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Landscape-scale GPP and carbon density inform patterns and impacts of an invasive tree across wet forests of Hawaii

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Abstract. Plant invasion typically occurs within a landscape-scale framework of abiotic and biotic conditions, often resulting in emergent feedbacks among environment, ecosystem functions, and the dominance of invasive species. Understanding the mechanisms underlying successful invasions is an important component of conservation and management efforts, but this has been poorly investigated in a spatially explicit manner. Knowing where and why invasion patterns change throughout the landscape enables managers to use context-specific controls on the spread of invasive species. Using high-resolution airborne imaging spectroscopy, we studied plant performance in growth within and across landscapes to examine the dominance and spatial distribution of an invasive tree, *Psidium cattleianum* (strawberry guava), in heterogeneous environmental conditions of a submontane Hawaiian tropical forest. We assessed invader performance using the GPP ratio index, which is the relative difference in remotely sensed estimates of gross primary productivity between canopies of guava and canopies of the invaded plant community. In addition, we used airborne LiDAR data to evaluate the impacts of guava invasion on the forest aboveground carbon density in different environments. Structural equation modeling revealed that substrate type and elevation above sea level interact and amplify landscape-scale differences in productivity between the invasive species and the host plant community (GPP ratio); differences that ultimately control levels of dominance of guava. We found shifts in patterns of forest carbon storage based on both gradual increase of invader dominance and changes in environmental conditions. Overall, our results demonstrate that the remotely sensed index defined as the GPP ratio provided an innovative spatially explicit approach to track and predict the success of invasive plants based in their canopy productivity, particularly within a landscape-scale framework of varying environmental factors such as soils and elevation. This approach may help managers accurately predict where invaders of forests, scrublands, or grasslands are likely to exhibit high levels of dominance before the environment is fully invaded.

Key words: Carnegie Airborne Observatory; ecosystem functions; environmental gradients; forest carbon stock; functional trait; gross primary productivity; invasive species; remote sensing.

Introduction

The spread of exotic plants in native forests varies according to the composition of the resident community (Mata et al. 2013), patterns of historical disturbance in the environment (DeGasperis and Motzkin 2007), and invader performance in establishment, maintenance, and growth (Alpert et al. 2000). These and other ecological processes interact with environmental factors, such as substrate type, temperature, and precipitation, causing the mechanisms and outcomes of invasions to be highly complex (Liao et al. 2008, Ehrenfeld 2010, Mata et al. 2013). Improving our understanding of invasion processes, and their response to environmental conditions, is central to predicting the spread of invasive species and, by extension, to controlling their negative outcomes. As we infer where invaders are more likely to succeed, we can more effectively target our control efforts against critical invasive species in particular habitats, minimizing costs and overall negative impacts.

Investigating differences in the functional traits of exotic and native plant species in different environments is an important step toward building links between invasion processes and environmental factors (e.g., Daehler 2003, Seipel et al. 2016). Plant functional traits express essential aspects of species morphology, ecophysiology, and life history, which combine to predict species survival and growth in a given habitat (Mcgill et al. 2006, Westoby and Wright 2006). Using trait-based approaches at the level of a leaf or individual plant, many studies have attempted to understand when and why some species are successful invaders (Daehler 2003, Richardson and Pyšek 2006). Successful plant invaders attain high abundance or dominance in the invaded habitat because they often have greater growth rate (Matzek 2011), resource use efficiency (Funk and Vitousek 2007) and reproductive output (Brooks and Jordan 2013) relative to local native species. Such differences between exotic and

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native species, however, may not always occur (Daehler 2003, Peñuelas et al. 2010) or may change along environmental gradients (Alpert et al. 2000). The spatially and temporally heterogeneous nature of invasion suggests that it is a context-dependent process. We therefore need investigations of performance and impacts of invasive species that are spatially explicit and cover large geographic areas. However, we currently lack studies that examine invasions using trait-based approaches at large spatial scales, and we do not know whether the ability of a species to invade habitats can be predicted with functional traits at landscape scale. If we can observe invasion processes in a spatially explicit manner, it may help managers to identify control strategies that incorporate the environmental variation across landscapes of interest.

Remote-sensing approaches have been effectively used to estimate canopy functional traits at the landscape scale. For instance, spectral data from airborne and satellite sensors have provided information on biochemical and physiological properties of the canopy, including pigment expression, photosynthetic light-use efficiency, and light interception (Asner and Vitousek 2005, Peñuelas et al. 2011, Flanagan et al. 2015). These remotely sensed canopy properties have been used to estimate gross primary productivity (GPP) at canopy to landscape scales (i.e., Asner et al. 2004, Clark et al. 2007, Tramontana et al. 2015). GPP is a key metric because it encapsulates both the photosynthetic efficiency of plants and their ability to absorb and harvest solar radiation. However, it remains extremely difficult to obtain field-based estimates of GPP across a wide range of environmental conditions (Geider et al. 2001), since leaf-level work is not always sufficient to predict whole-canopy processes, and since eddy covariance (flux) towers are labor intensive and cannot be deployed throughout heterogeneous landscapes. Remotely sensed estimates of GPP (canopy-level GPP) have become a powerful alternative to field-based methods, allowing for the estimation of carbon uptake per unit of time and canopy area (Field 1995, Clark et al. 2007, Peñuelas et al. 2011, Tramontana et al. 2015). For instance, Tramontana et al. (2015) show that satellite data are key drivers to improve accuracy in scaling up GPP estimates for large geographic areas, although the authors highlight that GPP estimates perform better in ecosystems with high variability in green biomass density. To reduce potential uncertainties in estimates of ecosystem level photosynthetic efficiency, some studies have used imaging spectrometers with high spectral resolution (e.g., Asner et al. 2006, Rascher et al. 2015). This technology can enhance the consistency in using vegetation indices to predict light use efficiency (LUE), which ultimately improves the accuracy to monitoring plant primary productivity from the sky (Peñuelas et al. 2011).

Airborne high-resolution imaging spectroscopy also has been used to map crowns of focal invasive species with overall accuracies that range between approximately 75% and 95% (e.g., Underwood 2003, Andrew and Ustin 2008, Asner et al. 2008*b*, Barbosa et al. 2016). Such high accuracies in mapping individual species have permitted the detection of initial stages of invasion (Barbosa et al. 2016). Combining maps of invasive species with estimates of canopy GPP may allow us to identify differences in productivity between an invader and the host plant community. In turn, this may help us to elucidate spatial patterns in the invasion process across varying spatial scales and environmental conditions. To date, however, remote-sensing approaches that estimate GPP have not yet been employed to study relationships between species performance in growth and invader dominance at the landscape level.

As exotic plants become dominant in a given landscape, they often alter canopy structure and species composition of forest communities (Sax and Gaines 2008, Powell et al. 2013), generating a cascade effect on ecosystem functions, such as nutrient, water, and carbon cycling (Asner and Vitousek 2005, Ehrenfeld 2010). Researchers have analyzed impacts of invasive species on ecosystem function by comparing invaded habitats with adjacent native counterparts (e.g., Ehrenfeld 2003, Hughes et al. 2014). However, native forests often show diverse levels of invader dominance (invasion severity), which lead to varying degrees of change in ecosystem functioning as landscapes are gradually invaded (Stohlgren and Rejmanek 2014). Consequences of gradual increases in alien plant dominance may be more pronounced where environmental conditions favor the growth of the invasive species relative to the native community, although this relationship is poorly understood at large spatial scales.

Here, we evaluated how environmental conditions affect invader primary productivity, dominance, and outcomes at a landscape scale, providing new insights into large-scale processes of species invasion. To do so, we introduce a new index, the "GPP ratio" that estimates the performance in growth of an invasive species in relation to the host plant community within a given landscape. We focused our study on the highly invasive tree species *Psidium cattleianum* (strawberry guava, hereafter guava) because it is recognized as a major threat to native Hawaiian forests as well as other forests throughout the world (Kueffer et al. 2010). In Hawaii, this species has invaded hundreds of thousands of hectares of native forest, replacing endemic and endangered local species (State of Hawaii, 2011). Using the GPP ratio technique developed here, combined with previously developed maps of guava canopy cover (Barbosa et al. 2016) and aboveground carbon density (ACD; Asner et al. 2011) at different elevations and substrate conditions, we addressed three questions: (1) To what degree do environmental conditions mediate differences in canopy GPP between a focal invasive tree (guava) and the host plant community (the GPP ratio) of a submontane Hawaiian tropical forest? (2) What is the relative importance of different environmental conditions and GPP ratio in predicting current levels of guava invasion in these forests? (3) How does invasion dominance of

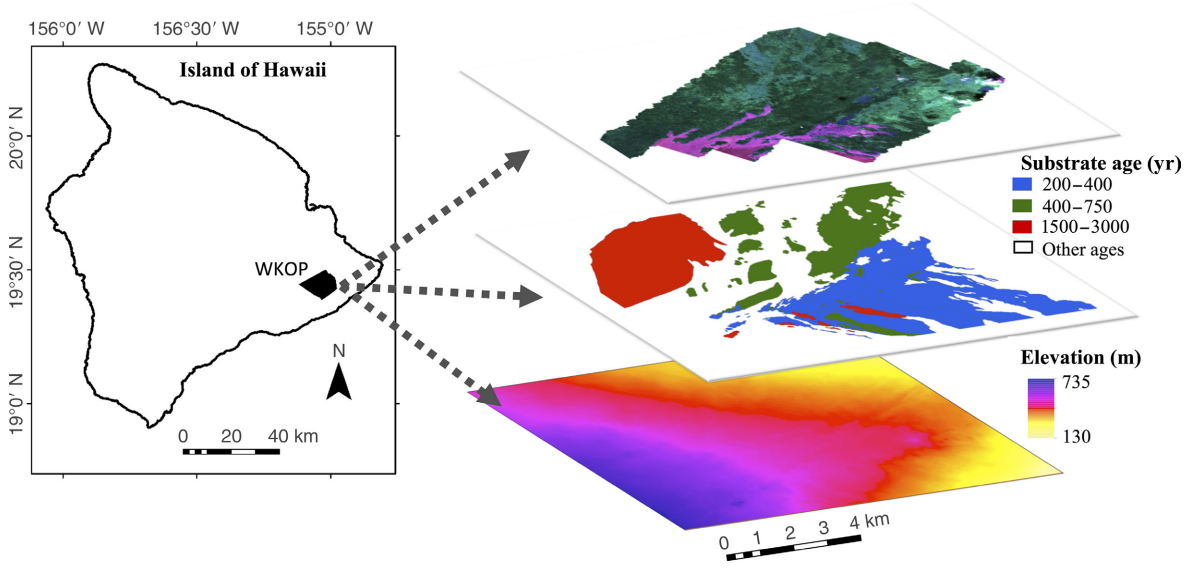

FIG. 1. The Island of Hawaii showing Wao Kele O Puna Forest Reserve (WKOP; fulfilled black polygon). False color composite map derived from Carnegie Airborne Observatory (CAO) Beta system, substrate age, and elevation above sea level of WKOP. [Color figure can be viewed at wileyonlinelibrary.com]

guava affect forest ACD? We expected maximum invasion under environmental conditions in which productivity inequality is highest between invasive and host species. We also expected significant shifts in forest carbon (C) storage based on both environmental and invasive gradients.

METHODS

Study site

Our study was conducted in the Wao Kele O Puna Forest Reserve (WKOP), Island of Hawaii and surrounding area (8873 ha; Fig. 1). Mean annual precipitation ranges from approximately 3000 to 4000 mm/yr, and mean annual temperature varies from 18° to 25°C (Giambelluca et al. 2014). Elevation steadily increases from 305 m to 640 m above sea level in an east-west direction. WKOP is located on the windward side of Kilauea volcano, where the reserve faces prevailing trade winds (Juvik and Nullet 1994). In these conditions, rain, temperature, and cloud cover often exhibit abrupt changes with increasing elevation (Giambelluca and Nullet 1991, Scholl et al. 2007). Because WKOP is located on an active volcanic area, substrate age varies from days to greater than 3000 years. Substrate age in Hawaii constrains soil nutrient availability (Vitousek 2004), where young and old substrates may exhibit lower nutrient availability than intermediate aged substrates (e.g., approximately 1000 yr). Variation in elevation and substrate age make WKOP a valuable area for investigations into how environmental gradients affect the success of exotic species in native forest landscapes.

WKOP encompasses the last remaining large region of lowland native rainforest in Hawaii. *Metrosideros polymorpha* (Ohia) is the most common native tree throughout WKOP. Lava flows determine substrate age-dependent stages of forest succession across Hawaiian landscapes (Zimmerman et al. 2008). As primary succession proceeds, lowland native rainforests exhibit increased compositional complexity with the presence of many native tree, fern, forb, and vine species (Hughes and Denslow 2005, Zimmerman et al. 2008). The understory vegetation includes, among others, *Psychotria hawaiiensis*, *Diospyros sandwicensis*, *Ilex anamola*, *Cibotium glaucum*, *Antidesma platyphyllum*, and *Cheirodendron trigynum*. Overall, this flora exhibits low species diversity and canopy structural complexity when compared with continental lowland rainforests (Zimmerman et al. 2008), and a few species dominate a broad range of successional stages and environmental conditions (Wagner et al. 1990).

In WKOP, *P. cattleianum* (guava) is the most prevalent alien tree species. Guava was intentionally introduced in Hawaii as a horticultural species in the early 1800s (Smith 1985, Wagner et al. 1990). However, it is now recognized as one of the most serious threats to native ecosystems in Florida, Puerto Rico, Reunion, Mauritius, Guam, Cook Islands, Fiji, French Polynesia, Palau, Samoa, and Norfolk Island (Lorence and Sussman 1986, Tunison 1991). Landscape-scale forest carbon stocks increase with substrate age, but this relationship is controlled by native vs. nonnative tree dominance (Hughes et al. 2014). Increases in elevation often lead to decreases in nutrient cycling and availability, which consequently reduce primary productivity (Raich et al. 1997). Elevation is an important and complex environmental variable in Hawaii as it merges factors such as precipitation, temperature,

wind patterns, and other climatic conditions (Juvik and Nullet 1994). In addition, WKOP has low levels of disturbance from human activities such as agriculture and ranching because it is a protected area.

Remote-sensing data

In January 2007, the Carnegie Airborne Observatory Beta system (CAO; Asner et al. 2007) acquired imaging spectroscopy data for the WKOP reserve using a sensor package that included the Airborne Visible and Infrared Imaging Spectrometer (AVIRIS). The CAO was flown at an altitude averaging 2.4 km above ground level, providing spectroscopic measurements at 2.4-m spatial resolution over an area of 8873 ha. The CAO Visible-to-Shortwave Infrared (VSWIR) imaging spectrometer measures spectral radiance in 427 channels spanning the 380–2510 nm wavelength range in 5-nm increments with nominally 6-nm spectral response function (full-width at half-maximum). Additional detector rows are used to monitor the instrument dark signal levels. These data were radiometrically and atmospherically calibrated in the laboratory following the flight using ACORN 5LiBatch (Imspec LLC., Palmdale, CA, USA) model, and a MODTRAN look-up table to correct for Rayleigh scattering and aerosol (see Asner et al. [2007] for details). Water absorption bands near 1450 nm and 1950 nm were removed, resulting in 161 spectral bands for analysis. We were interested in examining only leafy, well-lit vegetation; thus, prior to analysis we filtered the imagery to include only the pixels with a normalized difference vegetation index greater than 0.75 and mean near-infrared (850–1050 nm) reflectance greater than 20%. These leafy pixels (77% of the image) represent a controlled set of reflectance signatures that, theoretically, should be most indicative of surfaces containing vegetation; and consequently ideal for modeling GPP.

Invasive species map

We used a guava map developed by Barbosa et al. (2016), which estimated guava spatial distribution across WKOP (2.4-m spatial resolution) by combining the field inventory and CAO imaging spectroscopy data. Barbosa et al. (2016) mapped guava cover using a spectral unmixing classification framework; the methodological steps are summarized as follows: (1) the reflectance data from the CAO imagery were first transformed by applying minimum noise fraction (MNF) to the data (Green et al. 1988); (2) spectral endmembers of guava crowns were selected in the imagery based on field inventory; (3) a Mixture-tuned Matched Filtering (MTMF; Boardman et al. 1995) method were performed using the MNF outputs and the spectral endmembers to estimate the relative abundance of guava crowns within all pixels of the CAO imagery; (4) the continuous MTMF outputs, the matched filter (MF), were reclassified into presence and absence of guava guided by calibration with field data. The authors yielded a predicted guava canopy cover that explained 86% of the variation in field plot-based estimates of guava canopy cover. The predicted percentage of canopy cover within plots exhibited a root mean square error (RMSE) of 9% (Barbosa et al. 2016).

Using the guava cover map, we divided the entire WKOP forest reserve (Fig. 2) into 2.5-ha hexagons and then calculated invader dominance (guava canopy cover) as the proportional area of each hexagon covered by guava. Defining hexagonal grids in landscape analysis reduces the number of landscape units to cover a certain geographic area and minimizes bias in ecological analysis of neighborhood areas (Birch et al. 2007). The 2.5-ha hexagonal areas of WKOP were small enough to isolate local environmental conditions, but large enough to represent the local forest community. The guava map also allowed us to index pixels of CAO imagery into two groups: guava canopies and other plant species (i.e., the host plant community). We used results from this procedure to calculate differences in canopy GPP between guava and the host plant community (GPP ratio; see *Gross primary productivity ratio (GPP ratio)*) within the hexagonal landscapes.

Gross primary productivity ratio (GPP ratio)

GPP is the total carbon (C) uptake by vegetation, and it is often measured in Mg $C{\cdot}ha^{-1}{\cdot}yr^{-1}$. A common method for simulating GPP in ecosystems (Field 1995) uses the following equation:

$$\mathrm{GPP} = \mathrm{PAR} \times \mathrm{fAPAR} \times \mathrm{LUE} \quad (1)$$

where PAR is the incoming photosynthetically active radiation, fAPAR is the fraction of PAR absorbed by foliage (%), and LUE is the light-use efficiency. GPP is poorly known in tropical forests, and only a few studies have been able to validate large-scale GPP assessments with field data (Geider et al. 2001, Malhi et al. 2015). Using remote-sensed data, the normalized difference vegetation index (NDVI) is traditionally used to estimate fAPAR (as in Myneni and Hall 1995), and the photosynthetic reflectance index (PRI) is used to estimate LUE (Gamon et al. 1992, and reviewed in Peñuelas et al. 2011). The NDVI and PRI have been used to simulate canopy GPP over large areas (Asner et al. 2004, Clark et al. 2007, Peñuelas et al. 2011, Tramontana et al. 2015). PAR is often an input from field observations or meteorological models.

Here, we simulated the GPP ratio, as the ratio between estimated canopy GPP of guava (our focal invasive species) and the host plant community within a constrained area, hereafter referred to simply as the "host landscapes" (the hexagonal landscapes of 2.5 ha described in *Invasive species map*). The GPP ratio estimates the relative difference in canopy GPP between guava and community canopies, instead of measuring the actual canopy productivity. In addition, we modeled GPP within individual landscape units with small extent, reducing the variability in environmental conditions. Doing so has the added benefit of

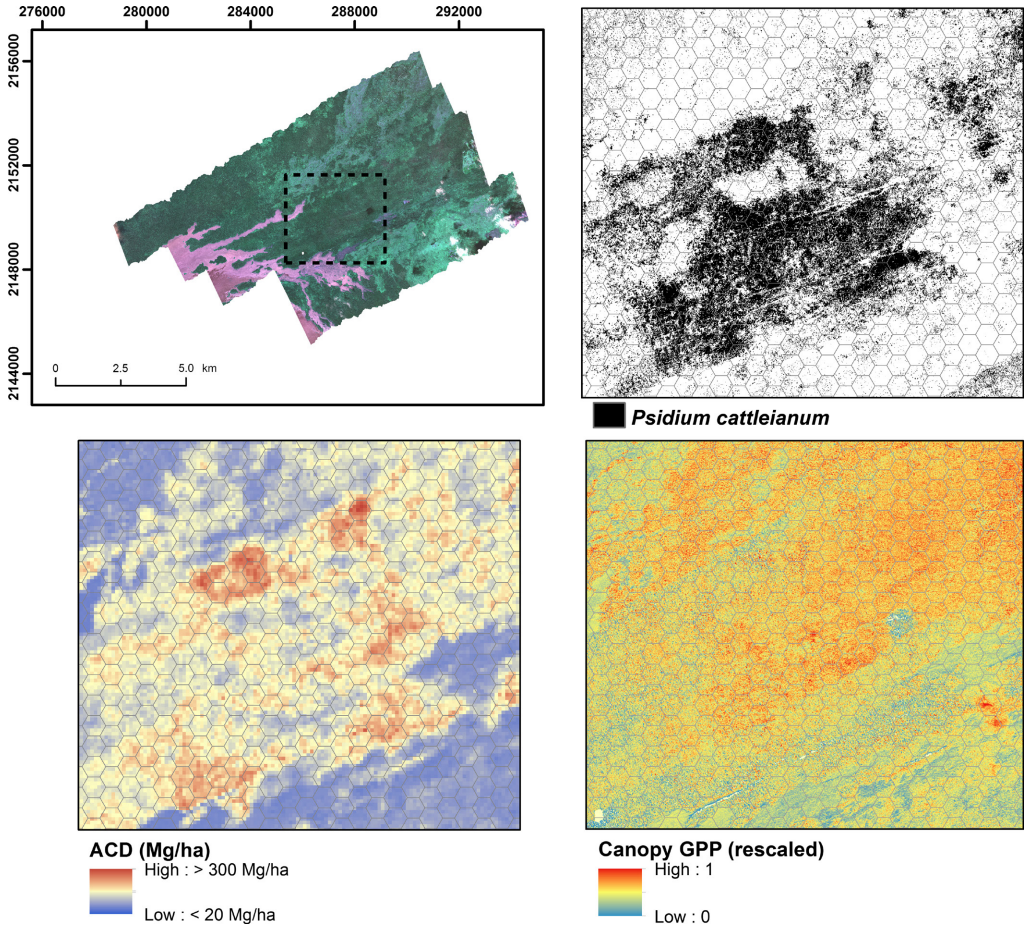

FIG. 2. False color composite map of the study area. Zoom maps for *Psidium cattleianum* spatial distribution (Barbosa et al. 2016), gross primary productivity (rescaled canopy GPP), and aboveground carbon density (ACD; Asner et al. 2011) within the dashed line extent located in the study area. Gray hexagonal lines represent the studied host landscapes (2.5 ha each). All the layers cover the entire extent of the false color composite map. Numbers in the upper left panel refer to geographic coordinates in UTM (Longitude, Latitude). [Color figure can be viewed at wileyonlinelibrary.com]

minimizing the effect of varying atmospheric aerosols and water vapor in the modeled GPP with remotely-sensed data, as well as image calibration errors, since the GPP ratio is a relative measure within each host landscape.

We calculated the GPP ratio of each host landscape (Fig. 2) using the following steps. First, we estimated the canopy GPP for all pixels of the CAO imagery with the NDVI and PRI (Table 1). Although the relationships between these vegetation indices and fAPAR or LUE may vary for different species, which can affect accuracy of GPP estimates, there is reasonable consistency in these relationships in several studies (see details in Peñuelas et al. 2011). We assumed that PRI values were already modulated by specific factors (e.g., precipitation, soil moisture, vapor pressure deficit, and temperature); therefore, we did not include these factors in the GPP ratio model. We expected that this modeling simplification does not affect our analysis of productivity efficiency because the GPP ratios were calculated using the relative difference in GPP within landscape units (2.5 ha), where minimal changes in environmental conditions occur. PAR was held constant because we can assume that it does not change within each hexagonal landscape.

The results of the canopy GPP (Table 1) were rescaled to values between 0 and 1, indicating minimum and maximum GPP in WKOP. Rescaling provided improved visualization of the results (Fig. 2), although it did not change the geographic pattern of the GPP ratio. In a second step, we spatially overlapped the canopy GPP outputs, the guava map (from *Invasive species map*), and the hexagonal landscapes. We then indexed the canopy GPP values within each hexagon into two groups: guava and other vegetation (host plant community). We then calculated the GPP ratio for each host landscape. That is, the mean canopy GPP of pixels previously indexed as guava in a given landscape, divided by the mean canopy GPP of pixels indexed as other plant species in the same host landscape (see Table 1). Where GPP ratios are greater than 1, we expected that guava productivity is greater than the host plant community, and this invasive

Table 1. Remote-sensing metrics used to simulate gross primary productivity (GPP) from the imaging spectroscopy data (Carnegie Airborne Observatory, CAO).

Index	Source
NDVI (fAPAR)	$(p800 - p680)/(p800 + p680)$
PRI (LUE)	$(p531 - p570)/(p531 + p570)$
PAR	1
Canopy GPP†	PAR × NDVI × LUE
GPP ratio‡	$\text{GPP ratio} = \dfrac{\text{Canopy GPP Guava}}{\text{Canopy GPP non Guava}} = \dfrac{\sum_1^{n(\text{guava})} \text{PAR} \times \text{NDVI} \times \varepsilon}{\sum_1^{n(\text{non guava})} \text{PAR} \times \text{NDVI} \times \varepsilon}$

Notes: NDVI = normalized difference vegetation index; PRI = photosynthetical reflectance index; p = wavelength values in nanometers; PAR = solar incident photosynthetically active radiation; fAPAR = the fraction of PAR absorbed by foliage (%); LUE (ε) = light use efficiency; Guava = strawberry guava (*Psidium cattleianum*).

†Canopy GPP outputs were rescaled into values between 0 and 1.

‡GPP ratio was calculated for each hexagonal landscape; *n* (Guava) are all pixels identified as *P. cattleianum* within a focal landscape; *n* (non Guava) are pixels classified as non *P. cattleianum,* also named as "other plant species" class.

species is likely to exhibit higher growth rates than the host plant community. In contrast, where GPP ratio is lower than 1, we expected guava to be less efficient for self-establishment and growth. As we calculated the ratio between canopy GPP of the invader and canopy GPP of the host plant community (GPP ratio), we assessed the degree of difference in canopy GPP within a given area (the host landscapes).

Environmental filters on species invasion

We evaluated the effect of substrate age and elevation on GPP ratio and guava dominance (canopy cover). We determined substrate age for all the hexagonal landscapes using lava flow maps (Trusdell et al. 2005). These maps classify lava flow into ranges of age, such as 200–400 yr BP. We filtered the data to select only the hexagons that had more than 75% of their area within substrate ages of 200–400 yr BP, 400–750 yr BP, and 1500–3000 yr BP. We excluded hexagons located on very young substrates (i.e., <5 yr BP), and those characterized by very broad age ranges (e.g., 400–1500 yr BP). We used an Advanced Spaceborne Thermal Emission and Reflection (ASTER) image to obtain a digital elevation model of the study area. We then calculated the mean elevation above sea level within each hexagon.

We computed structural equation models (SEM) to investigate environmental and biological factors that may control processes of guava invasion at the landscape scale, mainly searching for interactions between elevation, substrate age, and GPP ratio affecting guava cover. SEM uses the covariance among variables to build and test models with specific multistep pathways of influence on one or more final response variables, which can be illustrated as graphical representations of interdependent networks of relationships. SEM advances some traditional regression models, as it provides tools for simultaneous analysis of multiple layers of linkages (pathways) between independent and dependent variables, tests direct vs. indirect relationships, finds the partial contributions of correlated explanatory variables, and provides tools to select alternative models using maximum likelihood approaches (Grace and Bollen 2005).

Using SEM analysis, we evaluated elevation, substrate age, and GPP ratio as direct or indirect factors determining guava canopy cover within the hexagonal landscapes. Data distributions were log-transformed when necessary to ensure normality. Substrate age showed a nonlinear relationship with guava cover and canopy GPP; therefore, we implemented SEM using a nonlinear framework (Wall and Amemiya 2000). Because the landscape data came from spatially contiguous units, we estimated the magnitude of spatial autocorrelation in the model residuals and corrected the outputs of the SEM analysis (e.g., degree of freedom, standard errors, *Z* values, and *P* values) using the Moran *I* test (Harrison and Grace 2007, Matteson et al. 2013). In this procedure, we used the spatialCorrect function from the semTools package (semTools Contributors 2016) of the R programing language. We assessed the overall goodness of fit of the SEM models using χ^2 statistic, comparative fit index (CFI), and root mean square error of approximation (RMSEA). We determined the preferred (best-fit) model by selecting the model with lowest value of Akaike's information criterion (AIC; Burnham et al. 2011). We also searched for other statistically significant models by calculating the ΔAIC, which is the difference between the minimum AIC value and any other AIC. Models with ΔAIC < 2 were defined as good as the preferred model (Burnham et al. 2011). All statistical analyses were performed in R (R Development Core Team 2012).

Invasion impacts on forest carbon stock

At the spatial scale of the hexagonal landscapes, we analyzed the relationship between guava cover area and aboveground carbon density (ACD; Mg/ha). Guava cover was calculated as in *Invasive species map*. We obtained ACD data for our study area from a map produced and validated by Asner et al. (2011). These authors developed a 30-m resolution ACD map (Fig. 2) for the Hawai'i Island combining field measurements, light detection, and ranging data (LiDAR), and satellite-based imagery (LANDSAT and Advanced Spaceborne Thermal Emission and Reflection [ASTER]). Details on technical and methodological procedures are available in Asner et al. (2011).

We used this ACD map to calculate for each hexagonal landscape the mean carbon density (ACD_{mean}), the standard

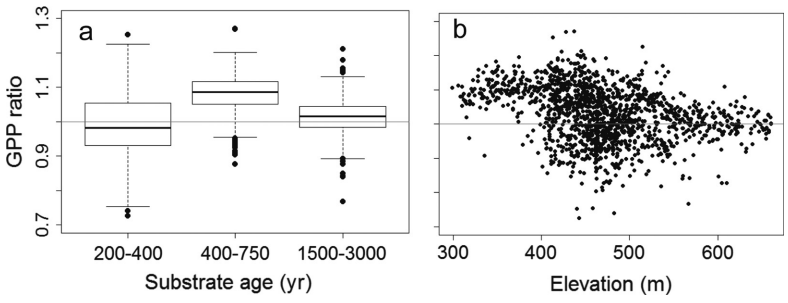

FIG. 3. Relationship between GPP ratio and environmental conditions (substrate age and elevation above sea level) for the host landscapes (total of 1440 hexagonal landscapes). (a) Median, upper and lower quartiles, minimal and maximum values, and outliers (points) for GPP ratio by substrate age. (b) Mean GPP ratio and mean elevation for each host landscape. Gray horizontal lines indicate where GPP ratio is 1, which indicates GPP of guava and other species is similar.

deviation of carbon density (ACD_{SD}), and the maximum ACD divided by mean ACD values ($ACD_{max/mean}$). We separated landscapes by substrate age (200–400 yr BP, 400–750 yr BP, and 1500–3000 yr BP) and elevation (i.e., below and above 520 m above sea level). We separated the elevation into these two classes, below and above 520 m, because the extent of guava invasion differed remarkably at this elevation threshold (as shown in *Results*; Fig. 5b). Finally, we analyzed the relationship between guava cover area and ACD using scatterplots and regression models.

RESULTS

Potential mechanisms driving plant invasion in the landscape scale

Landscape-scale GPP ratios ranged from 0.53 to 1.27. Overall, 75% of the host landscapes (hexagons of 2.5 ha) exhibited GPP ratios higher than 1, indicating that guava GPP at the landscape scale is higher than the mean GPP of the host plant community (other species) in most of the cases. GPP ratio was highest at the intermediate substrate age (i.e., 400–750 yr BP), followed by older (1500–3000 yr BP) and younger (200–400 yr BP) substrates (Fig. 3a, $P < 0.01$). Overall, GPP ratios showed a weak but significant decrease as elevation increased (Fig. 3b, $R^2 = 0.11$, $P < 0.01$). Nearly all host landscapes exhibited GPP ratios greater than 1 within the elevation range of 300–400 m (Fig. 3b), indicating that GPP of guava canopies was consistently higher than other canopies in this elevation range. GPP ratios were variable in elevations between 400 m and 520 m, while above 520 m, GPP ratio was usually close to 1.

Guava cover within the host landscapes spanned the entire range of possible values, from 0 to 100% of coverage, displaying interrelated spatial trends with GPP ratio, elevation and substrate age (Figs. 4 and 5). Guava cover was high in landscapes with high GPP ratio. However, the rate of increase in guava cover as GPP ratio increased was controlled by environmental conditions (Fig. 4), indicating that patterns in the relationship between guava cover and GPP ratio changed as substrate and elevation changed. For instance, the rate of increase

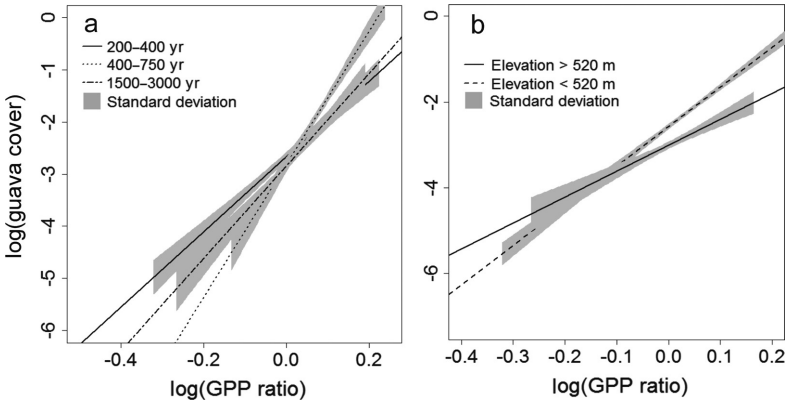

FIG. 4. Relationship between GPP ratio and the percentage of *P. cattleianum* (guava) canopy cover (measured as percentage of area), considering different environmental conditions: (a) substrate age of 200–400 yr ($R^2 = 0.23$, $P < 0.001$), substrate age of 400–750 yr ($R^2 = 0.32$, $P < 0.001$), and substrate age of 1500–3000 yr ($R^2 = 0.25$, $P < 0.001$). (b) Elevation above sea level < 520 m ($R^2 = 0.32$, $P < 0.001$) and elevation > 520 m ($R^2 = 0.18$, $P < 0.001$).

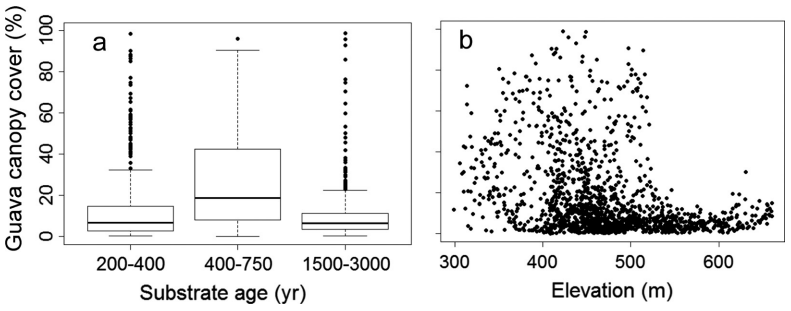

FIG. 5. (a) Median, upper, and lower quartiles, minimal and maximum values, and outliers (points) for the relationship between *P. cattleianum* (guava) canopy cover and substrate age. (b) Relationship between mean *P. cattleianum* canopy cover and mean elevation above sea level for each hexagonal landscape.

TABLE 2. Mean and standard deviation (in parenthesis) of GPP ratio, guava cover, and aboveground carbon density (ACD) in different combinations of substrate age (lava flow age) and elevation above sea level.

Substrate age (yr)	GPP ratio	Guava cover (%)	ACD (Mg/ha)	Number of landscapes
Elevation < 520 m				
200–400	0.99 (0.09)	13 (17)	46.2 (38)	477
400–750	1.08 (0.05)	28 (23)	76.2 (33)	465
1500–3000	1.03 (0.05)	15 (18)	85.6 (30)	191
Elevation > 520 m				
200–400	0.99 (0.08)	5 (5)	44.2 (33)	51
400–750	1.02 (0.04)	10 (9)	62.5 (28)	57
1500–3000	0.99 (0.05)	6 (4)	64.6 (13)	199

in guava cover as GPP ratio increased was higher in lava flows aged 400–750 yr BP (intermediary age) than in lava flows aged 200–400 yr BP or in lava flows aged 1500–3000 yr BP (Fig. 4a). Moreover, the rate of increase in guava cover was higher below 520 m than above this elevation as GPP ratio increased (Fig. 4b). Table 2 shows the simultaneous effect of elevation and substrate age on GPP ratio and guava cover.

Guava cover in substrates of 400–750 yr BP (intermediate age) was double that on substrates of 200–400 and 1500–3000 yr BP (Fig. 5a, $P < 0.01$). However, guava cover within all these substrate ages was highly variable. Substrates of 400–750 yr BP contained a total of 523 hexagonal landscapes, in which 18% presented guava cover higher than 50% of the landscape area. Five percent of the 527 hexagons located on 200–400 yr BP substrates and 2.8% of the 390 landscapes in 1500–3000 yr BP substrates showed guava cover higher than 50% of the landscape area. Guava cover exceeded 50% of hexagon areas only at elevations less than 520 m (Fig. 5b).

SEM analysis provided insight into the simultaneous and interactive effect of substrate age and elevation on guava cover (Fig. 6). In the SEM analysis, we tested models with different interactions among the following variables: substrate age, elevation, GPP ratio, and guava cover. However, the exclusive best-fit SEM model (Fig. 6; ΔAIC < 2; Weight = 0.68; $\chi^2 = 3.29$; CFI = 0.99, RMSEA = 0.04) revealed two pathways of environmental filters (controls) on guava invasion ($R^2 = 0.35$, $P < 0.001$). That is, elevation directly reduced guava cover ($r = -0.15$, $P < 0.001$), but it also did so indirectly, first by decreasing GPP ratio ($r = -0.20$, $P < 0.001$). In addition, substrate age affected guava cover only indirectly (Fig. 6), because GPP ratio mediated the effect of substrate age on guava cover ($r = 0.42$, $P < 0.001$). For instance, GPP ratio

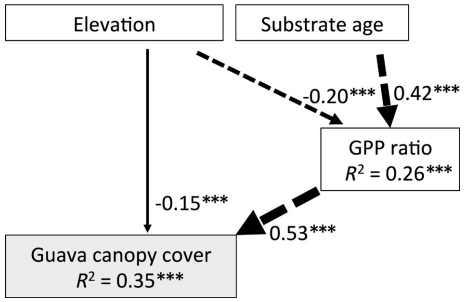

FIG. 6. Structural equation model (SEM) indicating the relative importance of direct and indirect pathways environmental conditions (elevation and substrate age) affect *P. cattleianum* (guava) invasion. The graph represents the most parsimonious model (weight = 0.68; $\chi^2 = 3.29$; CFI = 0.99, RMSEA = 0.04), showing respective variables (boxes) and directional connections (arrows). Arrow width and particular standardized coefficient (***$P < 0.001$) indicate the strength of the connection and the causal pathways of the relationship in a multivariate context. The standardized variables are dimensionless and have the same numerical range to allow direct comparison of respective effects on GPP ratio and guava cover. Dashed arrows indicate indirect pathways and continuous arrows are direct pathways of environmental conditions affecting *P. cattleianum* invasion process.

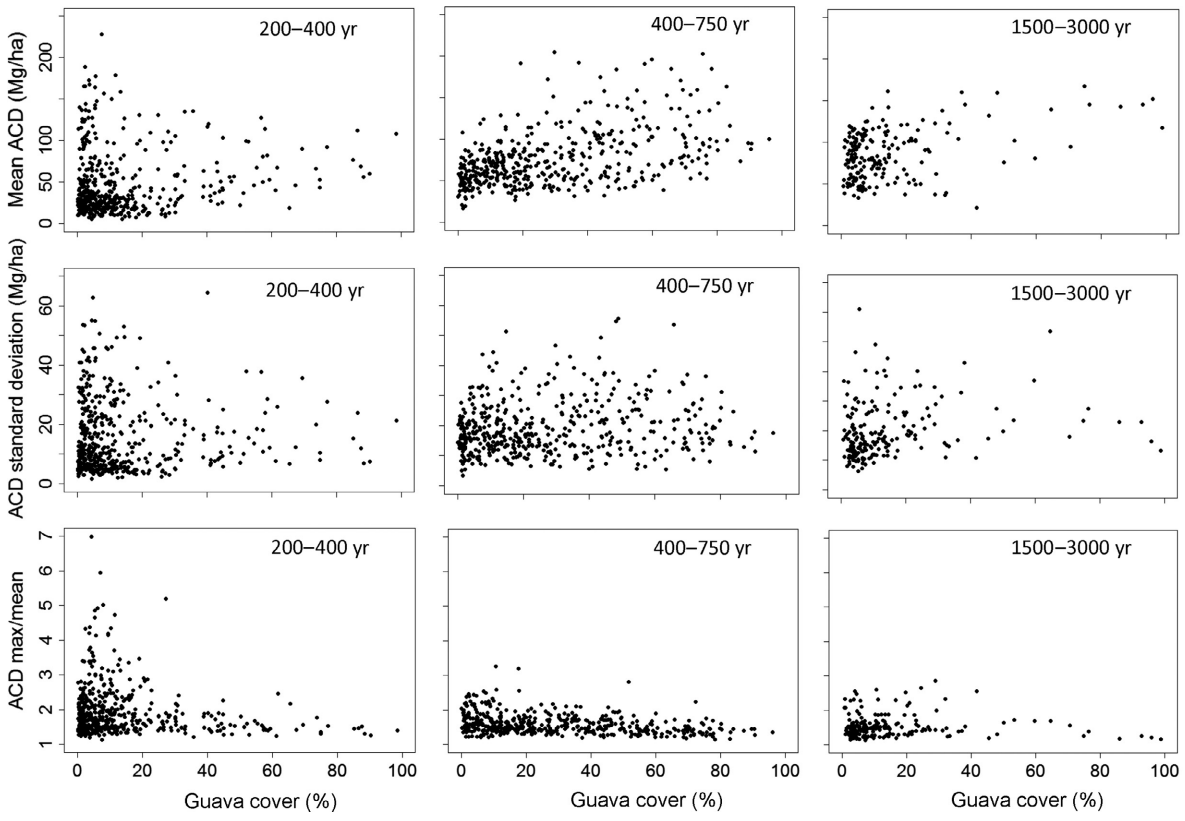

FIG. 7. Relationship between *P. cattleianum* (guava) cover and aboveground carbon density (ACD) in hexagonal landscapes located in elevation below 520 m. This relationship was partitioned by substrate age. ACD is shown as mean, standard deviation, and ratio between maximum and mean carbon density within each hexagonal landscape.

increased from young to intermediate substrate ages, and subsequently decreased on older substrates (Fig. 3a). Consequently, the change in GPP ratio was related to changes in guava cover. The moderate effect of GPP ratio on guava cover ($r = 0.53$, $P < 0.001$) highlights the importance of the indirect pathway driving the invasion process (Fig. 6; Appendix S1). As shown in Fig. 4, the relationship between GPP ratio and guava cover varied with elevation and substrate age. Because host landscapes are spatially contiguous units, these SEM outputs were adjusted considering spatial autocorrelation among the studied landscapes. Moran's I tests indicated significant spatial autocorrelation in the observed vegetation variables and also residual autocorrelation ($P < 0.05$ for both GPP ratio and *P. cattleianum* cover), resulting in a reduction in sample size from 1440 to 1186 landscapes. This adjusted sample size was used to recalculate the outputs of the SEM model (model parameters, standard error, and P value).

Invasion patterns affecting forest aboveground carbon density (ACD)

Mean ACD ranged from 3.8 to 228.1 Mg/ha across the host landscapes analyzed. Most of the landscapes (80%) showed mean ACD lower than 100 Mg/ha. ACD was affected by elevation and substrate age (Table 2). We evaluated the relationship between ACD and guava cover using only landscapes below 520 m of elevation because high levels of guava invasion were almost absent above this elevation (Fig. 5b). Although statistically significant, we did not find a well-defined effect of the gradual increase in guava cover on mean landscape-scale ACD (Fig. 7). For instance, ACD_{mean} increased somewhat as guava cover increased in intermediate (400–750 yr BP, $R^2 = 0.23$, $P < 0.001$) and older substrate ages (1500–3000 yr BP, $R^2 = 0.20$, $P < 0.001$), but this relationship was weaker in young substrate (200–400 yr BP, $R^2 = 0.01$, $P = 0.003$). In all cases, there was a reduction in the number of landscapes with very low ACD_{mean} values as guava cover increased. As invasion spread, ACD_{SD} slightly reduced in all substrate ages (Fig. 7; $R^2 = 0.03$, $P < 0.001$). The relationship between invasion and $ACD_{max/mean}$ in substrate age of 200–400 yr BP showed a particular pattern because there was a strong reduction in $ACD_{max/mean}$ values as landscapes showed guava cover higher than 20%.

DISCUSSION

Mapping an invasive plant distribution and modeling its GPP ratio, we found that elevation and substrate

factors were potential drivers of invader performance in productivity at the landscape scale, indicating where and how these environmental factors constrain invasion success. Our results indicate a variable but consistent decrease in GPP ratio in areas where stressful environments conditions are likely to occur. For example, when compared to intermediate substrate ages, young and old substrates can be stressful environments due to lack of soil development and depletion on nutrient availability, respectively (Vitousek 2004). In addition, elevations above approximately 550 m on the windward side of Hawaii Island show abrupt increases in cloud cover, higher rainfall, and temperature reduction due to prevailing northeasterly winds (Giambelluca and Nullet 1991, Scholl et al. 2007). As we demonstrated in the SEM analysis, the above mentioned environmental conditions interact, which may constrain the success of strawberry guava at invading habitat as indexed to gross primary productivity. In some cases, guava also outperformed the host plant community in some of the stressful habitats, although it happened with a lower frequency. The high GPP of the strawberry guava in some of the nutrient poor soils and higher elevations indicates that the species may invade a large portion of Hawaii Island, albeit with a lower overall rate of spread or intensity.

Our results suggest GPP ratio is a potential index to reveal patterns of invader performance in growth in relation to the host plant community. Differential performance between or among species is a key factor driving species coexistence (Chesson 2000, Adler et al. 2007), and may suggest why and where invaders become dominant in a community (Cothran et al. 2015). General invasibility–performance relationships have been found using plant traits measured at the leaf or individual levels (Daehler 2003, Funk and Vitousek 2007, Peñuelas et al. 2010), but not yet at large spatial scales that include both the invader population and the entire "host" plant community. Here, we show that the use of GPP ratio, a landscape-scale attribute, helped to explain invasion mechanisms. Even if the relatively short time since initial invasion is a constraint on our ability to predict long-term invasion outcomes (Gilbert and Levine 2013), we argue that GPP ratio may indicate invader performance in growth in initial or intermediate phases of invasion. GPP ratio is an integration of environmental conditions, phylogenetic origin of the focal species, resource use efficiency, and local competition (both intraspecific and interspecific). Together, these factors limiting plant productivity determine species coexistence (Chesson 2000).

Alpert et al. (2000) and Daehler (2003) already suggested that invader performance is driven by environmental conditions and is context dependent; we have found this to be true at the landscape scale in Hawaiian forests as well. In our system, invader performance was related to environmental filters, even when the species is growing at different densities, developmental stages, or location in the study area. Environmental conditions also constrain plant establishment and dispersal, determining invasion success (Brooks and Jordan 2013). Therefore, we have found that the same invader performance in productivity (GPP ratio) can show greater invasion success (dominance) in a more favorable environment compared to those that are more stressful. Overall, these results indicate that we may apply the relationship between relative performance in productivity, invasion dominance, and environmental conditions to identify where the focal invader is likely to successfully spread. In addition, GPP ratio may be broadly used to estimate the relative performance of the invader across climatically and structurally different vegetation types when the spatial location of the focal invader is known. Our understanding of large-scale and spatial-explicit species relative performance (GPP ratio) may help resource managers to prioritize monitoring and controls where exotic species tend to be successful invaders.

The coarse spatial resolution of environmental data, such as digital elevation model and substrate type, may limit studies of relationships between GPP ratio and invasion. For instance, fine-scale environmental conditions, such as nutrient availability or temperature, may be driving invasion within small areas due subtle spatial variation in hydrology, soil depth, and localized nutrient availability. We used the assumptions that NDVI and PRI are proxies for fAPAR and LUE, respectively, which ultimately were used to calculate GPP ratio. Physiological and structural differences between canopies may determine subtle changes in the relationship between remote-sensing indices and fAPAR or LUE (Grace et al. 2007). However, studies have also found strong consistency in using these vegetation indices to predict landscape-scale and multi-canopy productivity (Peñuelas et al. 2011). Another potential limitation in our particular case is the fact that plant productivity may be related to performance differences between two strawberry guava varieties, plants with red (*P. cattleianum* var. *cattleianum*) or yellow (*P. cattleianum* var. *lucidum*) fruits, which both occur across these landscapes. Trees with yellow fruits are more likely to invade places at high elevation because they may perform better than trees with red fruits in these conditions (T. Johnson, *unpublished data*). Another likely factor determining strawberry guava invasion in the study area over the last several decades is periodic dieback of the keystone native Hawaiian canopy tree species *Metrosideros polymorpha* (Mueller-Dombois and Boehmer 2013). Death of *M. polymorpha* increases the canopy and sub-canopy light environment that benefits strawberry guava growth and spread (Asner et al. 2008*a*). This interaction can be expected to be exacerbated by the arrival of a new pathogen in Hawaii, *Ceratocystis fimbriata*, which is lethal to *M. polymorpha* (Keith et al. 2015, Mortenson et al. 2016). Prevalence of this pathogen in *M. polymorpha* may also depend on substrate and rainfall, adding a further layer to the influence of these environmental factors in guava tree invasion.

In our study landscapes, strawberry guava showed a large range of variation in cover (invasion severity). We

expected that a continuum of cover would lead to a continuum of impacts on the ecosystem (Stohlgren and Rejmanek 2014), i.e., forest carbon storage, mediated by environmental conditions. However, we often found that the same degree of strawberry guava cover shows diverse outcomes in landscape-scale carbon stock. The variability of outcomes decreased as strawberry guava cover increased in substrates of 200–400 yr BP and 1500–3000 yr BP, but we found the opposite (i.e., increase in variability) in substrates of 400–750 yr BP (Fig. 7). Asner et al. (2009) highlight that environmental conditions mediate the magnitude or importance of a particular invasive species on changes in carbon stock. Although some studies have found contrasting outcomes of invasion on forests carbon stocks and fluxes (i.e., Hughes and Uowolo 2006, Liao et al. 2008, Asner et al. 2009, Hughes et al. 2014), our results demonstrate in particular how subtle increases in invasion severity change forest carbon storage. Together, these studies suggest species-specific and density-specific effects of invasion on losses or gains of forest carbon stock. Different outcomes of invasion for carbon stock may also be the result of patterns in diversity and population dynamics of native forests. In addition, invaders may regulate long-term changes in carbon fluxes and pools by indirect effects, such as changing nutrient availability, primary production, or species composition (Peltzer et al. 2010). These previous studies indicate why it is difficult to define a general principle of the relationship between increasing cover of invasive species and changes in carbon stock. While strawberry guava invasion did not markedly alter the total carbon stock on our study area, we found a decrease on ACD_{SD} and $ACD_{max/mean}$ as invasion increased. Therefore, this invasive species appears to homogenize the carbon stock within the landscapes, potentially due the long-term replacement of big native trees. Strawberry guava cover below and above 20% showed different ranges of carbon stock traits (i.e., ACD_{mean}, ACD_{SD}, and $ACD_{max/mean}$; Fig. 7), which suggest a potential threshold in the relationship between the progress of invasion and changes in forest carbon stock.

In sum, our knowledge about outcomes of continuum ranges of invasion severity and potential invasion thresholds may help us to prioritize management strategies that prevent negative impacts before invaders produce abrupt shifts in ecosystems function. In addition, the GPP ratio can also be a useful tool to study plant invasion, simplifying the forecast of coexistence mechanisms between invaders and the host plant community (Adler et al. 2013). This methodological approach may be used in any forest, shrub, or grass vegetation areas where canopies of both focal invasive species and host plant community are mapped and remote-sensing data are available for modeling GPP. Our understanding of large-scale invasion mechanisms may help us to narrow management efforts to focal areas where control measurements may be more effective.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1445/full

Data Availability

Data associated with this paper are available in figshare: https://figshare.com/s/9867849e4756e3d50dd9