Journal of Ecology

BRITISH ECOLOGICAL SOCIETY

Journal of Ecology 2017, **105**, 1462–1474 doi: 10.1111/1365-2745.12855

SPECIAL FEATURE: LONG-TERM DYNAMICS AND IMPACTS OF PLANT INVASIONS

Ecosystem vs. community recovery 25 years after grass invasions and fire in a subtropical woodland

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Summary

1. Despite a large body of research documenting invasive plant impacts, few studies have followed individual invaded sites over decades to observe how they change, and none have contrasted how compositional impacts from invasion compare to ecosystem-process impacts over a multi-decadal time-scale.

2. Using direct measurements of plant density and composition and of ecosystems processes, we evaluate how ecosystem structure, above-ground net primary production (ANPP), and above-ground and soil nutrient pools compare over 25 years since fire and C4 grass invasions disrupted seasonally dry Hawaiian woodlands. We compare structure and function between primary woodland that has never burned and is largely native species-dominated, with sites that had been the same woodland type but burned in alien-grass-fuelled fires in the 1970s and 1980s. The sites have not experienced fires since 1987.

3. We report here that woody plant composition and structure continue to be dramatically changed by the initial invasions and fires that occurred 25 years ago and invaders continue to dominate in burned sites. This is reflected in continued low plant carbon pools in burned compared to unburned sites. Yet ANPP and N storage, which were dramatically lower in the initial decade after invasive-grass fuelled fires, have increased and are now indistinguishable from values measured in intact woodlands. Soil carbon pools were resilient to both invasion and fire initially and over time.

4. Above-ground net primary production has recovered because of invasion of burned sites by a non-native N-fixing tree rather than because of recovery of native species. This invasive N-fixing tree is unlikely to return C storage of the invaded sites to those of unburned woodland because of its tissue and growth characteristics and its interactions with invasive grasses. It does not facilitate native species but rather promotes a persistent invasive grass/N-fixer savanna.

5. *Synthesis.* We conclude that fire, an unusual disturbance in this system, has perpetuated the dominance of these sites by invasive species and that despite the dramatic recovery of above-ground net primary production and N pools, the ecosystem continues to be in a distinctly different state than the pre-fire, pre-*Melinis* community. Thus, despite the absence of further disturbance (fire), there is no evidence that succession towards the original ecosystem is occurring. The fact that N pools and above-ground net primary production recover because of a new invader (*Morella faya*), highlights the unpredictability of ecosystem trajectories in the face of altered regional species pools.

Key-words: alternative states, ANPP, disturbance, ecosystem processes, exotic species, long-term impacts, net primary productivity, resilience, secondary invasions

Introduction

Disturbances in terrestrial systems can dramatically shift species composition to dominance by non-native, invasive species, some of which stall succession and create alternative stable states (e.g. Hobbs & Humphries 1995; D'Antonio, Dudley & Mack 1999; Suding, Gross & Houseman 2004; Diez *et al.* 2012). These species can create alternative states by establishing strong priority effects (e.g. Didham, Watts & Norton 2005; Fukami & Nakajima 2011) or generating positive feedbacks (Klironomos 2002; Reinhart & Callaway 2004). It is a matter of speculation whether strongly invaded

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ecosystems, in the absence of further disturbance, will eventually return to uninvaded trajectories as priority effects or positive feedbacks decline (Lundberg & Moberg 2003; Yelenik & D'Antonio 2013). Invader-dominated states may be transitional if propagules of potential colonists (native or not) are widespread (e.g. Didham, Watts & Norton 2005; Fukami & Nakajima 2011), and the physical environment and stable pools of soil organic matter (SOM) have not been dramatically altered during disturbance and invasion.

Despite hypotheses about when invader-dominated states should be transitional, there is a general lack of data concerning the long-term impacts of invasive plant species on ecosystem structure and functioning, particularly after disturbance (Strayer *et al.* 2006; Strayer 2012). By contrast, there is a growing body of knowledge on the impact of invaders on ecosystem function in the short term (e.g. Vitousek & Walker 1989; D'Antonio & Vitousek 1992; Ehrenfeld 2003; Mack & D'Antonio 2003a; Yelenik, Stock & Richardson 2004; Vila *et al.* 2011). This lack of long-term knowledge hinders an understanding of the recovery of important ecosystem properties including species composition, above-ground net primary productivity (hereafter, ANPP), N cycling, and carbon (C) and nitrogen (N) pools after disturbance and invasion. It is therefore not known whether some ecosystem properties such as ANPP are more resilient than other properties such as species composition, and how changes in these properties over time relate to changes in invader dominance.

Disturbance is often associated with invasion in terrestrial ecosystems. Disturbances reduce plant biomass and associated nutrient pools and uptake, and can initially reduce ANPP (Hicke *et al.* 2012; McLauchlan *et al.* 2014). The extent to which ecosystem properties such as ANPP, SOM pools and species composition are resilient to disturbance—particularly in the face of invasion—has been less well studied but is of current interest due to concerns over carbon sequestration (Jandl *et al.* 2007; Magnani *et al.* 2007) and concerns over ecosystems reaching 'tipping points' beyond which they do not return to prior trajectories (Turner 2010). Over the past two decades, many studies have documented the influence of plant species composition, disturbance (Jandl *et al.* 2007) and invasion (Liao *et al.* 2008) on soil C and N cycling, ANPP and nutrient pools. If a single disturbance causes a large-scale plant invasion, then ecosystem properties such as SOM and ANPP may be altered for decades particularly if invaders remain dominant (McLauchlan *et al.* 2014). Many invasive plant species enhance net primary productivity in ecosystems they invade (Vila *et al.* 2011) because they can access resources unavailable to residents thereby increasing accumulation and retention of nutrients (Liao *et al.* 2008; Vila *et al.* 2011). Invaders that enhance disturbance frequency or intensity, such as fire-associated grasses (D'Antonio & Vitousek 1992; Mack & D'Antonio 1998; Rossiter *et al.* 2003), can cause loss of nutrients stored in plant material (e.g. Mack, D'Antonio & Ley 2001), while simultaneously reducing the ability of resident species to re-establish through priority competition (e.g. Hughes & Vitousek 1993). They thus could create a persistent low productivity plant community. While a few studies have documented short-term *negative* impacts of invaders (coupled with disturbance) on ANPP (e.g. Mack, D'Antonio & Ley 2001), the low productivity 'state' has not been followed over time.

In this study, we evaluate the long-term ecosystem effects of plant invaders that promote and respond positively to fire in seasonally dry, primary successional woodlands in Hawaiʻi Volcanoes National Park, USA. These sites were studied intensively in the 1990s when it was found that fires, whose spread was promoted by invasive C_4 grasses, eliminated many native species (Hughes, Vitousek & Tunison 1991; Hughes & Vitousek 1993; D'Antonio, Hughes & Tunison 2011). While sediment charcoal clearly demonstrates that fire occurred in the quaternary history of Hawaiʻi (S. Hotchkiss, unpubl. data), there is no consensus today on how burned ecosystems should respond over multi-decadal time periods. A few native Hawaiian species regenerate immediately post-fire while many do not (D'Antonio, Tunison & Loh 2000; Tunison, D'Antonio & Loh 2000; Loh & Daehler 2008; Ainsworth & Kauffman 2009, 2010). It is not clear whether net primary productivity and other ecosystem properties will return to values of the pre-fire environment over decadal time-scales. Continued persistence of invaders or the incursion of other invaders may affect the trajectory of these systems.

Here we evaluate how ecosystem structure (woody species densities and composition as well as grass cover), ANPP and C and N pools have changed in the 25 years since the last of two fires burned sites that were formerly open-canopy native *Metrosideros polymorpha* Gaud. woodlands with a dense understorey of native shrubs. These primary successional sites were invaded by non-native perennial bunch grasses (*Schizachyrium condensatum* Kunth (Nees) and *Andropogon virgincus* L.) in the 1960s and 1970s, changing the understorey fuel bed (Tunison, D'Antonio & Loh 2000). After fires in 1970 and 1987, a mat-forming, African grass (*Melinis minutiflora* P. Beauv.) quickly became dominant (Hughes, Vitousek & Tunison 1991), suppressing regeneration of native woody species (Hughes & Vitousek 1993; D'Antonio, Hughes & Tunison 2011). In the 1990s, 7–8 years post-fire, ANPP was approximately 65% lower in burned compared to unburned woodland and above-ground nutrient pools were also dramatically lower (Mack, D'Antonio & Ley 2001). Yet soil N and C (unpublished) pools were unaffected by fire history suggesting the potential for return to pre-fire ANPP. From a community composition perspective, recent work has shown that 20+ years after the last fire sites are still largely grass-dominated (D'Antonio, Hughes & Tunison 2011), and N cycling rates are similar to unburned (Yelenik & D'Antonio 2013). Woody cover has increased in the grasslands and in particular an invasive N-fixing tree is increasing in density and cover across the region (Yelenik & D'Antonio 2013) which could affect ANPP.

We specifically evaluate whether ecosystem properties are consistent with the resilience predicted to occur after disturbance in primary successional systems (Peltzer *et al.* 2010), or whether invasive grasses continue to dominate and ANPP remains substantially lower than in unburned sites. If ANPP has remained low, then soil C pool sizes may have diverged between the woodland and the grassland sites. We ask the following specific questions: (i) How do woody species densities and composition, and total ANPP, and the components contributing to it, compare in burned vs. unburned woodland sites? (ii) How do the relative contributions of the life-form components of ANPP compare between current measurements and the 1990s when the sites were early in post-fire succession? and (iii) Is there evidence that ecosystem N and C pools in burned sites are converging towards the unburned woodland sites in the 25 years since fire? Because unburned woodland sites continue to be largely undisturbed and the woody plants that dominate them are relatively slow growing, we predicted that biomass and soil N and C pools will have changed little in 25 years, and ANPP will still be dominated by native woody plants. By contrast we predict that the burned sites, although still invasive grass-dominated, will show increased ANPP compared to the past due largely to recent invasion by non-native N-fixing trees not native woody plants (Yelenik & D'Antonio 2013). We likewise predict that soil C and N pools will be similar to the past or lower in the burned sites because of decades of low NPP and persistent grass dominance prior to this recent invasion of the N-fixing tree. We also predict relatively little change in soil pools because of the slow nature of change in these large nutrient pools.

Study site description

The study sites are on Kilauea Volcano in Hawai'i Volcanoes National Park, Hawai'i, USA. They are between 850 and 910 m in elevation and annual precipitation is approximately 1500 mm (D'Antonio, Hughes & Tunison 2011). There is a dry season from late April and extending typically into September (D'Antonio, Hughes & Tunison 2011; Fig. S1, Supporting Information). Because of the strongly seasonal rainfall, and the elevation, we refer to the area as seasonal submontane dry woodland.

The sites are on pahoehoe lava flows approximately 750–1000 years old overlain by volcanic ash creating entisol soils (mapped as Ustipsamments). The top 30 cm of soil is largely derived from ash deposited in the 1700s. Where soils are deeper than 30 cm, the surface (30–40 cm) ash is underlain by fine cinder and occasionally by an older ash layer that appears to comprise an undated buried A horizon (M.G. Kramer and C.M. D'Antonio, unpubl. data). The weighted average of cation exchange capacity for the surface 30 cm in a core from unburned and burned woodland yielded values of 20·5 and 22·8 respectively (M.G. Kramer and C.M. D'Antonio, unpubl. data). We have no information on the sulphur status of the soils or pre- and post-fire phosphorus. Tissue *P*-values suggest that plants are not *P* limited here (D'Antonio & Mack 2006).

The burned and unburned sites we studied are part of what was once continuous primary successional 'ōhi'a (*M. polymorpha)* woodland. Typical of primary successional woodland in this region, unburned sites are dominated by an open canopy of *M. polymorpha* with a dense understorey of native shrubs primarily of *Leptocophylla tameiameia* Cham. & Schltdl (pukiawe), *Osteomeles anthyllidofolia* Sm. (Lindl) ('ūlei), *Dodonaea viscosa* Jacl. ('a'ali'i) and *Wikstroemia*

Fig. 1. (a) Typical understorey near base of the dominant tree, *Metrosideros polymorpha* in unburned site (Summer 2011). (b) One of 10 surveyed density plots in unburned woodland (2011). Tape shows one edge of plot. (c) Matrix of *Melinis minutiflora* after wet season green up with scattered woody plants in a burned (TB) site. *Morella faya* individuals are large, dense and in background (Fall 2011). (d) One of surveyed density plots in a burned (TB) site. Light green individuals represent *Dodonaea viscosa* shrubs and darker green larger woody plants are *M. faya* (Summer 2011). Photos by Carla D'Antonio. [Colour figure can be viewed at wileyonlinelibrary.com]

phillyraeifolia A. Gray (ʻākia) and a sparse understorey of native sedges and lichens (Fig. 1, and see D'Antonio, Hughes & Tunison 2011). Introduced perennial grasses are abundant in the woodland understorey and include *S. condensatum* (beardgrass) and *M. minutiflora* (molasses grass). By contrast, those woodland sites that burned in 1970 and 1987 are dominated by a carpet of *M. minutiflora*, with common *D. viscosa* shrubs within the matrix of grass (D'Antonio, Hughes & Tunison 2011). Also present are scattered individuals of the non-native, N-fixing tree, *Morella* (formerly *Myrica*) *faya* (Aiton) (Fig. 1). Annual plants are lacking in both burned and unburned sites. We refer to the two habitats we sample within as, unburned woodland (UB in Tables and Figures) and burned woodland (TB in Tables and Figures). TB stands for twice burned because all burned sites studied here burned twice (1970, 1987). Both fires burned with high intensity according to National Park Service Personnel (Tunison, Loh & Leialoha 1995). Within each habitat, we sampled five 'sites' (Table S1). Sites are flat, vegetated swales at least 100 m in length and approximately 20 m wide, adjacent to transects sampled in the past (Hughes, Vitousek & Tunison 1991; D'Antonio, Hughes & Tunison 2011). They are a minimum of 200 m from one another in a landscape of undulating pahoehoe lava ridges and vegetated swales.

Materials and methods

ABOVE-GROUND COMPOSITION/DENSITY AND PRODUCTION OF WOODY SPECIES

To assess plant density and biomass in the two habitats, we established ten 10 m × 10 m unburned and eleven 10 m × 10 m burned plots and measured density, basal diameter (BD) and height of all woody individuals present keeping track of them by species thus obtaining woody species composition and density estimates. We measured all stems of individuals with multiple stems. These plots were adjacent to transects that have been regularly surveyed since 1988 and are described elsewhere (Hughes, Vitousek & Tunison 1991; D'Antonio, Hughes & Tunison 2011). We used allometric relationships (Table S2) created by harvesting 10–20 individuals of each marked woody species in each habitat, to convert BD to woody plant biomass. Before harvest we measured their BD and height. We separated biomass into stems vs. 'leafy twigs' (small stems with leaves). Biomass of each vegetation component was weighed in the field and a subsample returned to the laboratory, weighed, dried for 3 days at 60°C, and reweighed to correct field weights for tissue % moisture. Regressions were generated for each species using BD, BD^2, height (H), H^2, BDH, BD^2H or BDH^2 against total biomass. Regressions predicting biomass with the highest R^2 values were chosen for conversion of surveyed plants to standing biomass. For the dominant tree in the woodland, *M. polymorpha*, we used biomass regressions from Aplet & Vitousek (1994), as well as unpublished data provided by G. Aplet, separating trees by basal circumference and using different equations for different size classes. Samples obtained for % moisture were ground with a Wiley Mill and Wig-L-Bug Dental Amalgamator (Crescent Dental, Elgin, IL, USA) for %C and %N (UHH Analytical Laboratory, Hilo, HI, USA) to estimate standing C and N pools, and plant N uptake (nitrogen taken up by a plant in 1 year).

We used the per individual growth rate of woody species, scaled up by the censuses for woody species density and initial size to estimate ANPP. Within each of the five sites per habitat (Table S1), we marked the base of a minimum of ten individuals of all woody species that comprised >5% understorey cover (see D'Antonio, Hughes & Tunison 2011), using weather resistant paint in February of 2011. If there were fewer than 10 individuals in the area, we marked all of them. We measured BD with a dbh tape (≥1 cm stem) or with digital callipers (<1 cm stem) at the site of the paint. When individual shrubs had more than one main stem at base, we marked and measured each stem separately marking three stems per individual shrub. If there was high variation in stem size, we attempted to sample across that variability. We also measured the height of all marked individuals. A total of 52 shrubs (206 stems) and 11 trees (48 stems) were marked in the Unburned Woodland, and 49 shrubs (97 stems) in the Twice Burned. *Morella faya* was considered a shrub. These same individual stems were resampled in March 2012 to obtain a 1-year woody growth increment.

Finally, we calculated annual growth increment to estimate change in biomass between 2011 and 2012. We used habitat and species-specific (unburned vs. burned), growth increment averages to estimate growth of every stem in the density census and used the predicted 2012 stem diameter to calculate 2012 biomass, and annual above-ground growth. To measure site level ANPP, we added in ANPP of grasses and annual litterfall of woody species as described below.

ABOVE-GROUND GRASS PRODUCTION AND COMPOSITION

Above-ground net primary production of perennial grasses is difficult to measure and controversial (Scurlock, Johnson & Olson 2002). We coupled a sequential harvest technique to assess min and max live biomass across the year, with a census of grass per cent cover. We harvested biomass plots that were as close to 100% cover as possible and then used grass % cover taken in random subplots in each site (see below) to convert estimates to grass biomass on a per area basis across sites. Min/max live biomass techniques are the most commonly used measurements of grass production (Scurlock, Johnson & Olson 2002). This was not however, the same technique used by Mack, D'Antonio & Ley (2001), who used standing peak biomass of 1 year's leaves and stems sampled from randomly arrayed plots, to estimate grass ANPP.

For sequential grass harvests, we selected two 0·5 × 0·5 m plots with approximately 100% grass cover within each of the five sites per habitat and harvested the plots to the ground. We did this every 2 months for 14 months (November 2010 to February 2012), selecting new plots at each time point. Harvests were separated into live vegetative, live reproductive, and standing dead material, and litter and weighed damp. Subsamples were weighed, dried for 3 days at 60°C, and then reweighed to convert field-moist samples to dry weight. Biomass per m^2 was adjusted by % grass cover data taken across the sites (described below). Samples that were obtained for % moisture were also ground with a Wiley mill (#20 mesh) and Wig-L-Bug Amalgamator for %C and %N content (UHH Analytical Laboratory) to estimate standing C and N pools, and plant N uptake.

We harvested two plots per site (=10 plots per habitat) for *M. minutiflora*, the dominant grass. In unburned sites, *S. condensatum* was common although largely dead. Unlike *Melinis* it does not form 100% cover. We harvested plots with the highest per cent cover we could find, counted the number of individual plants and calculated biomass per plant, although there were never distinct relationships. Thus, *S. condensatum* biomass may be underestimated. We looked across sample dates to find maximum and minimum live vegetative and reproductive biomass per harvested quadrat in each site, not necessarily taking the two maximum or minimum values from the same sample date for each site. We used the equation (Live[stems and leaves]$_{max}$ + Reproductive$_{max}$) − (Live[stems and leaves]$_{min}$ + Reproductive$_{min}$) to estimate ANPP in these high-density plots (Scurlock, Johnson & Olson 2002). We averaged ANPP per habitat per species before correcting with per cent cover census data (below). We did not harvest *S. condensatum* in burned sites because living plants were rare. Yet because it had a small per cent cover in burned censuses, we used ANPP rates from unburned corrected with per cent cover data from burned to estimate *S. condensatum* ANPP in burned.

We censused per cent cover of *M. minutiflora* and *S. condensatum* in ten 1 × 1 m subplots within plots where woody plant density and size were censused. In the unburned, we measured subplots within all density plots where as in the burned we used only five of these because grass cover was high and uniform (see D'Antonio, Hughes & Tunison 2011). For *S. condensatum*, bundle density was obtained in these plus 10 other randomly places 1 × 1 m plots per site. Finally, we used the average ANPP at 100 per cent cover multiplied by actual per cent cover data of the species, to estimate ANPP for each grass species in the two habitats. We did not measure sedge production because living sedges were rare.

ANNUAL LITTERFALL

To measure annual litterfall, we lined 60 × 60 cm plastic horticultural trays with 1-mm window-screen mesh and installed them with six traps being placed at regular intervals along a transect through the middle of each site. Traps were checked every 3 months for 1 year, which entailed collecting all litter within the trap, returning it to the laboratory, drying it and weighing it. Litter was not separated by species. Litter from each sample date was summed over the year and an average annual total calculated per site and then per habitat. This was added to the species level production measurements to get total ANPP.

COMPARISONS OF ANPP IN 1990S VS. THIS STUDY

A goal of this study was to compare the components of ANPP between past and current measurements. Direct statistical comparisons of ANPP could not be done because of differences in methodologies for measuring grass ANPP. Instead, we qualitatively compare the proportion of total ANPP contributed by each of the components measured. Data from the 1990s were obtained through Mack (1998) and Mack & D'Antonio (2003b).

N AND C PLANT AND LITTER POOL CHARACTERIZATION

To estimate total standing C and N pools in each site, we used the BD data from the census plots, allometric relationships between BD and biomass of different plant parts (e.g. trunk, twigs, leafy twigs), and the %C and %N content of different woody plant material from the harvests for allometric relationships. We used %C and %N content that was averaged across species, habitat and plant part (e.g. leafy twigs). For grass N pools, we used standing dead, and live vegetative and reproductive biomass from harvest plots averaged across sample dates and habitat and multiplied this by the per cent cover found in the census plots. We then multiplied grass biomass of each component part (vegetative, reproductive) per unit area by %C and %N for that part found in the biomass harvests. To calculate plant N uptake, we multiplied the %N of each plant specific part by the amount that plant part contributed to ANPP.

To calculate the amount of N stored in litter at the soil surface, we collected three randomly placed 30 × 30 cm plots in each site, two times per year (October 2012, March 2013). All litter within the quadrat was collected down to the point at which no recognizable leaves, twigs or fruits were present, dried at 60°C for 3 days and weighed. Subsamples were ground for N and C analysis in bulk. The two dates are averaged to obtain one pool size and N and C content for each habitat type.

To sample roots, we took three, 3 cm diameter × 10 cm deep soil cores per site under random points through the middle of each site, sieved them and hand-picked both coarse and fine roots. Roots that were obviously dead were excluded. We were interested solely in the standing root biomass pool that was as close to live as possible and could be clearly separated from SOM. Sampling was done in August 2012 and March 2013 and averaged. Samples were rinsed, dried, weighed and ground for CN analysis. Per core averages were converted to roots per m^2 using bulk density values obtained from the soil coring and the surface area of the core. We sampled only the top 10 cm because depth to bedrock varied wildly and this depth was consistent. This is meant as a comparative and not exhaustive description of surface root pools.

SOIL N AND C POOL SAMPLING

To calculate C and N stored in soil, we sampled the soil in three locations randomly chosen along transects through each site using a 3·9-cm wide soil corer. At each location, the soil was sampled in increments including 0–5, 5–10, 10–20 and 20–30 cm from surface. Each sampling location had to have at least 35 cm of soil or a new location was chosen. Because most biological activity is in the top 30 cm, and because of the high variability in soil depth, we focused only on the 0–30 cm layer of soil. Before sampling, the litter-O horizon was removed, and coring began at the level where no recognizable leaves or plant parts could be identified. Each core section was sieved through 2-mm mesh. Exact volumes and total dry weight were used to calculate bulk density. Soil C and N were measured on subsamples after samples were ground in a mortar and pestle. Subsamples were rolled in tin caps and analysed on a Fison's Carlo Erba CN Analyzer (Beverly, MA, USA). Per cent C and N were multiplied by bulk density to obtain C and N per cm^3 of soil and then converted to per m^2 by layer.

We assessed δ^{13}C of surface (0–5 cm) and deepest (20–30 cm) soil cores to assess the contribution of C_4 (invasive grass) carbon to the otherwise C_3 (native) soil carbon pool. δ^{13}C was analysed on sieved, dried and ground (mortar and pestle) samples from all the cores. Analyses were conducted at the UH-Hilo Analytical Laboratory using a Thermo-Finnegan Delta V IRMS.

STATISTICAL ANALYSES

All statistical analyses were conducted using JMP versions 11 and 12. Most tests were one-way ANOVAs with habitat as a fixed effect, or two-way ANOVAs (habitat = fixed, soil depth = fixed) unless otherwise noted in figure legends. *Morella faya* data were log$_{10}$ transformed for analyses due to unequal variances/non-normal distributions.

Results

ANPP AND WOODY PLANT DENSITY AND COMPOSITION

Total ANPP (2011–2012) was not statistically distinguishable between the two habitats (Fig. 2a). In the unburned woodland, ANPP was distributed relatively evenly among shrubs, trees, grasses, *M. faya* and litterfall (Figs 2a and 3). While the native tree *M. polymorpha*-dominated standing biomass (Fig. 2b), it contributed little to ANPP because of its slow growth rates; on average the BD of *M. polymorpha* increased by 1·5% per year. By contrast the BD of the invasive tree *M. faya*, a new contributor to ANPP compared to the past (Fig. 3), increased by 17·4% per year (Table 1). This led to per tree production rates of *M. polymorpha* being 2·6 ± 7·0 kg year^{-1} vs. 26·4 ± 5·2 kg year^{-1} for *M. faya*. In contrast to the unburned sites, burned ANPP was dominated by grass and *M. faya* growth. *Morella faya* was present in the unburned woodland and comprised a similar density (Fig. 4) but was more productive (per tree) in the burned sites (Table 1).

Native shrub production made up approximately one quarter of ANPP in the unburned woodland and it was substantially greater there than in burned sites (Fig. 2a) largely reflecting dramatic different in native shrub densities and composition between habitats (Fig. 4). The shrub *D. viscosa* was the only shrub common in both habitats. Per individual it was substantially less productive in burned sites where it had lower height growth rates (Table 1). Overall shrub production was 20 times higher in the unburned compared to burned sites because of the prevalence and high density of other native shrubs primarily *L. tameiameia* and *O. anthyllidifolia* (Fig. 4). These species can occasionally be found in burned habitat and they appear to be growing well there (Table 1) but their overall densities were so low that their contribution to production was negligible.

Grass production was more important in burned compared to unburned sites (Figs 2 and 3), largely because of the high cover of *M. minutiflora* in burned sites and the low cover of living *S. condensatum* in unburned sites (data not shown). As a result, standing live grass biomass was three times higher in the burned than unburned woodland (Fig. 2b) and grass contributions to ANPP were higher in the burned as well (Fig. 2a).

In comparing components of ANPP between our current measurements and the 1990s, the single most obvious difference is the new contribution of *M. faya* to current production at both sites (Fig. 3). Its enormous increase (from 0 to 63% of ANPP) in the burned is mirrored by a similar decline in the relative contribution of grasses. *Morella faya* contributions in the unburned also increased, but this was substantially less (from 0 to 21%) and shrubs also increased as a proportion of total as well leading to an overall increase in ANPP compared to the past (Fig. 3). Grass production declined as a fraction of total production in unburned sites most likely because the dramatic decrease in *S. condensatum* was not compensated by the increase that did occur in *M. minutiflora* cover and productivity.

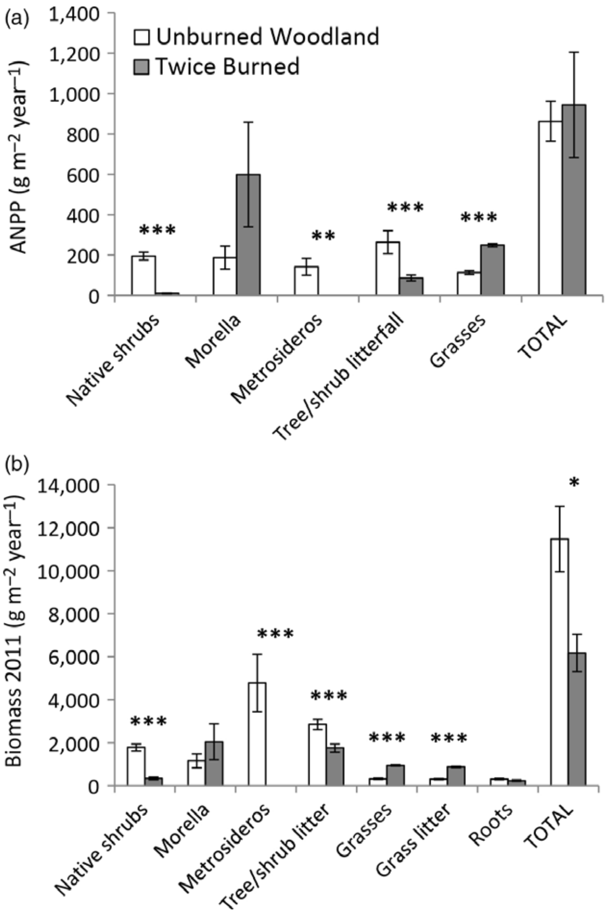

Fig. 2. (a) Above-ground net primary productivity (ANPP) components and totals and (b) biomass pools in plants, roots and litter in burned (TB) and unburned habitats (UB). Bars are means ± 1SE. Asterisks denote that habitats show significant differences with *t*-tests at the *P ≤ 0·05, **P ≤ 0·01 and ***P ≤ 0·001 levels. Woody plant biomass and ANPP (TB: *n* = 11; UB: *n* = 10); grass biomass and ANPP (TB: *n* = 5; UB: *n* = 10); litterfall, *n* = 5; and standing litter and roots, *n* = 20. *Morella faya* data were log$_{10}$ transformed for analyses due to unequal variances/non-normal distributions.

PLANT C AND N POOLS

Carbon pools were greater in unburned than burned sites primarily because of large C pools in *M. polymorpha* (Fig. 5a). While this species is slow growing and thus a small contributor to annual ANPP, it retains a large amount of standing carbon. Indeed our standing stock estimates are low given that we did not census the dead standing *M. polymorpha*. Yet dead trees are common in these woodlands, and they would possibly nearly double the standing pools of C in unburned as found in Mack, D'Antonio & Ley (2001). In contrast, there were no standing dead *M. polymorpha* in the burned sites because most dead trunks were incinerated in the second fire (Mack, D'Antonio & Ley 2001).

Tree and shrub litter biomass at the soil surface was significantly greater, as were C pools of litter, in unburned as compared to burned (Figs 2b and 5a). This is consistent with higher tree and shrub ANPP in unburned and also with the higher C:N ratio of the litter produced by native woody species that dominate these sites (Table S3).

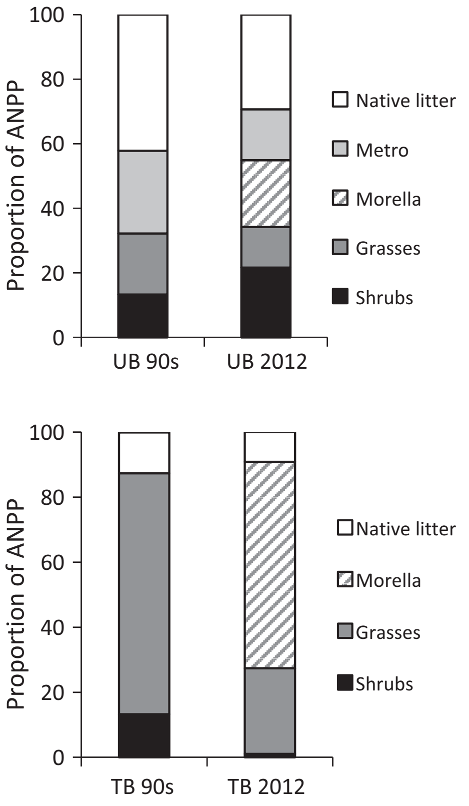

Fig. 3. Proportion of above-ground net primary production (ANPP) due to different vegetation components in 1994–1995 vs. 2011–2012. TB, burned; UB, unburned woodland; Metro, *Metrosideros polymorpha*.

Root biomass (Fig. 2b) in the sampled zone (0–10 cm) did not differ between habitats, although there was a trend towards higher standing root biomass in the unburned woodlands (303 g m^{-2} in UB, 235 g m^{-2} in TB, $P = 0{\cdot}11$). This was reflected again by a trend towards higher standing pools of root C in these sites ($P = 0{\cdot}08$) (Fig. 5a).

Total plant N pools were similar between habitats (Fig. 5b), due to the large contribution by *M. faya* in the burned sites, which more than compensated for the lack of native woody species. This invasive tree had 2·6 times greater %N in its leaves, and 3·3 times greater %N in its stems than *M. polymorpha*. Its higher biomass in burned sites counteracted the native woody pools present in unburned woodland. Litter N pools were higher in unburned than burned sites, whereas grass litter pools were higher in the latter.

ANNUAL N AND C ADDITION INTO PLANT POOLS

Similar to patterns in plant N and C pools (Fig. 5a,b), annual N uptake into vegetation was greater in burned than unburned habitats (Fig. 6b). This was due to high N accumulation in *M. faya*, an N-fixer. This thus represents new N being added to the ecosystem, assuming *M. faya* is actively fixing (supported by ^{15}N in leaf tissue, August-Schmidt and D'Antonio unpublished data from these sites). Yet *M. faya*

Table 1. Average (±1SE) basal diameter (BD), height, BD growth rate, height growth rate and above-ground net primary production (ANPP) per individual in unburned and burned sites for all woody species with >5% cover

	Unburned woodland					Burned				
	BD (cm)	H (cm)	BD GR (% per year)	H GR (% per year)	ANPP (g year^{-1} ind^{-1})	BD (cm)	H (cm)	BD GR (% per year)	H GR (% per year)	ANPP (g year^{-1} ind^{-1})
DODVIS	**2·0** (±0·1)	84·2 (±5·9)	3·7 (±1·2)	5·1 (±3·0)	**79** (±9)	**2·4** (±0·1)	84·8 (±4·5)	4·0 (±0·9)	1·3 (±0·8)	**21** (±2)
LEPTAM	2·5 (n/a)	74·7 (3·7)	4·8 (±1·0)	6·6 (±1·9)	188 (±17)	2·1 (±0·1)	80·0 (n/a)	8·4 (±2·4)	7·1 (±3·0)	205 (n/a)
METPOL	14·4 (±2·3)	389·5 (±47·4)	1·5 (±0·6)		2556 (±827)					
MORFAY	**8·6** (±1·6)	318·0 (±39·6)	**11·9** (±1·1)		**5280** (±1550)	**28·6** (±9·7)	341·0 (±42·0)	**17·4** (±2·1)		**58 264** (±26 684)
OSTANT	1·1 (±0·1)	74·2 (±39·6)	7·7 (±3·0)	2·3 (±1·4)	32 (±2)	1·1 (±0·1)	52·9 (±12·1)	6·3 (n/a)	2·3 (±1·4)	28 (±2)

Numbers in bold represent values that are statistically distinguishable at the $P \leq 0{\cdot}05$ level using *t*-tests with habitat as a fixed effect.
DODVIS, *Dodonaea viscosa*; LEPTAM, *Leptocophylla tameiameia*; METPOL, *Metrosideros polymorpha*; MORFAY, *Morella faya*; OSTANT, *Osteomeles anthyllidifolia*.

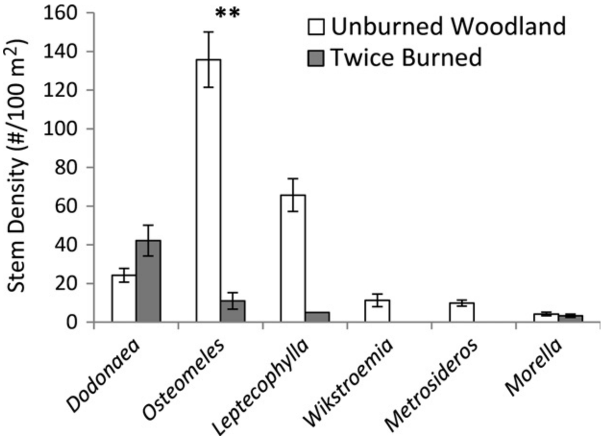

Fig. 4. Density of dominant trees and shrubs in unburned woodland and burned (twice burned) habitats. Asterisks denote that habitats show significant differences with *t*-tests at the $P \leq 0·01$ level. *Dodonaea viscosa* was significant at the $P = 0·06$ level. N for woody plant density: UB = 10, TB = 11.

has lower %C in wood and thus lower C:N ratios than native woody plants and so does not enhance C pools compared to unburned.

SOIL C AND N POOLS

Total soil carbon pools in the top 30 cm of soil were not different between the burned and unburned (Table 2, $P = 0·134$). The only layer to differ in soil carbon was the 10–20 cm layer, which had more C in the burned compared to the unburned sites (Table 2). This was the result of higher % soil C in the burned: bulk density was not different (Table 3).

In contrast to C, total soil N was higher in burned compared to unburned soils with habitat differences largely driven by the difference in %N in the 0–5 cm layer (Tables 2 and 3). C:N ratios tended to reflect these differences in the surface soil layer: the ratio was almost double in the unburned compared to the burned soils due to this difference in %N (Table 3). There were no other differences in C:N values across depths. Bulk density did not differ significantly between habitats, although there was a trend towards lighter bulk density in 0–5 cm cores in unburned compared to burned. This difference accounts for around half of the difference in N pool size between burned and unburned habitat. Even though total soil N in upper soil levels in burned is higher than unburned, soil net N mineralization is not different between habitats (Yelenik & D'Antonio 2013).

There were significant differences in soil $\delta^{13}C$ between habitats, reflecting the larger inputs from C_4 grasses in the burned habitat compared to the unburned. Soil $\delta^{13}C$ in the unburned was more depleted in ^{13}C both in the surface and at depth compared to the burned sites (Table 4). Differences were more prominent in surface layers (0–5 cm) as seen in a habitat by depth interaction (two-way ANOVA with habitat and depth as fixed effects, and an interaction effect, $n = 5$: habitat, $P < 0·001$; depth, $P = 0·195$; habitat × depth, $P = 0·005$). The contribution of C_4 grasses to soil C as a % of soil C was six times as great in burned surface soils compared to unburned and 2·5 times as great at depth (20–30 cm).

Discussion

Our data clearly demonstrate that although composition, density and biomass of *native woody plants* have not recovered (Table 1, Fig. 1) in the 25 years since the last fire burned through these former woodlands, ANPP has converged between unburned and burned sites (Fig. 2). The lack of recovery of composition is consistent with a recent multisite analysis of fire effects in *Metrosideros* forests across Hawai'i (Wasser 2015) and it appears unlikely that the native woodland will ever recover (see Hughes & Vitousek 1993; D'Antonio, Hughes & Tunison 2011). The recovery of ANPP in burned sites, however, is due to the invasion of a non-native N-fixing tree into the grassland where *M. minutiflora* remains as a dominant. Thus, although invasive grass dominance remains strong in burned sites, the relative contributions of each life-form to the components of ANPP have shifted. Despite the apparent resilience of ANPP and N pools, above-ground C pools are still greatly diminished in the burned habitats. Thus compositionally, this ecosystem is still in an alternative state although that state has transitioned to a savanna, co-dominated by *M. minutiflora* and *M. faya*. Fukami & Nakajima (2011) suggested quantitatively that alternative states are best viewed as transitional because priority effects of early colonists are unlikely to remain strong. In this case, the slow breakdown of *M. minutiflora's* priority effects led to succession towards a low-diversity *M. faya/ M. minutiflora* savanna (Yelenik & D'Antonio 2013). This ecosystem is thus an example of a system where disturbance (fire) hastened a transition to 'no analogue' communities that will continue for decades (Turner 2010). These novel communities retain few elements of the original community and present new challenges to ecosystem managers (Hobbs, Higgs & Harris 2009).

PLANT INVADER EFFECTS ON ANPP

In a meta-analytic review of plant invader impacts on ecosystem processes, Liao *et al.* (2008) found that invaders overall significantly increase ANPP (mean response ratio = 83% increase). This 'generality' does not apply in our study system. In the first decade after invasion and fire, Mack, D'Antonio & Ley (2001) clearly demonstrated *a decline* in ANPP with fire and invasion because of the loss of native woody species and the inability of grasses to compensate for this loss. While we found that ANPP is now similar between burned and unburned sites, we found no evidence that ANPP will be enhanced in burned *M. minutiflora*-invaded sites above unburned because grass dominance still limits woody establishment (Yelenik & D'Antonio 2013).

We believe that the reason our study is an outlier from Liao *et al.* is due to the direction of life-form change with invasion: fires here drove a catastrophic shift from a tall statured, woody plant-dominated ecosystem to a grass-dominated one of much lower stature, and diversity. *Melinis minutiflora*, cannot compensate for the lost leaf area and growth potential of the taller and more architecturally complex woody species. In many of the studies cited by Liao *et al.* (2008), invaders consisted of larger life-forms compared to the flora that they invaded (see Harcombe, Cameron & Glumac 1993; Lett *et al.* 2004). Other studies in their meta-analysis evaluated invaders entering systems with little competition from residents (e.g. Vitousek & Walker 1989; Hughes & Denslow 2005).

In ecosystems where invaders trigger a change in disturbance regime that leads to herbaceous species replacing woody ones, we expect ANPP and long-term above-ground carbon pools to be reduced by disturbance particularly if the disturbance intensity is high, as was reputed to be the case in these systems. Studies of cheatgrass (*Bromus tectorum*)-fuelled fires in the Great basin deserts of the western USA demonstrate reduced carbon storage in invaded and burned ecosystems (Bradley *et al.* 2006) compared to unburned. The persistence of such an impact, and its potential for reversal, depend on the diversity (and traits) of native species that could compete with the post-disturbance invader and ultimately recolonize these sites over time (Didham, Watts & Norton 2005). Our system, like Great Basin sagebrush–cheatgrass systems, has a low diversity of dominant woody species, which contributes to low native woody plant recovery.

CARBON STORAGE AND ANPP

In the last two decades, there has been great interest in how plant composition and forest management practices influence carbon storage because of the importance of C sequestration as a strategy to offset fossil fuel emissions (e.g. Canadell & Raupach 2008). Several studies have shown that increases in ANPP due to increases in woody plants do not always result in increased ecosystem C storage, consistent with our study: we found that ANPP is converging between the habitats because of succession towards a grass/*M. faya* savanna, but C storage is still different because above-ground C remains lower and soil C storage is unchanged. The still lower above-ground C pool in burned sites is due to the lack of recovery of the C-storing, slow-growing native plants that dominate unburned woodland and the much higher standing tree

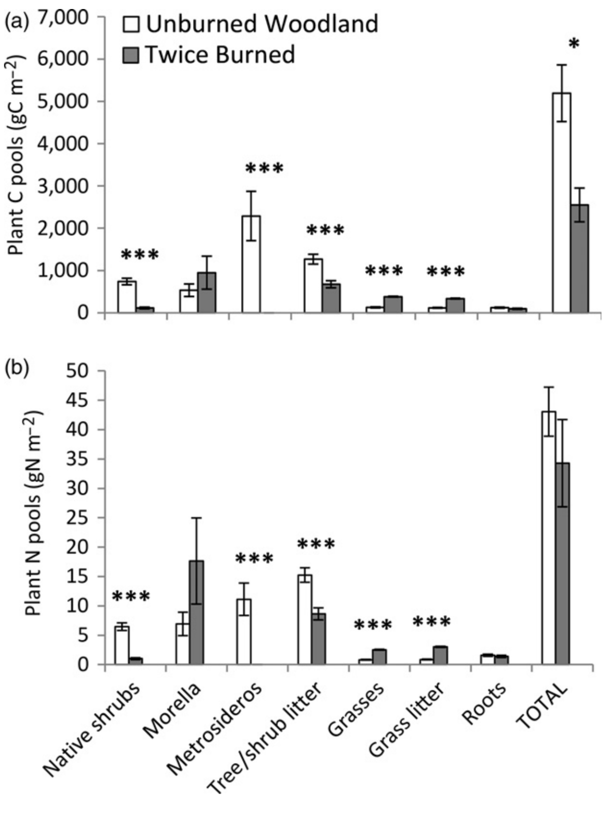

Fig. 5. Pools of (a) carbon and (b) nitrogen in plants, roots and litter in burned (TB) and unburned (UB) habitats. Bars are means ± 1SE. Asterisks denote that habitats show significant differences with *t*-tests at the $*P \leq 0{\cdot}05$, $**P \leq 0{\cdot}01$ and $***P \leq 0{\cdot}001$ levels. Woody plant pools (TB: $n = 11$; UB: $n = 10$); grass pools (TB: $n = 5$; UB: $n = 10$); and woody litter and roots, $n = 20$. *Morella faya* data were $\log_{10}$ transformed for analyses due to unequal variances/non-normal distributions.

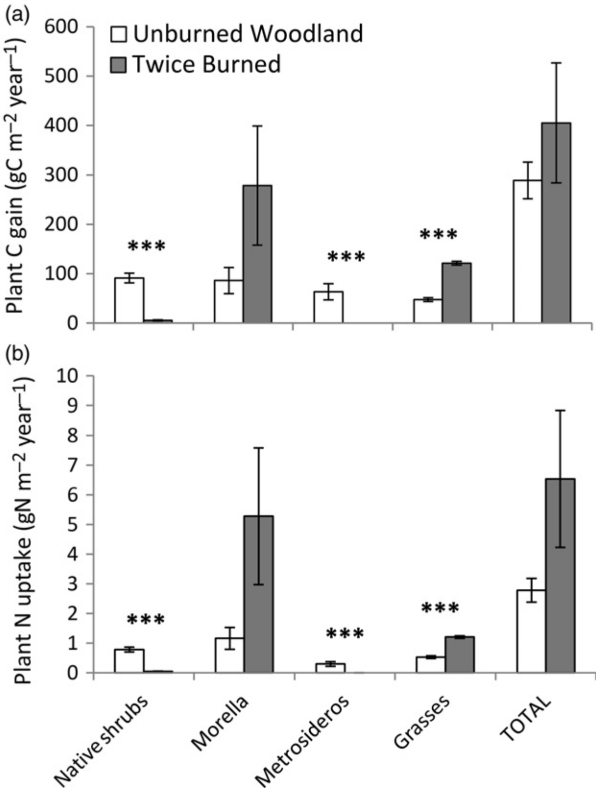

Fig. 6. Plant (a) carbon accrual and (b) nitrogen uptake as measured by above-ground growth x tissue C and N content, unburned and burned (twice burned) habitat. Bars are means ± 1SE. Asterisks denote that habitats show significant differences with *t*-tests at the $*P \leq 0{\cdot}05$, $**P \leq 0{\cdot}01$ and $***P \leq 0{\cdot}001$ levels. Woody plant pools (UB: $n = 10$; TB: $n = 11$), grass pools (UB: $n = 10$; TB: $n = 5$). *Morella faya* and TOTAL (all species) data were $\log_{10}$ transformed for analyses due to unequal variances/non-normal distributions.

Table 2. Soil carbon and nitrogen pools (g m^{-2}) in unburned (UB) and burned (TB) habitats between 2011 and 2013. Values = means of three coring locations in each of five sites per habitat with standard error in parentheses. F-values represent results of ANOVA with location nested within site. Nesting factor always $P > 0·10$. d.f. for habitat effect = 1, 28. %N and C are presented in Table 3. Values obtained for individual cores were converted to g m^{-2} using bulk density for each soil layer. F-(only shown for $P < 0·10$) and P-values in table below are for each soil layer. Analysis of pool distributions by depth was not done here because of differences in soil volume in the different depth fractions

	C pool (g m^{-2})			N pool (g m^{-2})		
Depth (cm)	UB	TB	F, P	UB	TB	F, P
0–5	3094·5 (220·8)	2795·1 (121·1)	$P = 0·245$	110·9 (8·9)	155·5 (7·5)	14·69, $\boldsymbol{P < 0·001}$
5–10	2304·7 (167·3)	2409·1 (118·8)	$P = 0·619$	132·0 (10·7)	146·0 (9·9)	$P = 0·352$
10–20	3321·0 (270·4)	4183·8 (256·8)	4·75, $\boldsymbol{P = 0·038}$	209·6 (16·6)	250·6 (15·3)	3·31, $\boldsymbol{P = 0·079}$
20–30	2976·1 (212·3)	3185·4 (234·1)	$P = 0·53$	179·4 (12·8)	191·0 (13·1)	$P = 0·543$
Total	11 592·7 (637·2)	12 573·4 (437·4)	$P = 0·134$	623·0 (33·7)	743·1 (25·7)	9·26, $\boldsymbol{P = 0·005}$

Bold indicates P values of <0·10 suggesting statistical significance or a strong trend.

Table 3. Soil bulk density, % nitrogen (N), % carbon (C), and C:N ratio of unburned (UB) and burned (TB) habitats between 2011 and 2013. Because the significance of nesting factors (site within habitat) were always >0·12, it was excluded from further models. Values therefore represent means where $N = 15$. Standard errors are in parentheses. Lower case letters indicate significant differences using one-way ANOVAs with habitat as a fixed effect for each depth, and Tukey tests at $P < 0·05$ significant values. The bottom row gives statistics for two-way ANOVAs with depth and habitat as fixed effects, as well as an interaction term. F and P-values are shown only when $P < 0·10$

	Bulk density (g soil cm^{-3})		Soil %N		Soil %C		Soil C:N	
Depth (cm)	UB	TB	UB	TB	UB	TB	UB	TB
0–5	0·42a (0·03)	0·49a (0·02)	**0·46b (0·02)**	**0·60a (0·03)**	**13·54a (1·13)**	**10·77b (0·67)**	**30·12b (2·90)**	**18·12a (0·50)**
5–10	0·67b (0·04)	0·70b (0·04)	0·40bc (0·048)	0·44b (0·03)	7·15c (0·64)	7·30c (0·55)	17·68a (0·60)	16·84a (0·60)
10–20	0·77b (0·06)	0·74b (0·07)	0·29cd (0·03)	0·35bcd (0·04)	4·69d (0·42)	5·81cd (0·51)	16·11a (0·40)	16·74a (0·50)
20–30	0·94c (0·04)	0·81c (0·03)	0·23d (0·03)	0·25d (0·02)	3·67d (0·37)	4·20d (0·37)	16·86a (0·70)	16·62a (0·40)
F, P	Depth: $F = 36·98$, $P < 0·001$ Depth*Habitat = 2·153, $P = 0·09$		Habitat = 9·46, $P < 0·003$ Depth: $F = 34·49$, $P < 0·001$		Depth: $F = 65·47$, $P < 0·001$ Depth*Habitat: $F = 3·85$, $P = 0·016$		Depth*Habitat: $F = 16·51$, $P = 0·004$	

Bold indicates P values of <0·10 suggesting statistical significance or a strong trend.

biomass in unburned both today and in the past (Mack, D'Antonio & Ley 2001). These native species build up a high C:N surface litter layer (Table S3) and higher C in their wood—all traits that would lead to higher above-ground ecosystem C storage.

Table 4. $\delta^{13}C$ values of soil organic carbon and plant leaves from unburned and burned sites. ^{13}C values are means from five samples (each a composite of five samples) from each habitat. Leaf ^{13}C values are means from 5 to 25 samples per type (C_4 vs. C_3) depending on habitat and plant type. Proportion of SOC (soil organic carbon) from C_4 calculated with simple mixing model

	Unburned	Burned
$\delta^{13}C$ soil		
0–5 cm	−26·03	−20·94
20–30 cm	−25·43	−22·45
$\delta^{13}C$ plant leaves		
C_4	−13·71	−13·41
C_3 (native woody)	−26·03	−25·94
Proportion SOC from C_4		
0–5 cm	6·28	39·90
20–30 cm	10·94	27·29

Bold indicates P values of <0·10 suggesting statistical significance or a strong trend.

Below-ground increases in C have been observed when forest is converted to pasture (Guo & Gifford 2002), a conversion similar to the change from woodland to grassland induced by fire and invasion in our sites. Yet we did not see an increase in soil C storage in the grassland despite decades of grass domination. Both habitats stored roughly 12 000 g m^{-2} of C in soil. The lack of increase in soil C may be because microbes and decomposition processes also respond to vegetation change, and increased respiratory losses, such as might be induced by *M. minutiflora* with its dense above-ground litter layer could result in lack of additional soil C accumulation.

Above-ground net primary production in our burned sites has come to be dominated by the invasive N-fixing tree, *M. faya*, a change from 25 years ago (Fig. 3). Elsewhere, woody plant invasion of grassland has been found to drive down soil C at precipitation >1000 mm offsetting gains in above-ground C with woody invasion (Jackson *et al.* 2002). Yet our results are not consistent with this: soil C storage was statistically similar among habitats (11 592 g m^{-2} in woodland vs. 12 573 g m^{-2} in burned), while the plant and litter C pool together was twice as high in the woodland (5191 g m^{-2} vs. 2550 g m^{-2}). Ash soils tend to have high capacity for C storage (Torn *et al.* 1997; Kramer *et al.* 2012) and so may be buffered from C loss as the vegetation changes. Thus, despite clear differences in the nature of vegetation inputs to soil as estimated from delta ^{13}C values of soil (Table 4), soil C pools remain similar in overall size. While this is consistent with at least one review of soil C pools in forested ecosystems, it contrasts with studies that report increases in soil C pools with N-fixation in some forested systems (Johnson & Curtis 2001). If N-fixers alleviate N limitation and do not become limited by other nutrients (like P), then soil C pools may increase over time.

FIRE AND TIPPING POINTS IN DRYLAND FOREST ECOSYSTEMS

Many dry forest ecosystems experience fire as a regular periodic disturbance and the trajectory of ANPP after fire appears to depend on the recruitment of trees (Mack *et al.* 2008; Turner 2010). Similarly, ANPP in burned grasslands can be strongly enhanced by woody plant recruitment because woody species typically have much greater leaf area and thus much greater potential for annual growth (Lett *et al.* 2004; Knapp *et al.* 2008). In our system (1500 mm mean annual precipitation [MAP]), recruitment of only one native shrub species, *D. viscosa*, occurred in the initial post-fire decade. This species, however, has low leaf area and contributes minimally to ANPP (Fig. 2a). Tree recruitment did not occur until the second post-fire decade (by non-native *M. faya*), such that now ANPP is approaching that of unburned sites despite substantially lower tree density overall. Thus, the high contribution of individual *M. faya* trees to ANPP in burned sites (Figs 1–3) suggests that like other post-fire woodland or forested ecosystems in the world, tree density will drive ANPP. In wetter Hawaiian forests, Asner *et al.* (2006) found that *M. faya* had consistently higher Leaf Area Index than *M. polymorpha* and grew 16–44% more rapidly, which is consistent with our data (Table 1). These fundamental differences in growth rate explain the convergence of ANPP between unburned and the burned habitats.

Does the relationship between tree density and ANPP plateau as ecosystems develop? In our system, the answer depends on ultimate *M. faya* density. In other work (C. M. D'Antonio & S. G. Yelenik, in review), we found that established *M. faya* in these sites enhance grass N status several metres beyond the canopy edge which in turn should enhance grass growth (D'Antonio & Mack 2006). Enhanced grass cover should reduce *M. faya's* further invasion because as seedlings, *M. faya* plants do not compete well with dense *Melinis* (Yelenik, D'Antonio & August-Schmidt 2017). Thus, *M. faya* abundance should plateau without achieving canopy closure because it enhances a competitor beyond its canopy edges suppressing its further recruitment. In the woodland however, where *M. faya* is also invading, it grows more slowly (Table 1) likely as a result of greater competition from native woody species. Asner *et al.* (2010) studying nearby *M. faya*-invaded sites at higher MAP (2000–3000 mm rain per year) found that its invasion did not lead to net changes in above-ground C pools. They used Lidar and hyperspectral imaging to evaluate contributions of *M. faya* to above-ground C in five sites and concluded that the elimination of understorey species via competition from the dense *M. faya* canopy compensates for C sequestered in *M. faya* trees. In our burned sites *M. faya* replaces species with much lower biomass (*M. minutiflora*), but in the unburned, increases in its growth may be compensated by reduced growth and eventual loss of native woody species. Thus, our unburned sites are more akin to some of those studied by Asner *et al.* (2010), while the burned sites are much different. Overall, adding more *M. faya* to unburned will likely not enhance either ANPP or C storage because of interactions and compensation with native understorey species.

Laurance *et al.* (2011) identified dry land forests and savanna/woodlands in Australia as ecosystems are vulnerable to tipping points due to changing fire regimes. The ecosystems we studied here experienced only two fires yet they are far from the composition and C storage of the ecosystems from which they were derived and we are predicting that they are unlikely to arrive back to those conditions. Fire has occurred in the quaternary history of Hawai'i yet most of these species did not evolve with a regular fire regime, nor did they evolve with competitors like these African grasses whose dominance can be triggered by a single fire (Hughes, Vitousek & Tunison 1991; D'Antonio, Hughes & Vitousek 2001). As a result, the ecosystem is vulnerable to long-term change even from a single disturbance. Didham, Watts & Norton (2005) suggested that alternative stable states or long transitions occur when abiotic conditions are harsh and where trait diversity is limited. The ecosystems we studied have both a harsh dry season (April through August) and limited trait diversity. In addition, the shallow soil limits water-holding capacity making the ecosystems perhaps harsher than might be revealed by MAP. Thus, this ecosystem fits with predictions of when and where invaders dominated states will be persistent (Didham, Watts & Norton 2005) even despite resilience of ANPP.

Conclusions

We found that ANPP, soil C pools and total plant and soil N pools are resilient to fire and invasion, but that native woody plant density and composition and plant C pools are not. Our results contrast with reviews that suggest that invaders increase ANPP above uninvaded sites (Liao *et al.* 2008; Vila *et al.* 2011) and highlight that the recovery of ANPP comes about because of a new arriving invader and not recovery of native woody species. Thus, generalities (see Liao *et al.* 2008; Vila *et al.* 2011) can mask important context-specific impacts of invaders. The life-form/traits of the invader needs to be considered when predicting impacts on ANPP: a grass moving into a woody ecosystem, triggers a lowered ANPP at least for a decade, while an invasive tree then counteracts that change.

In low-diversity ecosystems such as those studied here, invaders contribute to long-term compositional change towards no analogue communities despite the recovery of ANPP and N pools. Our study thus highlights the need for caution in defining ecosystem resilience. Measured as simply ‘recovery of ANPP and N pools’ towards a reference ecosystem, the system appears to be resilient. Yet, from a species composition and structure (density) perspective, these ecosystems do not recover from invasion and fire. Like native woody species metrics, plant C pools are sensitive to fire and invasion and did not recover over this multi-decadal time-scale because the loss of *M. polymorpha* was not compensated by invasion of *M. faya*. Our study suggests untapped potential for above-ground C storage which could be achieved through restoration of slow-growing, high C:N woody plants in burned sites (Ostertag *et al.* 2015). The fate of these sites if not managed over the next decade will ultimately depend on the dynamics *M. faya*, which enhances *M. minutiflora* beyond its canopy thus potentially limiting its own recruitment.

Authors’ contributions

C.M.D. and S.Y. conceived of the original research in this paper based on earlier work done by M.C.M. and C.M.D.; S.Y. and C.M.D. carried out field work; S.Y. compiled the data and led analysis of plant data, C.M.D. led analysis of soils, M.C.M. was responsible for 1990s data; all authors contributed to data interpretation; C.M.D. led the writing and all authors contributed critically to the drafts.

Acknowledgements

The authors acknowledge the following individuals for field and laboratory assistance: J. Batemen, B. Buckley, N. DiManno, T. D’Antonio-Dudley, T. Kalei, S. Ma, G. Ravenhurst, and V. Vincent. Logistical support and site access were provided by Rhonda Loh and Sierra McDaniel with Resources Management at Hawai‘i Volcanoes National Park. We also thank Greg Aplet for raw data on ‘ōhi‘a (*Metrosideros*) allometric equations. We thank R. Loh, J. Ross, L. Flory and two anonymous reviewers for comments on the manuscript. This research was funded by National Science Foundation DEB 1029168 and two REU supplements. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We have no conflicts of interest to declare.

Data accessibility

Data associated with the figures and tables in this manuscript can be found at https://knb.ecoinformatics.org/#view/knb.1302.1 (Yelenik 2017).

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Received 4 February 2017; accepted 5 June 2017
Handling Editor: Luke Flory

Supporting Information

Details of electronic Supporting Information are provided below.

Figure S1. Monthly rainfall across the sampling periods (a) 1994 to 1996 and (b) 2011 to 2013.

Table S1. Sampling design and terms.

Table S2. Allometric equations for biomass.

Table S3. Carbon to nitrogen ratio of litter collected from UB and TB sites.