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Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands

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Abstract. Invasive nonnative grasses have altered the composition of seasonally dry shrublands and woodlands throughout the world. In many areas they coexist with native woody species until fire occurs, after which they become dominant. Yet it is not clear how long their impacts persist in the absence of further fire. We evaluated the long-term impacts of grass invasions and subsequent fire in seasonally dry submontane habitats on Hawai'i, USA. We recensused transects in invaded unburned woodland and woodland that had burned in exotic grass-fueled fires in 1970 and 1987 and had last been censused in 1991. In the unburned woodlands, we found that the dominant understory grass invader, *Schizachyrium condensatum*, had declined by ~40%, while native understory species were abundant and largely unchanged from measurements 17 years ago. In burned woodland, exotic grass cover also declined, but overall values remained high and recruitment of native species was poor. Sites that had converted to exotic grassland after a 1970 fire remained dominated by exotic grasses with no increase in native cover despite 37 years without fire. Grass-dominated sites that had burned twice also showed limited recovery despite 20 years of fire suppression. We found limited evidence for "invasional meltdown": Exotic richness remained low across burned sites, and the dominant species in 1991, *Melinis minutiflora*, is still dominant today. Twice-burned sites are, however, being invaded by the nitrogen-fixing tree *Morella faya*, an introduced species with the potential to greatly alter the successional trajectory on young volcanic soils. In summary, despite decades of fire suppression, native species show little recovery in burned Hawaiian woodlands. Thus, burned sites appear to be beyond a threshold for "natural recovery" (e.g., passive restoration).

Key words: alien species; biological invasions; climate; grass/fire cycle; Hawaiian dry forest; invader impacts; long-term impacts, Melinis minutiflora; Morella faya; *nitrogen limitation, plant succession;* Schizachyrium condensatum.

Introduction

An extensive literature now documents the impacts that invasive nonnative (hereafter "exotic") plant species can have on community and ecosystem processes (e.g., Vitousek 1990, D'Antonio and Corbin 2003, Levine et al. 2003). For many invaders, removal is logistically or financially impractical particularly if they have become widespread prior to the recognition of their impacts (e.g., Hobbs and Humphries 1995). Given the limited funding typically available for plant control, it is important to prioritize species for management. Identifying whether deleterious effects of invaders are long- or short-term can help this prioritization. In particular, understanding the influence of plant invaders on long-term successional trajectories is critical.

Nonnative plants can invade native-dominated habitat either through superior competitive ability or by taking advantage of disturbances (Hobbs and Huenneke 1992, D'Antonio et al. 1999). In the first case, invaders may coexist with native species over a long timescale and slowly replace them. Shifts in composition will depend on how factors such as climate that influence growth and competitive interactions fluctuate over time. Where invaders have become dominant after a disturbance, they are more likely to remain dominant if they establish conditions that interfere with recruitment of native species even if seed sources of the latter are readily available. Alternatively, invaders may set up resource conditions that feedback negatively so that they are eventually replaced by other species (native or not). Lastly, initial invaders may facilitate other invaders via direct or indirect pathways (Simberloff and von Holle 1999, Richardson et al. 2000, Yoshida and Oka 2004). With the exception of studies of New Zealand succession (see McQueen et al. 2006) and California grasslands (see Stromberg and Griffin 1996), few long-term studies exist of plant invasions (Strayer et al. 2007). Some studies in New Zealand suggest that initial invaders die and are replaced by native species over time (Wilson 1994),

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although the "new native" trajectory might differ from that without the "invader" (e.g., Sullivan et al. 2007). Others studies have demonstrated that invaders persist for decades and retard succession (e.g., Lee et al. 1986, Stromberg and Griffin 1996). Still others have argued that invasion by one species can facilitate invasion by other nonnative species (Williams 1983, Simberloff and von Holle 1999, Richardson et al. 2000, Yoshida and Oka 2004), resulting in accelerating and long-term losses of native species, a process referred to as "invasional meltdown" (Simberloff and von Holle 1999).

In Hawaii, perennial C_4 grasses from Africa and the Americas have invaded dry and seasonally dry habitats from sea level up to 2000 m. Their impacts on fire regimes have been well documented (Tunison et al. 2001), and the subsequent impact of grass-fueled fires on native species and ecosystem processes in seasonally dry woodlands have been well studied (Hughes et al. 1991, Hughes and Vitousek 1993, D'Antonio et al. 1998, 2000, 2001, Mack et al. 2001, Mack and D'Antonio 2003*a*, *b*). In a detailed survey of burned and contiguous unburned woodland, Hughes et al. (1991) documented that (1) *Schizachyrium condensatum*, a New World bunchgrass co-dominated the unburned woodland understory with native shrubs. D'Antonio et al. (1999) demonstrated competitive impacts of this species on growth and recruitment of these native woody species. (2) Although *S. condensatum* persists after fire, it is largely replaced by the African grass, *Melinis minutiflora,* and total exotic grass cover increases. (3) Native species decline dramatically with a single fire, and even more dramatically with two fires. Hughes and Vitousek (1993) experimentally demonstrated that the low-light condition created by the dense-growing *M. minutiflora* interfered with recovery of native species after fire, yet *M. minutiflora* persists in its own shade and litter. We do not know however, whether these grasses persist over time if fire suppression continues. Also it is not known how patterns of dominance will change given ongoing strong climate warming in Hawai'i (Giambelluca et al. 2008).

One reason why succession might occur in burned sites is that *M. minutiflora* can be strongly N limited in young Hawaiian soils (D'Antonio et al. 2001, D'Antonio and Mack 2006). Mack et al. (2001), and D'Antonio and Mack (2006) demonstrated that *M. minutiflora*'s dominance of burned sites promotes rapid N cycling as had been suggested in shrublands on Moloka'i (Asner and Beatty 1996). D'Antonio et al. (2001) and D'Antonio and Mack (2006) further demonstrated that *M. minutiflora* benefits from high mineral N. Hence, its effects on soils in burned sites might be viewed as a short-term positive feedback. However, Mack (1998) also demonstrated that soil N losses are high in *M. minutiflora*-dominated sites due to asynchrony in the timing of N mineralization compared to plant uptake (D'Antonio and Mack 2006). This might result in lower grass productivity and the breakdown of *M. minutiflora*'s dominance. Indeed, we demonstrated that *M. minutiflora*'s productivity was constrained by N availability within eight years of the second fire (D'Antonio and Mack 2006). If ecosystem N declines, then other species such as the invasive N-fixing tree, *Morella faya* (prev. *Myrica faya*) might benefit. Alternatively, native species that tolerate low N conditions may reestablish. One of our primary objectives was thus to determine how fire suppression influences species composition in *M. minutiflora* dominated sites that have not reburned.

To evaluate long-term impacts of exotic grass invasions and fire suppression in these woodlands, we revisited the same sites established by Hughes et al. (1991) and compared newly obtained cover values with data from the same plots sampled in 1991. We were specifically interested in (1) whether native species continue to persist in invaded unburned primary woodland or whether exotic grass cover has increased and native species have declined (this might be predicted on the basis of our past research, which demonstrated strong competitive effects of *S. condensatum* on native woody species in the unburned woodland [D'Antonio et al. 1998]); (2) whether native species have begun to recover in burned woodlands that have now been 37 and 20 years without fire; (3) whether twice-burned (37 and 20 years ago) sites have a different trajectory than once burned ones; and (4) whether the original invaders that dominate after fire are replaced by more recently arriving invaders over these longer timescales.

METHODS

Study sites

The study sites were located on 500–1000-year-old pahoehoe lava flows in the seasonal submontane zone of Hawai'i Volcanoes National Park (hereafter HAVO; Holcomb 1987). All sampled locations were between 800 m and 900 m elevation. The sites were all within an area that had been contiguous woodland dominated by the evergreen tree *Metrosideros polymorpha* prior to the first fire that burned through the area in 1970. They are all on ash-derived soils that range in depth from protruding pahoehoe lava to 1 m of soil. The soil is classified as an Entisol and is not differentiated into horizons with the exception of an O (organic) horizon at the soil surface. The understory of the unburned woodland is dominated by *S. condensatum* and evergreen C_3 shrubs, the composition, cover, and productivity of which have been described in detail in previous studies (Hughes et al. 1991, D'Antonio et al. 1998 and Mack et al. 2001).

The forests in this area are classified as seasonal submontane woodland because of their elevation and seasonal climate (Mueller-Dombois and Fosberg 1974). We obtained climate records from HAVO Fire Cache (Fig. 1). The annual average rainfall over this period is 158 cm with ~5 months/year having an average of only 5 cm. This dry season typically occurs from April into early September and is punctuated by rare summer rain events. Average annual temperature is 21°C.

Grasses began to invade these woodlands in the early1960s (Tunison et al. 2001, Smith 1985). Beginning with the first grass-fueled fire recorded within HAVO (1969), dry and submontane forests began to be fragmented by these fires. Based on a 40-year record prior to grass invasions, fire return intervals were likely extremely low (probably >200 years), as was average fire size (<3 ha; Tunison et al. 2001). Since the 1960s, fire frequencies have quadrupled and fire size has increased >40 times despite active fire suppression by the National Park Service (Tunison et al. 2001).

Regarding the exact region of this study, a large fire in 1987 reburned part of the woodland area burned in 1970, but also burned adjacent woodland that had not previously burned. The resulting mosaic of burn conditions allowed Hughes and Tunison in 1988 to establish five sites in each of the following four burn conditions (hereafter "habitats") within this region: (1) woodland that has never burned (hereafter UB or unburned), (2) woodland that burned once in 1987 (YB or young burned), (3) woodland that had burned once in 1970 (OB or old burn) and (4) woodland that had burned both in 1970 and 1987 (TB or twice burned). These burn habitats are technically pseudoreplicated because the "sites" within each "habitat" were all burned in the same fire and are not fully spatially interspersed with the sites of other habitats/burn conditions. However, all habitats were originally part of a continuous woodland expanse on identical aged lava with identical ash soil, and all experience the same climate and are similar in elevation. So there is no a priori reason why habitats should be different, except for the recent burn history.

Each "site" was a somewhat flat vegetation-filled swale between pahoehoe tumuli (outcroppings) and within which a 100 m long and 10 m wide belt of vegetation was designated. Sites were marked with T posts at either end. Hughes et al. (1991), and later C. D'Antonio and R. F. Hughes (*unpublished data*), sampled each site using two parallel 100 m long transects randomly located within the belt area. All of the sites are a minimum of one/half-hour walk from Kipuka Nene Road. They have no public trails to or within them. Plant invaders that appear in these sites likely disperse into the area via birds, feral hogs, or by wind. A small amount of feral hog activity is evident in some of these sites.

Sampling methods

We relocated all sites originally established by Hughes et al. (1991) and censused them during October 2007 using point-intercept sampling. In each of the 20 sites, using a random numbers table, we sampled two parallel 100-m transects located between 0 and 10 m, within the 100 m long × 10 m wide belt established by Hughes et al. (1991). On each transect, points were sampled at 50-cm intervals, resulting in the census of 200 points per line and 400 points per site (see Plate 1). At each point we recorded all species touching a vertical, 1 cm wide, 2 m tall pole. These species "hits" will henceforth be referred to as "understory cover." A single sampled point could have multiple species hits so the total cover of all species on a transect was always greater than 100%. We did not distinguish whether encountered individuals of native species were seedlings, saplings, or mature adults. Rather, we simply noted if they were hit by the pole. We recorded the height (and identity) of the tallest understory plant to hit the pole and the substrate under the sampled point below any plants. Substrate designations included rock, bare soil, lichen, moss, plant litter, or tree trunk. We sampled canopy cover by evaluating whether there was a canopy tree above the 2-m pole at each point. We also recorded whether the *M. polymorpha* canopy was live or dead.

Species identification was based on Wagner et al. (1999) and Wagner and Herbst (2002). Initially we had

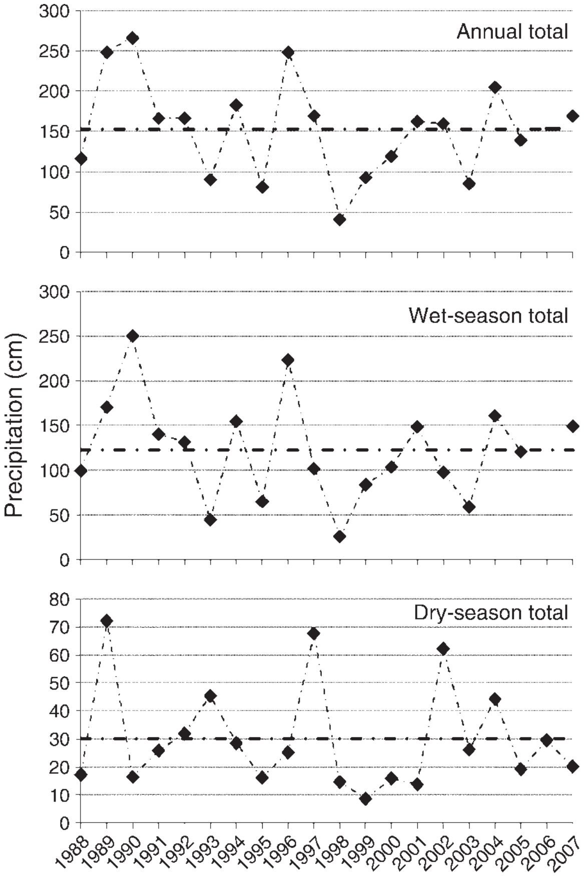

FIG. 1. Precipitation records for the Kipuka Nene weather station, Hawai'i Volcanoes National Park, Hawaii, USA. Dry season is defined here as April through August. Wet-season data are September through March. Seasonal values are shown as total rainfall across the season. Wet-season data for 2006 are missing. The dashed horizontal lines across each panel represent averages for the 20-year period.

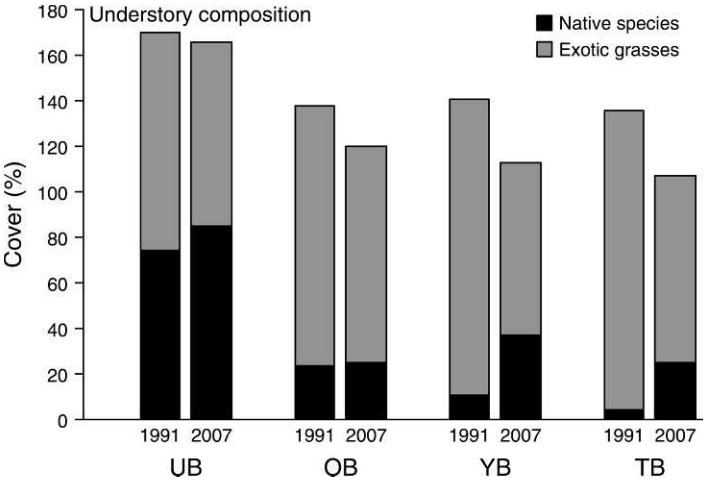

FIG. 2. Mean absolute cover of native and exotic understory species along point-intercept transects in 1991 and 2007 on old lava fields in Hawai'i Volcanoes National Park. Abbreviations are: UB, unburned; OB, old burn; YB, young burn; and TB, twice burned. Understory is defined as plants <2 m in height that touched the point-intercept pole at any time. Histograms represent means of the five sites per habitat. Standard errors are not shown. Relevant statistics are found in the *Results*.

tried to separate the native understory sedges *Carex wahuensis*, and *Morelotia gahniiformis* (formerly *Gahnia gahniiformi*). However, since many individuals were not in flower or fruit and could not be reliably identified, we combined these sedges into one category.

Our sampling methods were not the same as the original procedure reported by Hughes et al. (1991) when the sites first established. They used line-intercept sampling. We felt that for the multilayered canopies typical of these sites, their method was less accurate. Hence, we did not directly compare their data published in 1991 with the 2007 data. As a baseline against which to compare the 2007 data, we used instead unpublished data taken on these same 40 transects by C. D'Antonio and R. F. Hughes in 1991. Their methods (and the researchers) were identical to the 2007 census. For canopy sampling in 1991, we recorded whether the tree canopy in burned sites was alive or dead so that we could estimate canopy survival after the 1987 fire. In the unburned habitat, however, we did not separate live from dead *Metrosideros* because there was very little dead *M. polymorpha* canopy at that time. D'Antonio et al. (2001) used these same methods in 1998, but only twice-burned and unburned habitats were sampled. Thus, for some UB comparisons, we report here values from all three sample dates (1991, 1998, 2007). All sampling was conducted in the fall or early winter when *Melinis minutiflora* was near peak biomass. *Schizachyrium condensatum* typically does not grow during this time, having reached peak biomass in summer. For ease of future sampling, we mapped the location of each site using a Trimble GPS.

Data analysis

At each site we totaled the number of each species or substrate type hits encountered and divided by 400 (200 hits per transect × 2 transects per site). Average values were obtained for a given habitat by averaging the five sites per habitat (hereafter, $n = 5$). As mentioned previously, Hughes et al. (1991) used a different sampling method so we did not include their 1988 data in our analyses. Instead we used two-way ANOVA to compare differences among sites and dates (1991 vs. 2007) for each species or species group (e.g., native understory species). We did not use repeated-measures ANOVA because we did not resample identical transects and we were interested in average change across habitats rather than following specific transects.

RESULTS

Unburned woodlands

Metrosideros polymorpha, the dominant native tree, occupied the canopy of 40% of the points along each unburned transect in 1991, but this had declined to 18% by 2007 and only 60% of this was alive. Much of the dead canopy cover may have been due to the two-spotted leaf hopper (Alyokhin et al. 2001, Lenz and Taylor 2001), which began to affect *M. polymorpha* upslope of these sites in the early 1990s and is associated with tree death although the mechanism of death is not known (J. T. Tunison, *unpublished data*).

Despite changes in the tree canopy, native understory cover in UB woodlands did not change significantly between dates remaining around 78% cover (Fig. 2). Dominance by the shrub *Leptecophylla tameiameiae* (formerly *Styphelia tameiameiae*) remained unchanged: It persisted as the most common shrub species occurring in 34% of sampled understory across time (Fig. 3). There was a trend toward an increase in cover of the second-most common shrub, *Osteomeles anthyllidifolia* (Fig. 3). All other native species were unchanged. Several species that were rare (<0.0025%) in 1991, such as the native grass *Eragrostis variabilis*, the lily *Dianella sandwicensis,* and the tree *Pittosporum terminaliodes*, continued to be rare but still present in 2007. They occurred in the same sites within the UB habitat in 2007 as in 1991.

Nonnative grass cover declined by 13% over the observation period (Figs. 2 and 4). This was due to a

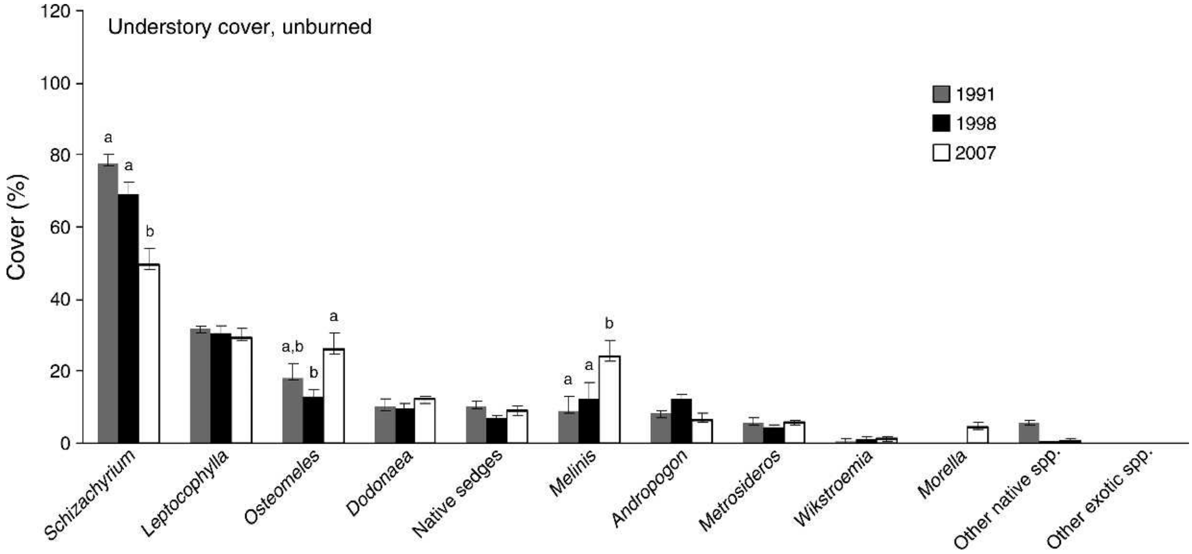

FIG. 3. Mean (±SE) percent cover of understory (all plants <2 m tall encountered on transects) plants in unburned woodland (UB) sites ($n = 5$) in 1991, 1998, and 2007. Nonnative species are *Schizachyrium, Melinis, Andropogon,* and *Morella*. All other species or groupings are native. Different lowercase letters indicate statistical differences using post hoc Tukey tests, $P < 0.06$. The 1998 data are from D'Antonio et al. (2001).

36% decline in *Schizachyrium condensatum* (Figs. 3 and 4), and dead bunches of this species were common. At the same time, cover of *Melinis minutiflora* increased by 182% (from 9.3% to 24%; $t = 19.3$; df = 1, 8; $P = 0.002$; Fig. 4), although this increase did not compensate for the decline in *S. condensatum*. On a site by site basis, the increase in *M. minutiflora* did not correlate with the decline in *M. polymorpha* canopy cover ($R^2 = 0.02$, $P < 0.76$). Examination of all three census dates for the UB suggests that the decline in *S. condensatum* was larger during the latter half of this 19-year period (Fig. 3). The increase in *M. minutiflora* was greater during this time as well.

One notable new nonnative species found in 2007, was the tree, *Morella faya* (formerly *Myrica faya*). It was absent from all UB transects in 1991 but occurred in all five sites, on 9/10 transects in 2007 although at low cover (Fig. 3). Its presence contributed to an increase in exotic richness from 3.2 per site in 1991 to 4.0 per site in 2007.

Changes in burned sites

As with the unburned sites, by 2007 exotic grass cover had declined in all burned sites (year, $F_{3,32} = 235.981$, $P < 0.0001$; Figs. 2 and 4). (The >100% values in 1991 were due to the overlapping canopies of *M. minutiflora* and *S. condensatum*.) In once-burned habitats the decline was due to a decrease in *S. condensatum,* but in the TB it was due to a decrease in both grasses (*Schizachyrium,* year, $F_{1,32} = 111.49$, $P < 0.001$; *Melinis,* habitat × year, $F_{3,32} = 5.612$, $P < 0.003$; Fig. 4). By 2007, average canopy height of *M. minutiflora* had declined by 25 cm relative to 1991 (Table 1). Along with the cover decline of *M. minutiflora* in TB, its height decreased more in TB than in the other habitats (Table 1).

Native cover increased significantly over time in burned sites (year, $F_{1,32} = 20.01$, $P < 0.001$; Fig. 2) due to increases occurring in TB and YB (habitat × year, $F_{3,32} = 2.65$, $P < 0.06$; TB across years, Tukey <0.05, $P < 0.06$; YB across years, Tukey <0.05, $P < 0.008$). In the TB, the only common native species at either time was *Dodonaea viscosa*, a species known to recruit after fire (Tunison et al. 1994, 1995). The cover change between 1991 and 2007 was likely a result of its growth. In 1991 individuals were small and only three *D. viscosa* individuals were recorded as "tallest canopy" from all 10 transects. By contrast, >240 individuals were recorded as the tallest canopy in 2007. In addition, the proportion of the native cover comprised of *D. viscosa* increased from 75% in 1991 to 86% in 2007. *D. viscosa* absolute cover also increased in the YB between years (5.9% to 15.1%), but its relative contribution to total native cover declined from 57% to 41%. By contrast, the absolute cover of *Osteomeles anthyllidifolia* increased by 350% and its relative contribution to native cover increased by 10%. This species increased across all habitats (year, $F_{1,32} = 8.73$, $P < 0.006$; habitat × year, $F_{3,32} = 1.64$, $P < 0.19$), but was still <2% cover in OB and TB. Although we did not specifically search for seedlings, we saw no evidence that it was recruiting into OB or TB. Individuals occurred in rocky outcroppings where they likely escaped the original fire. In the OB, native cover was unchanged but the cover of dead *D. viscosa* increased from <1% to 6%, and large dead *D. viscosa* individuals were common.

Despite small increases in native plant cover, the dominant understory shrub in the unburned woodland,

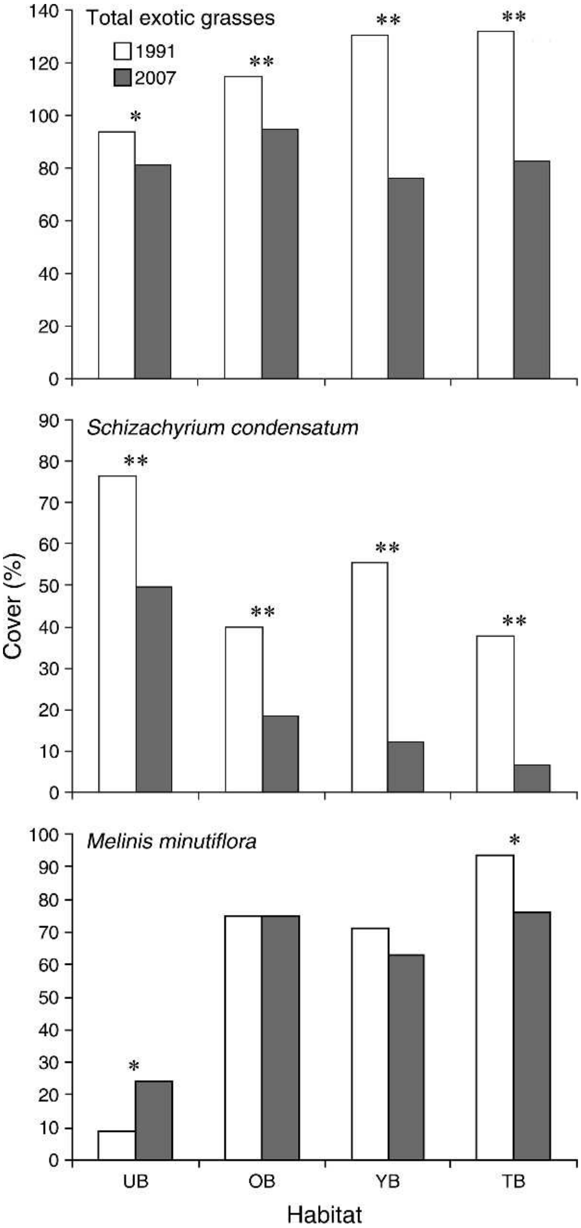

FIG. 4. Mean cover of exotic grasses along transects through the five sites per habitat ($n = 5$). Standard errors are not shown, but asterisks indicate statistical differences between dates within a habitat using a post hoc Tukey test. See Fig. 2 for a description of abbreviations.

* $P < 0.05$; ** $P < 0.01$.

L. tameiameiae, remained rare across all burned habitats. Single individuals were observed in rocky outcroppings where they likely escaped consumption by fire and some of these were encountered on transects. No individuals were encountered away from rocky outcroppings.

The only burned habitat having any live cover of the UB dominant native tree *M. polymorpha* in both 1991 and 2007 was YB. In 1991, several trees not killed by the original fire had partial live canopies or epicormic sprouts above 2 m contributing to canopy cover of 3% across the YB sites. No *M. polymorpha* was encountered in the understory (<2 m). By 2007, several trees damaged in the fire had large resprouting stems emerging from their bases, and they were recorded here as understory cover. No new sapling trees were observed. Live canopy cover was again only present in the YB and had only increased by 0.5% compared to 1991. A second native tree, *Sophora chrysophylla*, increased slightly in three OB and one YB sites between 1991 and 2007. These same sites had a small amount (<1%) of *S. chrysophylla* in 1991.

The only nonnative species to consistently increase over time in the burned sites was *Morella faya*. In 1991, this species occurred in only three of the 15 burned sites. By 2007 it occurred in 14 out of 15 burned sites and had increased to 12% understory (<2 m) cover in TB and 2% and 3% cover in OB and YB, respectively. The lack of variance for *M. faya* cover in 1991 (mostly zeros) precludes ANOVA, but the data suggest a faster increase in TB than in the other habitats. *M. faya* also reached canopy height in the TB transects at a greater frequency than in YB and OB (canopy cover = 5.5% in TB vs. An average 1% in YB and OB). No other nonnative species were detected in 2007 that were not detected in 1991. In fact, richness of exotic species declined on some transects due to the near disappearance of the exotic grasses *Andropogon virginicus* and *Sporobolus africanus* that were uncommon in 1991 and absent in 2007.

Unburned vs. burned sites

Despite an increase in total native understory species richness (Table 2) and cover in the burned sites between 1991 and 2007, native species still had dramatically lower values in all burned habitats compared to the UB (Fig. 2, Table 2). The YB sites were the most similar to the UB in terms of native richness, and shrub and *M. polymorpha* cover, yet they still were significantly reduced for all categories. Nonetheless, using the UB as a reference habitat, the YB showed the greatest "recovery." Although the YB and OB had similar values for native richness and *D. viscosa* cover, the rest of their native cover came from different sources. In OB, native richness was a mixture of *D. viscosa*, the small tree *S. chyrsophylla*, sedges, and *O. anthyllidifolia*. By contrast, the YB largely lacked *S. chrysophylla* and had few sedges, but had a higher cover of *O. anthyllidifolia* and had resprouting *M. polymorpha* in the understory. The TB was the most divergent from the UB sites: Native cover that was not *D. viscosa* was either the vine *Cocculus coronopifolia* (present in two sites) or *O. anthyllidifolia,* and richness was consistently low.

The forest floor of all sites was dominated by plant litter both sample times (Table 3). However, the UB consistently had greater lichen cover on the soil than burned habitats (Table 3), which all lacked lichens on

TABLE 1. Height (cm) of two exotic grasses and the native shrub *Dodonaea viscosa* along point-intercept transects on old lava fields in Hawai'i Volcanoes National Park, Hawaii, USA.

	Melinis		*Schizachyrium*		*Dodonaea*	
Habitat	1991	2007	1991	2007	1991	2007
Unburned	59.3^{a} (4.3)	44.8^{c} (2.7)	88.6^{a} (2.5)	$64.3^{b,c}$ (2.2)	83.4^{a} (7.4)	78.3^{a} (3.2)
Young burn	81.3^{b} (2.8)	42.5^{c} (2.6)	100.3^{a} (2.5)	45.4^{d} (3.6)	…	62.3^{a} (3.7)
Old burn	74.2^{b} (3.4)	50.6^{c} (4.4)	76.6^{b} (1.4)	$66.9^{b,c}$ (2.4)	105.3^{b} (4.6)	87.5^{a} (3.8)
Twice burned	$71.6^{a,b}$ (1.9)	39^{c} (1.7)	90.8^{a} (2.6)	60.9^{c} (5.0)	…	74.8^{a} (3.9)

Notes: Values were recorded for a species only when it was the tallest species at the sampled point, biasing data toward average maximum, not true, height. Values were averaged for each site and then for each habitat ($n = 5$ sites/habitat). Lowercase letters indicate comparisons among both habitats and years for a given species using a Tukey test. The same lowercase letters indicate values that are indistinguishable at $P > 0.06$. Values in parentheses are SE. Ellipses indicate no data possible due to a lack of plants in the appropriate size category in those habitats. For *Dodonaea*, cross-year comparisons were made with a t test for unburned (UB) and old burn (OB) only because no canopy shrubs were present in young burn (YB) or twice burned (TB) sites in 1991.

both dates. Bare soil was rare and similar in amount across habitats and over time. Feral pig activity was obvious and noted in the UB in 1991, but the only other habitat where it occurred then was the OB. In 2007, pig activity was rare everywhere.

The unburned and burned sites continued to differ in which exotic grass species was dominant. *S. condensatum*, although in decline everywhere, was still dominant in the UB while *M. minutiflora* was still relatively rare there, but dominant in the burned sites. Exotic species richness averaged between 3.0 and 4.0 across habitats and years and did not change over time. It tended to be higher in burned (4.0) compared to unburned (3.6) sites. *M. minutiflora* and *S. condensatum* were the most common nonnative species in both burned and unburned sites, with *M. faya* third in 2007. Several exotic species occurred sporadically, but were never abundant, in burned sites. These included *Sporobolus africanus, Desmodium incanum*, *Melinis repens* (formerly *Rhyncoletrum repens*), and *Nephrolepis multiflora*. Unburned transects did not have these species. Twice-burned sites consistently had the lowest overall exotic as well as native richness.

DISCUSSION

Trajectory of unburned woodlands

We found that the composition of the unburned woodland understory has changed very little over 17 years: It is not undergoing obvious successional change. This is despite a decline in cover of the canopy tree *M. polymorpha*. The dominant shrub in 1991, *Leptecophylla tameiameiae*, is still the dominant today. One of the other two codominant native shrubs, *O. anthyllidofolia*, increased since 1991. Other than this increase, woody cover and composition at the sites was unchanged. No previously absent species recruited except for *M. faya,* which was still uncommon in 2007. Initially rare native species, such as *Wikstroemia phyllraeifolia*, *Eragrostis variabilis*, *Dianella sandwicensis*, and *Pittosporum terminaliodes*, were still rare and in the same exact sites as in 1991. Overall, this suggests a relatively stable native assemblage. This might be expected given the relatively dry climate of this region and documentation of slow succession on young volcanic soils in dry climates (e.g., Aplet et al. 1998).

Our data do not support a consistent competitive effect of *S. condensatum* on native species in unburned woodlands. D'Antonio et al. (1998) demonstrated that during the early 1990s, *Schizachyrium condensatum* competed with native woody species (both shrubs and trees) for nitrogen and possibly water, resulting in reduced growth, reproduction, and recruitment of native woody seedlings. Yet our current data do not support a long-term effect of the grasses: It is *S. condensatum*, and not the native species, that have declined. The presence of the grass understory, however, may slow increases in native woody species that would otherwise occur, but

TABLE 2. Native species richness along point-intercept transects.

	Native species richness (number of species)			
Habitat	1991	Among habitat	2007	Across years (P)
Unburned	7.6 (0.51)	a	7.4 (0.40)	
Young burn	4.2 (0.37)	b	5.2 (0.49)	<0.024
Old burn	3.8 (0.40)	b	4.4 (0.40)	
Twice burned	1.6 (0.24)	c	2.8 (0.58)	<0.068

Notes: Values are averages of the total species found per site within a habitat. Although richness increased across years ($F_{1,32} = 7.28$, $P < 0.01$), the increase was not consistent among habitats (interaction, $F_{3,32} = 2.112$, $P < 0.11$). Across-year comparisons within particular habitats are shown for Tukey tests only when $P < 0.10$. Lowercase letters in the center column indicate comparisons among habitats ($F_{3,32} = 44.85$, $P < 0.001$) using a post hoc Tukey test where $P < 0.05$. Values in parentheses are SE. Analyses were performed on log-transformed data.

TABLE 3. Percent cover of surface substrate types encountered on woodland floor along point-intercept transects.

Habitat	Lichens		Plant litter		Bare soil	
	1991	2007	1991	2007	1991	2007
Unburned	12.3^{a} (1.8)	7.5^{b} (1.0)	86.4^{a} (1.2)	$83.5^{a,b}$ (1.6)	3.7^{a} (0.6)	$2.0^{a,b}$ (0.4)
Young burn	0.9^{c} (0.3)	0.5^{c} (0.2)	$83.3^{a,b}$ (2.7)	$83.5^{a,b}$ (2.3)	1.4^{b} (0.15)	1.4^{b} (0.15)
Old burn	1.7^{c} (0.5)	1.6^{c} (0.9)	86.3^{a} (1.0)	$80.6^{a,b}$ (1.5)	$2.4^{a,b}$ (0.7)	1.5^{b} (0.2)
Twice burned	0.15^{c} (0.15)	0.5^{c} (0.1)	77.5^{b} (2.6)	$83.2^{a,b}$ (1.1)	$3.3^{a,b}$ (1.2)	3.8^{a} (0.7)

Notes: Lowercase letters indicate comparisons among habitats and years for a given species using Tukey tests. Identical lowercase letters indicate values that are indistinguishable (here defined as $P > 0.06$). Values in parentheses are SE.

without uninvaded sites for comparison we cannot know this.

In contrast to the native species assemblage, the nonnative grass composition of the unburned woodland has changed since our 1991 measurements. *Schizachyrium condensatum* has declined dramatically and appears to be being partially replaced by *M. minutiflora*, a species which *S. condensatum* previously reduced via preemptive competition (D'Antonio et al. 2001). This direction of change will be unfavorable for the long-term persistence of these sites for two reasons: (1) *M. minutiflora* is a very strong competitor and thus might have a more negative influence on the demography of native species than did *S. condensatum* (Hughes and Vitousek 1993, D'Antonio et al. 2001), and (2) fires fueled by this species are much more detrimental for native species than fires with only *S. condensatum* as fuel (Tunison et al. 1995, D'Antonio et al. 2000). Hence, the long-term trend towards increases in *M. minutiflora* in unburned woodland could ultimately contribute to the demise of this woodland type when fire occurs.

Why is *S. condensatum* declining in the unburned woodland? The initial invasion occurred during a period when these woodlands were being grazed by feral goats (Doty and Mueller-Dombois 1966, Mueller-Dombois and Fosberg 1974). *S. condensatum* and *Andropogon virginicus* were described as the original grass invaders (Doty and Mueller-Dombois 1966, Smith and Tunison 1992) and are considered unpalatable to goats, while most of the woody species and *M. minutiflora* are considered palatable (Baker and Reeser 1972). Goats were removed in the early1970s. D'Antonio et al. (2001) demonstrated that *M. minutiflora* had the potential to dominate the woodland understory, but its invasion was slowed by the prior establishment of *S. condensatum*. In seedling competition *M. minutiflora* can outcompete *S. condensatum* under all tested conditions, but when its seedlings germinate near adult *S. condensatum* their growth and survival are low. Nonetheless, it can persist and slowly increase in these woodlands. The decrease in *S. condensatum* cover we observed, however, is apparent even in portions of individual sites not invaded by *M. minutiflora* suggesting a more widespread cause of *S. condensatum* decline than competition with *M. minutiflora*.

The climate record during this period (Fig. 1) shows a strong drought in the late 1990s. When D'Antonio et al. (2001) surveyed the UB in 1998, dead bunches of *S. condensatum* and *A. virginicus* were common. The climate after this drought also tended to be drier than during the first seven years of this study (Fig. 1). The only native species to disappear from the unburned between 1991 and 2007 was the small rush, *Luzula hawaiiensis,* a species associated with wetter conditions. The ecophysiology of *Schizachyrium* vs. *Melinis* is consistent with drought-induced compositional change: Although both are C_4 grasses, *S. condensatum* (Tribe Andropogoneae) is within the clade of C_4 species that utilize the NADP-ME pathway, while *Melinis* (Tribe Paniceae) is within the NAD-ME C_4 group (Ghannoum et al. 2002). The latter clade is known to be more drought tolerant than the former (Ghannoum et al. 2002), which is consistent with our observation that *M. minutiflora* declined little (only significantly in TB) during this drier period, while *S. condensatum* declined strongly across all sites. Also, Giambelluca et al. (2008) found marked warming in Hawaii over the past 30 years above 800 m, close to the elevation of these sites (800–900 m). Warming could exacerbate the effects of low rainfall. Fluctuations in climate can change competitive interactions between grasses and woody species (Scholes and Archer 1997) and may have favored woody species at the expense of grasses in UB. The native woody species at these sites are known to occur from sea level to 2000 m (Wagner et al. 1999), and thus may be adapted to a wider range of climate conditions than the grasses. Also when sites were first surveyed, the woody species may have been recovering from decades of goat browsing, which had likely reduced their competitive potential.

We found no evidence that invasive grasses in UB woodlands facilitated the establishment of other invaders. "Invasional meltdown" in the absence of fire does not appear to be occurring, despite an abundance of understory exotic grasses for decades. Only one invading species was observed in 2007 that was absent in 1991. This small tree, *M. faya,* has been invading the woodlands upslope from these sites since the 1980s (see Vitousek et al. 1987, Vitousek and Walker 1989, Camrath et al. 1992). Its invasion into our unburned sites is slow. D'Antonio and Mack (2001) demonstrated that *M. faya* invasion into the UB is slowed by the incumbent effects of exotic grasses. Over the long term, a decline in vigor of *S. condensatum* could accelerate *M.*

PLATE 1. A transect through an "old burn" woodland site in the seasonal submontane zone of Hawai'i Volcanoes National Park. This site burned once in a fire in 1970, though the trees in the far backgound did not burn. The dominant cover is made up of the African grass, *Melinis minutiflora*, and in the foreground are dead individuals of the native shrub *Dodonaea viscosa* which likely recruited after the original fire and then matured and died. Live *D. viscosa* are also visible. Photo credit: C. M. D'Antonio, November 2007.

faya invasion, but less so where *M. minutiflora* has replaced *S. condensatum*. Invasion of the unburned woodland by *M. faya* could facilitate death of more *M. polymorpha* because *M. faya* is a preferred host for the twin-spotted leaf hopper and population build-up of the leaf-hopper causes increased attack on *M. polymorpha* (Lenz and Taylor 2001, Aloykhin et al. 2004).

Do burned sites recover with prolonged fire suppression?

Grass-fueled fires can have very long-term effects: OB sites burned only once 37 years ago, but show no evidence of succession towards a native, woody dominated condition. By contrast the YB, which also burned only once, is undergoing some directional change towards a more native woodland condition. Nonetheless, there was no evidence of recruitment of the two species that dominate unburned sites (*L. tameiameiae* and *M. polymorpha*). This lack of native species recovery is consistent with observations from elsewhere of a lack of ecosystem recovery when species are subjected to disturbance regimes outside the realm in which they have evolved (e.g., Whisenant 1990, D'Antonio et al. 1999, Stylinski and Allen 1999, Suding et al. 2004). Here, a single fire appears to have effects even with 37 years of fire suppression. The stability of this "savanna" is consistent with grass/tree models where grasses have a strong competitive effect on recruitment of the woody species (Scholes and Archer 1997).

Differences between the OB and YB, which both have burned only once, highlight the complex nature of fire effects and successional trajectories. In neither the 1970 fire nor the 1987 fire, were direct measures of fire intensity available. Fire severity, however, can be assessed by vegetation condition (Brooks et al. 2004). When evaluated a year after fire (Hughes et al. 1991), some YB sites had live *Metrosideros polymorpha*, a species known to be susceptible to high intensity fire (Tunison et al. 1995), suggesting that they did not burn with high intensity. By contrast, the OB sites had no living *M. polymorpha*, suggesting higher fire intensity. Differences in their successional pathways may result from this variation: Both habitats are on the same-aged lava, at identical elevation, subject to the same climate, and all had ash-derived soils of identical age. The sites also differ in their proximity to the remaining expanse of unburned woodland with most YB sites being closer to unburned woodland that most OB sites. Thus, native-seed input could be greater into the YB sites. However, the OB site with the lowest native recovery is immediately adjacent to an expanse of unburned woodland arguing against the importance of seed supply.

Lack of recovery of native species in sites degraded by disturbance or introduced species has been proposed to be due to alterations in site physical conditions, competition with introduced species or seed limitation of native species (Suding et al. 2004). Mack and D'Antonio (2003*b*) did not find strong differences in physical site conditions between burned and unburned sites. Likewise, despite the potential for microclimate/fire feedbacks in these sites (Freifelder et al. 1998), no further fires have occurred. So, recurrent fire is not constraining regeneration of native woodland. Rather, we believe that introduced grasses, particularly *M. minutiflora* with its dense litter and strong shading, preempt light thereby reducing native-species establishment. Hughes and Vitousek (1993) found that seedlings densities were relatively high in YB and TB sites postfire (1988), particularly seedlings of *Dodonaea viscosa*. Seedlings typically occurred beneath the canopies of mature individuals of the same species (see their Table 1). Furthermore, biomass of native-shrub seedlings grown in areas cleared of grasses was greater (in some cases by several orders of magnitude) compared to areas with intact grass canopies. It is thus clear that, if native seeds or seedlings are present beneath exotic grasses, they are generally not capable of growing up through them, with the exception of *D. viscosa*. Ainsworth and Kauffman (2008) in an extensive evaluation of regenerative potential of native Hawaiian woody species after lava-ignited fires in nearby but wetter sites found that all 19 of the native species studied, including most of the ones in the UB here, demonstrated some postfire regeneration. However, as in our sites, recovery was suppressed in some of their sites by rapidly regrowing or invading nonnative species of ferns and grasses (Ainsworth and Kauffman 2010). In one of their sites these invaders even suppressed the regrowth of basal sprouts of *Metrosideros*.

It is possible that so long after fire and with little new seed input from within the sites, native species are now seed limited in burned habitat such that even if the grasses dieback, native recovery is unlikely. Where more mesic forests have burned in Hawaii, regeneration of several native species from newly dispersed seed and from the seedbank is known to occur (Ainsworth and Kauffman 2008). However, little is known about seed bank longevity for most native species in this region. They do not germinate readily from soil samples from our sites (C. M. D'Antanio, *unpublished data*), and Drake (1998) has shown that in a nearby more mesic forest the seeds of native woody plants are relatively short lived. Thus, if management actions were to reduce exotic-grass cover, it may be necessary to supplement the native seedbank to promote native regeneration.

Grass/soil feedbacks and succession

Previous studies (Mack et al. 2001, Mack and D'Antonio 2003*a*, *b*, D'Antonio and Mack 2006) suggest that TB sites have the potential for greater N loss than unburned areas because of their dominance by *M. minutiflora*. This dense, matted grass is inactive for January–March after it has set seed, yet it covers the soil so densely that light levels at the soil surface are near zero and nothing can recruit (Hughes and Vitousek 1993). Winter is a period of high N mineralization and heavy rainfall yet limited *M. minutiflora* uptake (Mack and D'Antonio 2003*a*, D'Antonio and Mack 2006). This should result in high nitrate losses. Moreover, results from Hughes and Vitousek (1993) indicated that pools of available soil N (i.e., ammonium and nitrate) were much higher in YB sites compared to the TB following the 1987 fire, suggesting that stocks of N may have been depleted already in TB. Because *M. minutiflora* is strongly responsive to N and was N limited by 1996, (D'Antonio and Mack 2006), it may have a negative feedback on its own persistence by promoting conditions that lead to ecosystem N decline. In our current survey we observed that the average height of *M. minutiflora* in the TB was significantly lower than the height observed in 1991, and we observed patches of completely dead *M. minutiflora*. We also saw declines in *M. minutiflora* cover and height in the YB, but did not see the large masses of dead *M. minutiflora* there. Also *M. minutiflora* increased in the unburned woodlands during this same time suggesting that regional climate is not responsible for its decline in the TB.

We hypothesize that the fertility of the soils in the TB sites is declining. This is consistent with our observation that the TB habitat was the most invaded by *Morella faya* of all habitats. *M. faya* is a nitrogen-fixing tree. Its success as a seedling is influenced by light availability and it may do poorly within dense grass (Lipp 1994). Indeed, it was least common on the OB transects, where *M. minutiflora*'s height was greatest. Its success in the TB may be indicative of a negative soil–plant feedback.

Why aren't native species taking advantage of reduced competition in sites where the vigor of *M. minutiflora* is declining? We believe this is because the *M. minutiflora* mats still cover the soil surface with >30 cm of grass stems and litter. If seedlings of native species do appear, they likely grow slowly as we have observed elsewhere, particularly in competition with grasses (Hughes and Vitousek 1993, D'Antonio et al. 1999). By contrast, seedlings of *M. faya* can grow fast most likely because of their ability to fix atmospheric N (Vitousek et al. 1987).

Conclusions

The habitat created as a result of grass invasion and subsequent fire in this region continues to be a grass-dominated savanna with a low diversity of scattered shrubs. Thus, in the absence of further fire or other forms of disturbance (e.g., animals), this assemblage appears to be relatively stable under current climate. Unlike other savanna environments around the world, fire suppression is not obviously leading to an increase in woody species (Scholes and Archer 1997). However, the N-fixing tree *M. faya* may eventually increase enough to reduce the probability of fire spread, a negative feedback observed with other woody species invading flammable savanna vegetation elsewhere (Scholes and Archer 1997, Stevens and Beckage 2009). The more rapid increase in *M. faya* in twice-burned sites compared to unburned, is the only evidence we found for "invasional meltdown."

The general lack of native species recovery in burned sites suggests that management must be active if native species are to be restored to these habitats. In particular, the dense grass canopy must be broken up to increase resources for native seedlings.

Native species in unburned woodland appear to persist well and the exotic grass species, *S. condensatum,* which has co-dominated these sites for decades, is in decline. Thus, although fueling the initial fires, *S. condensatum* does not now appear to be a substantial management concern as it is declining across these sites. However, an "invasion treadmill" (sensu Thomas and Reid 2007) maybe occurring: As *S. condensatum* declines, it is being partially replaced by *M. minutiflora*, a species of greater management concern.

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