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Vulnerability and resilience of forest ecosystems to plant invasions in the islands of Tahiti and Moorea

(Society archipelago, French Polynesia)

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Vulnerability and resilience of forest ecosystems to plant invasions in the islands of Tahiti and Moorea (Society archipelago, French Polynesia)

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Abstract

Biological invasions are a major threat to biodiversity, especially in the more vulnerable island ecosystems. Invasive alien plants can change forest composition, structure and dynamics, by outcompeting native trees and/or interfering with their regeneration. On the tropical oceanic islands of Tahiti and Moorea, more than 30 plant species are invading native forests and threatening endemic and indigenous plant species. In order to assess the vulnerability of forests, we measured basal area, stems number, seedlings density and species richness of all woody species in seven 10 x 20 m plots in Tahiti and ten 20 x 20 m plots in Moorea. We compared some of our results with data obtained in the last 2-8 years. Our study shows that the mid-elevation rainforests below 1,100 m in Tahiti is more invaded by alien trees while montane cloud forests seem to be more resistant to invasion. However, the herbaceous strata at high elevation is also invaded by the subshrub *Rubus rosifolius* which may have an impact on woody species regeneration. No significant changes of the forest structure and composition with time were found in Tahiti. On Moorea, any clear pattern of forest structure and composition was observed in the low and mid-elevation rainforests. Nevertheless, only two invasive trees, *Miconia calvescens* and *Spathodea campanulata*, occurred in the mid-elevation rainforests where the native trees seem to regenerate more efficiently on ridge habitat. Restoration attempts might be more effective in the mid-elevation invaded rainforests of Tahiti and Moorea where native tree seedlings recruitment does occur.

Keywords: invasive plants, forest dynamics, island ecosystems, regeneration, seedlings

Contents

Introduction

Biological invasion is defined as the establishment and spread of non-indigenous (or alien, non-native, exotic) species. Human activities have vastly increased dispersal distances of thousands of species. The mixing of species and functional groups that have never been associated during their evolutionary history amplifies the trend toward the global homogenization of biota. Humans increase the arrival rate, population propagule pressure, the availability of modified habitats and all of which facilitate the establishment and spread of introduced biota (Rejmanek and Simberloff, 2011). It has been shown that anthropogenic activity is, in some places, the most important factor determining an invasive species pattern in natural areas (Frankel et al., 1995; Kueffer et al., 2010). Invasive alien species can affect all components of an environment, from ecosystem processes (Dyer and Rice, 1999; Kourtev et al., 2003; Mack et al., 2001; Vitousek and Walker, 1989) to biodiversity patterns (Brown and Gurevitch, 2004) and community structure (Brown et al., 2006; Frankel et al., 1995; Gratton and Denno, 2005). A wide range of ecosystem functions can be affected by alien invasive plant species, like geomorphological processes, nutrient cycles, fire regimes, and native species seedling recruitement (Frankel et al., 1995; Rejmanek and Simberloff, 2011; Yelenik and D'Antonio, 2013).

Some ecosystems seem to be more susceptible to introduction than others, with island communities suffering the highest accretion of exotics while desert and savanna communities suffer the least (Brockie et al., 1988; Lonsdale and Braithwaite, 1991). The « island syndrome » referring to morphological, ecological, ethological and genetic changes of communities and populations in a situation of geographical remoteness and confinement includes a lower number of species (compared to mainlands), high endemism, interspecific competition easing off and vulnerability faced with disturbances (Blondel, 1995). Island communities which have been remote for a long time, live in so particular and different conditions compare to those prevailing on mainlands that they form a co-adapted and highly structured ensemble (Blondel, 1995; Simberloff, 2009). It makes them vulnerable to invasion, especially when the new species is introduced by human (Elton, 1958). Invasive alien plant species have significant ecological and economic impacts especially on islands ecosystems (Lee, 2011; Roderick and Vernon, 2009; Schmidt et al., 2012) where they are particularly competitive towards native species, which may be unable to easily preempt the available resources (Denslow, 2003). Moreover, invasive alien species are mostly generalist and can displace the native flora (Blondel, 1995; Lee, 2011). On an island, the introduction of only one species can have dramatic consequences on the diversity of a whole ecosystem (Blondel, 1995): In the Hawai'i Volcanoes National Park, it has been shown that one single invasive plant species is able to modify the characteristics of a whole ecosystem (Vitousek and Walker, 1989).

Disturbances can play a critical role in alien plant invasions. They provide entry points for introduced species and suitable habitats for their expansion (Eschtruth and Battles, 2009; Hobbs, 2011). Alien plants that are able to respond favorably to fluctuating post-disturbance conditions will most likely establish and spread (Brown et al., 2006). Therefore, some invasive alien plant species are even able to colonize in primary forest (Brown et al., 2006) and become themselves a disturbance or contribute to altering natural disturbance regimes (Hobbs, 2011).

Forest ecosystems are affected by natural disturbances (treefall gaps, cyclones, landslides, floods) which influence the spatial and temporal composition of forest patches (Puig, 2001; Vargas G. et al., 2013). Forest composition, structure and dynamics are dependent on the response of tree regeneration to site conditions, disturbances and management practices (Gray et al., 2005; Grubb, 1977). The successful regeneration of a plant species in a specific place depends on many processes like the production of viable seeds, flowering, pollinisation, setting and dispersal of seeds through space and time, germination, establishment and spread. It also depends on the characteristics of the site including size and shape, orientation, nature of the soil, litter, other plants, animals, and microorganisms present in this place (Grubb, 1977). As mentioned before, invasive alien plant species can limit native plant growth, change species composition, and alter plant succession trajectories (Brown et al., 2006; Lichstein et al., 2004) and prevent native species recovery (Yelenik and D'Antonio, 2013).

This present study was conducted in the tropical rainforests of two small and remote Pacific islands, Tahiti and Moorea. Both have a relatively high floristic richness because of the wide diversity of ecological habitats that occur along the elevation gradient (Chevillotte et al., 2014). The arrival of the first European explorers in French Polynesia led to massive destruction of native habitats, overuse of natural resources and a dramatic increase in the number of introduced alien plants and animals. Consequently, 1558 alien species were inventoried in French Polynesia in 2008, 57 of them are considered invasive (Fourdrigniez and Meyer, 2008) including 35 legally declared a threat to biodiversity. All of them have been introduced since the arrival of the first European explorers (Meyer et al., 2008). 33 of them are found in Tahiti and Moorea (Meyer et al., op. cit). The most dominant is the small tree *Miconia calvescens*, introduced as an ornamental plant in 1937, which has caused severe impacts on biodiversity and forest dynamics (Meyer and Florence, 1996). By decreasing the light in the understory, *Miconia calvescens* caused the decline of many endemic plant species in French Polynesia (Meyer and Florence, op. cit.). This plant invader now covers 80,000 ha on the island of Tahiti and 2,500 ha on Moorea. In 2000 a bio-control pathogen agent, the fungus *Colletotrichum gloeosporioides f. sp. miconiae* (C.g.m) was release in Tahiti in order to weaken the *Miconia calvescens* growth and spread (Meyer and Killgore, 2000). This fungus has caused anthracnosis and partial defoliation of *Miconia calvescens* (Fourdrigniez and Taputuarai, 2009) and favoured the recruitment of native plants, including rare threatened endemic plants, by enhancing the light availability in the understory (Meyer et al., 2007). Other dominant invasive trees found in Tahiti and Moorea forests are the African tulip tree *Spathodea campanulata* and the strawberry guava *Psidium cattleianum* (Pouteau et al., 2013).

The study of the long-term dynamics of mixed native and non-native plant communities may help to better predict the vulnerability of particular island ecosystems to invasions (Kueffer et al., 2010).

Our specific goals are:

- to assess the diversity and abundance of endemic, indigenous and introduced woody plant species in permanent plot set up on an elevation gradient in Tahiti and in three different sites on Moorea in 2014;

- to highlight the changes of these plant communities with time, by studying their basal area over years and their seedling recruitment which constitute the reflection of the future forests in Tahiti and Moorea.

Materials and methods

Study sites

This study is conducted in French Polynesia, in the Society Archipelago (15°-18° S, 148°154°W), on two high volcanic tropical islands: Tahiti (17°35' S 149°30' W) and Moorea (and 17°33' S 149°50' W). Tahiti is between 0.5 and 1 Myr. (Bonneville, 2009) Moorea is between 1.5 and 1.8 Myr (Le Dez et al., 1998). Tahiti is the largest and highest island in French Polynesia, covering 1,045 km² and reaching 2,241 m at its highest peak. Moorea, located 20 km from Tahiti, is 142 km² with a highest peak at 1,207 m (Laurent et al., 2004; Meyer and Salvat, 2009). The climate of the Society Islands is wet tropical (annual mean temperatures between 25°C to 27°C at sea level), with important rainfalls during the warm and humid season, from November to April (Laurent et al., 2004). In our study sites, the annual average rainfall is comprised between 2,300 and 3,500 mm (Laurent et al., 2004).

The French Polynesian islands are located more than 5,000 km away from the nearest continents. Because of their geographic isolation, relatively young geological age and small size, their native terrestrial fauna and flora are impoverished in terms of species numbers. However, isolation and habitat diversity, has resulted in high species endemism. In French Polynesia 550 of the 880 native vascular plant species are endemic (62 % endemism) with a high number of endangered species: 47 threatened plants species according to the IUCN Red Lists (Meyer and Salvat, 2009). One of the main threats to the French Polynesian tropical rainforests are invasive alien plant species such as *Miconia calvescens* (Meyer and Florence, 1996).

On Tahiti, two sites located on the leeward coast (Mt Aorai, Mt Marau) were selected for this study because of their accessibility. A total of fourteen 10 x 10 m permanent plots were set up at 7 different altitudes between 600 and 1,320 m in mid-elevation rainforests to high elevation cloudforests (Fig.1) (Table 1). Because the topography did not permit to install

20 x 10 m permanent plots, at each elevation, two 10 x 10 m plots were studied and data from both plots were gathered together in order to be analyzed as data from one 10 x 20 m plot. On Moorea, three study sites were selected (Opunohu valley,Vaianae valley, Mt Mouaroa) with a total of ten 20 x 20 m permanent plots located between 190 and 500 m in low- to mid-elevation rainforests (Fig.2). Each of the ten 20 x 20 m plots was split in four 10 x 10 m plots (Table 1).

Structure and composition of the shrub and tree layer

In this study, the shrub and tree layer refers to the shrubs and trees between 1.3 m and the top of the canopy.

In all plots set up on the islands of Tahiti and Moorea, the diameter at breast height (1.3 m) of stems of all woody species was measured in order to calculate the "native basal area" for all indigenous and endemic plants and the "alien basal area" for all non-native naturalized species. A tree basal area is the cross-sectional area of a tree trunk measured at breast height. In trees it is measured through the diameter, usually at breast height (DBH) (Mueller-Dombois and Ellenberg, 1974). Basal area is expressed in cm^2/m^2.

The basal area was calculated using this formula:

$$\text{Basal area} = \left[\Sigma \; (\pi \times DBH^2) / 4 \right] / \text{plot area}$$

The alien species basal area provides an index of the degree of invasion in each plot whereas the native species basal area provides an index of resistance to invasion.

The number of stems of native and alien species has been counted as well as the number of species. Using stems abundance of each species, Simpson's S index was calculated for each plot. The Simpson's S index is an evenness index, its value is the probability that two randomly selected individuals from a community will be the same species. The larger the value, the less diverse the community must be. If there is only one single species in the community, the value would be one, as you would be bound to find the same species each time you sampled at random. The formula for Simpson's S index is:

$$S = \Sigma \; (n / N)^2$$

n is the total number of stems of a particular species in the plot, N is total number of stems in the plot (Gardener, 2013).

McNaughton I index has also been calculated for each plot using stems abundance for each species. This index is a dominance index and it expresses the percentage of stems of the two most dominant species in a plot. The formula for the McNaughton I index is:

$$I = [(n_1 + n_2) / N] \times 100$$

n_1 is the total number of stems of the most abundant species in the plot, n_2 is the total number of stems of the second most abundant species in the plot, N is the total number of stems in the plot (McNaughton, 1968).

Woody species seedlings

Two different sampling methods were used to determine which one was better to sample most of the seedlings woody species. The first one consists of sampling 20 m² in the 100 m² plot by setting up twenty 1 x 1 m quadrats, the second method consists of sampling the same surface with five 2 x 2m plots. The first method allowed to count more woody species in the quadrats than the second method (Appendix A) and was thus selected for data analysis.

In Tahiti, all 100 m² permanent plot were divided in one hundred 1 x 1m quadrats. In order to avoid edge effects, the 32 quadrats placed at the boundary of the plot were excluded from the study. Among the other 68 quadrats, twenty 1 x 1m quadrats were randomly selected (Fig.4) using the ALEA() function and the EQUIV(PETITE.VALEUR()) function on the Calc spreadsheet of the Apache Openoffice ™ 4.1.0 software ("Apache OpenOffice ™ 4.1.0," 2014). In each randomly selected quadrats, all woody seedlings and saplings smaller than 1.3 m in height were counted. The non-woody species were not counted with the exception of the alien subshrub *Rubus rosifolius.* At each elevation, data of both 100 m² plots were gathered together, so a total of forty 1 x 1 m quadrats were used to estimate mean seedlings density at each elevation. Only twenty 1 x 1m quadrats were used to compare seedlings densities in measured in 2013/2014 with seedlings densities measured in 2012 (Savea, 2012).

In Moorea, all the 400 m² permanent plot were split in four 100 m² plots. Two diagonally opposite 100 m² plots were randomly selected in order to measure woody species seedlings density. These two selected plots were also divided in one hundred 1 x 1 m quadrats. In each of the two 100 m² selected plots, twenty 1 x 1 m quadrats were randomly selected in the same way than Tahiti (Fig.4). In these quadrats, the same methodology was used to measure woody species seedlings density.

In Moorea and Tahiti, the evenness index, Simpson's S index (2) as well as the dominance index, Mc Naughton I index (3) were also calculated for the woody species community in the herbaceous layer (from 0 to 1.3 m), on the 40 m² area studied in each plot. We also counted the number of alien and native woody species in the herbaceous layer in 10 x 20 m plots in Tahiti and 20 x 20 m plots in Moorea.

Data analysis

Statistical analysis was carried out using the R free Software (R Core Team, 2013).

Structure and composition of the shrub and tree layer

In 2014

In Tahiti and Moorea, the differences between native and alien species basal areas in the different plots were compared in order to assess a pattern of native and alien basal area along an elevation gradient. The proportion between native and alien stems abundance in the plots were compared as well as the number of native and alien species. In the two first cases a

ChiSquare test was run, and a Fisher test was used to compare the number of native and alien species between the plots (Poinsot, 2005, 2004). Then, « pairwise proportional tests » which perform pairwise comparisons between pairs of proportions with correction for multiple testing (R Core Team, 2013) were used in the three cases.

Woody species seedlings

In Tahiti, the woody species seedling abundances of the two groups of species (native and alien) in the different plots were compared using a Kruskal-Wallis test (Poinsot, 2005, 2004) followed by a « Pairwise Wilcoxon Rank Sum Tests » which performs pairwise comparisons between group levels with corrections for multiple testing (R Core Team, 2013) in order to assay a pattern of native and alien seedling abundance along an elevation gradient. Woody seedlings abundances measured on a 20 m^2 area in three plots of Tahiti (AOR-600, AOR-900 and AOR-1000) in 2013/2014 were also compared with woody seedlings abundances measured as part of former studies carried out in 2012 (Savea, 2012), using the same tests.

In Moorea, woody species seedling were counted for the first time in 2014. The abundance of the two groups of species (native and alien) in the different plots were compared using a Kruskal-Wallis test (Poinsot, 2005, 2004) and a « Pairwise Wilcoxon Rank Sum Tests » too, in order to assess a pattern of native and alien seedling abundance along an elevation gradient and to be a benchmark for future surveys.

For each island, a Fisher test (Poinsot, 2005, 2004) was run to compare the native and alien woody species richness between the different plots.

Comparison over time

In Tahiti, the proportion between native and alien species basal area, number of stems and number of species were compared with time in three 10x10 m plots at AOR-600, AOR-900 and AOR-1000 plots where basal area were measured as part of former studies carried out in 2005, 2007 and 2008 in AOR-600 and AOR-900 plots and in 2007 and 2008 in AOR-1000 plot (Fourdrigniez and Taputuarai, 2009) performing a ChiSquare test followed by a « pairwise proportional test ».

In Moorea, the proportion between native and alien species basal area, number of stems and number of species were also compared with time in all plots with former measurements carried out in 2010 (Fraisse, 2010) and 2006 (Chevillotte et al., 2014) performing the same tests as in Tahiti plots.

Correlation test

Spearman and Pearson correlation tests have been carried out in order to find interrelation between the different measured variables.

Results

TAHITI

Structure of the shrub and tree layer

Basal area

The proportion between alien and native species basal area are significantly different between the plots below and above 1,000 m elevation (p-value < 0.001). The basal area bar chart (Fig.4) shows that below 1,000 m elevation, alien species basal areas are higher than 35 cm^2/m^2 and native species basal areas are smaller than 2 cm^2/m^2 in our plots. However, from 1,000 m elevation alien species basal areas in our plots are lower than 30 cm^2/m^2 and native species basal areas are higher than 15 cm^2/m^2. Above 1,200 m elevation, the native species basal area is higher than the alien species basal area.

Stems density

The proportion between alien and native species stems number is also significantly different between high and low elevation (p-value < 0.001) (Fig.4). In plot below 1,100 m elevation, more than 90% of the stems are alien species stems whereas in plot from 1,100 elevation they are less than 60% (Appendix B).

Even if no correlation has been found between elevation and alien or native basal area or stems density (Table 2), our data shows that shrub and tree layer community structure is significantly different below and above 1,000 m or 1,100 m elevation.

In the plots of Tahiti, native species basal area is negatively correlated with alien species basal area (p-value < 0.05) and native species stems density is also negatively correlated with alien species stems density (p-value < 0.05).

Composition of the shrub and tree layer

Species richness

Regarding the number of species, the proportions between the number of alien and native species are not significantly different between plots in Tahiti (Table 3). But correlation test shows that native species richness in the shrub and tree layer is positively correlated with elevation (p-value < 0.001) (Table 2). Indeed, from 1,100 m elevation, the number of native species is higher than 8 in all plots whereas it is lower than six below 1,100 m elevation (Appendix B). In Tahiti native species diversity is more important at high elevation.

In the other hand, native species stems density is positively correlated with native species richness in shrub and tree layer (p-value < 0.05) (Table 2) which means that in plot where the native species richness is important, the number of native species stems is higher.

Evenness and dominance

Simpson's S index of shrub and tree layer is negatively correlated with the altitude in the plots of Tahiti (p-value < 0.05) (Table 2). Indeed, Simpsons's S index is comprised between 0.7 to 0.95 from AOR-600 to AOR-1000 whereas it is lower than 0.35 from plot MAR-1100 to AOR-1300 (Table 3), indicating that the stems on the plots are not evenly distributed between the species.

The McNaughton I index is higher than 95 from AOR-600 to AOR-1000 which mean that more than 95 percent of the stems belong to only two species in these plots whereas it is lower than 69 from AOR-1100 to AOR-1300. Actually, the shrub and tree layer in low elevation plots are more invaded by alien woody species than higher elevation plots, especially by the invasive plant species *Miconia calvescens* which is the species with the higher number of stems in all plots below 1,100 m elevation (Appendix B).

<u>Woody seedlings</u>

Alien vs native

The seedlings density of alien woody species in the study plots in Tahiti is significantly higher than the native seedlings density in AOR-600, MAU-800 and AOR-1000 (p-value < 0.01) while there is no significant difference between alien and native species seedlings density at higher elevation (Fig.5).

It is interesting to note that in the Tahiti plots, the alien woody species seedlings density is positively correlated with alien woody species stems density (p-value < 0.01) whereas the native woody species seedlings density is not correlated with the native woody species stems density (Table 2). It seems that the more alien stems number there are, the more there will be alien woody species seedlings in the plots and it is not the same for native woody species.

There is also a negative correlation between alien seedlings density and native woody species richness in the shrub and tree layer (p-value < 0.05) (Table 2), which means that more rich is the shrub and tree layer with native species, less the non-native species are able to regenerate.

Regarding the number of woody seedling species, the distribution of alien and native species are not significantly different between the plots in Tahiti (Table 3). The Simpson's S index of woody seedlings species is not correlated with elevation (Table 2). This index, in the shrub and tree layer as in the herbaceous layer, has the most important value in AOR-1000 plot. In this plot, if you randomly choose 2 seedlings in the 40 m^2 sampling are, you have 81 % of chance that they are from the same species, in this case the *Miconia calvescens.* The Mc Nauhgton I index higher values in the herbaceous layer are in the MAU-800 and in the AOR-

1200 plots, respectively 95.45 and 100 (Table 2). These values are explained by the fact that a few number of seedlings (44 and 8) and a few number of species (3 and 2) where sampled in these plots (Appendix C). In MAU-800, 95.45 % of the sampled seedlings are *Miconia calvescens* or *Psidium cattleianum*, in AOR-1200, 100 % of the sampled seedlings were *Miconia calvescens* or endemic species belonging to the genera *Myrsine* (Appendix C).

Alien woody species

Alien species seedlings density is negatively correlated with elevation (p-value < 0.05) (Table 2. There is a strong decrease of alien species seedlings density between 1,000 m and 1,100 m (Fig.5) which indicates that high elevation forest are relatively intact (almost not invaded) by alien species seedlings. However, in AOR-1200 and AOR-1300 plots, the herbaceous layer is invaded by the invasive subshrub *Rubus rosifolius* and alien species seedling density is negatively correlated with *Rubus rosifolius* density in our plots set up in Tahiti (Table 2). In all studied plots, among all species present in quadrats, the invasive species *Miconia calvescens* has the higher density of seedlings, except in AOR-600 where the invasive tulip tree *Spathodea campanulata* has the most important seedling density in the quadrats (Appendix C).

Native woody species

The density of native woody seedlings seems to decrease above 1,100 m in our plots (Fig.5) even if this decline is not significant. In the two higher plots, native species regeneration is almost absent on the ground and this is not related to forest invasion (Table 2 and Fig.4). This can be explained by the fact that most of the seedlings we observed in high elevation plots were not found on the ground, but as epiphyte on living trunk and tree fern stipes. Thus, our experimental design doesn't permit to quantify all the seedlings of woody species present in the plots.

<u>Change with time</u>

Structure and composition of the shrub and tree layer

No difference was observed in the proportion between alien and native species basal area with time in plots where basal area has been measured for nine years (AOR-600 and AOR-900) or seven years (AOR-1000) (Fig.6). AOR-600 and AOR-900 are still very invaded by the two dominant invasive alien species: *Miconia calvescens* and *Spathodea campanulata* (Appendix C). In these plot, alien species basal area is higher than 30 cm^2/m^2 and native basal area is lower than 1 cm^2/m^2 over the nine past years. In AOR-1000 native basal area is higher than alien basal area. Even if alien basal area seems to have increased between 2008 and 2014, the proportions of native and alien basal area have not significantly changed yet.

There is also no difference of proportion between alien and native species stems number or species richness over time in these plots (Table 3). No significant change has been noticed over the past nine or seven year in these three plots.

Seedlings density

In 2012, there was a significant difference between AOR-600 and AOR-900 alien species seedling densities (Fig.7). But this difference was not observed in 2013. In 2012 and 2013 alien seedlings density have been higher than native seedlings density in AOR-600 plot (p-value < 0.001). At low elevation (600 m) the regeneration of alien woody species is more important than the regeneration of native woody species. A more long term survey could allow to observe a possible change of this two groups of seedlings.

A former study was carried out in 1994 (Meyer, 1994) in a plot set up in the same area than our AOR-600 plots. This former plot was placed between our two 10 x 10 m plots forming. At this time, only three alien woody species were present in the herbaceous strata as seedlings or young plants (< 1.3 m tall): *Miconia calvescens*, *Spathodea campanulata* and *Syzygium cumini*. A total of 13 woody species, including four native species are found today in our AOR-600 plots (Appendix C).

MOOREA

Structure of the shrub and tree layer

Basal area

In Moorea, the proportions between alien and native species basal area were different between some plots but these differences did not allow to assess a pattern of alien and native species basal area either along an elevational gradient or between sites (Vaianae, Opunohu, Mouaroa) (Fig.8). For example OPU1 is a low elevation plot in Opunohu valley and its proportions between basal areas are significantly different from OPU2, a low elevation plot in the same valley (p-value < 0.01), but not significantly different from MOU1 which is a higher elevation plot on the ridge of Mouaroa and VAI4 which is also at higher elevation in the valley of Vaianae (Fig.8). Proportions between alien and native woody species basal area in plots of Moorea does not seem to be structured either along an elevational gradient or in different sites.

Stems density

The same conclusion is made with proportion between alien and native species stems density in the plots of Moorea where some closed plots present significant differences and some distant plots are not different in terms between proportion between alien and native number of stems (Fig.8) (Appendix D). Alien and native woody stems density in the plots of Moorea does not seem to be structured either along an elevational gradient or in different sites.

It can be noticed that OPU1 plot has the higher native species stems density and OPU2 plot has the higher native species basal area, both of them are the lower elevation plots (Fig.8).

In Moorea, the alien species stems density is negatively correlated with the alien species richness in the shrub and tree layer (p-value < 0.05) (Table 4). We observed that the invasive tree *Miconia calvescens* tends to form monospecific cover in the plots of Mouaroa (Appendix D).

In plots of Moorea, as it is observed in Tahiti, native species basal area is negatively correlated with alien species basal area (p-value < 0.05) and native species stems density is also negatively correlated with alien species stems density (p-value < 0.05) (Table 4).

Composition of the shrub and tree layer

Species richness

Regarding the number of species, the distribution of the alien and native species are not significantly different between the plots in Moorea (Table 5). In Moorea, the alien species richness is correlated with elevation, but negatively in this case, unlike the alien species richness in Tahiti (Table 3 and Table 4). Indeed, above 400 m elevation, only two alien species remain in our plots, *Miconia calvescens* and *Spathodea campanulata,* which are the two dominant invasive trees in Tahiti and Moorea (Appendix E).

Evenness and dominance

Simpson's S index of shrub and tree layer is comprised between 0.10 and 0.70 in the plots of Moorea (Table 5) but does not seem to be arranged along an altitudinal gradient since no correlation has been found between Simpson's index value and elevation (Table 4). Actually, the higher values of this index are found in the plots located at 250 m (VAI1) and 500 m elevation (MOU3) while its lower values are found in the plots located at 200 m (OPU2) and 400 m elevation (MOU1) (Table 5). In all the plots of the Opunohu valley Simpson's S index is lower than 0.3 (Table 5). The stems of these 3 plots are relatively evenly distributed between species.

VAI1 and MOU3 plots has also the higher McNaughton I index value, respectively 89.97 and 86.12 (Table 5). It means that in VAI1 plots, more than 89 % of the stems are 2 species, the invasive tree *Miconia calvenscens* with a mean of 0.77 stems per m² and the indigenous species *Freycinetia impavida* with a mean of 0.03 stems/m² (Appendix D). In MOU3 more than 86 % of the stems belong to *Miconia calvescens* species with a density of 1.28 stems per m² and to the indigenous species *Crossostylis biflora* species with 0.09 stems/m² (Appendix D). VAI1 and MOU3 plots are highly dominated by *Miconia calvescens*. The two lower values of Mcnaughton I index are also in OPU1 (25.81) and MOU1 (39.52) (Table 5) attesting that they are the most even study plots in term of stems distribution.

Woody seedling

Alien vs native

Alien species seedling density and native species seedling density are significantly different (p-values < 0.001) in four plots in Moorea: VAI3 (235 m), OPU4 (300 m), VAI4 (365 m) and MOU3 (500 m) (Fig.9). Even if native species seedlings density is positively correlated with elevation (p-value < 0.05) and alien species seedlings density is not (Table 4), the latter is still significantly more important than native seedlings in the higher plot (MOU3) (Fig.9).

In Moorea plots, as observed in Tahiti plots, the introduced woody species seedlings density is negatively correlated with the native species richness in the shrub and tree layer (p-value < 0.001).

The Simpson's S index of woody seedlings species is not correlated with elevation in this island (Table 4). The higher value of the Simpson's S index are in MOU3 plot (0.78), VAI4 plot (0.67) and OPU4 plot (0.44) (Table 5). These three plots are the less even regarding the number of stems per species. The lower Simpson's S index value are in VAI2 plot and MOU1 plot (Table 5). The stems in these two plots are relatively evenly distributed between all the species. The McNaughton I index confirm these facts as MOU1 and VAI2 plots has also the lower value of McNaughton I index (Table 5) and the higher values are in MOU3 plot (92.43), OPU4 plots (88.57) and VAI4 (85.71) plots (Table 5). The two dominant species in MOU3 are the *Miconia calvescens* (1.13 seedlings/m²) and the indigenous species *Crossostylis biflora* (0.06 seedlings/m²) (Appendix E). The two dominant species in OPU4 re the *Miconia calvescens* (0.05 seedlings/m²) and the introduced invasive species *Merremia peltata* (0.025 seedlings/m²) (Appendix E). The two dominant species in VAI4 are *Miconia calvescens* (0.03 seedlings/m²) and the invasive African tulip tree *Spathodea campanulata* (0.065 seedlings per m²) (Appendix E). These three plots are dominated by the invasive tree *Miconia calvescens*.

Alien woody species

The higher plot MOU3 (500 m elevation) present the higher density of the alien species seedlings and it is significantly different with all other plots (p-values < 0.05) (Fig.9). Opunohu site is the only one where alien species seedling densities in the plots are not significantly different (Fig.9).

Alien woody species seedling density is negatively correlated with alien species richness, as well of the shrub and tree layer (p-value < 0.01) as of the herbaceous layer (p-value < 0.05). It seems that if there is less alien species on the plot, more the remaining alien species are able to regenerate.

Native woody species

In the plots of Moorea, the native woody species seedling density is positively correlated with elevation (p-value < 0.05) (Table 4), higher plots present the higher native species seedlings densities (Fig. 9). In the five higher plot, from 345 to 500 m elevation, native species seedling densities are not significantly different (Fig.9). Native woody species seem to regenerate efficiently at these altitudes. A comparison of native seedling density between the 3 differents sites (Mt Mouaroa, Vaianae and Opunohu) shows that the density is the most significantly different on the ridge of Mouraoa (p-value < 0.01) whereas densities in Vaianae and Opunohu are not significantly different each other (Fig.9). This can be explained by the fact that Vaianae and Opunohu are similar habitat (valleys) and Mouaroa is a ridge. In addition, the plots in Vaianeae and Opunohu valleys are all comprised between 190 ans 365 m elevation, whereas Mouaroa plots are located between 400 and 500 m elevation (Table 1).

It is interesting to notice that native woody species seedlings density in Moorea is correlated with shrub and tree layer species richness as well as herbaceous layer species richness (p-value < 0.05 and <0.01) (Table 4). The more important the species richness is, the more efficiently native woody species seem to be able to regenerate. Regarding the number of woody seedling species, the distribution of alien and native species are not significantly different between the plots in Moorea (Table 5).

Change with time

Structure and composition of the shrub and tree layer

The comparison between basal area measured in 2014 and basal area measured in 2010 and 2006 shows that the proportion between native and alien species basal area in our plots has significantly changed with time in three plots of Moorea (Fig.10). The alien and native species basal area distribution has significantly changed between 2006 and 2014 in OPU2 (p-value < 0.05) and VAI3 (p-value < 0.03) plots where a decrease of alien basal area with time was observed (Fig.10). In VAI3, a tree fall gap occured in 2010 (Fraisse, 2010) since when the alien basal area has slowly increased. In OPU4 plot, alien and native basal area distribution has significantly changed between each measurement: in 2006, 2010 and 2014 (p-value < 0.05). In 2006, alien species basal area was higher than native species basal area, in 2010, they were relatively similar and in 2014, native species basal area is now higher than alien species basal area. In these plots, the forest structure has changed for the last eight years, the native species basal area becoming more and more important. Although these plots are located between 200 and 300 m elevation, they seem resilient to invasive plant species.

Proportion between alien and native species stems number were different with time in the three plots OPU4, VAI3 and MOU1. In OPU4 and VAI3, the percentage of native stems increased significantly during the four last years -(p-value < 0.001 and p-value < 0.01) and which can also explain the increase of native basal area in these plots. In MOU1, the significant increase of the percentage of native stem number occurred between 2006 and 2010 (p-value < 0.01).

Regarding the species richness, there is no difference of proportion between alien and native species number over time in the plots of Moorea.

Discussion

Forest vulnerability to plant invasion

TAHITI

Our results show that in Tahiti, alien woody species basal area and number of stems are more important below 1,000-1,100 m elevation. Mid-elevation rainforests are relatively vulnerable to plant invasion compared to high elevation forest. The dominance of a few number of species, and particularly of the invasive alien tree *Miconia calvescens* in mid-elevation forests is confirmed by the relative high Simpson's S index and McNaughton I index.

In the low and mid-elevation rainforests, the regeneration of alien woody species is more important than the native woody species up to 1,000 m elevation. A longer term survey could allow to observe a possible change of these two groups of woody seedlings. In Tahiti, the more invaded the shrub and tree layers are and the more able to regenerate the alien species are, this fact highlight the invasiveness on alien woody species. It should be taken in account for future management practice, as the uprooting of invasive alien species could limit their regeneration.

Above 1,100 m elevation, the native and alien woody species regeneration is almost absent on the ground even if native species are more present in the shrub and tree strata. The high elevation forest doesn't seem to be able to regenerate by themselves on the ground in Tahiti. Further study should take in account herbaceous and subshrub species such as *Rubus rosifolius* which invade the high elevation herbaceous layer plot and could affect the woody species regeneration.

MOOREA

Regarding the composition, even if the mid-elevation forests seem resistant to many alien species, the remaining non-native alien species are two alien invasive species: *Miconia calvescens* and the African tulip tree *Spathodea campanulata* which strongly threat the biodiversity in French Polynesia (Meyer et al., 2008).

In Moorea plots, less the species richness is and more the alien species seem able to regenerate on the ground. Actually, we observed on the field that in poor species richness forest ecosystem, *Miconia calvescens* tend to form monospecific cover in the forest of Moorea as it has been observed for twenty years in Tahiti (Meyer and Florence, 1996).

On the top of Mt Mouaroa ridge, in mid-elevation forest, alien woody species regenerate more efficiently. It seems that the alien species community doesn't need to be rich in species to be able to regenerate efficiently. Less there are alien species, more the remaining species, *Miconia calvescens* and *Spathodea campanulata*, seem able to regenerate and invade the herbaceous layer.

At low elevation forest, native woody species appear to regenerate less compared to mid-elevation forest. Low elevation forest seems less resilient than mid-elevation forest, even if this latter is more invaded by invasive alien trees above 500 m elevation.

Forest resilience and resistance to plant invasion

TAHITI

The high elevation forest in Tahiti, both in term of structure and composition, appeared to be more resistance to woody plant invasion. The resistance of the forest seems to be correlated with elevation as high elevation forest seems to be almost free from any alien species. Our study show a relative resistance or resilience (if there are natural disturbances) of forest at higher elevation toward invasions by alien woody plant species, as it has been observed in high elevation montane in the Hawaiian islands (Daehler, 2005). High-elevation environments appear to be less affected by invasions because of the harsher climatic conditions and comparatively low human population densities and it has been assumed that this situation will not change substantially in the future (MA, 2003).

But it could be just a switch from alien woody species invasion to alien herbaceous or subshrub species invasion at higher elevation as the subshrub *Rubus rosifolius* seems to dominate the herbaceous layer at high elevation in Tahiti.

Morever, a global study has shown that the higher mountain, across wide climatic and latitudinal range, harbor ecosystems where invasion by non-native species has carefully begun, and where science and management have the opportunity to respond in time (Pauchard et al., 2008).

The regeneration of the forest at high elevation on the ground is very low. Natural regeneration of high elevation forest seems to be mainly epiphytic on ferns as it has been shown in La Réunion island (Rivière et al., 2008) and in Hawaiian rainforest (Medeiros et al., 1993). Further studies should be conducted on the seedlings growing on the ground as well as epiphytes using a more adapted protocol. For example by a survey of seedlings on living trunck between ground level and 1-2 m in height.

We note a higher ability of native woody species to regenerate at lower elevation, which should be taken in account for future management practice (e.g. restoration) at low elevation (600-900 m) forest in the island of Tahiti.

More importantly is the species richness and the less the non-native species seems to be able to regenerate in Tahiti forest ecosystem, so it is possible the native species richness has a negative impact on the alien species regeneration. This information could be another available avenue for research on the resistance mechanism of the rainforest and the implementation of possible restoration project in the forest of Tahiti.

The study of the regeneration over the two last years did not permit to highlight any changes as the period of time was short and the sampling area was smaller in 2012. However, the fact that no native species were observed in the herbaceous layer 20 years ago in the same area (Meyer, 1994) whereas 4 species were counted in 2013 can be the result of the introduction of the biocontrol agent *C.g.m.* in 2000 allowing the sunlight to reach the ground by causing anthracnosis and defoliation of the invasive alien tree *Miconia calvescens.* Further seedling density survey on a longer period and larger area would possibly show a trend on the native and alien species regeneration.

MOOREA

In our study the forest structure in Moorea does not seem to be organized either along an elevational gradient or in different sites. No particular pattern could be deduced from our measurements about the vulnerability to plant invasion of the forest of Moorea. Indeed some low elevation forests seem to be relatively resilient to plant invasion. The Opunohu valley seems, in term of number of stems per species, more even and less invaded by *Miconia calvescens* compared to two other study sites.

Native species seem to regenerate more efficiently above 300 m elevation and more particularly on the ridge habitat which should be taken in account for future management practice in the island of Moorea.

As it was observed in Tahiti, the most important is the native species richness and the less the non-native species seems to be able to regenerate in Moorea forest ecosystems, so it is possible the native species richness has a negative impact on the alien species regeneration. This information could be another available avenue for research on the resistance mechanism of the rainforest and the implementation of possible restoration project in the forest of both islands.

More plots should be set up on the three studied sites (Opunohu, Vaianae, Mouaroa) and on higher elevation sites in order to have a more important elevational gradient. Indeed, in our study, the amplitude of our altitude gradient was only 300 m and not help to highlight the effect of elevation on the forest structure and a possible resistance of high altitude forest to woody plant invasion as it is observed in Tahiti. It is not easy to set up an elevational gradient in Moorea as the relief is really steep and it has been difficult to find an appropriate site to set up at least a 10 x 10 m plot.

Conclusion

Our study highlight the invasion of the mid-elevation rainforests of Tahiti and the relative resistance of the montane cloud forest to alien woody species invasion. Our data on seedling recruitment also show that native woody species are able to regenerate in the mid-elevation forests of Tahiti whereas their regeneration is very low on the ground in the cloud forest. But this result might be related by the sampling bias, as commonly native and endemic seedlings are found as epiphytes and not on the ground at high elevation. The cloud forests of Tahiti is also invaded by the subshrub species *Rubus rosifolius*, indicating that our experimental design has to be modified and improved in order to take into account all form of regeneration and invasion in further survey.

Our study did not permit to highlight the effect of elevation on the regeneration and invasion of the rainforests of Moorea. However the ridge of Mt Mouaroa at about 500 m elevation seems to be a better habitat for the regeneration of native species but even more for alien woody species, especially the invasive alien tree *Miconia calvescens* which tend to form monospecific cover where the native species richness is low.

Overall our study highlights the urgently need for management practice and long term survey in both island of Moorea and Tahiti, particularly vulnerable, at low and mid-elevation, to woody alien plant invasion.

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Figure caption

Fig.1 Map of Tahiti and location of studied plots

Fig.2 Map of Moorea and location of studied plots

Fig.3 Example of a sampling plan on a 10 x 10 m plot: map of a 10 x 10 m plot divided into 1 x 1 m quadrats. In grey: 20 randomly selected quadrats.

Fig.4 Alien and native woody species basal area and stems density in the plots of Tahiti in 2014.
Black bars indicate the alien woody species basal area, grey bars indicate the native woody species basal area, the darker grey line shows alien woody species stems density, the light grey line shows native woody species stems density.

Fig.5 Mean density (± S.E.) of alien and native woody species seedlings and mean density of *Rubus rosifolius* in the plots of Tahiti in 2014.
The black line indicates the alien woody species seedlings mean density, the grey line shows the native woody species mean density, the broken line indicates the *Rubus rosifolius* mean density.

Fig 6 Alien and native woody species basal area with time in three plots of Tahiti.
Black bars indicate the alien woody species basal area, grey bars indicate the native woody species basal area.

Fig.7 Alien and native woody species seedlings mean density (± S.E.) in 2012 and 2013/2014 in the plots of Tahiti.

Fig.8 Alien and native woody species basal area and stems density in the plots of Moorea in 2014.
Black bars indicate the alien woody species basal area, grey bars indicate the native woody species basal area, the darker grey line shows alien woody species stems density, the light grey line shows native woody species stems density.

Fig.9 Alien and native woody species seedlings mean density (± S.E.) in the plots of Moorea in 2014.
The black line indicates the alien woody species seedlings density, the grey line shows the native woody species.

Fig.10 Alien and native woody species basal area with time in the plots of Moorea.
Black bars indicate the alien woody species basal area, grey bars indicate the native woody species basal area.

Table 1: location, elevation and G.P.S. coordinates of the 17 studied plots

Island	**Site**	**plot**	**Latitude**	**Longitude**	**elevation (m)**	**G.P.S. Tracking device**
Tahiti	Aorai	AOR-600	-17.564686	-149.528944	615	Garmin 62 S
Tahiti	Marau	MAR-800	-17.5963889	-149.56583333333336	820	Garmin map 60
Tahiti	Aorai	AOR-900	-17.581597	-149.515656	995	Garmin 62 S
Tahiti	Aorai	AOR-1000	-17.5788889	-149.51916666666668	1005	Garmin map 60
Tahiti	Marau	MAR-1100	-17.6055556	-149.54638	1140	Garmin 62 S
Tahiti	Aorai	AOR-1200	-17.5846389	-149.50769	1220	GPS Trimble SL
Tahiti	Aorai	AOR-1300	-17.58789	-149.50547	1315	GPS Trimble SL
Moorea	Opunohu	OPU1	-17.54184889	-149.82937968	230	Garmin 62s
Moorea	Opunohu	OPU2	-17.54178653	-149.8299529	195	Garmin 62s
Moorea	Opunohu	OPU4	-17.54535837	-149.83970367	300	Garmin 62s
Moorea	Vaianae	VAI1	-17.5495748	-149.84163315	250	Garmin 62s
Moorea	Vaianae	VAI2	-17.54681142	-149.84227722	345	Garmin 62s
Moorea	Vaianae	VAI3	-17.5499506	-149.84187434	235	Garmin 62s
Moorea	Vaianae	VAI4	-17.5486111	-149.8413888888889	365	Garmin map 60
Moorea	Mouaroa	MOU1	-17.54575621	-149.84281614	400	Garmin 62s
Moorea	Mouaroa	MOU2	-17.5466667	-149.84583333333333	480	Garmin 60 csx
Moorea	Mouaroa	MOU3	-17.54578155	-149.84859605	500	Garmin 62s

Table 2: Results of correlation tests performed between the different variables measured in Tahiti.
N.S. indicates there is no significant correlation
** indicates a p-value lower than 0.05, **: a p-value lower than 0.01, ***: a p-value lower than 0.001.*
(+) indicates a positive correlation, (-) indicates a negative correlation.

STL means in the shrub and tree layer, HL means herbaceous layer.

		Native species					**Alien species**					**Elevation**	**Rubus density**
		Basal area	Stems density	Seedlings density	SR STL	SR HL	Basal area	Stems density	Seedlings density	SR STL	SR HL		
	Basal area		N.S.	N.S.	N.S.		*(-)		N.S.			N.S.	
	Stems density	--		N.S.	*(+)			*(-)	N.S.			N.S.	
Native species	Seedlings density	--	--		N.S.	N.S.	N.S.	N.S.	N.S.			N.S.	N.S.
	Species richness STL	--	--	--		N.S.			*(-)	N.S.		*(+)	
	Species richness HL			--	--				N.S.	N.S.	N.S.	N.S.	N.S.
	Basal area	--		--				N.S.	N.S.	N.S.	N.S.	N.S.	
	Stems density		--	--			--		**(+)	N.S.	N.S.	N.S.	

Alien species	Seedlings density	--	--	--	--	--	--	--		N.S.	*(+)	*(-)	*(-)
	Species richness STL				--	--	--	--	--		N.S.	N.S.	
	Species richness HL					--	--	--	--	--		N.S.	N.S.
All species	Species richness STL											*(+)	
	Species richness HL											N.S.	N.S.
	Simpson's S Index STL											*(-)	
	Simpson's S Index HL											N.S.	
	Rubus density											***(+)	

Table 3: Species richness, values of Simpson's S index and values of McNaughton I index in the 7 plots of Tahiti.
The value of Simpson's S index is the probability that two randomly selected individuals from a community will be the same species.
The value of the Mc Naughton I index expresses the percentage of the two most dominant species in the plot.

	Plots	**AOR-600**	**MAR-800**	**AOR-900**	**AOR-1000**	**MAR-1100**	**AOR-1200**	**AOR-1300**
Shrub and tree layer	Native species richness	3	4	5	3	10	9	13
	Alien species richness	2	4	2	2	1	2	1
	Simpson's S index	0.78	0.83	0.85	0.92	0.32	0.32	0.18
	McNaughton I index	97.29	95.81	95.36	97.70	68.66	65.36	50.51
Herbaceous layer	Native species richness	4	2	7	3	10	2	6
	Alien species richness	10	3	1	4	2	1	1
	Simpson's S index	0.2	0.69	0.47	0.81	0.18	0.63	0.51
	McNaughton I index	52.94	95.45	79.31	94.81	51.43	100	84.61

Table 4: Results of correlation tests performed between the different variables measured in Moorea.
N.S. indicates there is no significant correlation.
** indicates a p-value lower than 0.05, **: a p-value lower than 0.01, ***: a p-value lower than 0.001.*
(+) indicates a positive correlation (-) indicates a negative correlation.

STL means in the shrub and tree layer, HL means species richness herbaceous layer.

		Native species					**Alien species**					**Elevation**
		Basal area	Stems density	Seedlings density	SR STL	SR HL	Basal area	Stems density	Seedlings density	SR STL	SR HL	
	Basal area		N.S.	N.S.	N.S.		*(-)		N.S.			N.S.
	Stems density	--		N.S.	N.S.			*(-)	N.S.			N.S.
Native species	Seedlings density	--	--		*(+)	**(+)	N.S.	N.S.	N.S.			*(+)
	Species richness STL	--	--	--		N.S.			N.S.	N.S.		N.S.
	Species richness HL			--	--				N.S.	***(-)	N.S.	*** (+)
	Basal area	--		--				N.S.	N.S.	N.S.		N.S.
	Stems density		--	--			--		** (+)	*(-)		N.S.
	Seedlings	--	--	--	--	--	--	--		** (-)	* (-)	N.S.

Alien species	density								
	Species richness STL	--	--	--	--	--		N.S.	** (-)
	Species richness HL	--				--	--		N.S.
All species	Species richness STL								N.S.
	Species richness HL								** (+)
	Simpson's Index STL								N.S.
	Simpson's Index HL								N.S.

Table 5 : Species richness, values of Simpson's S index and values of McNaughton I index in the 10 plots of Moorea.
The value of Simpson's S index is the probability that two randomly selected individuals from a community will be the same species.
The value of the Mc Naughton I index expresses the percentage of the two most dominant species.

	Plots (elevation)	**OPU2 (190 m)**	**OPU1 (230 m)**	**OPU4 (300 m)**	**VAI3 (235 m)**	**VAI1 (250 m)**	**VAI2 (345 m)**	**VAI4 (365 m)**	**MOU1 (400 m)**	**MOU2 (480 m)**	**MOU (500 m**
Shrub and tree layer	Native species richness	11	8	7	5	8	11	7	13	11	13
	Alien species richness	7	6	6	4	5	5	3	4	2	2
	Simpson's S index	0.10	0.21	0.28	0.36	0.70	0.26	0.36	0.15	0.40	0.65
	McNaughton I index	25.81	47.85	72.31	74.55	89.97	69.39	64.67	39.52	74.59	86.1
Herbaceous layer	Native species richness	4	6	4	8	9	8	10	12	20	20
	Alien species richness	7	7	7	5	6	4	5	10	3	3
	Simpson's S index	0.26	0.26	0.44	0.40	0.19	0.18	0.67	0.13	0.36	0.78
	McNaughton I index	63.33	62.50	88.57	81.21	53.42	51.47	85.71	40.00	67.20	92.4

Fig.1

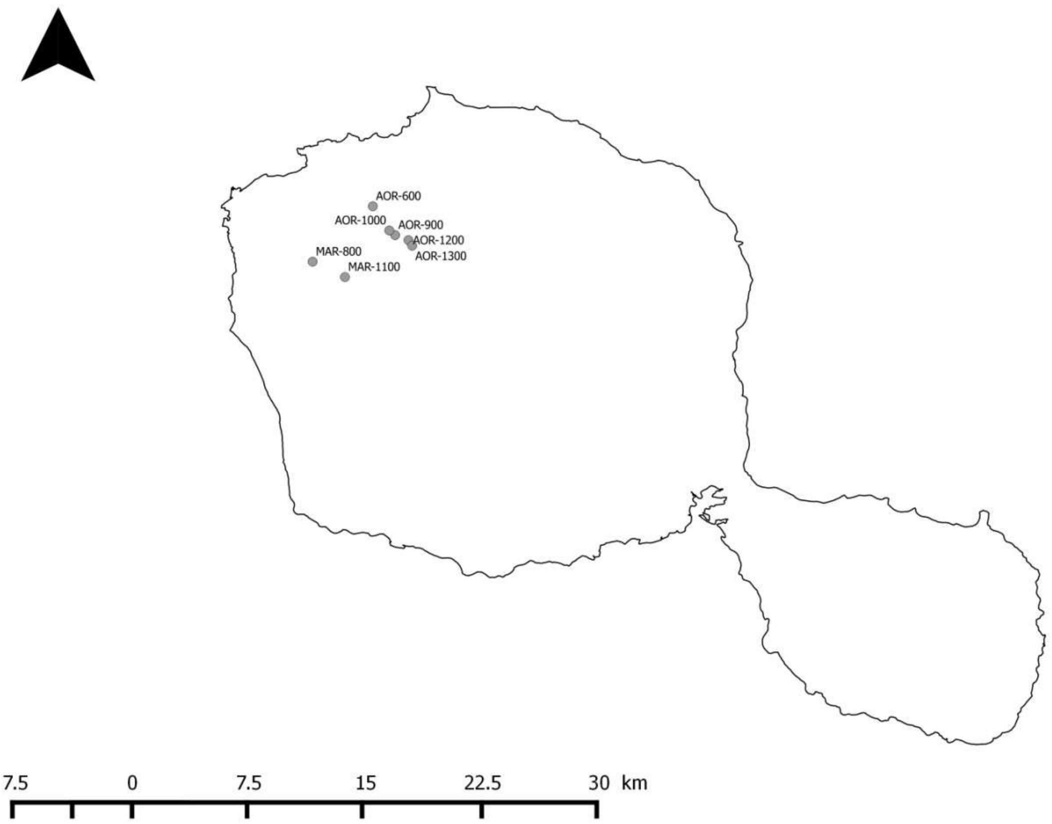

AOR-600
AOR-1000
AOR-900
AOR-1200
AOR-1300
MAR-800
MAR-1100
7.5
0
7.5
15
22.5
30 km

Fig.2

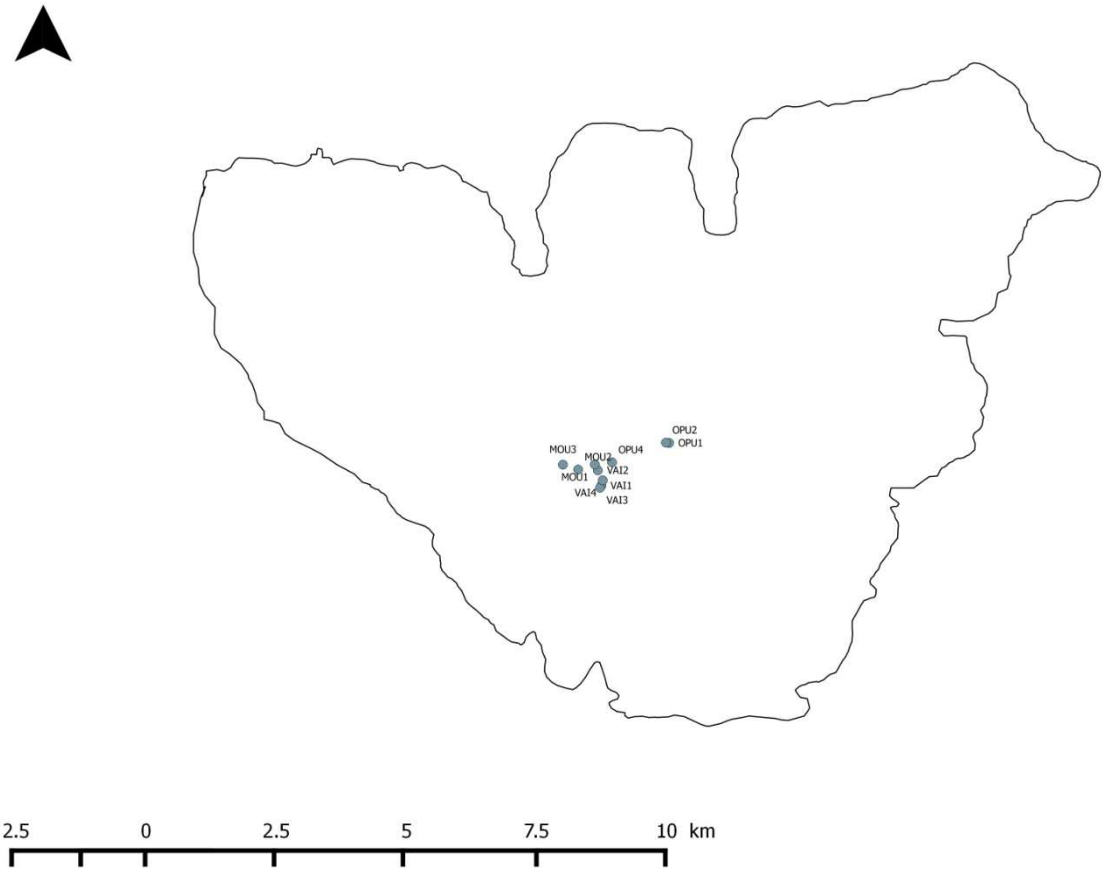
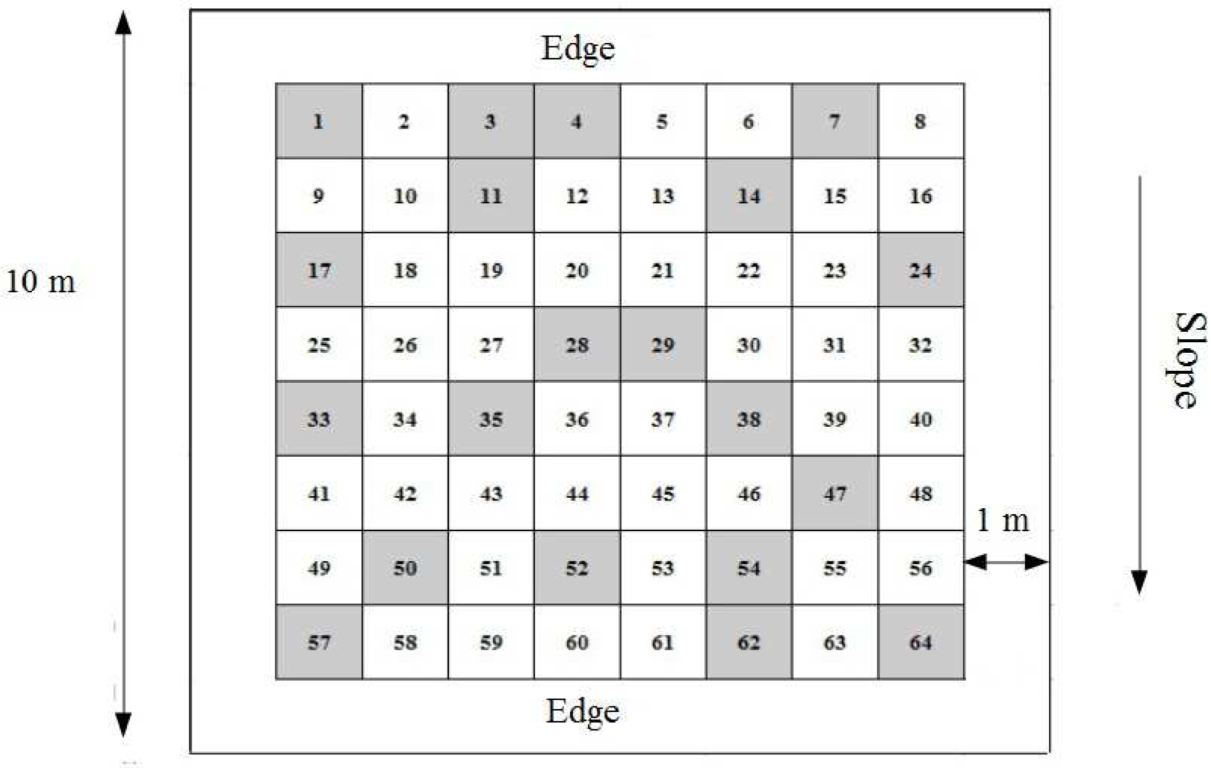

OPU2
OPU1
MOU3
OPU4
MOU2
VAI2
MOU1
VAI1
VAI4
VAI3
2.5
0
2.5
5
7.5
10 km

Fig.3



Edge
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
Edge
10 m
1 m
Slope

Fig.4

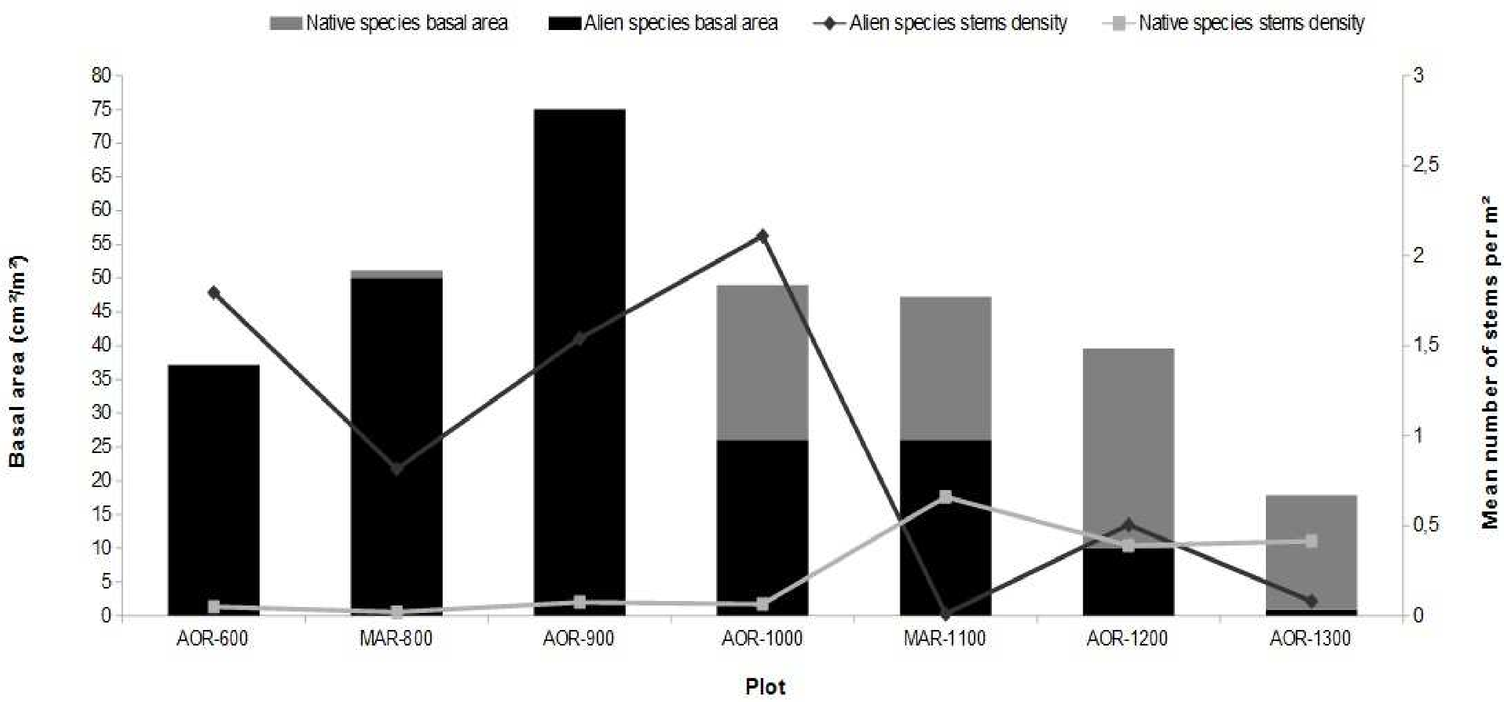
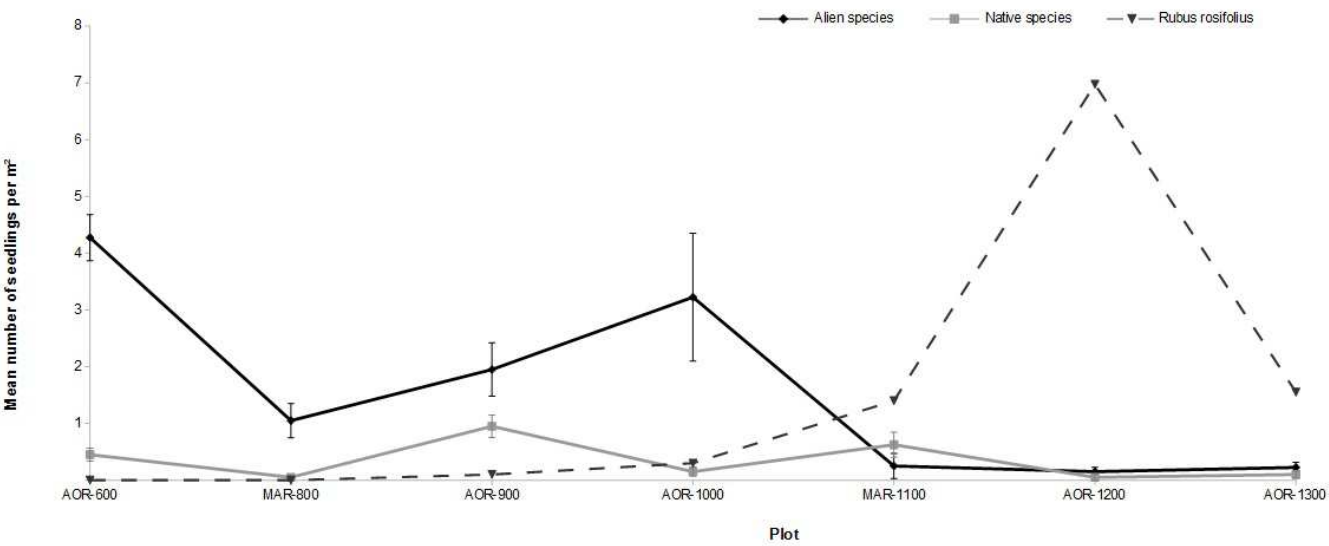
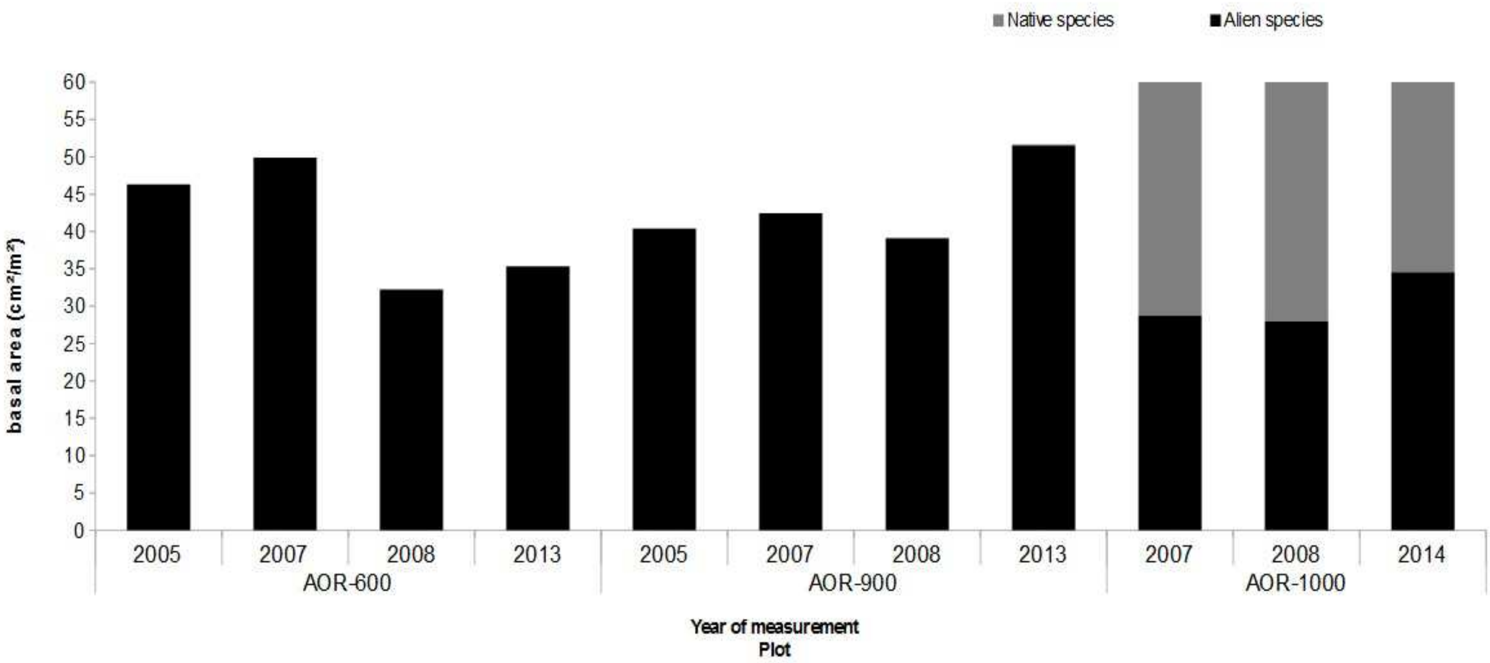

Native species basal area
Alien species basal area
Alien species stems density
Native species stems density
Basal area (cm²/m²)
Mean number of stems per m²
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
3
2,5
2
1,5
1
0,5
0
AOR-600
MAR-800
AOR-900
AOR-1000
MAR-1100
AOR-1200
AOR-1300
Plot

Fig.5



Alien species
Native species
Rubus rosifolius
Mean number of seedlings per m²
8
7
6
5
4
3
2
1
AOR-600
MAR-800
AOR-900
AOR-1000
MAR-1100
AOR-1200
AOR-1300
Plot

Fig.6



Native species
Alien species
60
55
50
45
40
35
30
25
20
15
10
5
0
basal area (cm²/m²)
2005
2007
2008
2013
AOR-600
2005
2007
2008
2013
AOR-900
2007
2008
2014
AOR-1000
Year of measurement
Plot

Fig.7

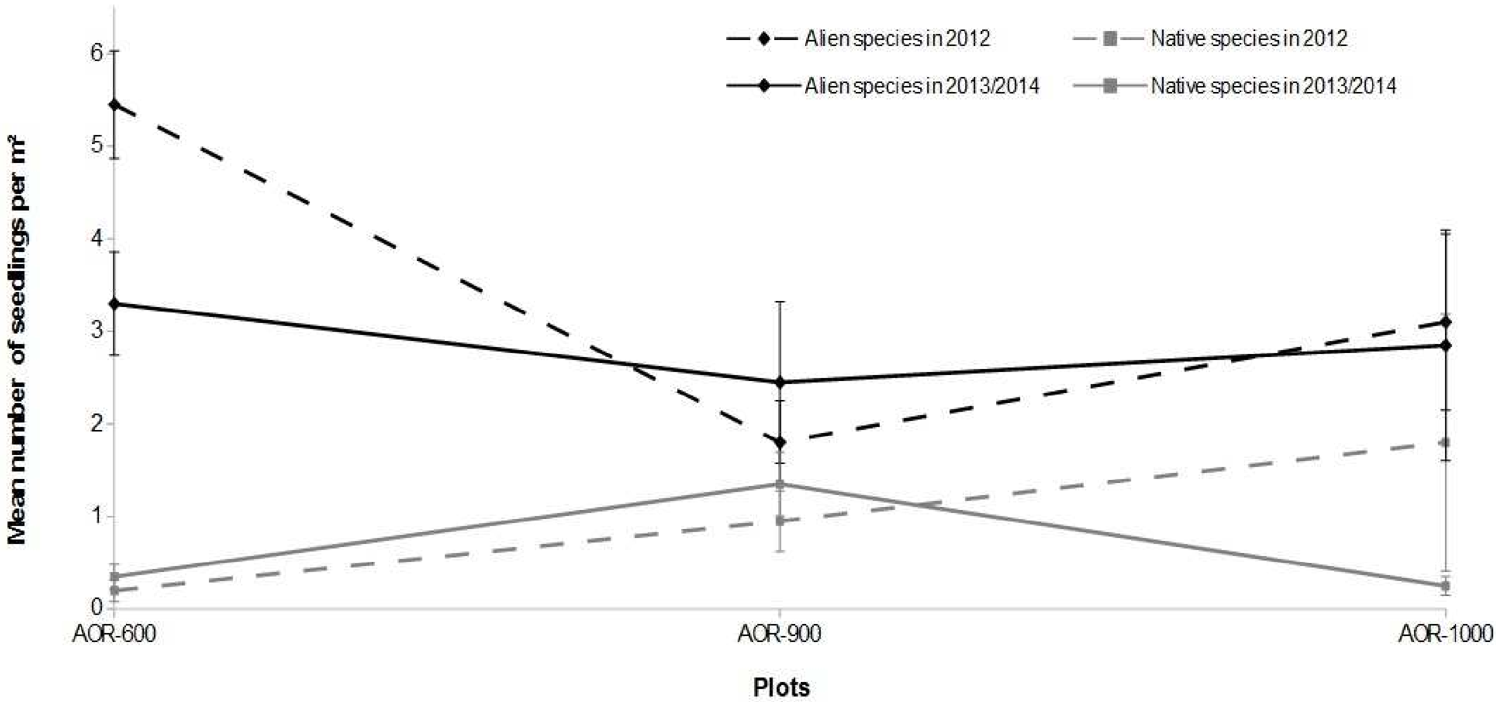

Alien species in 2012
Native species in 2012
Alien species in 2013/2014
Native species in 2013/2014
Mean number of seedlings per m²
0
1
2
3
4
5
6
AOR-600
AOR-900
AOR-1000
Plots

Fig.8

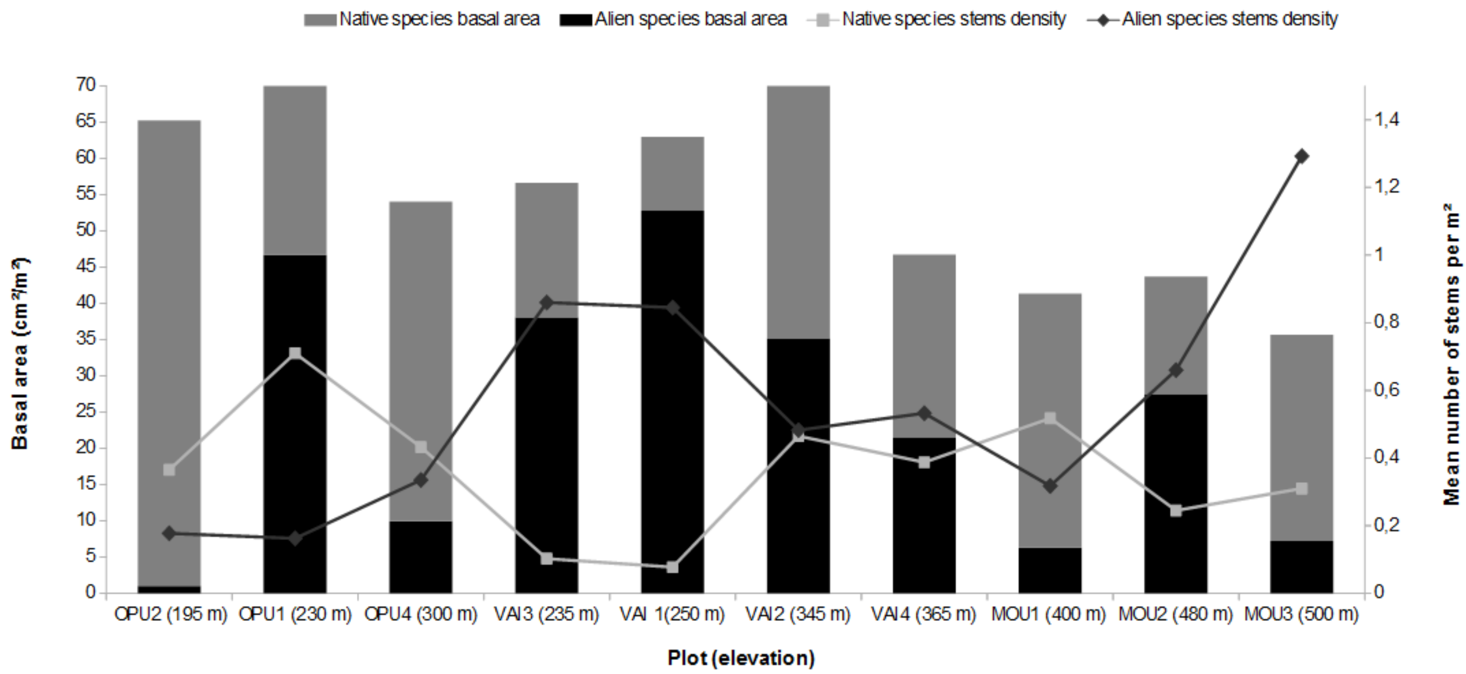
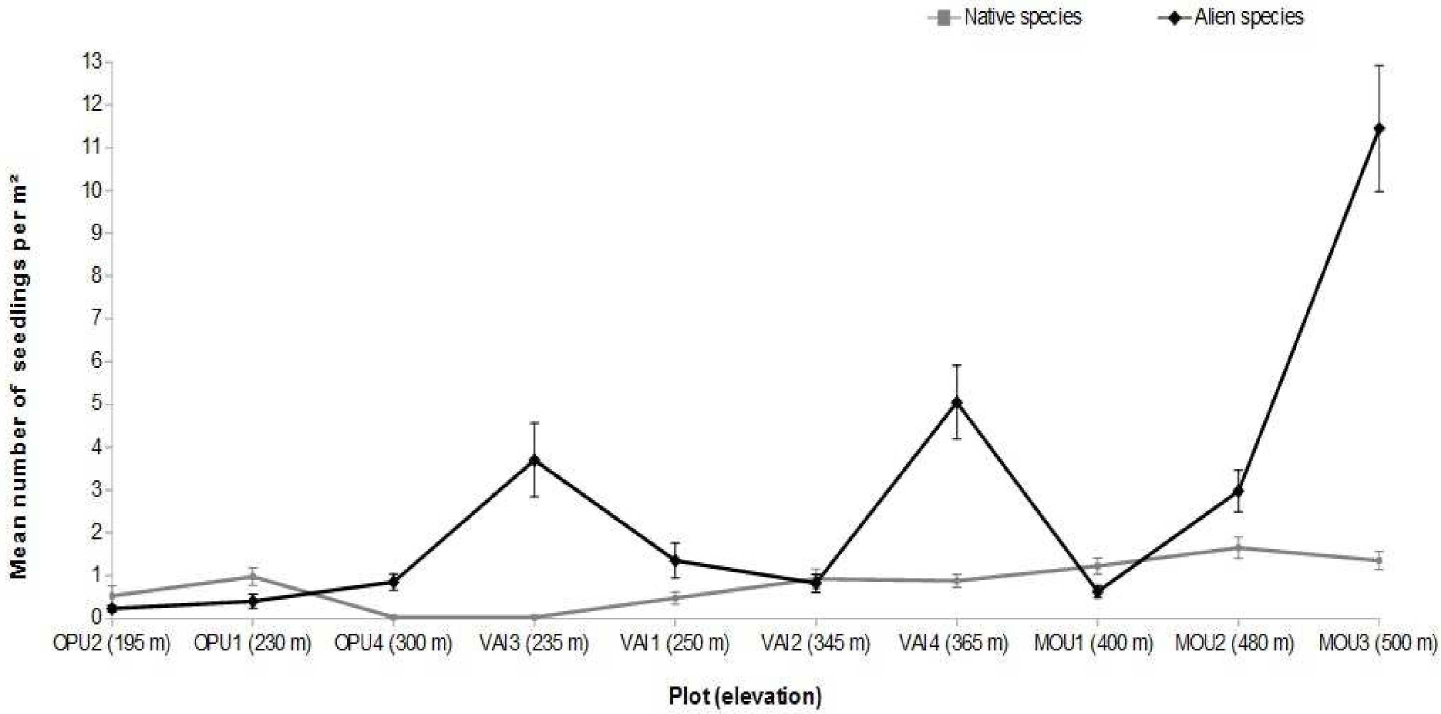
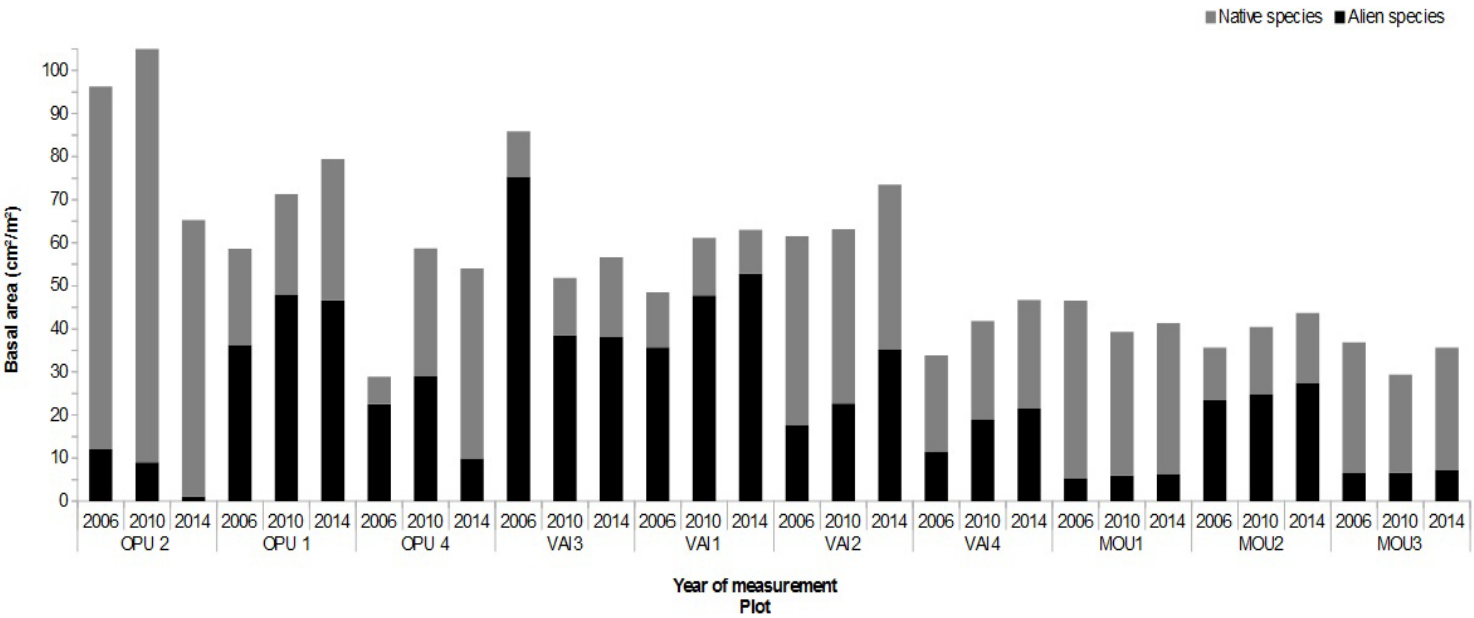

Native species basal area
Alien species basal area
Native species stems density
Alien species stems density
Basal area (cm²/m²)
Mean number of stems per m²
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
1,4
1,2
1
0,8
0,6
0,4
0,2
0
OPU2 (195 m)
OPU1 (230 m)
OPU4 (300 m)
VAI3 (235 m)
VAI 1(250 m)
VAI2 (345 m)
VAI4 (365 m)
MOU1 (400 m)
MOU2 (480 m)
MOU3 (500 m)
Plot (elevation)

Fig.9



Native species
Alien species
Mean number of seedlings per m²
13
12
11
10
9
8
7
6
5
4
3
2
1
0
OPU2 (195 m)
OPU1 (230 m)
OPU4 (300 m)
VAI3 (235 m)
VAI1 (250 m)
VAI2 (345 m)
VAI4 (365 m)
MOU1 (400 m)
MOU2 (480 m)
MOU3 (500 m)
Plot (elevation)

Fig.10



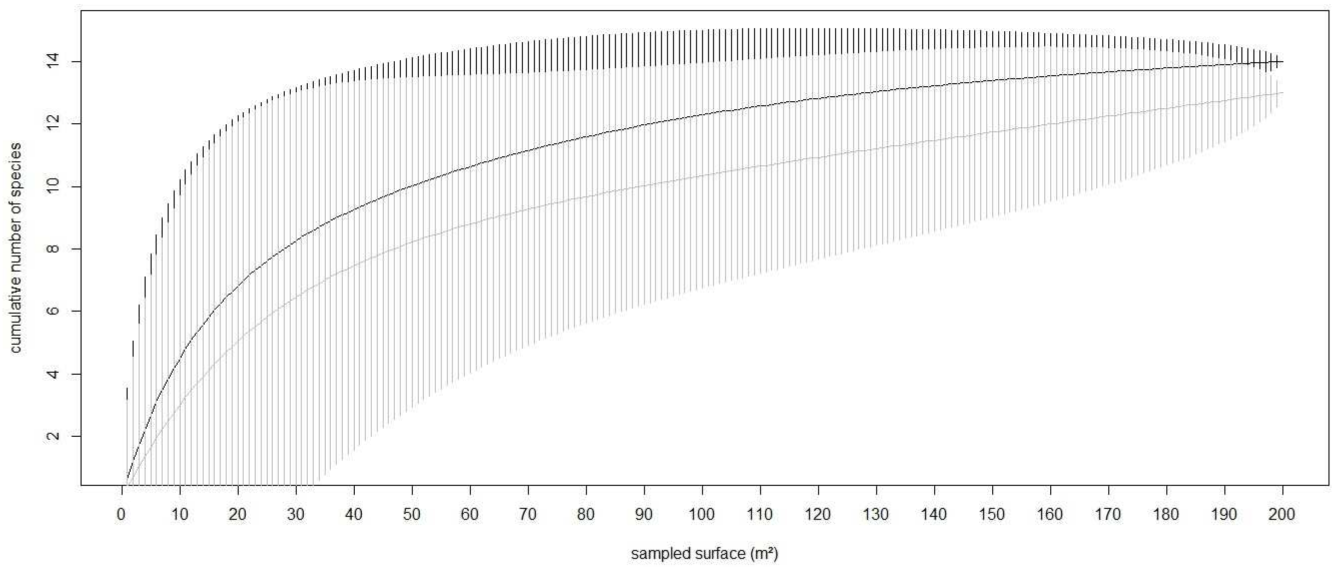
Native species
Alien species
Basal area (cm²/m²)
0
10
20
30
40
50
60
70
80
90
100
2006
2010
2014
OPU 2
OPU 1
OPU 4
VAI3
VAI1
VAI2
VAI4
MOU1
MOU2
MOU3
Year of measurement
Plot

Appendix

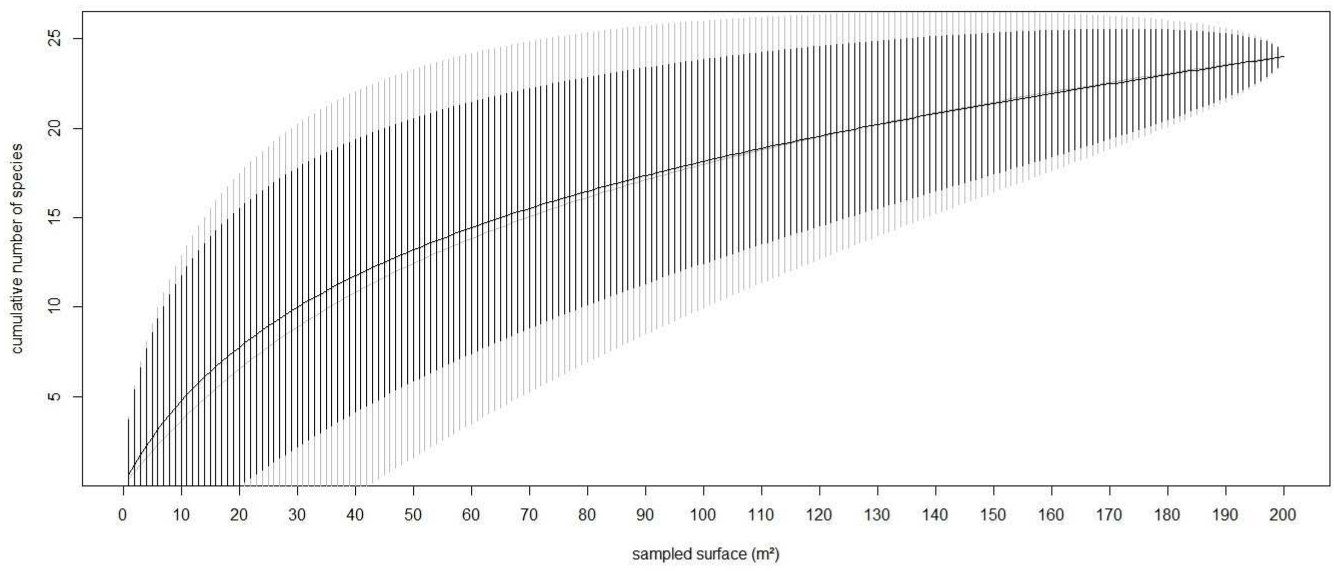
Appendix A

Species accumulative curves in AOR-600 plot and in MOU2 plot .
Black curves indicate the species accumulative curves using the 1 x 1m sampling method, grey curves show the species accumulative curves using the 2 x 2m sampling method.

AOR-600 species accumulative curves



MOU2 species accumulative curves



Appendix B

Number of stems higher than 1.3 m of woody species with their biogeographical status in each 20 x 10 m plots in Tahiti.

POL: alien species introduced by Polynesians

EUR: alien species introduced by Europeans

End. Eas. Pol. : species endemic to Eastern Polynesia

End archipelago: species endemic to the Society archipelago

End island: species endemic to the island of Tahiti

Underline species are invasive alien species

Species	**Family**	**Biogeographical status**	**AOR-600**	**MAU-800**	**AOR-900**	**AOR-1000**	**MAU-1100**	**AOR-1200**	**AOR-1300**	**Total**
Cordyline fruticosa	Dracaenaceae	POL		1						1
Psidium cattleianum	Myrtaceae	EUR		8						8
Miconia calvescens	Melastomataceae	EUR	324	152	298	418		97	16	1305
Spathodea campanulata	Bignoniaceae	EUR	35	2	10	4	2			53
Tecoma stans	Bignoniaceae	EUR						4		4
Alstonia costata	Apocynaceae	Indigenous					2	8	10	20
Cyathea affinis	Cyatheaceae	Indigenous		1	1		70	11	34	117
Cyathea societarum (medullaris)	Cyatheaceae	Indigenous		1			6	16	2	25
Freycinetia impavida	Pandanaceae	Indigenous	6	1				20	13	40
Ilex anomala	Aquifoliaceae	Indigenous								0
Metrosideros collina	Myrtaceae	Indigenous								0
Macropiper latifolium	Piperaceae	Indigenous						7	2	9
Rhus taitensis	Anacardiaceae	Indigenous	3							3
Streblus anthropophagorum	Moraceae	Indigenous								0
Wikstroemia coriacea	Thymelaeaceae	End Eas. Pol.	1							1
Ascarina polystachya	Chloranthaceae	End archipelago					9		7	16
Coprosma sp.	Rubiaceae	End archipelago								0
Coprosma taitensis	Rubiaceae	End archipelago					22	5	1	28
Cyrtandra apiculata	Gesneriaceae	End archipelago			8					8
Meryta sp.	Araliaceae	End archipelago								0
Myrsine cf. ovalis	Myrsinaceae	End archipelago						2		2
Myrsine sp. 1	Myrsinaceae	End archipelago							1	1
Myrsine sp. 2	Myrsinaceae	End archipelago							3	3
Myrsine sp. 3	Myrsinaceae	End archipelago			1					1
Ophiorrhiza subumbellata	Rubiaceae	End archipelago				7				7
Pipturus polynesicus	Urticaceae	End archipelago					1			1
Reynoldsia verrucosa	Araliaceae	End archipelago								0
Vaccinium cereum	Ericaceae	End archipelago								0
Weinmannia parviflora	Cunoniaceae	End archipelago				5	1	7	1	14
Cyrtandra cf. taitensis	Gesneriaceae	End island						2		2
Cyrtandra Induta	Gesneriaceae	End island								0
Cyrtandra mucronata	Gesneriaceae	End island					15		3	18
Cyrtandra Nadeaudii	Gesneriaceae	End island					2		5	7
Fuchsia cyrtandroides	Onagraceae	End island								0
Leptecophylla pomarae	Ericaceae	End island								0
Melicope tahitensis	Rutaceae	End island							1	1
Psychotria marauensis	Rubiaceae	End island					4			4
Psychotria cf. speciosa	Rubiaceae	End island			1					1
		Alien species stems	**359**	**163**	**308**	**422**	**2**	**101**	**16**	**1371**
		Native species stems	**10**	**3**	**11**	**12**	**132**	**78**	**83**	**329**
		Total number of stems	**369**	**166**	**319**	**434**	**134**	**179**	**99**	**1700**
		Total number of species	**5**	**7**	**6**	**4**	**11**	**11**	**14**	**58**

Appendix C

Number of seedlings of woody species in the 40 m² sampling area of each plots of Tahiti.

POL: alien species introduced by Polynesians

EUR: alien species introduced by Europeans

End. Eas. Pol. : species endemic to Eastern Polynesia

End archipelago: species endemic to the Society archipelago

End island: species endemic to the island of Tahiti

Unid: unidentified

Underline species are invasive alien species

Species	Family	Biogeographical status	AOR-600	MAU-800	AOR-900	AOR-1000	MAU-1100	AOR-1200	AOR-1300	Total
Spathodea campanulata	Bignoniaceae	EUR	67		1	7	1			76
Tecoma stans	Bignoniaceae	EUR	9							9
Miconia calvescens	Melastomataceae	EUR	23	36	77	121	9	6	9	281
Ardisia elliptica	Myrsinaceae	EUR	5							5
Pimenta dioica	Myrtaceae	EUR	32							32
Psidium cattleianum	Myrtaceae	EUR		6						6
Syzygium jambos	Myrtaceae	EUR	5							5
Passiflora Suberosa	Passifloraceae	EUR	25			1				26
Stachytarpheta urticifolia	Verbenaceae	EUR	1							1
		Unid alien species	2							2
Rhus taitensis	Anacardiaceae	Indigenous	2							2
Alstonia costata	Apocynaceae	Indigenous					1			1
Jasminum didymum	Oleaceae	Indigenous			1					1
Cyclophyllum barbatum	Rubiaceae	Indigenous	1							1
Psychotria sp	Rubiaceae	Indigenous			15					15
Unidentified native species 1	Urticaceae	Indigenous					1			1
Unidentified native species 2		Unid indigenous			1					1
Unidentified native species 3		Unid indigenous			1					1
Unidentified native species 4		Unid indigenous							2	2
Xylosma suaveolens	Flacoutiaceae	End Eas. Pol.	2							2
Allophylus rhomboidalis	Sapindaceae	End Eas. Pol.			1					1
Wikstroemia coriacea	Thymelaeaceae	End Eas. Pol.	13							13
Weinmannia parviflora	Cunoniaceae	End archipelago					9			9
Glochidion sp.	Euphorbiaceae	End archipelago			3		1			4
Cyrtandra sp.	Gesneriaceae	End archipelago			1				1	2
Myrsine sp.	Myrsinaceae	End archipelago			9			2		11
Coprosma taitensis	Rubiaceae	End archipelago			6	3	5			14
Ophiorrhiza subumbellata	Rubiaceae	End archipelago				1				1
Ophiorrhiza tahitensis	Rubiaceae	End archipelago							1	1
Cyrtandra cf. taitensis	Gesneriaceae	End island				1	5			6
Cyrtandra mucronata	Gesneriaceae	End island					3			3
Psychotria cf. speciosa	Rubiaceae	End island				1				1
Psychotria marauensis	Rubiaceae	End island		2						2
		Alien species seedlings	**169**	**42**	**78**	**129**	**10**	**6**	**9**	**443**
		Native species seedings	**18**	**2**	**38**	**6**	**25**	**2**	**4**	**95**
		Total number of seedlings	**187**	**44**	**116**	**135**	**35**	**8**	**13**	**538**
		Total number of species	**13**	**3**	**11**	**7**	**9**	**2**	**4**	**33**

Appendix D

Number of stems higher than 1.3 m of woody species with their biogeographical status in each 20 x 20 m plots in Moorea.

POL: alien species introduced by Polynesians

EUR: alien species introduced by Europeans

End. Eas. Pol. : species endemic to Eastern Polynesia

End archipelago: species endemic to the Society archipelago

End island: species endemic to the island of Tahiti

Underline species are invasive alien species

Species	**Family**	**Biogeographical status statut**	**OPU 1**	**OPU 2**	**OPU 4**	**VAI1**	**VAI2**	**VAI3**	**VAI4**	**MOU1**	**MOU2**	**MOU3**	**Total**
Merremia peltata	Convolvulaceae	POL		1									1
Aleurites moluccana	Euphorbiaceae	POL		22	1		1		2				26
Inocarpus fagifer	Fabaceae	POL	11							1			1
Artocarpus altilis	Moraceae	POL			7								7
Syzygium malaccense	Myrtaceae	POL	3	23	20		1	56		56			156
Morinda citrifolia	Rubiaceae	POL	1	3		1							4
Spathodea campanulata	Bignoniaceae	EUR	7		4	24	7	76	6	10	48	4	179
Cecropia peltata	Cecropiaceae	EUR						1					1
Miconia calvescens	Melastomataceae	EUR	39	21	96	308	177	211	205	60	216	513	1807
Psidium guajava	Myrtaceae	EUR	4		6								6
Coffea arabica	Rubiaceae	EUR		1		3	7						11
Coffea liberica	Rubiaceae	EUR				2							2
Alstonia costata	Apocynaceae	Indigenous									8	12	20
Cyathea affinis	Cyatheaceae	Indigenous									6	1	7
Barringtonia asiatica	Lecythidaceae	Indigenous		18									18
Fagraea berteroana	Loganiaceae	Indigenous							36	1			37
Hibiscus tiliaceus	Malvaceae	Indigenous	39	9	24		39		58	56	6		192
Jossinia reinwardtiana	Myrtaceae	Indigenous	5	9						1			10
Pisonia tahitensis	Nyctaginaceae	Indigenous		5		1	14	5		8	3	2	38
Freycinetia impavida	Pandanaceae	Indigenous		26	126	13	37	19	14	72	5	8	320
Macropiper latifolium	Piperaceae	Indigenous					6						6
Crossostylis biflora	Rhizophoraceae	Indigenous				7	53	6	33	37	54	39	229
Cyclophyllum barbatum	Rubiaceae	Indigenous	73	30	5		5			1			41
Neonauclea forsteri	Rubiaceae	Indigenous	18	7	6	3	9	7	6	3	7	5	53
Tarenna sambucina	Rubiaceae	Indigenous				2				1		1	4
Boehmeria virgata	Urticaceae	Indigenous										2	2
Xylosma suaveolens	Flacourtiaceae	End Eas. Pol.	4		1					7			8
Hernandia ovigera	Hernandiaceae	End Eas. Pol.					2				1	1	4
Serianthes myriadenia	Mimosaceae	End Eas. Pol.				1							1
Lepinia taitensis	Apocynaceae	End archipelago							2				2
Meryta lanceolata	Araliaceae	End archipelago	1			1							1
Weinmannia parviflora	Cunoniaceae	End archipelago									1	21	22
Claoxylon taitense	Euphorbiaceae	End archipelago		3									3
Glochidion manono	Euphorbiaceae	End archipelago		4	3		1			1			9
Macaranga attenuata	Euphorbiaceae	End archipelago										1	1
Cyrtandra vestita	Gesneriaceae	End archipelago					3						3
Cyrtandra sp.	Gesneriaceae	End archipelago									3		3
Astronidium sp.	Melastomataceae	End archipelago										30	30
Myrsine sp.	Myrsinaceae	End archipelago								1			1
Pittosporum taitense	Pittosporaceae	End archipelago	16	1									1
Ixora mooreensis	Rubiaceae	End Island	128	34	8	3	17	4	6	18	4	1	95
		Alien species stems	**65**	**71**	**134**	**338**	**193**	**344**	**213**	**127**	**264**	**517**	**2201**
		Native species stems	**284**	**146**	**173**	**31**	**186**	**41**	**155**	**207**	**98**	**124**	**1161**
		Total number of stems	**349**	**217**	**307**	**369**	**379**	**385**	**368**	**334**	**362**	**641**	**3362**
		Total number of stems	**14**	**17**	**13**	**13**	**16**	**9**	**10**	**17**	**13**	**15**	**41**

Appendix E

Number of seedlings of woody species in the 40 m² sampling area of each plots of Moorea.

POL: alien species introduced by Polynesians

EUR: alien species introduced by Europeans

End. Eas. Pol. : species endemic to Eastern Polynesia

End archipelago: species endemic to the Society archipelago

End island: species endemic to the island of Tahiti

Unid: unidentified

Underline species are invasive alien species

Species	Family	Biogeographical status	OPU 1	OPU 2	OPU 4	VAI1	VAI2	VAI3	VAI4	MOU1	MOU2	MOU3	Total
Merremia peltata	Convolvulaceae	POL		1	10					1			12
Dioscorea pentaphylla	Dioscoreaceae	POL							1				1
Cordyline fruticosa	Dracaenaceae	POL								1			1
Aleurites moluccana	Euphorbiaceae	POL		2									2
Inocarpus fagifer	Fabaceae	POL	2			1							3
Artocarpus altilis	Moraceae	POL			1								1
Syzygium malaccense	Myrtaceae	POL		4	1			38		10			53
Chrysalidocarpus madagascariensis	Arecaceae	EUR							1				1
Elephantopus mollis	Asteraceae	EUR	2										2
Spathodea campanulata	Bignoniaceae	EUR	1		1	26	7	23	6	8	10	4	86
Miconia calvescens	Melastomataceae	EUR	*10*	*2*	*21*	*13*	*17*	*83*	*194*	*4*	*108*	*453*	905
Passiflora maliformis	Passifloraceae	EUR				8							8
Passiflora suberosa	Passifloraceae	EUR									1	1	2
Coffea arabica	Rubiaceae	EUR				6	8	4					18
Stachytarpheta cayennensis	Verbenaceae	EUR	1							1			2
Rhus taitensis	Anacardiaceae	Indigenous				1							1
Alstonia costata	Apocynaceae	Indigenous										2	2
Barringtonia asiatica	Lecythidaceae	Indigenous		6									6
Jossinia reinwardtiana	Myrtaceae	Indigenous	3	13									16
cf Pisonia	Nyctaginaceae	Indigenous					1						1
Macropiper latifolium	Piperaceae	Indigenous					1					6	7
Crossostylis biflora	Rhizophoraceae	Indigenous							4		17	23	44
Cyclophyllum barbatum	Rubiaceae	Indigenous	11	1		5	4		4	5	2		32
Morinda myrtifolia	Rubiaceae	Indigenous										1	1
Tarenna sambucina	Rubiaceae	Indigenous				2		1	2				5
Unid. Native species 4		Unid indigenous										2	2
Unid. Native species 5		Unid indigenous									3	1	4
Unid. Native species 6		Unid indigenous									1		1
Unid. Native species 7		Unid indigenous									2		2
Unid. Native species 8		Unid indigenous								1			1
Unid. Native species 9		Unid indigenous	1										1
Unid. Native species 10		Unid indigenous								1			1
Xylosma suaveolens	Flacoutiaceae	End Eas. Pol.				1	9		5	17	4	7	43
Hernandia ovigera	Hernandiaceae	End Eas. Pol.					2						2
Allophylus rhomboidalis	Sapindaceae	End Eas. Pol.				2	1		3	9	15	1	31
Wikstroemia coriacea	Thymelaceae	End Eas. Pol.									1	2	3
Lepinia taitensis	Apocynaceae	End archipelago							5				5
Meryta lanceolata	Araliaceae	End archipelago							1				1
cf. Macaranga attenuata	Euphorbiaceae	End archipelago									2		2
Macaranga cf taitensis	Euphorbiaceae	End archipelago				1							1
cf Claoxylon	Euphorbiaceae	End archipelago				1							1
Phyllanthus urceolatus	Euphorbiaceae	End archipelago								1			1
Cyrtandra sp.	Gesneriaceae	End archipelago										2	2
Cyrtandra cf apiculata	Gesneriaceae	End archipelago									2		2
Myrsine sp.	Myrsinaceae	End archipelago								1	2	2	5
Pittosporum taitense	Pittosporaceae	End archipelago							1	1	6	2	10
Ixora mooreensis	Rubiaceae	End Island	24	1	1	6	18		10	13	9	3	85
Unidentified species 1	Unid	Unid	1										1
Unidentified species 2	Unid	Unid							1				1
Unidentified species 3	Unid	Unid								1			1
Unidentified species 4	Unid	Unid										1	1
Unidentified species 5	Unid	Unid										1	1
Unidentified species 6	Unid	Unid										1	1
Unidentified species 7	Unid	Unid									1		1
		Alien species seedlings	**16**	**9**	**34**	**54**	**32**	**148**	**202**	**25**	**119**	**458**	**1097**
		Native species seedings	**39**	**21**	**1**	**19**	**36**	**1**	**35**	**49**	**66**	**54**	**321**
		Unidentified species	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**3**	**7**
		Total number of seedlings	**56**	**30**	**35**	**73**	**68**	**149**	**238**	**75**	**186**	**515**	**1425**
		Total number of species	**10**	**8**	**6**	**13**	**10**	**5**	**14**	**16**	**17**	**19**	**54**