in understanding the long-term effects of damage to vegetation, particularly in tropical forests and on islands (Barrios-Garcia and Ballari 2012).

Tree ferns (order: Cyatheales) are a major understory component of many forests globally (Tropicos.org). Tree fern trunks are also important for forest regeneration because they facilitate epiphytic establishment of woody plants (Bellingham and Richardson 2006; Gaxiola et al. 2008; Inman-Narahari et al. 2013). Woody seedlings may grow or survive better on tree ferns than other substrates (Bellingham and Richardson 2006), especially where ungulate rooting and grubbing prevent seedling establishment in mineral soil (Hone 2002; Cole et al. 2012). However, feral pigs bore into tree fern trunks to consume the starchy inner pith, resulting in substantial damage (Giffin 1978; Thomson and Challies 1988) that may also reduce woody seedling abundance and diversity.

The objective of this study was to determine the extent of feral pig damage and its effects on the growth and survival of endemic tree ferns (*Cibotium* spp.) and woody (non-tree fern) seedling abundance in Hawaiian forest where both tree fern and feral pig densities are high. In Hawai'i, feral pigs are likely a hybrid of Polynesian (*Sus scrofa vittatus*) and European (*Sus scrofa scrofa*) introductions (Nogueira-Filho et al. 2009). In Hawaiian wet forest, tree ferns comprise both a large proportion of forest basal area (Drake and Mueller-Dombois 1993; Kellner and Asner 2009) and up to 50–80 % of feral pig diet (Giffin 1978). Despite obvious damage to native vegetation (Nogueira-Filho et al. 2009; Cole et al. 2012), feral pigs are ubiquitous in Hawaiian ecosystems because management is both extremely costly (approximately $450,000/year in Hawai'i's three national parks; Pimentel et al. 2000) and often complicated by the prominence of feral pigs as a cultural, food, and recreational resource (O'Brien 1987; Maguire 2004). In this study, we concentrate exclusively on the ecological impacts of feral pigs, while fully recognizing that socio-economic aspects may be equally as important in defining management goals.

We tested the hypothesis that feral pig damage would decrease tree fern survival, frond and trunk growth, and epiphytic woody seedling abundance. To quantify feral pig damage, we developed a standardized damage index, which has been noted as a particular need for feral pig studies (Campbell and Long 2009). We also hypothesized that feral pigs would affect woody seedling establishment on tree ferns by both consuming tree ferns trunks (thereby decreasing area for seedlings to establish) and by knocking over trunks (thereby increasing the horizontal surface area available for seedlings). To address these hypotheses, we explored the relationships between feral pig damage, tree fern growth angle (standing, leaning, semi-prone, or prone), and native woody seedling abundance on tree fern trunks. The results of this study provide valuable information about how feral pigs affect forest ecosystems, particularly where tree ferns are a dominant component.

## Methods

### Study site

We conducted this study in the Laupāhoehoe Forest Dynamics Plot of the Hawai'i Permanent Plot Network (HIPPNET; www.hippnet.hawaii.edu) in the Hawai'i Experimental Tropical Forest on the Island of Hawai'i (19° 55′ N, 155° 17′). The HIPPNET is part of the Smithsonian Tropical Research Institute Center for Tropical Forest Science plot network (www.ctfs.si.edu). The Laupāhoehoe Forest Dynamics Plot is a 4 ha permanent plot located at 1,200 m elevation in subtropical lower-montane wet forest (Holdridge 1947) with a mean annual rainfall of 3,400 mm (Giambelluca et al. 2013) and a mean annual temperature of 16 °C (T. Giambelluca, *unpub. data*). Slopes average 30° (±SE 0.41°; range 0°–72°) and the overall aspect is northeast with substantial micro-topographic variation (R. Ostertag, *unpub. data*). Substrate is 4 to 14 k years old with soils developed from weathered volcanic ash classified as moderate to well-drained hydrous, ferrihydritic, isothermic Acrudoxic Hydrudands in the Akaka series (websoilsurvey.nrcs.usda.gov). The canopy is dominated by *Metrosideros polymorpha* (H. Lév.) H. St. John and *Acacia koa* A. Gray and the midstory is dominated by *Cheirodendron trigynum* (Gaudich.) A. Heller and *Cibotium* spp. Three tree fern species in the Cibotiaceae family (*Cibotium chamissoi* Kaulf., *Cibotium glaucum* (Sm.) Hook. & Arn, and *Cibotium menziesii* Hook.), collectively comprise 28 % of total stems and 46 % of total stand basal area within the Forest Dynamics Plot (R. Ostertag, *unpub. data*). Precise feral pig densities are unavailable for the study site, but estimates in similar Hawaiian forests range from 12.1 animals/km$^2$ in an adjacent forest (Hess et al. 2006) to as high as 31 animals/km$^2$ on the Island of Maui (Anderson and Stone 1993).

### Vegetation sampling

Within the 4 ha study plot, every native woody individual (including trees, shrubs, and tree ferns) $\geq$1 cm DBH was identified, measured, and mapped in 2008–2009. Of the 3,384 tree ferns present in the 4 ha forest dynamic plot that were $\geq$50 cm tall, we randomly selected 200 *C. glaucum* and 200 *C. menziesii* by matching previously assigned tag numbers with a sequence of randomly generated numbers. We included only 196 *C. menziesii* in the study because four individuals of the original 200 selected were misidentified in the original census. We further included all 42 individuals of a rarer species found within the plot, *C. chamissoi*, for a total sample size of 438 individuals of the three species. For each selected tree fern, we measured trunk length from the base to where the stipes separate from the trunk, and marked a fixed point on the trunk to ensure consistency across repeated measurements. We also counted the number of fronds that were at least 50 % expanded, 50 % whole, and 50 % green. *Cibotium* spp. often grow at an angle which may influence tree fern survival, feral pig damage, and the number of native woody (non-tree fern) seedlings that establish on tree fern trunks. To explore these possible relationships, we recorded the angle of each tree fern as standing (growing primarily vertically), leaning (growing at an angle >45° and <90°), prone (growing primarily horizontally in contact with the ground), or semi-prone (growing partially upright and partially horizontally in contact with the ground; these were most likely individuals that were once prone but had begun to re-grow vertically).

In 2010, we re-located 435 of the original 438 individuals and recorded the extent of feral pig damage using a custom damage index (DI): none (DI = 0), light (DI = 1, evidence of rutting on the trunk), moderate (DI = 2, holes bored into trunk; Fig. 1a), and heavy (DI = 3, trunk completely severed; Fig. 1b). We separately recorded tree fern survival, classifying any tree fern without live fronds as dead. In addition, we quantified the abundance of native woody seedlings growing on each tree fern by using the following seedling abundance categories: none, 1–10, 11–50, and >50 individuals. We excluded up to 27 individuals from one or more analyses due to measurement inconsistencies between censuses (sample sizes given in Table S1).

### Statistical analyses

We conducted all analyses in R (R Development Core Team 2012) and evaluated significance at $\alpha = 0.05$. To standardize the effects of feral pig damage on growth of *Cibotium* spp. across a range of tree fern sizes, we calculated the percent change in trunk length and number of fronds between years [((2010 measurement–2009 measurement)/2009 measurement) × 100]. We performed ANOVAs and post hoc Tukey's tests (Ott and Longnecker 2001) with damage index

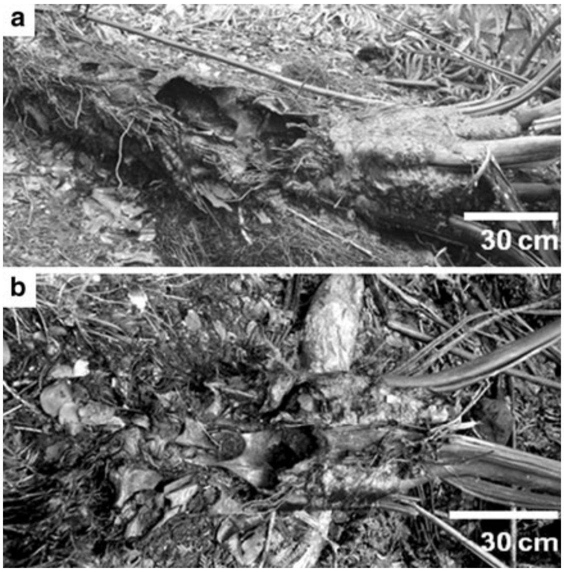

**Fig. 1** *Cibotium glaucum* tree fern with (**a**) moderate damage (holes bored into trunk), and (**b**) heavy damage (trunk completely severed)

and/or species as explanatory variables and percent change in number of fronds or percent change in trunk length as the dependent variable. To determine the relationship between survival and feral pig damage, we performed logistic regression (Ott and Longnecker 2001) on survival versus damage index with all species pooled and separately. To determine whether damage index was associated with species or tree fern angle, and if seedling abundance on tree ferns was associated with damage index or tree fern angle, we conducted Fisher's exact tests of independence using the 'fisher test' procedure in R (Fisher 1922). We used Fisher's exact tests because it is recommended over Chi square analysis when counts in any category are <5, as found in our study (Agresti and Wackerly 1977). Where we found significant associations from Fisher's tests, we calculated 95 % simultaneous Bonferroni confidence intervals to identify specific associations among categories (Byers et al. 1984). This technique applies a Bonferroni Z statistic to calculate simultaneous confidence intervals based on observed frequencies (Byers et al. 1984). We examined the association between woody seedling abundance and tree fern trunk length by examining the means and 95 % confidence intervals of tree ferns within each seedling abundance category.

## Results

Feral pig damage to tree ferns was widespread throughout the 4 ha study site, variable across the three *Cibotium* species, and associated with overall decreased growth and survival. Of 435 tree ferns relocated in 2010, 87 % were undamaged, 4.8 % were lightly-damaged, 6.4 % were moderately-damaged, and 1.6 % were heavily-damaged (Table S1). The probability of being heavily-damaged (DI = 3) varied among species (*C. chamissoi:* 4.8 %; *C. glaucum:* 2.0 %; and *C. menziesii*: 0.5 %; $P = 0.007$; $n = 435$; Fig. 2, Table S1). Additionally, damage affected the probability of survival for each species differently (DI × species interaction $F_{1,2} = 3.2$, $P = 0.041$; Fig. 3). When grouped into two categories of no to light damage (DI = 0 + 1) versus moderate to heavy damage (DI = 2 + 3), survival rates decreased by 100 % for *C. chamissoi* (100 to 0 %, respectively), 35 % for *C. menziesii* (99 to 64 %, respectively), and 25 % for *C. glaucum* (98 to 73 %, respectively; Fig. 3). For all species pooled, annual survival was higher for undamaged and lightly-damaged tree ferns (DI = 0 + 1; 65 %) versus moderately- and heavily-damaged tree ferns (DI = 1–3; 99 %; $F_{1,435} = 47$, $P < 0.001$). Of the 16 individuals that died over the 1 year study, 75 % were damaged by feral pigs (DI = 1 + 3). Of these, 31 % were moderately-damaged and 44 % were heavily-damaged.

Percent change in the number of fronds and trunk length became more negative with increasing damage by feral pigs (Fig. 4). The mean proportion of fronds lost over time increased from 6.2 % for undamaged to 19 % for lightly-damaged to 21 % for moderately-damaged and 100 % for heavily-damaged tree ferns, and differed significantly among damage categories when analyzed for all species combined ($F_{3,403} = 2.4$, $P < 0.001$; Fig. 4). On average, trunk length increased by 4 % for undamaged tree ferns and decreased by 50 % for heavily-damaged tree ferns ($F_{3,403} = 52$, $P < 0.001$; Fig. 4), and percent change in trunk length differed significantly among damage indices when analyzed across all species combined ($F_{3,415} = 2.9$, $P = 0.034$; Fig. 4). In addition, the effects of damage on trunk length differed among species (DI × species interaction $F_{3,415} = 18.2$, $P < 0.001$), while there was no significant interaction between damage index and species for percent change in fronds. In absolute terms, the trunk length of undamaged tree ferns for all species

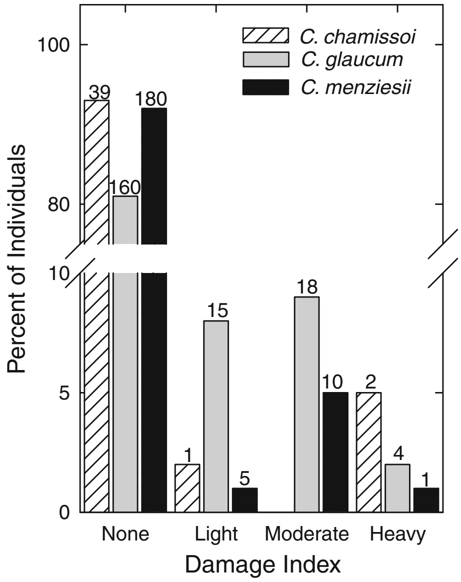

**Fig. 2** Percent of tree ferns in each damage index category by species (damage indices defined in "Methods"); numbers above the *bars* represent sample sizes

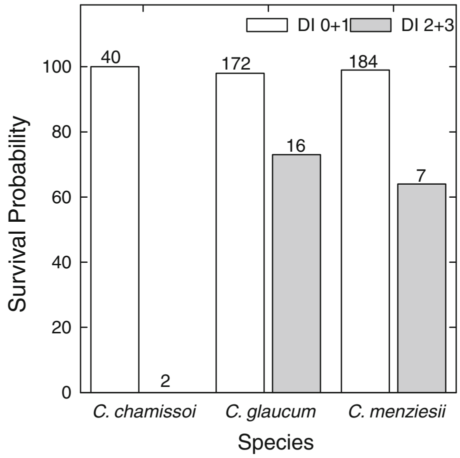

**Fig. 3** Survival probabilities for tree ferns grouped into two categories of no to light damage (DI = 0 + 1) versus moderate to heavy damage (DI = 2 + 3); note that no heavily-damaged *C. chamissoi* survived. Sample sizes are shown above *bars*. Logistic regression on survival versus damage index for all species pooled and for each species separately *P*-values all <0.001

pooled increased by 6.6 cm (±SE 0.5) over 1 year, and decreased by 26.5 cm (±SE 20.5), on average, for moderately- and heavily-damaged tree ferns combined. Undamaged tree ferns had 4.3 fronds (±SE 0.11) while damaged tree ferns (DI = 1–3) had 2.6 fronds (±SE 0.11) when averaged over all species (values for differences in trunk length and frond number by species in Table S2).

Damage index was significantly associated with species and tree fern angle, and woody seedling abundance on tree ferns was associated with DI and tree fern angle (sample sizes and observed versus expected values with 95 % Bonferroni confidence intervals in Tables S1–7). There was a significant association between species and damage index (Fisher's test $P = 0.006$, $n = 435$), where lightly-damaged

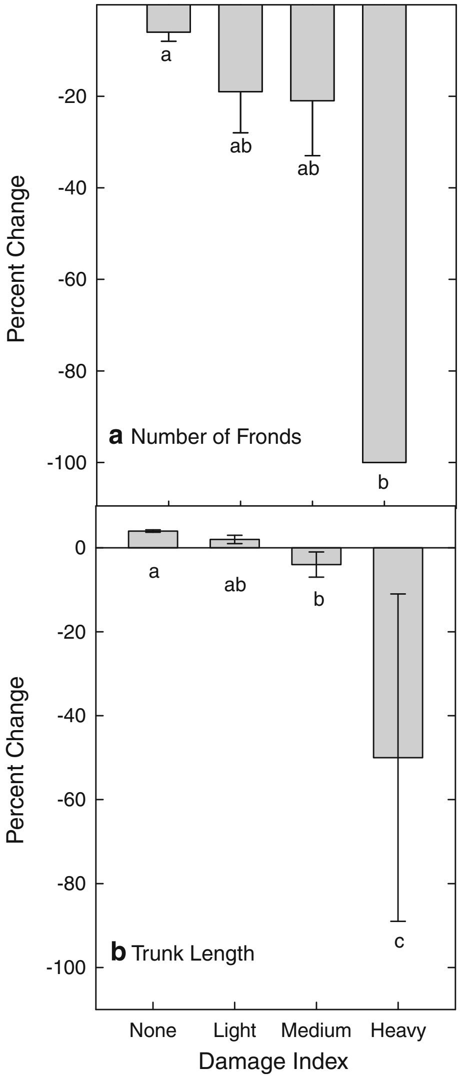

**Fig. 4** Mean percent change in (**a**) the number of fronds and (**b**) trunk length for all tree fern species pooled. Error bars represent ±1 SE from the mean; sample sizes in Table S1. *Letters* indicate significant differences among damage indices from Tukey's tests

tree ferns were more likely to be *C. glaucum* and moderately-damaged tree ferns were less likely to be *C. chamissoi* (Table S4). The overall association between damage index and tree fern angle was also highly significant (Fisher's test $P < 0.001$; $n = 412$). Undamaged tree ferns (DI = 0) were more likely to be standing and less likely to be prone, whereas all damaged tree ferns (DI = 1–3) were less likely to be standing and more likely to be prone (Fig. 5; Table S5). Additionally, moderately-damaged tree ferns were most likely to be semi-prone. Seedling abundance category was associated with both damage index and tree fern angle (Fisher's test all $P < 0.001$; $n = 435$). Both lightly- and heavily-damaged tree ferns were less likely than expected to have abundant seedlings (>50 seedlings), and moderately-damaged tree ferns were less likely to have no seedlings (Fig. 6, Table S6). Standing tree ferns usually had no seedlings and seldom had >11 seedlings, leaning tree ferns seldom had >50 seedlings, and semi-prone tree ferns usually had 11–50 seedlings (Table S7). However, seedling abundance also varied with tree fern length such that larger tree ferns tended to have more seedlings (Table S8).

## Discussion

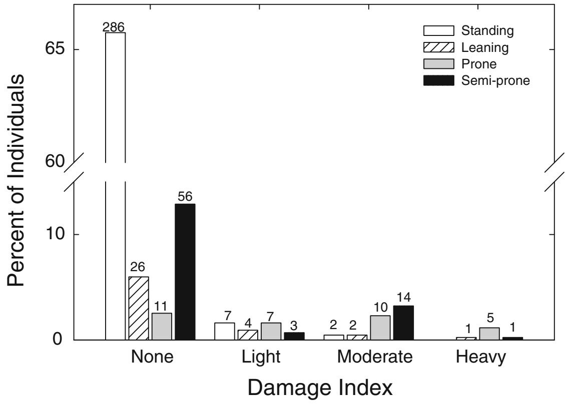

**Fig. 5** The association between damage index and tree fern angle for all tree fern species pooled (Fisher's exact tests of independence $P < 0.001$); note that no heavily-damaged tree ferns were standing; numbers above the *bars* represent sample sizes

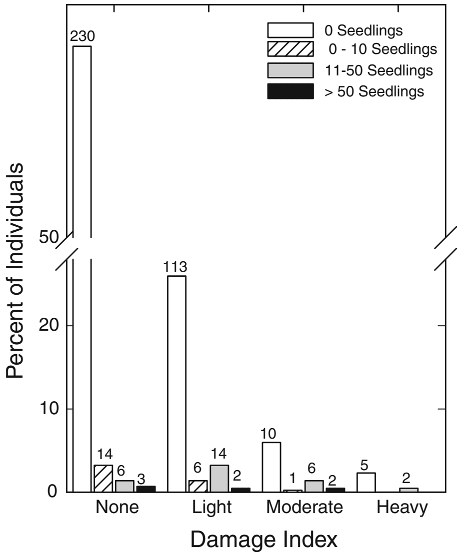

**Fig. 6** The association between damage index and woody seedling abundance on tree fern trunks for all tree fern species pooled (Fisher's exact tests of independence $P < 0.001$); numbers above the *bars* represent sample sizes

This study adds to the growing body of knowledge on how non-native ungulates impact the structure and function of forest ecosystems (Nuñez et al. 2010). Consistent with previous studies, we show that feral pigs can alter forest dynamics (Weller et al. 2011; Barrios-Garcia and Ballari 2012; Cole et al. 2012), in this case by reducing tree fern growth and survival and by damaging an important substrate for native woody seedling epiphytic recruitment. Although feral pig damage to other types of vegetation has been previously documented (Barrios-Garcia and Ballari 2012), ours is the first study to quantify the extent and magnitude of feral pig damage to tree ferns. The results of this study should be useful for forest restoration and conservation where both tree ferns and feral pigs are present.

These data support the hypothesis that feral pig damage decreases tree fern growth and survival. In particular, the majority of tree fern mortality was strongly associated with feral pigs. In contrast to undamaged tree ferns, moderately- and heavily-damaged tree ferns lost substantial trunk length. Even light damage, likely caused by feral pigs rubbing against trunks (e.g., to remove skin parasites; (Baker 1979; Heinken et al. 2006)), was associated with 50 % lower trunk length increment than that of undamaged individuals. In turn, trunk length increment for undamaged tree ferns corresponded with previous studies reporting 2–7 cm annual trunk length increment in *Cibotium* spp. (Walker and Aplet 1994; Durand and Goldstein 2001). Further, damaged tree ferns had half as many fronds as undamaged tree ferns, which likely reduces growth, survival, and reproduction—tree ferns with more fronds have a correspondingly larger frond area (Arcand et al. 2008), thereby increasing plant-level photosynthesis and spore production (Durand and Goldstein 2001). We note that tree ferns frequently resprout from epicormic buds, thus actual mortality may be lower than that reported here. We further note that the number of fronds also decreased for undamaged tree ferns, likely because annual rainfall at the study site was 11 % lower in 2010 than the 40 year average (Giambelluca et al. 2013; R. Ostertag, *unpub. data*). However, the decrease in frond numbers for undamaged individuals was significantly less than the decrease found for damaged individuals. Overall, these data are consistent with earlier studies that found high tree fern mortality where ungulates were present (Friday et al. 2008) and increased tree fern recruitment and growth following feral ungulate removal from Hawaiian forests (Scowcroft 1992; Weller et al. 2011; Cole et al. 2012).

Damage to *C. chamissoi* was relatively more extensive than to *C. glaucum* or *C. menziesii*. Specifically, the probability of being heavily-damaged was twice as high as for *C. chamissoi* than for *C. glaucum*, and no heavily-damaged *C. chamissoi* survived, although sample sizes were low due to the relative rarity of *C. chamissoi*. Previous studies have also found feral pig predation to vary by species (Mayer et al. 2000). For example, feral pigs were found to preferentially feed on native versus invasive tree ferns in Hawai'i (Durand and Goldstein 2001). The relative rarity of *C. chamissoi* compared to other *Cibotium* spp. could be related to feral pig preference for this species, or it may have always been less common in Hawaiian forests (Buck 1982). More research on interspecific differences among tree ferns that may affect their palatability to feral pigs and vulnerability to damage would support conservation and management of these species.

As hypothesized, epiphytic woody seedling abundance and tree fern angle co-varied with feral pig damage, although causality was unclear. Feral pigs topple tree ferns during foraging, but may also predate tree ferns that fall naturally because they are easier to access (Baker 1979). We propose that the positive association between woody seedling abundance and feral pig damage was driven by the correlated associations between seedling abundance and tree fern angle, and damage index and tree fern angle. Specifically, native woody seedlings were less abundant on standing tree ferns, likely because seedlings establish more readily on the horizontal surfaces provided by prone and semi-prone individuals. However, prone and semi-prone tree ferns were more likely to be damaged by feral pigs, reducing the overall area available for epiphytic woody seedling establishment. Because feral pigs largely eliminate the establishment of native plants in mineral soil in Hawaiian forests (Cole et al. 2012), most native species are restricted to epiphytic establishment in the presence of feral pigs and tree ferns provide ~50 % of all epiphytic establishment sites in these forests (Iwashita 2012; Inman-Narahari et al. 2013). In particular, the dominant canopy species in Hawaiian forest (*Metrosideros polymorpha*) is largely restricted to epiphytic establishment (Iwashita 2012; Inman-Narahari et al. 2013). Additionally, feral pigs facilitate the distribution and establishment of non-native invasive plants. As a result, feral pigs are expected to have large impacts on the future structure of these forests via direct impacts on tree ferns, and indirect impacts on the epiphytic establishment of woody seedlings and invasion by non-native plants.

In conclusion, invasive feral pigs had substantial negative effects on native tree ferns and alter native plant community dynamics. Because feral pigs are one of the most widely-distributed and potentially destructive invasive species and tree ferns and feral pigs co-occur in many regions globally (Tropicos.org; Barrios-Garcia and Ballari 2012), it is likely that feral pigs also substantially impact other ecosystems via damage to tree ferns. In some ecosystems, removal of invasive mammals does not lead to full recovery (Coomes et al. 2003). However, many questions remain about the resilience of tree ferns to disturbance, and if that resiliency would differ between tree ferns endemic to islands versus continental species. Future studies in both island and mainland areas should further investigate the long-term effects of feral pig damage to tree ferns on future forest structure and diversity. This research provides the first quantification of these effects and contributes to new insights on interactions among invasive mammals and keystone native plants.

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