Geoderma 279 (2016) 53–60

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Soil and hydrological responses to wild pig (*Sus scofa*) exclusion from native and strawberry guava (*Psidium cattleianum*)-invaded tropical montane wet forests

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ARTICLE INFO

Article history:
Received 15 January 2016
Received in revised form 24 May 2016
Accepted 29 May 2016
Available online 6 June 2016

Keywords:
Throughfall
Runoff
Soil erosion
Fecal bacteria
Feral pigs
Strawberry guava

ABSTRACT

The structure and function of many ecosystems are threatened by non-native, invasive plant and animal species. Globally, invasive trees alter interception, evapotranspiration, water use, and throughfall, while wild pigs (*Sus scofa*) have been introduced and now invade widely ranging ecosystems, with impacts to soil and groundcover, and as a consequence, infiltration, runoff and water quality. In a resource management context, physical, chemical and biological control methods can limit the impact of plants on native biodiversity while fence building and animal removal can limit the effects of non-native ungulates on ecosystems. These expensive treatments have documented biodiversity benefits, but few studies have quantified hydrological effects of such management. Using paired fenced/unfenced runoff plots in native and *Psidium cattleianum*-invaded Hawaiian tropical montane forests, we examined the independent and interactive effects of strawberry guava (*Psidium cattleianum*), a highly invasive tree in tropical islands and wild pigs on runoff amount, soil erosion rates and fecal indicator bacteria (FIB). We sampled 18 events spanning a 22 month period, and found that: 1) pigs are less active in invaded forests; 2) higher stem densities in invaded forests were associated with lower soil erosion and runoff rates compared to native forest; 3) reduced canopy cover and greater pig activity in native forests resulted in higher runoff volumes, soil erosion rates, and runoff FIB content; and 4) unfenced plots had more bare soil, less vegetation cover and greater soil FIB (*Escherichia coli*, total coliforms, enterococci) compared to fenced plots. These results point to the importance of understanding the independent and interactive effects of multiple invaders on watershed function. In this study system, removal of an invasive tree without fencing may actually lead to an increase in disturbance, with impacts to both biodiversity and hydrological properties.

1. Introduction

The introduction of non-native plants and animals has resulted in negative impacts to native ecosystems worldwide (Campbell and Long, 2009). These introductions can drive significant changes to plant community composition (Hughes and Denslow, 2005; Baker, 1986) but also structure (Asner et al., 2008), function (Krull et al., 2013), and over time, the dynamics of native ecosystems. These impacts can be severe and managing for invasive species threats costs land management agencies billions of dollars annually (Apollonio et al., 2010; Ditomaso, 2000). While a great deal of scientific attention has been directed to understanding benefits of such management on composition and structure of native biodiversity, impacts to ecosystem function, especially by multiple plant and animal invaders, have been understudied.

The European boar (*Sus scrofa*) has been introduced to North America (Kay and Bartos, 2000), and across widely ranging islands (Nogueira-Filho et al., 2009). These ungulates consume native plants, disturb soils, and spread non-native species (Coblentz, 1978), resulting in increased erosion and altered hydrology. This is especially true in tropical island forests. In Hawai'i, European pigs were introduced by explorers in the 17th and 18th Centuries (Nogueira-Filho et al., 2009, Bruland et al., 2010), quickly interbred with domesticated pigs that had been released, becoming a self-sustaining hybrid wild pig population this is most densely populated in wet forests (Cuddihy and Stone, 1990). Feral pigs in Hawai'i, which will subsequently be referred to as wild pigs, produce large litters (5–7 piglets), are reproductive year round, and achieve densities as high as 20–30 pigs km^{-2} (Pavlov et al., 1992, Hess et al., 2006). These life history traits, combined with a lack of predators in Hawai'i, have resulted in high densities that, because of terrain, are difficult to control.

Pig behavior (e.g., browsing, rooting, digging, trampling) alters forest understory by disrupting soil, exposing roots, increasing bare ground

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http://dx.doi.org/10.1016/j.geoderma.2016.05.021

and damaging vegetation, changing soil hydraulic conductivity and increasing nutrient loss in runoff (Sidle et al., 2006; Singer et al., 1984). Wild pigs dig for soil invertebrates (Diong, 1982, Hess et al., 2010), disturbing the topsoil (Krull et al., 2013), reducing the litter layer and mixing the topmost soil horizons (Cooray and Mueller-Dombois, 1981). Because island vegetation evolved in the absence of ungulates, the effects of grazing mammals on island plant communities are particularly apparent (Beverley and Wilson, 1985). Pigs consume native species (Murphy et al., 2014) and facilitate the proliferation of non-native vegetation (Huenneke and Vitousek, 1990). Following pig removal, Cole and Litton (2014) found that ground-rooted plants, bryophyte cover, and litter increased while exposed soil declined. The loss of understory plants and litter degrades a watershed's ability to retain water and increases soil erosion (Ryder and Fares, 2008). In Hawai'i, vegetative groundcover captures fog drip and rainfall, making a substantial contribution to the water budget (Ziegler and Giambelluca, 1998).

In addition to their effect on infiltration and runoff, ungulates impact runoff water quality by introducing pathogenic bacteria (Pavlov et al., 1992). Fecal indicator bacteria (FIB), such as *Escherichia coli* and enterococci, are commonly used to assess fecal contamination in soils (Dunkell et al., 2011b) and water (Strauch et al., 2014). Tropical soils support the growth of pathogenic bacteria and their erosion can be a source of contamination to surface waters (Hardina and Fujioka, 1991).

Monotypic stands of non-native vegetation, such as strawberry guava, pose a different but also important threat to watershed hydrology (Calder and Dye, 2001 Huenneke and Vitousek, 1990). The spread of *Psidium cattleianum*, introduced to Hawai'i from Brazil in the 1800s, alters community composition by shading understory species and displacing epiphytic communities; increasing canopy evaporation and stem flow while reducing cloudwater interception and throughfall (Mair and Fares, 2010, Safeeq and Fares, 2012, Mudd and Giambelluca, 2006, Takahashi et al., 2011). *Psidium cattleianum* spreads clonally through rhizomes and produces large quantities of fruit that pigs consume and distribute (Huenneke and Vitousek, 1990). While it stands to reason that there are likely to be interactive, even synergistic effects of pigs and *P. cattleianum* on these montane wet forests, few studies have examined physical and biological effects of co-occurring invasive species (Strayer et al., 2006). To address existing knowledge gaps, we established six replicate pairs of fenced and unfenced runoff plots (fence treatment) in native and *P. cattleianum*-invaded forests (forest treatment). We hypothesized that *P. cattleianum*-invasion would: alter forest composition and structure by simplifying biodiversity and greatly increasing individual stems in the 0–5 cm DBH size class (Hypothesis 1; H1); modify soil structure by increasing soil density and reducing porosity (H2); reduce retention of rainfall and so increase runoff and soil erosion (H3). We further hypothesize that excluding pigs would reduce disturbance and so increase vegetation groundcover (H4), reduce soil and runoff FIB (H5), and reduce runoff volume and soil erosion (H6) compared to unfenced plots. Finally, we hypothesized combined, feral pigs and *P. cattleianum* would act in additive fashion to increase surface runoff and soil erosion (H7).

2. Methods

2.1. Study area

In June 2012, 12 plots (2 forests × 3 sites per forest × 2 plots per site) were established in the Laupāhoehoe Wet Forest (LWF) section of the Hawai'i Experimental Tropical Forest. The LWF is a 4990 ha protected area established in 2007 on windward Hawai'i Island. The canopy is dominated by native species including ōhia (*Metrosideros polymorpha*) and koa (*Acacia koa*), while the mid-canopy is dominated by native tree ferns, hāpu'u (*Cibotium glaucum*), and the native trees olapa (*Cheirodendron trigynum*), pilo (*Coprosma ochracea*) and kawau (*Ilex anomala*). Geological age of underlying substrate is 4000–14,000 year old weathered volcanic tephra, with deep, moderately well drained soils over lava composed of silty clay loam in the Honokaa and Akaka series (Acrudoxic Hydrudands); consisting of a surface layer of dark-brown silty clay loam about 15 cm thick and a dark brown to very dark grayish brown silty clay sub-soil about 150 cm thick (Soil Survey Staff, 2012).

2.2. Site selection and design

Three sites were located in *P. cattleianum*-invaded forest at 840 m above sea level (a.s.l.) and three sites in native dominated forest at 1260 m a.s.l. Sites were identified within areas of 4–12% slope and final site selection was determined by proximity to existing road networks, woody debris cover, slope homogeneity, and canopy cover. Each site has one fenced (pigs excluded) and one unfenced 10 × 4 m area as depicted in Dunkell et al. (2011a). Each runoff plot was then delineated by 10 cm plastic flashing installed around the edges of a 1.2 × 4 m rectangle within the area to prevent runoff entering from outside the plot and oriented on the down slope direction to capture runoff. The fence was established with 1.524 m (5 ft) metal posts on the corners and midpoints of a rectangle equidistant from the runoff plot. At the base of each plot, metal collectors were installed to funnel runoff into a standard plastic bucket. To prevent overflow from large rainfall events, connectors excluded half of all runoff from entering the bucket and runoff volumes were subsequently doubled and converted to mm ha^{-1}.

2.3. Groundcover and pig activity survey

Groundcover and pig activity were determined 17 months and 38 months after plot installation. To assess the ground cover of each plot, six parallel transects were established at 60 cm intervals from the runoff collector to the top of the plot. At 5 cm intervals along each transect, groundcover was determined as: bare soil, rock, litter, coarse woody debris, standing dead plant, root, and live plant. Coarse woody debris was defined as any piece of wood > 2 cm in diameter while litter included leaf, detritus, or wood pieces < 2 cm in diameter. Data presented only considers the first groundcover dataset.

Pig activity was surveyed visually using 12 m transects from the center of each site in each of the four cardinal directions based on methods developed by Anderson and Stone (1994) and Pavlov et al. (1992). Visual signs of pig activity correlate well with actual densities of pig populations in Hawaiian forests (Hess et al., 2006) along with relative changes in pig densities (Scheffler et al., 2012). The presence of fresh (within a few weeks) rooting or digging, foraging, scat, tracks, and trails 1 m from either side of transects were recorded at 10 cm intervals. All activities were combined and the frequency of pig activity was determined following the removal of fenced portions as the pig activity index. Pig activity was assessed in both wet season (December 2013) and dry season (August 2015).

2.4. Forest composition and canopy cover

In January 2014, plot vegetation characteristics were assessed using standard forest inventory techniques (Kauffman and Donato, 2012). Within a 10 m radius circular plot centered between the runoff plots, all trees > 5 cm diameter at breast height (DBH) were counted, identified to species, and measured. Within a 2 m radius circle similarly centered between the plots, all plants were counted, identified, and measured. Species richness was calculated as the total number of species. Biodiversity was calculated using the inverse Simpson's (D′) diversity index (Morris et al., 2014). Trees within the 10 m circle were scaled to the hectare. All plants within runoff plots were also counted, identified, and measured regardless of DBH.

Canopy cover was determined by taking photographs using a Cannon EOS 5D high resolution digital camera (Canon Inc., Melville, NY, USA; only zenith angles 0–60° were used) with a 15 mm hemispherical lens mounted 1 m off the ground above each runoff plot and oriented towards magnetic north (Olivas et al., 2013). For each photograph, leaf area index (LAI) and percent (%) openness were calculated using WinSCANOPY™ Pro software (Version 2006, Regent Instruments Inc., Québec City, Québec, Canada). LAI-2000 original values were calculated using the linear average method (Lang, 1986).

2.5. General soil properties

To examine differences in soil profiles, three replicate soil cores from the upper 20 cm were taken using a 1 cm diameter soil corer from within each fenced site but outside of the runoff plot in January 2014. Each core was divided into 4 cm lengths and stored separately in sealed plastic bags. Samples were then processed for soil moisture (%), bulk density (g cm^{-3}), and organic matter (%) in the lab after the removal of rocks and large roots. Soil samples were weighted (wet weight) in pre-weighted paper bags and dried at 60 °C for one week. Dry weight was then measured and soil moisture was quantified as the difference between wet and dry weight, divided by wet weight subtracted from one. Bulk density was calculated as the sample dry weight divided by the sample volume, and organic matter was determined by weighting samples following combustion at 500 °C for 3 h (Maynard and Curran, 2008).

2.6. Canopy rainfall and throughfall

Canopy rainfall was provided by the Laupāhoehoe climate tower at 1100 m a.s.l., approximately equidistant between the invaded and native forest plots. Canopy rainfall during activation was determined as total rainfall between 12:00 on activation day and 12:00 on collection day. Throughfall was measured using six standard all-weather rainfall gauges (Productive Alternatives, Inc., Fergus Falls, MN) per site ($n = 3$ fenced, $n = 3$ unfenced) installed on separate 1.52 m metal posts around the perimeter of each plot. Relative throughfall was calculated as the ratio of mean plot throughfall ($n = 3$) to canopy rainfall during activation for each forest.

2.7. Runoff activation and data collection

Approximately once per month from November 2012 to April 2014 all runoff plots were activated. Activation began with emptying throughfall gages and adding a small aliquot (~5 mL) of mineral oil to prevent evaporation. Runoff collectors, connectors, and buckets were cleaned of all soil and debris using wet paper towels and sanitized with alcohol wipes (Great Value® 283.4 g disinfecting wipes). Collector and connector levels were checked and adjusted as needed. Soil moisture was measured for each plot as detailed in the following section. During activation in the largest storm events, throughfall exceeded the capacity of the gauges (284.6 mL) and the runoff buckets filled up to their maximum volume (18,848 mL), so an underestimate of maximum values were used.

Data collection occurred when a storm event was observed within ~7 days of activation, although events had to be estimated due to the remoteness of site location. Throughfall gauges were averaged by plot and runoff depth was measured using a meter stick in five locations in each bucket and averaged. Runoff volume (mL) was then calculated based on a standard equation for a cylinder volume (radii = 13 cm). For analysis of runoff sediment and bacteria, runoff was stirred and then sampled using a 500 mL acid-washed HDPE bottle. For half of all activations, a sample was taken for FIB quantification using a 100 mL sterile Wirl-Pak bag and transported on ice.

2.8. Determination of gravimetric soil moisture

Soil moisture was assessed at activation by taking a one centimeter diameter soil core from the top 5 cm of soil, 30 cm outside of each plot corner ($n = 4$ per plot). Samples were pooled in sterile plastic bags and placed on ice for transport to the laboratory. The pooled soil sample was weighed in a pre-weighed paper bag and dried at 60 ° C for one week. Soil moisture (%) was calculated following re-weighing as described earlier.

2.9. Analysis of soil erosion

Total suspended solids (TSS) in runoff samples were determined by vacuum filtration using pre-combusted and pre-weighed 45 mm G/F filters (Watman Inc., Kent, United Kingdom) and a Buchner funnel. Sample filters were dried at 60 °C for 1 week and reweighed for dry mass (DM) to the nearest 0.01 mg. TSS was calculated as the DM minus filter weight divided by volume of filtered solution (mg L^{-1}). Samples were then combusted at 500 °C for 3 h and reweighed to calculate ash-free dry mass (AFDM). Percent (%) runoff TSS organic matter was calculated as AFDM DM^{-1}. Soil erosion (mg soil $event^{-1}$) was calculated as the product of runoff volume and TSS. Organic soil erosion (mg soil $event^{-1}$) was calculated as the product of % runoff TSS organic matter, TSS and runoff volume. Soil erosion and organic soil erosion were then scaled to t ha^{-1} for comparison.

2.10. Soil and runoff bacteria analysis

Quantification of soil bacteria was after Myers et al. (2007), where 5.00 g of soil taken from pooled soil samples, stored in a sterile Wirl-Pak™ bag, are mixed with 100 mL of sterile 0.15 M NaCl solution, and shaken on a rotary shaker table at 100 rpm for 45 min. Solutions were permitted to settle for 5–10 min and from the top of the solution, 10 mL aliquots were transferred to each of two new sterile Wirl-Pak™ bags. Solutions were brought up to 100 mL (10× dilution) with sterile water and analyzed for total coliforms and *E. coli* bacteria using Colilert™ defined substrate in one bag and *Enterococci* spp. using Enteroelert™ in the other bag (IDEXX Laboratories, Westbrook, ME, USA). Bags were shaken for 90 s, let sit for 60 s, heat-sealed in QuantiTray-2000™ trays (IDEXX Laboratories, Westbrook, ME, USA) and incubated at 36 °C (Colilert™) or 40 °C (Enteroelert™) for 24 h. Results were enumerated under ultraviolet (680 nm) light (enterococci and *E. coli*) and under ambient light (total coliforms). The brightest wells were counted as positive following comparison to a sterile water control and the most probable number (MPN) of colony forming units was calculated based on the IDEXX QuantiTray MPN table with a detection limit of 24,190 MPN 100 mL^{-1}. To determine runoff bacteria concentration, the same procedure was utilized as for soil bacteria starting with a 10 mL aliquot of sample obtained from the collection bucket and transferred to each of two sterile Wirl-Pak™ bags. Final values were scaled to 100 mL (10× dilution). For statistical analyses, all MPN values were $\log_{10}(x + 1)$-transformed.

2.11. Data analysis

Categorical groundcover data were analyzed using a contingency table analysis testing the null hypothesis that the observed frequency of each groundcover did not differ from the expected for each plot. Comparisons between fenced and unfenced plots and between native and invaded forests were also made using a Wilcoxon sign-rank non-parametric *t*-test. Using each cardinal direction per site as an independent value ($n = 12$ per forest), we used a two-way ANOVA to compare pig activity between forests and years. For the soil cores, soil moisture, bulk density, and % organic matter were averaged at each depth among the nine replicates for each forest. We tested the null hypothesis that there were no differences between forest types or among depths using a two-way repeated measures analysis of variance (RM-ANOVA) with soil depth as the repeated factor to eliminate pseudoreplication.

Relationships between canopy rainfall 48 h prior to activation and soil moisture at activation were examined for each treatment using regression analysis. We tested the null hypothesis that there was no effect of forest on the mean difference in throughfall and relative throughfall using one-way RM-ANOVA ($\alpha = 0.05$). We also used a RM-ANOVA to test the independent and interactive effects of forest and fencing treatments on runoff volume, TSS, % runoff TSS organic matter, soil erosion and organic soil erosion as well as $\log(x + 1)$-transformed soil FIB values. Due to the large number of tests and relatively small sample sizes, Spearman non-parametric correlations were used to examine relationships between mean throughfall, soil moisture, runoff volume, runoff TSS, runoff TSS organic matter (%), and runoff organic soil erosion. Differences in regression slopes of runoff volume, soil erosion and organic soil erosion with throughfall were compared for each forest and fencing treatment using analysis of covariance (ANCOVA) with $\log(x + 1)$-transformed values. To examine relationships between soil FIB and runoff FIB, we also used Spearman correlations due to the limited sample sizes and non-normal distributions. Statistical analyses were computed using SigmaPlot (Version 12.0, Systat Software, Inc., Chicago, IL).

3. Results

3.1. Groundcover, vegetation and canopy cover analysis among treatments

Groundcover differed across forest and fencing treatments ($\chi^2 = 1155$, degrees of freedom, df = 44, $p < 0.0001$) with more bare soil in unfenced plots (7.6%) compared to fenced plots (1.7%) and native forest plots with more bare soil (8.3%) than *P. cattleianum*-invaded forest (1.1%) plots (Fig. 1). Plant cover made up a greater percentage of groundcover in native forest (13.2%) compared to invaded forest (1.6%). Invaded forest plots tended to have slightly more (mean ± SD) basal area (116.9 ± 28.1 m^2 ha^{-1} vs. 100.6 ± 16.7 m^2 ha^{-1}) but substantially greater stem densities (4785 ± 447 ha^{-1} vs. 2472 ± 239 ha^{-1}) than native forest plots. *Psidium cattleianum* stem densities and basal areas within invaded runoff plots ranged from 4167 to 104,167 ha^{-1} and from 25,000 to 371,458 m^2 ha^{-1} per plot, respectively. Percent openness (mean ± SD) of the canopy was greater in native forest sites (9.9% ± 2.67%) compared to invaded sites (5.9% ± 2.4%) as was LAI (Table 1). Invaded plots had greater species richness (range: 8 to 10 species) compared to native forest plots (each site had 5 species), but lower species diversity compared to native forest plots (Table 1). Mean (±SD) pig activity index for native forest sites in 2013 was 5.51 (±1.82) sightings m^{-1} versus to 0.40 (±0.27) sightings m^{-1} for invaded sites. By comparison, native forest sites in 2015 had an index of 2.84 (±1.31) sightings m^{-1} compared to 0.45 (±0.48) sightings m^{-1} for *P. cattleianum* plots resulting in a significant difference between forests ($F = 131.83$, df = 1,44, $p < 0.001$) and years ($F = 17.45$, df = 1,44, $p < 0.001$) with a significant interaction effect ($F = 14.79$, df = 1,44, $p < 0.001$) due to between year differences in activity in native forest.

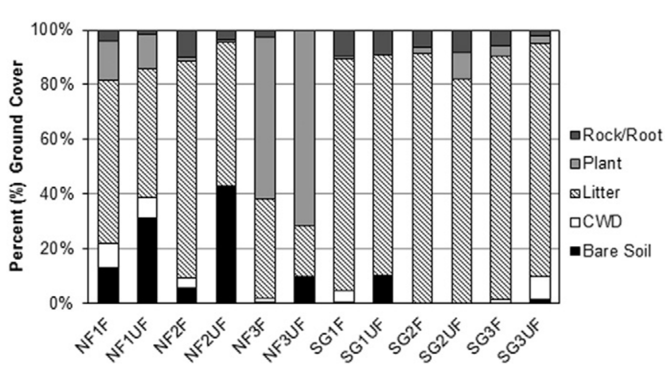

Fig. 1. Mean percent (%) ground cover for native forest (NF) and *P. cattleianum* (strawberry guava, SG)-invaded forest, fenced (F) and unfenced (UF) runoff plots ($n = 6$). CWD = coarse woody debris (>2 cm diameter) in the Hawai'i Experimental Tropical Forest, Hawai'i Island.

3.2. Soil properties and soil bacteria

Soil moisture was similar at all depths for native forest soils but increased at depth in invaded forest soils (Fig. 2). Bulk density increased with depth in both vegetation types and percent organic matter declined with depth in both forests, but the organic matter decline was greatest in *P. cattleianum* forest sites. Significant forest and depth effects are provided by Table 2. Soil FIB was measured 10 times over 16 months from September 2012 to March 2014. Overall, unfenced plots in both the native and invaded forests had greater mean and maximum FIB values (Fig. 3) resulting in a significant forest effect for enterococci and total coliforms and a significant fencing effect for *E. coli* (Table 3).

3.3. Throughfall, soil moisture and runoff

From November 2012 to April 2014, 16 of 18 activations successfully captured runoff. Canopy rainfall during activation ranged from 0.254 to 495.3 mm. Mean (±SE) throughfall across all activations and sites was 88.3 mm (±17.4 mm), with no significant difference between native (79.2 ± 23.5 mm) and invaded forest (97.4 ± 26.0 mm) plots (Supplemental Fig. S1). Relative throughfall (mean ± SE; unitless) was greater in the invaded forest (1.024 ± 0.11) compared to the native forest (0.777 ± 0.06) resulting in a significant effect of forest type ($F = 5.13$, df = 1,16, $p = 0.038$).

Soil moisture at activation was positively correlated with canopy rainfall for the previous 48 h (Supplemental Fig. 2) and the correlation was slightly stronger for native forest plots. Overall, soil moisture at activation was significantly greater in *P. cattleianum* sites ($F = 37.4$, df = 1,62, $p < 0.001$) but not between fencing plots ($F = 0.60$, df = 1,62, $p = 0.44$) and there was no forest ∗ fencing interaction ($F = 1.32$, df = 1,62, $p = 0.25$). Fencing treatments within each forest differed significantly in soil moisture at activation (Tukey HSD, $p < 0.05$).

Four activations occurred >200 mm of throughfall (December 2012, February, November, and December 2013), and four had <10 mm of throughfall. Two plots (one invaded unfenced and one native fenced) only recorded runoff for five events, while most other plots recorded runoff in at least nine events. Runoff volume differed significantly across activation dates and increased with increasing throughfall for all sites (Supplemental Fig. 3). There was a significant forest and almost a significant forest*fencing interaction effect on runoff volume (Table 4), but no significant differences in the slopes of the regression lines between throughfall and runoff ($F = 0.34$, df = 1,3, $p = 0.80$). However, correlations between throughfall and runoff volume were statistically stronger for unfenced plots in both native and invaded forests compared to fenced native and invaded forests (Supplemental Table 1).

3.4. Soil erosion

Runoff TSS, soil erosion and organic soil erosion were each positively correlated with throughfall in all treatments (Supplemental Table 1; Supplemental Fig. 3). Mean runoff TSS varied from 4.44 to 103.16 mg L^{-1} in the native forest and from 2.80 to 99.11 mg L^{-1} in the invaded forest. There were significant forest effects, but no fencing or forest ∗ fencing interaction effects on runoff TSS (Table 4). There was a forest effect on total soil erosion ($F = 8.57$, df = 1,16, $p = 0.01$) but no fencing effect driven by larger runoff volumes in the native forest plots. The event sampled with the highest soil loss was November 2013, where unfenced native forest plots averaged 2.03 and 1.35 t ha^{-1} $event^{-1}$ of total soil erosion and organic soil erosion, respectively, compared to fenced native forest plots, which averaged 0.86 and 0.63 t ha^{-1} $event^{-1}$, respectively. There were no significant differences in the slopes of the regression lines between throughfall and soil erosion ($F = 0.76$, df = 1,3, $p = 0.521$) or organic soil erosion ($F = 0.33$, df = 1,3, $p = 0.81$).

There was a significant interaction effect on mean % organic matter with the largest values (mean ± SE) in the invaded fenced sites

(82.5% ± 1.38%) (Table 4). There was a significant forest ($F = 8.79$, df = 1,13, $p = 0.009$) and almost a significant fencing ($F = 3.95$, df = 1,13, $p = 0.06$) effect on soil organic matter erosion, with the largest values (mean ± SE) in native fenced plots (0.0498 ± 0.0133 t ha^{-1} $event^{-1}$) and the smallest in invaded unfenced plots (0.0127 ± 0.0028 t ha^{-1} $event^{-1}$).

3.5. Runoff bacteria

Runoff FIB was correlated with runoff TSS, although maximum FIB detection limit was reached a number of times (Supplemental Fig. 3). During some activations, certain plots had minimal runoff and no soil erosion resulting in low FIB values (as identified in Section 3.3), while other plots had large runoff volumes with high soil erosion leading to high overall variability and no forest or fencing effects on runoff FIB (Table 4). While runoff enterococci and *E. coli* tended to be greater in unfenced plots compared to fenced plots, high variation among sites prohibited the detection of a significant fencing effect and there were no clear trends between soil and runoff FIB values across treatments (Fig. 4; Supplemental Table 2).

4. Discussion

The introduction of wild pigs has dramatically altered ecosystems worldwide (Campbell and Long, 2009), but few studies have been able to quantify their effect on water and soil resources (Dunkell et al., 2011a, Ziegler and Giambelluca, 1998). Additionally, concurrent changes in vegetation cover are expected to alter forest hydrology (Giambelluca et al., 2007, Mair and Fares, 2010, Mudd and Giambelluca, 2006) and the interactions between vegetation and ungulates are of particular interest to watershed managers. We found that *P. cattleianum* invasion affected pig activity, forest composition and structure (supported H1), soil structure (supported H2), soil moisture, and runoff volume (supported H3). Pig activity in unfenced plots altered groundcover (supported H4), soil *E. coli* (supported H5), runoff, and soil erosion (supported H6) compared to fenced plots. While unfenced, invaded forests had the greatest mean soil FIB and mean runoff FIB, we found no interaction effects on soil FIB, runoff volume or runoff TSS (not supported H7). The lack of significant interaction effects between *P. cattleianum* invasion and pigs would be due to complications between study design and the many additional interactions among canopy vegetation, groundcover, soil and hydrology that we were unable to monitor or there may not be significant interaction effects.

4.1. Forest and pig effects on throughfall, runoff and soil erosion

We initially expected differences between the native and invaded forests in throughfall and stem flow would drive differences in runoff and soil erosion, with larger pulses of overland flow (Mair and Fares, 2010, Takahashi et al., 2011). This expectation also lines up with modeling results that suggest that hydrology effects of *P. cattleianum* at the watershed scale increases runoff and storm flows while reducing groundwater recharge and baseflow (Strauch et al., in review). While it is possible that stem flow increased in runoff plots in the invaded forest, we did not directly measure this variable and *P. cattleianum* stem densities were relatively low overall in the invaded runoff plots compared to heavily invaded lower elevation forests (Strauch et al., in review). The *Psidium cattleianum* biomass in heavily invaded stands represents greater than 10% basal area but can have densities as great as 4000 stems ha^{-1} (personal observation). *Psidium cattleianum* forests have a more closed canopy, increasing interception and canopy evaporation while reducing throughfall. Further, differences in throughfall rainfall intensity may affect the removal of fecal bacteria transported in runoff (Blaustein et al., 2016). Modeled mean annual rainfall was slightly greater in invaded forests and these results would also be expected if invaded forest canopy rainfall was also consistently greater (Giambelluca et al., 2011). Alternatively, differences in canopy rainfall may mitigate the forest effect on throughfall. Native forest runoff could be attributed to increased throughfall due to reduced canopy interception, but no throughfall differences between forests suggests that reduced interception may instead have led to greater rainfall energy and more runoff compared to invaded forests.

Runoff and erosion differences between forests may also be due to differences in groundcover that affected infiltration. Invaded forests had more litter cover and less vegetation cover that would otherwise protect the soil surface from erosion. Soil differences between forests (soil moisture and % organic matter) also indicate that native forest soils are more homogenous due to rooting (Singer et al., 1984). And so while changes in forest composition may alter watershed dynamics, our current study design does not allow us to differentiate underlying mechanisms.

Despite the observed wild pig activity, we found no statistical effects of fencing on runoff or soil erosion, likely due to the short time-frame presented here. Current results only consider the first 22 months following fencing, the effects of which can take years to manifest (Dunkell et al., 2011b). In line with this interpretation, while no differences in runoff volume or soil erosion were observed during the first two large rainfall events (December 2012 and February 2013), we did observe greater soil erosion in unfenced native forest plots during the last two events (November 2013 and December 2013), possibly a function of increased differences in bare soil between plots (Singer et al., 1984). Using a similar setup of paired runoff plots on O'ahu Island, Dunkell et al. (2011b) found no significant fencing effect on runoff within the first year of plot establishment. By contrast, after seven years of soil recovery, Vtorov (1993) found that soil porosity outside of a pig enclosure was more than three-fold higher than within the enclosure. We did not find any synergistic effects of *P. cattleianum* and pigs that enhanced surface runoff and soil erosion. However, we found that wild pigs were more active in native forests, perhaps because high stem densities and dense, shallow root structures of *P. cattleianum* impede the movement and rooting of pigs. *Psidium cattleianum* can also reduce the growth of native understory species favored by pigs (Huenneke and Vitousek, 1990), but this may be offset by fruit production by *P. cattleianum*.

Table 1
Elevation (m), pig activity index, tree basal area (m^2 ha^{-1}) and stem density (ha^{-1}), diversity (Simpson's D) slope (%), canopy cover (% openness) and canopy cover (leaf area index; LAI) of paired (fenced/unfenced) runoff plots in the Hawai'i Experimental Tropical Forest, Hawai'i Island.

Site	Forest	Elevation (m)	Pig activity index at 17 months (m^{-1})	Pig activity index at 38 months (m^{-1})	Basal area (m^2 ha^{-1})	Stem density (ha^{-1})	*P. cattleianum* Basal Area (m^2 ha^{-1})	Simpson's D' diversity index	Slope (%)		Canopy cover (% openness)		Canopy cover (LAI)	
									Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
NF1	Native	1340	4.98	0.45	119.3	2482.8	0.00	1.87	8.5	8.5	10.9	9.9	3.41	2.97
NF2	Native	1340	3.27	0.22	95.6	2705.6	0.00	2.33	11.0	9.5	7.7	7.5	3.27	3.49
NF3	Native	1340	4.27	0.37	87.0	2228.2	0.00	2.38	5.5	5.5	14.6	8.6	4.20	4.37
SG1	Invaded	840	0.49	0.11	94.3	5252.1	14.692	1.82	8.0	8.5	2.6	3.3	3.40	3.72
SG2	Invaded	840	0.19	0.19	108.1	4742.8	14.795	1.53	8.5	8.5	6.7	7.4	2.74	2.94
SG3	Invaded	840	0.57	0.28	148.4	4360.9	16.357	1.43	7.0	7.0	7.6	8.0	3.12	3.08

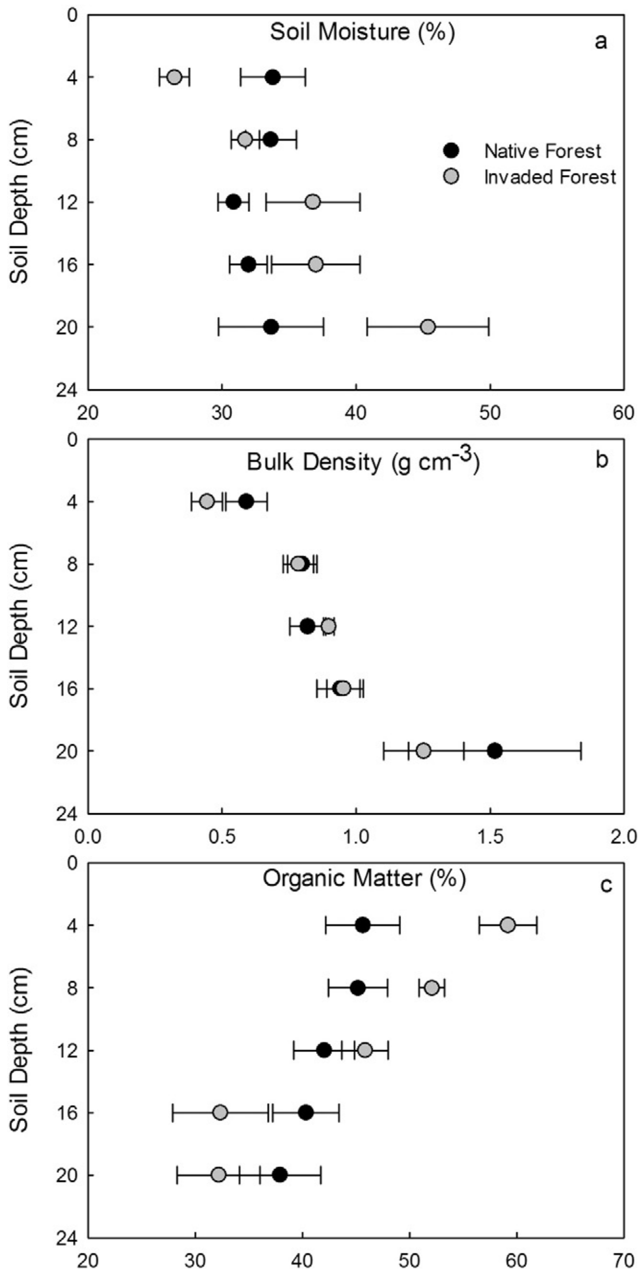

Fig. 2. (a) Mean (±standard error) soil moisture (%), (b) mean bulk density (g cm^{-3}) and (c) mean percent (%) organic matter for soil core segments ($n = 9$) at increasing (0–20 cm) depths from plots 19 months after fencing in the Hawai'i Experimental Tropical Forest, Hawai'i Island.

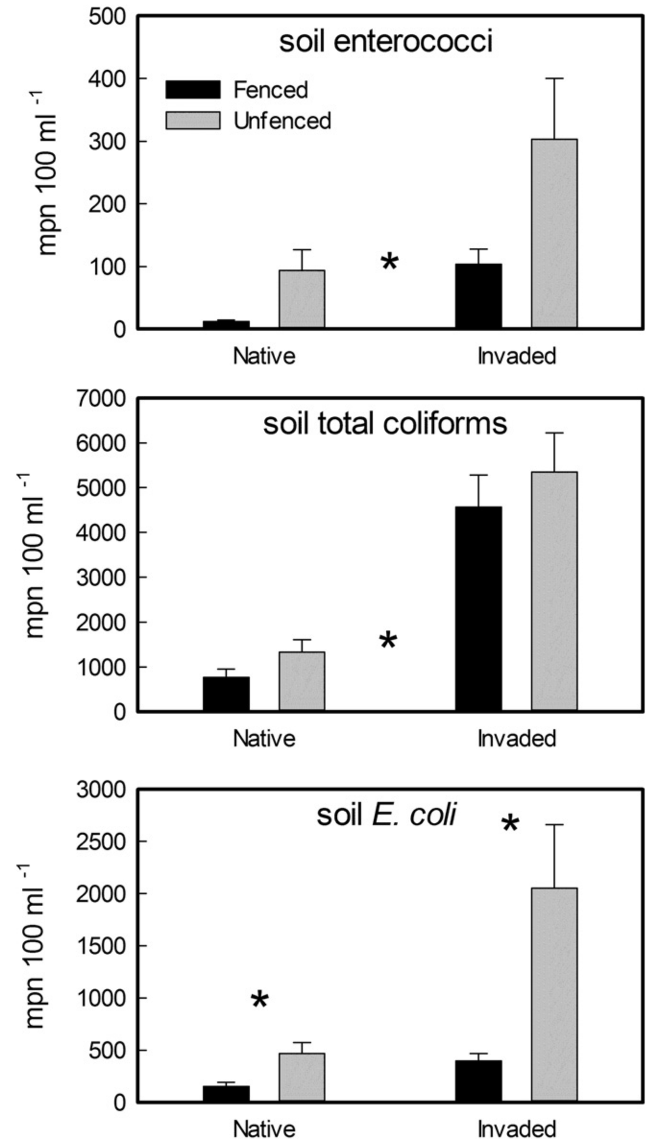

Fig. 3. Mean (±standard error) soil fecal indicator bacteria ($n = 30$) at activation in native and *P. cattleianum*-invaded forests for fenced and unfenced runoff plots in the Hawai'i Experimental Tropical Forest, Hawai'i Island. Stars between bar sets indicate significant forest effects while stars above bar sets indicate significant fencing effects.

4.2. Feral pig effects on soil and runoff bacteria

The transport of fecal bacteria from animal waste in surface runoff is often impacted by groundcover and vegetation (Stout et al., 2005).

Table 2
Two-way repeated measures analysis of variance *F*-values testing the effect of forest (native vs. *P. cattleianum*-invaded) and soil depth (0–20 cm at 4 cm increments) on percent (%) soil moisture, bulk density (g cm^{-3}) and % organic matter.

	% soil moisture		Bulk density		% organic matter	
	df	F	df	F	df	F
Forest	1	0.548	1	0.377	1	0.110
Depth	4	7.830**	4	6.426**	4	13.289***
Forest * depth	4,16	9.065***	4,16	0.307	4,16	4.651*

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 3
Two-way repeated measures analysis of variance sum of squares (SS) and *F*-value results for mean log(x + 1) transformed soil enterococci, total coliforms, and *E. coli* with forest (native vs. invaded) and fencing (fenced vs. unfenced) fully fixed factors and a forest * fencing interaction effect from 10 collection dates from October 2012 to April 2014 (N = 40; df = 1,9).

	Soil enterococci		Soil total coliforms		Soil *E. coli*	
	SS	F	SS	F	SS	F
Forest	5.016	6.44*	4.86	11.90**	0.502	0.54
Fencing	0.497	2.54	0.53	3.68	1.363	6.23*
Forest * fencing	0.001	0.005	0.15	1.16	0.976	1.95

* $p < 0.05$.
** $p < 0.01$.

Table 4
Two-way repeated measures analysis of variance sum of squares (SS) and *F*-value results for mean runoff volume, total suspended solids (TSS), and TSS % organic matter with forest (native vs. *P. cattleianum*-invaded) and fencing (fenced vs. unfenced) fully fixed factors and a forest ∗ fencing interaction effect from 16 collection dates from October 2012 to April 2014 ($N = 64$; df = 1,14). Two-way repeated measures analysis of variance sum of squares (SS) and *F*-value results for log(x + 1)-transformed mean runoff enterococci, total coliforms, and *E. coli* from 9 collection dates from October 2012 to April 2014 (N = 54; df = 1.8).

Runoff	Forest		Fencing		Forest ∗ fencing	
	SS	F	SS	F	SS	F
Volume	59,152,807	6.42*	1,077,012	0.48	6,083,645	4.02
TSS	3042	14.03**	612	1.16	431	0.77
TSS % organic matter	415	3.06	393	3.51	265	9.23**
Enterococci	0.111	0.25	1.244	2.43	0.400	0.60
Total coliforms	0.183	0.44	0.497	0.95	1.611	1.69
E. coli	0.025	0.121	0.603	3.26	0.001	0.002

* $p < 0.05$.
** $p < 0.01$.

While warm, moist tropical soils can sustain populations of fecal bacteria (Fujioka et al., 1998), pig activity was expected to enhance soil bacteria via fecal inputs. Within one year following fence construction we found signs that soil FIB in fenced plots declined compared to unfenced plots, but effects were not significant. Although Dunkell et al. (2011b) found no differences in soil FIB in the first year of data collection, Bovino-Agostini (2012) found a fencing effect three years post-fence construction on O'ahu. Runoff FIB levels in unfenced plots were in line with other studies of wildlife impacted water resources (Strauch, 2011).

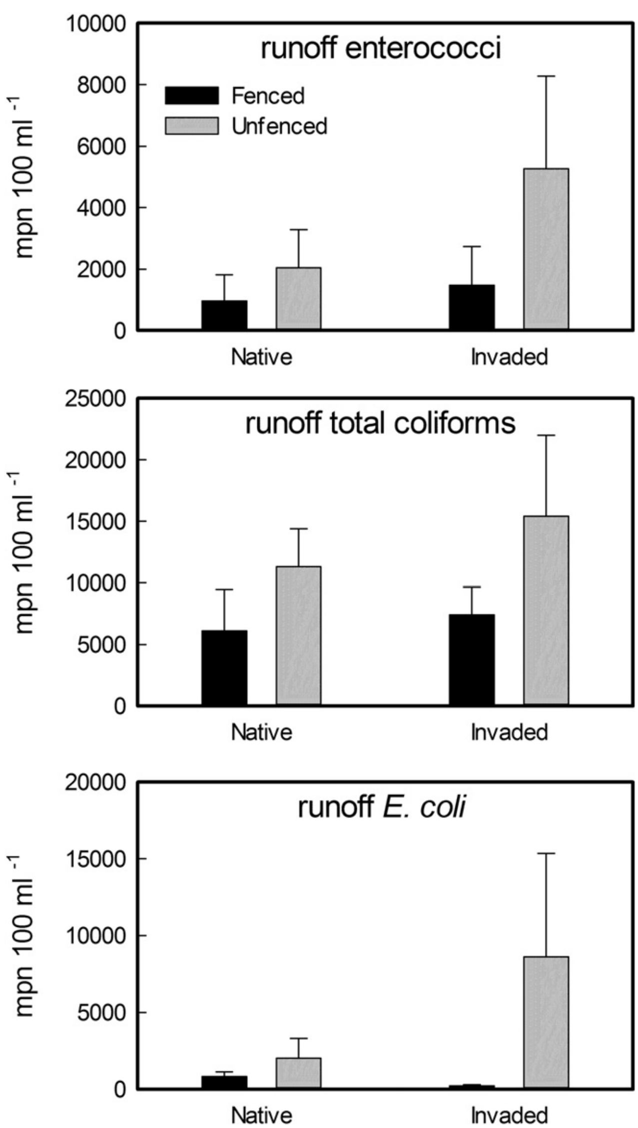

Fig. 4. Mean (±standard error) runoff fecal indicator bacteria ($n = 19$) at activation in native and *P. cattleianum*-invaded forests for fenced and unfenced runoff plots in the Hawai'i Experimental Tropical Forest, Hawai'i Island.

5. Conclusions

The continued invasion of native forests by non-native plant and animal species has serious consequences for watershed function and erosion. Our short-term study demonstrates that fencing can increase groundcover vegetation and reduce soil FIB. The behavioral link between *P. cattleianum* and pig activity was surprising and demonstrates that vegetation-driven pig behavior may exert as large an influence on ecosystem and watershed function as either fencing or plant control treatments. This clearly highlights that watershed management needs to address both vegetation and ungulate problems concurrently, as protecting native forests from one type of invasive species in isolation may leave the habitat vulnerable to alterations by the other.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.geoderma.2016.05.021.

Acknowledgements

R. Tingley provided assistance with the slope analysis. Support in the field was provided by P. Foulk, T. Frauendorf, T. Sowards, and R. Tingley. S. Hess provided useful comments on an earlier draft. Special thanks to the State of Hawai'i, as well as the USDA Forest Service for site access. Funding was provided by the USDA Forest Service (Research Joint Venture #10-JV-11272177-030 grant to G. Bruland) and the McIntire-Stennis Forestry Research grant (HAW00108-M) to G. Bruland as well as institutional support by the University of Hawai'i.

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