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Recovery of native forest after removal of an invasive tree, *Falcataria moluccana*, in American Samoa

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Abstract Invasive species are among the greatest threats to global biodiversity. Unfortunately, meaningful control of invasive species is often difficult. Here, we present results concerning the effects of invasion by a non-native, N_2-fixing tree, *Falcataria moluccana*, on native-dominated forests of American Samoa and the response of invaded forests to its removal. We sampled species richness, seedling and stem densities, biomass, and soil inorganic N status in native-dominated forests, and in forests invaded by *F. moluccana* where it was subsequently removed. While total biomass of intact native forests and those invaded by *F. moluccana* did not differ significantly, greater than 60% of the biomass of invaded forest plots was accounted for by *F. moluccana*, and biomass of native species was significantly greater in intact native forests. Biomass of native Samoan tree species following removal of *F. moluccana* accumulated rapidly from 128 Mg ha^{-1} immediately after tree girdling treatment to 185 Mg ha^{-1} following 8 years of post-removal recovery, at which point biomass of *F. moluccana*-removal plots did not differ significantly from native-dominated forest plots. Native trees exhibiting early successional traits accounted for a large portion of aboveground biomass in these forests where frequent large-scale disturbance events (i.e., tropical cyclones) are a salient feature. We suspect that this is the single most important reason why *F. moluccana* removal is a successful management strategy; once *F. moluccana* is removed, native tree species grow rapidly, exploiting the legacy of increased available soil N and available sunlight. Seedling densities of *F. moluccana* were high in invaded forest stands but effectively absent following only 3 years of forest recovery; a result likely due to the shade cast by reestablishing native trees. Although *F. moluccana* is a daunting invasive species, it exhibits characteristics that make it vulnerable to successful control: it is easily killed by girdling or herbicides, and its seeds and seedlings do not tolerate shade. These characteristics, combined with the important capacity for rapid growth exhibited by many of Samoa's native trees, provide conditions and opportunities for successful, long-term control of *F. moluccana* across lowland forests of American Samoa. Caution should be exercised, however, in anticipating comparable management success in the control of *F. moluccana* elsewhere, as post-removal responses of invaded forest communities may differ dramatically from what has been documented in American Samoa.

Keywords Invasive species · Disturbance · Pacific Islands · Samoa · Biomass · Richness · Soil nitrogen · Succession

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Introduction

Invasive species pose one of the greatest threats to global biodiversity in general (Vitousek et al. 1997; Mack et al. 2000; Millennium Ecosystem Assessment 2005) and to native biodiversity of islands in particular (Denslow 2003; Reaser et al. 2007; Kueffer et al. 2010; Castro et al. 2010). Unfortunately, meaningful control of invasive species to protect and sustain native biodiversity is often difficult even at small scales, much less across broad landscapes with challenging terrain (Ostertag et al. 2009; Norton 2009). Effective control may prove even more problematic in cases where the invasive species have the capacity to alter ecosystem function as well as community composition and structure (Vitousek 1990); for example, when invasive grasses change fire regimes (D'Antonio and Vitousek 1992) or N_2-fixing trees increase available soil N in primary succession settings (Vitousek et al. 1997). In such instances, functional thresholds may be crossed to the degree that return to pre-invasion states is considered impractical (Hobbs et al. 2009).

The literature is replete with examples of intractable and persistent invasions (Elton 1958), but successful control of particular invasive species have also been documented (Simberloff 2009a; Jäger and Kowarik 2011). Mack et al. (2000) attribute successful control to three key factors: (1) sufficient and persistent funding of control approaches; (2) widespread support for action from agencies and the public; and (3) the presence of exploitable characteristics in the target invader (e.g., shade intolerance, sensitivity to herbicides or fire, vulnerability to specific pathogens and/or insects that may serve as effective bio-control agents) that make control efforts feasible and effective. An important additional corollary to this last factor is that the invaded ecosystem itself exhibits particular structural or functional characteristics that will enable it to respond positively to the removal/control of a given invasive species. If such response characteristics can be maintained, resilience to invasion and sustained maintenance of the integrity of the native ecosystem are possible (Funk et al. 2008).

On the island of Tutuila, American Samoa, an aggressive field campaign has been ongoing since 2001 to eliminate the introduced, N_2-fixing tree, *Falcataria moluccana* (Miquel) Barneby and Grimes (formerly known as *Albizia falcataria* (L.) Fosberg, *Paraserianthes falcataria* (L.) Nielsen, and *Albizzia moluccana* Miguel) within the boundaries of the National Park of American Samoa (NPSA) as well as in adjacent areas. Invasive species control in general, and control of *F. moluccana* in particular, is considered a high priority as Samoa's forests are important constituents of the Pacific Ocean's Polynesia/Micronesia biodiversity hotspot (Myers et al. 2000). By themselves, these islands support some of the most intact native ecosystems of any Pacific Island group, including littoral communities, wetlands, as well as lowland, montane and cloud rainforests (Mueller-Dombois and Fosberg 1998; Whistler 2002). The continued existence of lowland rainforest vegetation in particular is not typical of most islands of the Pacific, where the majority of such forests have been converted to agriculture of one form or another (Hunt and Kirch 1997). Though humans have occupied the Samoan Islands for at least 3,000 years, deforestation on steep slopes of Tutuila Island for cultivation has been relatively limited and localized, though certainly not absent. However, tropical cyclones occur frequently, and adaptation to such disturbances appears to be a salient feature of the flora of Samoa (Webb et al. 2011).

F. moluccana has invaded large areas of the forests of the NPSA and neighboring areas on Tutuila Island; it is also present in Independent (or Western) Samoa (Space and Flynn 2000; Space and Flynn 2004). A nitrogen-fixing tree, *F. moluccana*—also known as tamaligi in Samoa—is native to the Moluccas, New Guinea, New Britain, and the Solomon Islands (Wagner et al. 1999). The species likely was first introduced to Samoa on the island of Upolu perhaps as early as the 1830s and was thought to have spread to Tutuila Island in the early 1900s. It was noted present in Samoa by Christophersen (1938) during the 1930's, and was mentioned as occurring in the backyards of residents of Pago Pago by the 1950s (M. H. Sesepasara, personal communication). By the 1980's *F. moluccana* was noted as locally common within NPSA boundaries (Whistler 1980; Whistler 1994) and by 2000, approximately 35% of Tutuila Island—or ca. 6,725 ha—was infested with *F. moluccana*, prompting NPSA efforts to begin control of this species (Togia, unpublished data).

Aided by its N_2-fixing capacity, *F. moluccana* grows well on a variety of soil types, including degraded sites (Otsamo 1997; Otsamo 2002) and

acidic or nutrient-poor soils (DeBell et al. 1989; Panjaitan et al.1993). It has been noted to be among the fastest growing trees in the world (Soerianegara and Lemmens 1994). In Hawaii where it has become naturalized, this species is well known for its rapid growth and large size at maturity; canopy heights can reach 10 m in 2-year-old stands, and 20-year-old individuals may be 30 m tall with trunk diameters up to 80 cm (Walters 1971). In well-developed stands, the broad, umbrella-shaped canopies of large individuals often coalesce into one extensive monotypic canopy capable of covering hectares to square kilometers (Hughes and Denslow 2005).

Our objectives in this study were to determine how *F. moluccana* invasion affects the composition, biomass, and soil nitrogen availability of native-dominated Samoan forests and how these parameters respond to the removal of *F. moluccana*. To do this we sampled species composition and richness, density of seedlings and woody stems, biomass, and soil inorganic N status in native-dominated forests, forests invaded by *F. moluccana*, and forests in which *F. moluccana* populations had become well established but were subsequently removed a given number of years prior to sampling.

Methods

Study area

Study sites were located on the northwest side of Tutuila Island of American Samoa, part of the archipelago that includes the islands of Savai'i and

Table 1 Forest type and management treatment, elevation, location, and land stewardship of research plots in and adjacent to the National Park of American Samoa, Tutuila Unit

Forest/treatment	Plot location (UTM coordinates)			Elevation	Land
Type	Plot label	North	East	a.s.l (m)	Stewardship
Intact-native forest	111	530,321	8,421,426	200	NPSA
Intact-native forest	112	530,292	8,421,501	154	NPSA
Intact-native forest	113	530,298	8,421,535	172	NPSA
Intact-native forest	114	530,348	8,421,548	171	NPSA
Intact-native forest	115	530,240	8,421,506	175	NPSA
Tamaligi controlled in 2007	101	529,029	8,419,942	157	Fagasa village
Tamaligi controlled in 2007	102	529,048	8,419,902	186	Fagasa village
Tamaligi controlled in 2007	103	529,020	8,419,883	200	Fagasa village
Tamaligi controlled in 2007	104	529,004	8,419,920	141	Fagasa village
Tamaligi controlled in 2007	105	529,104	8,420,304	198	Fagasa village
Tamaligi controlled in 2006	106	529,901	8,421,091	66	NPSA
Tamaligi controlled in 2006	107	529,942	8,421,074	68	NPSA
Tamaligi controlled in 2006	108	530,452	8,421,469	234	NPSA
Tamaligi controlled in 2006	109	530,446	8,421,418	251	NPSA
Tamaligi controlled in 2006	110	530,352	8,421,475	227	NPSA
Tamaligi controlled in 2003	321	530,219	8,421,342	239	NPSA
Tamaligi controlled in 2003	322	530,469	8,420,969	166	NPSA
Tamaligi controlled in 2003	323	530,430	8,421,039	153	NPSA
Tamaligi controlled in 2003	324	530,877	8,421,825	278	NPSA
Tamaligi controlled in 2003	325	530,527	8,421,489	269	NPSA
Tamaligi controlled in 2001	316	530,827	8,420,939	182	Fagasa village
Tamaligi controlled in 2001	317	530,782	8,420,925	179	Fagasa village
Tamaligi controlled in 2001	318	530,730	8,420,943	172	Fagasa village
Tamaligi controlled in 2001	319	533,729	8,420,988	175	Fagasa village
Tamaligi controlled in 2001	320	530,763	8,421,012	160	Fagasa village

Upolu (i.e., the Independent State of Samoa). Tutuila is a high volcanic island (maximum elevation, 653 m) approximately 13,700 ha in size located in the South Pacific Ocean (14°18′S, 170°41′W); it originates from a hot spot on the Pacific plate that manifested as shield volcanism of Pago Volcano between 1.54 and 1.28 Ma years ago (McDougall 1985).

The climate of Tutuila is characterized as tropical, and weather patterns are primarily determined by its proximity to the equator and exposure to northeasterly trade winds. Mean annual precipitation is substantial and varies according to the island's topographic features, averaging 3,200 mm for coastal areas to as much as 5,000 mm on windward upper slopes. Precipitation also varies seasonally. A dry season occurs from June to September and a wet season occurs from October to May. Mean monthly temperatures vary only slightly, ranging from 26 (July) to 28°C (January); Maximum July temperatures range from 32°C in coastal areas to 26°C in upland areas and minimum January temperatures range from 24°C in coastal areas to 21°C in upland areas (Daly et al. 2006).

Study sites were located within or adjacent to the National Park of American Samoa (NPSA) (Table 1, Fig. 1). Elevation of study plots ranged from 66 to 200 m above sea level (a.s.l.) and the mean elevation for all plots was 183 m a.s.l. (Table 1). Soils in this area are described as belonging to the Fagasa Family and are classified as fine, hallositic, isohyperthermic Typic Hapludolls. They are derived from volcanic ash and residuum from basic igneous rock and are moderately deep (50 cm) and deep (100 cm) well-drained soils occurring on ridges and very steep terrain (slopes are 70–130%; Nakamura 1984).

The flora of the Samoan Archipelago consists of approximately 540 native angiosperm species (Whistler 1992), partitioned into 283 genera in 95 families, as well as 230 species of ferns and fern allies. Vegetation of forest plots sampled in this study have been classified as lowland hill forest (Webb and Fa'aumu 1999) comprised of several native tree species, most dominant being *Planchonella samoensis*, *Dysoxylum* spp., *Canarium* spp., *Rhus taitensis, Myristica inutilus, Hibiscus tiliaceus, Syzygium inophylloides, Eleocarpus ulianus, Neonauclea forsteri,* and *Macaranga stipulosa* ("Appendices 1 and 2"). Several non-native trees also are present in these forests, notably *Cananga odorata* and the Polynesian introduction, *Inocarpus fagifer* (Whistler 2002). Collectively, these native-dominated forests provide critical habitat and sustenance for native fruit bats

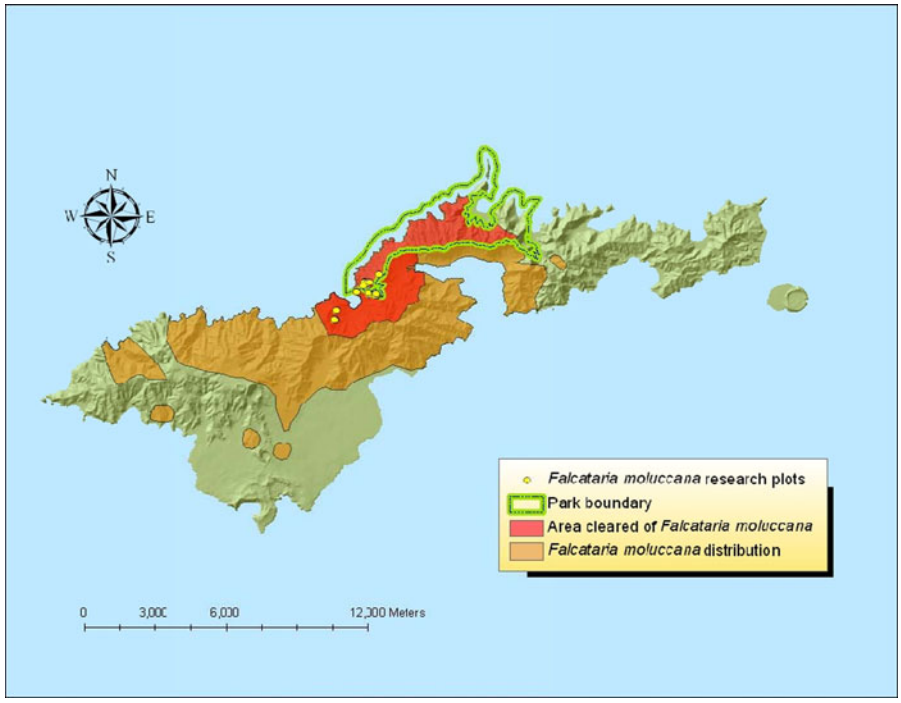

Fig. 1 Map of Tutuila Island indicating the boundary of the National Park of American Samoa—Tutuila Unit (*green line*). *Red areas* are those in which *Falcataria moluccana* have been killed via girdling; *orange areas* are those currently infested by *F. moluccana*. *Yellow dots* indicate locations of forest plots

(*Pteropus tonganus* and *P. samoensis*) and a wide variety of native and endemic birds (Banack 1998; Freifeld 1999; Webb et al. 1999). They also are culturally significant as sources of many traditional practices, medicines, fibers, timber, weaving materials, carving materials, and items used for adornment and decoration (Whistler 2000).

While humans have inhabited and utilized the resources of the Samoan archipelago for millennia (Hunt and Kirch 1997), extensive forested areas remain, likely as a consequence of the difficulty cultivating crops on steep portions of the island. In 1985, forest cover on Tutuila was estimated at 53% (Cole et al. 1988), and the NPSA remains nearly completely forested from the coastal zone up to high ridges approximately 300 m above sea level.

Like many Pacific islands, American Samoa occasionally experiences large-scale, cataclysmic disturbances from cyclones (Mueller-Dombois and Fosberg 1998). Visher (1925) noted an annual frequency of two to three potentially destructive cyclones in the general area around Samoa, and Elmqvist et al. (1994) documented the destructive effects of such large-scale, severe events on the structure of Samoan forests. Additionally, Samoa experiences more frequent but less cataclysmic disturbances in the form of cyclone "near misses", tropical storms, and tropical depressions; together these create what has been termed a 'chronic disturbance' regime (Webb et al. 1999, 2011). In total, disturbances from cyclones, whether large or small, have played a potent evolutionary role in shaping the composition, structure, and function of Samoa's native forests (Webb and Fa'aumu 1999; Webb et al. 2006).

Study design

To investigate the effects of *F. moluccana* invasion and its subsequent removal on the composition, structure and function of native-dominated forests, we established study plots in five treatment areas that provided a chronosequence of forest succession following *F. moluccana* removal. These included native-intact forest stands that had never been invaded by *F. moluccana* and forest stands in which numerous large (i.e., >1 m diameter at dbh) *F. moluccana* individuals had become established, typically at densities averaging 11 individuals per 0.10 ha and with an average diameter of 47 cm dbh. Because *F. moluccana* does not tolerate shade, very few if any saplings (i.e., <10 cm dbh) were encountered along with the larger mature trees. Across the forested landscape, patches of *F. moluccana* trees were girdled and killed in 2001, 2003, 2006, and 2007, respectively. Trees were girdled by NPSA field crews of 2–6 people, who incised the bark of each at its base and manually peeled the bark up the trunk in large strips. This was done around the entirety of the trunk, resulting in a 1–3 m wide section where the outer bark was removed. Following girdling, individual trees died gradually but inevitably; complete canopy defoliation typically occurred between 6 months to a year following treatment, after which time the girdled individual might remain within the forest for several years before falling over or falling apart in place. Specific areas where *F. moluccana* individuals were present and subsequently killed have been mapped by NPSA staff (Togia, unpublished data). Together, these plots provide a chronosequence of time since *F. moluccana* removal (Table 1, Fig. 1). As with chronosequence study designs conducted elsewhere (Johnson 1992; Linder 1998), we recognize that differences between plots in a chronosequence can occur because of unique site characteristics (i.e., slope position, initial species composition, and potential prior land use) rather than because of succession. However, the *F. moluccana* patches identified by NPSA staff for control in a given year were selected in a haphazard fashion that demonstrated no bias with regard to subsequent forest recovery. As such, although initial conditions likely differed among patches, such differences were randomly distributed across treatment years.

Five, 18 m radius forest plots were established in each of the five study areas. In the four *F. moluccana*-removal stands, each forest plot was located in an area that contained the trunks of 5–10 large remnant *F. moluccana* snags that had been girdled at the designated time prior to sampling. This was done to ensure that mature *F. moluccana* individuals had in fact invaded these study plots in the past. Each plot encompassed an area of 1,018 m^2 (i.e., approximately 0.10 ha) and consisted of various sized nested subplots. Species identity and dbh (1.37 m height) were determined for each tree 10 cm or greater in diameter encountered in the entirety of each 18 m radius plot. In cases where buttresses were present on trees at dbh, diameter measurements were taken at a height above the buttress to provide a more accurate measurement.

All trees ≥10 cm dbh were labeled with aluminum tags to allow for accurate re-measurement on an annual basis. Smaller trees, i.e., those ≥2 cm and <10 cm in diameter (dbh) were identified to species and their diameters recorded within each 9 m radius subplot nested within the 18 m radius forest plot. The diameter and identity of all saplings, shrubs, or vines <2 cm at dbh and at least 1.37 m tall were determined within a 6 m radius subplot. Seedlings and small saplings <1.37 m in height were counted and identified to species in four 0.5 m^2 quadrats located within each nested plot.

Biomass was calculated for live tree and sapling components of each forest stand. Biomass of each tree >10 cm dbh was estimated using the following equation from Chave et al. (2005) for wet forest stands:

$$(\mathrm{AGB})_{\mathrm{est}} = \rho * (\exp(-1.239 + 1.9801 * \ln(\mathrm{D}) + 0.207 * (\ln(\mathrm{D}))^2 - 0.0281 * (\ln(\mathrm{D}))^3))$$

where $(\mathrm{AGB})_{\mathrm{est}}$ is the estimated aboveground biomass of each tree (kg); ρ is wood specific gravity (g cm^{-3}) determined for each tree species; and D is diameter (cm) measured at 1.37 m from the forest floor. Species-specific wood density values were obtained from a global wood density database (Zanne et al. 2009) and from other published sources (Reyes et al 1992; Asner et al. 2011). In cases where species specific values were not available from the literature, we used a mean of species values from the same genus. In the few cases where genus-specific values were unavailable, we used a value of 0.50 g cm^3.

Biomass of trees <10 cm at 1.37 m height (dbh) was estimated using the following equation from Hughes et al. (2000):

$$(\mathrm{AGB})_{\mathrm{est}} = \exp(4.9375 + (1.0583 * (\ln(\mathrm{D}^2)))) * 0.0114$$

where notations are as described above, and 0.0114 is the correction factor to account for the back transformation (Baskerville 1972).

Biomass of vines was estimated using the following equation from Schnitzer et al. (2006):

$$(\mathrm{AGB})_{\mathrm{est}} = \exp(-1.484 + 2.657 * (\ln(\mathrm{D})))$$

All plots were measured at least twice on an annual basis to provide necessary plot-specific biomass accumulation information. Native intact forest plots and forest plots in which *F. moluccana* had been removed in 2006 and 2007 were measured in 2007, 2008, and 2009. Forest plots in which *F. moluccana* had been removed in 2001 and 2003 were measured in 2008 and 2009. Species richness was also determined within each forest plot through visual surveys and species identification.

Indices of available soil N (i.e., NO_3^--N and NH_4^+-N) were sampled within each forest plot using resin bags (Binkley and Matson 1983) during 2007 and 2008 sampling efforts. Each 6 × 7.5 cm resin bag was made of monofilament polyester silkscreen fabric (86 mesh), filled with 6 g of mixed-bed exchange resin (IONAC NM-60 H1/OH2 form, type I, beads,16–50 Mesh; J. T. Baker; Phillipsburg, New Jersey, USA). At the beginning of each sampling period, resin bags were placed approximately 5 cm deep at two different locations within each forest plot (n = 10/study area). In 2007, bags were recovered after an 11 day in situ period; in 2008 bags were recovered after a 23 day in situ period. Once recovered, bags were rinsed with deionized water to remove attached soil, and shaken vigorously to remove excess water. Bags were immersed in 100 mL of 1 mol/L KCl solution in sealed sample cups and agitated on a shaker table for 6 h. After shaking, KCl extracts were analyzed colorimetrically for NO_3^--N and NH_4^+-N (Technicon AAI Sampler [Technicon, Emeryville, California,USA] and Scientific AC 200 Colorimeter [Westco Scientific Instruments; Danbury, Connecticut, USA]) by the University of Hilo, Marine Sciences Laboratory (Mulvaney 1996). Resin-captured soil N was sampled on two separate occasions (August 2007 and August 2008). In the few instances that resin bags were damaged by animals in the field, these samples were discarded from subsequent analyses. Results are expressed as μg ion per g resin per day and represent indices of soil inorganic N availability rather than actual soil inorganic N pools or transformation rates.

Statistical analysis

One of our primary objectives was to compare the change over time of the forest stands where *F. moluccana* had invaded and been subsequently killed prior to sampling (Table 1) against the intact native forest stands in which *F. moluccana* had not invaded. To do so, we recognized that the levels of the dependent variables (i.e., total biomass, stem and

seedling densities, species richness, and soil inorganic N availability) depend on the time since treatment and that some plots were measured during more than 1 year. As such, we used a model employing fixed mean values for both *F. moluccana*-invaded forest and native-intact forest plots for each year of measurement. In the case of *F. moluccana*-invaded plots, we incorporated an additional additive term based on the years since treatment or elapsed time since treatment.

Analysis of the effect of time since treatment

We utilized the usual general linear mixed model with the following notation:

$$y_{ijk} = \mu_{ik} + \beta \times e_{ijk} + \epsilon_{ijk}$$

where y_{ijk} was the measurement for forest type i ($i = N$ is for native-intact and $i = T$ for *F. moluccana*-invaded), plot j, and time period k; μ_{ik} was the overall effect of forest type i measured in year k; β was the slope associated with the linear change of the *F. moluccana*-invaded plots since initial removal, e_{ijk} was the number of elapsed years with $e_{ijk} = 0$ when $i = N$; and ϵ_{ijk} is the residual error with $\epsilon_{ijk} \sim N(0, \sigma_i^2)$ and $\mathrm{Cov}(\epsilon_{ijk}, \epsilon_{i'j'k'}) = \sigma_i^2 \rho^{|k-k'|}$ when $i = i'$ and $j = j'$ and $\mathrm{Cov}(\epsilon_{ijk}, \epsilon_{i'j'k'}) = 0$ otherwise. This covariance accounted for the serial correlation (ρ) induced by repeated measurements on the same plots. The correlation between measurements on two successive years is ρ, the correlation between measurements separated by 2 years is ρ^2, between 3 years is ρ^3, etc.

For elapsed years (e) from 0 to 8 we were interested in comparing the mean responses of native-intact and *F. moluccana*-invaded forest types during any particular year k. That comparison corresponded to a linear function of some of the fixed effects parameters:

$$(\mu_{T,k} + \beta \times e) - \mu_{N,k}$$

As measurements were taken in 2007, 2008, and 2009, we selected $k = 2008$ to make the comparisons. We used 95% confidence limits to express the precision of estimating those differences.

$$\mu_{T,2008} + \beta \times e - \mu_{N,2008}$$

Using the estimates of the above coefficients from the analysis (*i.e.,* $\hat{\mu}_{T,2008}$, $\hat{\mu}_{N,2008}$, and $\hat{\beta}$) and their associated variances and covariances, we constructed 95% confidence intervals for these differences.

The 95% confidence interval for the difference was

$$\hat{\mu}_{T,2008} + \hat{\beta} \times e - \hat{\mu}_{N,2008} \pm 1.96 \times se_{\text{Difference}}$$

where $se_{\text{Difference}}$ is the estimated standard error of the difference of the two predicted means. To see which estimated baseline values did not provide evidence of a significant difference (at the 5% significance level), we plotted the elapsed years, e, against

$$\hat{\mu}_{T,2008} + \hat{\beta} \times e \pm 1.96\, se_{\text{Difference}}$$

This provided a single figure to depict the trend of *F. moluccana*-invaded forest types *and* the size and precision of the difference between the *F. moluccana*-invaded forest type means from the estimated native-intact forest baseline, rather separate figures for the trend and the difference.

Analysis of annual change

The aforementioned model characterized the average annual change for both *F. moluccana*-invaded and native-intact forest types. Native-intact forest plots measured in 2007 and 2009 exhibited a mean change defined by

$$\Delta_N = (\mu_{N,2009} - \mu_{N,2007})/2$$

This was the case whether or not measurements were taken in 2008. Similarly, in *F. moluccana*-invaded plots, the mean change from 2007 to 2009 where the number of elapsed years since removal in 2007 is e and is given by

$$\begin{aligned}\Delta_T &= \frac{\mu_{T,2009} + \beta \times (e+2) - (\mu_{T,2007} + \beta \times e)}{2} \\ &= \frac{\mu_{T,2009} + 2\beta - \mu_{T,2007}}{2}\end{aligned}$$

For variables with measurements taken in just 2008 and 2009, the mean annual change is

$$\Delta_N = \mu_{N,2009} - \mu_{N,2008}$$

$$\begin{aligned}\Delta_T &= \mu_{T,2009} + \beta \times (e+1) - (\mu_{T,2008} + \beta \times e) \\ &= \mu_{T,2009} + \beta - \mu_{T,2008}\end{aligned}$$

Confidence intervals for the estimated changes were produced with PROC MIXED software from SAS (SAS/STAT software, Version 9.2 of the SAS System for Windows).

Analysis of initial values

An additional analysis was performed on the initial values of one *F. moluccana*-invaded stand prior to *F. moluccana* removal (i.e., the forest stand in which the *F. moluccana* individuals within and adjacent to the study plots had been removed in 2007). These values were compared to the initial measurements of native-intact plots. A linear model was formulated as follows:

$$y_{ij} = \mu_i + \epsilon_{ij}$$

where y_{ij} is the measurement on plot j of forest type i, μ_i is the mean for forest type i, and $\epsilon_{ij} \sim N(0, \sigma_i^2)$. Confidence intervals for the difference in forest type means $(\mu_T - \mu_N)$ also were produced by PROC MIXED software from SAS System for Windows (SAS/STAT software, Version 9.2 of the SAS System for Windows.). In addition, several of the figures were generated using the statistical package R (R Development Core Team 2010).

Results

Forest stands in which large *F. moluccana* individuals occurred were significantly different from intact native forest stands with regard to composition and structure. Prior to removal of *F. moluccana*, total biomass of native-intact forests and forests invaded by *F. moluccana* did not differ significantly (Fig. 2). However, more than 60% of the biomass in the invaded forest was accounted for by *F. moluccana* individuals, and biomass of native species was significantly greater in intact native forests (88% of total) relative to *F. moluccana*-invaded forests (30% of total; Fig. 2).

Removal of *F. moluccana* trees via girdling led to large initial differences in both total above ground biomass and biomass accounted for by native species; native intact forest plots contained 90% higher total biomass and 86% greater native tree biomass than *F. moluccana* removal plots immediately following girdling (Fig. 3a, b). Introduced non-native trees such as *I. fagifer* and *C. odorata* constituted a relatively small proportion of total aboveground biomass in these forests immediately following removal; they contributed only 30 Mg ha^{-1} to native-intact forest plots (12% of total biomass) and 12 Mg ha^{-1} to *F. moluccana* removal plots (9% of total biomass); collectively, biomass of non-native trees did not differ significantly between native-intact forest and removal plots (Fig. 3c).

Biomass accumulation following *F. moluccana* removal was rapid. Biomass accumulated from an initial estimated value of 128 Mg ha^{-1} immediately following removal to 185 Mg ha^{-1} following 8 years of post-removal recovery, at which point total biomass of removal plots was not significantly different from native-intact plots (Fig. 3a). This represented an average biomass accumulation rate of 7.1 Mg ha^{-1} year^{-1}; a response almost entirely due to biomass accumulation by native tree species, which, immediately after *F. moluccana* removal, exhibited biomass values that were 50% less than native-intact forest plots, but recovered to where they were not significantly different from native-intact values following 8 years of succession (Fig. 3b). In contrast, biomass of non-native species in removal plots was roughly equivalent to native-intact plots and did not change over the post-removal recovery period (Fig. 3c). Whereas we observed dramatic increases in native tree biomass following *F. moluccana* removal, we did not see commensurate increases in non-native tree biomass. Most biomass in native-intact forest and removal plots consisted of trees >10 cm dbh (98 and 97% of total, respectively; data not shown).

Total stem densities in removal plots were comparable to those in native-intact forest plots immediately following removal. After 8 years of post-removal forest recovery, however, total stem densities were 70% higher in removal plots relative to native-intact plots (Fig. 4a). As with trends in total biomass, native species accounted for the majority of total stem density in both native-intact (92% of total) and *F. moluccana* removal plots (84% of total). Total stem density values were similar between native-intact and removal plots immediately following removal, but were significantly greater in removal stands following 8 years of post-removal recovery (Fig. 4b). Non-native species contributed little to total stem density values in both native-intact (8% of total) and removal plots (16% of total) immediately following removal, although an important invasive understory species, *Clidemia hirta* was relatively abundant (248 stems ha^{-1} or 5% of total stem density) with study plots where *F. moluccana* had been removed in 2006

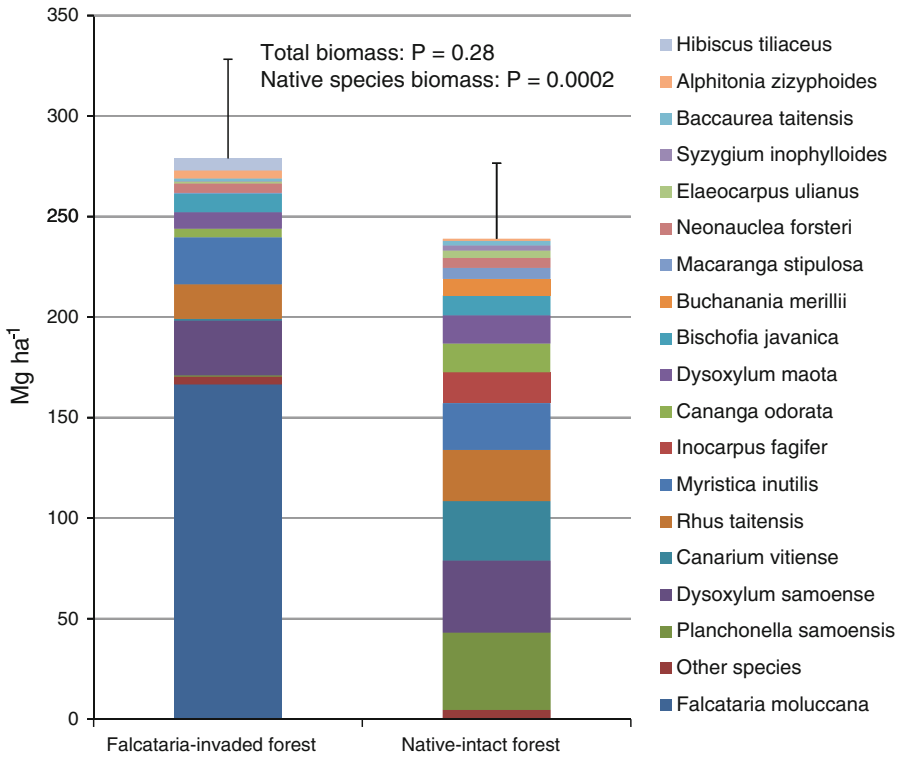

Fig. 2 Mean biomass values for native intact forest plots and *F. moluccana*-invaded forest plots (N = 5 in each case) on Tutuila Island, American Samoa. Colors indicate species-specific contributions to total biomass values. *Error bars* are standard errors of total biomass values. *P* values are derived from two-tailed t tests

("Appendix 2"). After 7 years of post-removal recovery, densities of non-native species in removal plots remained low (Fig. 4c).

Species richness totals were dominated by native species in both native-intact and removal plots (89 and 80% of total, respectively). After *F. moluccana* removal, total species richness and native species richness did not differ significantly between native-intact and removal plots (Fig. 5a, b). However, both total species richness and native species richness increased with time in removal plots, and were significantly greater than values in native-intact plots following 8 years of post-removal recovery (Fig. 5a, b). In contrast, estimated values of non-native species richness in removal plots were significantly greater than those in native-intact plots immediately following *F. moluccana* removal. After 8 years of post-removal recovery, non-native species richness values had declined to where they no longer differed from values in native-intact plots (Fig. 5c).

Regarding soil N dynamics, both total inorganic N and nitrate (NO_3^--N) values were three and five times higher, respectively, in *F. moluccana* removal plots compared to native-intact forest plots immediately after removal (Fig. 6a, b). Following only 3 years of post-removal forest succession, total inorganic N and nitrate values had declined to the point where they no longer differed from relatively low values of native-intact forest plots. Estimated values of ammonium (NH_4^+-N) in *F. moluccana* removal plots did not differ significantly from those in native-intact forest plots immediately after removal, but as with trends of total inorganic N and nitrate, ammonium values were virtually zero after only 5 years of post-removal succession (Fig. 6c).

Native seedling densities were not significantly different between native-intact and *F. moluccana* removal plots at any point across the 8 year period of the post-removal recovery period (Fig. 7a). Native species accounted for 86% of total seedling densities in native-intact forest plots, but accounted for only 45% of total seedlings in removal plots immediately following removal. This was due to high densities of *F. moluccana* seedlings (3.6 individuals m^2) present immediately following removal (Fig. 7b). After only 3 years of post-removal recovery *F. moluccana* seedling densities declined to virtually zero in removal plots. At that point they were not significantly different from *F. moluccana* densities in native-intact forest plots, which were effectively zero at all time points (Fig. 7b, c).

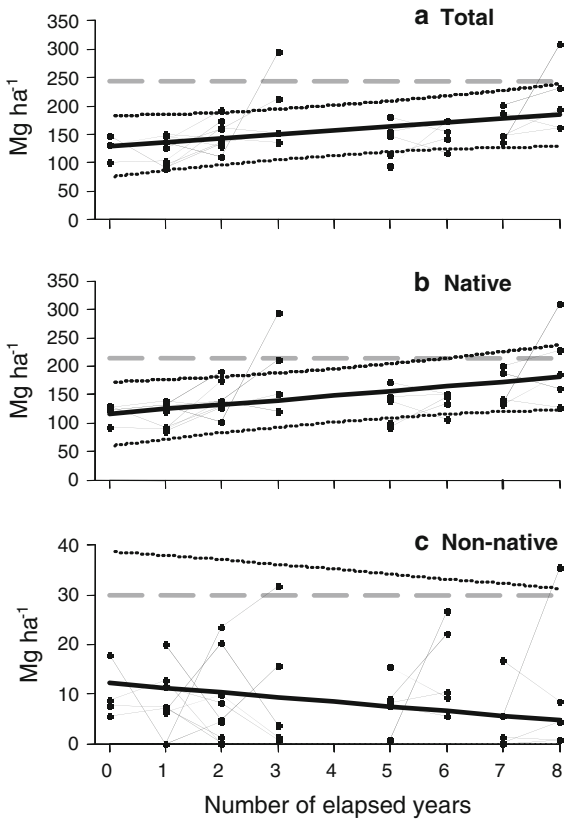

Fig. 3 *Trend lines* for total aboveground biomass (**a**), aboveground biomass of native species (**b**), and aboveground biomass of non-native species (**c**) in intact native forest (*dashed line*) and recovering forests following *F. moluccana* removal (*solid line*) on Tutuila Island, American Samoa. X-axis denotes the time since removal. *Dotted lines* denote 95% confidence interval of recovering forest biomass. *Thin black lines* denote trajectories of individual plots measured over consecutive years; *open circles* denote one-time measures of individual plots. Native-intact values differ significantly ($P \leq 0.05$) from *F. moluccana*-removal plots where the native-intact trend line (i.e., the *dashed line*) falls outside the confidence intervals of the *F. moluccana*-removal plots (i.e., *dotted lines*)

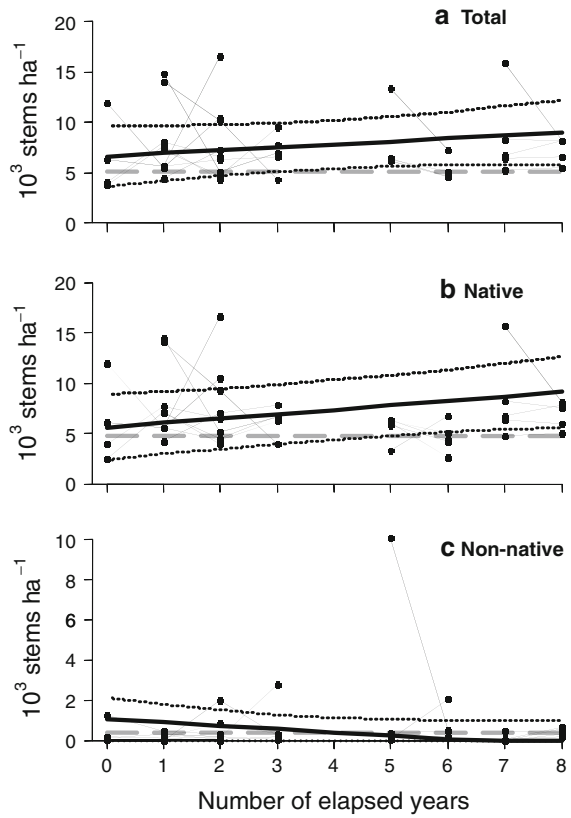

Fig. 4 Trend lines for all tree densities (**a**), native tree densities (**b**), and non-native tree densities (**c**) in intact native forest (*dashed line*) and recovering forests following *F. moluccana* removal (*solid line*) on Tutuila Island, American Samoa. X-axis denotes the time since removal. *Dotted lines* denote 95% confidence interval of recovering forest biomass. *Thin black lines* denote trajectories of individual plots measured over consecutive years; *open circles* denote one-time measures of individual plots. Native-intact values differ significantly ($P \leq 0.05$) from *F. moluccana*-removal plots where the native-intact *trend line* (i.e., the *dashed line*) falls outside the confidence intervals of the *F. moluccana*-removal plots (i.e., *dotted lines*)

Discussion

Our results demonstrate the strong influence of *F. moluccana* on the structure, composition, and functioning of native forests of Tutuila Island, American Samoa. That *F. moluccana*-invaded forests exhibited equivalent levels of total biomass but significantly lower biomass of native tree species suggests that this invasion replaces, rather than augments, the biomass of native trees in these forests. This is similar to findings of Hughes and Denslow (2005) who showed that *F. moluccana* replaces native-dominated lowland wet forests in Hawaii. It must be noted, however, that the native-dominated forests likely had been disturbed to some degree prior to the invasion of *F. moluccana*, and such disturbances actually may have been the catalyst for invasion by this species. Given the presence of agricultural species (e.g., *Artocarpus altilis, Cocos nucifera* and *Morinda citrifolia*) within some study plots ("Appendices 1 and 2"), we suspect that *F. moluccana* invasion into some portions of our areas of interest may have been preceded by small-scale disturbances such as land clearing for cultivation.

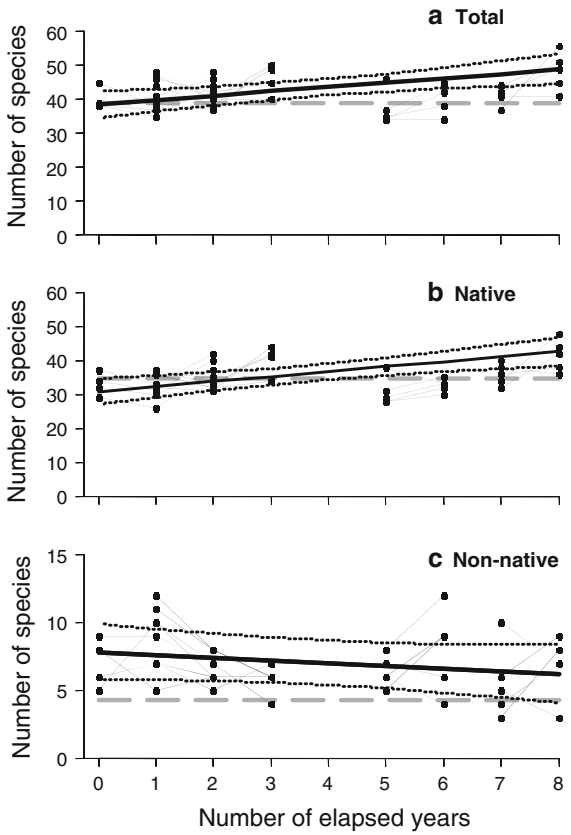

Fig. 5 *Trend lines* for the number of all species (**a**), the number of native species (**b**), and the number of non-native species (**c**) in intact native forest (*dashed line*) and recovering forests following *F. moluccana* removal (*solid line*) on Tutuila Island, American Samoa. X-axis denotes the time since removal. *Dotted lines* denote 95% confidence interval of recovering forest biomass. *Thin black lines* denote trajectories of individual plots measured over consecutive years; *open circles* denote one-time measures of individual plots. Native-intact values differ significantly ($P \leq 0.05$) from *F. moluccana*-removal plots where the native-intact trend line (i.e., the *dashed line*) falls outside the confidence intervals of the *F. moluccana*-removal plots (i.e., *dotted lines*)

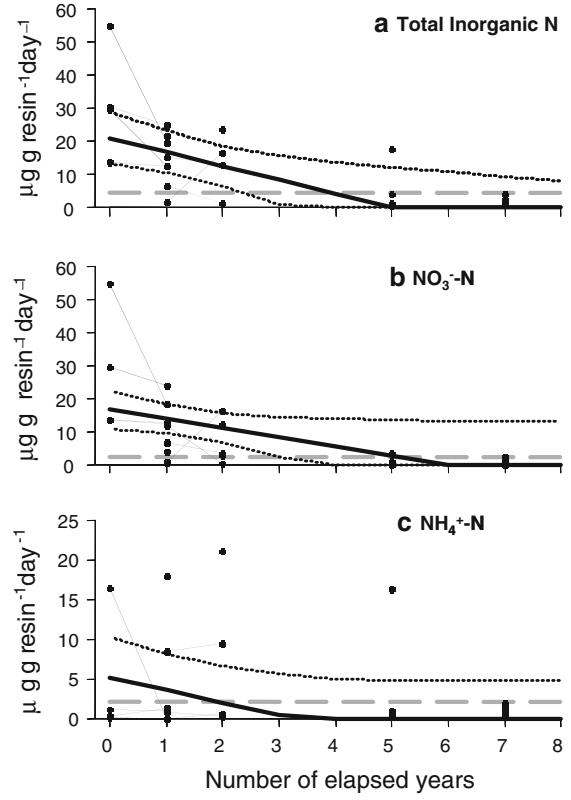

Fig. 6 *Trend lines* for resin-captured total inorganic N (**a**), resin-captured nitrate (**b**), and resin-captured ammonium (**c**) in intact native forest (*dashed line*) and recovering forests after *F. moluccana* removal (*solid line*) on Tutuila Island, American Samoa. X-axis denotes the time since removal. *Dashed lines* denote 95% confidence interval of recovering forest biomass. *Thin black lines* denote trajectories of individual plots measured over consecutive years; *open circles* denote one-time measures of individual plots. Native-intact values differ significantly ($P \leq 0.05$) from *F. moluccana*-removal plots where the native-intact trend line (i.e., the *dashed line*) falls outside the confidence intervals of the *F. moluccana*-removal plots (i.e., *dotted lines*)

Cyclone events are also are relatively common occurrences in Samoa and *F. moluccana* invasion may have occurred following one or more of these storms. As such, although *F. moluccana* may alter the secondary plant succession after disturbance, it should not be considered as the sole or preeminent driver of changes in composition and structure of these forests.

The marked increase in soil available N associated with *F. moluccana* presence in Samoan forests was also similar to patterns of increase in soil available N associated with *F. moluccana* invasion of Hawaii's lowland wet forests (Hughes and Denslow 2005; Hughes and Uowolo 2006) and with the presence of *F. moluccana* stands in plantation settings on Hawaii Island (Binkley 1997). Vitousek and Walker (1989) documented similar increases in available soil N associated with invasion by another non-native, N_2-fixing tree, *Myrica faya* (now known as *Morella faya*), in montane forests of Hawaii Volcanoes National Park. This is a common and expected result of invasion by N-fixing tree species into communities where such species are absent or uncommon (Ehrenfeld 2003). While not determined in this current

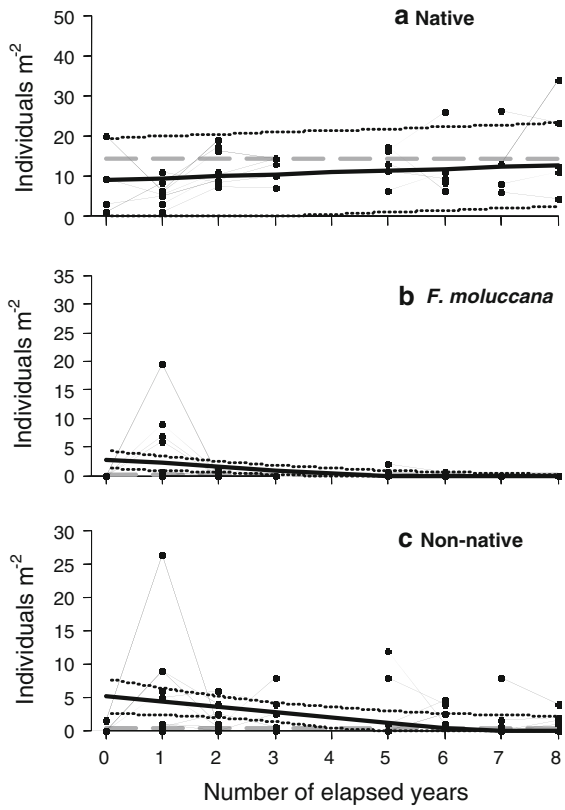

Fig. 7 Trend lines for densities of native seedlings (**a**), *F. moluccana* seedlings (**b**), and non-native seedlings (**c**) in intact native forest (*dashed line*) and recovering forests following *F. moluccana* removal (*solid line*) on Tutuila Island, American Samoa. X-axis denotes the time since removal. *Dashed lines* denote 95% confidence interval of recovering forest biomass. *Thin black lines* denote trajectories of individual plots measured over consecutive years; *open circles* denote one-time measures of individual plots. Native-intact values differ significantly ($P \leq 0.05$) from *F. moluccana*-removal plots where the native-intact *trend line* (i.e., the *dashed line*) falls outside the confidence intervals of the *F. moluccana*-removal plots (i.e., *dotted lines*)

study, Hughes as Denslow (2005), documented inputs of N via a litterfall collected under *F. moluccana* invaded forests that were as high as 250 kg N ha^{-1} $year^{-1}$. This differs from results of Kueffer (2010) and Kueffer et al. (2008), who found that the presence of *F. moluccana* did not facilitate seedling growth or increase nutrient turnover on phosphorus-poor soils of the Seychelle Islands, likely because primary production and decomposition were limited by phosphorus availability rather than nitrogen availability.

In contrast to the *F. moluccana* invasion scenario on young lava flows of Hawaii (Hughes and Denslow 2005), where *F. moluccana* virtually eliminated the dominant native tree species (i.e., *Metrosideros polymorpha*) and facilitated the invasion of additional non-native trees (i.e., *Psidium cattleianum*), many of Samoa's native tree species commonly found in native lowland forest stands were also present, albeit often at lower abundances, in *F. moluccana*-invaded stands (Fig. 2, "Appendices 1 and 2"). This may be one of the keys to successful recovery of native forest regeneration following *F. moluccana* removal: a sufficient diversity of native trees, including some exhibiting early successional, pioneer-type functional traits, was present at adequate abundances when control measures occurred to ensure recapture of these areas by native components. The rate of recovery following girdling was rapid, averaging 7.1 Mg ha^{-1} $year^{-1}$; a value within the range of biomass accumulation rates documented for secondary forests recovering following cultivation (6.2–8.7 Mg ha^{-1} $year^{-1}$; Alves et al. 1997; Silver et al. 2000) and for forests recovering from hurricane disturbances (5.4–16.3 Mg ha^{-1} $year^{-1}$; Scatena et al. 1996; Mascaro et al. 2005).

The relatively rapid accumulation of biomass—particularly of native tree species—following *F. moluccana* removal can be largely attributed to the particular characteristics of the native Samoan forest community. Webb and Fa'aumu (2006) estimated biomass in three 1.2 ha forest plots in NPSA; two plots were located in undisturbed wet forest stands and exhibited biomass values of 206 and 282 Mg ha^{-1}, respectively; these values are comparable to the mean value of native-intact forest stands sampled in this study (i.e., 244 Mg ha^{-1}). More importantly, these authors noted that 38% of the common native forest trees sampled in their study could be classified as successional (i.e., regenerating readily in disturbed forest), and that this proportion is substantially higher than what was documented in lowland rainforests of Panama, where successional species accounted for only 8% of the total species evaluated (Welden et al. 1991). Webb and Fa'aumu (2006) attribute this difference to the relatively frequent disturbances, whether high intensity, large-scale cyclones that create extensive openings in forest canopies or smaller, more frequent, low intensity disturbances caused by tropical storms and/or cyclone near misses (Pierson et al. 1996; Webb et al. 2011). Forest gaps, large and small, tend

to favor fast-growing, light-loving species (Denslow 1987; Hubbell and Foster 1987).

It is not surprising that a very large proportion of native trees encountered in our forest plots were those classified by Webb and Fa'aumu (2006) as having early successional, disturbance-adapted characteristics. Such species accounted for approximately 20% of the aboveground biomass in native-intact forests and 34–57% of aboveground biomass in *F. moluccana*-removal forest stands and ("Appendix 1"). We suspect that this is the single most important reason why girdling and killing *F. moluccana* is a successful management strategy in forests of American Samoa; once *F. moluccana* is removed, native tree species are poised to exploit available resources and recapture gaps resulting from *F. moluccana* girdling, defoliation, and eventual death. Equally important, biomass and stem densities of non-native species other than *F. moluccana* did not increase throughout the post-removal period; all of the increases were attributable to native trees. Thus, it appears from results that once management activities redirect the successional trajectory by killing the mature *F. moluccana* individuals in the overstory, the native-dominated forest community is capable of regaining dominance. This dynamic stands in stark contrast to results from experimental removal of the non-native, N_2-fixing tree, *Morella faya* from forests of Hawaii Volcanoes National Park, where successful reestablishment and recovery of native forest species following girdling of the non-native, N_2-fixing tree is much less certain given the presence of highly competitive non-native species (Loh and Daehler 2008). It should be noted, however, that *Clidemia hirta*, an acknowledged invasive understory weed in Hawaii and elsewhere (Peters 2001; DeWalt et al. 2004; Baret et al. 2006), was present at relatively high densities (248 individuals ha^{-1}) in some of our *F. moluccana*-removal plots ("Appendix 2"). Although biomass of these individuals was low on average ((23 g $individual^{-1}$; "Appendix 1"), this may represent an incipient invasion into these areas, and should be addressed accordingly by managers.

The high levels of available soil N present immediately following *F. moluccana* removal likely amplified the rapid biomass accumulation of native tree species. Elevated soil N has been associated with *F. moluccana* dominated stands in natural forest settings as well as plantations in Hawaii as well as India (Binkley 1997; Otsamo 2002; Hughes and Denslow 2005). While girdling and killing *F. moluccana* certainly eliminated long-term N inputs from this highly productive N_2-fixing tree, the initial pulse of N resulting from the steady defoliation of *F. moluccana* canopies after girdling created an environment of abundant light and available soil N that likely fueled rapid growth in native tree species and recovery of a closed, native-dominated forest canopy. Tree species that exhibit early successional life strategies are often capable of capitalizing on short-term resource pulses (Reich et al. 1994; Navas et al. 2010). Our results provide strong evidence for this: the relatively large amounts soil inorganic N present immediately following *F. moluccana* removal dramatically declined, approaching low levels exhibited in soils of the native-intact stand in less than 3 years. Such changes coincided with significant increases in native tree species biomass over the same time period. Previous studies addressing disturbances such as deforestation and fire have documented large increases in nutrient availability (Daubenmire 1968; Matson et al. 1987). Where species are able to capitalize on such resource increases, they will likely gain the competitive advantage as succession proceeds (Wilson 1988; Hughes and Vitousek 1993). Previous studies also demonstrate that pioneer tree species exhibit high leaf N contents, high capacities to respond to increased soil N availability, and a high capacity for leaf nitrate assimilation (Aidar et al. 2003). Reich et al. (1994), Lawrence (2001), and Siddique et al. (2010) also document positive growth responses with increased N availability in pioneer tropical tree species.

Our results also indicate that, as with available soil N levels, seedling densities of *F. moluccana* declined immediately following girdling actions. It has been noted that although *F. moluccana* reaches reproductive maturity in as little as 3–6 years and produces copious amounts of seed that are viable in the soil seed bank for months to years (Parrotta 1990), germination and seedling growth is highly constrained by light availability. Seedlings do not tolerate shading and germinate in abundance only where both the overstory canopy and the forest floor are open enough to allow sufficient light penetration (Soerianegara and Lemmens 1994). In *F. moluccana*-invaded areas of Hawaii, light levels as high as 20% of ambient were not sufficient to promote *F. moluccana* seed germination and growth, and no small saplings were present beneath *F. moluccana* dominated forest stands, much

less beneath close-canopy native-dominated forest (Hughes and Denslow 2005). Although we did not measure light availabilities in any of our forest plots on Tutuila Island, we did observe complete canopy closure of the recovering native forest in *F. moluccana*-removal forest stands over the 8-year period of post-removal succession. As such, we strongly suspect that the underlying mechanism constraining *F. moluccana* re-establishment is the rapid recapture of the overstory canopy in these areas—and concomitant forest floor light suppression—by native Samoan tree species exhibiting early successional characteristics (Webb et al. 2011).

It is important to recognize that the *F. moluccana*-invaded forests studied here still contained a substantial component of native species. It is not known whether such native trees were present due to some inherent capacity to persist in the presence of *F. moluccana*, or whether *F. moluccana* populations had not yet attained dominance to the point of excluding a great number of the native tree species. As such, our results regarding the rapid recovery of the native trees species must be regarded as limited to forests where *F. moluccana* is locally common (i.e., >50% of the aboveground biomass) within a matrix of native-dominated forest area. We did not include in our study extensive forests of near monotypic *F. moluccana* dominance where few native species might be present. Such monotypic forests do exist on Tutuila Island, and native forest recovery following *F. moluccana* removal may be severely constrained in these areas due to both a lack of adjacent propagule sources and anticipated rapid seedling recruitment from an abundant and extensive *F. moluccana* seedbed (Lockwood et al. 2005; Simberloff 2009b). In lieu of this, a strategy of active out-planting of fast-growing native tree species coupled with *F. moluccana* seedling control may be required in such areas.

If native Samoan tree species are adapted to small, forest gap forming disturbances and large-scale disturbances such as cyclones as we suspect (Webb et al. 2011), why wouldn't they, rather than *F. moluccana*, regain dominance in forest stands following such disturbances? We surmise that the reasons for this can be found in the growth characteristics of *F. moluccana*. Because this species becomes very tall, very fast (Walters 1971, Parrota 1990), in areas where its seedlings accompany recruitment of native species, *F. moluccana* will likely outpace native seedlings and saplings in the race to the overstory canopy as secondary succession proceeds. Further, since mature *F. moluccana* individuals attain heights well above those exhibited by most of the native Samoan tree species (Whistler 2004), *F. moluccana* will tend to attain and maintain overstory canopy dominance. As long as cyclones capable of defoliating extensive portions of the forest canopy occur at sufficient frequencies, we expect *F. moluccana* populations would persist and expand in the absence of ongoing management practices. As such, removal of mature *F. moluccana* individuals, re-establishment of native Samoan tree species, and exhaustion of the *F. moluccana* seed bank are necessary prior to subsequent large-scale disturbances in order to break the cycle of *F. moluccana* establishment and proliferation.

Overall, efforts to eliminate *F. moluccana* populations from the Tutuila unit of NPSA and adjacent lands meet the attributes that define successful invasive species control programs (Mack et al. 2000). First, significant funding was available to implement and execute *F. moluccana* control across the targeted areas of infestation. To date, NPSA field crews have killed over 6,000 mature trees ≥10 cm at dbh, restoring approximately 1,500 ha of native Samoan forest in the process. Second, widespread public knowledge of, and support for, the control effort has been cultivated through outreach and informational meetings with local village leadership, employment of villagers residing adjacent to areas of infestation, and use of media outlets on a consistent basis. Third, although *F. moluccana* poses daunting management challenges as a very large, fast-growing species that produces copious amounts of seed early on in its lifespan that maintain viability for months to years, it also exhibits characteristics that make it vulnerable to successful control: it is easily killed by girdling or herbicides and its seeds and seedlings are exceedingly shade intolerant. These characteristics, combined with the equally important capacity for rapid growth exhibited by many of the common native Samoan tree species, provide conditions and opportunities for successful, long-term control of *F. moluccana* across broad, forested landscapes of Tutuila Island.

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Appendix 1

See Table 2.

Table 2 Biomass (Mg ha^{-1}) all woody plant species, including vines, encountered in forest plots on Tutuila Island, American Samoa

Species	Native Intact	*F. moluccana* controlled 2001	*F. moluccana* controlled 2003	*F. moluccana* controlled 2006	*F. moluccana* controlled 2007
*Adenanthera pavonina**	0.7 ± 0.7	0.7 ± 0.4	6.5 ± 6.5	0.8 ± 0.8	0.0 ± 0.0
Aglaia samoensis	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Aidia racemosa	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Alphitonia zizyphoides	1.2 ± 1.2	2.5 ± 1.1	1.9 ± 1.7	6.1 ± 4.8	5.8 ± 3.6
Alyxia bracteolosa	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Antidesma sphaerocarpum	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
*Artocarpus altilis**	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.7	1.3 ± 1.0
Astronidium pickeringii	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Baccaurea taitensis	2.3 ± 2.3	0.7 ± 0.7	0.9 ± 0.9	0.0 ± 0.0	0.0 ± 0.0
Barringtonia asiatica	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.9 ± 0.9
Barringtonia samoensis	0.0 ± 0.0	0.0 ± 0.0	1.8 ± 1.8	1.7 ± 0.7	0.0 ± 0.0
Bischofia javanica	9.5 ± 8.8	0.4 ± 0.2	0.2 ± 0.2	2.6 ± 2.2	12.5 ± 5.3
Buchanania merillii	8.5 ± 4.7	6.1 ± 2.7	25.1 ± 17.3	0.0 ± 0.0	0.0 ± 0.0
Calophyllum neo-ebudicum	0.0 ± 0.0	0.0 ± 0.0	11.4 ± 9.1	0.0 ± 0.0	0.0 ± 0.0
Canarium mafoa	0.0 ± 0.0	0.0 ± 0.0	5.0 ± 4.8	0.0 ± 0.0	0.1 ± 0.1
*Cananga odorata**	12.8 ± 5.9	0.7 ± 0.5	1.8 ± 0.8	11.9 ± 4.9	7.1 ± 2.4
Canarium vitiense	30.7 ± 12.8	7.3 ± 3.9	6.1 ± 3.4	4.4 ± 4.2	1.5 ± 1.1
Citronella samoensis	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
*Clidemia hirta**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Cocos nucifera	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	6.3 ± 3.0	0.0 ± 0.0
*Cordia aspera**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Cordyline fruticosa	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Crossostylis biflora	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
*Dioscorea bulbifera**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Diospyros samoensis	0.0 ± 0.0	0.5 ± 0.4	2.8 ± 2.7	0.4 ± 0.4	0.0 ± 0.0
Dysoxylum huntii	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Dysoxylum maota	16.0 ± 7.2	1.4 ± 1.0	0.1 ± 0.1	10.1 ± 5.0	11.2 ± 4.5
Dysoxylum samoense	36.5 ± 25.0	19.9 ± 9.6	5.9 ± 5.6	9.8 ± 5.1	31.7 ± 8.2
Elaeocarpus floridanus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Elaeocarpus ulianus	4.0 ± 3.1	7.3 ± 3.4	1.4 ± 1.1	0.7 ± 0.6	1.2 ± 1.0
Elattostachys falcata	0.0 ± 0.0	1.1 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Epipremnum pinnatum	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.6 ± 0.2	0.2 ± 0.1
Fagraea berteroana	0.0 ± 0.0	0.0 ± 0.0	3.9 ± 2.9	0.0 ± 0.0	0.0 ± 0.0
*Falcataria moluccana**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Faradaya amicorum	0.6 ± 0.2	0.0 ± 0.0	0.3 ± 0.1	0.1 ± 0.1	0.0 ± 0.0

Table 2 continued

Species	Native Intact	*F. moluccana* controlled 2001	*F. moluccana* controlled 2003	*F. moluccana* controlled 2006	*F. moluccana* controlled 2007
Ficus scabra	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	0.5 ± 0.3	0.1 ± 0.0
Ficus tinctoria	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Flacourtia rukam	0.0 ± 0.0	0.7 ± 0.5	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
Freycinetia spp.	0.0 ± 0.0	0.2 ± 0.1	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Garuga floribunda	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Glochidion ramiflorum	0.0 ± 0.0	3.9 ± 3.2	0.6 ± 0.6	0.1 ± 0.1	0.0 ± 0.0
Gynochtodes epiphytica	0.0 ± 0.0	1.1 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Hedycarya denticulata	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Hernandia moerenhoutiana	0.6 ± 0.6	0.4 ± 0.4	2.0 ± 0.9	0.0 ± 0.0	0.0 ± 0.0
Hibiscus tiliaceus	0.0 ± 0.0	9.0 ± 8.1	17.8 ± 8.2	8.3 ± 4.4	3.0 ± 1.7
Hoya australis	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
*Inocarpus fagifer**	15.9 ± 12.0	3.4 ± 2.7	1.5 ± 1.5	0.8 ± 0.6	0.0 ± 0.0
Intsia bijuga	0.0 ± 0.0	0.0 ± 0.0	3.1 ± 3.1	0.0 ± 0.0	0.0 ± 0.0
Macaranga harveyana	0.5 ± 0.5	0.5 ± 0.3	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0
Macaranga stipulosa	6.3 ± 3.4	6.9 ± 2.8	5.2 ± 1.7	8.2 ± 4.9	0.2 ± 0.2
Meryta macrophylla	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
*Mikania micrantha**	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
*Morinda citrifolia**	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.5 ± 0.3	0.0 ± 0.0
Myristica hypargyraea	0.5 ± 0.5	0.0 ± 0.0	1.8 ± 1.5	0.0 ± 0.0	0.0 ± 0.0
Myristica inutilis	24.3 ± 3.0	29.8 ± 1.9	15.7 ± 4.8	15.0 ± 3.3	28.1 ± 6.0
Neonauclea forsteri	5.1 ± 3.8	10.6 ± 3.1	38.1 ± 22.1	32.5 ± 10.9	0.2 ± 0.2
Omalanthus nutans	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Palaquium stehlinii	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Piper graeffei	0.1 ± 0.0	0.2 ± 0.1	0.6 ± 0.2	0.2 ± 0.1	0.1 ± 0.0
Pipturus argenteus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Planchonella garberi	0.0 ± 0.0	3.8 ± 3.8	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Planchonella samoensis	43.5 ± 18.4	0.8 ± 0.7	10.5 ± 7.8	0.1 ± 0.1	0.1 ± 0.0
Polyscias reineckei	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Polyscias samoensis	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Psychotria insularum	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.0
Rhus taitensis	27.6 ± 18.1	24.0 ± 19.3	15.4 ± 6.2	28.8 ± 8.4	21.8 ± 13.4
Sterculia fanaiho	0.5 ± 0.5	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.0 ± 0.0
Syzygium inophylloides	2.6 ± 2.5	18.4 ± 9.3	21.8 ± 17.6	0.0 ± 0.0	0.4 ± 0.4
*Syzygium samarangense**	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Syzygium samoense	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0	0.0 ± 0.0
Terminalia richii	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Trema cannabina	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.4	0.0 ± 0.0
Unknown	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Native species total	221.8 ± 16.8	158.9 ± 14.6	202.0 ± 31.4	138.0 ± 8.2	119.5 ± 13.8
Introduced species total	29.5 ± 9.8	4.8 ± 3.1	9.9 ± 6.6	14.8 ± 4.1	8.4 ± 3.0
Grand total	251.3 ± 16.6	163.8 ± 12.9	211.9 ± 27.7	152.9 ± 10.3	127.9 ± 14.6

Values are mean + one standard. An asterisk (*) identifies a species as a non-native introduction

Appendix 2

See Table 3.

Table 3 Density (individuals ha^{-1}) of stems of all woody plant species, including vines, encountered in forest plots in and adjacent to the National Park of American Samoa, Tutuila unit

Species	Native Intact	*F. moluccana* controlled 2001	*F. moluccana* controlled 2003	*F. moluccana* controlled 2006	*F. moluccana* controlled 2007
*Adenanthera pavonina**	2 ± 2	12 ± 7	86 ± 40	2 ± 2	0 ± 0
Aglaia samoensis	18 ± 18	69 ± 40	79 ± 41	18 ± 18	0 ± 0
Aidia racemosa	18 ± 18	20 ± 17	8 ± 8	0 ± 0	0 ± 0
Alphitonia zizyphoides	2 ± 2	16 ± 9	8 ± 6	10 ± 3	10 ± 6
Alyxia bracteolosa	0 ± 0	79 ± 53	281 ± 281	141 ± 141	22 ± 22
Antidesma sphaerocarpum	16 ± 16	228 ± 102	33 ± 25	16 ± 10	0 ± 0
*Artocarpus altilis**	2 ± 2	0 ± 0	8 ± 8	53 ± 33	91 ± 43
Astronidium pickeringii	0 ± 0	0 ± 0	2 ± 2	0 ± 0	0 ± 0
Baccaurea taitensis	2 ± 2	2 ± 2	2 ± 2	0 ± 0	0 ± 0
Barringtonia asiatica	0 ± 0	0 ± 0	0 ± 0	0 ± 0	427 ± 427
Barringtonia samoensis	0 ± 0	0 ± 0	16 ± 16	96 ± 57	0 ± 0
Bischofia javanica	8 ± 6	4 ± 2	2 ± 2	10 ± 6	49 ± 16
Buchanania merillii	41 ± 27	18 ± 8	86 ± 72	0 ± 0	0 ± 0
Calophyllum neo-ebudicum	18 ± 18	0 ± 0	71 ± 49	0 ± 0	0 ± 0
Canarium mafoa	26 ± 17	0 ± 0	126 ± 67	0 ± 0	32 ± 32
*Cananga odorata**	35 ± 18	6 ± 4	41 ± 23	31 ± 11	81 ± 45
Canarium vitiense	31 ± 10	71 ± 52	45 ± 30	12 ± 10	25 ± 9
Citronella samoensis	8 ± 8	33 ± 33	0 ± 0	0 ± 0	0 ± 0
*Clidemia hirta**	0 ± 0	0 ± 0	0 ± 0	248 ± 162	0 ± 0
Cocos nucifera	0 ± 0	0 ± 0	0 ± 0	22 ± 10	0 ± 0
*Cordia aspera**	0 ± 0	0 ± 0	8 ± 8	0 ± 0	0 ± 0
Cordyline fruticosa	0 ± 0	332 ± 152	169 ± 61	61 ± 52	103 ± 103
Crossostylis biflora	0 ± 0	0 ± 0	43 ± 43	0 ± 0	0 ± 0
*Dioscorea bulbifera**	0 ± 0	0 ± 0	106 ± 71	88 ± 88	1,415 ± 1,415
Diospyros samoensis	26 ± 17	39 ± 17	195 ± 132	20 ± 17	76 ± 38
Dysoxylum huntii	0 ± 0	0 ± 0	8 ± 8	0 ± 0	0 ± 0
Dysoxylum maota	24 ± 8	10 ± 8	2 ± 2	14 ± 5	22 ± 10
Dysoxylum samoense	16 ± 6	14 ± 7	28 ± 23	173 ± 86	37 ± 9
Elaeocarpus floridanus	0 ± 0	8 ± 8	0 ± 0	0 ± 0	10 ± 10
Elaeocarpus ulianus	63 ± 32	20 ± 9	53 ± 31	31 ± 29	29 ± 20
Elattostachys falcata	0 ± 0	2 ± 2	0 ± 0	0 ± 0	0 ± 0
Epipremnum pinnatum	619 ± 161	53 ± 53	521 ± 334	1,533 ± 379	803 ± 212
Fagraea berteroana	0 ± 0	0 ± 0	41 ± 37	0 ± 0	0 ± 0
*Falcataria moluccana**	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Faradaya amicorum	405 ± 191	460 ± 375	399 ± 184	362 ± 243	111 ± 56
Ficus scabra	63 ± 60	140 ± 75	59 ± 40	12 ± 7	140 ± 65
Ficus tinctoria	57 ± 40	238 ± 165	35 ± 35	24 ± 24	341 ± 341
Flacourtia rukam	16 ± 10	59 ± 41	41 ± 26	28 ± 25	0 ± 0
Freycinetia spp.	0 ± 0	485 ± 294	316 ± 160	0 ± 0	0 ± 0

Table 3 continued

Species	Native Intact	*F. moluccana* controlled 2001	*F. moluccana* controlled 2003	*F. moluccana* controlled 2006	*F. moluccana* controlled 2007
Garuga floribunda	0 ± 0	0 ± 0	128 ± 128	0 ± 0	0 ± 0
Glochidion ramiflorum	0 ± 0	31 ± 27	65 ± 41	37 ± 21	0 ± 0
Gynochtodes epiphytica	0 ± 0	497 ± 184	35 ± 35	0 ± 0	0 ± 0
Hedycarya denticulata	26 ± 26	167 ± 88	0 ± 0	0 ± 0	0 ± 0
Hernandia moerenhoutiana	2 ± 2	4 ± 4	37 ± 26	0 ± 0	0 ± 0
Hibiscus tiliaceus	0 ± 0	65 ± 53	635 ± 257	159 ± 76	27 ± 11
Hoya australis	8 ± 8	0 ± 0	71 ± 71	53 ± 53	0 ± 0
*Inocarpus fagifer**	350 ± 294	6 ± 2	2 ± 2	6 ± 4	0 ± 0
Intsia bijuga	0 ± 0	0 ± 0	10 ± 10	0 ± 0	0 ± 0
Macaranga harveyana	55 ± 55	22 ± 19	0 ± 0	4 ± 2	0 ± 0
Macaranga stipulosa	49 ± 29	49 ± 20	147 ± 74	90 ± 71	2 ± 2
Meryta macrophylla	0 ± 0	0 ± 0	26 ± 26	0 ± 0	0 ± 0
*Mikania micrantha**	0 ± 0	88 ± 88	106 ± 106	248 ± 248	1,083 ± 1,025
*Morinda citrifolia**	0 ± 0	0 ± 0	2 ± 2	14 ± 10	0 ± 0
Myristica hypargyraea	2 ± 2	0 ± 0	12 ± 10	0 ± 0	0 ± 0
Myristica inutilis	888 ± 270	929 ± 141	523 ± 120	348 ± 106	1,002 ± 190
Neonauclea forsteri	18 ± 9	22 ± 8	106 ± 54	43 ± 9	2 ± 2
Omalanthus nutans	0 ± 0	10 ± 10	0 ± 0	0 ± 0	0 ± 0
Palaquium stehlinii	0 ± 0	0 ± 0	41 ± 23	0 ± 0	0 ± 0
Pipturus argenteus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	42 ± 42
Piper graeffei	865 ± 453	1,165 ± 456	1,456 ± 397	884 ± 315	1,248 ± 362
Planchonella garberi	8 ± 8	8 ± 8	120 ± 69	0 ± 0	0 ± 0
Planchonella samoensis	654 ± 279	250 ± 123	124 ± 49	84 ± 60	64 ± 28
Polyscias reineckei	0 ± 0	0 ± 0	59 ± 38	8 ± 8	0 ± 0
Polyscias samoensis	0 ± 0	0 ± 0	0 ± 0	8 ± 8	0 ± 0
Psychotria insularum	18 ± 18	2,132 ± 1,396	554 ± 273	106 ± 65	592 ± 237
Rhus taitensis	29 ± 17	65 ± 33	20 ± 7	61 ± 31	69 ± 42
Sterculia fanaiho	37 ± 29	84 ± 55	4 ± 2	43 ± 19	88 ± 36
Syzygium inophylloides	24 ± 21	472 ± 251	43 ± 26	0 ± 0	12 ± 12
*Syzygium samarangense**	94 ± 67	0 ± 0	57 ± 40	0 ± 0	0 ± 0
Syzygium samoense	0 ± 0	0 ± 0	4 ± 4	0 ± 0	0 ± 0
Terminalia richii	0 ± 0	0 ± 0	0 ± 0	24 ± 24	0 ± 0
Trema cannabina	0 ± 0	0 ± 0	0 ± 0	12 ± 12	22 ± 22
Unknown	0 ± 0	24 ± 24	0 ± 0	20 ± 17	0 ± 0
Total introduced	495 ± 344	136 ± 89	462 ± 90	792 ± 335	2,793 ± 2,460
Total native	4,179 ± 1,130	8,378 ± 1,935	6,909 ± 582	4,568 ± 671	5,457 ± 691
Grand total	4,639 ± 1,042	8,504 ± 1,916	7,303 ± 558	5,254 ± 517	8,078 ± 1,782

Values are mean + one standard

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