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Invasive grasses change landscape structure and fire behaviour in Hawaii

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BehavePlus; Fire modelling; Grass–fire cycle; Guinea grass; Hawaii; Land-cover change; *Megathyrsus maximus*

Nomenclature
Wagner et al. (1999) for all native Hawaiian species; USDA ARS-GRIN (www.ars-grin.gov/npgs/) for *Megathyrsus maximus*.

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Abstract

Questions: How does potential fire behaviour differ in grass-invaded non-native forests vs open grasslands? How has land cover changed from 1950–2011 along two grassland/forest ecotones in Hawaii with repeated fires?

Location: Non-native forest with invasive grass understory and invasive grassland (*Megathyrsus maximus*) ecosystems on Oahu, Hawaii, USA.

Methods: We quantified fuel load and moisture in non-native forest and grassland (*Megathyrsus maximus*) plots (n = 6) at Makua Military Reservation and Schofield Barracks, and used these field data to model potential fire behaviour using the BehavePlus fire modelling program. Actual rate and extent of land-cover change were quantified for both areas from 1950–2011 with historical aerial imagery.

Results: Live and dead fuel moisture content and fine fuel loads did not differ between forests and grasslands. However, mean surface fuel height was 31% lower in forests (72 cm) than grasslands (105 cm; $P < 0.02$), which drove large differences in predicted fire behaviour. Rates of fire spread were 3–5 times higher in grasslands (5.0–36.3 $m \cdot min^{-1}$) than forests (0–10.5 $m \cdot min^{-1}$; $P < 0.001$), and flame lengths were 2–3 times higher in grasslands (2.8–10.0 m) than forests (0–4.3 m; $P < 0.01$). Between 1950 and 2011, invasive grassland cover increased at both Makua (320 ha) and Schofield (745 ha) at rates of 2.62 and 1.83 $ha \cdot yr^{-1}$, respectively, with more rapid rates of conversion before active fire management practices were implemented in the early 1990s.

Conclusions: These results support accepted paradigms for the tropics, and demonstrate that type conversion associated with non-native grass invasion and subsequent fire has occurred on landscape scales in Hawaii. Once forests are converted to grassland there is a significant increase in fire intensity, which likely provides the positive feedback to continued grassland dominance in the absence of active fire management.

Introduction

It is generally well accepted that the synergistic effects of non-native grass invasion and repeated wildfire in the tropics reduce cover and abundance of native species (Loope 1998, 2004; Eva & Lambin 2000; Hoffmann et al. 2002; Hughes & Denslow 2005), often outcompeting native plant communities and converting forests into non-native grasslands (Hughes et al. 1991; D'Antonio & Vitousek 1992; Ainsworth & Kauffman 2010). In Hawaii, as with other tropical island ecosystems, grass invasion and increased fire frequency is particularly problematic because fire is not believed to have historically played a large role in the evolution of these unique island ecosystems, and current fires are primarily anthropogenic in origin (LaRosa et al. 2008). As a result, many native species do not possess adaptations to survive a regime of frequent fires (Rowe 1983; Vitousek 1992) or to recover following fire (D'Antonio et al. 2011), and often any woody plant re-establishment is non-native (Mandle et al. 2011). Prior studies have examined grass–fire interactions on tropical islands at the plot level (Hughes et al. 1991; Ainsworth & Kauffman 2010). One recent study in Hawaiian submontane forests, in particular, showed that non-native grasses remain dominant,

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with little native recovery, up to 37 yrs after fire and conversion of native forest to non-native grassland (D'Antonio et al. 2011). However, no study has quantified these type conversions to non-native grasslands over large spatial extents or long temporal scales.

Invasive grasses in the tropics alter the occurrence and behaviour of fires via a variety of both intrinsic (characteristics of the plants themselves) and extrinsic (arrangement of plants across the landscape) fuel properties (Brooks et al. 2004). Intrinsic fuel properties associated with type conversion from forest to grassland can include increased flammability due to lower fuel moisture (Brooks et al. 2004), total curing of grass (Andrews et al. 2006) and higher surface area to volume ratios (Hoffmann et al. 2012), followed by competitive superiority for above- and below-ground resources in the post-fire environment (Veldman & Putz 2011; Ammondt & Litton 2012). Extrinsic properties, in turn, can include increased horizontal fuel continuity (Brooks et al. 2004), changes in microclimate (Blackmore & Vitousek 2000; Hoffmann et al. 2002), increased fine fuel loads (Litton et al. 2006) and change in fuel packing ratios (Brooks et al. 2004; Hoffmann et al. 2004).

Highly flammable African pasture grasses have been introduced throughout the tropics where they are now widespread and problematic invaders (D'Antonio & Vitousek 1992; Williams & Baruch 2000). In addition to impacting fire regimes, these invasive grasses commonly alter carbon storage, forest structure (Litton et al. 2006) and nutrient dynamics (Asner & Beatty 1996; Mack et al. 2001). Once a fire does inevitably occur, the post-fire plant community is typically characterized by rapid non-native grass regeneration, which then predisposes these ecosystems to more frequent and higher intensity fires (Smith & Tunison 1992; Pyne et al. 1996; Blackmore & Vitousek 2000; LaRosa et al. 2008; Ainsworth & Kauffman 2010). This cycle of non-native grass invasion, fire and grass reinvasion (i.e. the invasive grass–widlfire cycle) is a common occurrence in tropical ecosystems that is thought to lead to large-scale land-cover change (D'Antonio & Vitousek 1992).

Megathyrsus maximus [Jacq.], previously *Panicum maximum* and *Urochloa maxima* [Jacq.], an African bunchgrass, was introduced to Hawaii for cattle forage and became naturalized in the islands by 1871 (Williams & Baruch 2000; Motooka et al. 2003; Portela et al. 2009). As in other tropical ecosystems, *M. maximus* quickly became problematic because it is adapted to a wide range of ecosystems (*e.g.* dry to mesic) where it alters flammability by dramatically increasing fuel loads and fuel continuity. Year-round high fine fuel loads with a dense layer of standing and fallen dead biomass maintain a significant fire risk throughout the year (Ellsworth et al. 2013). Because *M. maximus* recovers quickly following disturbance (i.e. fire, ungulate grazing, land-use change, etc.) and is competitively superior to native species (Ammondt & Litton 2012), many areas of Hawaii, as well as throughout the tropics, are now dominated by this non-native invasive grass.

Plot-level studies provide important insights into the relationships between non-native grass invasion, fire and type conversion from forest to grassland, but a greater understanding of these dynamics is only possible by examining these processes at the landscape scale (Brook & Bowman 2006; Levick & Rogers 2011). Furthermore, understanding the spatio-temporal dynamics of vegetation change over longer time scales can better elucidate the mechanisms driving vegetation change. Because the invasive grass–wildfire cycle has been well documented at the plot scale, the dominant paradigm on tropical islands is that fire shifts composition from woody communities to non-native grassland, that these changes persist over long time periods, and that the end result is a landscape that is increasingly dominated by non-native invasive grasses that have a much higher fire risk than the forests that they replaced. However, few studies in the tropics have looked at landscape vegetation cover patterns resulting from repeated fire and grass invasion at landscape scales (Blackmore & Vitousek 2000; Grigulis et al. 2005).

The objectives of this study were to: (1) use field data and fire modelling to compare fuels and potential fire behaviour in adjacent forests vs grasslands; and (2) measure the rate and extent of land-cover change at the grassland–forest boundary from 1950 to 2011 in and around two heavily utilized military installations on Oahu, Hawaii. We hypothesized that (1) fine fuel loads and heights would be lower and fuel moisture higher in forest plots than grass plots due to differences in understorey microclimate (Hoffmann et al. 2002) and shading (Funk & McDaniel 2010); (2) as a result of lower fuel heights and loads, modelled fire behaviour would be less severe (i.e. lower rates of spread, flame lengths and probability of ignition) in forest plots than in grass plots (Freifelder et al. 1998); and (3) rates of conversion from forest to grassland would increase through time over the past 50+ yrs due to increased grass cover and ignition sources (Beavers 2001). To test these hypotheses, we quantified fuels in forest and grassland plots, modelled potential fire behaviour, and quantified land-cover change from 1950 to 2011 with historical imagery.

Methods

Fuel quantification

Fuel loads in *M. maximus* -dominated open grassland (grass sites) and adjacent non-native forest with an invasive grass understorey (forest sites) were quantified in the summer

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of 2008 in the Waianae Kai Forest Reserve (forest: 367 m a.s.l.; MAP [mean annual precipitation], 1399 mm; MAT [mean annual temperature], 20 °C) (grass: 193 m a.s.l.; MAP, 1134 mm; MAT, 23 °C) and Dillingham Airfield (forest and grass: 4 m a.s.l.; MAP, 900 mm; MAT, 24 °C; T. Giambelluca, unpublished data) on the Waianae Coast and North Shore areas, respectively, on the Island of Oahu, Hawaii, USA (Fig. 1). All sites are dominated by *M. maximus* in the understorey. Forest sites are dominated by non-native trees, including *Leucaena leucocephala* (Lam.) De wit in the subcanopy and *Prosopis pallida* and *Grevillea robusta* in the overstorey. Soils at Dillingham Airfield are in the Lualualei series (fine, smectitic, isohyperthermic Typic Gypsitorrerts) formed in alluvium and colluvium from basalt and volcanic ash. Soils at Waianae Kai are in the Ewa series (fine, kaolinitic, isohyperthermic Aridic Haplustolls) formed in alluvium weathered from basaltic rock.

Within each of the two sites, three grassland and three forest plots were selected using USGS imagery in Google Earth 5.0 and an *a priori* knowledge of the understorey composition. Plot selection was based on continuous grass cover with little to no tree cover for grassland plots, and a continuous tree overstorey with *M. maximus* in the understorey for forest plots. Final plot selection was made randomly from all possible 50 × 50-m plot locations within the study area that met these criteria. In each grassland and forest site, the following fuel variables were measured: (1) total fuel loads (standing live and dead, and litter), (2) fuel composition (live grass, dead grass, standing trees, downed wood), (3) mean fuel height (calculated as 70% of maximum observed surface fuel height in each plot (Burgan & Rothermel 1984)) and (4) live and dead fine fuel

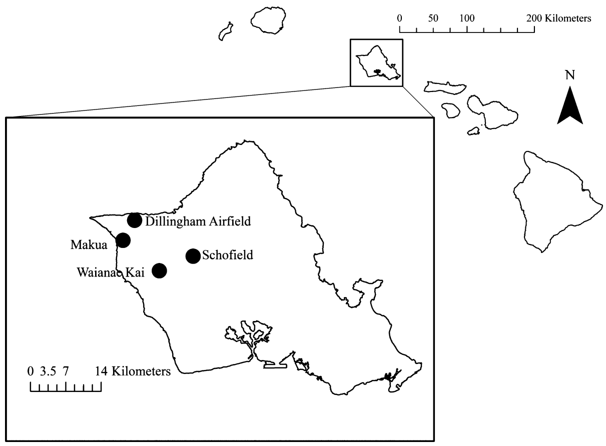

Fig. 1. Location of sites for grassland and forest fuel sampling and historical analysis on the Waianae Coast and North Shores of Oahu, Hawaii. Forest and grassland field sampling occurred at Dillingham Airfield and Waianae Kai Forest Reserve. Historical land-cover change analyses were conducted on imagery from Schofield Barracks and Makua Military Reservation.

moisture. To measure understorey fuels in each plot, three parallel 50-m transects were established 25-m apart, and all herbaceous fuel was destructively harvested in six 25 × 50-cm subplots at fixed locations along each transect (n = 18 plot^{-1}). This sampling design adequately captured the spatial variability in fuels at a given site (Ellsworth et al. 2013). Samples were immediately placed into sealed plastic bags to retain moisture. Within 6 h of field collection, all samples were separated into categories (live grass, standing dead grass, surface litter and downed wood), weighed, dried in a forced air oven at 70 °C to a constant mass (minimum 48 h), and reweighed to determine dry mass and moisture content relative to oven dry weight.

Live standing trees and standing and downed dead wood were also quantified in each grassland and forest plot. The DBH of *L. leucocephala* – the dominant woody species in all forest plots – in a single 1 × 50-m belt transects was measured in each forest plot. Total live tree biomass was determined using an existing species-specific allometric equation for *L. leucocephala* (Dudley & Fownes 1992). The utility of this allometry for estimating biomass in trees from the Waianae Kai field site was explored by harvesting trees across the widest possible range of sizes found (n = 20, DBH from 1.5 to 6.2 cm) and comparing observed vs predicted biomass. There was a strong correlation between predicted and observed biomass (r^2 = 0.95), indicating that the existing equation accurately estimates *L. leucocephala* biomass in our study sites. While other woody species occurred in the general study area, none were encountered in any of the sampling transects. Coarse downed woody fuels were sampled along three 50-m transects plot^{-1} using a planar intercept technique (Brown 1974). In addition, the height of the tallest blade of grass was measured in each subplot before clipping, and mean fine fuel height was recorded as 70% of the average maximum height across subplots (Burgan & Rothermel 1984).

Fire modelling

The fuels data described above were used to create a custom fuel model in the BehavePlus 5 Fire Modelling System (Andrews et al. 2005) to predict fire behaviour for each plot. Live and dead fuel heat contents were measured using bomb calorimetry (Hazen Research, Inc., Golden, CO, US). Previously published values of dead fuel moisture of extinction for *M. maximus* (Beavers 2001) and woody surface area to volume ratio for humid tropical grasslands (Scott & Burgan 2005) were used. Surface area to volume ratios for both live and dead fuels were measured on *M. maximus* individuals from Dillingham Airfield and Waianae Kai Forest Reserve (n = 20 overall using a LI-3100C leaf area meter (LI-COR, Lincoln, NB, US) and water displacement. After examining the range of wind

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speed data collected at the field sites, we selected an average 20-foot windspeed (15 km·h^{-1}) and an extreme 20-foot windspeed (30 km·h^{-1}) to simulate moderate and severe wind scenarios that were then applied to all sites. Wind adjustment factors of 0.4 and 0.3 were used for grass and forest plots, respectively, to adjust the wind speed collected by the RAWS weather stations (20-foot wind speed) to that at the vegetation height (surface wind speed, Andrews et al. 2005). Air temperature was obtained from adjacent RAWS station and fuel shading was measured with a hand-held densitometer. Output variables of interest from the fire behaviour model included: maximum rate of spread (ROS; m·min^{-1}), flame length (m) and probability of ignition (%).

Historical and spatial land-cover change analysis

Land cover classifications were made on orthorectified aerial photographs and 0.5-m spatial resolution multispectral Worldview-2 imagery for Makua Military Reservation (108 m a.s.l.; MAP, 864 mm; MAT, 23 °C) and Schofield Barracks (297 m a.s.l.; MAP, 1000 mm; MAT, 22 °C (Giambelluca et al. 2013); Fig. 1). Classified maps for Makua were derived from images for five time periods: 1962, 1977, 1993, and 2004 aerial photographs, and 2010 Worldview-2 scenes. Schofield land-cover maps were created for six time periods: 1950, 1962, 1977, 1992 and 2004 aerial photographs, and 2011 Worldview 2 scenes. The 2004 images for Makua and Schofield were high-resolution (0.3 m) USGS registered images with a positional accuracy that did not exceed 2.12 m RMSE (root mean square error). The other images were georeferenced to the 2004 images with a first-order polynomial warping (affine transformation) to achieve an average RMSE of 3.37 m and a maximum RMSE of 9.84 m. Worldview-2 images are high resolution (~0.5 m) with a positional accuracy of 12.2 m at the CE90 level.

Both Makua and Schofield site boundaries were digitized into polygon vector shapefiles using ArcGIS Desktop v 9.3.1 (ESRI, Redlands, CA, US). Each site was divided into two areas of interest (AOI): a grassland area on one side of a mowed fire break, which is heavily utilized for military training activities, and a forested area on the other side of the fire break, where little military activity occurs. While these areas were defined as grassland vs forest, each contains patches of both grass and woody cover as well as patches of more intensive utilization (i.e. developed military training areas). The ArcGIS data management tool *Create Fishnet* was used to divide the study sites into grids with a 50 × 50-m cell size and clip the grids to the site boundaries. After the grids were created, they were overlaid onto the images for classification.

Each cell was classified into one of seven cover classes at Makua: Grass, shrub, forest, bare, developed, military training area (MTA; highly disturbed area with minimal vegetative cover) and shadow/cloud (treated as No Data). The woody plant composition at Schofield is highly variable and forest and shrub cover classes are often indistinguishable from aerial images. At Schofield, shrub and forest cover classes were combined into a single mixed woody cover class, resulting in six cover classes for this site (grass, woody, bare ground, developed, MTA and No Data). The total area of each cover class was calculated for every time period within the two AOIs for both sites. Amounts and rates of land-cover change (expressed as average ha·yr^{-1}) were then extrapolated for each of the four AOIs over each time period.

Statistical analyses

General linear models were used to determine whether there were differences in live and dead fine fuel loads, fine fuel moistures, average fuel height, fire behaviour variables (ROS, flame length) and probability of ignition between grassland and forest plots, after controlling for differences in mean annual precipitation (MAP) among sampled plots. Because there is an elevation/precipitation gradient at Waianae Kai Forest Reserve, and forest plots were clustered ~150 m higher in elevation than grassland plots, MAP was included in the model to control for differences in environmental variables that may have potentially impacted fuels and fire behaviour. Site was treated as a random factor, plot type (forest or grassland) was treated as a fixed factor and MAP was used as a covariate. Live and dead fine fuel variables were log-transformed for analysis to meet model assumptions of normality and homogeneity of variance, but all results are presented herein as untransformed data. Minitab v 15 (Minitab, State College, PA, US) was used for all statistical analyses, and significance was assessed at $\alpha = 0.05$. For Fragstats spatial analyses, AOIs within sites are not independent, and only two sites were analysed, making statistical inference inappropriate. Therefore, this analysis was limited to an examination of temporal trends in patterns.

Results

Fuel quantification

After controlling for differences in MAP ($P < 0.01$), there were few differences in fine fuels between forest and grassland plots, with live fine fuels ranging from 2.1 to 5.9 Mg·ha^{-1} ($P = 0.86$), and dead fine fuels ranging from 10.4 to 19.5 Mg·ha^{-1} ($P = 0.89$; Table 1). Precipitation

Table 1. Live and dead fine fuel loads (in Mg ha^{-1}), fuel moisture (%) and maximum fuel height (cm) in open *M. maximus* ecosystems and forested ecosystems with a *M. maximus* understorey on leeward Oahu, Hawaii. MAP refers to the mean annual precipitation at each site. Means and SE are given for fuels variables at each site (N = 3). Significant model factors are indicated with bold font in the last three columns.

Variable	Dillingham Grass	Dillingham Forest	Waianae Kai Grass	Waianae Kai Forest	Model R^2 (%)	MAP	Site	Type
						(*P*-value)		
Live fine fuels	4.6 (0.9)	5.9 (3.9)	3.7 (0.4)	2.1 (1.0)	31.1	0.38	0.65	0.86
Dead fine fuels	19.5 (4.3)	19.5 (3.0)	13.7 (0.6)	10.4 (1.8)	51.4	0.52	0.80	0.89
Live fuel moisture	47.2 (3.6)	78.2 (13.1)	57.7 (9.0)	173.6 (27.3)	84.2	**0.02**	0.18	0.19
Dead fuel moisture	13.6 (2.3)	23.4 (6.8)	15.5 (2.9)	65.2 (31.4)	61.7	**0.05**	0.14	0.95
Max. fuel height	138.6 (9.7)	71.0 (3.0)	71.3 (10.7)	72.3 (12.0)	76.5	**0.02**	**<0.01**	**<0.01**

Table 2. Predicted fire behaviour under both moderate (15 km·h^{-1}) and severe (30 km·h^{-1}) wind conditions in open *M. maximus* ecosystems and forested ecosystems with a *M. maximus* understorey on leeward Oahu, Hawaii. MAP refers to the mean annual precipitation at each site. Means and SE are given for fire behaviour variables at each site (N = 3). Significant model factors are indicated in bold font in the last three columns.

Variable	Wind condition	Dillingham Grass	Dillingham Forest	Waianae Kai Grass	Waianae Kai Forest	Model R^2 (%)	MAP	Site	Type
							(*P*-value)		
Rate of Spread (m·min^{-1})	Moderate	14.9 (1.6)	2.7 (1.2)	5.8 (0.6)	0.4 (0.4)	91.0	**0.04**	**<0.01**	**<0.001**
	Severe	30.7 (3.1)	5.7 (2.6)	12.0 (1.2)	0.8 (0.8)	91.1	**0.04**	**<0.01**	**<0.001**
Flame Length (m)	Moderate	5.8 (1.0)	2.1 (0.5)	3.0 (0.2)	0.3 (0.3)	84.8	0.61	0.10	**<0.01**
	Severe	8.1 (1.4)	2.9 (0.8)	4.3 (0.3)	0.4 (0.4)	84.6	0.62	0.11	**<0.01**
Probability of Ignition (%)	Moderate	21.0 (7.0)	10 (10)	14.3 (5.6)	0.3 (0.3)	38.5	0.84	0.82	0.27
	Severe	21.0 (7.0)	10 (10)	14.3 (5.6)	0.3 (0.3)	38.5	0.84	0.82	0.27

was a strong predictor of both live (P = 0.02) and dead (P = 0.05) fuel moisture, but after controlling for MAP, fuel moistures did not differ significantly between forest and grassland (live, P = 0.19; dead, P = 0.95). Live fine fuel moisture ranged from 47 to 173%, and dead fine fuel moisture from 14 to 65%. Mean fuel height, however, was 31% lower in forests (72 cm) than in grasslands (105 cm; $P < 0.02$) after accounting for differences in MAP (Table 1).

Fire modelling

Despite few significant differences in fuels between forest and grassland, predicted fire behaviour differed greatly between these two land-cover types (Table 2). Under moderate wind conditions (15 km·h^{-1}), rate of modelled fire spread was 3–5 times higher in grassland (5.0–17.7 m·min^{-1}) than forest (0–5.0 m·min^{-1}; $P < 0.001$), and flame lengths were 2–3 times higher in grassland (2.8–7.2 m) than forest (0–3.0 m; $P < 0.01$). Under extreme wind conditions (30 km·h^{-1}), predicted rates of spread were 3–10 tines higher in grasslands (10.1–36.3 m·min^{-1}) than in forests (0–10.5 m·min^{-1}; $P < 0.001$); and flame lengths were 2–4 times higher in grasslands (3.9–10.0 m) than forests (0–4.3 m; $P < 0.01$). Probability of ignition was only >1% in a single forest plot (30%), ranged from 4 to 32% in grassland plots, and was not significantly different between cover types under either moderate or extreme wind conditions (P = 0.27; Table 2).

Historical and spatial land-cover change analysis

Invasive grassland cover increased in heavily utilized areas inside the firebreak at both Makua (total area 320 ha) and Schofield (total area 745 ha) at rates of 2.62 and 1.83 ha·yr^{-1}, respectively, over the entire 50+ yrs examined. More rapid rates of conversion (up to 7.41 ha·yr^{-1}) occurred before aggressive fire management practices were implemented in the early 1990s (Figs 2 and 3, Appendix S1–S3). At Makua, conversion from forest to grassland in the surrounding forest area (total area 1244 ha) was slower (1.78 ha·yr^{-1}) than in the grass area (Fig. 2). Unlike Makua, in the forest area at Schofield (total area 1576 ha) conversion of grassland to forest occurred at a faster rate (4.75 ha·yr^{-1}) than in grass areas (Fig. 3). Overall, change in land cover over time was more dynamic at Makua (Fig. 2) than at Schofield (Fig. 3), coinciding with large and frequent fires at Makua, and fewer hectares burned at Schofield.

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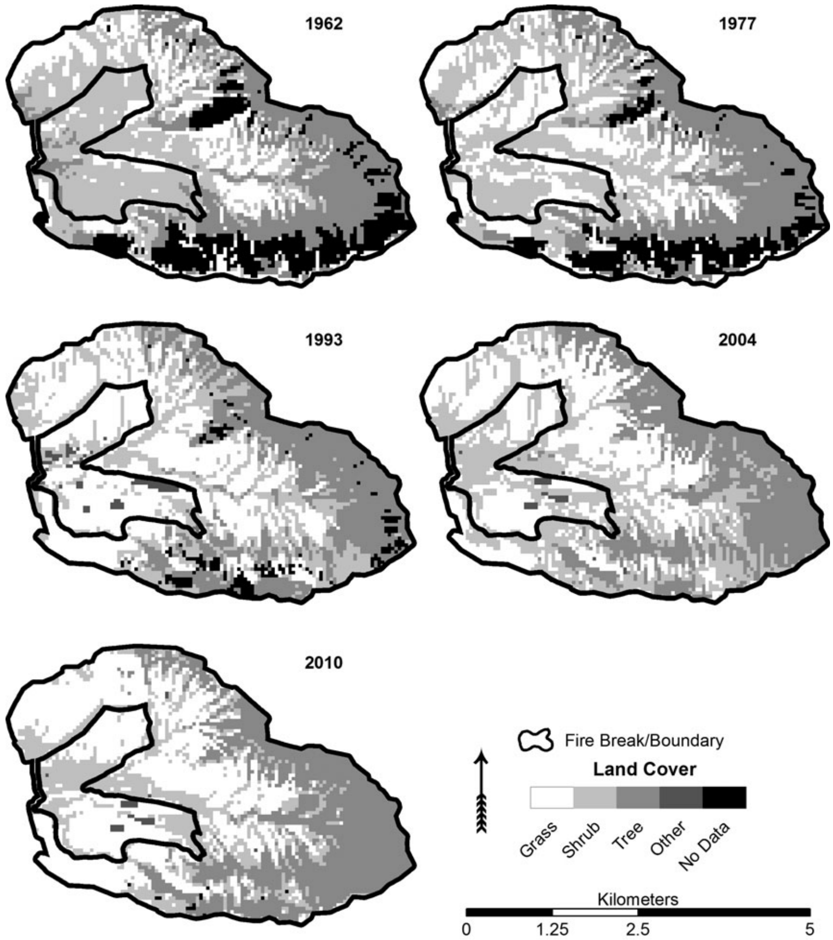

Fig. 2. Land cover at Makua Military Reservation on leeward Oahu, Hawaii, from 1962 through 2010. The area inside the firebreak is heavily utilized for military training activities, and fire is frequent. The area outside the firebreak has historically been forested, contains many threatened and endangered species and is impacted to a lesser extent by military activities and fire. Grassland areas are dominated by *Megathyrsus maximus*, shrub areas (Makua) are dominated by *Leucaena leucocephala*, and forest (Makua) and woody (Schofield) areas are dominated by a mixed non-native canopy.

Discussion

These results demonstrate large type conversions from forest to grassland have occurred over the past 50+ yrs, which have altered fuel heights and increased modelled surface fire spread and intensity, likely representing a positive feedback to grassland dominance. As hypothesized, increased fuelbed depth and an increased effect of wind at the fuel surface (Freifelder et al. 1998; Andrews et al. 2005) in grassland has led to the potential for more intense surface fire behaviour compared to forest. These data support previous work in Hawaii (Hughes et al. 1991; Freifelder et al. 1998) and elsewhere in the tropics (Williams & Baruch 2000; Hoffmann et al. 2002; Rossiter et al. 2003), demonstrating that, at the plot level, the synergistic effects of fire and non-native grass invasion can lead to a pervasive invasive grass–wildfire cycle.

While fire behaviour modelling is commonly used to predict fire behaviour under a given set of fuel conditions (Andrews et al. 2005), we recognize that predicted fire behaviour may not always mirror real world fire. However, the site-specific fuels and weather data that we used as input variables, as well as the close agreement with measured fire behaviour (Beavers 2001), give confidence that the predicted fire behaviour is a close approximation to actual fire behaviour given the same fuel and weather characteristics. However, changing conditions (i.e. wind speed and direction, topography, precipitation) can quickly alter fire behaviour (Pyne et al. 1996). It is important to note that while this paper dealt primarily with surface fire behaviour, in drought conditions it is possible that surface grass fires could transition into torching and crown fire behaviour under low fuel moisture conditions (Scott & Reinhardt 2001). Probability of ignition is calculated in

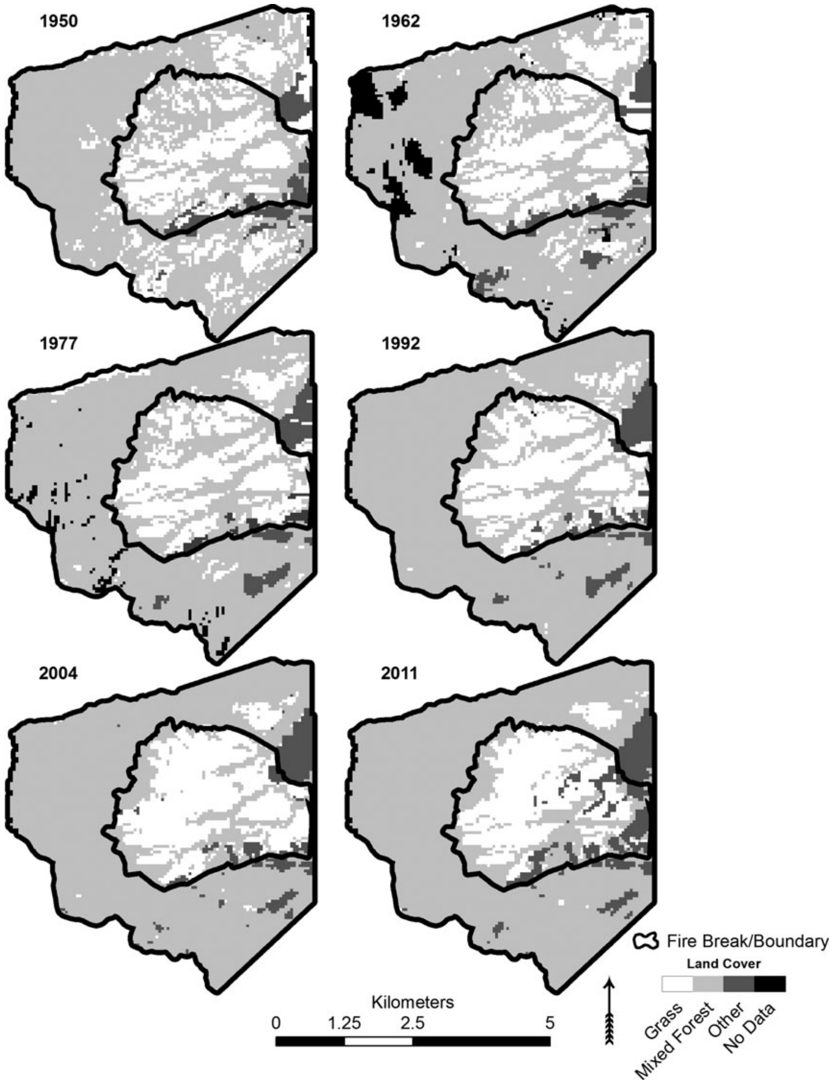

Fig. 3. Land cover at Schofield Barracks on leeward Oahu, Hawaii, from 1950 through 2011. The area inside the firebreak is heavily utilized for military training activities, and fire is frequent. The area outside the firebreak is maintained for woody species and is less affected by military activity and fire. Grassland areas are dominated by *Megathyrsus maximus*, shrub areas (Makua) are dominated by *Leucaena leucocephala*, and forest (Makua) and woody (Schofield) areas are dominated by a mixed non-native canopy.

BehavePlus using dead fuel moisture, air temperature and fuel shading from the sun. While there was no statistically significant difference between forest and grassland plots, it is important to note that only a single forest plot out of the six simulations had a probability of ignition > 1%. The one plot that was predicted to be more likely to ignite had the lowest dead fuel moisture (at 10%) of any plot sampled, and represented the extreme end of fuel moisture conditions previously reported for this fuel type (Ellsworth et al. 2013).

On a landscape scale, interactions among fire, grass invasion, non-native woody species and fire management appear to be complex (App. S4). Because it is generally accepted that repeated fires and the presence of non-native grasses lead to a landscape that is increasingly dominated by flammable grasslands, we expected to see an increase in the rate and extent of conversion in more recent years as compared to historical landscapes. While we acknowledge that the two valleys analysed in this study do not mirror all landscapes in the tropics, they do represent among the most highly impacted end of the spectrum in terms of utilization intensity and opportunities for fire ignition (i.e. frequent military training activities), and we expected to see rapid rates of land cover conversion. The mean trend over time in grassland areas was a reduction in woody cover with a concomitant increase in grass cover, as the

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dominant overstorey trees are generally top-killed and do not rapidly recover following fire (Harwood et al. 1997; Campbell & Setter 2002). In contrast, the mid-storey species is a prolific resprouter as well as a rapid recolonizer from seed following fire (Smith & Tunison 1992), thus contributing to the patches of rapid shrubby recovery seen at Makua (Fig. 2). In the forests, however, there were varied trends observed. At Makua, where fires have been larger and more frequent, the forest is slowly being replaced by grassland, with periods of shrub recovery between fires. Fire management has been difficult at this site (Beavers et al. 1999) due to low precipitation and fuel moisture, remoteness and common anthropogenic ignitions (i.e. military, arson, roadside).

At Schofield, grass cover decreased from 1950 to the present, while woody species increased (Fig. 3). While this area is inaccessible due to unexploded ordinance, we presume that most of the woody increase is due to the spread of non-native woody species, rather than a recovery of a very limited native plant component. Several factors may contribute to the differential response at Schofield. This site has ~16% higher precipitation than Makua (Giambelluca et al. 2013), with higher fuel moisture (Ellsworth et al. 2013). Additionally, fire managers have been successful at containing fires since improved fire management began in the 1990s (Beavers & Burgan 2001). While there are site-specific management concerns that have contributed to the patterns quantified, the implications of our results can be more widely extrapolated. *M. maximus* is widespread in distribution and is similar in fuel characteristics to other large tropical grasses (Kauffman et al. 1998; Williams & Baruch 2000; Jaramillo et al. 2003) where the invasive grass–wildfire connection has been documented (D'Antonio & Vitousek 1992).

From this study, it can be inferred that at a landscape scale, the invasive grass–wildfire cycle may not be the final endpoint for all fire-impacted and non-native grass-invaded tropical ecosystems, as is currently the paradigm in the science and management communities. A recent review of the impacts of woody invasive plants on fire regimes (Mandle et al. 2011) showed that, while most discussion centres around the effects of grass invaders, invasive woody plants can also alter ecosystem properties and patterns, impacting future fire regimes. A dominant non-native woody invader at Schofield, *Schinus terebinthifolius* Raddi (Beavers & Burgan 2001), may reduce fire intensity and spread (Beavers & Burgan 2001; Stevens & Beckage 2009), potentially offering an escape from the invasive grass–wildfire cycle (Mandle et al. 2011).

In summary, we investigated evidence for the dominant paradigm that grass invasion and subsequent fire lead to widespread conversion from forest to grassland and to increased frequency and severity of wildfire. While these results show that grasslands are prone to more extreme fire behaviour than forests, it was not always the case that increased flammability led to widespread increases in grassland cover across the landscape. In fact, some areas appear to be recovering a woody overstorey, albeit non-native, suggesting that active fire management is largely preventing further type conversion to non-native grasslands.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Change in grass, tree and shrub land-cover classes from 1962 to 2011 at Makua Military Reservation.
Appendix S2. Change in grass, woody and military training area land-cover classes from 1950 to 2011 at Schofield Barracks.
Appendix S3. Rates of land-cover change at Makua Military Reservation and Schofield Barracks from 1950 to 2011.
Appendix S4. Landscape metrics describing increasing homogeneity over time.