Tropical Rain Forest Recovery after Cyclone and Human Activity on Savai´i, Samoa

-A field study of tree species composition and distribution

View from the crater in Tafua-Tai taken by Sakura Netterling

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PREFACE

This study was initiated by Henrik Hedenås 2004 based on former studies by Thomas Elmqvist at Umeå University in 1990 and 1992 and Johan Hjerpe and Henrik Hedenås in1996 and 1997. The study was funded by the Swedish International Development Cooperation Agency (Sida) 2004 by authority from Mälardalens högskola and was carried out as a Minor Field Study 2005. The field work was conducted in Samoa during March – May 2005 with the assistance from Chief Moelagi Jackson President of Faasao Savai'i Society and local people in the area of villages Tafua-Tai and Taga.

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ABSTRACT

Keywords: Samoa, disturbance, cyclone, logging, rain forest, species diversity.

This MFS study was conducted in the island of Savai'i of State Samoa, performed as a follow up to a ten years previous study. The aim was to estimate the recovery of forest species diversity following two sequential cyclones that passed over the forest reserve of Tafua-Tai 1990 and 1991. We compared this natural disturbance to a cumulative natural disturbance as an extensive area suffered from a fire one month after the cyclone 'Ofa'. To broaden the work and to include a forestry aspect a comparison of human afflicted disturbance a survey was made in the area near Taga village. Here a substantial area had been clear-felled in the same time interval as the cyclones, and one harvested and logged just five years ago. We performed relative abundance analysis and compared the status of the forests as well as climber and vines ratio between the disturbance regimes. It was found that cumulative disturbance severely affected the area and opened it up to secondary forest species and vines which arrest crown growth. The severest damage was still found in the clear-felled area that during the fifteen years interval has not recovered and was significantly worse in all aspects to the other disturbed areas. One can interpret that the logged and harvested area which was five years old was as good as the cumulative natural disturbance area due to a more selective logging. However, both are still not as diverse and some of the most important mature forest species are missing. Invasive species such as *Funtumia elastica*, a shadow tolerant exotic species and a late introduction, show an alarming dominance in the naturally disturbed area.

SAMMANFATTNING

Nyckelord: Samoa, störning, cyklon, avverkning, regnskog, artrikedom.

Den här MFS studien utfördes på ön Savai'i i Samoa. Den är en uppföljande studie till en långtidsstudie som utfördes senast för 10 år sen (1995). Målsättningen var att uppskatta återhämtningen av den tropiska skogens artdiversitet efter två stora cykloner som passerade Tafua-Tai området 1990 respektive 1991. Vi jämförde den här naturliga störningen med en kumulativ störning som innebar en brand som drabbade delar av det cyclondrabbade området en månad efter cyklonen, "Ofa". Arbetet innefattar också en jämförelse med områden nära byn Taga där omfattande mänsklig störning i form av avverkning och sedemera boskapsskötsel skedde i samma tidsrymd som cyklonerna. Ett område avverkades totalt för 10-15 år sen och ett annat avverkades selektivt för 5 år sen. Vi utförde relativ artrrikedoms analyser och jämförde skogens uppbyggnad och antalet lianer och krypväxter i alla områden. Vi fann att den kumulativa störningen med cykloner och brand påverkade området kraftigt och öppnande upp det för sekundära arter. Den svåraste påverkan fanns i kalhygge området som efter 15 år inte hade återhämtat sig och var signifikant sämre i alla aspekter. Man kan tolka data från den selektiva avverkningen som att den är likvärdig som den kumulativa störningen av två stora cykloner och en brand men den är mycket mer påverkad än den naturliga störningen i det icke brända området. Många viktiga primära skogsarter saknas i dessa områden och diversiteten har inte återhämtat sig efter cykloner samt brand eller i det selektivt avverkade området. En skuggtålig exot, *Funtumia elastica*, har dessutom etablerat sin dominans inom det naturligt störda området.

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BACKGROUND OF SAMOA

The independent State of Samoa, formerly known as Western Samoa, formed 1st January 1962 is a South Pacific group of islands located in Oceania (13°35' S, 172°20' W), south of the equator about 800 km from Tonga and 2400 km northeast from New Zealand, nearly half way to Hawaii. The country land area is a total of 2,944 sq km. Samoa consists of two large islands Upolu and Savai'i (96% of the land area) together with eight smaller islands and uninhabited islets. (CIA -the World Factbook 2007)

The climate is tropical with a mean annual temperature of 26.5 °C, with little variation as the temperatures seldom rise above 29° C or fall below 24° C, with abundant rainfall (Samoan Sensation, NOAA, The Global Historical Climatology Network). There is a slight seasonal variation with rainy season from November to April and a dry season from May to October. Mean rainfall is about 2,900 mm per annum, but due to the rocky interior average annual rainfall varies from 5,000 to 7,000 mm on the southern windward side and 2,500 to 3,000 mm on the leeward side (Samoan Sensation; NOAA, The Global Historical Climatology Network). Humidity is high averaging about 80%. The terrain on the two large islands is a rocky rugged mountain interior with civilization mostly located on the surrounding lowlands of the narrow coastal plain (CIA -the World Factbook 2007). Mostly the landscape is an almost flat coastal plain, gradually passes into a region of gently rolling slopes, these in turn merge with the more strongly sloping (5-15°) foothills, which continue upwards until an upland or plateau. The highest point of Mauga Silisili 1,857 m a s is found on Savai'i (CIA -the World Factbook 2007).

It is estimated that Samoa has been inhabited for over three thousand years. Samoa has a population of 214,265 (2007 est.) with a density of 73 individuals per km^2. The population growth rates are 1.3% (2007 est.) with a fertility rate of 4.21 children born per woman. The population of Samoa consist of mainly the ethnic group Samoans (Polynesians), 92.6%. The languages spoken are Samoan (Polynesian) and English. Government type is a mix of parliamentary democracy and constitutional monarchy. The capital of Samoa is Apia and has an estimated 40 000 inhabitants. The GDP per capita is $ 2,100 (2005). 21.1 % of the land area is arable land and 24.3% are used for permanent crops. Natural resources are considered to be hardwood forests, fish and hydropower. The agricultural products are coconuts, bananas, taro, yams, coffee, and cocoa. Samoa's export commodities are fish, coconut oil and cream, copra, taro, automotive parts, garments and beer. The economy of Samoa has traditionally been dependent on development aid, family remittances from overseas, agriculture and fishing. The country is vulnerable to devastating storms due to its concentration of economy to the coastlands. Tourism is an expanding sector and in 2005 it accounted for 25% of GDP. (CIA -the World Factbook 2007)

CYCLONES

Samoa is located in the South Pacific cyclone belt. Ofa and Val ravaged terrestrial and marine environments in February 1990 respectively December 1991 (ReliefWeb). The cyclone Ofa caused 90% damage to tree crops (UNDRO 90/0301) and the subsequent Val destroyed nearly 90% of the vegetation on the northern side of Savai'i (UNDRO 91/1855) and destroyed 60% of the forests (UNDRO 91/1869). The cyclones had vast economic and public health effects as causes of ecological problems such as devastated coral reefs, marine life reduction, rain forest destruction and a following draught spell leading to prolonged shortage of staple foods (personal communication with natives). Ofa killed 8 people and left 25 000 people homeless, with 50% of the homes destroyed on Savai'i (ReliefWeb). The eye of the cyclone passed

about 60 nautical miles south of the Samoa, bringing the most destructive quadrant of the cyclone over the islands which sustained winds of 260 km/h (UNESCAP 2001). Ofa formed high storm waves causing serious reef damage along the western and northern shores. The cyclone Val was smaller with the eye of the cyclone passing over Savai'i with wind speeds on average of 170 km/h, but the impact of the cyclone was intense and worsened the damage done by Ofa (ReliefWeb, UNDRO 91/1841; The New York Times, 22 December 1991). Cyclone Val raged for approximately four days and hit 90% of the island, causing 13 deaths, leaving 95% homeless on Savai'i and resulting in a huge blow to Samoa's economy. On the 16th of February 2005, the cyclone Olaf, with winds of up to 250 km/h made a close pass of Samoa but luckily did not inflict any large visible damage to the forest or other ecological and economical assets (BBC, 6 February 2005). The impact of the cyclones has been a severe influence on Samoa's fragile ecology and the complex Polynesian culture.

SOIL STRUCTURE

All of Samoan islands are of volcanic oceanic origin and consist of basalt derived from magmatic material normal to the Pacific basin, only Savai'i could be considered volcanically active since in the beginning of the 18th century (between 1905 and 1911) there was a volcanic eruption from Mount Matavan where lava flowed down to the village Salealua (CIA -the World Factbook 2007, Bennett 2003). According to FAO Samoa's soil consist of low fertile volcanic latosols, which contain 7.8 -12.6% titanium oxides (FAO, Land and Water Information, Samoa National Report 2002). The most extensive soil order in Samoa is that derived from recent volcanic ash called Andisols found in the uplands. Inceptisols, together with Oxisols are also found in great areas in Samoa. Significant areas of Mollisols and Entisols are cultivated. Most Samoan soils have a pH between 5.5 and 7.5. The alkaline soils with pH above 7.5 include the coral sands along the coast. Soils of Samoa are generally extremely porous and excessively drained so vegetation may suffer from water shortage if there is no rain a week.

FLORA AND FAUNA

The environment of Samoa with its tropical climate supports a wide range of flora from tropical rain forests to scrublands, marshes, swamps and mangrove. Samoa is predominated by higher plants of which 90% of the 550 flowering plants; 95 plant families about 300 genera, are indigenous or native (Whistler 2002) about 30% are endemic to the archipelago (Whistler 2004). There are about 250 native and naturalized tree species. There is also a threat of invasive "alien" vegetative species which often have negative impact on both the economy and the environment. Invasive species is a threat through the reduction of grazing areas, reduction of crop yield, risk of threat to biodiversity, disruption of water flow, livestock poisoning and the formation of impenetrable thickets. Forest quality is further reduced by the subsequent invasion of highly aggressive non-native trees, not including the 22 tree species that have been naturalized over the past 170 years (Whistler 2004). Samoa has a limited land fauna of larger animals where flying foxes, land and sea birds, skinks and geckos play an important role to the forest community (Hjerpe et al. 2001). There is of course other fauna such as various insects and land crustaceans inhabiting the land of Samoa.

Flying foxes are the major pollinators and seed dispersers in these forests and both flying foxes and resident birds were affected by starvation as seed and fruit production was low in the cyclone devastated areas (Elmqvist 1994; Hjerpe et al. 2001). Since the cyclones 1990 and 1991 there has been increased effort within Samoa to rehabilitate and conserve the endangered flying fox population of Samoa and efforts to conserve endangered birds such as Tooth Billed pigeons and others. The avian community is also of high importance to the seed dispersal of the Samoan flora (Elmqvist 1994; Hjerpe et al. 2001). Samoa supports a total of

49 bird species of which 11 are endemic species and 7 are threatened by extinction (Government of Samoa 1998). Tooth Billed pigeon is threatened by deforestation for agriculture particularly combined with the severe effects of cyclones, e.g. in 1990 and 1991, when canopy cover was reduced from 100% to 27% (Elmqvist *et* al. 1994). Extractions of timber lead to further habitat losses due to the forest areas being converted to agriculture (Elmqvist *et* al. 1994). Hunting is also a further threat and although hunting is now illegal, birds are still shot in the seasonal harvest of unprotected pigeon species. Poaching was and is a towering problem to solve as food availability was scarce after the cyclones and Flying foxes and pigeons are thought of as delicacies and therefore are still hunted (personal communication; Government of Samoa 1998). Other current environmental issue is excessive fishing (Government of Samoa 1998).

SAMOAN FORESTS

In a global perspective the tropical forest of the world is now shrinking with about 5% each decade. A gross deforestation of 2.8 million hectares a year is estimated in Asia alone. FAO Global Forest Resources Assessment 2005 data shows that primary forests are being replaced by less diverse plantations and secondary forests (FAO "Global Forest Resources Assessment 2005" 2006). Samoa consists of 100% tropical rain forest with a high degree of endemism making it one of the biodiversity hotspots for conservation priorities (Myers *et* al. 2000). About 171,000 hectares or 60.4% of the land area of Samoa is forested (FAO "State of the World's Forests" 2007). Historically the rate of deforestation is high in Samoa and of great concern to the government. In 2000 37.2% of the land area was covered by closed forests canopy compared to 47% in 1992, directly after the two cyclones and 74% in1954 prior to the extensive timber-export-times between 1974 and 1987 (FAO "State of the World's Forests" 2001; Whistler 2002; Government of Samoa "Sustainable forest management programmes in Samoa" 2002). In contrast to this, according to FAO State of the World's Forests (2007), between 1990 and 2000, Samoa gained an average of 4,000 hectares of forest per year. This amounts to an average annual reforestation rate of 2.8% (FAO "State of the World's Forests" 2007). Between 2000 and 2005, the rate of forest change decreased to 0% per annum, all data conceived by remote sensing (FAO "State of the World's Forests" 2007, 2001, and 1999). In total, between 1995 and 2005, Samoa gained 31.5% of its forest cover, or around 41,000 hectares. However 32,000 of those hectares are forest plantations making it 78% of the gained forest during the 1990-2005 intervals (FAO "State of the World's Forests" 2007, 2001, and 1999). Samoa in 2005 consists of 171,000 hectares of primary forest in total with 64.3% modified natural forest (110,000 hectares), 17.0% semi-natural forests (29,000 hectares) and 18,7% (32,000 hectares) forest plantations (FAO "State of the World's Forests" 2007, 2001, and 1999). Ownership of forestland 2000 was 98.2 % publically owned and 1.8% privately owned. Still over 70% of the land in Western Samoa is held in customary ownership (FAO "Asia-Pacific Forestry Sector Outlook Study: Commentary on Forest Policy in the Asia-Pacific Region" 1997). Nevertheless, the remaining lowland forest from sea level to 600 m a s has been severely fragmented and the forest has mostly been converted to agricultural land. About 77% of the total land area of land holdings is under some form of cultivation. The remaining 23% comprises land under fallow (3%), bush (3%) or under non-agricultural use (17%). Thus any forest policy must be aware of this intricate political system, in which families strive for status and power, making a flexible customary land-tenure system mostly inflexible and less controllable by intricate country laws.

Preceding 1992 the rain forests of Samoa were threatened by extensive logging operation by foreign operation contractors and most of the lowland forest and foothill forest on Savai'i and Upolu have been highly modified (FAO "Sustainable Production, Intensification and Diversification of Agriculture, Forestry and Fisheries in Small Island Developing States"

1999). In 1993 the government banned export of logged unprocessed timber and banned all logging operations on the island of Upolu. In 1994 the government had approved some documents of legislation to improve the status of the forest management; those were the National Forest Policy 1995, Watershed Protection and Management Regulations 1992 and National Environment and Management Strategies (NEMS) 1993. In the same time period drafts on Code of Logging Practice (COLP) and the Reduced Impact Logging Guidelines (RIL) were made but have not yet been agreed on (FAO "Asia and the Pacific National Forestry Programmes: Update 34" 2000; Government of Samoa "Sustainable forest management programmes in Samoa" 2002). By these documents one constraint to logging licence was made; that no tree less than 30 cm dbh were allowed to be cut (Government of Samoa "What every potential investor needs to know" 2000). Still between 1977 and 1992 47% of the merchantable forest of Savaii was cleared at an average rate of 987 hectares per year. Though counted from 1978 to 1990 approximately 20% of the deforestation on Samoa was due to logging operation, but most 97% of logging was concentrated to the island of Savai'i (Government of Samoa "Sustainable forest management programmes in Samoa" 2002). At present time logging is still undergone in Savai'i. Between years of 2005-2006 the industrial round wood production produced 61,000 cubic meter and the consumption was 55,000 cubic meter. Sawn wood production equalled consumption and was a total of 21,000 cubic meters (FAO "State of the World's Forests" 2007). Export of 824 cubic meters sawn wood and veneer was recorded for 2002 (FAO, country profiles, Samoa)

Now the Tafua-tai village community forest is threatened by the city expansion of Salelologa. An industrial area is planned in the otherwise intact lowland forest area. Especially lowland rain forest is still highly threatened by forest degradation and by modern techniques the highland forest is becoming more accessible, therefore the threat shall not be underestimated due to the positive numbers from the Global Forest Resources Assessment 2005 from FAO. Deforestation is the most immediate environmental challenge in Samoa, arising chiefly from an expansion of agriculture (FAO "Asia-Pacific Forestry Sector Outlook Study: Commentary on Forest Policy in the Asia-Pacific Region" 1997; FAO "Proceedings of the Training Workshop on Forest Product Statistics" 2002). "Some concern has been expressed that the current level of wood production in Samoa, Solomon Islands and Tonga may not be sustainable" (FAO "Particular forestry issues and activities of interest to small island developing states" 1999). Unfortunately, it is the loss of non-timber forest products that is the greatest threat to the people of Samoa. In addition cooperative efforts that are necessary for local forest conservation are not favoured by the competitive aspect of the local forest policy system managed by customary ownership. (FAO Forestry Paper 140, Global Forest Resources Assessment 2000) (FAO "Global Forest Resources Assessment 2005" 2006; FAO "Asia-Pacific Forestry Sector Outlook Study: Commentary on Forest Policy in the Asia-Pacific Region" 1997).

INTRODUCTION

Earlier, tropical rain forests were considered as pristine areas untouched by large-scale disturbances and by man (Richards 1964). However, the importance of both large scale and small scale natural disturbances are recognised as fundamental for the development of structure, function and species diversity of rain forest ecosystems (Attiwill 1994; Molino & Sabatier 2001). There is also an increasing understanding that man caused disturbances also have affected the structure of tropical rain forests (Lugo 1995; Bayliss-Smith *et* al. 2003). However, today, in a global perspective the tropical forest of the world is now shrinking rapidly (FAO "State of the World's Forests" 2001), changing the prerequisites for forest diversity (Curran *et* al. 1999; Ghazoul & Mc Leish 2001; Elmqvist *et* al. 1994). Our knowledge of the effects of natural and anthropogenic disturbances on the diversity and regeneration of tropical rain forests especially in an island setting is still limited. This study was performed on the south coast of Savai'i, Samoa. Samoa is part of the Micronesia/Polynesia belt of biodiversity hot-spots for high conservational priorities (Myers *et* al. 2000). Any impact on this endemic rich island and its peers are a great threat to the global diversity and impact analysis of different disturbances are urgently needed. On a small island like Samoa any changes could have devastating results due to its small size and immigration limits. Samoa is in the middle of the cyclone belt, creating large natural disturbances, as well as a growing degree of human disturbances making the future of the Samoan rain forest an ideal case to study and learn from. Thus, Samoa gives a unique opportunity to study the rain forest recovery after different disturbances, in a relatively short distance from each other. There has been one study, in 1990-1991 that compared the tree species composition and diversity, following two severe cyclones in one area, and fire and cyclones in a nearby area, with the status of the forest prior to the disturbances (Elmqvist *et* al. 1994). Five years later the area was reinvestigated and the post cyclone tree establishment and mortality were monitored (Hjerpe *et* al. 2001). Studies have also been done regarding the importance of remnant trees for the recovery process (Elmqvist *et* al. 2001) and the importance of vertebrates, as seed vectors (Banack 1998).

DISTURBANCE VARIATION

Chazdon (2003) argue that the tropical forest must be seen through a model of flux and dynamism rather than a notion of climax and stability. Connell (1978) formed "the intermediate disturbance hypothesis" which states that a primary forest uphold an ongoing matrix of sequential succession under a less continuous mature forest cover ruled by moderate disturbance. This promotes rapid recruitment through seed dispersal. This consecutively ongoing succession impede interspecific competition exclusion as gaps form due to different low impact disturbances such as branch or tree fall or other subcanopy openings, as well as larger impact disturbances from wind-throw to cyclones or hurricanes or other major natural disturbances, which gives a pattern of diverse positive light conditions hoisting species richness by hindering domination from a few primary species (Connell 1978; Molino & Sabatier 2001). Hubbell *et* al. (1999) point out that this dynamic tree-by-tree replacement is fundamental to understanding tropical forest diversity. Sheil (2001) validates the model of increased species richness by disturbance but accentuate caution in generalizing too much as it is an oversimplified theory (Sheil & Burslem 2003). Sheil (2001) also suggest that stem-number and species-number correlation appears to reflect shared underlying successional processes rather than any other cause-effect relationship. Sheil (2001) found that Eggeling's series which Connell based "the intermediate disturbance hypothesis" on showed a consistency with successional progression. The guild classifications reveal increasing shade-tolerance across the series and increasing heights of canopy species. Stem numbers increase through tree colonisation until canopy space is filled and decreases as larger trees subsume

ever increasing proportions of the limited space (Sheil 2001). Sheil (2001) nonetheless finds it clear that abundance distribution have profound influence on net richness. Species co-existence occurs only when the periods of species persistence overlap. Sheil (2001) conclude that Eggeling-Connell's view implies that patterns of richness are short-lived or disturbance dependent. Molino & Sabatier (2001) edict that the recruitment limitation hypothesis do not preclude disturbance regimes as causes of variation in species richness and state that the intermediate disturbance hypothesis is a valid explanation for high species diversity in tropical forests. Vandermeer *et* al. (2000) states that the primary source of disturbance in the form of tree-fall gaps play an important role of maintenance of high diversity.

Subsequent to disturbance new tree stems enters in the form of small saplings, new seedlings, previously established seedlings, newly germinated seeds from seed bank and from newly arrived seeds (Vandermeer 1996). Connell (1978) suggest that disturbance increases the number of species in a community and Hubbell *et* al. (1999) propose that tropical rain forest species do not have enough time to competitively exclude one another between disturbance events. Denslow (1987) and others suggest another disturbance related hypothesis of "Gap phase dynamics" that maintain species richness and hinder competitive exclusion. Vandermeer (1996) stress the importance of large storms creating a "super gap theory" for diversity within high tree species communities. Vandermeer (1996) draws a connection to the even-aged monocultures self-thinning process, where biomass and density increase to a point where individuals start to die, the so called 3/2 thinning law used in silviculture. In the extreme of this notion biomass can in a site be so low that competition ceases to exist. He assumes that if competition is unrelated to species identity the "neutral competition hypothesis" can be used to estimate population size by relating to disturbance frequency and intensity. Vandermeer (1996) relates population size to number of species and thus to diversity. He presents a scenario where frequent strong disturbances gives a situation where biomass is dramatically reduced so repeatedly that recruitment will never have a chance to build up and self-thinning will not occur. Another example with frequent but weak disturbances also gives a low biomass and diversity in a similar manner but with a higher density/diversity over-all. If the frequent weak disturbances hit a species rich community Vandermeer (1996) presume that the disturbance does not destroy the established high biomass and high density/diversity community. In a situation of frequent strong disturbances Vandermeer assumes that biomass and diversity will be driven low. On the other hand the infrequent occurrence of strong disturbances allows density to build up, through subsequent recruitment, resulting in thinning before disturbance occurs again. Density will be maximal if the time between disturbances allows recruitment to run its course if it happens before thinning proceeds too far. Most important is that Vandermeer (1996) treat disturbance as a dynamic renewal process where competition is neutral. However, there are things to consider about these simplified theories such as if some individuals have some advantage over others in increasing their biomass competition it will provoke thinning more rapidly. The existence of pioneer trees introduces complications to the above picture, as they are not competitively equivalent to other species. They quickly invade disturbed areas, grow very rapidly and are extremely intolerant to shade. Due to this, pioneer tree species may not fit in this framework.

According to Chazdon (2003) strong wind forces such as cyclones and hurricanes generate secondary succession. Disturbance affects forest vegetation by creating spatial heterogeneity to varying degrees. In the model for species richness according to the gap phase theory we have a spatial mosaic of species where the pattern is constantly changing due to random disturbances (Tuner *et* al. 1998). The creation of a spatial mosaic is also prominent following mechanized logging, hurricanes and fires that create patches with some to non residual vegetation (Groove *et* al. 2000; Ginsberg 1998). Tuner *et* al. (1998) stress the importance of

presence or absence of residual vegetation for forest recovery, differentiating primary succession from secondary by the absence respectively the presence of residuals (Chazdon, 2003). Both del Moral & Bliss (1993) and Chazdon (2003) stress that the abundance of residuals could also be used as a measure of disturbance intensity. The impact of cyclonic storms as a natural force probably drives the species composition dynamics of Samoa. In addition to these naturally occurring disturbances, there are plenty of anthropogenic disturbances such as local consumption, shifting cultivation and to a lesser degree industrial logging activities. Thus, the effect of disturbance by natural forces is also dependent on land-use history. According to T.C. Whitmore (1999) stable primeval tropical rain forest in steady-state equilibrium is a myth. Disturbances of varying degree occur on several time-scales building up the dynamic matrix of species that characterizes the tropical forest system. All tropical forest would according to this be in various states of recovery. 60% of the world forest was classified as degraded forest, including secondary forest, degraded primary forest and degraded forest land (ITTO 2002).

First human impact on forest dates back to when humans started using fire. Barro Colorado Island is still recovering from human impact occurring over 300 years ago as proved by the establishment of emergent long-lived pioneer species and the fact that pioneer species and light demanding species are declining with a trend that is consistent with an old secondary forest (Sheil & Burslem 2003). This shows that anthropogenic disturbance can have effects on species composition and forest structure and thereby altering the landscape patterns in forests subjected to natural disturbances. Disturbances and recovery processes overlap spatially and temporarily in a forest stand where tree-falls and cyclones and other natural disturbance combined with anthropogenic disturbance create a complex mosaic as showed in the Luquillo Experimental Forest in Eastern Puerto Rico (Thompson *et* al. 2002).

TREE SPECIES COMPOSITION IN RELATION TO RESILIENCE AND RECOVERY

The responses of individual species to detrimental effects of disturbances are shown to be related to growth requirements of the species and a reflection of the site's history of recovery after disturbance. Sprouting by residual vegetation has been shown to play a significant role of re-establishing the stem density and richness after disturbances (Chazdon 2003; Uhl *et* al. 1988). Many species in wet and dry tropical forest have the capacity to resprout after severe damage. However in successional older stands regrowth by sprouting is of less importance (Chazdon 2003). Extensive resprouting endorses regeneration of species composition equal to the pre-disturbed mature forest (Vandermeer *et* al. 1995, 2000). According to Uhl *et* al. (1981) resprouting by root sprouts or stem coppice after cutting is a common regeneration mode in Venezuela. However, burning after cutting killed sprouts and reduced the seed bank. Kemmesheidt (1998) saw that over 59% of the regrowth originated from sprouts in slash-and-burn cultivations in Paraguay, and Murphy & Lugo (1986) found that resprouting dominated regrowth in a cut and cleared dry forest of Central America. Bellingham *et* al. (1995, 2000) also show that for a Jamaican forest resprouting was the mechanism leading to rapid recovery of species composition. Re-leafing of surviving residual trees and establishment of early successional species are the first steps of recovery, and was found to happen in following the years after the hurricane disturbance in Nicaragua (Mascaro *et* al. 2005). Residual vegetation promotes a rapid increase of biomass and species richness and tree density but not always a return to the pre-disturbance species composition (Guariguata & Ostertag 2001). Scatena *et* al. (1996) also saw that the biomass reached 86% of the pre-hurricane value. Re-leafing of residual trees is the fast action of restoring biomass, but there is a high mortality of residual trees by stress and damage in the standing population to account for a long period after disturbance affecting the tree species composition consequently (Guariguata & Ostertag 2001).

REGROWTH REQUIREMENTS

Dupuy & Chazdon (1998) states that seeds stored in the soil influence the course of regeneration and succession as an important source of new recruits following disturbance and that in mature primary forest seed rain and seed bank contribute equally. However, Dalling & Hubbell (2002) and Arriaga (2000) found early pioneer seedling community in large gap-formations of a secondary forest to reflect the soil seed bank composition. This could be explained by the findings of Saulei & Swaine (1988) that the composition and abundance of seeds in seed bank reflect the feature of neighbouring vegetation and the site history. Proximity of remnant intact forest patches promotes a more rapid recovery of species composition in disturbed areas depending on improved seed dispersal (Chazdon 2003). Slow recovery of species composition in secondary forest is often attributed to inadequate dispersal of late-successional species (Chazdon 2003; Whitmore 1989). Therefore, we can conclude which particular species that will colonize a site will depend first on soil seed bank composition and the vicinity of peripheral remnant species as sources of seed rain. Abundance and composition of seed bank depends on land-use history, landscape and floristic composition (Dupuy & Chazdon 1998). Regrowth in logging gaps occurs primarily from seeds and seedlings present at the time of felling (Uhl & Jordan 1984). Logging in its extreme has a negative effect on the seed bank resource when top soil is removed causing a lack of on-site propagules and as a consequence recovery is coupled to timing of forest seed dispersal which can strongly affect recovery rate (Guariguata & Dupuy 1997). As land-use intensity increases Guariguata & Ostertag (2001) stress that the importance of seedling recruitment from adjacent primary forest increases and seed bank relevance decreases since depletion of tree species in the seed bank most strongly impacts late successional species. Dupuy & Chazdon (1998) and Zimmerman *et* al. (1995) found that seed bank density differed significantly with land-use. They found that second growth after abandoned pastures had the highest density though consisting mostly of herbaceous seeds as trees species accounted for less than 5% of total seed abundance and forbs-herbs, shrub and vines represented more than 75% of both species richness and abundance in total. Those tree species found were of early successional species, with infrequent occurrences of late successional species in the seed bank can be attributed to the predominantly quick-germinating nature of pioneer seeds (Dupuy & Chazdon 1998). Dupuy & Chazdon (1998) found old-growth stands differed from abandoned pastures in that old growth stands had a low density but a homogenous species composition with higher amounts of tree species in the seed bank. Though their results did not indicate a significant variance to land-use related to species richness. The composition of the soil seed bank showed a closer similarity between selectively logged forest stand and old growth stands than to abandoned pasture second-growth stands (Dupuy & Chazdon 1998). They also found higher dissimilarities within selectively logged forest related to intensity. A major limitation to tree recruitment is seed dispersal especially following anthropogenic disturbance (Hubbell *et* al. 1999; Chazdon 2003). Dupuy & Chazdon (1998) found the soil seed bank to be an unlikely source for recruiting late successional tropical tree species. In addition, if seeds are to germinate other factors will come into play such as soil requirements, fertility, drainage, compaction, amount of incident of light and other abiotic resources affecting the microclimate (Chazdon 2003).

ASPECT OF THE DISTRIBUTION OF PIONEER TREES VERSUS SHADE TOLERANT CLIMAX SPECIES BEFORE AND AFTER THE DIFFERENT DISTURBANCES

Molino & Sabatier (2001) assert that Barro Colorado Island suffering from frequent long-term disturbances correspond to the decrease in species richness has locally led to a shift to a higher level of heliophilic species dominance in Barro Colorado Island. This paucity is suggested by Molino & Sabatier (2001) to be more inflicted by recruitment limitation as

found by Hubbell *et* al. (1999) than normally in a more species diverse forest with higher amount shade-loving species. Hubbell *et* al. (1999) promotes that gap formation enlarge available niches that will not necessarily be filled by the most adapted species. Instead the most abundant species that are in the right place at the right time act as recruits, indicating that dispersal limitation outweigh the intermediate disturbance hypothesis. Molino & Sabatier (2001) claim that pioneer occurrence and density should record the recent history of canopy gap tree-fall openings and that the percentage heliophilic stems more precisely reflects the continuum of light impermeability over mid and late successional low disturbance levels. Species composition is postulated to relate to the proportion of functional groups (Molino & Sabatier 2001). Molino & Sabatier (2001) postulate that species richness gave a humpbacked curve in relationship to percentage heliophilic and percentage pioneer stems as an indirect measurement to canopy gap openings increasing light permeability disturbance in line with the intermediate disturbance hypothesis. Vandermeer *et* al. (2000) found hurricane disturbance to differ from simple tree-fall disturbance. Vandermeer *et* al. (2000) using data sets from Hurricane Joan severed area at the Caribbean coast of Nicaragua concluded that pioneer species are limited in large disturbances and do not suppress other species unlike smaller disturbance patterns of succession.

Kitajima *et* al. (2005) shows that light utilization characteristics of crowns of tall mature trees in a tropical forest vary among species in relation to differences in their architecture and leaf arrangement patterns. Vertical distribution of leaves is greater than that found of herbaceous communities and can consequently support a wider range of morphologies e.g. trees, treelets, shrubs and vines and epiphytes (Kitajima *et* al. 2005). Many pioneer trees exhibit orthotropic (vertically inclined) shoots that successively produce leaves in spiral or dessucate phyllotaxy and such structures exhibit a clear gradient of self shading (Kitajima *et* al. 2005). Many late successional tree species have plagiotropic (horizontally inclined) shoots where the individual leaf is more subjected to among-branch shading (Kitajima *et* al. 2005). For light extinction the inclination of the terminal shoot seems to be more important than individual leaf inclination. It was found that later successional species exhibited greater total light extinction than early successional species and Kitajima *et* al. (2005) postulate that this could be an adaptive strategy to extract light resources and cast shade upon subdominant neighbours. They state that the successional stand of 15-20 years old do not show the heterogeneity of canopy structure shown in a late-successional forest of 75-100 years old.

ANTHROPOGENIC INFLUENCES ON FOREST DIVERSITY AND RECOVERY

Anthropogenic disturbances corresponding to commercial logging actions influence the severity of the disturbance in many ways as well as the rate and nature of the recovery processes in a tropical forest. Human impact can coincide with either primary succession or secondary succession such as landslides, volcanic eruptions, annual flooding depending on the degree of soil degradation and the impact to remnant vegetation (Chazdon 2003). In comparison human activity can be divided into degree of impact from low non-commercial normal native out-take to high impact large-scale harvesting for commercially valuable trees. Rates of recovery shown from research on abandoned farmland stress the importance of soil nutritional state for speed of recovery. Abiotic conditions of course determine the degree of disturbance and land-use intensity a forest can recover from (Swaine & Hall 1983). Chazdon (2003) proclaim that virtually all studies of post-agricultural recovery of tropical forest indicate that species composition transition to an old growth forest stand composition is a slower process than recovery of forest structure, soil nutrient stock or species richness. High nitrogen concentration in litterfall reflects domination of fast growing early successional species (Whitmore 1991; Ingle 2003). Skid-trails create highly patchy patterns of soil damage by compaction and light availability. Skid-trail scraping of ground has been found to provide

a seedbed for pioneers (Holdsworth & Uhl 1997). Guariguata & Dupuy (1997) and Jackson *et* al. (2002) found that top soil removal and soil compaction by logging tracks substantially retarded forest recovery. Guariguata & Dupuy (1997) observed that substrate compaction were evident after more than a decade after abandonment. This influences the microhabitat, impede root growth and restrict plant nutrient availability. Logging severely reduced organic matter due to top soil removal and sequential erosion of material with bleaching of nutrients in the soil (Guariguata & Dupuy 1997). At road edges, up-turned topsoil may facilitate establishment of small-seeded, light demanding tree species (Guariguata & Dupuy 1997). An increase of stem density in the logging-road edge of both small and large tree individuals was observed by Guariguata & Dupuy (1997). In addition, volcanic islands also suffer from erosion. Thus, through effects on species composition and forest structure, anthropogenic disturbance can determine landscape patterns sequentially to damage from natural disturbance regimes (Chazdon 2003). Therefore land-use history is important not to forget when considering events of disturbance. Boucher *et* al. (2001) compared post agricultural land to post-hurricane sites and found post-hurricane forest to be more similar to pre-hurricane forest than post-agricultural to pre-agricultural forests. Species of high importance were not found in post-agricultural sites (Boucher *et* al. 2001). Further, cattle grazing can be another important factor in selecting woody species in early phases of regeneration and impeding tree re-growth (Gillespie *et* al. 2000).

FIRE AS A DISTURBANCE REGIME

Fires that follow cyclones in tropical monsoon forest can have devastating effects (Bowman *et* al. 1999). Burned forests are often adjacent to actively used land that is maintained by fire. Holdsworth and Uhl (1997) consider virgin rain forest to be generally immune to fire in the Amazon but they found that with a rise of human impact to the forest the fire susceptibility rose. Holdsworth and Uhl (1997) show that a higher frequency of fire occurrences is due to the fact that burned sites are more prone to burn again. As selective logging has become an important land-use regime in the region, extracting 4-8 trees per ha reduces the canopy cover to about half and results in a patch formation. Large gaps are created that is more sensitive to fires, where only 5-6 rainless days during the dry season are enough to make the litter prone to ignite and Holdsworth and Uhl (1997) state that this phenomenon is not unique to the Amazon. Nykvist (1996) found that above ground biomass only recovered to 24% of previous forest biomass and that pioneer species *Macaranga* dominated the site after a severe fire in South-west Sabah, Borneo. He also found few primary species that were able to establish themselves by seed dispersal from adjacent undamaged area as they need a dispersal vector and often consist of rare species with few individuals that are more distantly spread. Dupuy & Chazdon (1998) saw that the annual and seasonal variation in seed production influenced the abundance of seeds deposited. Invading grasses and weedy vines can equal to combustible fuel when a dry spell hits the damaged forest stand (Uhl *et* al. 1981) and recurrent fires have the potential to totally eradicate trees from damaged land (Cochrane & Schulze 1999). Recovery often occurred through expansion of established forest patches. It shall be noted that a post-agricultural recovery period is a much longer process of succession than in a natural disturbance affected site (Chazdon 2003). Fire reduces the soil seed bank and if of a high intensity it will also limit sprouting (Uhl *et* al. 1981). Fire releases nitrogen resources, creating an environment more favouring fast growing species such as vines, shrubs and light loving pioneers (Holdsworth & Uhl 1997; Cochrane & Shulze 1990; Gerwing 2002).

Holdsworth & Uhl (1997) and Cochrane & Shulze (1990) press the need for careful planning to reduce gap size in selective logging to prevent fire prone conditions. Among others Holdsworth & Uhl (1997) suggest low-impact logging techniques such as pre-logging vine-cutting, skid-trail planning and directional felling as ways to reduce canopy loss. A similar

logging plan was tested by Forshed *et* al. (2006) with favourable results leaving a healthier residual stand. Holdsworth & Uhl (1997) found that 44% of 1010 trees larger than 10 cm in diameter at breast height died during the 1.5 yr period following the burn which they compared to the 3% that died in the unburned area during the same period. Considering only the trees actually touched by fire this figure rose to 55% that died after the fire. Holdsworth & Uhl (1997) drew the conclusion that the thin bark of tropical trees in the region makes them more vulnerable to fire. If more severely damaged where the fire caused deep scars or split or peeling of bark the mortality rose to 84%. Holdsworth & Uhl (1997) found that after four years mortality caused by fire was an issue, and the eventual fall of these trees still furthered increased gap formations, leaving the still standing trees more susceptible to wind-throw causing further alterations of the forest structure. Pioneer density following fire was at least 60% greater than recorded before the fire. Holdsworth & Uhl (1997) found the recruits of timber species were lowered by 80% due to the fire compared to unburned area. Unburned area showed only a 10% reduction in the same time interval. Sprouting was the most frequently used method to re-establish within primary forest species but as Holdsworth & Uhl (1997) point out those individual's timber value is often low. Holdsworth & Uhl (1997) found that the trajectory of forest regeneration shifted towards pioneer species due to the fire incident.

LIANAS AND INVASIVE SPECIES

Normally we think of lianas as a cause of domino effect in logging operations by dragging not only the cut downed tree but also the entangled ones. However cutting of lianas before logging also reduced liana proliferation in post-logging gaps (Gerwing 2002). Prolific species such as shrubs and vines are common in damaged areas as a cause of reduced shading and can be of hinder to the vertical growth of the forest by building up a matrix of vines covering all living and non-living trees as a heavy carpet (Schnitzer *et* al. 2000; Gerwing 2002; Forshed *et* al. 2006). Schnitzer *et* al. (2005) states that lianas and vines compose a severe competition for below ground resources particularly in low nutrient soils, affecting sapling above ground biomass and increasing mortality of pioneer species. Chazdon (2003) found signs that repeated cutting of regrowth prior to abandonment were of advantage to vegetative re-sprouting species as shrubs and vines. Not only lianas and vines can have negative impact on forest recovery since the damage leads to new successional ways where invasive non-native species can have an influence on forest composition. Seed rain from peripheral vegetation may favour species that did not originally occur on cleared sites (Chazdon 2003). Measurements of forest recovery can also track changes in economic value, by changes of distribution of various commercial and anthropologically valuable species (Chazdon 2003).

ANTHROPOGENIC VS. NATURAL

Differences in forest composition across Kolombangara, Solomon Island were according to Chazdon (2003) a reflection of different anthropogenic disturbances linked to settlement patterns rather than to differential cyclone impacts. Zimmerman *et* al (1995) found that legacies of human land-use history were more long-lasting than hurricane impacts at least in Puerto Rico. As human activity intensifies in an area the fauna is also most likely to be altered both in population size and in the actual species inhabiting the environment.

In slash and burn regimes early establishment of pioneers, either short or long-lived, is critical for the speed of recovery as they function as nutrient and carbon sinks that drive the process of succession forward (Brown & Lugo 1990). Post-agricultural anthropological recovery differs remarkably from natural disturbance recovery by a dominance of pioneer species in the initial phase in contrast to the dominance of residual vegetation as by hurricane or cyclone disturbances according to Burslem's and Whitmore's studies in the neotropics. The course of

succession through initial establishment of pioneers is a slower process than recovery by residual vegetation recruitment dominance (Chazdon 2003). Distance to adjacent old-growth forest is significant in all cases suggesting the importance of dispersal limitation. Interregional differences of rates of forest regrowth were explained by differences in soil fertility whereas intraregional variation depends on land-use type (Chazdon 2003). Logging disturbance vary widely due to their different impact dependent on the regime of logging conducted (Chazdon 2003). The base model for sustainable forest management presented by Harthorn (1995) is a low intensity, polycyclic, selective logging in concept to mimic canopy gap formation in contrast to clear cutting which afflict secondary succession to the same degree as landslides or post agricultural recovery situations. Cannon *et* al. (1998) proposed that reduction in dominance of commercial species following selective logging lead to an increased number of species among the individuals of small-tree recruits, mitigating effects of reduced density on species-area relations. Tree diversity may not decrease due to selective logging shown by Steege *et* al. (2002) in Central Guyana where logging of one species for 75 years did not change the species diversity in the area researched or the rank abundance of the investigated species. However the commercially attractive species density has declined due to low population growth and small numbers of seed trees. Density may not be a good factor to research actual impact of a disturbance. Density of stems and species richness of recruits after disturbance did not differ between logged forest and unlogged forest investigated by Chazdon (2003) and Molino & Sabatier (2001). We therefore can conclude that the most significant factor for recovery is the tree species composition.

OBJECTIVE

The long term goal is to help us attain knowledge of forest disturbance, a knowledge that can further sustainable forestry. Giving guidelines for how the valuable lowland forest of Samoa could be managed in an optimal way with a focus on high biodiversity of native species with not so severe disturbances to the ecosystem keeping with traditional local use. Thus, the overall objective of this study is to increase the understanding of island tropical rain forest resistance and resilience in relation to different disturbance regimes, i.e. natural disturbance (two severe cyclones since 1990), cumulative disturbance (two severe cyclones and one fire since 1990), harvesting five years ago and harvesting ten to fifteen years ago. More specific, the aim of the study is to evaluate if the (1) tree species diversity (2) number of tree individuals per site (i.e. abundance) are affected by fire and logging, and (3) if the regeneration differ between the forests subjected to different disturbance regimes.

MATERIALS AND METHODS

STUDY SITES

The study was conducted in an rain forest preserve with low impact of human activity adjacent to Tafua Tai on the Tafua peninsula (13°50'S, 172°20'W) and an area with high impact of human activity adjacent to the village of Taga (13°47'S, 172°29'W). Both study areas are on the island of Savai´i in the Archipelago of Samoa. Most of the study area is low relief lava plain below 30 m elevation with the highest elevation of 108 m found on the highest peak of the two volcanic cones in Tafua, i.e. the study was conducted in areas with an established lowland rain forest (Hjerpe *et* al. 2001).

According to Whistler (2004) there are 142 (+6 new) tree species, 138 (+6 new) excluding palm trees that are monocotyledons, in lowland to mid-elevation forest in the Archipelago of Samoa. The rate of endemic lowland tree species are 20.3% with a small insecurity of one species being endemic or not, but still is 19.6% without this one species. The rate of endemic lowland species found on Savai'i is 17.4%. Whistler found that 3 tree species have been introduced by Polynesians and 11 where from modern introduction, but there are 12 of unsure origin of spread. The vast majority of species found in Samoa are native (85%) (Whistler 2004). Whistler has covered of 57% of the tree species in Samoa, with littoral and high elevation species being excluded.
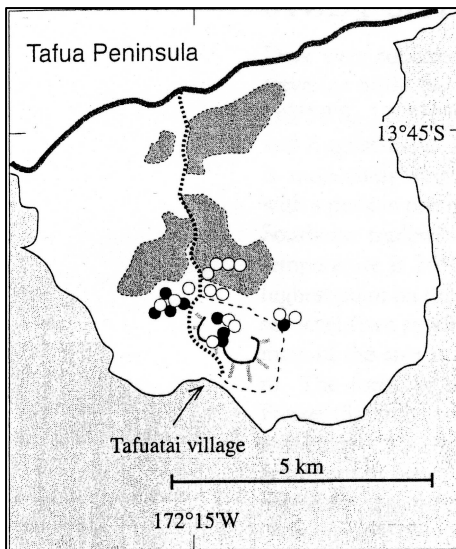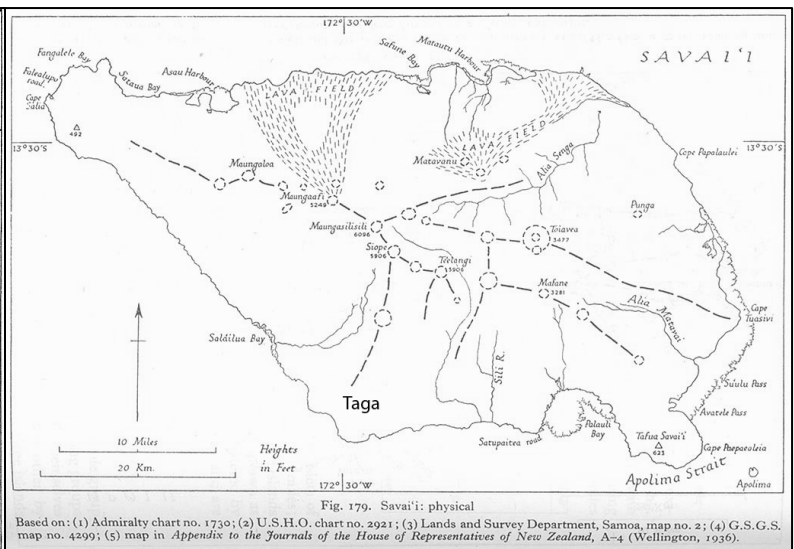

Figure 1 Tafua-Tai forest area   Figure 2 Taga forest area

LOCATION

The Tafua Rain Forest Preserve (ca 5000 ha) was chosen for the study since the preserve is the largest containing block of continuous lowland rain forest in Independent Samoa. Tafua on Savai'i was hit by two severe cyclones, Ofa in February 1990 and Val in December 1991 (Elmqvist *et* al. 1994). They restructured/reorganized the composition of tree species diversity in a short interval. Forest was dominated by *Pometia pinnata* and *Cananga odorata* prior to the cyclones. Five years later the area was dominated primary of pioneers as *Macaranga harveyana* (Hjerpe *et* al. 2001). Their combined effect resulted in tree mortality greater than 50% in the study area of Tafua (Elmqvist *et* al. 1994). Further, parts of the Tafua Rain Forest Preserve were subjected to another disturbance event. A fire one month after Ofa affected an area of approximately 750 ha in the preserve Elmqvist *et* al. 1994). In the burned area the mortality were as great as 90% (Elmqvist *et* al. 1994). There are areas in the preserve that have functioned as refuges that were subjected to less degree of the cyclones and not at all by the fire (Hjerpe *et* al. 2001). However, *Macaranga harveyana* was the totally dominating tree species five years after the fire (Hjerpe *et* al. 2001).

Taga was chosen since the areas with community owned forestland was harvested approximately at 1990 and respectively at 2000 and the area is situated only 25 km from the rain forest preserve. We had two different logging routines where one was a conventional one (clear-felled 10-15 years ago) and secondly a size-selective logging (harvested five years ago) where only trees above minimum diameter of 35 cm DBH counted as commercially valuable forest giving a more random selection of trees left. Previous to the harvests the forest were dominated by lowland rain forest with a large proportion of *Pometia pinnata* (Taga Chieftain, personal communication 2005). The study site of Taga was thus used as a comparison to estimate the human impact. Data was collected during March to May 2005. This gave us the opportunity to investigate different disturbances and in addition comparing to the disturbance by human activity since the natural events coincide with the human impact on the areas at Taga.

SAMPLING

To determine the forest structure after a large-scale natural force such as cyclonic storms and fire in comparison to human activity with high impact such as large-scale harvesting we established 26 20 X 20 m plots in two locations Tafua and Taga. Plot sites used by J. Hjerpe & H. Hedenås 1996 and 1997 based on the plots by T. Elmqvist 1990 and 1992 in Tafua were re-established with an a proximity of less 100 m according to old maps and directions. In total eleven plots were made in the unburned natural disturbance area (Nd) and five in the burned cumulative natural disturbed area (two cyclones and one fire since 1990; cNd). In Taga five human disturbed plots (Hd) in a 10-15 years old harvest area was randomized as well as in a five plots in the five year old harvested area. All plots were geographically pin-pointed by GPS and marked by coloration of tree stems in corners of the 20 X 20 m squares as well as guiding marks from the trail to the actual plot.

Two kinds of measurements procedures were used. First, for community dynamics 20x20 m square plots were established. At each of the 26 plots all living and dead trees (a dead tree equals bark absent and xylem dry and absence of leaves or shoots) over 5 cm DBH were noted. For each tree the following parameters were noted: Height (m) Circumference in mm then recalculated to diameter at breast height (DBH); Inclination (INC) of the tree grouped into classes 1=Standing straight; 2=Slightly Leaning; 3=Severe Leaning; 4=Lying but alive; Presence of buttress or stilt roots and quantity; Stratum, each tree was recognized as in Emergent layer (E), Canopy layer (C) or Understory layer (U), Tree crown (TC) as a

description of crown shape/form; Crown width (CW) recorded as the radius estimated in integer meters (m); Damage (DAM) class divided in 1=None; 2=Slightly; 3=Much; 4=Dead; Potential crop tree (PC) recognition. Climbers per tree are surveyed by number to a single tree and by size in circumference in mm then recalculated to diameter; Forest floor vegetation is given as a description to recognize if there been any human disturbance in the plot (any kind of human activity was recorded).

For each stand, percentage canopy cover was estimated with the use of a ''moose horn'' (Robinson, 1947) at eye height, which projects the canopy onto a quadratic grid, at five different locations, positioned as a cross in the stand. Canopy cover equals shade in the stand and is presented in percentage, recalculated to a mean in every plot. Further, basal area was calculated based on the tree diameter at breast height. Measurements and equipments used followed standard methods in forestry.

Second, in each 20 X 20 m plot 2 X 20 m transects were placed in a cross for the second procedure of measuring the regeneration process and tree recruitment. 1 X 1 m squares were laid along transects alternately on each side so the crossing would not result in bias, the small plots adding up to an amount of 40 for each large plot. In the 1 X 1 m survey area the height of all the seedlings, saplings and small trees less than 5 cm in DBH was recorded up to 3 meters height (all above was classed in to one group). The recruitment was then specified by species identity. Bushes and vines were not recorded, though sometimes it was hard to distinguish between bushes or trees. As a consequence of *Aidia racemosa* way of spreading and its behaviour of dividing into several stems in a thicket less than 1m in height above ground we decided to count thickets as one individual in the survey to minimize bias.

To identify species in the field, photographs of specimens of collected dry plant material from earlier studies conducted by Hjerpe & Hedenås 1996 and 1997 were used. New specimens were collected and dried; these were identified with help from Dr. W.A. Whistler, University of Hawaii, USA. Voucher specimens have been deposited in the herbarium UME, Department of Ecology and Environmental Science, Umeå University, Sweden.

DATA ANALYSIS

STAND CHARACTERISTICS

First, one-way ANOVA models are used in order to assess whether the stand characteristics, i.e. tree density, mean diameter at breast height, basal area, canopy cover and canopy height differ between the forest types. Second, Tukey Test is used as a post hoc test in order reveal where the significant difference is. In a few cases area a *Student's T-test* applied instead of a Tukey Test.

SPECIES ABUNDANCE AND DIVERSITY INDICES

First, one-way ANOVA models are used in order to assess whether number of tree species (<5 cm DBH) differ between the forests. Second, Tukey Test is used as a post hoc test in order reveal where the significant difference is. In a few cases a *Student's T-test* is applied instead of a Tukey Test.

Rank-abundance was drawn; these graphs show $\log_{10} p_i$ value for each species, beginning with most abundant ending with least abundant species (Whittaker 1965; Feinsinger 2001).

Further, the Shannon index *H'* were claculated for each size class for each forest type:
$$H = -\sum_{i=1}^{S} p_i \ln p_i \qquad p_i = \frac{n_i}{N} \qquad N = \sum_{i=1}^{S} n_i$$
Where p_i is the fraction of individuals belonging to the *i*-th species, and *S* the number of species found the species richness. p_i is the relative abundance of each species, calculated as the proportion of individuals of a given species (n_i) to the total number of individuals in the community (*N*). Maximum possible *H'*, $H_{max} = \ln S$ occurs when all species are present in equal numbers. Shannon index is invariant with respect to sample size, but rare species add to the value. Similarly, Shannon evenness or equitability denoted *J* is calculated by the proportion of *H'* by *H'$_{max}$* is constrained in between 0 to 1, and with less variation in populations between species *J* gets higher (Taylor *et* al. 1976; Begon *et* al. 2006).

Further, Berger-Parker dominance index *D* which is the relative abundance of the most common species (Hjerpe *et* al. 2001), was also calculated for each size class in each set of plots. The *Berger-Parker* diversity index is simply:
$$max_{1 < i < p_i}$$

Further, Jackknife Species richness estimate was also calculated:
$$S = n + \left(\frac{(n-1)}{n}\right)^k$$
It estimates the probability of missing some of the actual total number of species present in any count based on a sample population. Where, *S* is species richness, *n* the number of species and *k* the number of unique species (Gaston & Spicer 2004).

Furthermore, The Simpsons index *D* were claculated for each size class for each forest type:
$$D = \frac{\sum_{i=1}^{s} n_i(n_i - 1)}{N(N-1)}$$
Where *S* is the number of species, *N* is the total percentage cover or total number of organisms and n_i is the percentage cover of a species or number of organisms of a species. Note that $0 < D < 1$ with values near zero corresponding to highly diverse or heterogeneous ecosystems and values near one corresponding to more homogeneous ecosystems (Taylor *et* al. 1976; Begon *et* al. 2006).
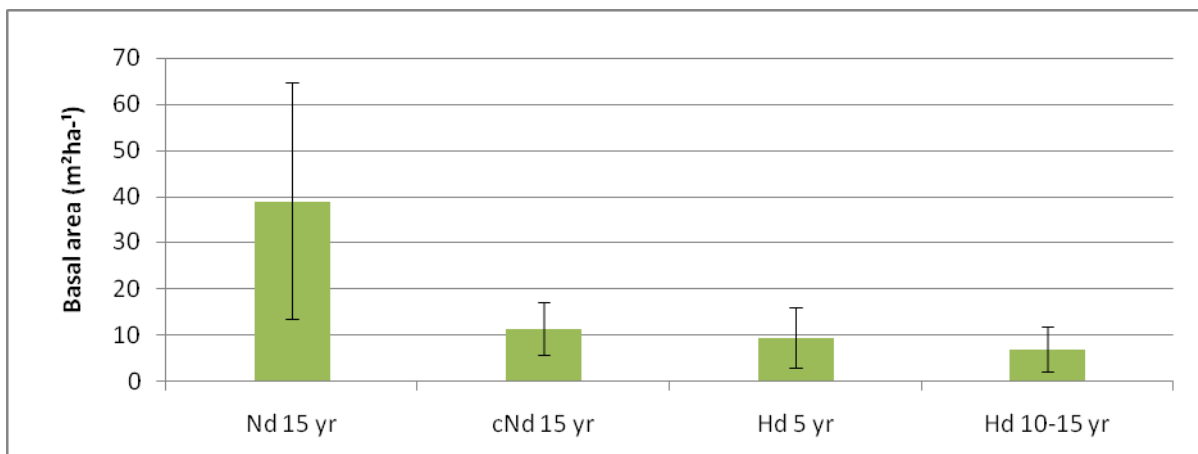
RESULTS

STAND CHARACTERISTICS

Figure 3 Mean stand basal area (±SD) per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).

Figure 4 Mean canopy cover (±SD) (crown closure) shown in percentage of shade per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).

The one-way ANOVA analysis revealed that mean basal area differed significantly between forest types ($F_{3,22}$-value = 12.08, $p < 0.001$; Fig. 3). The mean basal area is significantly higher in the forest with a natural disturbance regime (two cyclones since 1990) compared to the two forests harvested five and ten to fifteen years ago (Tukey test p-adj. = 0.034 and p-adj. = 0.019, respectively). It is also almost significantly higher mean basal area in the natural disturbed forest than in the cumulative disturbed forest (two cyclones and one fire since 1990; Tukey test p-adj. = 0.051). The mean basal area does not differ between the other forest types. Seen in figure 4 the one-way ANOVA analysis revealed that the canopy cover differed significantly between forest types ($F_{3,22}$-= 9.19value, $p < 0.001$;). The canopy cover is significantly higher in the natural disturbed forest compared to the two forests harvested five and ten to fifteen years ago (Tukey test p-adj. = 0.005 and p=0.004, respectively). There is also a significant higher canopy cover in the cumulative disturbed forest compared to the two forests harvested five and ten to fifteen years ago (Tukey test, p-adj. = 0.011 and p-adj. = 0.010, respectively). The canopy cover does not differ between the other forest types.
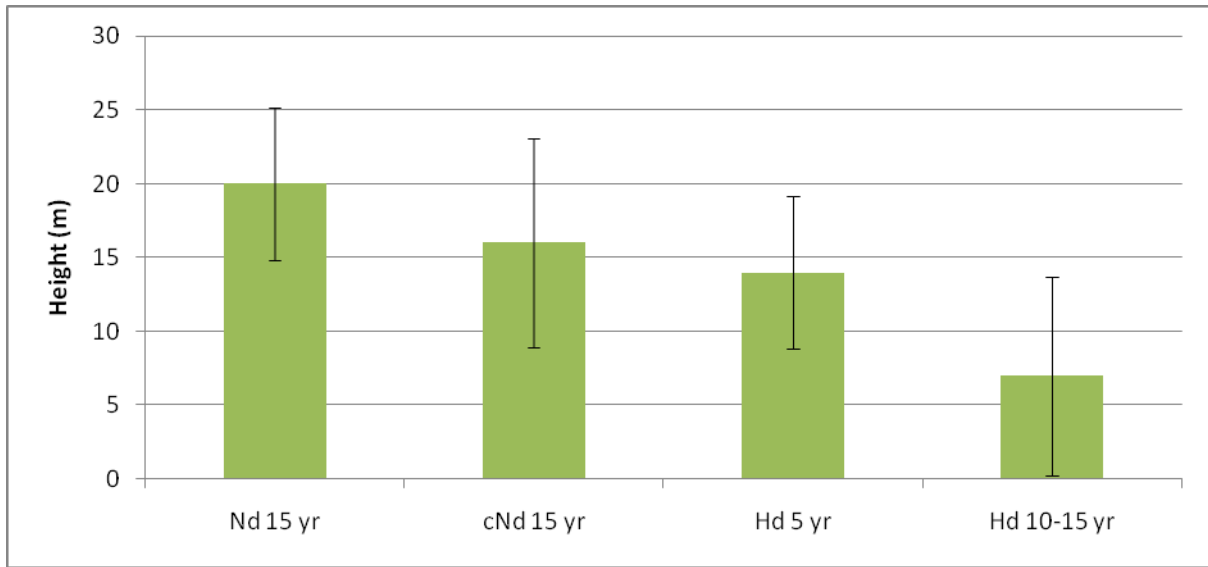
Figure 5 Mean canopy height (m) per per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).
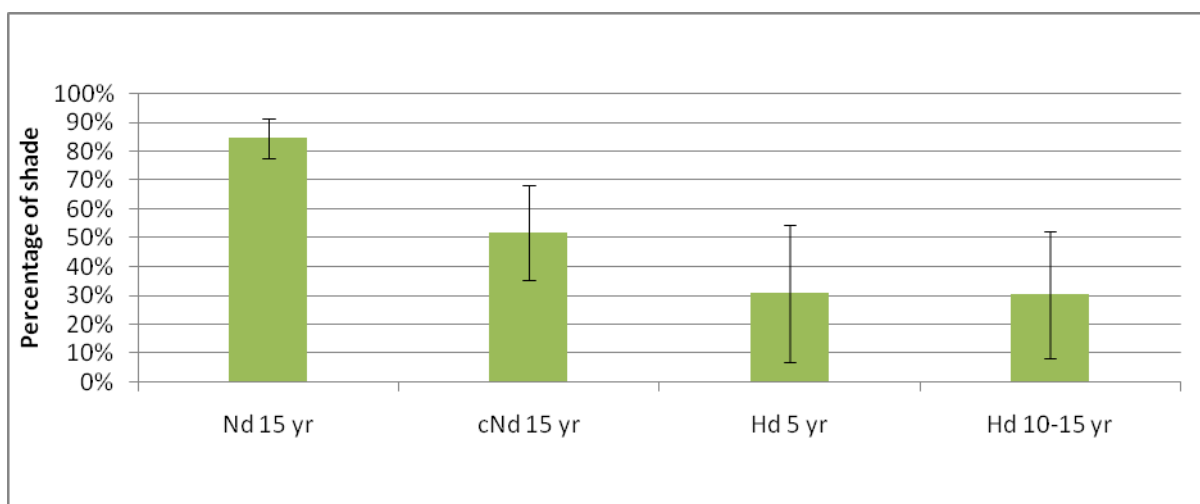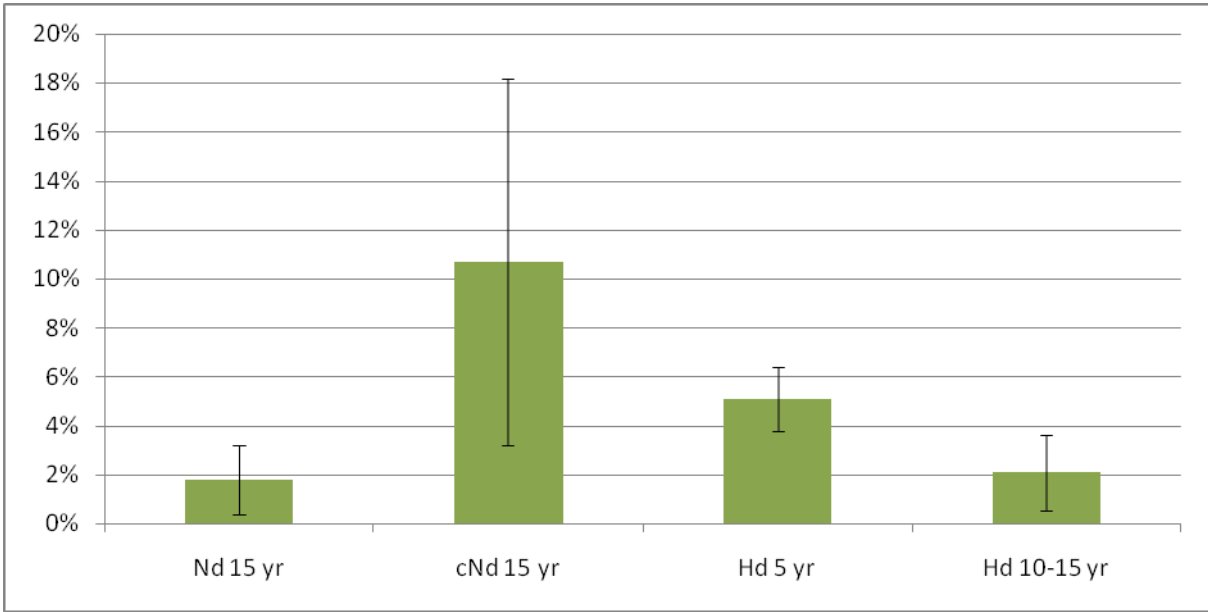

Figure 6 Ratio of mean vine and liana basal area per mean stand basal area per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).

The one-way ANOVA analysis revealed that the canopy height differed significantly between forest types ($F_{3,22}$-value= 6.40, p = 0.003; Fig. 5). The canopy height is significantly lower in the forest harvested five years ago than in the forest subjected to natural disturbance and compared to the cumulative disturbed forest (Tukey test, p-adj. = 0.002 and p-adj. = 0.037, respectively). The canopy height does not differ between the other forest types.

The one-way ANOVA analysis revealed that the ratio between mean vine and liana basal area per mean stand basal area differed significantly between forest types ($F_{3,22}$-value= 8.67, p < 0.001; Fig. 6). The ratio is significantly higher in the cumulative disturbed forest than in the natural disturbed forest (Tukey test, p-adj. < 0.001). The ratio is also higher in the cumulative disturbed forest than in the forest harvested 10-15 years ago (Tukey test, p-adj. = 0.004). The ratio does not differ between the other forest types.
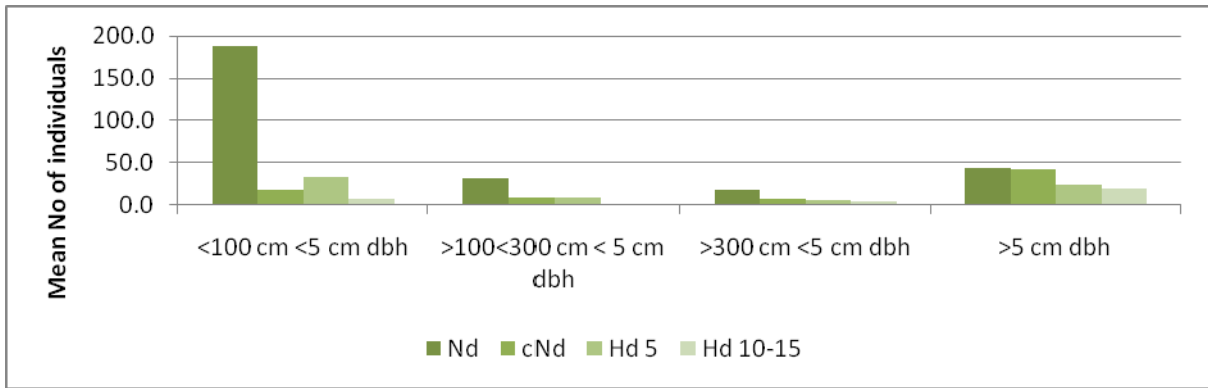
Figure 7 Mean number of individuals per plot in each size class and forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).

Figure 8 Mean number of species per forest type and size class, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).

	Nd	cNd	Hd 5	Hd 10-15
Total Rare	9	6	4.8	2.4
Total Species	23.7	15.8	13.2	4.2

Figure 9 Mean number of species totally with mean number of rare species per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).

The mean number of individuals (trees > 5cm DBH) per plot differs among the forest types and is highest in the natural disturbed forest and lowest in the forest harvested 10-15 years ago ($F_{3,22}$-value= 5.63, p = 0.006; Fig. 7). The mean number of individuals (trees > 5cm DBH) per plot is significantly higher in the natural disturbed forest than in the two forests harvested five and ten to fifteen years ago (Tukey test p-adj. = 0.044 and p-adj. = 0.011, respectively). The mean number of individuals (trees > 5cm DBH) does not differ between the other forest types. Further, there is a significant difference in the number of individuals between the natural disturbed forest compared to the other disturbances both in total (data not shown) and for all seedlings and saplings (<5 cm dbh; *Student t-test,* P: <0.05; Fig. 7). The other areas do not differ from each other except from when comparing the number of individuals in the cumulative disturbed forest with the number of individuals in the harvested forests 10-15 years ago.

SPECIES ABUNDANCE AND DIVERSITY

The mean number of tree species (> 5cm DBH) per plot differs among the forest types and is highest in the forest subjected to natural disturbance and lowest in the forest harvested 10-15 years ago ($F_{3,22}$-value= 10.66, p < 0.001; Fig. 8). The mean number of species (trees > 5cm DBH) per plot is significantly higher in the natural disturbed forest than in the two forests harvested five and ten to fifteen years ago (Tukey test p-adj. = 0.033 and p-adj. < 0.001, respectively). The mean number of tree species (trees > 5cm DBH) does not differ between the other forest types. The total mean number of rare species followed the same trend as the total mean numbers (Fig. 9). The rank abundance diagram, for the smallest size class, composed of seedlings, indicates a low evenness for the forest harvested ten to fifteen years ago (Fig. 10). It also indicates that the species richness is highest in the natural disturbed forest, moderate in both the cumulative disturbed forest and the forest harvested five years ago.

	<100 cm height, <5 cm dbh			
	Nd 15 yr	*cNd 15 yr*	*Hd 5 yr*	*Hd 10-15 yr*
H'	1,45	1,32	0,94	0,08
J	0,57	0,79	0,69	0,86
S	13,38	6,66	6,41	1,33
D	0,39	0,36	0,31	0,86

Figure 10 Rank abundance <100 cm height, >5 cm dbh per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and for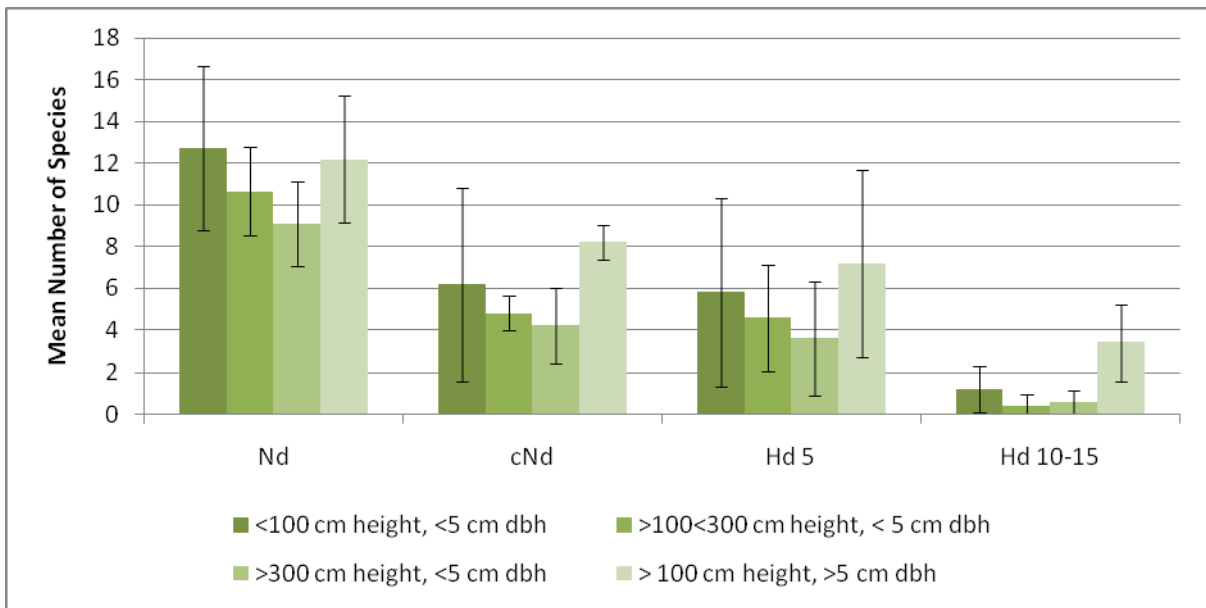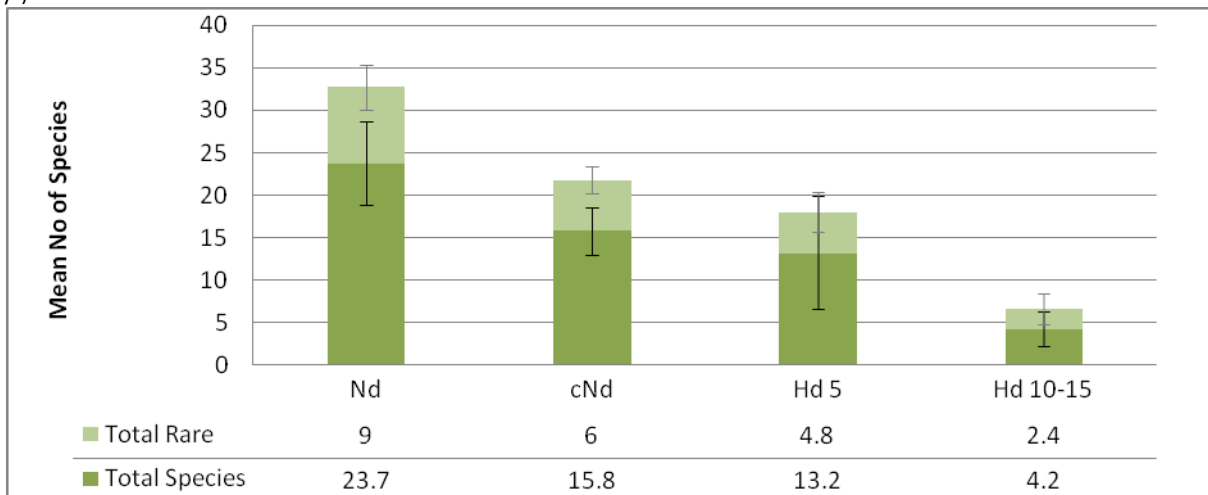est harvested ten to fifteen years ago (Hd 10-15 yr). Integrated in the rank abundance figures are the Shannon index value (H'), the Shannon evenness index (J), and the Jacknife estimate of species richness (S) and Berger-Parker dominance index (D).

	>100 cm <300 cm height, <5 cm dbh			
	Nd 15 yr	*cNd 15 yr*	*Hd 5 yr*	*Hd 10-15 yr*
H'	2,02	1,39	1,19	0,00
J	0,84	0,84	0,89	1,00
S	11,28	5,34	4,96	0,40
D	0,23	0,28	0,30	0,67

Figure 11 Rank abundance >100<300 cm height, < 5 cm dbh per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr). Integrated in the rank abundance figure is the Shannon index value (H'), the Shannon evenness index (J), the Jacknife estimate of species richness (S) and Berger-Parker dominance index (D).

All values derived from the Shannon index value (H'), the Shannon evenness index (J), and the Jacknife estimate of species richness (S) and Berger-Parker dominance index (D) are consistent with the shape of the rank abundance curve. The Shannon index by itself show a much clearer view of the drop of species abundance (Fig 10). The Berger-Parker dominant species shown in values (D) are, in order, *Funtumia elasctica*, *Morinda citrifolia*, *Dysoxylum spp.*, and *Macaranga harveyana*.

The rank abundance diagram, for the middle class, consisting of small saplings, displays, similar shapes as the smallest class, though the slope is even steeper in the forest harvested ten to fifteen year ago (Fig 11). The steep slope indicates a low species evenness and very low species richness in the forest harvested ten to fifteen year ago. Shannon index show a higher value of species richness in contradiction to the Shannon evenness index which display a lucid high value indicating low diversity. The dominant species shown in values (D) are, in order, *Aidia racemosa*, *Dysoxylum samoense*, *Aidia racemosa*, and *Macaranga harveyana*.

The largest class of young trees display similar shapes of the rank abundance curves as the other two previous rank abundance diagrams (Fig. 12). The shallow gradients of the forest subjected to cumulative disturbance and forest harvested five years ago both with moderate species richness site, and slope of the natural disturbance forest indicates higher species evenness in this size class than the smaller size classes. The dominant species shown in values (D) are, in order, *Aidia racemosa*, *Kleinhovia hospitata*, *Aidia racemosa*, and *Hibiscus tiliaceus*.

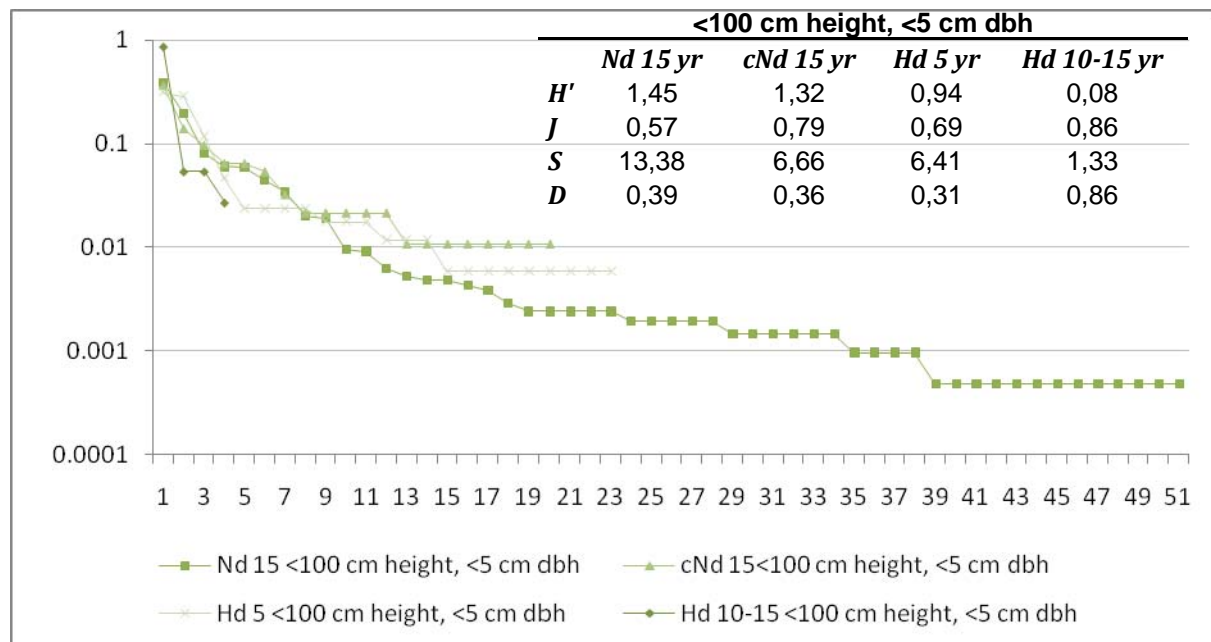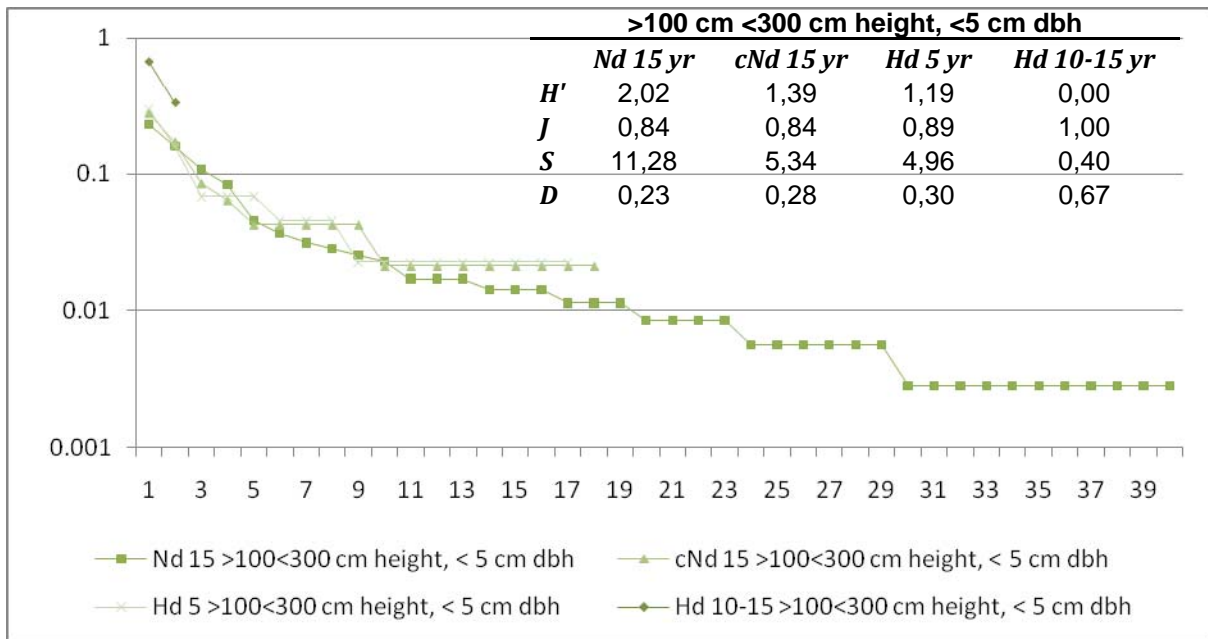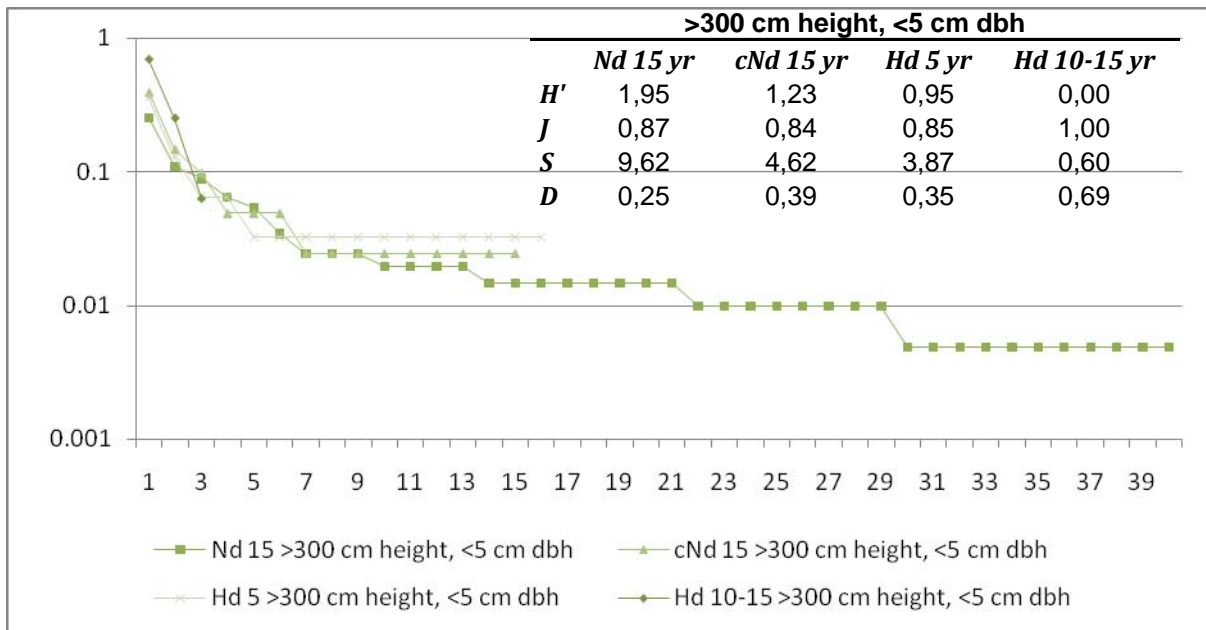**Figure 12** Rank abundance >300 cm height, <5 cm dbh per per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr). Integrated in the rank abundance figure is the Shannon index value (H'), the Shannon evenness index (J), the Jacknife estimate of species richness (S) and Berger-Parker dominance index (D).
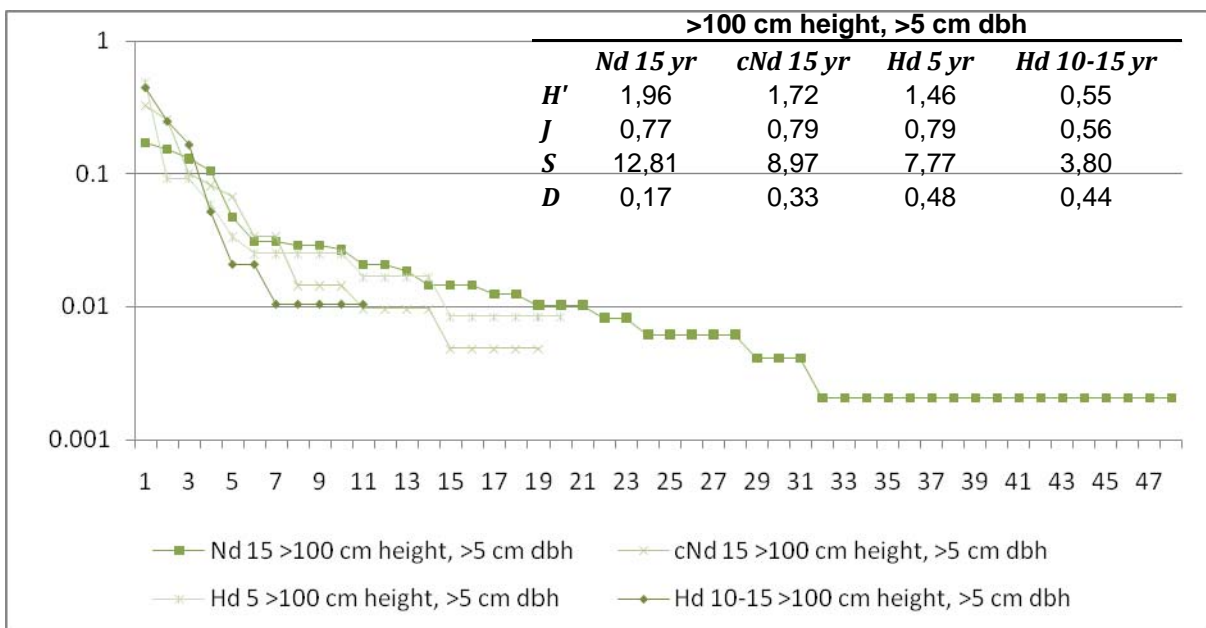
Figure 13 Rank abundance >100 cm height, >5 cm dbh per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr). Integrated in the rank abundance figure is the Shannon index value (H'), the Shannon evenness index (J), the Jacknife estimate of species richness (S) and Berger-Parker dominance index (D).

The tree size class, show less evenness i.e. a reduced variation of abundance of different species (Fig. 13). Species richness nevertheless exhibits an equal distribution amongst the forest types as seen before. However, forest harvested ten to fifteen year ago reveals a higher richness than shown for the other size classes. The dominant species shown in values (D) are, in order, *Funtumia elastica*, *Cananga odorata*, *Macaranga harveyana*, and *Hibiscus tiliaceus*.

	Total			
	Nd 15 yr	*cNd 15 yr*	*Hd 5 yr*	*Hd 10-15 yr*
H'	2,08	2,22	1,94	0,55
J	0,65	0,80	0,77	0,52
S	25,59	16,48	13,87	4,63
D	0,30	0,18	0,20	0,41
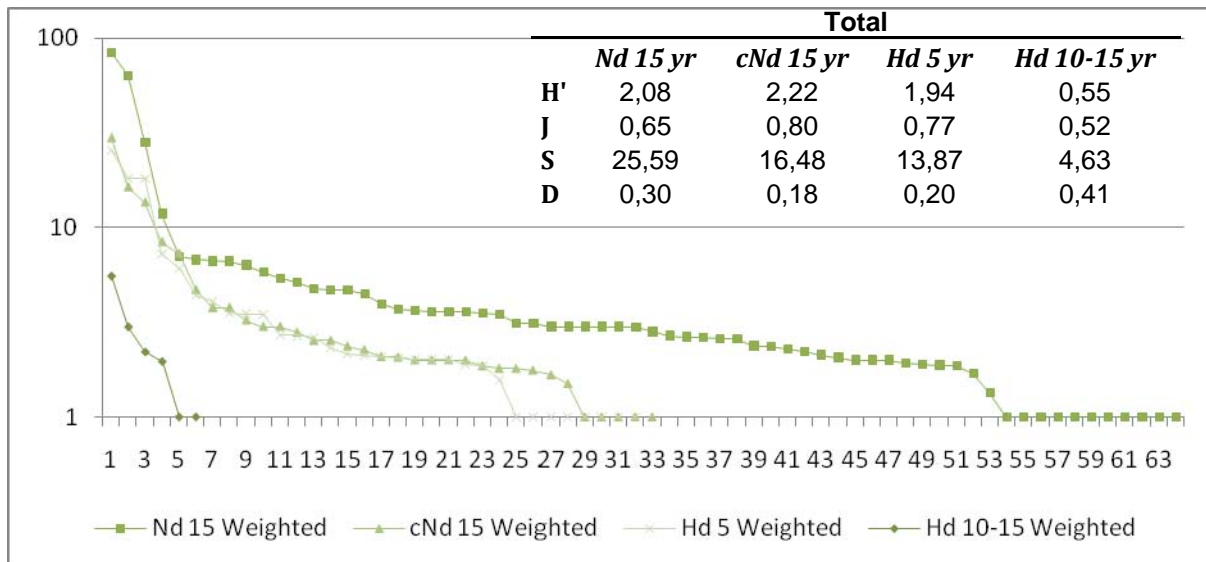
Figure 14 Weighted rank abundance per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).
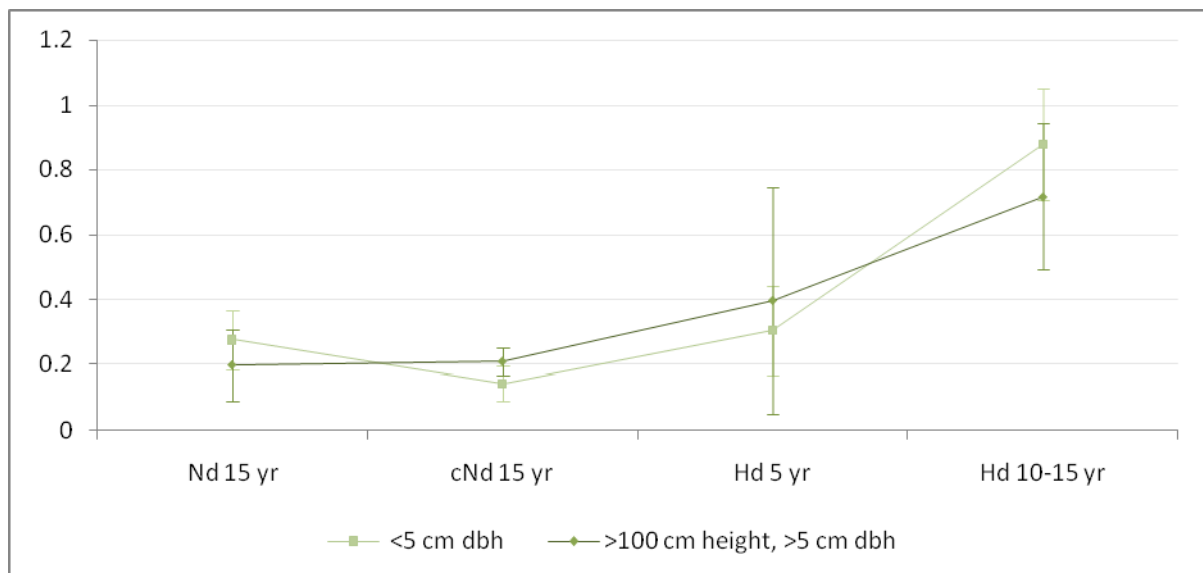
Figure 15 Simpson index showing values for trees (> 5 cm dbh) and seedlings and saplings (< 5 cm dbh) per forest type, i.e. natural disturbed forest (Nd 15 yr), cumulative disturbed forest (cNd 15 yr), forest harvested 5 years ago (Hd 5 yr), and forest harvested ten to fifteen years ago (Hd 10-15 yr).

The weighted total mean abundance of the sites supports the difference amongst the forest types subjected different disturbance regimes. The natural disturbed forest has the highest species richness and the most subtle slope indicating the highest species evenness (Fig. 14). The cumulative disturbed forest and the forest harvested five years ago is evidently grouped together even more than so than as before. Shannon index is equivalent for all but the forest harvested ten to fifteen years ago. Shannon evenness index support the rank abundance diagram with a higher variation of species and therefore a higher diversity. The forest harvested ten to fifteen years ago is yet again shown to have a high evenness due the smaller population found in this area.

Simpson index gives a value between 0 to 1 and is less sensitive to changes in species richness, with values near zero corresponding to highly diverse or heterogeneous ecosystems and values near one corresponding to more homogeneous ecosystems, i.e. less diverse. There is a significant difference between the natural disturbed forest and the cumulative disturbed

forest in the smaller size range of seedlings and saplings (<5 cm dbh) and for the total (*Student t-test,* P <0.02). There is no significant difference between the forest subjected to natural disturbances and the forest harvested five years ago, probably due to the great variation in the latter. The same pattern is found for the cumulative disturbed forest and the forest harvested five years ago. The pattern found in the forest harvested ten to fifteen years ago is significantly different from all the other forests in all size ranges (*Student t-test,* P < 0.01), except for all trees (>5 cm dbh) when comparing the two harvested forests on their own.

Table 1 to 4 in the appendix 1 illustrate the relative abundance of each species found of the tree size class (>5 cm dbh) in the different forest types. In the forest subjected to natural disturbances a single modern introduced invasive species appears at the top *Funtumia elastica* (17%) followed in position by a large long-lived pioneer, *Pometia pinnata* (15.3%), a species normally distributed in a mature lowland forest of Samoa. Among the relative abundant trees in the natural disturbed forest are two species normally found in secondary or disturbed forest, *Macaranga harveyana* (12.9%) a short lived fast growing pioneer species and a Polynesian introduced species, *Cananga odorata* (10.4%). In the fire ravaged cumulative natural disturbed forest the two most abundant species are *Cananga odorata* (32.5%) and the large long-lived pioneer *Rhus taitensis* (25.4%). The secondary forest species *Macaranga harveyana* (10.0%) is third in rank. Fourth is *Pometia pinnata* (8.1%) and fifth in rank is *Kleinhovia hospitata* (6.7%), also a secondary forest type. The dominating species are in the forest harvested five years ago, *Macaranga harveyana* (48.3%) followed in close to equal amounts of *Morinda citrifolia* (9.2%), a Polynesian introduction with a low invasive risk, and *Rhus taitensis* (9.2%) and another modern introduction, *Elaeocarpus grandis* (5.8%). In the most severely disturbed area, the forest harvested ten to fifteen year ago, the most dominating tree found is *Hibiscus tiliaceus* (44.3%) which form thick thickets competing out all other tree species. Followed by *Macaranga harveyana* (24.7%) and *Pometia pinnata* (16.5%).

Table 5 to 8 in the appendix 1 illustrate the relative abundance of each species found in the seedling and sapling size range (<5 cm dbh) in the separate forest types. We found that in the forest subjected to natural disturbances the invasive species *Funtumia elastica* (32.6%) dominated the forest floor. Second in relative abundance is *Aidia racemosa* (20.7%) which is a normal understory shrub or small tree. Third comes the shade tolerant *Diospyros samoensis* (7.4%) and at equal abundance the large long-lived pioneer *Pometia pinnata* (7.4%). The forest subjected to cumulative natural disturbances is dominated by *Morinda citrifolia* (24.2%). Followed by *Dysoxylum* spp. (17.0%) then by *Kleinhovia hospitata* (12.6%) both pioneer species and the later representative to secondary forest types. In fourth order is *Diospyros samoensis* (8.2%). In the forest harvested five years ago dominates the small tree (alternatively shrub) *Aidia racemosa* (29.8%) equally with *Dysoxylum spp* (22.0%). After them follows *Diospyros samoensis* (9.4%). Notably, the timber tree *Terminalia richii* (4.9%) is found in quite high amount as it is normally dispersed more sparsely. Dominating in the forest harvested ten to fifteen years ago is the secondary forest species *Macaranga harveyana* (67.9%) followed by the thicket forming *Hibiscus tiliaceus* (19.6%) and third by *Dysoxylum* spp. (8.9%).

DISCUSSION

This study assesses the rain forest dynamic following different disturbance regimes in Samoa, about 15 years after the disturbance. The first study showed that the combined effect of the two cyclones resulted in large immediate changes in structure and species composition of the Tafua forest (Elmqvist *et* al. 1994). The area subjected to a forest fire was even more adversely affected, with a tree mortality of more than 90 percent (Elmqvist *et* al. 1994). In the second survey of the forest nearly five years after the second cyclone distinct patterns of regeneration start to emerge (Hjerpe *et* al. 2001). Despite heterogeneity in the effect of the cyclones, strong differences are exhibited between the burned and the unburned parts of the forest. In addition this study compares the forest dynamic of the above studies with two forests subjected to harvesting. This study is unique as most of the studies concerning major cyclone and hurricane damaged have assessed the immediate effects of disturbance event (Frankling *et* al. 2004; Bellingham *et* al. 1995), but only few studies has followed the forest dynamic and recovery for more than longer time span (see e.g. Burslem *et* al. 2000).

In total 73 identified species were scored during the inventories, representing about 30% of the Samoan tree flora (Whistler 2002). The rate of endemic tree species of the scored species inventoried was 16% and as much as 68% of those were indigenous to Samoa (Whistler 2002). In accordance to the rate of 17% endemic tree species in total on Savai'i according to Whistler (2004).We also came across species that were of modern origin to the extent of 7% of sampled species. One of these of relatively recently introduced species is *Funtumia elastica,* a highly invasive species which we found in relative high abundance in the natural disturbed forest. Another 4% of the species were of Polynesian origin and are now considered naturalized. One of these is *Cananga odorata* which was frequent in all forest types. The highest number of species, 67 identified species, was found in the natural disturbed forest and the lowest number of species, 14 identified species, was found in the forest harvested ten to fifteen years ago. It is, however, important to point out that the samplings effort (number of plots) was more than double in the natural disturbed forest than in any of the other forest types. Nevertheless, the pattern remains when considering the Alfa diversity (mean number of species per plot) as it is highest in the natural disturbed forest and lowest in the forest harvested ten to fifteen years ago.

FOREST DYNAMICS 1990-2005 IN THE NATURAL DISTURBED FOREST AND THE CUMULATIVE DISTURBED FOREST

First, the number of species found in this study in the natural disturbed forest as well as in the cumulative disturbed forest is higher than in the survey conducted by Hjerpe *et* al. (2001) despite the fact that they had a higher sampling effort. This indicates that the number of trees species has increased in the Tafua rain forest during the last eight years of recovery.

Second, the tree density, 1111 stem per ha, after fifteen years of recovery in the natural disturbed forest is relative similar to the tree density found five years after the cyclones (Hjerpe *et* al. 2001). The present tree density in the natural disturbed forest is, however, considerably higher compared to prior the cyclones and immediately after the cyclones (476 and 225 stems per ha, respectively; (Elmqvist *et* al. 1994). However, there has been a more dramatic change in tree density in the cumulative disturbed area since the survey eight years before. The stem density has decreased with 46% in the cumulative disturbed area from 2294 stems per ha (Hjerpe *et* al. 2001), about five years, after the disturbance events to the present 1045 stems per ha. The tree density is still more than double prior to the cyclones. This indicates an intense density-dependent competition during forest recovery i.e. self-thinning (Westoby 1984; van Breugel 2006).

Third, our study also indicates that there has been a change in species composition during the last eight year of recovery (see appendix 2). Most notably is the decrease in relative abundance of the pioneer species *Macaranga harveyana* in both forest types. At present, the canopy is instead a mix of species. The most common is *Funtumia elastica* an exotic invasive species. Almost as common is *Pometia pinnata*, a native forest species common in intact lowland forest followed by *Macaranga harveyana*. The fourth species is *Cananga odorata* which suffered a very high mortality in the cyclones and consequently decreased dramatically in relative abundance. It regenerated abundantly from seeds during recovery and regained its position as the second most frequent tree species in the natural disturbed forest five years after the cyclones (Hjerpe et al 2001). Further, at present, the canopy is in the cumulative disturbed forest dominated by *Cananga odorata*. This species was very rare both as a mature tree as well as seedlings and saplings after five years of recovery in the cumulative disturbed forest (Hjerpe *et* al. 2001). Instead, Hjerpe *et* al. (2001) found that the dense canopy in the cumulative disturbed forest was exclusively made up by *Macaranga harveyana*. Among the saplings size class in the cumulative disturbed forest is another early successional species *Kleinhovia hospitata* (D=0.20, data not shown) dominating at present. A possible explanation is that the fire ravaged all larger standing trees in the cumulative natural disturbance area leaving more standing dead (data not shown) and open areas to be populated by secondary forest species. Due to the high dominance of secondary forest species Hjerpe *et* al. (2001) believed the recovery of the cumulative disturbed forest to be a noticeably slower process. Generally less species are found in the sapling size classes presumably due to that competition raises with age and few withstand being halted in growth to wait the moment of an opening in a forest canopy structure seen in figure seven. In general we found less species in the middle class seen in figure eleven and twelve. As shown by the steepness of the curves the competition for light and nutrients has started to take its toll on the number of individuals.

Furthermore, the index value of seedlings have not changed much in either the natural disturbed forest or in the cumulative disturbed forest since the survey conducted by Hjerpe *et* al. (2001). However, the Shannon index indicates a decrease in diversity in both forest types, although especially in the cumulative disturbed forest.

Thus overall the forest structure has changed from a *Pometia pinnata* dominated forest prior the cyclones to a forest mixed with secondary forest species and invasive species (appendix 2, data from before the cyclones). Species such as *Cananga odorata*, *Macaranga harveyana* and *Funtumia elastica* seems to be prime candidates to multiply following a disturbance action.

Fourth, the natural disturbed forest has a defined increase of canopy cover, at present 84%, since the canopy cover was as low as 27% in the natural disturbed forest immediately after the cyclones (Elmqvist *et* al. 1994). The canopy cover has increased for the cumulative disturbed forest, at present 52% since it was as low as 12% in the cumulative disturbed forest. However, the increase occurred during the first five year of recovery as Hjerpe *et* al. (2001) recorded a canopy cover as high as 49% percent already after five years of recovery.

Fifth, the natural disturbance canopy height was less than expected for a mature forest (Whistler 2002) and even lower in the cumulative disturbed forest. Both the low canopy cover as well as the relatively low canopy height indicate passed is not enough to stabilize a mature forest in particular not in the cumulative forest.

Comparing mean number of species data shows little has changed since ten years of recovery (23.7 and 15.8, respectively: figure 8).

COMPARING FOREST STRUCTURES AND TREE DIVERSITY AMONG FORESTS AFFECTED BY DIFFERENT DISTURBANCE REGIMES

The natural disturbance caused by the dual cyclones seems to be more evenly distributed considering species diversity and recovery has been steady. The forest harvested ten to fifteen years ago are still continuously disturbed by cattle grazing made worse by the fact that the harvest was illegal with a non-discriminate tree removal (local communication). The area harvested five years ago was logged in a restricted manner with a legislative minimum diameter class of 30 cm dbh consequentially left more trees of different species standing. If considering the forest harvested ten to fifteen years ago, this forest differs from all other areas when comparing all size classes except for trees between the human disturbance areas. This might be a consequence of the grazing and browsing pressure that hamper the tree seedlings of secondary forest type while facilitating grasses. The number of trees found in the forest harvested 10 -15years ago was slim to say the least with one population of *Hibiscus tiliaceus* growing in thickets in ONE plot making up the main total number of trees (D: 44%). All rank abundance curves showed the same trend, the natural disturbed forest display a higher variation of species followed by the forest harvested five years ago and the cumulative disturbance and last by the ten to fifteen years old human disturbance site with the immensely smaller population.

INVASIVE SPECIES AND LIANAS

In the article by Hjerpe *et* al. (2001) they state that the "severe large-scale disturbance may increase vulnerability of the plant community to invasion that can severely reduce biodiversity". This pattern is even more pronounced in this study as an invasive species *Funtumia elastica* is the most dominant species among the tree size class in the natural disturbed forest. Similarly, the seedling class of *Funtumia elastica* dominate the forest floor vegetation in the natural disturbed forest which still has the highest density of seedling throughout the different forest types. In the cumulative disturbed forest yet another introduced species, *Morinda citrifolia* of Polynesian introduction, rule the seedling class.

Further, the cumulative disturbed area has a high ratio of vines to tree stand basal area as a consequence severely sequestered recovery rate due to trees being smothered by vines and liana. The harvested forest (10-15 years ago) with equal recovery time showed almost no lianas when compared to the cumulative disturbed forest, despite its openness that ought to have a higher potential capacity to support vines suggesting that cattle grazing to be a major factor of vines scarcity or a false negative due to less tree stems, but personal observation hold the first theory to be more important.

The Samoan island is a volcanic young island when compared to Barro Colorado Island used by Hubbell *et* al. (1999) and age could be of great importance to the configuration and the status of the species pool (MacArthur & Wilson 1967). This is illustrated in the consequence of the dominance of *Funtumia elastica* in the natural disturbed area of the surrounding forest of Tafua-Tai. Samoa cannot have reached the dynamic equilibrium of Barro Colorado Island, Panama, that has a continual turnover of species and where the resilience to LID is high counted in recruitment per year (van Bloem *et* al. 2006). Generally rare species become extinct by differential elimination by density dependent competition (Wills *et* al. 1997). The endemic and indigenous species of Samoa seems to be sensitive to new immigrating species spread by human help, which get an opportunity to spread after a larger disturbance generating an unbalance in an otherwise stable community of species (PIER).

Thus genetic variation is related to island size as a consequence of population size. Frankham (1996) found species endemic to islands to have a lower allozyme variation than related mainland species supporting this theory. Lower genetic variation within an island population could be a factor for their greater vulnerability to random extinction in comparison to mainland populations (Frankham, 1996; Pearson *et* al. 2003). Size of land area of course influences the stability with smaller populations meaning vulnerable tree species in an community where a single tree of one species is found in an larger area, dependent of seed dispersal, when cut down or fallen will be more exposed to chance elimination and extinction by not having the same chance to spread as a more frequent inhabitant species raising the risk of chance extinction. The immigrating species we saw were more effective seed dispersers and therefore more competitive in their interaction even with indigenous secondary forest pioneer tree species increasing competition. Much is at stake for the Samoan tree community after a LID and after harsh human impact as clear cutting without restrictions or plantation treatments and most severe infliction seems to be the adding a cumulative disturbance as fire or grazing without any considerations of rehabilitating the area firstly destroyed by cyclone or harvesting of timber. According to MacArthur and Wilson's equilibrium theory the islands of Samoa could be considered as impoverished of species therefore more sensitive to disturbances coupled to new species introduction (Bellingham *et* al. 1995, MacArthur & Wilson 1967).

Not only opportunistic invading species and common pioneers thrive in a disturbed landscape with high light availability, but also vines, climbers and creepers will advance in such areas. This leads to reduced tree height and crown size caused by these opportunistic creeping plants covering all tree vegetation as a carpet, shading and also reducing water status in the soil hindering the recovery of primary forest Schnitzer *et* al. (2000, 2005).

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

Comparing the species composition and abundance before the cyclones indicated that the natural disturbed area has not fully restored species diversity to the level of a mature Samoan lowland forest. The forest areas surveyed are still more of a secondary forest type not fully recovered in either regime. Therefore the natural disturbance site will not hold all species that could be present in an undisturbed area, suggesting a reduced amount of mature trees and an unsecure future of seed resources. Further, it seems as if the specific mature forest species composition found by Whistler (2002) and Elmqvist *et* al. (1994) before the two cyclones 1990 and 1991 are exposed to a risk of being out competed by new immigrants as well as the risk of chance extinction. However, the forests in Samoa are probably adapted to cyclone disturbances and may recover. But, it is highly possible that people hamper the recovery process, as the forest comes down to simple weighing direct onetime income to the fact the forest is an important source of routine everyday living, as the forest solves some needs for food, house material and firewood etc. Further, our study revealed that the recovery process seems to be a much slower process in the forests subjected to unnatural disturbance regimes such as fire and logging than in the forest subjected to cyclones.

Thus, our conclusion is that cyclones have inflicted a change in forest composition that will take considerable time to recuperate from. This is inconsistent with Burlsem *et* al. (2000) who concluded that cyclone impacts had only short-term effects upon the tree species community. However, I agree with Burslem *et* al. (2000) that the effects of human disturbances causes do have a larger impact on the forest composition than cyclone caused disturbances. Thus the recovery process also seems to be an even more prolonged process in the harvested forests than in cyclone damaged forest. Further, in contrast to the Puerto Rican hurricane affected forest and to the Caribbean model of resilience against large infrequent disturbances (LIDs)

Samoa pacific islands native tree community seem to be more fragile due to many synergetic factors (Tuner *et* al. 1998; Brown *et* al. 2006; Van Bloem *et* al. 2006).

A sustainable forestry must be based on the natural forest's potential to regenerate. This means that for focal species seedling trees, "mother trees", must be allowed to remain adjacent or in the area harvested. This is especially important for shade tolerant and long-lived pioneer species (Hartshorn 1995). To facilitate this, harvesting should include restrictions in size and number of trees felled as well as cutting of lianas, replanting and maintaining of timber tree species harvested, leaving stand of seed trees, and a minimal use of heavy machinery to avoid soil erosion and compaction (Forshed *et* al. 2006). However this might not be economically practical and thus the only way may very well be to conserve the areas for the future (Bowles *et* al. 1998; Pearce *et* al. 2003). The Samoan people are also dependent on the non timber products from their tropical forest and thus it is essential to actively maintain the lowland forest not only for ecological reasons.

ACKNOWLEDGEMENTS

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ITTO. International Tropical Timber Organization: *http://www.itto.or.jp*

NOAA, The Global Historical Climatology Network *http://www.ncdc.noaa.gov/oa/climate/ghcn-monthly/index.php*

PIER, Pacific Island Ecosystems at Risk. Institute of Pacific Islands Forestry Plant threats to Pacific ecosystems: *http://www.hear.org/Pier/*

ReliefWeb, United Nations Department of Humanitarian Affairs (DHA):
Val: http://www.reliefweb.int/rw/rwb.nsf/db900sid/OCHA-64BS6W?OpenDocument
Ofa: http://www.reliefweb.int/rw/rwb.nsf/db900sid/ACOS-64CCQQ?OpenDocument&query=SAmoa%20Ofa
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APPENDIX 1

Tables showing species distribution in the different disturbance areas and in size classes.

Table 1 Relative abundance >5 cm dbh in the forest subjected to natural disturbances (two cyclones since 1990).

Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	>5 cm dbh, Nd 15
High	Shade tolerant secondary	M	U	None	*Funtumia elastica*	17.0%
	Pioneer Long-lived	I	C/E	Timber	*Pometia pinnata*	15.3%
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	12.9%
Low	Pioneer secondary	P	C	Timber	*Cananga odorata*	10.4%
		I	C/U	None	*Antirhea inconspicua*	4.7%
	Intermediate secondary	P	C	Timber	*Inocarpus fagifer*	3.1%
	Pioneer	P	C/U	NTFP	*Morinda citrifolia*	3.1%
	Pioneer Long-lived	I	C/E	Timber	*Rhus taitensis*	2.9%
	Pioneer secondary	I	C	NTFP	*Kleinhovia hospitata*	2.9%
	Pioneer	I	C	Timber	*Dysoxylum spp*	2.7%
		I	C	NTFP	*Myristica inutilis*	2.7%
High	Pioneer	M	C	Timber	*Adenanthera pavonina*	2.0%
High	Pioneer secondary	M	C	Timber	*Castilla elastica*	2.0%
		I	C	Timber	*Flacourtia rukam*	1.8%
	Shade tolerant	I	C	Timber	*Diospyros samoensis*	1.4%
		I	C/E	Timber	*Terminalia richii*	1.4%
		I	C/E	Timber	*Terminalia catappa*	1.2%
	Intermediate	I	C	NTFP	*Elattostachys falcata*	1.0%
	Pioneer secondary	I	C	Timber	*Planchonella samoensis*	1.0%
		I	C/U	None	*Citronella samoensis*	1.0%
	Shade tolerant	E	C	None	*Syzygium samoense*	0.8%
		I	U	NTFP	*Aidia racemosa*	0.8%
	Pioneer Long-lived	I	C/E	Timber	*Garuga floribunda*	0.6%
	Shade tolerant	I	C/U	NTFP	*Syzygium clusiifolium*	0.6%
		E	C	Timber	*Canarium mafoa*	0.6%
		I	C/U	NTFP	*Ficus scabra*	0.6%
		I	C	Timber	*Neonauclea forsteri*	0.6%
		I	C	NTFP	*Aglaia samoensis*	0.4%
		I	C	Timber	*Hernandia moerenhoutiana*	0.4%
		I	C	NTFP	*Sterculia fanaiho*	0.4%
	Intermediate	E	C	NTFP	*Cryptocarya elegans*	0.2%
	Intermediate	E	C	None	*Elaeocarpus ulianus*	0.2%
	Pioneer Secondary	I	U	NTFP	*Pipturus argenteus*	0.2%
	Pioneer secondary/ Coastal	I	C/U	NTFP	*Hibiscus tiliaceus*	0.2%
	Shade tolerant	E	C/U	NTFP	*Syzygium savaiiense*	0.2%
		I	U	None	*Antidesma sphaerocarpum*	0.2%
Low		M	U	None	*Carica papaya*	0.2%
		I	C	None	*Celtis harperi*	0.2%
		E	U	None	*Ficus godeffroyi*	0.2%
Low		-	-	None	*Ficus spp*	0.2%
		I	U	NTFP	*Ficus tinctoria*	0.2%
		E	U	None	*Ficus uniauriculata*	0.2%
		I	C	NTFP	*Guettarda speciosa*	0.2%
		I	U	NTFP	*Ixora samoensis*	0.2%
		I	C	NTFP	*Psydrax merrilli*	0.2%
		-	-	-	*Unidentified 14*	0.2%
		-	-	-	*Unidentified 15*	0.2%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

Table 2 Relative abundance >5 cm dbh, in the forest subjected to cumulative disturbances (two cyclones and one fire since 1990).

Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	>5 cm dbh, cNd 15
Low	Pioneer secondary	P	C	Timber	*Cananga odorata*	32.5%
	Pioneer Long-lived	I	C/E	Timber	*Rhus taitensis*	25.4%
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	10.0%
	Pioneer Long-lived	I	C/E	Timber	*Pometia pinnata*	8.1%
	Pioneer secondary	I	C	NTFP	*Kleinhovia hospitata*	6.7%
	Pioneer	I	C	Timber	*Alphitonia zizyphoides*	3.3%
	Pioneer	P	C/U	NTFP	*Morinda citrifolia*	3.3%
	Pioneer	I	C	Timber	*Dysoxylum spp*	1.4%
		I	C/U	NTFP	*Ficus scabra*	1.4%
		I	C	Timber	*Neonauclea forsteri*	1.4%
		I	U	NTFP	*Aidia racemosa*	1.0%
	Shade tolerant	I	C	Timber	*Diospyros samoensis*	1.0%
High	Shade tolerant secondary	M	U	None	*Funtumia elastica*	1.0%
		E	C	NTFP	*Medusanthera samoensis*	1.0%
		I	U	None	*Antidesma sphaerocarpum*	0.5%
		I	C	NTFP	*Myristica inutilis*	0.5%
		I	C	NTFP	*Psydrax merrilli*	0.5%
	Shade tolerant	I	C	Timber	*Syzygium inophylloides*	0.5%
	Shade tolerant	E	C/U	NTFP	*Syzygium savaiiense*	0.5%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

Table 3 Relative abundance >5 cm dbh, in the forest harvested five years ago.

Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	>5 cm dbh, Hd 5
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	48.3%
	Pioneer	P	C/U	NTFP	*Morinda citrifolia*	9.2%
	Pioneer longlived	I	C/E	Timber	*Rhus taitensis*	9.2%
Low	Intermediate	M	C	Timber	*Elaeocarpus grandis*	5.8%
	Pioneer	I	C	NTFP	*Glochidion ramiflorum*	3.3%
Low	Pioneer secondary	P	C	Timber	*Cananga odorata*	2.5%
	Intermediate	I	C	Timber	*Elaeocarpus floridanus*	2.5%
		I	C	NTFP	*Myristica inutilis*	2.5%
	Pioneer longlived	I	C/E	Timber	*Pometia pinnata*	2.5%
		I	C	NTFP	*Sterculia fanaiho*	2.5%
	Shade tolerant	I	C	Timber	*Diospyros samoensis*	1.7%
		I	C	Timber	*Flacourtia rukam*	1.7%
	Pioneer secondary	I	C	NTFP	*Omalanthus nutans*	1.7%
	Pioneer secondary	I	C	Timber	*Planchonella samoensis*	1.7%
		I	U	NTFP	*Aidia racemosa*	0.8%
		E	C	Timber	*Canarium mafoa*	0.8%
	Pioneer	I	C	Timber	*Dysoxylum maota*	0.8%
		I	C/U	NTFP	*Ficus scabra*	0.8%
	Pioneer Long-lived	I	C/E	Timber	*Garuga floribunda*	0.8%
	Shade tolerant	I	C/U	None	*Syzygium carolinense*	0.8%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

Table 4 Relative abundance >5 cm dbh, in the forest harvested 10-15 years ago.

					>5 cm dbh, Hd 10-15	
Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	*Species*	
	Pioneer secondary	I	C/U	NTFP	*Hibiscus tiliaceus*	44.3%
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	24.7%
	Pioneer Long-lived	I	C/E	Timber	*Pometia pinnata*	16.5%
Low	Pioneer secondary	P	C	Timber	*Cananga odorata*	5.2%
	Pioneer	P	C/U	NTFP	*Morinda citrifolia*	2.1%
	Pioneer secondary	I	C	NTFP	*Trema cannabina*	2.1%
	Shade tolerant	E	U	None	*Anacolosa insularis*	1.0%
	Pioneer	I	C	Timber	*Dysoxylum samoense*	1.0%
	Intermediate	E	C	None	*Elaeocarpus ulianus*	1.0%
	Pioneer Long-lived	I	C/E	Timber	*Garuga floribunda*	1.0%
	Pioneer secondary	I	U	NTFP	*Pipturus argenteus*	1.0%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

Table 5 Relative abundance <5 cm dbh in the forest subjected to natural disturbances.

Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	<5 cm dbh, Nd 15
High	Shade tolerant secondary	M	U	None	*Funtumia elastica*	32.63%
		I	U	NTFP	*Aidia racemosa*	20.69%
	Shade tolerant	I	C	Timber	*Diospyros samoensis*	7.40%
	Pioneer Long-lived	I	C/E	Timber	*Pometia pinnata*	7.37%
High	Pioneer	M	C	Timber	*Adenanthera pavonina*	5.15%
		E	C	Timber	*Canarium mafoa*	3.78%
		I	C/E	Timber	*Terminalia richii*	3.63%
		I	C/U	None	*Antirhea inconspicua*	3.09%
	Pioneer	I	C	Timber	*Dysoxylum spp*	2.37%
		I	C	NTFP	*Myristica inutilis*	1.30%
		I	C	NTFP	*Barringtonia samoensis*	1.22%
	Shade tolerant	I	C	Timber	*Syzygium inophylloides*	1.11%
	Pioneer Long-lived	I	C/E	Timber	*Garuga floribunda*	0.88%
	Pioneer	P	C/U	NTFP	*Morinda citrifolia*	0.61%
	Intermediate	E	C	NTFP	*Cryptocarya elegans*	0.53%
	Intermediate	I	C	NTFP	*Elattostachys falcata*	0.53%
		E	C	NTFP	*Mammea glauca*	0.53%
	Shade tolerant	E	C	None	*Syzygium samoense*	0.50%
		E	C	None	*Palaquium stehlinii*	0.46%
	Pioneer secondary	I	C	NTFP	*Omalanthus nutans*	0.42%
	Intermediate secondary	P	C	Timber	*Inocarpus fagifer*	0.34%
	Shade tolerant	I	C	Timber	*Planchonella samoensis*	0.34%
	Shade tolerant	I	C	NTFP	*Syzygium clusiifolium*	0.34%
		I	C	Timber	*Flacourtia rukam*	0.31%
	Shade tolerant	E	U	None	*Anacolosa insularis*	0.31%
		I	C/U	None	*Citronella samoensis*	0.31%
		I	C	Timber	*Neonauclea forsteri*	0.31%
		I	C	NTFP	*Aglaia samoensis*	0.27%
		I	U	NTFP	*Psychotria insularum*	0.27%
		E	U	None	*Ficus godeffroyi*	0.23%
		I	C/E	Timber	*Terminalia catappa*	0.23%
Low	Pioneer secondary	P	C	Timber	*Cananga odorata*	0.19%
		I	U	None	*Garcinia myrtifolia*	0.19%
	Pioneer secondary	I	C	NTFP	*Kleinhovia hospitata*	0.15%
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	0.15%
		I	U	None	*Tarenna sambucina*	0.15%
		-	-	-	*Unidentified 7*	0.15%
	Pioneer	I	C	NTFP	*Glochidion ramiflorum*	0.11%
	Pioneer Long-lived	I	C/E	Timber	*Rhus taitensis*	0.11%
	Shade tolerant	I	C/U	NTFP	*Diospyros elliptica*	0.11%
Low		M	U	None	*Carica papaya*	0.11%
		I	U	NTFP	*Ixora samoensis*	0.11%
		-	-	-	*Unidentified 15*	0.11%
	Shade tolerant	I	C	NTFP	*Planchonella garberi*	0.08%
		I	C/U	NTFP	*Erythrospermum accuminatissimum*	0.08%
		I	U	NTFP	*Ixora amphipholia*	0.08%
		I	C	None	*Sapindus saponaria*	0.08%
	Intermediate	I	C	Timber	*Elaeocarpus floridanus*	0.04%
		E	C	Timber	*Canarium vitiense*	0.04%
		I	U	None	*Garcinia vitiense*	0.04%
		I	C	NTFP	*Guettarda speciosa*	0.04%

Continued					<5 cm dbh, Nd 15	
Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	
Low		M	U	None	*Musa spp*	0.04%
		I	C/U	NTFP	*Premna serratifolia*	0.04%
		I	C	NTFP	*Sterculia fanaiho*	0.04%
		-	-	-	*Unidentified 1*	0.04%
		-	-	-	*Unidentified 11*	0.04%
		-	-	-	*Unidentified 12*	0.04%
		-	-	-	*Unidentified 2*	0.04%
		-	-	-	*Unidentified 3*	0.04%
		-	-	-	*Unidentified 4*	0.04%
		-	-	-	*Unidentified 5*	0.04%
		-	-	-	*Unidentified 6*	0.04%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

Table 6 Relative abundance <5 cm dbh, in the forest subjected to cumulative disturbances

					<5 cm dbh, cNd 15	
Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	
Low	Pioneer	P	C/U	None	*Morinda citrifolia*	24.2%
	Pioneer	I	C	Timber	*Dysoxylum spp*	17.0%
	Pioneer secondary	I	C	NTFP	*Kleinhovia hospitata*	12.6%
	Shade tolerant	I	C	Timber	*Diospyros samoensis*	8.2%
		I	U	NTFP	*Aidia racemosa*	6.0%
	Pioneer Long-lived	I	C/E	Timber	*Rhus taitensis*	4.4%
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	3.3%
High	Shade tolerant secondary	M	U	None	*Funtumia elastica*	2.7%
		I	C/U	None	*Antirhea inconspicua*	1.6%
	Pioneer	I	C	NTFP	*Glochidion ramiflorum*	1.6%
		-	-	-	*Unidentified 9*	1.6%
		I	C	NTFP	*Barringtonia samoensis*	1.1%
Low	Pioneer secondary	P	C	Timber	*Cananga odorata*	1.1%
		E	C	Timber	*Canarium mafoa*	1.1%
	Intermediate	E	C	None	*Elaeocarpus ulianus*	1.1%
		E	C	NTFP	*Medusanthera samoensis*	1.1%
		I	C	NTFP	*Myristica inutilis*	1.1%
	Pioneer secondary	I	C	NTFP	*Omalanthus nutans*	1.1%
	Pioneer secondary	I	C/U	NTFP	*Premna serratifolia*	1.1%
	Shade tolerant	I	C/U	None	*Syzygium carolinense*	1.1%
	Shade tolerant	I	C	Timber	*Syzygium samarangense*	1.1%
	Pioneer	I	C	Timber	*Alphitonia zizyphoides*	0.5%
		E	C	NTFP	*Mammea glauca*	0.5%
Low		M	U	None	*Musa spp*	0.5%
		I	C	Timber	*Neonauclea forsteri*	0.5%
		E	C/E	Timber	*Palaquium stehlinii*	0.5%
	Pioneer Long-lived	I	C/E	Timber	*Pometia pinnata*	0.5%
		I	C	NTFP	*Psydrax merrilli*	0.5%
	Shade tolerant	I	C	Timber	*Syzygium inophylloides*	0.5%
		-	-	-	*Unidentified 10*	0.5%
		-	-	-	*Unidentified 8*	0.5%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

Table 7 Relative abundance >5 cm dbh, in the forest harvested five years ago.

Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	
		I	U	NTFP	*Aidia racemosa*	29.8%
	Pioneer	I	C	Timber	*Dysoxylum spp*	22.0%
	Shade tolerant	I	C	Timber	*Diospyros samoensis*	9.4%
		I	C/E	Timber	*Terminalia richii*	4.9%
	Pioneer secondary	I	C/U	NTFP	*Premna serratifolia*	4.1%
	Pioneer secondary	I	U	NTFP	*Pipturus argenteus*	3.3%
	Pioneer secondary	I	C/U	NTFP	*Omalanthus nutans*	2.9%
Low	Intermediate	M	C	Timber	*Elaeocarpus grandis*	2.0%
	Intermediate	E	C	None	*Elaeocarpus ulianus*	2.0%
	Pioneer	I	C	NTFP	*Glochidion ramiflorum*	2.0%
	Pioneer	P	C/U	NTFP	*Morinda citrifolia*	2.0%
High	Pioneer	M	C	Timber	*Adenanthera pavonina*	1.6%
		I	C	None	*Crateva religiosa*	1.6%
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	1.6%
		I	C	Timber	*Syzygium inophylloides*	1.6%
		I	C/U	None	*Syzygium carolinense*	1.2%
		I	C	NTFP	*Barringtonia samoensis*	0.8%
		I	C/U	NTFP	*Ficus scabra*	0.8%
		I	C	NTFP	*Flacourtia rukam*	0.8%
		I	U	NTFP	*Psychotria insularum*	0.8%
	Pioneer secondary	I	C	NTFP	*Aglaia samoesis*	0.4%
Low	Pioneer secondary	P	C	NTFP	*Cananga odorata*	0.4%
Low		M	U	None	*Carica papaya*	0.4%
	Intermediate	E	C	NTFP	*Cryptocarya elegans*	0.4%
	Intermediate	I	C	Timber	*Elaeocarpus floridanus*	0.4%
		E	U	None	*Ficus godeffroyi*	0.4%
		I	U	NTFP	*Ficus tinctoria*	0.4%
	Pioneer Long-lived	I	C/E	Timber	*Garuga floribunda*	0.4%
	Intermediate secondary	P	C	Timber	*Inocarpus fagifer*	0.4%
		I	C	NTFP	*Myristica inutilis*	0.4%
		I	C	Timber	*Neonauclea forsteri*	0.4%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

Table 8 Relative abundance >5 cm dbh, in the forest harvested 10-15 years ago.

Threat[1]	Light Class	Origin[2]	Stature[3]	Status[4]	Species	
	Pioneer secondary	I	C/U	NTFP	*Macaranga harveyana*	67.9%
	Pioneer secondary/ Coastal	I	C/U	NTFP	*Hibiscus tiliaceus*	19.6%
	Pioneer	I	C	Timber	*Dysoxylum spp*	8.9%
Low		M	U	None	*Carica papaya*	1.8%
	Pioneer secondary	I	C/U	NTFP	*Omalanthus nutans*	1.8%

1. Threat: High= High invasive risk, low= low invasive risk (PIER)
2. Origin: M=Modern; I=Indigenous; E=Endemic.
3. Stature: U=Understory; C=Canopy; E=Emergents.
4. Status: NTFP=Non Timber Forest Products.

APPENDIX 2

Tables showing previous collected data over species distribution in earlier studies.

Table 9 Relative abundance of trees (>5 cm dbh) from before cyclones and straight after in the natural disturbed forest.

		>5 cm in dbh		
Species	Before Cyclones	After 'Ofa'	*Species*	After 'Val'
Pometia pinnata	25.0%	31.1%	*Pometia pinnata*	34.2%
Cananga odorata	22.1%	10.9%	*Dysoxylum spp*	15.1%
Aglaia samoensis	12.3%	10.3%	*Planchonella samoensis*	11.2%
Syzygium inophylloides	10.8%	10.9%	*Syzygium inophylloides*	8.5%
Mammea glauca	10.0%	9.8%	*Mammea glauca*	5.8%
Dysoxylum spp	7.1%	8.1%	*Aglaia samoensis*	5.2%
Planchonella samoensis	5.8%	8.8%	*Inocarpus fagifer*	4.8%
Garuga floribunda	2.9%	4.1%	*Cananga odorata*	4.6%
Inocarpus fagifer	2.0%	3.0%	*Garuga floribunda*	4.6%
Diospyros samoensis	1.0%	2.1%	*Diospyros samoensis*	2.3%
Canarium vitiense	<0.5%	<0.5%	*Canarium vitiense*	<0.5%
Flaucortia rukam	<0.5%	<0.5%	*Flaucortia rukam*	<0.5%
Guettarda speciosa	<0.5%	<0.5%	*Guettarda speciosa*	<0.5%
Kleinhovia hospita	<0.5%	<0.5%	*Kleinhovia hospita*	<0.5%
Myristica inutilis	<0.5%	<0.5%	*Myristica inutilis*	<0.5%
Psydrax merrilli	<0.5%	<0.5%	*Psydrax merrilli*	<0.5%
Rhus taitensis	<0.5%	<0.5%	*Rhus taitensis*	<0.5%
Tabernaemotana pandacaqui	<0.5%	<0.5%	*Tabernaemotana pandacaqui*	<0.5%
Terminalia catappa	<0.5%	<0.5%	*Terminalia catappa*	<0.5%
Alphitonia zizyphoides	<0.5%	0%	*Alphitonia zizyphoides*	0%

Data from Elmqvist, Rainey, Pierson, and Cox 1994

Table 10 Relative abundance of trees (>5 cm dbh) after five years of recovery in the natural disturbed forest (Nd) and in the cumulative disturbed forest (cNd).

	>5 cm in dbh		<5 cm in dbh	
Species	After 5 yrs Nd	After 5 yrs cNd	After 5 yrs Nd	After 5 yrs cNd
Macaranga harveyana	42.1%	85.8%	7.2%	69.7%
Cananga odorata	15.0%	1.9%	7.8%	29.5%
Pometia pinnata	12.4%	1.1%	28.3%	2.8%
Antirhea inconspicua	6.9%	<1.0%	2.4%	3.0%
Inocarpus fagifer	3.4%	0%	1.2%	0%
Myristica inutilis	3.0%	0%	8.4%	0%
Kleinhovia hospita	2.6%	1.4%	<1.0%	<1.0%
Dysoxylum spp	2.1%	<1.0%	9.4%	2.9%
Mammea glauca	1.7%	<1.0%	10.8%	6.9%
Syzygium inophylloides	1.7%	0%	9.9%	0%
Diospyros samoensis	1.3%	<1.0%	38.4	48.1%
Rhus taitensis	<1.0%	7.4%	1.7%	21.3%
Aglaia samoensis	<1.0%	0%	3.9%	0%
Planchonella samoensis	<1.0%	0%	5.9%	0%
Canarium mafoa	<1.0%	0%	6.1%	0%
Garuga floribunda	0%	<1.0%	0%	15.4%
Aidia racemosa	<1.0%	<1.0%	91.4%	6.2%
Citronella samoensis	<1.0%	0%	1.20%	0%
Cryptocarya elegans	<1.0%	0%	4.20%	0%
Elattostachys falcata	<1.0%	<1.0%	1.2%	9.3%
Erythrospermum aquminatissimum	<1.0%	0%	2.4%	0%
Ficus godeffroyi	<1.0%	0%	7.0%	0%
Ficus scabra	<1.0%	<1.0%	1.4%	2.6%
Funtumia elastica	<1.0%	<1.0%	2.4%	9%
Morinda citrifolia	<1.0%	<1.0%	3.5%	30%
Planchonella garberi	<1.0%	<1.0%	19.6%	21.8%

Data from Hjerpe, Hedenås, and Elmqvist 2001

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