Title: Effects of anthropogenic wildfire in low-elevation Pacific island vegetation communities in French Polynesia

Running head: Anthropogenic wildfire impacts on Pacific island flora

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Summary for the non-specialist reader: Wildfire at low elevations in remote Pacific islands is poorly characterized but likely all anthropogenic in origin. We show that wildfire in already heavily invaded low-elevation plant communities can lower native plant species richness, while increasing the relative abundance of non-native species. Wildfire also reduces the differences in plant communities among sites, and may exacerbate invasive species problems on Pacific islands by selecting for non-native, fire-adapted species over native ones.

Abstract

Anthropogenic (or human-caused) wildfire is an increasingly important driver of ecological change on Pacific islands including southeastern Polynesia, but fire ecology studies are almost completely absent for this region. Where observations do exist, they mostly represent descriptions of fire effects on plant communities before the introduction of invasive species in the modern era. Understanding the effects of wildfire in southeastern Polynesian island vegetation communities can elucidate which species may become problematic invasives with continued wildfire activity. We review what is known about fire effects in low elevation plant communities in Polynesia. We also investigate the effects of wildfire on vegetation in three low-elevation sites (45-379 m) on the island of Mo'orea in the Society Islands, French Polynesia, which are already heavily impacted by past human land use and invasive exotic plants, but retain some native flora. We analyze plants in categories: natives, those introduced by Polynesians before European contact (1767 C.E.), and those introduced since European contact. Burned areas have the same or lower mean species richness than paired unburned sites. Although wildfire does not affect the proportions of native and introduced species, it may increase the abundance of introduced species on some sites. Non-metric multidimensional scaling indicates that unburned plant communities are more distinct from one another than are those on burned sites. We discuss conservation concerns for particular native plants absent from burned sites, as well as invasive species (including *Lantana camara* and *Paraserianthes falcataria*) that may be promoted by fire in the Pacific.

Introduction

The ecological effects of fire in tropical Pacific island ecosystems have received little attention in most of the Pacific island groups (Nunn 1990). Despite the potential importance of wildfires for conservation, public health, and human-environment interactions, almost nothing is known about how contemporary wildfire affects plant communities in the Pacific outside of Hawai‘i (Hughes *et al.* 1991; D’Antonio and Vitousek 1992; Hughes and Vitousek 1993; Freifelder *et al.* 1998; D’Antonio *et al.* 2000, 2001; Ainsworth and Kauffman 2009, 2010, 2013; Angelo and Daehler 2013; Ellsworth et al. 2014), with few studies in New Caledonia (McCoy et al. 1999), western Polynesia (Hjerpe *et al.* 2001; Elmqvist *et al.* 2002; Franklin 2007) and Guam (Athens and Ward 2004). Furthermore, human-caused wildfires are increasingly occurring on Pacific islands today (Trauernicht *et al*. 2015).

French Polynesia is similar to the Hawaiian Islands in terms of isolation from potential colonizing species, climate, geology, topography, and flora, including shared congeners that have similar fire responses. Indeed, Hawai‘i may be the best model for hypothesizing about the role of fire in French Polynesia. There are substantial differences between the island groups, however, including total land area (3500 km^2 and 16,600 km^2 for French Polynesia and Hawai‘i, respectively), population size (~286,000 people vs. 1.4 million), lack of volcanic activity in French Polynesia for ~1M years (except infrequently on Mehetia), the presence of a potentially important lightning-driven fire regime at high elevations in French Polynesia compared to a lack of lightning activity in Hawai‘i (P. Ortéga, *pers. comm.*), and overall species differences. There has been no assessment of average size or intensity of fires in this region, and no published studies of the causes of fires. News outlets report an increasing number of fires each year, but

records held by local fire stations are difficult to obtain, and records held by local authorities on firefighting efforts are not publically available (Newman 2014; Newman, *manuscript*), making the news reports hard to verify. However, because there are no other ignition sources, all low-elevation fires can be assumed to be human-caused, including open burning, which is common for waste removal and agriculture. Ignition density and local population size are highly correlated on Mo'orea, although the largest wildfires are apparently caused by agricultural burning (J-M Hokaupoko, *interview*, 2011; Newman 2014; Newman, *manuscript*). Droughts, seasonal rainfall variability, and leeward/windward differences in climate likely all affect fire activity, but these relationships have not been well studied. Furthermore, differences in ecological effects of natural wildfires (from lightning and volcanoes) and more recent human-caused fires have not been evaluated for most of remote Oceania.

The purpose of this paper is to review what is known about wildfire's ecological effects in low elevation plant communities of the Remote Pacific generally, and through analysis of paired field sites, establish what role human-caused wildfire has in low-elevation plant communities in French Polynesia in the modern, post-European contact era. These results may have implications for conservation efforts in southeastern Polynesia and elsewhere in Oceania.

Fire effects in pre-modern Pacific Island plant communities

Fire has been widely invoked by archaeologists and paleoecologists as a means by which humans transformed Pacific island landscapes (Dodson and Intoh 1999; Kirch 2000; Mann *et al.* 2008). Certain vegetation communities in the Pacific have been considered to be associated with fire (Papy 1954; Mueller-Dombois and Fosberg 1998), but most Pacific island plant communities

are not considered to support active fire regimes of the type seen in some continental communities of similar climate (*e.g.* Cochrane 2003; but see Hunter-Anderson 2009).

Early botanists in the Pacific remarked on extensive fernlands and grasslands on certain islands. These communities were usually described as near-monocultures, dominated by either the native fern *Dicranopteris linearis* (Gleicheniaceae) or several species of grass. In some cases, including modern examples of these fernlands and grasslands, these take the form of "savannas" with scattered emergent trees such as *Metrosideros* and *Commersonia* (Florence 1997). For example, *Dicranopteris* fernlands are common in the Cook, Society, Austral, and Hawaiian islands. Notable areas with grassland include the Gambier Islands, leeward parts of Fiji (where savanna is known by the Fijian name *talasiqa*), the Mariana Islands, and the western Caroline Islands of Palau and Yap in Micronesia (Mueller-Dombois and Fosberg 1998).

Although these communities are widespread, Mueller-Dombois and Fosberg (1998) proposed that either these plant communities are not natural, or they represent post-disturbance communities because of their extremely low diversity, and because no other plant species are restricted to these communities (*i.e.* these communities contain no habitat specialists). Such conclusions were likely influenced by local knowledge that these plants grow back following wildfire. Archaeologists came to similar conclusions using pollen and charcoal records, and have argued that widespread "pyrophytic" grassland and fernland zones resulted from the use of fire by the first colonizing humans (Kirch 2000; Athens and Ward 2004; but see Hunter-Anderson 2009). These archaeological studies suggest that fire, in combination with other human impacts, transformed the mid- and low-elevation vegetation of oceanic Pacific islands from forest to pyrophytic fernlands and grasslands.

Despite obvious effects of fire in the vegetation communities of Pacific islands, there are few quantitative studies of wildfire effects on vegetation over the vast area in which they are dispersed. Wildfire has been shown to interact with other disturbance regimes (*i.e.* cyclones) in Samoa (Hjerpe *et al.* 2001; Elmqvist *et al.* 2002) and Tonga (Franklin 2007), and negatively impact the recruitment of late successional dominants (Franklin 2007). In New Caledonia, fire is implicated in the ecology of *maquis* scrublands (McCoy 1999), a vegetation community without parallel elsewhere in the remote tropical Pacific (Perry and Enright 2002). Like the research from Hawai‘i, these studies imply poor recovery of moist Pacific island forests. Few records and no formal studies exist for French Polynesia of the ecological effects of fire activity. In a detailed survey of Society Islands vegetation, Papy (1954) reported an association of *Dicranopteris* and grasses with fire, and suggested that the former can resprout from rhizomes following wildfire. He also observed that certain woody plants (*Metrosideros collina*, *Melastoma denticulatum*, and *Dodonaea viscosa*) are often associated with areas that have burned. These observations are similar to those from Hawai‘i for *Dodonaea viscosa* and *Metrosideros polymorpha* (D’Antonio *et al.* 2000; Ainsworth and Kauffman 2009).

The Hawai‘i-specific fire effects studies primarily have been conducted within Hawai‘i Volcanoes National Park on the island of Hawai‘i (“Big Island”; but see Ellsworth *et al.* 2014). They span a range of habitat types and elevations within the park (to 1200 m), where some fires are human-ignited and others are lava-ignited. Although a considerable number of native woody and tree fern species in wet and mesic forests show some ability to persist after wildfire through resprouting or germination following lava-ignited wildfire (Ainsworth and Kauffman 2009), and some native herbaceous species appear to sprout only following repeated wildfires that destroy litter (Ainsworth and Kauffman 2013), most evidence suggests that wildfires increase abundance

of introduced herbaceous and grass species. Fires promote invasion of introduced herbaceous species in forests (Ainsworth and Kauffman 2010), native tree and tree fern death (D'Antonio *et al.* 2000; Ainsworth and Kauffman 2013), and the replacement of native communities with invasive grasslands (Hughes *et al.* 1991; Hughes and Vitousek 1993; D'Antonio *et al.* 2000; Ainsworth and Kauffman 2013). These introduced herbaceous and grass communities restrict native seedling recruitment (Ainsworth and Kauffman 2010) and are even more susceptible to future fires, perpetuating a grass-fire cycle (D'Antonio and Vitousek 1992; Freifelder *et al.* 1998). It has been shown that wildfires can mediate transitions between dominance by different invasive grasses (Hughes *et al.* 1991; D'Antonio *et al.* 2001). The upward expansion in elevation of fire-adapted grasses has also been documented (Angelo and Daehler 2013). Although French Polynesia lacks a volcano-driven fire regime, its vegetation communities are similar to Hawaiian ones, and may show similar responses to anthropogenic wildfire.

This study

In this study, we examine vegetation changes associated with wildfires at low elevations (< 380 m) on the island of Mo'orea in the Society archipelago of French Polynesia (see Fig. 1). We investigate how low-elevation plant communities differ between burned areas and nearby comparison areas that have no known recent burn history, and expect wildfire to have substantial effects on the plant communities in our study. The comparison areas do not represent natural vegetation communities, but instead are secondary forests dominated by introduced species that have regrown in areas burned or cultivated by humans following human colonization ~1000 yr BP (Mueller-Dombois and Fosberg 1998; Kirch 2000). Native forests in French Polynesia, which

harbor most remaining endemic plant and invertebrate diversity, are primarily restricted to higher elevations (Meyer 2010), and do not naturally experience large wildfires.

Given what is known from previous observations from other islands, we hypothesize that burned areas will have a significantly different vegetation community from unburned areas. We expect that grasses and ferns, especially *Dicranopteris linearis*, will be present at higher proportions in burned areas than in unburned areas. We also expect that burned areas will contain more introduced species and higher abundances of introduced species than are present in unburned comparison areas, but that native (especially herbaceous) vegetation will persist or recolonize burned sites (Ainsworth and Kauffman 2009; 2013). We investigate whether site or burned status (burned or unburned) is more significant in explaining species diversity and abundance in plots. We examine which plant species are present, through colonization, regrowth, or persistence, in burned areas. One aim of this study is to identify which of the species existing in an already highly modified plant community are likely to become more abundant or invasive after wildfire.

Methods

We conducted research on the island of Mo'orea, French Polynesia (17°32'S, 149°50'W) during the austral-spring dry season of October and November 2013 (Fig. 1). The wetter summer season lasts from December-April (21-29C, ~123cm/month precipitation), and the drier winter season lasts from May-November (19-25C, ~230cm/month precipitation). Large rainfall events are still relatively common in the mostly dry winter months, however. Winds are generally stable and dominated by southern tradewinds, although powerful wind events, including cyclones, occur somewhat regularly (http://mcr.lternet.edu/general_information/climate/). Weather station

measurements provided by the Moorea Coral Reef Ecosystem LTER for August 2006-October 2010 report monthly average temperatures ranging from 24.5 C-27.2 C, and monthly cumulative rainfall between 0.8mm-716.8mm (Washburn *et al*. 2013).

Study sites

We worked at three sites, each containing two study areas: a post-wildfire ("burned") area that was paired with a nearby, unburned ("comparison") areas. Post-wildfire sites represent a variety of times since fire disturbance, total burned area, original vegetation communities, elevations, slopes, aspects, and microclimates. We chose to work in previously defined sites (following Koehler 1999), where burned and comparison areas at a single site have the same or very similar slopes, aspects, average rainfalls, and soil types (Bonvallot *et al.* 1993). The seasonality and severity of the burns were not controlled for, and the post-wildfire climatic conditions are not known, each of which can influence species richness and abundance in post-wildfire communities. Extreme variation in microclimates at these sites was not explicitly controlled for, and we therefore clarify that this collection of sites in not meant to represent plant community succession for different-aged sites.

Study sites varied in location, time since burn, and other characteristics, but were all located on the wetter side of the island (Table 1). Site 1 is located at the Col des Trois Cocotiers (accessible via the "Three Coconuts trail") on the saddle between Mount Tohi'e'a and Mount Mou'aroa. The fire of interest originated from a small campfire at the top of the ridge (J.-Y. Meyer, *pers. comm.*) in 2004 (9 years before this survey was conducted), burning <1 ha. The site receives an average annual rainfall of 4500-5000mm, was characterized in 1993 as having an average annual temperature of 20-22.7°C (Bonvallot *et al.* 1993), and is in direct sunlight

throughout the day when there are no clouds. The slope at this site varies with a maximum of 30°. The adjacent comparison area is similar to the burned area but receives slightly more shade, and is located to the west of the burned area.

Site 2 is also located on the southwest side of the island, north of the town of Ha'apiti. According to Koehler (1999), the fire originated in 1995 (18 years before survey) from a noni (*Morinda citrifolia*, or "*nono*" in Tahitian) fruit plantation and traveled up the slope of a west-facing ridge for approximately 1 km. The width of the burned area is ~300 m, with a total area of ~4 ha. The slope of this site averages approximately 25°, and the ridge can receive direct light for the entire day. The average annual precipitation is 1720-2000 mm, with an average annual temperature of >22.7° C (Bonvallot *et al.* 1993). The adjacent comparison area is located to the northeast of the burned area.

Site 3 is located on the southwest side of the island, southeast of Ha'apiti. According to Koehler (1999), the wildfire occurred in 1991 (22 years before this survey was conducted), and originated from a pile of burning waste in a cemetery on the outskirts of Ha'apiti. The fire traveled along a west-facing ridge for approximately 1.5 km. The total burned area is ~5 ha, nowhere exceeding 250 m in width, and the slope is ~25° along the entire length of the burned site (Koehler 1999). The ridge receives direct sunlight for the majority of the day, the average annual precipitation at the site is 2000-2350mm, and the average annual temperature is >22.7°C (Bonvallot *et al.* 1993). The adjacent comparison area is located to the southeast of the burn. Center points of all burned and comparison areas, and total area burned were estimated using Google Earth (Google 2013).

Field surveys

Each of the paired study areas at three sites (Sites 1, 2, and 3) comprises a post-wildfire burned area and an adjacent, unburned comparison area. Five transect lines were placed in each of the six total burned and comparison areas, for a total of 30 transects. Vegetation was sampled at 4m intervals along each transect (starting at the zero point, for a total of 13 samples per transect and n = 390 data points) at all sites along points on a 50m transect tape, using a method modified from the Line Interception Method (Canfield 1941).

For each burned and comparison area, all individuals of vascular plant species touching and directly above a vertical measuring post were recorded. These were counted and identified to the species level in the field if possible, and photographs were taken for later verification. For plants that could not be field-identified, samples were collected for examination at the University of California, Berkeley Gump Station using online and printed plant identification keys (Moorea Digital Flora Project, Murdock 1999; Whistler 1995). Samples and photographs were verified through expert opinion (of J.-Y. Meyer, R. Tapatuarai, and J. Nitta). Voucher specimens collected from each site have been deposited in the University Herbarium (UC) at the University of California, Berkeley.

Analyses

Plant species were categorized by origin as native or introduced, and within the category of introduced species, a distinction was made between “Polynesian introduction” and “modern introduction” (post European contact) for analysis (Table 2). Historical presence was assessed by consensus and expert opinions including the following: Austin (1991), Butaud *et al.* (2008), Butaud (2010), Florence (1997, 2004), Florence *et al.* (2007), McCormack (2007), Meyer

(2004), J.-Y. Meyer (*pers. comm*.), J. Nitta (*pers. comm*.), Prebble (2008), and Whistler (1996, 2009).

Line-intercept transect data were used to calculate relative frequencies of species' abundances for burned and comparison areas at each of the three study sites. Relative frequencies were calculated as total number of individuals in each species pooled across all five transects in one study area. Total species richness was calculated as number of species encountered on all transects in each area. Plants were organized by presence in burned areas, control areas, or both, and graphed by these categories for further examination. Differences between species richness by category of origin was assessed with Pearson's Chi-squared tests for proportions, with the null hypothesis that the burned areas have the same proportions of species richness by category of origin as the comparison areas, and the alternate hypothesis that they do not. Similar calculations were made for relative frequencies of observed abundances.

To test the relative importance of site (SITE) and burned or unburned status (STATUS) in determining the plant community in an area, we constructed a set of Gaussian-distributed generalized linear models (GLMs) for species richness, and a set of Poisson-distributed GLMs for count data, which corresponds to observed abundance at each transect point. We included an interaction effect of SITE*STATUS in each model. Akaike's Information Criterion adjusted for small sample sizes (AIC*c*) was applied to each model set for model selection.

For plant data in each survey area, we calculated a non-metric multi-dimensional scaling test (NMDS) using a Bray-Curtis dissimilarity matrix to assess community-level differences among sites and between burned and comparison areas, using individual transects as data points. Bray-Curtis NMDS analyses evaluate community composition and structure. We employed Wisconsin double standardization (using R package "vegan" "metaMDS" analysis, Solymos *et*

al. 2015). Results of the NMDS were evaluated using analysis of similarities (ANOSIM in R software package "vegan"). Homogenization of plant communities was assessed by applying an ANOVA, followed by a Tukey's Honestly Significant Differences Test, on the Bray-Curtis transformed NMDS (using the function "betadisperser" in the "vegan" R package). A significant value of the ANOVA *F*-test would indicate that the burned areas are different from the control areas in terms of community homogenization (measured in distance to the centroid of each group in ordination space).

All analyses were conducted in "R" version 3.1.3 (R Core Team 2015), with additional packages "vegan" version 2.3-0 (Oksanen *et al.* 2015), "MASS" version 7.3-34 (Venables and Ripley 2002), "AICcmodavg" version 2.1-1 (Mazerolle 2017), and "MuMIn" version 1.15.6 (Bartoń 2009).

Results

Fire effects on species composition

Wildfire at all surveyed sites had large effects on the species composition of the resulting communities, compared to unburned areas. Certain native species, such as *Dicranopteris linearis* and *Commersonia bartramia* appeared only in burned areas. Plants fell into three categories: those that were only present in unburned areas (23 species), those that were only present in burned areas (11 species), and those that were present in both burned and unburned areas (23 species) (Fig. 2). Although these species might be placed in different categories with data from additional sampling, our results suggest that there is a significant component of the low-elevation plant community that is directly benefitting from wildfire activity and are present only in burned areas. Of these, pineapple (*Ananas comosus*) is a fruit crop that may have been planted following

the fires, and therefore likely does not represent a "naturalized" species benefitting from fire. Papaya (*Carica papaya*), on the other hand, does seem to benefit from fire in western Polynesia (Franklin 2007) although we are not aware of evidence that it is naturalized in southeastern Polynesia where this study took place. Similarly, *Inocarpus fagifer* (Fabaceae) is a large tree that may have persisted through a low-intensity fire, so its presence in one burned area may not be reflective of its response to fire. Persistence of overstory trees in low-intensity burns may be more common, and such observations should be noted in future studies on this topic. *Dicranopteris linearis*, as discussed previously, appears to be an aggressive colonizer of post-wildfire sites, and like the native *Metrosideros collina*, is only present in areas that have been burned. This is consistent with observations of the pyrophytic *Dicranopteris* savanna noted previously. One observation of the native tree *Phyllanthus manono* (syn. *Glochidion manono*) in a burned area is interesting to the natural history of this species, but it was not noted if this was an individual that had resprouted or grown from seed.

Of the species present in both burned and unburned areas, *Hibiscus tiliaceus* is native and is the most abundant, followed by an aggressive modern invasive, *Paraserianthes falcataria*. This species (syn. *Falcataria molluccana*, *Albizia falcataria*) has been identified as having disproportionate effects on species loss in tropical systems it invades (Pyšek *et al.* 2012). Of the control-area only plants, notable are coconut (*Cocos nucifera*), which may have been planted; a host of native species which may be highly fire-intolerant, including *Ixora mooreensis* and *Xylosma suaveolens*, a large number of native fern species, and a problematic invasive species, *Miconia calvescens*, which densely invades otherwise undisturbed areas (Meyer and Florence 1996).

Fire effects on species richness and abundance

Burned and unburned comparison sites contained a total of 57 vascular plant species (one club moss, 13 ferns, 14 monocots, and 29 eudicots; Table 2). Lichens and mosses were not included in this study. Of these, 54 plant species were identified to the species level. Each of three unknown species was given a unique identifier for analysis. At comparison sites, 46 species were found in total, with 34.8% native species, 17.4% Polynesian introduced species, and 41.3% modern introduced species (with three unidentified species of unknown origin). By comparison, 34 species were found in burned sites, 38.2% of which were natives, 5.9% Polynesian, and 50.0% modern introductions (Fig 3-4). Abundances varied on a site-to-site basis, with wildfire increasing observed abundances at two of three sites, and sharply increasing observed abundance at Site 2.

Model selection on GLMs for species richness (Table 3) showed that two models had near-equal explanatory power, and we therefore present model averages of a model of species richness ~ SITE + SPECIES, and a model that contains an interaction between the two measured explanatory variables: SITE + SPECIES + SITE*SPECIES. We found that comparison areas had greater species richness than burned areas **(P = 0.004)**; Site 1 had the greatest species richness, though this effect was not as great when SITE by SPECIES interactions were considered (Table 4). GLM analysis of observed abundances (Table 3) produced three models within ΔAICc = 2 of one another, all containing STATUS as an explanatory variable. Model averaging on these three top ranked models yielded the following (Table 5): unburned "comparison" status had higher abundance generally than burned areas **(P = 0.079)**, though the effect size was relatively small (0.152). As was the case for the species richness GLM, the high point estimate and statistical

significance of the intercept in each case indicates that more nuanced models with higher explanatory power could be developed.

Fire effects on proportions of native and introduced species

Species richness was compared between study areas by category of origin (Fig. 3). Pearson's Chi-squared tests for proportions show no differences between proportions of species in the native, Polynesian introduction, and modern introduction categories for burned and unburned areas at each site (χ^2= 1.43, df = 2, P = 0.434 for 9-year burned and unburned areas at Site 1; χ^2 = 3.65, df = 2, P = 0.161 for 18-year burned and unburned areas at Site 2; and χ^2 = 3.58, df = 2, P = 0.167 for 22-year burned and unburned areas at Site 3). When modern and Polynesian introductions are grouped into one "introduced species" category, this result does not change, that is, there are no significant differences between proportions of native and introduced species by native versus introduced categories (P-values on χ^2 tests are all > 0.2).

Relative abundances of all individuals in vegetation communities were also compared across burned and control areas in three sites by category of origin (Fig. 3). Here, Pearson's Chi-squared tests show significant differences between proportions of abundances of individuals in the native, Polynesian introduction, and modern introduction categories for burned and unburned areas at each site (χ^2 = 7.523, df = 2, $\boldsymbol{P = 0.023}$ for Site 1; χ^2 = 10.697, df = 2, $\boldsymbol{P = 0.005}$ for Site 2; and χ^2 = 76.705, df = 2, $\boldsymbol{P < 10^{-5}}$ for Site 3). When modern and Polynesian introductions are grouped into one "introduced species" category, results are still significant (though not as strongly so) (P = 0.09 for Site 1**;** $\boldsymbol{P = 0.005}$ for Site 2; and $\boldsymbol{P = 0.01}$ for Site 3). Wildfire significantly increased the relative abundance of individuals in the "introduced species" category at Sites 1 and 3, but decreased the relative abundance of introduced species at Site 2.

Fire effects on plant communities

Community differences were assessed with a two-dimensional NMDS. Results were plotted with individual points representing a single transect. Results converged in three iterations, for a calculated stress = 0.160, Procrustes root mean squared error = 1.64e-05, and maximum residuals = 2.98e-05. An analysis of similarities gives values for the ANOSIM test statistic $R = 0.709$, with $\boldsymbol{P = 0.001}$, meaning that compositional differences between groups (in this case burned and unburned areas) are significantly greater than within groups.

As shown in Fig. 5, there was no overlap in the points between the burned and unburned comparison areas, visually indicating large differences between burned and unburned communities in ordination space. Points for each of the comparison areas were highly clustered but did not overlap with sites of different ages, indicating substantial differences in communities between different unburned comparison areas. In contrast, points for the burned areas are highly mixed and essentially indistinct from each other, and within-site spread of points in NMDS-ordination space is larger for the burned areas than for the comparison areas. Community level differences in burned and comparison areas were tested with an ANOVA followed by a Tukey's Honestly Significant Differences Test on the Bray-Curtis transformed NMDS. We find that the results are not significant between groups ($F_{1,28} = 0.417$, $P = 0.524$). These results are similar to those produced by a related test, the permutation test for homogeneity of multivariate dispersions (not shown). The significance level of the ANOVA does not change if the data are first normalized by Euclidian distances ($F_{1,28} = 1.902$, $P = 0.179$) (Oksanen 2015). Our results do not support the hypothesis of vegetation community homogenization due to presence of non-native species.

Discussion

We have shown that even in an already heavily impacted plant community, wildfire creates communities that lack distinguishability between sites, whereas unburned comparison sites remain relatively distinct from one another. Wildfire does not appear to change the proportion of species in a community by their category of origin (*i.e*. native, Polynesian introduction, or modern introduction), but it significantly lowered diversity at one of three sites (Site 2). Counter to our original hypothesis, we did not find that there were more introduced species in burned areas than unburned ones. These results taken together provide evidence that wildfire impacts on the native community of plants vary from site to site, and are likely related to microclimate or other environmental drivers affecting the original vegetation community that were not measured in this study.

We found, as previous studies have, that *Dicranopteris linearis* colonized burned areas. We did not find higher presence of grasses, as has been noted in Hawai‘i, however, it should be noted that all our study sites were located on the wet side of the island, and that non-native grasses are present in abundance only on the dry side of Mo’orea. A study designed to sample the dry side of Mo’orea would likely discover additional problematic invasives. Although only sixth most abundant among invasives, *Lantana camara* is a modern introduction that is probably of higher concern than some of the more abundant species. Fire-*Lantana* interactions, including the possibility of a “fire cycle” or positive feedback between the two, are of special concern and have been reported from continental tropical areas (Fensham *et al.* 1994; Duggin and Gentle 1998; Hiremath and Sundaram 2005; Berry *et al.* 2011). Although its flammability and other fire adaptations compared to other vegetation in this system are not known, *Lantana camara* is bird-

dispersed in French Polynesia (Spotswood *et al.* 2012), and so has the potential to increase its range rapidly through seed dispersal. *Lantana camara* is designated by the French Polynesian government as one of the most serious invasive plants in the country (Meyer and Butaud 2007).

Our results demonstrate that wildfire on Mo'orea causes significant changes in plant communities, reducing distinguishability of communities between sites, increasing abundances of introduced species in burned areas, and changing community membership by facilitating colonization by *Dicranopteris linearis* as well as non-native species that have known positive fire feedback interactions. These changes are present in all post-wildfire sites (including the oldest site of 22 years). Long-term changes to the vegetation community that promote non-native and fire-prone species could be especially harmful on small tropical islands because they are more susceptible to invasion, and the plant diversity is already relatively low (Elton 1958; Vitousek *et al.* 1996).

Pacific islands invasives are comparatively understudied (Pyšek *et al.* 2012), and a general understanding of disturbance ecology across Pacific islands is absent. Our results may be generalizable to other islands both within the Society Islands chain and elsewhere in French Polynesia and southeastern Polynesia, where the original vegetation communities are similar to those on Mo'orea, and the invasive species available to colonize post-wildfire sites come from the same pool of available species. These results are important in light of frequent recent reports of wildfire events in local news media from multiple islands in French Polynesia (Newman*, manuscript*), and because both wildfire frequency and total burned area per year may increase in future years with climate change, presence of invasive species, increasing populations that rely on fire for agricultural and waste management, and other changes in human land use.

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Figure legends.

Figure 1.

Map of the Pacific region showing the the region containing French Polynesia (dark outline) and the island of Mo'orea. Other island chains mentioned in this study are also labeled.

Figure 2.

Species recorded in burned and comparison areas, arranged by relative abundance. Data represent all individuals recorded at all sites, and are grouped by presence in burned areas, comparison areas, or both.

Figure 3.

Species richness shown as total (A) and proportional (B) measurements; and observed abundances of species (C) and their proportions (D) measured at sampling points in burned and unburned areas at 3 sites. Data represent individuals measured at 13 points each along 5 transects in burned and comparison areas for each of 3 sites (n = 390 data points). Plants are grouped into native, Polynesian introduction, and modern introduction categories.

Figure 4.

Box plots comparing species richness and observed abundance across burned and comparison areas ("Status") and three sites.

Figure 5.

Non-metric multidimensional scaling (NMDS) plot showing differences in plant community composition between transects from each site. Points that are closer together have a higher degree of similarity. Each point represents a single transect; burned area data are represented in red, and comparison plot data are represented in black. Post-fire areas have larger and more overlapping ranges in this parameter space than do unburned areas.

Tables.

Table 1. Summary of characteristics for burned and unburned comparison sites. Centers of burned areas were determined from aerial photos.

Name of site and location	Age (year of burn)	Condition	GPS coordinates	Elevation (m)	Size of burned area	No. species (no. observations)
Site 1: Col des Trois Cocotiers	9 years (2004)	burned	17°32'49.9”S 149°50’32.5"W	374	< 1 ha	26 (179)
	(NA)	comparison	17°32’47”S 149°50’35”W	379	(NA)	30 (331)
Site 2: North of Ha’apiti	18 years (1995)	burned	17°33’10.39”S 149°52’14.63”W	154	~4 ha	18 (150)
	(NA)	comparison	17°33’4.09”S 149°52’3.68”W	146	(NA)	21 (212)
Site 3: Southeast of Ha’apiti	22 years (1991)	burned	17°33’30.44”S 149°51’50.48”W	120	5 ha	13 (160)
	(NA)	comparison	17°33’40.98”S 149°51’53.15”W	45	(NA)	17 (167)

Table 2. Plant species recorded at the three study sites, categorized by broad taxonomic groups. Species are also categorized by their historical presence in the Society Islands: *e.g.*, native, introduced by humans before 1767 C.E. ("Polynesian introductions"), or introduced by humans since 1767 C.E. ("modern introductions"). Lichens and mosses were not included in this study.

Historical Presence *	**Type of Plant**	**Species**
Native	Club mosses	*Lycopodiella cernua*
	Ferns	*Angiopteris evecta*
		Arachniodes aristata
		Asplenium australasicum
		Blechnum patersonii
		Davallia solida
		Dicranopteris linearis
		Diplazium ellipticum
		Lygodium reticulatum
		Nephrolepis hirsutula
	Monocots	*Freycinetia impavida*
		Pandanus tectorius
	Eudicots	*Cyclophyllum barbatum* (*Canthium barbatum*)
		Commersonia bartramia
		Fagraea berteroana
		Hibiscus tiliaceus
		Ipomoea littoralis
		Ixora mooreensis
		Metrosideros collina
		Neonauclea forsteri

		Phyllanthus manono (syn. *Glochidion manono*)
		Xylosma suaveolens
Polynesian Introduction	Monocots	*Cocos nucifera*
		Cordyline fruticosa
		Dioscorea bulbifera
		Miscanthus floridulus
		Musa X paradisiaca (cultivar)
		Zingiber zerumbet
	Eudicots	*Inocarpus fagifer*
		Syzygium malaccense
Modern Introduction	Ferns	*Adiantum trapeziforme*
		Diplazium proliferum
	Monocots	*Ananas comosus*
		Centotheca lappacea
		Dypsis madagascariensis
		Melinis repens
		Spathoglottis plicata
	Eudicots	*Falcataria moluccana* (syn. *Paraserianthes falcataria, Albizia falcataria*)
		Carica papaya
		Elephantopus mollis
		Emilia fosbergii
		Lantana camara
		Mangifera indica

		Merremia peltata
		Miconia calvecens
		Mikania micrantha
		Passiflora foetida
		Polyscias scutellaria
		Psidium guajava
		Rubus rosifolius
		Spathodea campanulata
		Stachytarpheta urticifolia
		Syzygium cuminii
		Tecoma stans
Unknown Origin	Fern	unknown fern 1
	Fern	unknown fern 2
	Monocot	unknown grass 1

* Historical presence was assessed by consensus and expert opinions including the following references: Austin 1991, Butaud *et al.* 2008, Butaud 2010, Florence 2004, Florence 1997, Florence *et al.* 2007, McCormack 2007, Meyer 2004, J.-Y. Meyer (*pers. comm*.), J. Nitta (*pers. comm*.), Prebble 2008, Whistler 1996, and Whistler 2009.

Table 3. Model selection for species richness and for abundance. Models are shown in rank order of AIC*c* support. Here, *k* = number of parameters in model; AIC*c* = Akaike's Information Criterion value corrected for small sample sizes; ΔAIC*c*= difference of AICc value compared to the next best-supported model; w_i = AIC*c* weight (a measure of strength of evidence for each model); Cumulative *w* = total model AIC*c* weights for best models in rank order; and LL = Log-Likelihood.

Ranked models for *y* = SPECIES Model family = Gaussian	*k*	AIC*c*	ΔAIC*c*	w_i	Cumulative *w*	LL
y = SITE + STATUS	5	164.33	0	0.53	0.53	-75.91
y = SITE + STATUS + SITE:STATUS	7	164.54	0.21	0.47	1	-72.72
y = SITE	4	179.21	14.88	0	1	-84.81
y = STATUS	3	183.74	19.41	0	1	-88.41
y = 1	2	190.3	25.98	0	1	-92.93

Ranked models for *y* = ABUNDANCE Model family = Poisson	*k*	AIC*c*	ΔAIC*c*	w_i	Cumulative *w*	LL
y = SITE + STATUS + SITE:STATUS	7	237.02	0	1	1	-108.96
y = SITE	4	253.67	16.66	0	1	-122.04
y = SITE + STATUS	5	254.89	17.88	0	1	-121.2
y = 1	2	255	17.98	0	1	-125.28
y = STATUS	3	256.13	19.11	0	1	-124.6

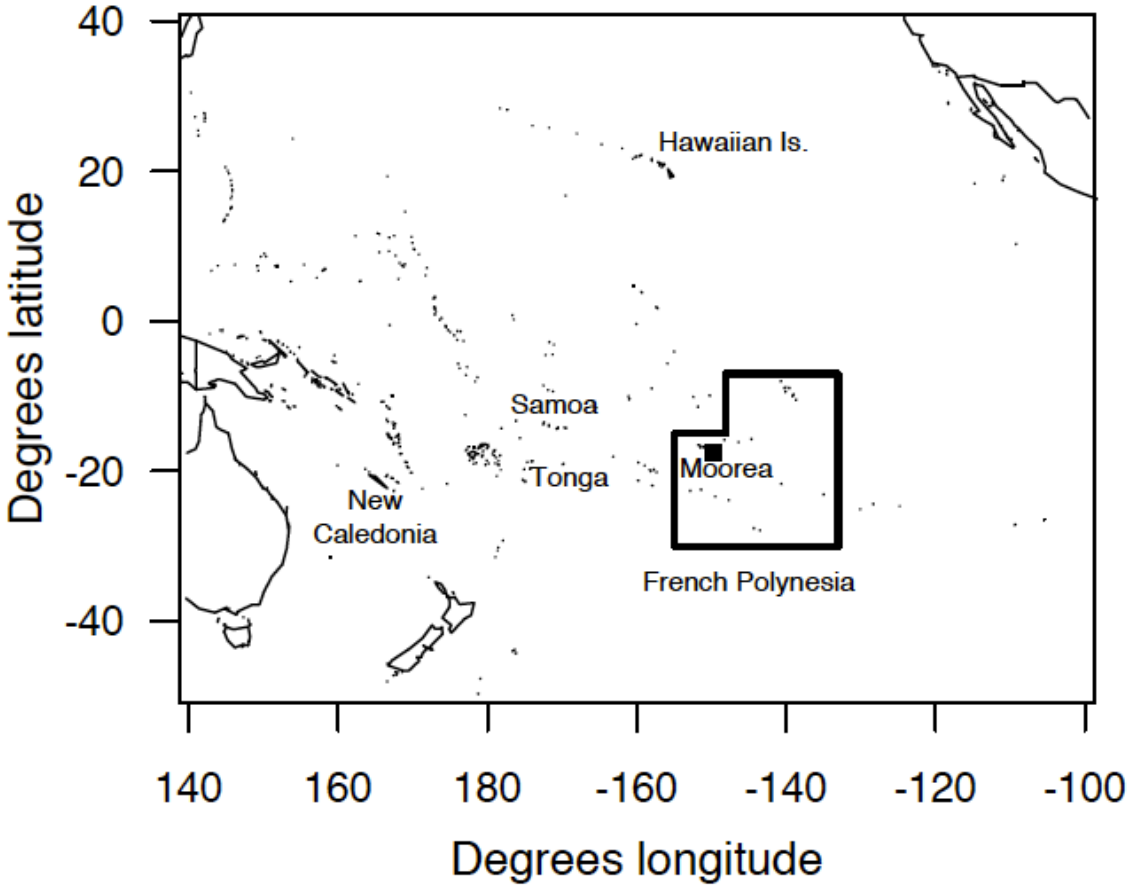
Table 4. Fixed effect parameter estimates from GLM analysis of total species richness, averaged from the top two AIC_c-selected models. Significant parameters are printed in **bold**.

Parameter	Point Estimate	Standard error	*P*-value
Intercept	**11.383**	**1.581**	**< 0.001**
SITE THREE	**-6.38**	**2.266**	**0.006**
SITE TWO	**-5.569**	**2.139**	**0.012**
STATUS (Comparison)	**7.234**	**2.448**	**0.004**
SITETHREE:STATUS (Comparison)	**-6**	**2.733**	**0.037**
SITETWO:STATUS (Comparison)	**-5.2**	**2.733**	**0.071**

Table 5. Fixed effect parameter estimates from GLM analysis of total abundance, from the top AIC_c-selected model. Significant parameters are printed in **bold**.

Parameter	Point Estimate	Standard error	*P*-value
Intercept	**3.68819**	**0.0973**	**< 0.001**
SITE	-0.06368	0.0410	0.138
STATUS (Comparison)	**0.15209**	**0.0831**	**0.079**
SITE:STATUS (Comparison)	0.04208	0.0707	0.570

Figure 1.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-40
Degrees latitude
Hawaiian Is.
Samoa
Tonga
Moorea
New
Caledonia
French Polynesia
140
160
180
-160
-140
-120
-100
Degrees longitude

Newman *et al*.: Anthropogenic wildfire impacts on Pacific island flora

Figure 2.

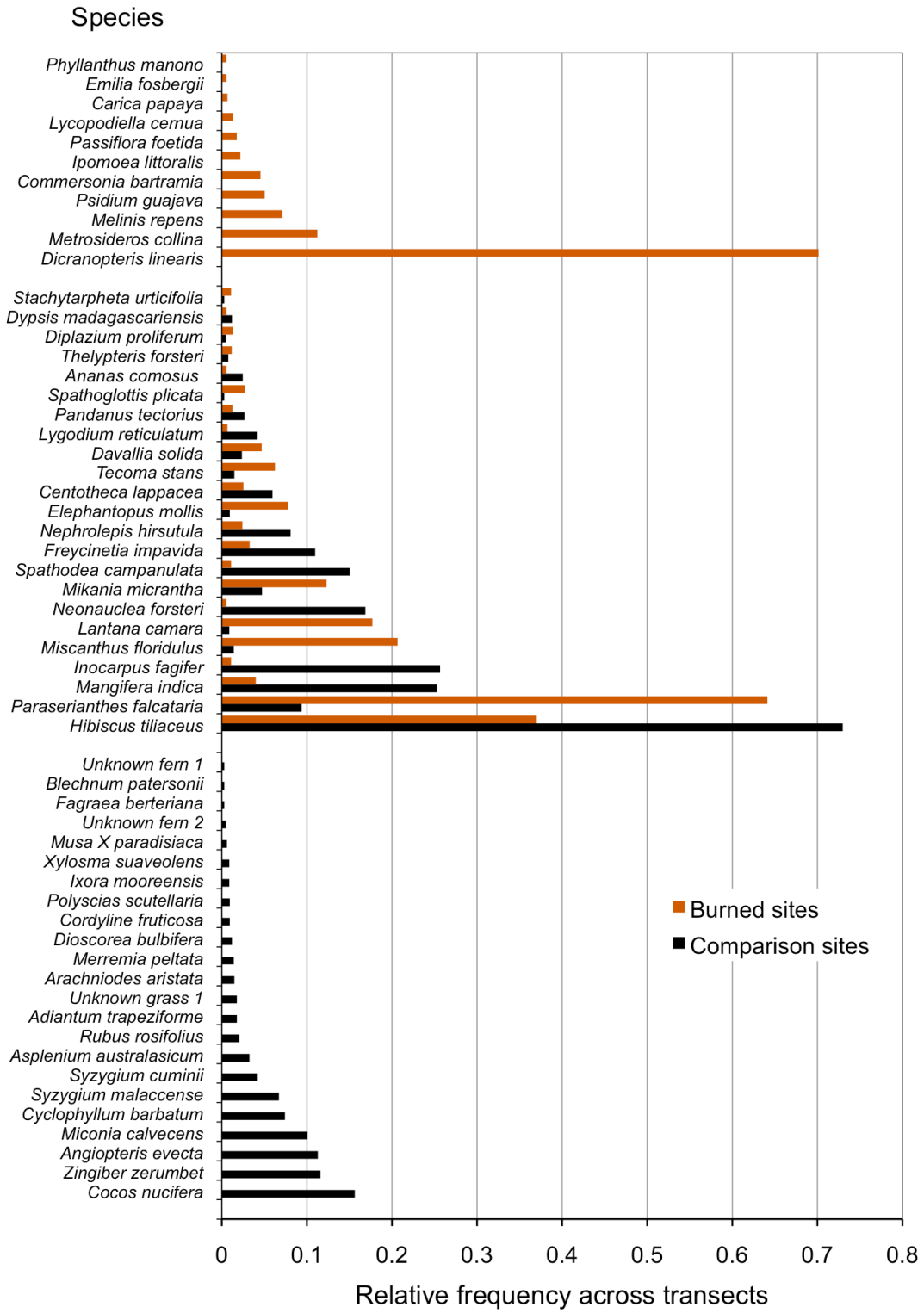
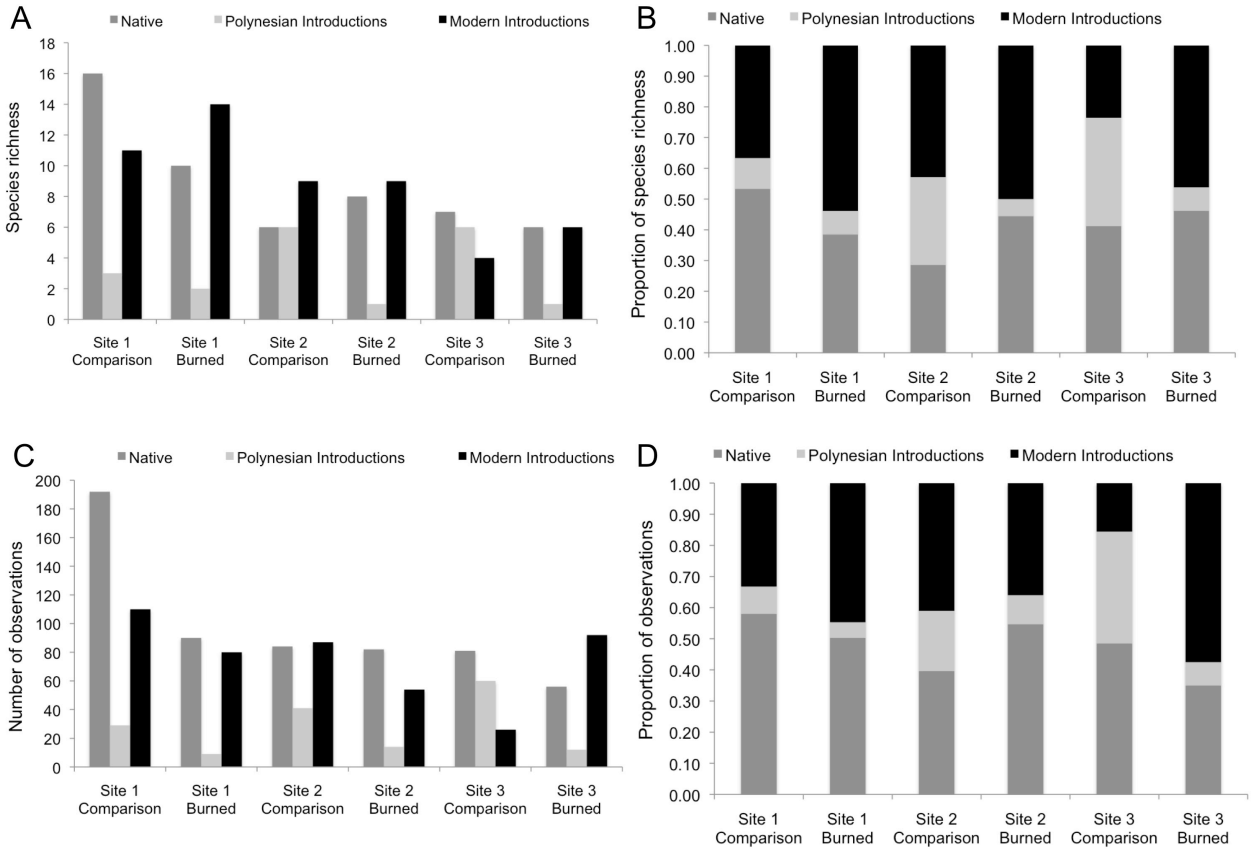


Figure 3.


A
Native
Polynesian Introductions
Modern Introductions
Species richness
0
2
4
6
8
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12
14
16
18
Site 1 Comparison
Site 1 Burned
Site 2 Comparison
Site 2 Burned
Site 3 Comparison
Site 3 Burned
B
Native
Polynesian Introductions
Modern Introductions
Proportion of species richness
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
Site 1 Comparison
Site 1 Burned
Site 2 Comparison
Site 2 Burned
Site 3 Comparison
Site 3 Burned
C
Native
Polynesian Introductions
Modern Introductions
Number of observations
0
20
40
60
80
100
120
140
160
180
200
Site 1 Comparison
Site 1 Burned
Site 2 Comparison
Site 2 Burned
Site 3 Comparison
Site 3 Burned
D
Native
Polynesian Introductions
Modern Introductions
Proportion of observations
0.00
0.10
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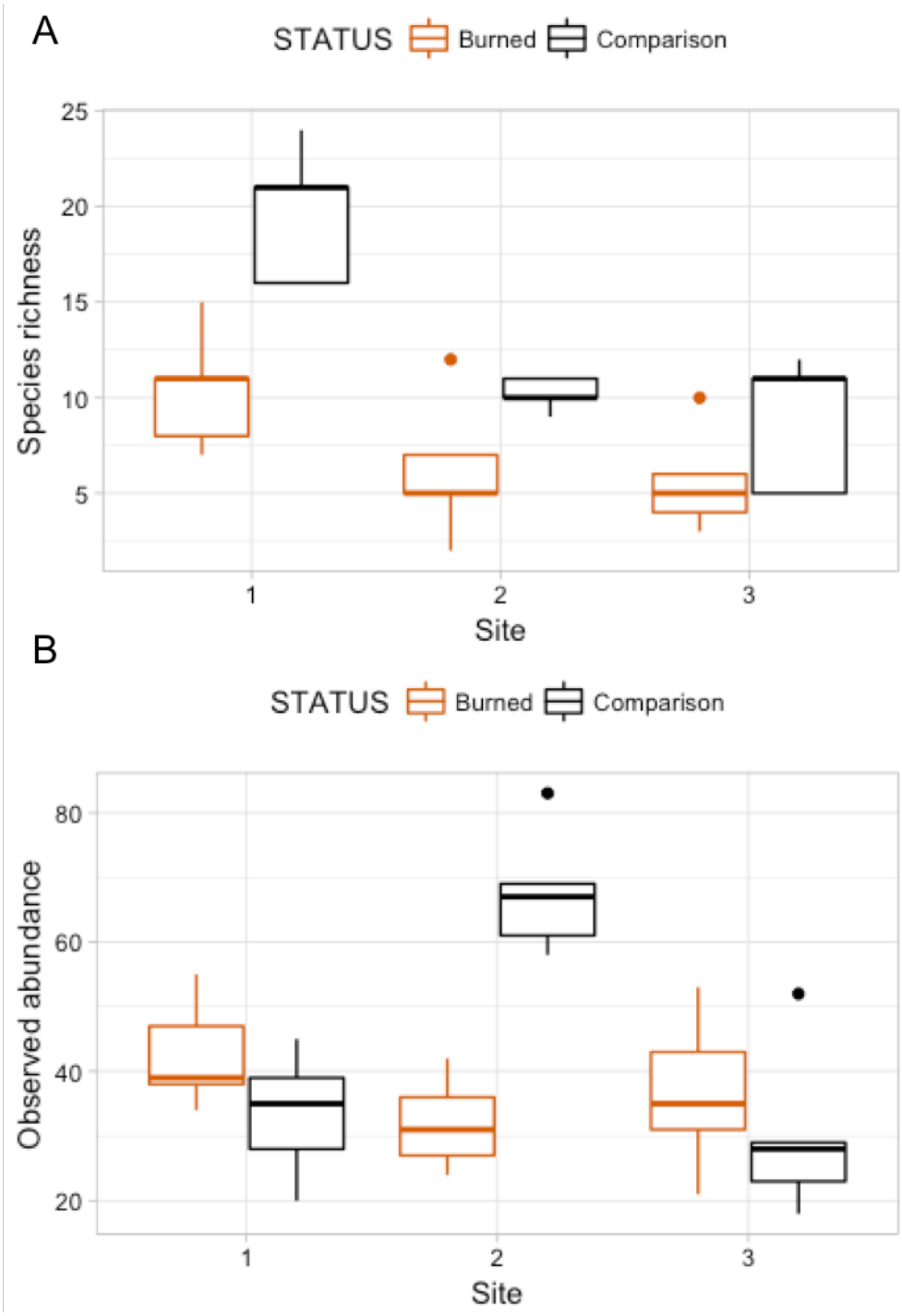
1.00
Site 1 Comparison
Site 1 Burned
Site 2 Comparison
Site 2 Burned
Site 3 Comparison
Site 3 Burned

Figure 4.


A
STATUS
Burned
Comparison
Species richness
25
20
15
10
5
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Site
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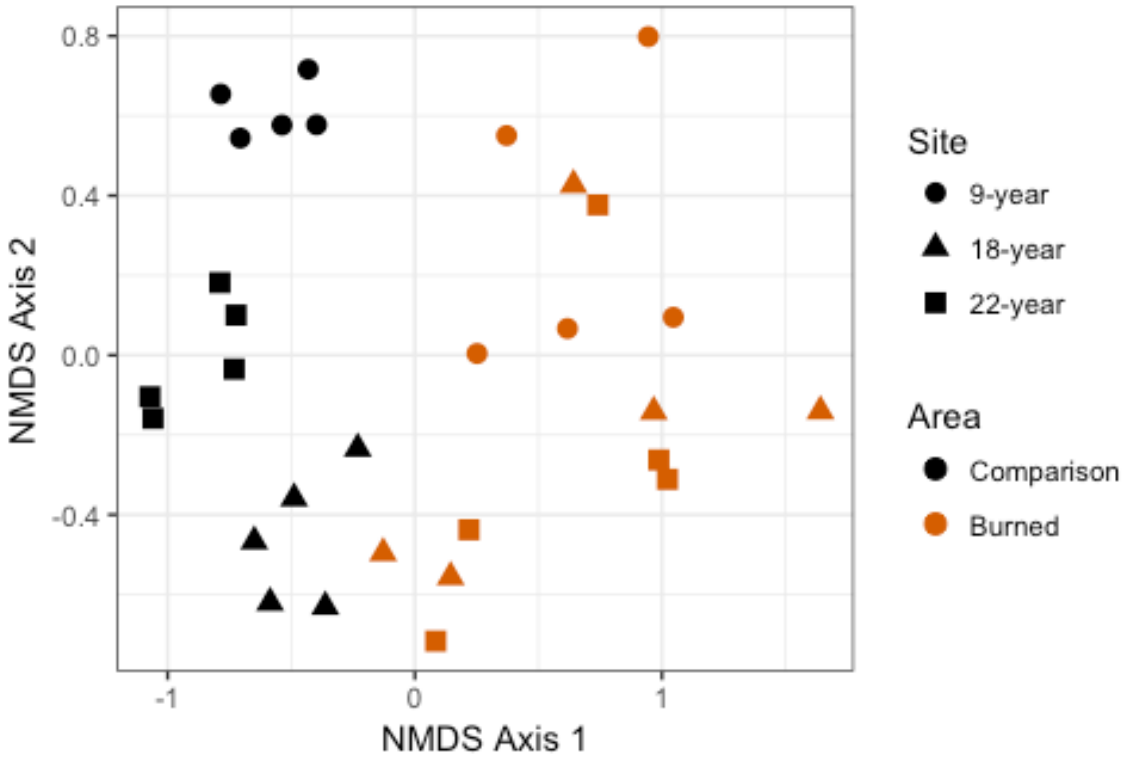
STATUS
Burned
Comparison
Observed abundance
80
60
40
20
1
2
3
Site

Figure 5.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0.4
0.0
-0.4
NMDS Axis 2
-1
0
1
NMDS Axis 1
Site
9-year
18-year
22-year
Area
Comparison
Burned