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Relationships between soil macroinvertebrates and nonnative feral pigs (*Sus scrofa*) in Hawaiian tropical montane wet forests

Nathaniel H. Wehr · Creighton M. Litton · Noa K. Lincoln · Steven C. Hess

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Abstract Nonnative feral pigs (*Sus scrofa*) are recognized throughout the New World as a highly significant introduced species in terms of ecosystem alteration. Similarly, nonnative soil macroinvertebrates (e.g. earthworms, ground beetles) invade and alter the structure and function of native habitats globally. However, the relationship between feral pigs and soil macroinvertebrates remains largely unknown. This study analyzed relationships between these taxa using nine sites located inside and outside of feral pig management units representing a ~ 25 year chronosequence of removal in tropical montane wet forests in Hawai‘i. Soil macroinvertebrates were sampled from plots categorized as: actively trampled by feral pigs, actively rooted by feral pigs, feral pigs present with no signs of recent activity, or feral pigs

removed over time. In total, we found 13 families of primarily nonnative soil macroinvertebrates. Plots with active trampling correlated with lower total macroinvertebrate abundance, biomass, and family richness. Plots with active rooting were correlated with higher abundance of nonnative earthworms (*Lumbricidae* and *Megascolicidae*) and ground beetles (*Carabidae*). The abundance, biomass, and biodiversity of macroinvertebrates did not vary with time since feral pig removal. Collectively, these results indicate: (1) trampling by feral pigs negatively influences soil macroinvertebrates; (2) feral pigs either modify habitats while rooting thereby facilitating earthworm and ground beetle habitat use or selectively seek out target prey species of soil macroinvertebrates; and (3) removal of feral pigs has minimal impacts on soil macroinvertebrates over time. These results are important globally due to the broadly overlapping ranges of *S. scrofa* and nonnative macroinvertebrates.

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Introduction

Nonnative feral pigs (*Sus scrofa*) alter ecosystem processes and biodiversity throughout temperate and tropical ecosystems worldwide (Anderson and Stone

1993; Campbell and Long 2009; Wehr et al. 2018), and their activity has been shown to affect soils (Bueno et al. 2013; Long et al. 2017; Singer et al. 1984; Wehr et al. 2019), plant communities (Cole and Litton 2014; Drake and Pratt 2001; Setter et al. 2002), animal abundance and distribution (Atkinson and LaPointe 2009; Galetti et al. 2015; Keuroghlian et al. 2009), and watershed function (Browning et al. 2008; Cuevas et al. 2010; Dunkell et al. 2011; Strauch et al. 2016). In 2000, the management of feral pigs cost ~ \$800 million in the United States alone (Pimentel et al. 2000) and has likely increased notably since. Due to their widespread environmental alterations, fencing and the subsequent removal of feral pigs is a commonly utilized management strategy to protect native ecosystems (Wehr et al. 2018).

In general, the effects of feral pigs on the physical, chemical, and biological properties of soils are poorly understood compared to their alterations of above-ground plant communities (Long et al. 2017; Spear and Chown 2009). Prior research has, however, shown that trampling, rooting, wallowing, and the deposition of feces and urine alter soil processes that indirectly alter plant communities (Bueno et al. 2013; Wardle and Bardgett 2004; Wehr et al. 2018). The presence of feral pigs has been shown to alter soil structure via reduced aggregate stability and increased compaction (Bueno et al. 2013; Long et al. 2017), which can in turn affect soil macroinvertebrate communities (Vtorov 1993). In addition, feral pig rooting and wallowing has been associated with increased soil carbon, nitrogen, and phosphorous, increased pH, and increased volumetric water content and water-filled pore space in Hawaiian tropical montane wet forests (Long et al. 2017). Further, the alteration of understory plant communities by feral pigs likely leads to alterations in soil macroinvertebrates given the close linkages between above- and belowground biota (Wardle et al. 2004).

Soil macroinvertebrate species are frequently introduced and invasive, including > 4500 introduced species of nonnative invertebrates in the United States, with more than half of these introductions occurring in Hawai'i alone (Pimentel et al. 2000). Further, soil macroinvertebrates compose more than 98% of all non-microbial soil fauna worldwide, with vertebrates representing the remaining 2% (Decaëns et al. 2006). Many of these soil macroinvertebrates inhabit the upper layers of soil and aid in the fragmentation and

decomposition of leaf litter and can decrease understory recruitment, thereby altering the overall structure of forest habitats by increasing soil nutrient availability (Bernier 1998; Buse et al. 2008; Lavelle et al. 2006; Meyer et al. 2011; Negrete-Yankelevich et al. 2008; Snyder and Hendrix 2008). Soil macroinvertebrate species are sensitive to soil chemical and physical properties, including pH (Huerta and van der Wal 2012; Kuperman 1996), nutrient content (Huerta and van der Wal 2012; Warren and Zou 2002), soil texture, soil organic matter content, and litter density (Ponsard et al. 2000), all of which can be altered by feral pigs (Bueno et al. 2013; Hobbs 1996; Long et al. 2017; Siemann et al. 2009; Singer et al. 1984; Wirthner et al. 2012).

Feral pigs target soil macroinvertebrates, including snails, beetles, and earthworms, as a food source while rooting, and the importance of soil macroinvertebrates as a protein source in the diets of feral pigs has been well-documented (Diong 1982; Massei and Genov 2004; Meads et al. 1984; Parkes et al. 2015). While rooting for prey items such as soil macroinvertebrates, feral pigs can disturb up to 200 m² of soil daily, generating pits averaging depths of ~ 10 cm (Anderson and Stone 1993; Hancock et al. 2015; Meads et al. 1984). Importantly, feral pig rooting has been shown to occur more frequently when prey species are readily available in the top layer of soils, such as following rain events and in places where the soil has been previously disturbed (Elledge et al. 2013; Krull et al. 2016; Laznik and Trdan 2014). As such, feral pig rooting has been correlated to higher abundance and/or diversity of earthworms in a variety of environments (Bueno and Jiménez 2014; Lincoln 2014; Taylor et al. 2011). However, mechanistic explanations of these patterns have not been determined. As such, given that feral pigs are nonnative throughout much of the world and can drastically alter ecosystems, understanding their relationship with soil macroinvertebrates as a target food source is of great importance, particularly in light of the worldwide spread of nonnative macroinvertebrate species (Barrios-Garcia and Ballari 2012; Hendrix et al. 2008; Pimentel et al. 2000).

To better understand the potential relationship between feral pigs and soil macroinvertebrates, we asked the following questions: (i) How do rooting and trampling by feral pigs correlate to the abundance, biomass, and biodiversity of soil macroinvertebrates?;

and (ii) How does the abundance, biomass, and biodiversity of soil macroinvertebrates change over time following the removal of feral pigs? To address these questions, we examined soil macroinvertebrate communities from plots characterized by active rooting, active trampling, no recent activity despite feral pigs being present, and after 13, 15, 16, 23, and 25 years following feral pig removal. We hypothesized that: (H1) soils actively trampled by feral pigs would have lower abundance, biomass, and biodiversity of soil macroinvertebrates (Vtorov 1993); (H2) soils with active feral pig rooting would have higher abundance, biomass, and biodiversity of nonnative soil macroinvertebrates (Elledge et al. 2013; Krull et al. 2016); and (H3) soil macroinvertebrate abundance, biomass, and biodiversity would increase over time following feral pig removal (Decaëns et al. 2006; Taylor et al. 2011).

Methods

Study site

This study utilized a previously established chronosequence (~ 13–25 years since removal) of large feral pig removal management units (117–1024 ha) on the eastern side of Mauna Loa Volcano in the Ola‘a Tract of Hawai‘i Volcanoes National Park and the adjacent Pu‘u Maka‘ala Natural Area Reserve on the Island of Hawai‘i (Cole and Litton 2014). The experimental design consists of nine sites located in areas of canopy-intact native tropical montane wet forest classified as *Metrosideros polymorpha/Cibotium* spp. (Wagner et al. 1999). Sites range in elevation from 1140 to 1370 m above sea level, with mean annual temperatures between 14.4 and 15.9 °C and mean annual precipitation between 2910 and 3985 mm with no distinct seasonality (1920–2012) (Giambelluca et al. 2013). All study sites occur on 2000–10,000 year-old tephra-derived andisols from two closely related soil series: Puauulu (medial over ashy, aniso, ferrihydritic over amorphous, isothermic Aquic Hapludands) and Eheuiki (medial, ferrihydritic, isothermic Typic Hydrudands) (NRCS 2010). These soils are characterized by deep, moderately well-drained soils formed from basic volcanic ash deposited over basic lava with slopes of 2–5% (Cole and Litton 2014; Long et al. 2017; NRCS 2010). Forests surrounding the

enclosures are managed for limited recreational hunting of feral pigs (Cole and Litton 2014), with densities estimated at 0.6–16.3 feral pigs/km² (Scheffler et al. 2012).

The nine sites are arranged in pairs with five having feral pigs removed and four having feral pigs present (a single feral pig present site serves as the pair for two feral pig removal sites). In each of the sites with feral pigs present, three sampling plots were established representing areas with soil actively rooted by feral pigs, soil actively trampled by feral pigs, and soil with no recent sign of feral pig activity. In these sites, each of the plots was systematically selected to represent the three categories of feral pig activity by assessing feral pig activity 2 and 4 months prior to sampling. Trampled plots represent relatively narrow corridors throughout the forest formed by feral pig movement, which have previously been associated with increased soil compaction (Vtorov 1993). Rooted plots represent areas with widespread (average of 21 m² of rooted soil) and repeated rooting, which is typically associated with mixing of soil layers, decreased soil compaction, and increased nutrient cycling (Singer et al. 1984). In the five sites representing the chronosequence of feral pig removal, three plots at each site were established in areas representing 13, 15, 16, 23, or 25 years since removal (Cole and Litton 2014). Within each site, plots were located randomly and 75–200 m apart. Across all plots, canopy cover was controlled for by placing each plot within 1 m of the base of a randomly selected mature tree fern (*Cibotium* spp.).

Data collection

Prior to assessing soil macroinvertebrate communities, localized feral pig sign was recorded along two 25 m transects extending north and south from the center of each plot. The presence/absence of recent feral pig sign was determined at 1 m intervals along the transects. Additionally, percent litter cover was assessed on the surface of our plots. The soil macroinvertebrate community in each plot was sampled in soil pits excavated to 30 cm depth, width, and length, resulting in 27,000 cm³ total soil volume, including surface litter, in the center of each plot (Chan and Munro 2001; Lincoln 2014). Once excavated, the soil was sieved through 6.4 mm mesh to overcome clumping. All macroinvertebrates were

extracted by hand from both the mesh and the sieved soils. To ensure that no earthworms escaped collection by burrowing below the excavated pits and to sample potential species residing at lower depths, a solution of 75 g of powdered mustard in 2 L of water was poured into the bottom of each pit (Chan and Munro 2001; Nuutinen et al. 2001; Pelosi et al. 2014). However, no additional earthworms or other soil macroinvertebrates were obtained using this method.

Sampled macroinvertebrates were identified to family; more accurate taxonomic classifications were not possible due to similarities among related taxa. Voucher specimens for each taxonomic group were collected in a solution of 70% isopropyl alcohol for identification in the laboratory and were then stored in the University of Hawai‘i at Mānoa Insect Museum. Images of specimens are available on Scholarspace, the University of Hawai‘i at Mānoa’s open-access repository (Wehr 2018). The status of each taxa was determined from prior literature as either native, nonnative, or unknown. Length was recorded for the first 25 specimens collected for each family from each plot. Once 25 individuals were collected, additional specimens were only counted, with their length estimated from the mean of the first 25 specimens sampled. For earthworms, a subsample was collected from each site, dried for 48 h at 50 °C, weighed, processed in a muffle furnace at 400 °C for 24 h, and weighed again to estimate ash-free dry biomass to convert length measurements into biomass estimates (Hale et al. 2004). For all other soil macroinvertebrates, only length was recorded, and this measurement served as a proxy for biomass and a standardized value across taxa.

Statistical analyses

All statistical analyses were conducted using R-Studio statistical software version 3.4.3 (R Team 2018). To compare the abundance, biomass, and biodiversity of soil macroinvertebrates across each of the plot categories (rooting, trampling, no activity, and time since removal), Kruskal–Wallis rank sum tests were used because of the non-parametric, categorical nature of the data. For those comparisons found to be statistically significant, Dunn’s test of multiple comparisons using rank sums was used to explore differences in distributions of soil macroinvertebrates between individual categories (package: <dunn.test>). Finally,

linear regression analyses were used to model the relationship between soil macroinvertebrates and time since feral pig removal, as well as percent litter cover and the presence of soil macroinvertebrates. Because of the small sample size, tests were considered to be significant at or below $\alpha = 0.10$ for Kruskal–Wallis rank sum tests and linear regressions, and at or below $\alpha = 0.05$ for Dunn’s tests (Long et al. 2017). Additionally, Bonferroni corrections were applied to systematic analyses in order to correct for family-wise error rates when making multiple comparisons ($m = 6$).

Results

Across all plots, we collected 2352 total specimens from 13 unique families representing 11 orders (Table 1). Combined, earthworms (*Lumbricidae*, *Megascolicidae*, and juveniles) accounted for ~ 42% of total individuals sampled and ~ 60% of total soil macroinvertebrate biomass. *Julidae* was the second most common taxa accounting for ~ 31% of all individuals sampled and ~ 24% of total biomass. *Hemiptera* individuals were the third most abundant sampled (~ 14%), while *Lithobiidae* individuals represented the third largest amount of biomass (~ 6%).

Trampling resulted in a decrease of 74% in mean abundance ($T = 2.09$, $p = 0.02$), a decrease of 79% in mean biomass ($T = 2.63$, $p = 0.004$), and a decrease of 41% in mean family richness ($T = 2.40$, $p = 0.008$) of all soil macroinvertebrates compared to plots with no activity (Fig. 1a–c). Comparatively, rooting did not result in significant differences in total macroinvertebrate abundance, biomass, or family richness when all specimens were combined in comparison to plots with no feral pig activity (Fig. 1a–c). In addition, time since feral pig removal did not correlate to significant differences in the abundance, biomass, or family richness of soil macroinvertebrates (Fig. 1a–c).

Trampling resulted in marginally significant decreases in both the abundance and biomass, respectively, of individual taxonomic groups including *Hemiptera* ($T = 1.81$, $p = 0.04$; $T = 1.83$, $p = 0.03$), *Lepidoptera* ($T = 2.33$, $p = 0.01$; $T = 2.61$, $p = 0.005$), *Oxychilidae* ($T = 1.84$, $p = 0.03$; $T = 1.83$, $p = 0.03$), and *Parasitidae* ($T = 1.69$, $p = 0.05$; $T = 1.69$, $p = 0.05$) when compared to plots

Table 1 Soil macroinvertebrate taxa collected during this study, their current status in Hawai'i, the total number and relative percentage of specimens found, and their total and relative length (mm), serving as a proxy for biomass, combined across all sites

Taxa	Status	Total N	% Total N	Total length	% Total length
<i>Arionidae</i>	Nonnative ^a	3	< 1.0	9	< 1.0
<i>Carabidae</i>	Unknown	22	< 1.0	60	< 1.0
<i>Geophilidae</i>	Native ^b	16	< 1.0	262	1.6
<i>Hemiptera</i>	Unknown	334	14.2	662	4.1
<i>Julidae</i>	Nonnative ^c	731	31.1	3967	24.3
Juvenile earthworms	Nonnative ^d	797	33.9	5098	31.2
<i>Lepidoptera</i>	Unknown	56	2.4	348	2.1
<i>Lithobiidae</i>	Unknown	145	6.2	993	6.1
<i>Lumbricidae</i>	Nonnative ^d	164	7.0	3112	19.1
<i>Megascolicidae</i>	Nonnative ^d	31	1.3	1608	9.9
<i>Oniscidea</i>	Unknown	13	< 1.0	70	< 1.0
<i>Oxychilidae</i>	Unknown	23	< 1.0	77	< 1.0
<i>Parasitidae</i>	Unknown	10	< 1.0	10	< 1.0
<i>Talitridae</i>	Unknown	7	< 1.0	43	< 1.0
All macroinvertebrates	N/A	2352	100.0	16,319	100.0
All earthworms	Nonnative ^d	992	42.2	9818	60.2

Please reference ^a(Hayes 2015), ^b(Chamberlin 1953), ^c(Hoffman 1997), and ^d(González et al. 2006)

with no activity. Comparatively, rooting correlated to marginal increases in the abundance of both earthworms, including *Lumbricidae*, *Megascolicidae*, and juveniles combined ($T = -1.67$, $p = 0.05$; Fig. 1d), and *Carabidae* ($T = -2.38$, $p = 0.009$; Fig. 1e). There were no significant changes over time with feral pig removal among any individual taxa of soil macroinvertebrates. However, *Lepidoptera* abundance did show a marginal but non-significant negative linear trend following time since feral pig removal ($n = 6$, $F = 4.66$, $p = 0.10$, $r^2 = 0.42$).

Litter cover was negatively and linearly related to earthworm abundance ($n = 8$, $F = 6.5$, $p = 0.04$, $r^2 = 0.44$), but not biomass. Litter cover was not correlated to the abundance or biomass of any other taxa, but was negatively correlated with the presence of localized feral pig sign at each plot ($n = 26$, $F = 37.75$, $p < 0.001$, $r^2 = 0.59$). This included significant differences between rooted and trampled plots and nearly all other plot categories ($n = 8$, $\Sigma^2 = 23.02$, $p < 0.001$; Fig. 1f), with specific decreases in litter cover associated with rooting ($T = 3.51$, $p < 0.001$; Fig. 1f) and trampling ($T = 2.85$, $p = 0.002$; Fig. 1f).

Discussion

Given that only four families showed individually significant decreases in trampled sites (*Hemiptera*,

Lepidoptera, *Oxychilidae*, and *Parasitidae*) and collectively made up < 20% of the total population and < 10% of the total biomass, our results indicate that, in general, soil macroinvertebrate species are less abundant in sites trampled by feral pigs. The decreased presence of soil macroinvertebrates at trampled sites is in-line with our original hypothesis based on work by Vtorov (1993) in similar forests, who documented that soil macroinvertebrate species are negatively influenced by soil compaction, which has been associated with feral pigs in our study site (Long et al. 2017), as well as *S. scrofa* activity globally (Bueno et al. 2013). This result is suggestive of a larger pattern whereby soil trampling by ungulates could decrease the survival of soil macroinvertebrates in trampled microhabitats worldwide.

In contrast to trampled sites, we originally hypothesized that we would observe an increase in soil macroinvertebrate abundance and biomass at sites rooted by feral pigs. However, this hypothesis largely was not supported. Instead, only earthworms (*Megascolicidae*, *Lumbricidae*, and juveniles combined) and ground beetles (*Carabidae*) were found in greater abundance in the presence of feral pig rooting. This result is of particular interest because earthworms and ground beetles are important food sources for feral pigs (Diong 1982; Massei and Genov 2004; Parkes et al. 2015). Additionally, other studies have shown that feral pigs tend to return to sites they have

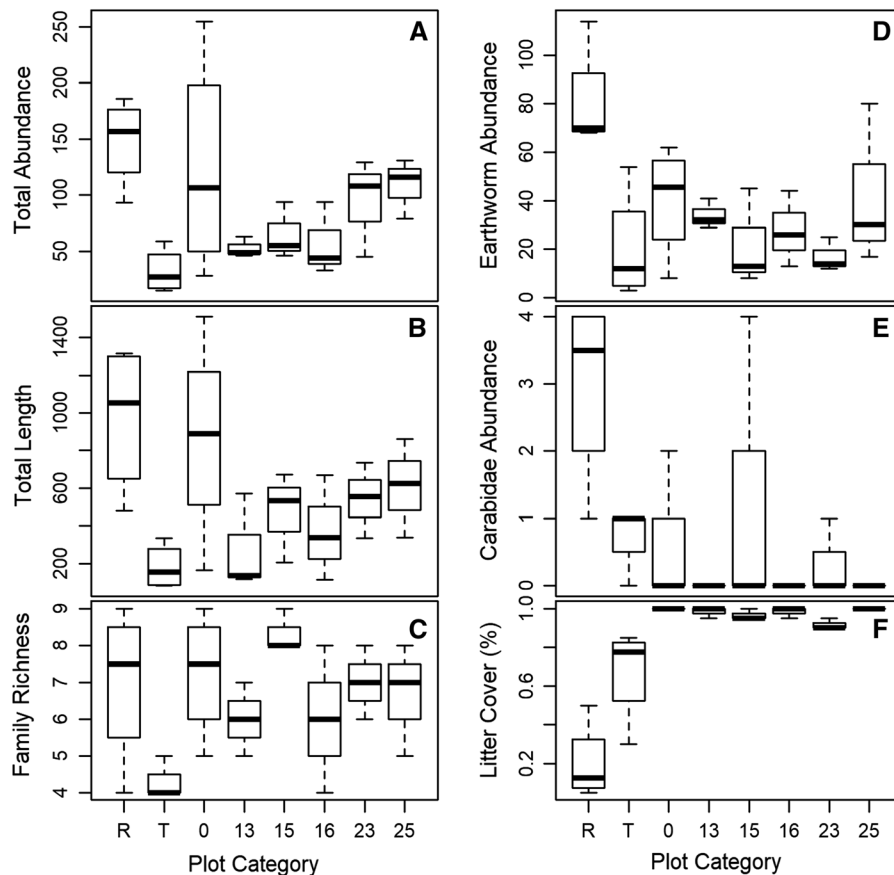


Fig. 1 Comparisons of six continuous variables labeled along the y-axes including: **a** total abundance of all soil macroinvertebrates; **b** total length (mm) (i.e. biomass) of all soil macroinvertebrates; **c** the family richness of soil macroinvertebrates; **d** the abundance of all earthworms combined including *Lumbricidae*, *Megascolicidae*, and juveniles; **e** the abundance of *Carabidae*; and **f** the percent litter cover, at each plot type. These plot types are labeled along the x-axes: “R” representing plots with active rooting; “T” representing plots with active trampling; “0” representing plots with pigs present, but no recent activity; and 13, 15, 16, 23, and 25 representing years since feral pig removal (for R, T, and 0, $N = 4$; for 13, 15, 16, 23,

and 25, $N = 3$). Dunn’s tests indicated that trampling resulted in lower abundance ($T = 2.09$, $p = 0.02$; **a**), biomass ($T = 2.63$, $p = 0.004$; **b**), and family richness ($T = 2.40$, $p = 0.008$; **c**) of all soil macroinvertebrates combined compared to plots with no activity. Rooting correlated to marginal increases in the abundance of both earthworms, including *Lumbricidae*, *Megascolicidae*, and juveniles combined ($T = -1.67$, $p = 0.05$; **d**), and *Carabidae* ($T = -2.38$, $p = 0.009$; **e**). Litter cover was explained by localized feral pig activity, with specific decreases in litter cover associated with rooting ($T = 3.51$, $p < 0.001$; **f**) and trampling ($T = 2.85$, $p = 0.002$; **f**)

previously rooted despite harvesting target food sources during rooting (Elledge et al. 2013; Krull et al. 2016). In our study, rooted plots were only sampled after rooting had occurred across a 4 month time period. It is therefore likely that the earthworms and ground beetles should have been recently and consistently depredated by feral pigs prior to data collection. If the earthworm and ground beetle populations were not being depredated, it is unlikely that feral pigs would repeatedly root at these sites because there would not be an energetic benefit. We therefore

propose two possible explanations for these results: (1) *Worm-Farming Hypothesis*—alterations to soils (e.g., increased mixing of soil and organic material) from feral pig rooting increases earthworm and ground beetle presence; or (2) *Truffle-Worm Hypothesis*—feral pigs actively select sites for rooting that have higher earthworm and ground beetle abundance.

In support of the *Worm-Farming Hypothesis*, rooting by feral pigs has been specifically associated with increases in soil carbon, nitrogen, phosphorous, pH, and soil moisture, decreased soil compaction, and

increased mixing of organic material (Cuevas et al. 2012; Long et al. 2017; Singer et al. 1984). These soil alterations could potentially facilitate the increased presence of earthworms observed in our rooted plots due to earthworms' general preference for soils with mixed organic and mineral material (Doube et al. 1997). Mechanistically, this would be possible because both families of earthworms present in our study system begin reproducing 1–2 months after birth with short cocoon incubation times, making it possible for earthworms to replenish over short time periods in the ideal conditions resultant from feral pig rooting (Butt 1993; Edwards et al. 1998; Karmegam and Daniel 2009; Venter and Reinecke 1988). In the case of ground beetles, while they would be unlikely to reproduce quickly enough to overcome feral pig predation, they are capable of greater dispersion than earthworms and may recolonize rooted areas to prey upon repopulating earthworms (Lövei and Sunderland 1996). If the *Worm-Farming Hypothesis* is supported, it would be indicative of a facilitative relationship between feral pigs, earthworms, and ground beetles whereby these taxa synergistically accelerate the environmental alterations of one another as invasive species in native Hawaiian ecosystems. As such, this relationship would provide supporting evidence of the invasional meltdown hypothesis (Simberloff and Von Holle 1999). However, it is important to note that this invasional meltdown likely would have only occurred historically mirroring the introduction of feral pigs and earthworms. Presently, this invasional meltdown would therefore be limited to range expansion fronts resulting from climate change because feral pigs have largely maximized their use of available habitat in Hawai'i.

The *Truffle-Worm Hypothesis*, however, is equally likely in our study system. Mechanistically, *Truffle-Worm Hypothesis* suggests that feral pigs selectively choose to root in areas with a greater abundance of earthworms and ground beetles. Supporting this hypothesis, feral pigs have long been recognized as having adaptations for the consumption of belowground food resources (Hatley and Kappelman 1980). This adaptation is, however, most commonly associated with truffles (*Tuber* spp.) that produce an aromatic compound similar to *S. scrofa* sex pheromones (Patel 2012). As such, it may be possible that feral pigs are capable of seeking out areas with greater availability of belowground food resources, but the

mechanism for this targeted predation remains unclear. If the *Truffle-Worm Hypothesis* is true, repeated rooting in these areas could be explained by high availability of food, and the presence of ground beetles could be explained by the high presence of earthworms as a target food source (Lövei and Sunderland 1996). The increased presence of earthworms and ground beetles would then be explained by some other environmental factor not directly associated with rooting behavior. In this study, we are unable to definitively determine which of these two explanations (i.e. *Worm-Farming Hypothesis* or *Truffle-Worm Hypothesis*) best addresses the high abundance of earthworms and ground beetles at rooted sites. However, given our knowledge of this ecosystem and the prevailing patterns of existing literature, we would suggest that *Worm-Farming Hypothesis* is the more likely explanation and that studies examining this mechanism would be a useful and needed avenue for future research.

Considering sites where feral pigs were removed, our initial hypothesis was that soil macroinvertebrate abundance, biomass, and biodiversity would increase over time following feral pig removal due to the release of top-down predation. However, our results did not support this hypothesis. As such, we conclude that the removal of feral pigs largely does not affect soil macroinvertebrate communities over decadal time scales.

Our results indicated a negative correlation exists between earthworms and litter cover. Three potential explanations for this are that: (1) feral pig activity alters both earthworms and litter cover independently; (2) litter cover influences earthworm abundance; or (3) earthworm abundance influences litter cover. Previous research has shown that earthworms decreased the volume of leaf litter (Bohlen et al. 1997) and that earthworm populations were correlated to canopy cover, and consequently leaf litter (Lincoln 2014; Ponsard et al. 2000). Our results similarly lend support to the third explanation. However, while we did observe a negative correlation between earthworm abundance and leaf litter, this did not mirror patterns of feral pig activity. Specifically, trampled plots had the lowest abundance of earthworms despite having an intermediate amount of leaf litter cover. These plots therefore contrasted the pattern we observed in litter cover's influence on earthworms and indicated that the alterations to earthworm abundance were better

explained by feral pig activity independently, which supports the first proposed explanation.

Conclusions

This study corroborates results previously reported by Vtorov (1993) suggesting that trampled habitats contain fewer soil macroinvertebrates making up less biomass likely due to soil compaction. Additionally, the high presence of earthworms and ground beetles in areas where they were consumed by feral pigs is a novel result suggesting that rooting, a common strategy used by feral pigs to forage for target prey species, either correlates with increases in the presence of earthworms and ground beetles (i.e. *Worm-Farming Hypothesis*) or with feral pigs' ability to intentionally seek out and uncover earthworms and ground beetles as target belowground food sources (i.e. *Truffle-Worm Hypothesis*). If rooting does alter soil conditions favorably for earthworms and ground beetles, this result would support the existence of a facilitative relationship between these taxa and feral pigs. Conceptually, this result would support the invasional meltdown hypothesis (Simberloff and Von Holle 1999). Alternatively, if feral pigs are capable of seeking out soil macroinvertebrates as prey, this result would provide evidence suggesting feral pigs are capable of targeting and uncovering earthworms as belowground food resources. Regardless of the correct hypothesis, our study identifies the existence of a close relationship between feral pig activity and the soil macroinvertebrate community broadly. In particular, the negative effects of trampling and potential interactions of rooting provide insight into this relationship, information useful in future examinations of soil macroinvertebrate species broadly, in the presence of *S. scrofa*.

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