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ORIGINAL PAPER

Landscape level effects of invasive plants and animals on water infiltration through Hawaiian tropical forests

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Abstract Watershed degradation due to invasion threatens downstream water flows and associated ecosystem services. While this topic has been studied across landscapes that have undergone invasive-driven state changes (e.g., native forest to invaded grassland), it is less well understood in ecosystems experiencing within-system invasion (e.g. native forest to invaded forest). To address this subject, we conducted an integrated ecological and ecohydrological study in tropical forests impacted by invasive plants and animals. We measured soil infiltration capacity in multiple fenced (i.e., ungulate-free)/unfenced and native/invaded forest site pairs along moisture and substrate age gradients across Hawaii to explore the effects of invasion on hydrological processes within tropical forests. We also characterized forest composition, structure and soil characteristics at these sites to assess the direct and vegetation-mediated impacts of invasive species on infiltration capacity. Our models show that invasive ungulates negatively affect soil infiltration capacity consistently across the wide moisture and substrate age gradients considered. Additionally, several soil characteristics

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known to be affected by invasive ungulates were associated with local infiltration rates, indicating that the long-term secondary effects of high ungulate densities in tropical forests may be stronger than effects observed in this study. The effect of invasive plants on infiltration was complex and likely to depend on their physiognomy within existing forest community structure. These results provide clear evidence for managers that invasive ungulate control efforts can improve ecohydrological function of mesic and wet forest systems critical to protecting downstream and nearshore resources and maintaining groundwater recharge.

Keywords Invasive ungulates · Soil infiltration capacity · Tropical forest ecohydrology · Invasiveimpacts on ecosystem services

Introduction

Invasive species have transformed the structure and function of native ecosystems at a global scale. In addition to changes to plant community composition and associated fauna, plant and animal invasions can have dramatic direct and indirect effects to ecosystem processes such as soil nutrient cycling, primary productivity, and hydrological cycles (Levine and D'Antonio 2003; Ehrenfeld 2010; Catford 2017). In particular, invasion of forest ecosystems may disrupt some of Earth's most productive, high-quality reliable sources of freshwater (Neary et al. 2009). Quantifying and understanding the differences in hydrological function between native and invaded systems can provide essential information to watershed managers responsible for maintaining water flows critical to forest health and downstream anthropogenic needs.

Past research shows that shifts in vegetation life form, such as woody encroachment of arid landscapes or alteration of tropical forested landscapes to exotic grass pastures, incur dramatic hydrological shifts (Le Maitre et al. 1996; Bruijnzeel 2004; Huxman et al. 2005; Bonell et al. 2010; Muñoz-Villers and McDonnell 2012; Vasquez-Valderrama et al. 2020). While it may be more challenging to detect ecohydrological disruptions of within-system invasions (e.g. native forest to invaded forest) when compared to an invasive-driven type shift (e.g. forest to grassland conversion), research indicates ecohydrological impacts of invasion may still be significant. It has been proposed that non-native plants with different life history strategies or traits than native species are most likely to alter ecosystem function (Vitousek and Walker 1989; Ehrenfeld 2010) including ecosystem-scale evapotranspiration rates, water flow paths (via root size and depth), runoff, and erosion (Cavaleri and Sack 2010; Catford 2017). Indeed, Cavaleri and Sack (2010) found in a meta-analysis comparing native and invasive species with the same life form, that invasive species often had higher transpiration rates at the leaf scale, but that at the whole plant or landscape-scale, this did not translate into higher evapotraspiration rates in invaded systems except in warmer, wetter environments.

Invasive animals can also have direct and indirect impacts on ecohydrological processes, although the directionality of these has been more challenging to generalize. Singer et al. (1984) found that pig rooting decreased bulk density and hence increased infiltration in sites at the Great Smoky Mountains National Park in the Southeastern United States. In contrast, Long et al. (2017) found that sites with feral pigs (*Sus scrofa*) had higher bulk density, and reduced porosity and stable soil aggregates when compared to those where pigs had been removed across forested sites in Hawaii. Indirectly, feral animals can impact soils by altering plant communities and thus rooting depths, organic matter inputs, water interception and other processes that impact hydrological cycles (Nuñez et al. 2008; Leopold and Hess 2017). Co-invasion by exotic plants and animals can also lead to synergistic and/or interactive effects. For example, the high stem densities of strawberry guava (*Psidium cattleianum*) in invaded Hawaiian forests were correlated with less rooting by pigs, leading to native forests having more pig activity and greater erosion than invaded stands (Strauch et al. 2016).

There is considerable evidence documenting how land cover change alters forest hydrologic function across nearly all continents, even post-reforestation (see Filoso et al. 2017; Bonnesoeur et al. 2019). However, it is unclear the degree to which within-system invasion transformation impacts ecohydrologic function; to-date most studies evaluating changes to ecohydrologic function include nearly or fully converted landscapes compared to native systems (Giambelluca 2002). These strong contrasts do not directly capture changes in ecohydrologic function under the levels of invasion where conservation efforts are more feasible and could prevent further land cover conversion.

In Hawaii, ecosystems have experienced dramatic and widespread invasion by non-native plants and animals. Nearly one third of mesic and wet forests are already dominated by invasive plant species and disturbed by feral pigs and other ungulates (Jacobi et al. 2017a). While these mesic and wet forests cover just 28% of Hawaii's land area (Jacobi et al. 2017a), they receive 50% of precipitation across the state (Giambelluca et al. 2013), likely having large impacts on water cycling and island-wide freshwater resources. Preserving forest hydrologic function is of particular concern in Hawaii, which is prone to drought conditions across ecosystem types, and has limited water resources as an island-state (Frazier et al. 2018). There have been studies investigating how land-use change, invasive species, and restoration have altered hydrological processes, although these are generally focused on broad comparisons between forested areas, grasslands, and bare soil areas, or very limited in range (Wood 1971; Ziegler and Giambelluca 1998; Perkins et al. 2012; Strauch et al. 2016, 2017). Due to the unreplicated nature of conservation and restoration projects that are large enough to affect water cycling, as well as steep topographic gradients and substrate age differences between locations, many past studies necessarily include a single or unpaired site design (Ziegler and Giambelluca 1998; Takahashi et al. 2011; Perkins et al. 2014; Dudley et al. 2020). To date, a landscape-scale perspective of the impacts of invasive plants and animals on hydrological processes in Hawaii is lacking.

Here we use a landscape-scale approach to ask how invasive plants and animals are affecting water infiltration within invaded tropical forests. We use soil infiltration as a common metric between these sites, since it is a widely used, inexpensive, repeatable measure indicative of the partitioning between runoff and infiltration. We sampled multiple fenced (i.e., ungulate-free)/unfenced and native/invaded forests along moisture and substrate age gradients across the islands of Hawaii and Kauai. Within these forests we characterized forest composition and structure and soil characteristics to assess the effects of invasive species on soil infiltration capacity. We predicted that sites with native, undisturbed forests would have higher rates of infiltration compared to invaded, disturbed sites, and younger substrates would have higher rates of infiltration compared to older substrates with soils containing higher amounts of clay.

Methods

We measured variables representing ecological, environmental and physical characteristics previously documented to influence infiltration capacity at the local scale (Fig. 1) using a paired site sampling regime. We quantified differences among native and invaded forests (N/I sites), and fenced and ungulate damaged unfenced forests (F/U sites) across mesic and wet environments on Hawaii and Kauai Islands. To minimize the influence of unmeasured variables in these comparisons, N/I sites and F/U sites were always placed near each other (mostly within 100 m distance). We define each management treatment below:

Native sites A majority (> 50%) of cover of both overstory and understory layers are native. For this study we focused on forest sites with the tree canopy dominated by keystone species ohia, *Metrosideros polymorpha*, or ohia/koa, *Acacia koa*.

Invaded sites Majority of understory cover either strawberry guava, *Psidium cattleianum*, Himalayan ginger, *Hedychium gardnerianum*, or non-native grasses. Tree canopy was dominated by ohia or ohia/koa, or strawberry guava.

Fenced ungulate-free sites Majorities (> 50%) of both canopy and understory layers are dominated by native species with the tree canopy dominated by ohia or ohia/koa. Areas within fences contain no sign of ungulate damage. To the authors' knowledge, all fenced sites had been ungulate-free for at least 5 years at the time they were sampled.

Unfenced ungulate-damaged sites Same forest composition as fenced sites, but in unfenced areas with clear signs of ungulate damage (rooting, trails, etc.). Given the distribution of ungulates across the islands of Hawaii and Kauai in the areas we sampled, most ungulate damage in the forests we sampled was likely caused by non-native feral pigs.

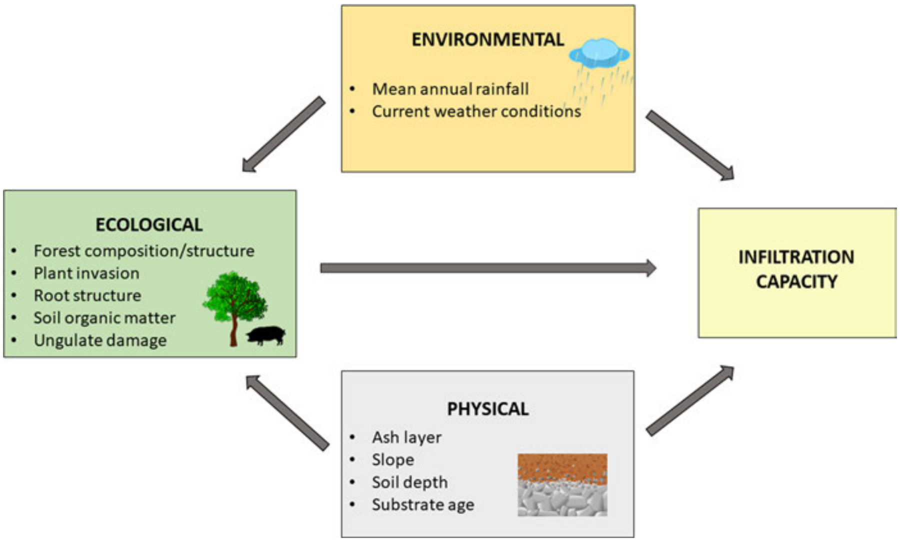

Fig. 1 Conceptual diagram of the factors measured in this study to investigate how ecological, environmental and physical characteristics of a site influence infiltration capacity

No interaction between treatments were considered (e.g., fenced native vs. unfenced non-native sites) given the challenges in site selection (see below) and many rare or impossible interactions (e.g., fenced invaded sites). Additionally, we wanted to identify possible distinctions between effects of invasive plants and ungulates on forests in Hawaii; the interactive effects of invasive plants and ungulates has been well-documented in Hawaii and elsewhere (Simberloff and Von Holle 1999; Siemann et al. 2009; Leopold and Hess 2017). Instead, all native/invaded site pairs were located in unfenced areas, except for sites within Hawaii Volcanoes National Park (Nahuku, Kipuka Puaulu, Kipuka Ki).

Sampling along substrate age and moisture gradients

To ensure our efforts were relevant to the wider Hawaiian landscape, we attempted to replicate N/I and F/U site pairs across the clear substrate age and moisture gradients that have been shown to shape vegetation and soil patterns across the state (Kitayama and Mueller-Dombois 1995; Asner and Vitousek 2005). Furthermore, given a focus on mesic and wet forests, only areas with a greater than 50% canopy cover were considered. To select candidate areas across mesic and wet forests, we used the Price et al. (2007) moisture zone map available for the entire state. We excluded areas in the dry moisture zone as they contribute little to statewide rain catchment, and also have very few native and ungulate-free managed areas. Sites spanned a precipitation gradient of 1658 to 6218 mm/year.

We subdivided the landscape into three substrate age classes (young/medium/old) based on U.S. Geological Survey geology maps for the state (Sherrod et al. 2007). These age cutoffs were specific to moisture zone to account for the moisture-related differential rate of soil development (Chadwick et al. 1999). For wet forests, the young substrate age class spanned 0–10 K years; the medium age spanned 10–30 K years; and the old substrate age class spanned all soil > 30 K old. For mesic forests, the young substrate age class also spanned 0–10 K years; the medium age spanned 10–140 K years; and the old substrate age class spanned all soil > 140 K old. The young substrate age class encompasses a spectrum of soil development conditions as this age group is still largely affected by the high variability of lava flow topology and deposition of fine-grained tephra. The medium to old substrate cutoff represents the start of greater clay concentration and higher heterogeneity in soil that affects water retention and allows for lateral water movement such as lateral pan formation.

Site selection

We created a structured site selection process across Hawaii and Kauai Islands to ensure full consideration of the relevant factors beyond moisture zone and substrate age given the complex nature of our site criteria. First we conducted a GIS analysis where we excluded highly degraded and unvegetated areas (Price et al. 2007); very young primary succession areas with little soil and vegetation (Price et al. 2007); non-forested areas (Jacobi et al. 2017b); and areas far from road access, given the logistics of carrying field equipment. Additionally, with assistance from local land managers, we compiled information on all fenced areas across Hawaii and Kauai Islands to identify candidate sites with/without ungulate damage. To narrow our selection further, we removed areas with $> 30\%$ slope from consideration because our infiltration methods required relatively flat ground for measurements. We reviewed candidate sites with local land managers and evaluated suitability using Pictometry® (EagleView Technologies Inc., Rochester, New York, USA) aerial imagery. Lastly, we visited and evaluated over 100 potential study site pairs to ensure suitability for infiltration measurements (minimum soil depth of 5 cm), minimum stand size (> 20 m radius) and vegetation characteristics matching our four treatments described above, identifying a total of 40 sites for sampling purposes (Fig. 2). All sites were named according to their moisture zone, substrate age, management status, and site pair number (e.g., WYF1/WYU1 are the first paired fenced/unfenced site in wet young substrate areas).

Sites and plot sampling design

Within each site in a given site pair, 17 plots were selected where we measured infiltration capacity, vegetation, soil and other local environmental characteristics. The number of plots per site was determined by a power analysis using previously collected infiltration data from other sites in Hawaii (Perkins et al. 2018).

The 17 plots were placed in a radial design where, besides the plot at site center, two plots were placed along each of 8 cardinal and intercardinal directions along a radius of 15 or 20 m (Supplemental Fig S1). Radius size was dependent on stand size, and spacing of plots along the radius was calculated to ensure at least a 6.5 m distance between plots. We used this radial sampling design to minimize potential bias in our plot locations. While infiltration measurements can vary widely over very short distances (Gupta et al. 2006), we tested for spatial autocorrelation between plots by comparing variability of nearby plots to variability across all plots within a site. These analyses confirmed that our infiltration measurements were independent.

At each plot within a site, independent measurements were made including: (1) infiltration measurements; (2) soil hydrophobicity measurements; (3) compositional and structural vegetation surveys; (4) ungulate damage surveys; (5) soil organic matter (SOM), particle size and depth assessments; and (6) weather conditions. Each of these measurements and surveys are detailed in Table 1. Because of the expected influence of the immediate surrounding environment on infiltration, which is the focus of our research project, nearly all other measurements and surveys were done within a 3-m radius from plot center. Special use permits were acquired prior to conducting research activities.

Infiltration measurements

To reduce the influence of soil disturbance from field team activities, infiltration rate in each of the plots was measured first. Infiltration capacity was assessed by measuring field-saturated hydraulic conductivity (Kfs), a measure of the ability of water to move through soils. We used portable, falling-head, small-diameter (20 cm) single-ring infiltrometers that allow relatively rapid measurements (Nimmo et al. 2009). This method, which employs an analytical formula for Kfs, compensates for both variable falling-head and subsurface radial spreading that unavoidably occurs with small infiltrometer ring size (Perkins et al. 2012).

To avoid subjective sampling bias for Kfs measurements, we installed an infiltrometer ring at the center of each plot. In a few cases when large rocks or roots were present, the infiltrometer was offset as little as possible from plot center. We inserted infiltrometer rings 5 cm into the soil by pounding them evenly across the rim. When necessary, we cut roots around the infiltrometer rings to avoid disruption to the soil within the ring insertion area. After installation, the litter layer within the ring was removed and the height of the infiltrometer above ground was measured on

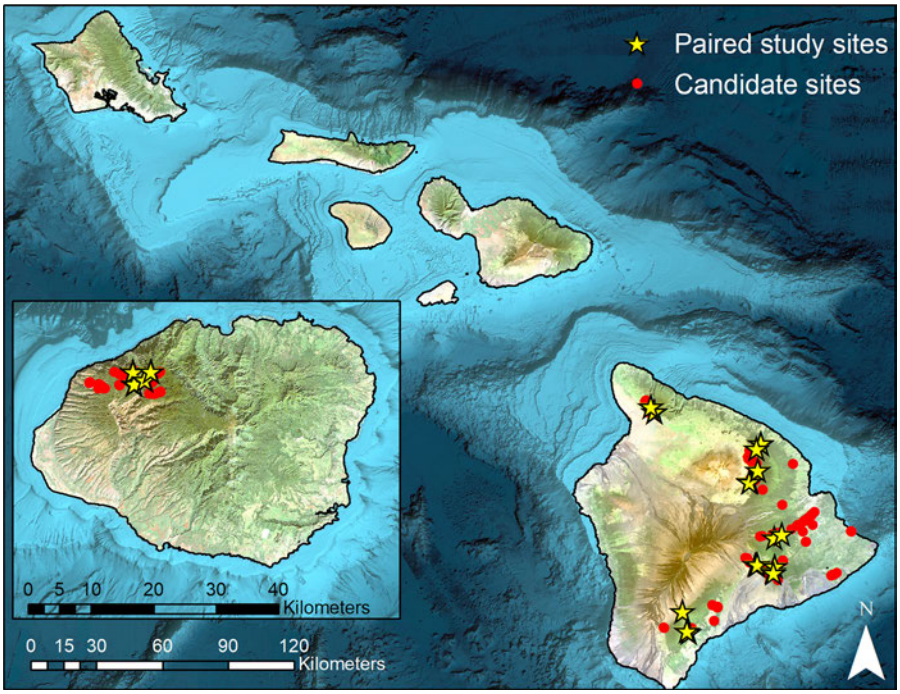

Fig. 2 Candidate study sites (red dots) and 39 final study sites (yellow stars) across Hawaii (far right) and Kauai (left inset) Islands. Access to one planned site was ultimately not possible. Landsat-7 image courtesy of the U.S. Geological Survey

four locations around the ring to calculate infiltrometer depth.

We made three sets of measurements to estimate Kfs at each plot. The first two sets of measurements were done by pouring 1 L of water (equivalent to 6.4 mm of precipitation, in total) into the infiltration ring and measuring the time necessary for the water to be fully infiltrated into the soil. The third measurement set, done shortly after the first two, was made by pouring 2 L of water into the infiltrometer and then measuring the depth of water inside the infiltrometer at set 30 s intervals since pour. For these depth by time measurements, at plots where infiltration rates were slow (i.e., the preceding 1 L measurements took > 10 min), we deployed automated camera systems to monitor depth changes over time that allowed us to conduct multiple infiltration measurements at once. In a few plots where infiltration was extremely fast, the third measurement set was similar to the first two where we measured the time required for 2 L of water to be fully infiltrated into the soil. In total, at each plot we used 4 L of water for infiltration measurements.

We used the mean value from the last two measurements of the 2 L infiltration test taken at each plot to estimate Kfs. However, when necessary we excluded the last measurement as it often had a higher measurement error associated with measuring water depth as it neared irregular soil surfaces (Supplemental Fig S2). In these cases, we used the second and third to last measurements. Kfs was calculated following the approach by Nimmo et al. (2009) where we used these measurements along with dimensions and geometry of the infiltrometer, and depth of soil penetration to estimate Kfs for each pour. We also performed hydrophobicity and preferential flow measurements at each plot along with our infiltration measurements. However, due to relatively wet field conditions, both hydrophobicity and preferential flow measurements were challenging to perform and showed little variation across all plots in the study.

Compositional and structural vegetation survey

We recorded total plant cover at each plot using both a densiometer and expert ocular estimates. We used the densiometer readings to ensure a standardized assessment of vegetation cover. Total cover above the forest floor (1 m height) was estimated using the common

Table 1 List of variables measured at each site

Variable	Variable type	Measurement scale
Treatment: native/invasive	–	Site
Treatment: fenced/unfenced	–	Site
Site moisture zone	Climate	Site
Site substrate age	Soil	Site
Percent sand	Soil	Site
Percent silt	Soil	Site
Percent clay	Soil	Site
Soil organic matter (lab)	Soil	Site
Field-saturated conductivity: Kfs	Soil	Plot
Soil depth	Soil	Plot
Soil organic matter (expert estimate)	Soil	Plot
Soil large roots (expert estimate)	Soil	Plot
Ungulate damage (expert estimate)	Ungulate damage survey	Plot
Ungulate damage (quadrat estimate)	Ungulate damage survey	Plot
Total cover at 1 m height	Vegetation survey	Plot
Densiometer cover	Vegetation survey	Plot
Canopy cover	Vegetation survey	Plot
Relative canopy native tree cover	Vegetation survey	Plot
Proportion of ohia in canopy native tree cover	Vegetation survey	Plot
Understory woody cover	Vegetation survey	Plot
Relative understory native woody cover	Vegetation survey	Plot
Understory fern cover	Vegetation survey	Plot
Litter cover	Vegetation survey	Plot
Bare soil cover	Vegetation survey	Plot
Current weather	Weather	Plot
Past weather	Weather	Plot

Description of variables is provided in methods

method of averaging four individual densiometer readings per plot, with one facing each cardinal direction (Lemmon 1956). These measurements were used to anchor all subsequent cover estimates. We devised a rapid assessment ocular method to characterize forest structure and composition within a 3 m radius area around the plot center. In this assessment, the forest was divided into three strata that were evaluated separately: forest floor, understory, and canopy. The forest floor layer included all vegetation up to a height of 1 m. To avoid separately estimating partial cover of plants with foliage both below and above a height of 1 m, plants with live foliage starting below 1 m height were entirely included within the forest floor layer. This made the assessment of cover much easier and adaptable to differing conditions, and mostly affected cover estimates of the climbing fern, uluhe (*Dicranopteris* spp.) and Himalayan ginger. The understory layer extended from the top of the forest floor layer (1 m) to the top of the hapuu ferns (tree ferns, *Cibotium* spp.) or 5 m height when these were not present. The canopy layer extended from the top of the hapuu (or 5 m height) to the tallest tree crowns.

Within each of these strata, the absolute and proportional cover of woody, herbaceous, and fern cover was visually assessed and the relative dominance of native/invasive species evaluated. Individual cover estimates for dominant native/invasive forest species were also recorded (e.g., ohia, uluhe, hapuu, Himalayan ginger, strawberry guava). Over 55 different forest structure indices were collected and further derived from these vegetation surveys (Supplemental Table S1).

Ungulate damage surveys

We recorded two indicators of ungulate disturbance at each plot: quantitative and expert ocular estimates. Indices of disturbance within the plot were recorded loosely following methods described by Stone et al. (1991). Our quantitative estimate was based on the number of quadrants within a 3 m radius from plot center, excluding a 0.5 m center radius (see Supplemental Fig S3), that exhibited signs of ungulate disturbance varying from 0 (no sign) to 4 (ungulate sign within all 4 quadrants). Our second disturbance estimate was based on an expert assessment of the wider surrounding plot area, utilizing a 1–4 scale (1- None; 2- Slight; 3- Moderate; 4- High).

Soil surveys and sampling

Expert-based soil surveys were conducted at each plot. After the removal of the litter layer, an observer recorded soil dryness on a 1–5 scale (1 = very dry, 5 = saturated), and SOM as the proportion of soil volume within the infiltration ring composed of dead organic matter and plant roots. Soil depth was measured in cm at the site of infiltration measurements using a probe, with measurements up to a maximum of 120 cm. A garden trowel was used to collect 240–480 mL of soil below the litter layer down to approximately 5 cm depth at each plot. Samples were collected either directly beneath or to the right of soil collars, and below the root layer; fine roots were avoided. Samples were refrigerated until analysis. Soil samples from each plot were stirred and sieved to create a homogenous sample and oven-dried at 35 °C until weight stabilized. Approximately 30 mL of soil volume were collected from each sample and combined at the site level. Combined soil samples were submitted to a diagnostic laboratory to determine the proportion of sand, silt, and clay. All 39 sites were analyzed. Four samples were used completely during this process and not available for further analyses: WOI2, WON2, WOF2, WOU2. After soil composition analysis, samples were analyzed to determine organic matter content at the site-level. Approximately 30 g of soil from each sample was sieved to 2 mm to homogenize samples and eliminate large organic matter objects, dried overnight at 100 °C, and weighed. Soils were then ashed at 500 °C for at least 12 h and re-weighed. The proportion of organic matter in the soil was calculated by subtracting ashed-weight from dry weight, and dividing by the dry soil weight. To minimize error, the process was repeated and the average proportion of organic matter was recorded.

Weather conditions

Basic weather condition data were recorded at each plot. Past weather was recorded on a 1–5 scale, ranging from 1 = much drier than usual, and 5 = much wetter. Current rain, cloud cover and wind conditions were also recorded. Rain, and current and past weather conditions can influence infiltration and hydrophobicity measurements (Tricker 1981; Cerdà 1996). All expert-based estimates were done by the same observer throughout the study.

Data processing, analysis and modeling

We employed some gap-filling routines to address missing data. Because some modeling approaches require complete observations for each plot considered, excluding entire plots from the analysis when 1 of > 60 candidate predictor variables were missing would be too onerous. Given a > 0.8 correlation between quadrat and expert based ungulate damage assessment, we used quadrat-based estimates to fill missing expert estimates from 18 plots (2.7% of the data). Similarly, because of the lack of enough soil samples, lab measured SOM was missing for 4 of our 19 sites. To fill these gaps, we created a linear model between lab-based SOM and expert-based SOM estimates, and interpolated missing values. For all other variables, if for any given site there were less than 5 plots with missing data, we replaced the missing values with the mean value across all plots in the site. In-practice, this led to a very small number of substitutions (60 data points, or $\sim 0.1\%$ of the dataset).

To identify which local environmental factors correlated consistently with our primary measure of infiltration capacity, Kfs, we focused on identifying consistent correlations across landscape classes and management treatments. Hence for each factor considered, we evaluated the direction of correlation across all plots, across moisture zones, and substrate age in a total of six correlation tests.

To reduce collinearity in our model fits, we removed variables highly correlated with one another, and variables that had little or no correlation to our dependent variable in the correlation analyses. We merged silt and clay soil content variables by adding their combined percent content after discovering that the particle size analysis method used likely underestimated the percent clay content, particularly in the Hawaii Island sites. From the 86 variables available, we limited our models to consider 33 candidate predictor variables (Supplemental Table S2).

Following our correlation analysis, we developed regression models to best understand the relative importance and interaction between the variables associated with Kfs across mesic and wet Hawaiian forests. We used a linear forward and backwards stepwise model fitting procedure to construct a parsimonious model from the large set of vegetation, soil, and landscape level potential predictors of Kfs.

Prior to modeling we attempted to transform each candidate predictor variable using an approach that yields the most normalized data distribution (Peterson and Cavanaugh 2019). For each variable, we considered multiple transformations (log, square root, arcsin, exponential, Lambert, Box Cox and Yeo-Johnson) and used repeated cross-validation to estimate the out-of-sample performance of each transformation to select whether and how data were transformed for analyses (Supplemental Table S3; see example in Supplemental Fig S4). All data processing and analysis steps were done programmatically and directly from the raw data collected using the R statistical programming environment. All datasets collected for this study are publicly available (Fortini et al. 2020).

Results

A total of 39 sites were sampled, including 663 plots (Fig. 2; Supplemental Table S4), representing 19 site pairs across substrate age and moisture conditions (and one fenced site where access to its corresponding unfenced site was not possible). All sites were measured between the period of July and December 2017 to avoid the wettest part of the wet season in the state. Due to limited access across the island, sites in Kauai were spatially clustered on the Alakai plateau.

Many variables correlated well and consistently with Kfs across all plots and when subdivided by moisture zone, substrate age, or management treatment categories (Table 2). Regarding invasion related factors, both estimates of ungulate damage were consistently and negatively associated with Kfs (Fig. 3). Additionally, several other vegetation variables that showed some degree of correlation with Kfs seem indicative of differing degrees of ungulate damage (e.g., native herbaceous cover in forest floor). In terms of correlates with native/invasive plant variables, proportion of invasive grass in floor herb cover was consistently negatively correlated with Kfs while ohia canopy cover (the dominant tree species in native forests in Hawaii) was consistently positively related to Kfs. Non-native Himalayan ginger cover was also consistently positively related to Kfs.

Beyond native/invasive effects, we found several consistently positive correlations between Kfs and vegetation cover, including total woody cover (Fig. 4). While ohia canopy cover, native canopy cover, and total native woody cover were consistently and positively related to Kfs, total woody cover and densiometer cover were also positively related to Kfs.

Soil characteristics were consistently correlated to Kfs. Greater percent litter cover and SOM were associated with higher Kfs (Fig. 5). In contrast, several variables describing weather conditions (current rain, and past weather conditions) were consistently negatively correlated with Kfs, showing that if it had recently rained or was wetter than usual, Kfs tended to be lower. This reflects the known effect of moisture content at the time of infiltration measurement (Chowdary et al. 2006; Nimmo et al. 2009) and lends support for using paired sampling and other methods to minimize differences in measurement conditions as employed in our study.

We found a high correlation (Pearson's R = 0.773) between densiometer and ocular total cover estimates despite the fact that ocular estimates included only a 3 m radius area, whereas densiometer estimates included a wider canopy area. This correlation indicates optical estimates were adequate for estimating fractional cover across our plots. Quadrat and expert ungulate disturbance assessments were also strongly correlated (Pearson's R = 0.867), indicating that optical expert estimates were representative of plot-level ungulate damage. Correlation between expert and lab-based SOM values was moderately strong (Pearson's R = 0.51). Because ocular estimates were collected for each plot and were generally highly correlated with other more quantitative methods, we opted to use ocular estimates of canopy cover and

Table 2 Consistent correlations between plot-level log Kfs and vegetation and soil characteristics across all plots, across moisture zones, and substrate age classes

Variable	All	Mesic	Wet	Young	Medium	Old
Soil organic matter expert estimate	0.33*	0.19*	0.39*	0.22*	0.34*	0.50*
Soil conditions	− 0.33*	− 0.07	− 0.46*	− 0.42*	− 0.22*	− 0.40*
Wider ungulate damage ocular estimate	− 0.19*	− 0.37*	− 0.14*	− 0.27*	− 0.29*	− 0.15*
Percent litter cover	0.26*	0.30*	0.28*	0.14*	0.19*	0.28*
Absolute total woody cover	0.23*	0.10	0.30*	0.10	0.29*	0.27*
Absolute total native woody	0.20*	− 0.05	0.33*	0.06	0.31*	0.29*
Past weather	− 0.21*	0.12	− 0.29*	− 0.32*	− 0.19*	− 0.23*
Ohia cover in canopy	0.20*	− 0.06	0.30*	0.27*	0.04	0.31*
Native tree cover in canopy	0.16*	− 0.12	0.28*	0.15*	0.04	0.27*
Native herbaceous cover in forest floor	0.21*	− 0.05	0.26*	0.10	0.27	0.18*
Ginger cover in forest floor	0.15*	0.18	0.18*	0.26*	NA	0.16
Current rain conditions	− 0.16*	0.04	− 0.19*	− 0.26*	− 0.09	− 0.10
Densiometer canopy cover	0.04	0.11	0.01	− 0.14*	0.11	0.21*

Only variables that had at least 5 of 6 correlations agreeing in direction are presented. Generally accepted correlation values are as follows: weak correlation values (positive or negative) range from 0.1–0.3; moderate correlation values from 0.3–0.7, and strong correlation values are those > 0.7. *denotes statistical significance at $p \leq 0.05$

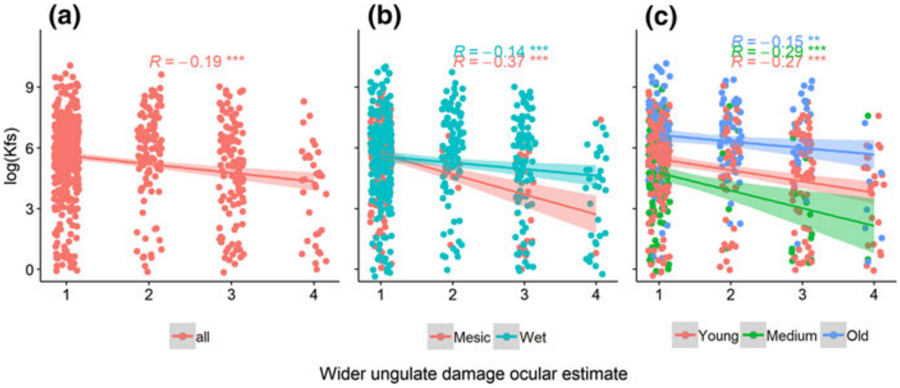

Fig. 3 Ungulate damage (based on a 1–4 scale: 1-None; 2-Slightly disturbed; 3-Disturbed; 4-Very disturbed) was consistently negatively associated with Kfs across landscape classes and management regimes, but in general correlation (R) was weak. *$p < 0.1$, **$p < 0.05$, ***$p < 0.01$. Associations across **a** all data, **b** moisture zones, and **c** substrate age. Shaded areas represent the 95% confidence interval of the linear fit between variables

SOM variables as predictors in modeling efforts and did not further consider densiometer or lab-based data. This approach also helped reduce collinearity in the dataset.

Kfs regression models

The final model for Kfs explains about 40% of Kfs variation and is statistically significant (F14, 648 = 25.34, $p < 0.001$; Fig. 6). We further parameterized a mixed effect model with site pair as a random factor to account for the potential effect of site in our model. Comparison of models with and without the random factor showed plot pair did not improve model fit using Akaike information criterion (AIC) values (Burnham and Anderson 2002), and therefore was not explored further.

Results show Kfs varies in relation to several vegetation, site, and soil related variables (Table 3). The sign of most regression coefficients match our expectations with relation to Kfs. For instance, SOM, canopy cover, and presence of large roots are all

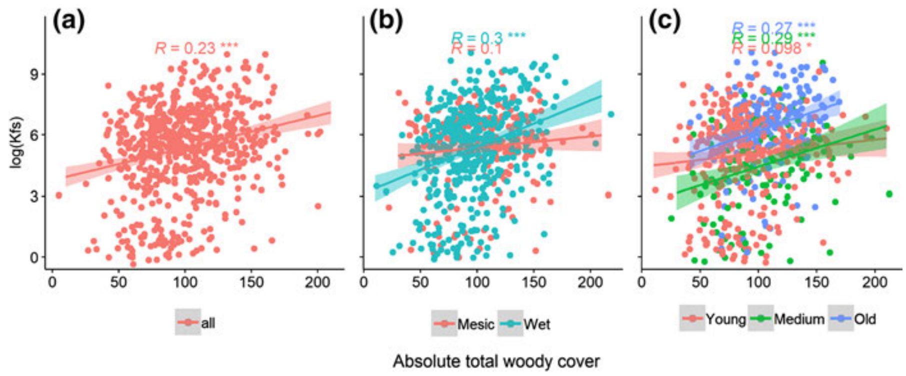

Fig. 4 Percent total woody cover was consistently positively correlated to Kfs. *$p < 0.1$, **$p < 0.05$, ***$p < 0.01$. Associations across **a** all data, **b** moisture zones, and **c** substrate age. Shaded areas represent the 95% confidence interval of the linear fit between variables

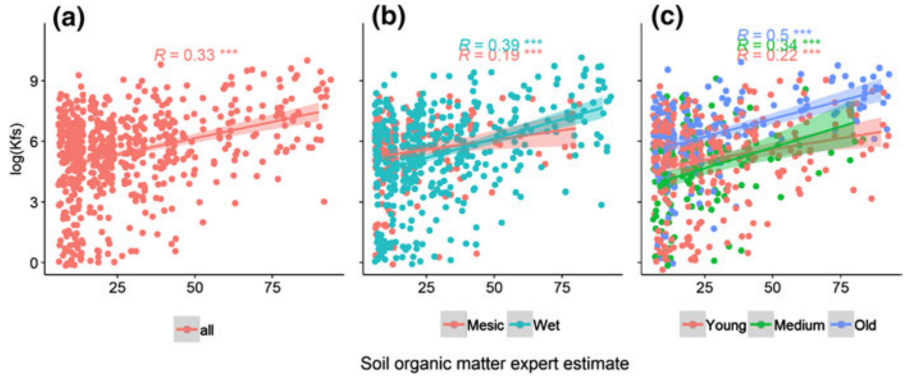

Fig. 5 Percent soil organic matter was consistently correlated to Kfs across landscape classes. *$p < 0.1$, **$p < 0.05$, ***$p < 0.01$. Associations across **a** all data, **b** moisture zones, and **c** substrate age. Shaded areas represent the 95% confidence interval of the linear fit between variables

positively related with Kfs, while ungulate damage and site slope were negatively related to Kfs. While the final model corroborates the effect of ungulates on infiltration capacity, only a few native/invasive predictors help explain Kfs variation. Grass cover was found to have a negative effect on Kfs whereas ohia canopy cover had a positive effect on infiltration capacity. Himalayan ginger cover was positively correlated to Kfs in previous analyses, although it was not a significant factor in our final model. Native woody cover at the forest floor had a small but statistically significant negative effect on Kfs.

Older substrates were associated with higher Kfs in our final model. Additionally, several other factors in our Kfs model were related to soil characteristics: SOM, presence of recent ash layer, presence of large roots, and bare soil cover. While current soil conditions were factors shown to influence Kfs, mean annual precipitation was not a significant factor in the final model.

We parameterized linear models including two-way interactions among predictors to explore if any meaningful interactions could further explain variation in Kfs. While the resulting model with interactions had an R^2 close to 0.5 ($R^2 = 0.47$), many interaction terms were of unclear biological interpretation, making the overall model with interactions much less useful for understanding drivers of Kfs and were not considered further. Lastly, to ensure our model results were not driven by remaining collinearity between predictor variables, we created a partial least square model and a ridge regression model that showed most relations we observed between Kfs and the stepwise linear model predictors were robust to collinearity.

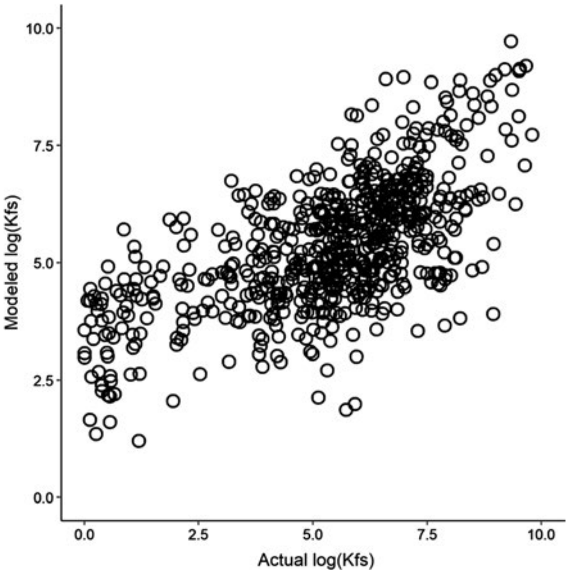

Fig. 6 Actual versus modeled log-transformed Kfs (mm/hr), based on final stepwise fitted model

Modelled response of Kfs to vegetation and soil-related plot conditions

Despite the strong correlations and statistically significant models relating Kfs to plot level variability in multiple vegetation and soil characteristics, we found no statistically significant site-level differences between fenced vs. unfenced or native vs. invaded sites. This was not only true when pooling all data, but also when looking at data within moisture zone and substrate age categories (Supplemental Fig. S5). In fact, controlling for moisture zone and substrate age potential differences in Kfs, analysis of variance (ANOVA) and linear mixed effect models (with site pair as random variable) showed no significant differences between native/invaded and fenced/unfenced sites. This lack of scaling of results from plot to site level is partly due to multiple factors in our model varying independently of one another across plots within each site and possibly obfuscating site-level effects.

Discussion

The suite of environmental, vegetation, and soil characteristic data collected allowed us to systematically test how variables ranging from canopy cover to SOM influence infiltration capacity, and to explore relations among these variables. Median Kfs rates were generally very high (633 mm/hr) across the forests considered in our study. This value is 3 times larger than the mean Kfs rate of 203 mm/hr found for

Table 3 Stepwise linear regression variables in the final model, their coefficients, relative importance in the model, and statistical significance

Variable	Coefficient	Variable importance	Pr(>|t|)
Soil organic matter (expert estimate)	0.44	5.42	< 0.001
Island age: Hawaii old	1.60	5.27	< 0.001
Ungulate damage (expert estimate)	− 0.39	4.43	< 0.001
Soil conditions	− 0.43	4.34	< 0.001
Island age: Hawaii medium	− 1.12	4.01	< 0.001
Absolute grass cover on forest floor	− 0.38	3.78	< 0.001
Site ash layer present	0.92	3.36	< 0.01
Absolute native woody cover on forest floor	− 0.28	3.29	< 0.01
Island age: Kauai old	0.78	2.65	< 0.01
Large roots (expert estimate)	0.01	2.59	0.010
Site elevation	0.26	2.27	0.024
Absolute ohia canopy cover	0.01	2.22	0.027
Absolute forest floor cover	0.19	2.16	0.031
Absolute woody cover on understory	0.17	2.06	0.040
Site slope	− 0.21	2.04	0.042
Soil depth	0.17	2.01	0.045
Bare soil cover	− 0.15	1.88	0.061
Absolute tree canopy cover	0.01	1.78	0.075

Variables are sorted by descending order of importance. Variable importance is a measure of each model variable's influence relative to the null model. Pr(>|t|) is the *p*-value for the two-tailed t-test of the distribution for each variable all previous measurements associated with tree and shrub vegetation in Hawaii (Perkins et al. 2018) and 3–10 times greater than other tropical forests (Bonell et al. 2010; Zimmermann et al. 2010; Hassler et al. 2011). Similar to previous studies, Kfs rates across our measured plots varied remarkably from 170 mm/hr to 2641 mm/hr (5 and 95 percentiles, respectively). Our combined island age variable was most important in determining Kfs in our models. Yet, surprisingly, there were no significant interactions between island age and the other model predictor variables, which would have indicated substrate-specific differences in how these predictors (e.g. ungulate damage) affect infiltration as has been found across other tropical forests (Zimmermann and Elsenbeer 2008; Zimmermann et al. 2010; Lozano-Baez et al. 2019). Aside from island-age, high Kfs rates were largely driven by a suite of forest structure variables, and lack of ungulates and their associated impacts.

Past research indicates invasive plants and disturbance of vegetation and substrate by feral ungulates may have large effects on local and downstream water resources because of differences in water-use efficiency and soil-related effects (Kagawa et al. 2009; Cavaleri et al. 2014; Strauch et al. 2016; Long et al. 2017; Litton and Cole 2018). Other studies indicate that invasive species, both plant and animal, have altered whole-watershed water balances (Giambelluca and Luke 2007; Giambelluca et al. 2008; Strauch et al. 2017), groundwater recharge (Engott 2011; Brauman et al. 2012, 2015) and led to downstream and near-shore ecological effects (Stock et al. 2011). Results of this study demonstrate that, while less extreme than a type shift from native forest to invaded grassland, within-system transformations (e.g. native forest to invaded forest) can still affect infiltration rates.

Effects of ungulates on infiltration capacity

Our results indicate that ungulate disturbance clearly negatively affected infiltration capacity across rainfall and substrate age gradients. This was expected as ungulates are known to disrupt soil structure, affect soil aggregate stability (Beever et al. 2006), and compact soils (Vtorov 1993; Beever et al. 2006). In Hawaii, ungulates are known to cause soil disturbance through trampling, creating wallows, digging, and indirectly causing erosion by exposing soils during bioturbation activities (Smith 1985; Stone and Anderson 1988; Long et al. 2017). There is also a substantial amount of research documenting negative effects ungulates have on additional soil characteristics important for infiltration (Long et al. 2017; Leopold and Hess 2017). In particular, feral pigs are common in mesic and wet Hawaiian forests and are known to transform forest structure above and belowground (Barrios-Garcia and Ballari 2012; Leopold and Hess 2017).

Beyond the direct importance of ungulate damage on local infiltration capacity, our final model indicates indirect effects of ungulates on infiltration capacity through other soil-related predictors of Kfs. For instance, bare soil cover, which is known to increase with ungulate disturbance (Cole et al. 2012), was negatively associated with Kfs. Bare soil cover combined with the presence of ungulates can cause soil compaction (Asner et al. 2004) and compound the reduction in infiltration capacity. We also found that soil depth and soil organic matter were important predictors of infiltration capacity, both of which can be affected by ungulate damage (Long et al. 2017). Lastly, a few forest structural indices such as woody understory cover and forest floor cover in our final model were consistently negatively correlated with ungulate damage, illustrating how increased ungulate damage could indirectly decrease Kfs via vegetation effects.

Invasive versus native plant impacts on infiltration

Results show mixed patterns in terms of invasive versus native plant impacts on forest infiltration. The negative effect of invasive grasses on infiltration capacity was clear and corroborates past studies in Hawaii that show grasslands have significantly lower soil hydraulic conductivity than native forest (Perkins et al. 2012). Invasive grasses are particularly problematic in Hawaiian forests because their shallow, matt-forming root systems limit soil water storage to near-surface layers relative to deeper-rooted vegetation and can slow rates of infiltration. Invasive grasses also compete directly with native seedlings in wet, mesic and dry habitats across Hawaii (Anderson et al. 1992; Cabin et al. 2000; Yelenik et al. 2017) and after disturbance in other tropical forest systems (Veldman and Putz 2011), creating a positive feedback loop that can quickly modify forest structure and ecosystem function. In contrast, while Himalayan ginger cover was not part of our final model, it was consistently positively correlated with increased infiltration capacity in our study, likely because of its large and dense rhizomatous root system and large inputs of leaf litter that could increase soil organic matter content. The presence of large roots (regardless of plant species) was a predictor for increased infiltration capacity in our final model. Large roots can provide preferential flow for water to move quickly through soil. While the presence of Himalayan ginger enhanced infiltration locally, its wider ecological effects are dramatic and include competition which can effectively exclude native woody species recruitment (Gardner and Davis 1982; Minden et al. 2010).

Ohia canopy cover was a significant predictor of Kfs in our final model. It is important to note that this model links ohia, a keystone species in Hawaiian forests (Mertelmeyer et al. 2019), to a function critical to watershed health. It is not clear if this relation between ohia cover and infiltration is driven by particular characteristics of ohia rooting and canopy structure, or whether ohia cover simply serves as an indicator of ecosystem integrity in our forest data and model. Because total woody canopy cover was also part of our final model, it indicates ohia cover has an effect on infiltration apart from overall canopy cover.

Aside from this ohia relation, across the forest floor, understory or canopy layers, we found no infiltration association to other woody native/invasive indicators except an unexpected negative relationship between Kfs and native woody cover on the forest floor. This may be partially explained by native-dominated Hawaiian forests generally having more open forest floors and understories than invaded counterparts. Broad attention has been given to the potential ecosystem effects of strawberry guava invasion on native Hawaiian forests (Diong 1982; Smith 1985; Takahashi et al. 2011; Strauch et al. 2016). While it was challenging to find extremely invaded strawberry guava stands next to native-dominated stands for comparisons (see study limitations below), it was still surprising to find no clear effects of this species on localized infiltration capacity.

Forest structure and infiltration

In addition to the few clear and significant links between native/invasive plant dominance on local soil infiltration capacity, it is important to recognize how invasion may change some of the forest structure characteristics that our model associated with infiltration capacity. One-third of predictors of Kfs in our study included plot-level forest structure variables, adding to previous work demonstrating the influence of forest structure on soil–water processes (Catford 2017). Canopy cover, forest floor cover, woody understory cover, bare soil and soil organic matter are some of the determinants of infiltration capacity based on our model of Kfs, and plant invasion can drastically affect these forest structure characteristics and consequently infiltration. For instance, understory plant invasion has been linked to exposed soil surfaces which can increase erosion and runoff (Nanko et al. 2015) and understory canopy of keystone species hapuu have been reduced in the presence of invasive ungulates (Cole et al. 2012).

Research has shown many ecosystem properties in Hawaii are not clearly dependent on native/non-native status (D'Antonio et al. 2017). Indeed, Cavaleri and Sack (2010) found growth form to be the predominant determinant of water use at the ecosystem scale, and only when native and invasive species had different growth forms did water use increase by invasives. With regards to litter cover or SOM, while it can be true that invasive species are more nutrient use inefficient, and have leaf litter with high nitrogen that decomposes faster, this is certainly not always the case (Funk and Vitousek 2007). This may be especially relevant on Hawaii Island which is more nutrient limited and tends to have invaders with similar leaf traits to native species (Vitousek and Farrington 1997). More broadly, in wet and mesic habitats, invaders and natives tend to be fairly similar from a functional perspective (Henn et al. 2019), and it is only in more arid environments that grasses, which have distinctly different traits than native woody species, become more prevalent thus potentially leading to larger changes in ecosystem properties such as SOM, water infiltration, or transpiration (Catford 2017). However, in Hawaii unlike many other tropical regions, grasses are able to competitively exclude forest species in mesic and wet forests as well, changing forest structure and causing ecohydrologic disruptions (Holscher et al. 2005; Yelenik et al. 2017).

Limitations, future work and conclusions

Owing to high within-site variability, the observed reductions in Kfs correlated with increased ungulate presence was not statistically significant at the site (i.e., forest stand) level. Nevertheless, there were clear overall reductions in the highest Kfs values across both moisture and age gradients as ungulate disturbance increased, which could cause reductions in infiltration across the site and result in increased surface flow. Our sample-design avoided steep slopes generally associated with increased surface flow, which would compound effects associated with ungulate disturbance. Infiltration capacity was driven by a complex set of factors, and these factors varied widely across plots within each site. For example, all sites were selected based on having a minimum of 50% canopy cover, and greater where possible. Despite this, canopy cover at the 3 m radius plot-scale yielded cover estimates ranging from 0–90%, and some within-site canopy cover estimates having greater than a 50% range. Soil depth and bare soil cover were also highly variable within sites. This unbiased, paired site design was extremely challenging to apply at the landscape-scale because there is typically a wide invasion gradient between completely native forest sites and heavily invaded forest sites. Given the additional constraints in site selection (large and homogeneous stands for multiple plot measurements, accessibility, etc.) our native/invasive site pairs likely overrepresented a transition zone where invasion was less pronounced.

It is important to remember that the wider issue of invasive driven differences to water yields of forests is not driven only by infiltration (Wohl et al. 2012). For example, invasion of Hawaiian wet forests, specifically by strawberry guava, was shown to reduce precipitation available for groundwater recharge due to reduced cloud water interception (Takahashi et al. 2011), and there were dramatic differences in throughfall between grazed and ungrazed native forests in a study by Brauman et al. (2010). Both studies asserted that vegetation structure and characteristics were likely responsible for these differences. A future approach to further investigate effects of invasive species on infiltration and other metrics of water yield could focus comparisons on identifying the primary mechanisms by which invasion can affect above and below ground forest structure and then sample sites according to structural differences and/or plant traits irrespective of species.

This study fills a gap in the literature with regards to tropical forest invasion. While there are numerous studies of forest conversion and reforestation effects on ecohydrology in the tropics, we tested and detected differences between intact and invaded forests, demonstrating that all forests are not equal with regards to metrics of watershed health. Even more, we detected differences in infiltration across native-canopied forests. We provide clear evidence for land managers that ungulate removal efforts likely improve ecohydrologic function to mesic and wet forest systems critical to protecting downstream and near-shore resources, as well as groundwater recharge. These findings underscore the importance of early intervention to recover ecohydrological health, especially when considered with the body of literature showing that reforestation efforts have yet to fully restore hydrologic function to previously-invaded systems.

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