

# A Comparative Study of the Floristic Diversity and Structure of Relictual Littoral and Swamp Forests in the Island of Tahiti (French Polynesia, South Pacific)<sup>1</sup>

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**Abstract:** Littoral and swamp forests are among the most threatened native plant communities in the island of Tahiti (South Pacific) due to past and present anthropogenic pressures such as agriculture, urbanization, pollutions, and invasive alien species, including the mangrove tree *Rhizophora stylosa*. In order to provide reference data that are crucial to implement appropriate conservation and restoration strategies in these habitats, we assessed the composition and structure of seven littoral and swamp forests types in eighteen 10 × 20 m plots considering three different strata (trees and lianas, epiphytes, and understory). Forest types were compared using common diversity indices (e.g., Shannon index, Simpson index, and Pielou evenness) and indicator values. Results show that native submangrove swamp forests dominated by the tree *Talipariti tiliaceum* and the large erect fern *Acrostichum aureum* were the most species-rich, while introduced *Rhizophora* mangroves had an almost monospecific composition in the trees, lianas, and understory strata. The diversity of trees and lianas was higher in littoral forests with the highest understory cover in *Talipariti-Barringtonia asiatica* and *Talipariti-Inocarpus fagifer* plant communities. Surprisingly, epiphyte diversity and abundance were higher in swamp forests with lower canopy, especially in the mixed swamp forest with both *A. aureum* and *R. stylosa*. These counter-intuitive results highlight the potential role of introduced species in creating novel microhabitats suitable for the development of some native epiphytes. Conservation and restoration projects should however focus on the use of native species to maintain these remnant littoral and swamp habitats in Tahiti and other high volcanic islands of the Society archipelago, rather than non-native and potentially harmful species such as *R. stylosa*.

**Keywords:** conservation, forest structure, hybrid habitat, novel ecosystem, mangrove, restoration, submangrove, wetland

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LITTORAL (OR COASTAL) and swamp forests (or lowland forested wetlands) are among the most threatened native plant communities in the Pacific Islands due to past and present anthropogenic pressures such as land clearance for agriculture, urbanization or mining, pollution, harvesting of species, degradation through drainage, and invasive alien species (Ash and Ash 1984). Conservation and restoration of mangrove or mangal swamps (i.e., forests composed of trees mainly belonging to the Rhizophoraceae family) have received a lot of attention because of the ecosystem services they provide (Gilman et al. 2006), but relatively few studies have been conducted in other types of swamp forests (Stemmermann 1981, Scott 1993, Thaman et al. 2005, Ellison 2009).

In the Society Islands (French Polynesia, South Pacific), littoral forests have been among the most disturbed terrestrial ecosystems in relation with anthropogenic activities since the first Polynesians settled a thousand years ago (Kahn and Sinoto 2017, Stevenson et al. 2017), and probably even more since the Europeans colonized the islands at the end of the 19<sup>th</sup> century. Similarly, swamp forests already affected by taro (*Colocasia esculenta*) plantations during the pre-European period, continue to decline due to urbanization, pollution (Mueller-Dombois and Fosberg 1998) but also to non-native species invasions such as the mangrove *Rhizophora stylosa* that was introduced in the Society Islands in the early 1930's (Taylor 1979, Woodroffe 1987, Meyer et al. 2021). Only a few coastal areas remain relatively undisturbed, especially on the east coast and the peninsula of Tahiti (e.g., the seashore cliffs of Te Pari, Florence 1993; Meyer 2007). Except for some brief qualitative descriptions in Tahiti (Papy 1951–1954, Florence 1993, Mueller-Dombois and Fosberg 1998, Meyer 2016) and in high volcanic islands throughout the Pacific region such as western Polynesia (Samoa and Tonga) (Whistler 1980, 1992, 2002, Sykes 1981, Franklin et al. 2006), and Hawaii (Erickson and Puttock 2006), few quantitative analyses of plant assemblages found in littoral native forests have been carried out.

The main goals of the study are: (1) to assess the composition and structure of plant communities in different littoral and swamp forest types; and (2) to test the hypothesis that floristic diversity is significantly different between forest types by using several diversity index, especially in *R. stylosa* mangroves compared to native forests. The collected quantitative data can be used as a reference database on plant composition of threatened littoral and swamp habitats in high volcanic islands for future conservation and restoration projects.

## MATERIALS AND METHODS

### *Study Areas*

The high volcanic island of Tahiti (17° 38' S, 149° 30' W) in the Society archipelago is the largest island of French Polynesia with a land surface of 1,045 km<sup>2</sup>, and the highest summit at 2,241 m elevation (Mont Orohena). It is also the most populated island with ca. 190,000 inhabitants censused in 2017 (ISPF 2017). The island is formed by two ancient volcanoes connected by the narrow, low-elevation isthmus of Taravao: Tahiti Nui (ca. 30 km in diameter) aged between 0.8 and 1.4 million years old, and the peninsula of Tahiti Iti (Figure 1) (ca. 22 km by 13 km) between 0.2 and 0.4 million years old (Brousse et al. 1985, Guillou et al. 2005). The climate is tropical oceanic with a mean annual temperature of 26.5°C and annual rainfall of about 1,700 mm in the coastal plain of the leeward coast of Tahiti Nui, reaching 4,000 mm on the windward coast and in Tahiti Iti, and up to 8,000 mm in the center of Tahiti Nui (Laurent et al. 2004). The island of Tahiti has the richest native plant diversity of the ca. 120 French Polynesian islands, with 460 species of which 224 are endemic to French Polynesia (49% of endemism) and 107 strictly endemic to the island (23%; Chevillotte et al. 2019). The native vegetation of Tahiti can be divided into two main types: (1) an azonal vegetation, not related to climatic factors but rather to substrates of different nature and age, including coastal vegetation, littoral and para-littoral forests (on rocky cliffs, up to 200–300 m elevation, Florence

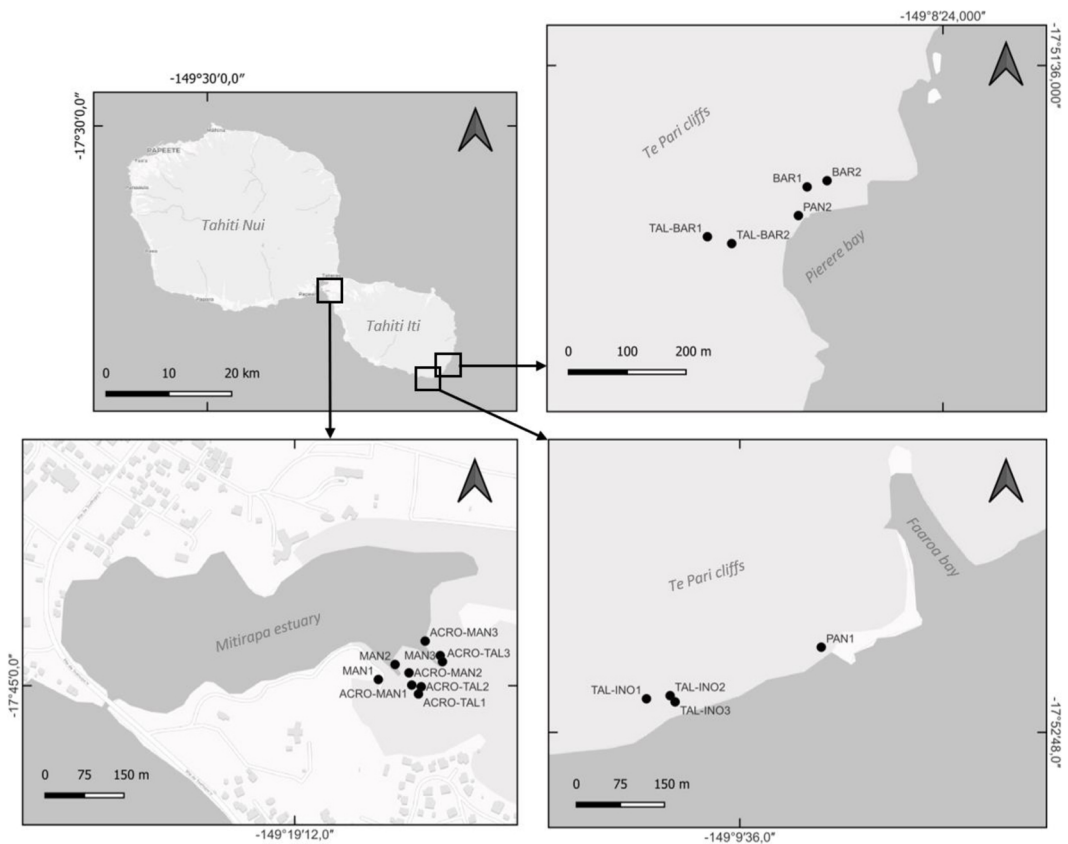


FIGURE 1. Location of the study sites and plots in the island of Tahiti (French Polynesia). The seven studied forest types according to the two main habitats are: MAN = *Rhizophora* mangrove, ACRO-MAN = *Acrostichum-Rhizophora*, and ACRO-TAL = *Acrostichum-Talipariti* for the swamp habitats; BAR = *Barringtonia*, PAN = *Pandanus*, TAL-INO = *Talipariti-Inocarpus*, and TAL-BAR = *Talipariti-Barringtonia* for the littoral habitats.

and Lorence 1997), and wetlands; (2) a zonal vegetation structured along elevation belts, related to climatic factors (rainfall and temperature) that includes dry to semi-dry, mesic, wet or rainforests, cloud forest and subalpine vegetation (Papy 1951–1954, Florence 1993, Meyer 2007, Meyer and Salvat 2009).

Our study was conducted in Tahiti Iti (Figure 1) in several lowland areas preserved from human disturbance and urbanization, that is, with relatively intact native vegetation, except for the mangrove and the mixed swamp forests types. Among the two studied habitats (littoral and swamp), seven main forest types were observed and sampled: (1) introduced *Rhizophora stylosa* mangroves, (2) mixed native

*Acrostichum*-introduced *Rhizophora* swamp forests, (3) native *Acrostichum-Talipariti tiliaceum* (syn. *Hibiscus tiliaceus*) submangroves, (4) native *Barringtonia asiatica*, (5) native *Pandanus tectorius*, (6) native *Talipariti*-naturalised *Inocarpus*, and (7) native *Talipariti-Barringtonia* littoral and para-littoral forests (Figure 1).

#### Experimental Design and Data Collection

Sites were sampled between February and April 2022. In each forest type, 10 × 20 m plots were set up and georeferenced (Garmin GPSMAP® 78) with two or three replicates depending on the forest surface (Figure 1). The main plot selection criterion was the presence of an homogenous vegetation

(structure and composition), to isolate each specific forest types. In each plot, ten  $2 \times 2$  m quadrats were set up along a 20 m transect.

At the plot scale, all individuals of woody plant species with diameter at breast height (dbh)  $\geq 5$  cm were identified, counted, and their dbh measured. Epiphytic vascular plants were also identified and their relative percentage cover were assessed on all living trunks and stems between 0 and 3 m in height among those above 5 cm diameter. In each quadrat, we visually estimated cover (percentage of ground cover) of each species found in the understory layer (less than 1 m in height), including the erect stipe of the large fern *Acrostichum aureum* and epiphytes on lying trunks. Based on these measures, we calculated several variables in order to characterize the vegetation composition and structure on each plot.

### Diversity Indices

Species diversity is one of the most widely considered variables for assessing ecosystem biodiversity (Chiarucci et al. 2011). The mean local species diversity at local scale quadrats was estimated by using diversity indices at plot-level for trees and epiphytes and quadrat-level for the understory layer. We chose to select several of the most commonly used indices, in order to compare and complement their values, as they all have both advantages and weaknesses. The simplest index is the species richness ( $S$ ) or alpha diversity, that is, the number of species found in a defined area (e.g., plot or quadrat). The Shannon index (Shannon and Weaver 1949)

$$H' = -\sum_{i=1}^S p_i \log_2 p_i,$$

where  $p_i = n_i/N$ ,  $n_i$  is the individual number of species  $i$  and  $N$  is the individual number of all species. This index considers both species richness and evenness and represents the uncertainty with which we can predict which species will be one randomly selected individual in the community. If the community contains of only one monodominant species, the uncertainty is zero; the more species-rich the community is, the more uncertainty increases. However, if a community has many species but one of them

prevails, uncertainty will not be so high, since there is high probability that a randomly selected individual will be the most abundant species. Thus, the maximum value of  $H'$  for community of given richness occurs at situation where all species represent the same relative proportion. The second widely used index is the Simpson index (Simpson 1949),  $D = \sum p_i^2$ .  $1 - D$  which also considers both richness and evenness but, compared to Shannon, it is more influenced by evenness than richness. It represents the probability (ranging from 0 to 1) that two randomly selected individuals will be of the same species. Here, we chose to use the reciprocal Simpson index ( $1 - D$ ) since it varies in the same direction as Shannon.

The Pielou evenness index (Pielou 1966),  $J' = \frac{H'}{H'_{\max}} = \frac{H'}{\log(S)}$ , which is the ratio of the observed value of the Shannon index to its maximum value, was also calculated to study the degree of equality in species abundance in a sample. It is minimum ( $J' = 0$ ) when one species dominates.

Diversity indices were calculated on the basis of the basal area for trees and lianas, and the mean percentage cover for epiphytes in each plot. For understory species, indices were calculated on the percentage of plant cover in each quadrat.

### Data Analysis

Statistical analyses were computed with R software (version 4.0.4) (R Core Team 2019). Diversity indices were calculated using the *diversity* function of the package “Vegan” (Oksanen et al. 2022). Data were tested for normal distribution (Shapiro-Wilk test), homoscedasticity (Levene test), and independence (Durbin-Watson test), respectively with the packages “Stats” (R Core Team 2019), “Car” (Fox and Weisberg 2019), and “lmtest” (Zeileis and Hothorn 2002). Comparisons between the structure parameters (trees and stems density, basal area, epiphytes frequency and understory plant cover) and diversity indices of the seven forests were performed with one-way ANOVAs when all the required conditions of applications were met, or non-

parametric Kruskal–Wallis tests when they were not. When results significantly differed, pairwise multiple comparisons were performed with Bonferroni or Dunn’s post-hoc test, respectively (tests for non-equal sample sizes between groups) (package “FSA”; Ogle et al. 2020).

Diversity indices values were also compiled by stratum and compared between the two habitats (i.e., swamp vs. littoral forests) using non-parametric Wilcoxon–Mann–Withney  $U$  test. Indicator species analysis (Dufrière and Legendre 1997) was computed for each stratum to determine indicator values or “indval” (the average of relative abundance and frequency) for species in each forest (indval function, package “labdsv”; Roberts 2019). The indval approach looks for species that are both necessary and sufficient, that is, if you find that species you should be in that forest type, and if you are in that forest type, you should find that species. The indval index reaches its maximum value (1) when a species is found in a single forest type and in all samples of the forest type. We chose to consider a species as an indicator if it obtained at least the threshold value of 0.25, which

corresponds to the presence of the species in at least 50 % of the samples of the forests, and/or that its relative abundance reaches at least 50 %. This index was calculated on basal area for trees and lianas, and on the percentage cover for the two other strata (i.e., epiphytes and understory).

## RESULTS

### Structure and Composition of Forest Types

A total of 857 individual trees and 1,206 stems (dbh  $\geq$  5 cm) were measured on our eighteen study plots set up in seven forest types, representing a total study area of 3,600 m<sup>2</sup>. Significant differences in the structure of these forests were found on the averages of basal area, density of trees and lianas, and density of stems, but not on the frequency of epiphytes nor the plant cover in the understory (Table 1). The density of trees and lianas, as well as the stem density, are higher in *Acrostichum-Rhizophora* swamp forests and significantly distinct from *Talipariti-Inocarpus* littoral forests. Despite their low density of trees and stems, *Talipariti-Inocarpus* forests have the significant maximum basal area due

TABLE 1

Forests Structure in the 10 × 20 m Plots, According to the Number of Trees, Lianas, Stems (dbh  $\geq$  5 cm), Basal Area (BA), Percentage of Plant Cover in the Understory (in 2 × 2 m Quadrats), and Epiphyte Frequency (% of Occurrence on Living Trunks and Stems)

Forest Types ( <i>n</i> = Number of Plots)	Density of Trees and Lianas (Trees or Lianas per m <sup>2</sup> )	Density of Stems (Stems per m <sup>2</sup> )	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Epiphyte Frequency (%)	Plant Cover in the Understory (%)
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
<b>Swamp forests</b>					
<i>Rhizophora</i> mangrove ( <i>n</i> = 3)	0.20 ± 0.10 <sup>ab</sup>	0.45 ± 0.16 <sup>bc</sup>	43.6 ± 5.9 <sup>ab</sup>	22.8 ± 32.9 <sup>a</sup>	28.5 ± 12.3 <sup>a</sup>
<i>Acrostichum-Rhizophora</i> ( <i>n</i> = 3)	0.38 ± 0.10 <sup>b</sup>	0.56 ± 0.10 <sup>c</sup>	48.9 ± 8.9 <sup>ab</sup>	53.7 ± 30.4 <sup>a</sup>	30.2 ± 4.7 <sup>a</sup>
<i>Acrostichum-Talipariti</i> ( <i>n</i> = 3)	0.31 ± 0.09 <sup>ab</sup>	0.34 ± 0.08 <sup>abc</sup>	18.0 ± 5.5 <sup>a</sup>	44.6 ± 20.5 <sup>a</sup>	33.4 ± 17.7 <sup>a</sup>
<b>Littoral and para-littoral forests</b>					
<i>Talipariti-Barringtonia</i> ( <i>n</i> = 2)	0.15 ± 0.00 <sup>ab</sup>	0.18 ± 0.01 <sup>ab</sup>	35.8 ± 7.9 <sup>ab</sup>	9.6 ± 1.4 <sup>a</sup>	60.6 ± 22.9 <sup>a</sup>
<i>Talipariti-Inocarpus</i> ( <i>n</i> = 3)	0.13 ± 0.02 <sup>a</sup>	0.17 ± 0.02 <sup>a</sup>	53.7 ± 11.7 <sup>b</sup>	14.2 ± 9.8 <sup>a</sup>	66.8 ± 26 <sup>a</sup>
<i>Pandanus</i> ( <i>n</i> = 2)	0.20 ± 0.01 <sup>ab</sup>	0.21 ± 0.01 <sup>ab</sup>	42.8 ± 22.9 <sup>ab</sup>	1.2 ± 1.6 <sup>a</sup>	51.5 ± 3.1 <sup>a</sup>
<i>Barringtonia</i> ( <i>n</i> = 2)	0.22 ± 0.03 <sup>ab</sup>	0.28 ± 0.1 <sup>abc</sup>	39.9 ± 3.6 <sup>ab</sup>	0.7 ± 1.0 <sup>a</sup>	15.9 ± 0.2 <sup>a</sup>

Forest types names are based on tree species dominance and the presence of the large erect native fern *Acrostichum aureum*. Within a column, different letters indicate significant differences between forest types (ANOVA followed by post-hoc multiple comparisons tests using Benjamini–Hochberg correction for *p*-values).

to the large trunk of the Polynesian chestnut *Inocarpus fagifer*. Epiphytes frequency was the highest in native *Acrostichum-Talipariti* submangroves and in mixed *Acrostichum-Rhizophora* swamp forests, whereas plant cover in the understory was the highest in the two *Talipariti-Barringtonia* and *Talipariti-Inocarpus* littoral forest types.

We identified a total of 45 plant species in 31 families in the seven forest types, including seven trees and one liana (*Decalobanthus peltatus*) with a dbh  $\geq 5$  cm, 18 species found as epiphytes on living trunks and stems and 38 species in the understory (Table 2). Four taxa were identified at the genus level only, and three at the family level (including two fern species in the family Hymenophyllaceae and Dryopteridaceae, and a palm seedling) because the plants were too small or young (i.e., not fertile) to be morphologically determined. Most of the species were native (29), seven were ancient Polynesian introductions, and nine European or modern introductions. A total of 23 species were present in one forest type only (e.g., the two native *Dendrobium* epiphytic orchids in mixed *Acrostichum-Rhizophora* swamp forests), and no species were found in every studied forest. The most frequent species were the native tree *Talipariti tiliaceum* found in all forest types except the *Rhizophora* mangroves, and the epiphytic fern *Microsorium grossum* (syn. *Phymatosorus grossus*) in all but the *Barringtonia* forests. Moreover, five species are only found in both swamp and littoral forests (the common tree *T. tiliaceum*, the large erect fern *A. aureum*, the grass *Centotheca lappacea* and the two ferns *Davallia solida* and *M. grossum*) while the others are specific to one of the two habitats (swamp vs. littoral).

Forest composition was also distinguished by indicator species including six trees, three epiphytes and 13 understory species (Table 2). Indicator values confirmed the dominant tree species characterizing the different forest types (e.g., *B. asiatica* in *Barringtonia* forests), and highlighted their characteristic species assemblages in the epiphytic and understory strata. For example, in the epiphyte stratum, *A. elliptica* and *D. solida* are associated with

native *Acrostichum-Talipariti* submangroves whereas *Ctenopteris contigua* and *D. solida* are characteristic of mixed *Acrostichum-Rhizophora* swamp forests.

The biogeographical status of species in each stratum are different between forest types (Figure 2). Native *Acrostichum-Talipariti* submangroves are exclusively composed of native trees (100% of *T. tiliaceum*), with some European introduced species in the understory and as epiphytes (44% and 57%, respectively). Littoral and para-littoral forests are dominated by native species regardless of the stratum ( $\geq 82\%$  for trees and lianas, 100% for epiphytes, and  $\geq 68\%$  in understory), except the canopy stratum of *Talipariti-Inocarpus* forests with the large Polynesian introduced tree *I. fagifer* (70%). As expected, *Rhizophora* mangroves and mixed *Acrostichum-Rhizophora* swamp forests are strongly dominated by European introductions, both for trees (constituting respectively 100% and 99% of the canopy, mainly *R. stylosa*) and understory species (respectively 99% and 36%, mainly *R. stylosa* and *A. elliptica*).

#### Species Diversity in Forest Types

Native *Acrostichum-Talipariti* submangroves have the highest total species richness among all the forest types, with 18 species recorded considering the all different strata, whereas *Barringtonia* littoral forests have the lowest richness with only seven species, followed by the introduced *Rhizophora* mangroves with nine species (Figure 3). For the tree and liana strata, the two littoral *Talipariti-Inocarpus* and *Pandanus* forests have significant higher species richness. The understory species richness is significantly lower in introduced *Rhizophora* mangroves and in *Barringtonia* littoral forests. Despite the relatively high epiphytic species richness found in native submangroves and mixed *Acrostichum-Rhizophora* swamp forests, they were found not to significantly differ from other forest types ( $p = 0.06$ ), probably due to strong variations in standard deviation and the low number of replicates per forest type.

TABLE 2

Comparison of the Seven Forest Types According to Their Species Composition (Arranged in Alphabetical Order of Scientific Name) in Different Strata, Basal Area for Trees and Lianas, Frequency for Epiphytes and Plant Cover for the Understory Species

Species	Family	n	Status	Swamp Forests			Littoral and Para-Littoral Forests			
				<i>Rhizophora</i> mangroves 3	<i>Acrostichum- Rhizophora</i> 3	<i>Acrostichum- Talitpariti</i> 3	<i>Talitpariti- Barringtonia</i> 2	<i>Talitpariti- Inocarpus</i> 3	<i>Pandanus</i> 2	<i>Barringtonia</i> 2
<b>Trees and lianas (basal area in m<sup>2</sup> ha<sup>-1</sup>)</b>										
<i>Barringtonia asiatica</i>	Lecythidaceae	N					7.5 ± 0.7	0.1 ± 0.1	12.1 ± 0.7	37.2 ± 4.2
<i>Coos nucifera</i>	Areaceae	PI							8.8 ± 7.7	
<i>Decalobanthus peltatus</i>	Convolvulaceae	EI					0.2 ± 0.2	0.1 ± 0.1		
<i>Inocarpus fagifer</i>	Fabaceae	PI						37.1 ± 9.7		
<i>Morinda citrifolia</i>	Rubiaceae	PI						0.2 ± 0.3		
<i>Pandanus tectorius</i>	Pandanaceae	N							21.8 ± 14.4	
<i>Rhizophora stylosa</i>	Rhizophoraceae	EI		48.8 ± 9.1						
<i>Talitpariti tiliaceum</i>	Malvaceae	N		0.1 ± 0.2	18.0 ± 5.6	28.2 ± 6.9	16.2 ± 6.3	0.07 ± 0.09	2.7 ± 0.6	
<b>Epiphytes (% of occurrence on living trunks and stems between 0 and 3 m)</b>										
<i>Acrostichum aureum</i>	Pteridaceae	N		4.0 ± 6.9						
<i>Adenanthera pavonina</i>	Fabaceae	EI			0.7 ± 1.2					
<i>Arcisia elliptica</i>	Myrsinaceae	EI			33.3 ± 11.6					
<i>Asplenium nidus</i>	Aspleniaceae	N						13.0 ± 8.7		0.5 ± 0.7
<i>Crepidomanes humile</i>	Hymenophyllaceae	N			0.3 ± 0.6					
<i>Crepidomanes bipunctatum</i>	Hymenophyllaceae	N		0.7 ± 1.2	2.0 ± 3.5					
<i>Ctenopteris contigua</i>	Hymenophyllaceae	N		0.7 ± 1.2	2.0 ± 3.5					
<i>Davallia pectinata</i>	Grammitidaceae	N			6.7 ± 4.0					
<i>Davallia solidata</i>	Davalliaceae	N		0.3 ± 0.6	0.3 ± 0.6					
<i>Davallia solida</i>	Davalliaceae	N		20.0 ± 29.5	43.0 ± 29.8	17.0 ± 20.1	1.5 ± 2.1			
<i>Dendrobium biflorum</i>	Orchidaceae	N		9.3 ± 12.1						
<i>Dendrobium involutum</i>	Orchidaceae	N		6.0 ± 9.5						
<i>Lepisorus spicatus</i>	Polypodiaceae	N		0.3 ± 0.6	0.3 ± 0.6					
<i>Microsorium grossum</i>	Polypodiaceae	N		1.0 ± 1.7	6.7 ± 11.5	2.5 ± 3.5	3.7 ± 6.4	1.0 ± 1.4		
<i>Nephrolepis</i> spp.	Nephrolepidaceae	N			5.7 ± 7.4	4.0 ± 5.7	2.0 ± 3.5			
<i>Ophioglossum pendulum</i>	Ophioglossaceae	N			1.0 ± 1.0					
<i>Psilotum complanatum</i>	Psilotaceae	N			0.3 ± 0.6					
<i>Schefflera actinophylla</i>	Araliaceae	EI		0.3 ± 0.6	12.3 ± 18.0					
<i>Teniophyllum fasciola</i>	Orchidaceae	N		1.0 ± 1.0	2.7 ± 2.9					





TABLE 2

Species	Family	Status	<i>n</i>	Swamp Forests			Littoral and Para-Littoral Forests			
				<i>Rhizophora</i> mangroves	<i>Acrostichum- Rhizophora</i>	<i>Acrostichum- Talipariti</i>	<i>Talipariti- Barringtonia</i>	<i>Talipariti- Inocarpus</i>	<i>Pandanus</i>	<i>Barringtonia</i>
				Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Areaceae	Areaceae	EI				0.02 ± 0.03				
<i>Pandanus tectorius</i>	Pandanaceae	N								<b>11.4 ± 9.2</b>
<i>Rhizophora stylosa</i>	Rhizophoraceae	EI		<b>28.2 ± 12.8</b>	1.3 ± 1.8					
<i>Schefflera actinophylla</i>	Araliaceae	EI		0.1 ± 0.2	1.0 ± 1.6					
<i>Talipariti tiliaceum</i>	Malvaceae	N			0.02 ± 0.03		<b>0.4 ± 0.2</b>	0.02 ± 0.03		<b>4.4 ± 2.2</b>
<i>Tectaria lessoni</i>	Dryopteridaceae	N								
<i>Vigna marina</i>	Fabaceae	N		0.2 ± 0.3						
<i>Vigna</i> sp.	Fabaceae	EI								
<i>Zingiber zerumbet</i>	Zingiberaceae	N					34.4 ± 29.2	36.0 ± 13.7		0.03 ± 0.04

*n* = number of plots. Biogeographical status (according to [Chevillotte et al. 2019](#)). N = native; PI = Polynesian introduction; EI = European introduction. Indicator species for each forest are shown in bold.

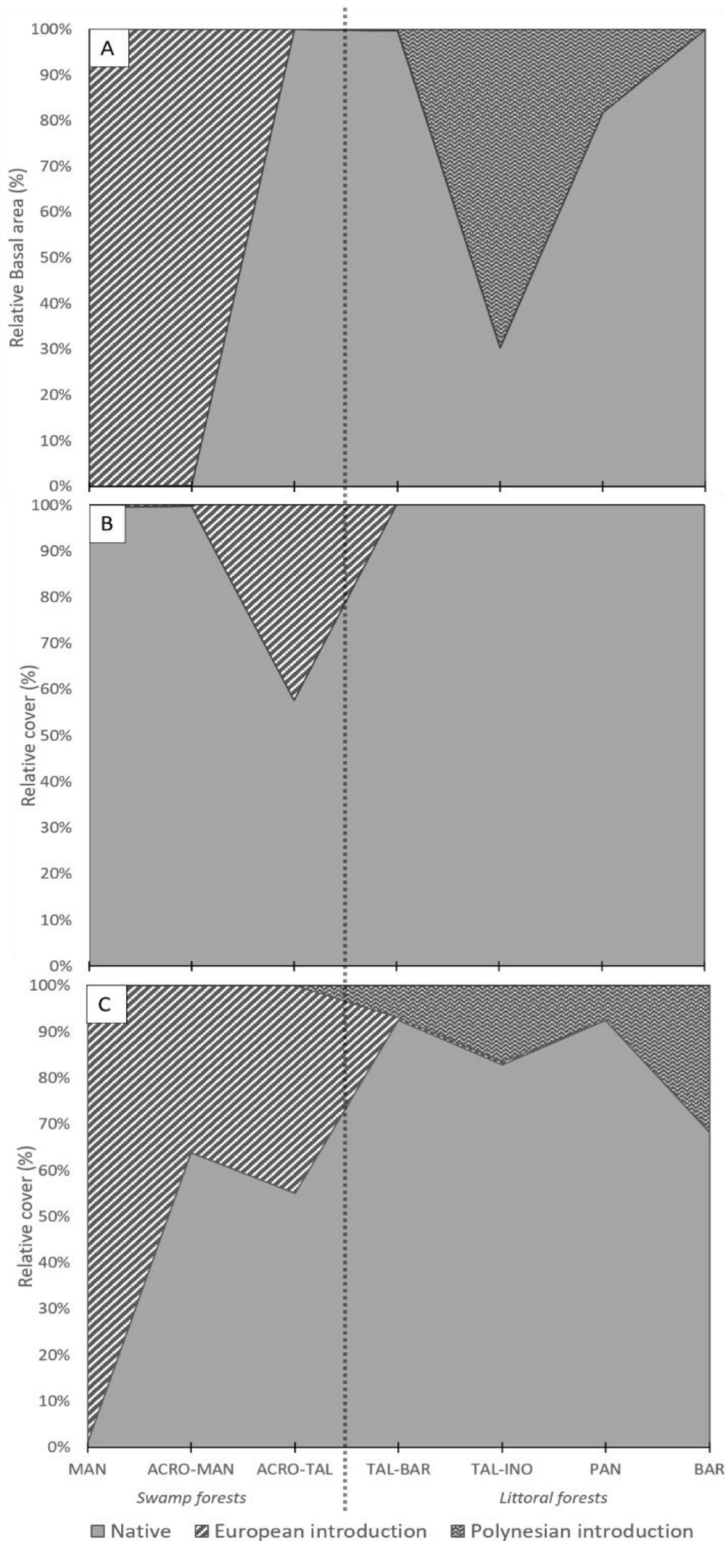


FIGURE 2. Forest composition in terms of specific biogeographical status across the seven forest types: (A) basal area of trees and lianas, (B) epiphytes cover, and (C) cover in the understorey layer. The proportions shown indicate average values across plots within forest types. The dotted line separates the two main habitats (swamp vs. littoral).

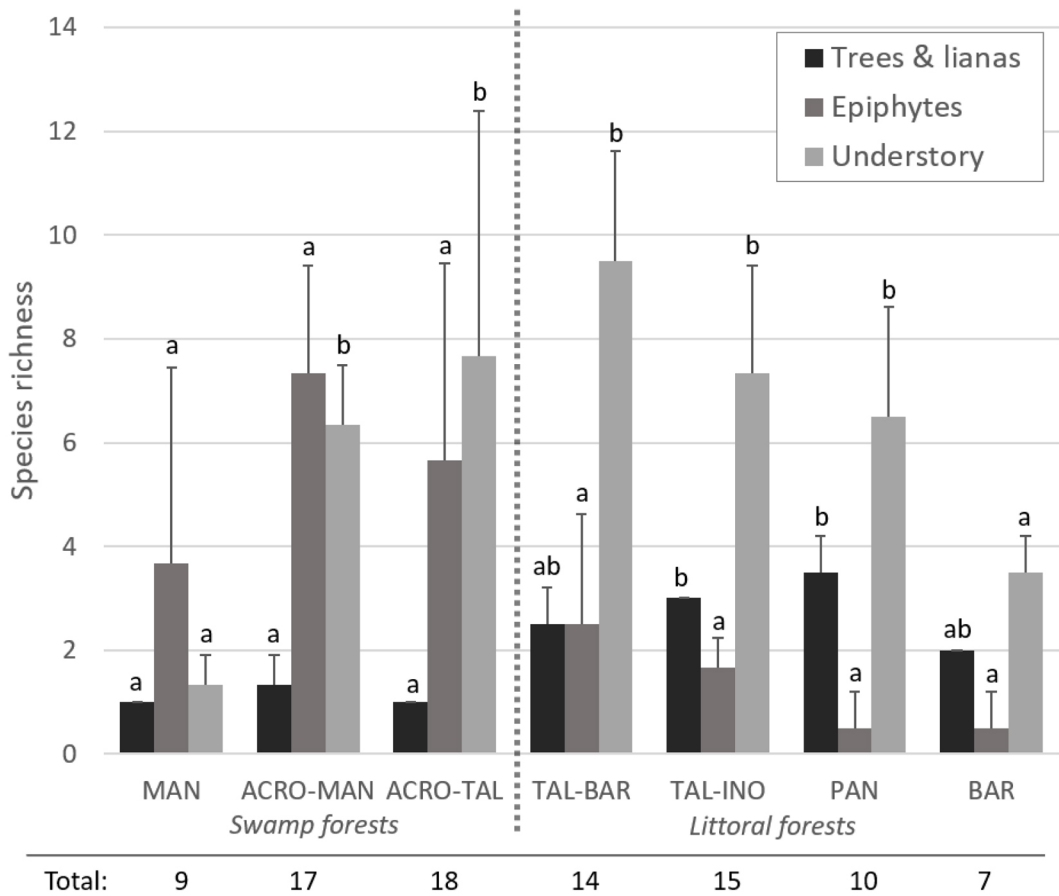


FIGURE 3. Species richness (mean ± SD) by stratum, and total species richness for the seven forest types. Comparisons were performed between forests for each stratum separately with Kruskal–Wallis test and Dunn’s post-hoc test. The dotted line separates the two habitats (swamp vs. littoral).

As Shannon and Simpson diversity indices follow the same pattern (Figure 4), we used only the Shannon index to describe the species diversity in the different forest types (Table 3). Shannon diversity and Pielou evenness are maximum in *Pandanus* forests for the tree and liana stratum, and for the understory ( $p < 0.01$  for both indices) whereas introduced *Rhizophora* mangroves and *Barringtonia* forests have the lowest species diversity in the understory ( $p < 0.001$ ; Figure 5; Table 3). Shannon and Pielou indices for epiphytes are maximum in mixed *Acrostichum-Rhizophora* swamps and native *Acrostichum-Talipariti* sub-mangroves, while they are minimum in *Pandanus* and *Barringtonia* littoral forests,

but with no significant difference between forests.

At the habitat level (swamp vs. littoral forests), there are significant differences in diversity for every strata (Figure 6). Swamp forests have a lower diversity than littoral forests for the trees and lianas and for the understory ( $p < 0.001$ ), but a significantly higher diversity in epiphytes.

#### DISCUSSION

##### Comparison Between Habitats and Forest Types

SWAMP FORESTS, MANGROVES, AND SUBMANGROVES — Our studied *Acrostichum-Talipariti*

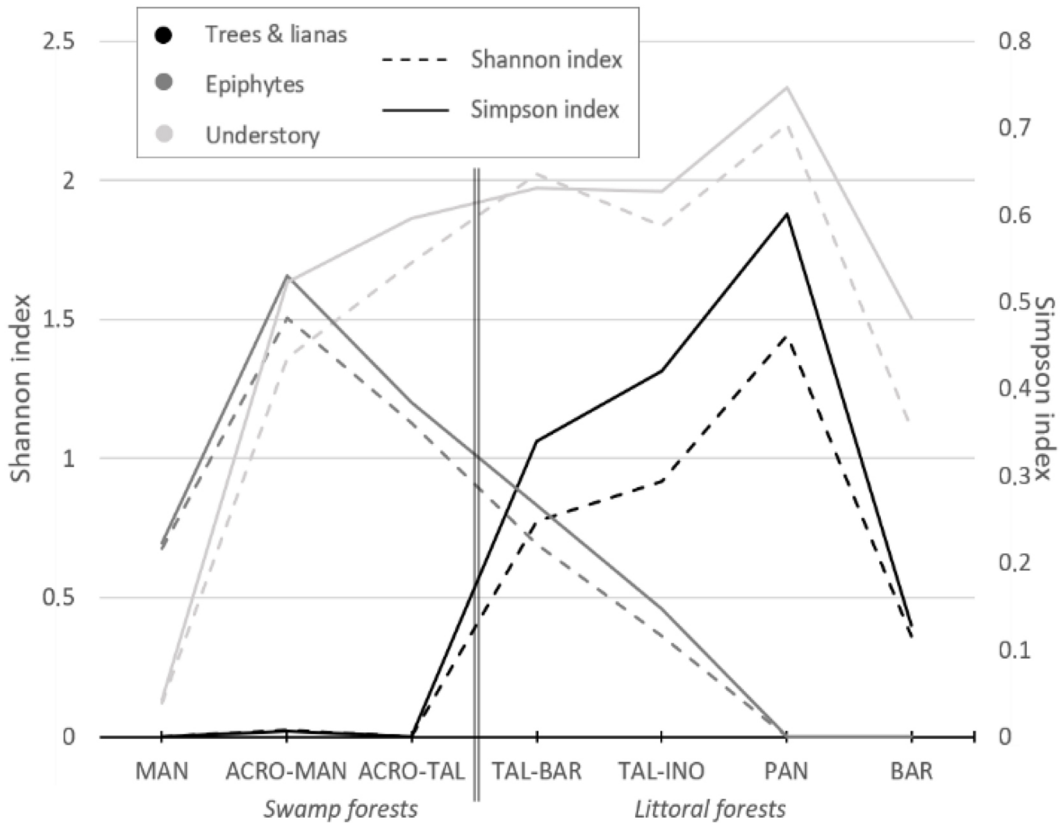


FIGURE 4. Shannon and Simpson index (mean) by strata in the seven forests. The vertical line separates the two habitats (swamp vs. littoral).

TABLE 3

Diversity Comparison Between the Seven Forests According to the Shannon Index and Pielou Evenness (Mean  $\pm$  SD) in Each Stratum (Kruskal–Wallis with Dunn’s Test for Trees and Lianas and for Understory, ANOVA for Epiphytes)

Forest Types (n = Number of Plots)	Shannon (Mean $\pm$ SD)			Pielou Evenness (Mean $\pm$ SD)		
	Trees and Lianas	Epiphytes	Understory	Trees and Lianas	Epiphytes	Understory
<b>Swamp forests</b>						
<i>Rhizophora mangrove</i> (n = 3)	0.00 $\pm$ 0.00 <sup>a</sup>	0.68 $\pm$ 0.82 <sup>a</sup>	0.12 $\pm$ 0.21 <sup>a</sup>	0.00 $\pm$ 0.00 <sup>a</sup>	0.32 $\pm$ 0.28 <sup>a</sup>	0.12 $\pm$ 0.21 <sup>a</sup>
<i>Acrostichum-Rhizophora</i> (n = 3)	0.02 $\pm$ 0.04 <sup>a</sup>	1.51 $\pm$ 0.43 <sup>a</sup>	1.36 $\pm$ 0.03 <sup>cd</sup>	0.02 $\pm$ 0.04 <sup>ac</sup>	0.54 $\pm$ 0.15 <sup>a</sup>	0.52 $\pm$ 0.06 <sup>bc</sup>
<i>Acrostichum-Talipariti</i> (n = 3)	0.00 $\pm$ 0.00 <sup>a</sup>	1.13 $\pm$ 0.60 <sup>a</sup>	1.70 $\pm$ 0.74 <sup>d</sup>	0.00 $\pm$ 0.00 <sup>a</sup>	0.47 $\pm$ 0.11 <sup>a</sup>	0.60 $\pm$ 0.07 <sup>a</sup>
<b>Littoral and para-littoral forests</b>						
<i>Talipariti-Barringtonia</i> (n = 2)	0.78 $\pm$ 0.01 <sup>ab</sup>	0.69 $\pm$ 0.98 <sup>a</sup>	2.02 $\pm$ 0.69 <sup>cd</sup>	0.63 $\pm$ 0.21 <sup>bc</sup>	0.35 $\pm$ 0.49 <sup>a</sup>	0.62 $\pm$ 0.15 <sup>a</sup>
<i>Talipariti-Inocarpus</i> (n = 3)	0.92 $\pm$ 0.13 <sup>b</sup>	0.36 $\pm$ 0.33 <sup>a</sup>	1.83 $\pm$ 0.20 <sup>cd</sup>	0.58 $\pm$ 0.08 <sup>bc</sup>	0.36 $\pm$ 0.33 <sup>a</sup>	0.65 $\pm$ 0.06 <sup>acd</sup>
<i>Pandanus</i> (n = 2)	1.44 $\pm$ 0.04 <sup>b</sup>	0.00 $\pm$ 0.00 <sup>a</sup>	2.20 $\pm$ 0.32 <sup>c</sup>	0.81 $\pm$ 0.11 <sup>b</sup>	0.00 $\pm$ 0.00 <sup>a</sup>	0.83 $\pm$ 0.03 <sup>b</sup>
<i>Barringtonia</i> (n = 2)	0.36 $\pm$ 0.08 <sup>ab</sup>	0.00 $\pm$ 0.00 <sup>a</sup>	1.11 $\pm$ 0.08 <sup>b</sup>	0.36 $\pm$ 0.08 <sup>ab</sup>	0.00 $\pm$ 0.00 <sup>a</sup>	0.63 $\pm$ 0.15 <sup>bd</sup>

Within a column, different letters indicate significant differences between forests ( $p$ -value  $\leq$  0.05).

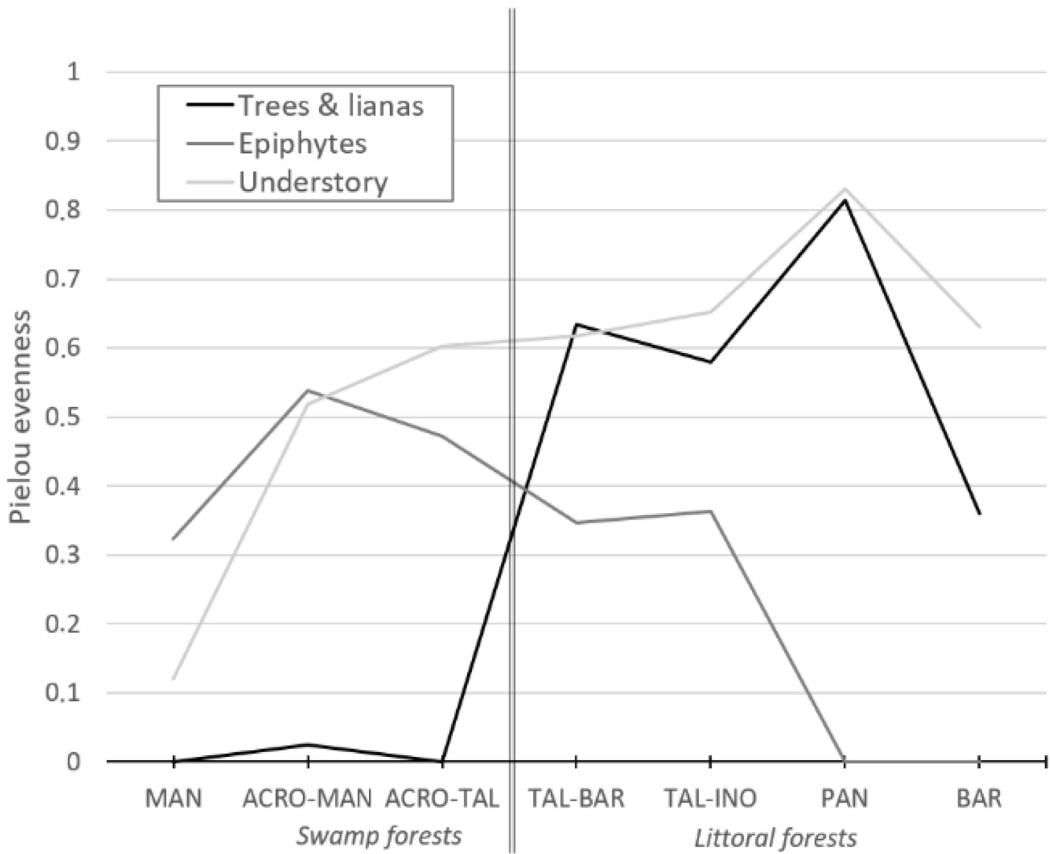


FIGURE 5. Pielou evenness (mean) by strata in the seven forests. The vertical line separates the two habitats (swamp vs. littoral).

submangrove forest type corresponds to the “*Hibiscus-Acrostichum* swamp” described by Florence (1993) among the “littoral azonal vegetation” found in Tahiti. This forest type is

also called “submangrove islets” (*îlots de submangrove* in French) by Papy (1951–1954) or “almost-mangrove swamp” by Mueller-Dombois and Fosberg (1998), although the

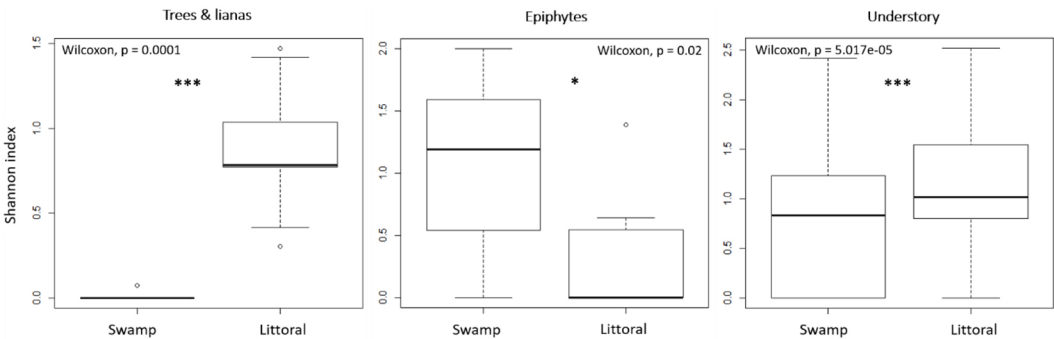


FIGURE 6. Comparison of Shannon index between swamp and littoral forests in the three strata (Wilcoxon–Mann–Whitney *U* test; \* $<0.05$ , \*\* $<0.01$ , \*\*\* $<0.001$ ).

native tree *Thespesia populnea* and the introduced large tree *Terminalia catappa* have not been recorded in our plots but are found outside in the Mitirapa estuary (Meyer and Fabre Barroso 2022). It is interesting to note that a similar forest type also called “submangrove islets” is described by Rivals (1952) in the island of La Réunion (Mascarenes, Indian Ocean). The large erect fern *Acrostichum aureum*, although rare in La Réunion, is found in Mauritius (Mascarenes) in association with the mangrove species *Bruguiera gymnorhiza* and *Rhizophora mucronata* (Blanchard 2000). In the Hawaiian Islands, where mangroves are also naturally absent, “coastal wetland shrublands” dominated by *Talipariti tiliaceum* are found in coastal streams, marshes and ponds, with *Terminalia catappa* as a co-dominant species (Gagné and Cuddihy 1990). These authors mentioned that “there are no representative extant native examples” of what they considered native coastal wet forests, and “only a single alien community is recognized,” the mangrove *Rhizophora mangle*-*Bruguiera sexangula* (incorrectly identified as *B. gymnorhiza* in Wagner et al. 1990, see Allen et al. 2000) that have been introduced after 1900 and spread along muddy coastlines to become invasive in many Hawaiian Islands (Allen 1998).

The floristic composition of introduced *Rhizophora* mangroves had never been described in French Polynesia until this study. In the Samoan islands where mangrove is native, Whistler (1980, 2002) has described “*Rhizophora* mangrove scrubs” dominated by *Rhizophora mangle* (syn. *R. samoensis*) with the occasional presence of *Acrostichum aureum* on the margin of mangrove forests (or sometimes in openings within the forest), corresponding to our observations in our *Rhizophora* mangroves, but even more in the understory of our mixed *Acrostichum*-*Rhizophora* swamp forests. He also recorded some epiphytic species, including several of them which are common in our studied swamp forests, that is, the ferns *Davallia solida*, *Microsorium grossum*, *Ophioglossum pendulum*, and other species belonging to the genera *Ctenopteris* and *Psilotum*, as well as some *Dendrobium* orchids such as *D. biflorum* also found in our mixed *Acrostichum*-*Rhizophora* swamp forests. Meyer et al. (2021)

mentioned the existence of a mixed forest between native submangroves and introduced *Rhizophora* mangroves on the islands of Tahiti and Moorea, and suggested that mangroves have invaded native littoral swamp forests, forming a “novel” or “neo-ecosystem” (sensu Hobbs et al. 2006, 2009, 2013) or a hybrid habitat (Meyer et al. 2015) where native species co-occur with naturalized non-native species. Interestingly, the tree basal area (43.6 m<sup>2</sup>/ha) of *Rhizophora stylosa* mangrove found in Tahiti appears to be much higher than those dominated by *R. apiculata* (23 m<sup>2</sup>/ha) in the Philippines where it is naturally present (Dangan-Galon et al. 2016). By comparison the basal area of the invasive *R. mangle* in Hawaii is reaching 37.5 m<sup>2</sup>/ha with up to 2.44 trees/ha (Allen 1998).

LITTORAL AND PARA-LITTORAL FORESTS — Our *Pandanus* and *Barringtonia* littoral forests fall into the “rocky littoral vegetation” of Florence (1993) who described a *Pandanus*-*Barringtonia* forest, whereas we separated them into two forest types, following Whistler (1980, 2002) in the Samoan islands, who distinguished “*Pandanus* scrubs” and “*Barringtonia* littoral forests.” Indeed, Whistler’s description corresponds to the floristic composition of these two forest types found in the seacliffs of Te Pari in the peninsula of Tahiti, notably given the presence of the bird’s nest fern *Asplenium nidus* in the understory and as epiphytes. Despite floristic similarities, the structure of our *Barringtonia* littoral forests differs from that of the “*Barringtonia*/*Hernandia* littoral forest type” described by Franklin et al. (2006) in Samoa, the former having a basal area almost two times lower (40 vs. 68 m<sup>2</sup>/ha) but a stem density three times higher than the latter (0.28 vs. 0.10 stems/m<sup>2</sup>).

Our two littoral and para-littoral forests dominated by the tree *Talipariti tiliaceum* are mainly riparian forests (i.e., located in the surroundings of streams and wetlands, see Meyer 2016) described by Florence (1993) as low-elevation mesic *Hibiscus*-*Mangifera* degraded forests or wet *Hibiscus*-*Etilingera* native forests, and also called “adlittoral” vegetation by Papy (1951–1954). Whistler (2002: 55) described “freshwater swamps” by

differentiating the “*Hibiscus* swamp forests” from the “*Inocarpus* swamp forests” and from the “*Barringtonia* swamp forests,” but he explained that these tree species can sometimes occur mixed together (“*Hibiscus sometimes shares dominance with other tree species, making these areas difficult to classify*”), as we have observed in our study sites.

### *Comparison of Species Diversity*

Littoral and swamp forests are relatively species-poor compared to wet and cloud forests in Tahiti (Florence 1993, Meyer 2011) in relation to the particular ecological conditions of those habitats (e.g., sea spray, tidal flooding, muddy or sandy substrate). For instance, tree species richness was between one and five and the Shannon index between 0.00 (monospecific) and 1.44 in our plots while tree species richness was in the range 14–50 and Shannon in the range 0.72–3.32 in higher-elevation vegetation sampled in the neighbouring island of Moorea (Chevillotte et al. 2014).

The tree layer is often dominated by one or two species while greater variations in diversity are observed for epiphytes and the understory. Most mangroves do not contain a significant amount of non-tree or understory vegetation (Snedaker and Lahmann 1988). Our study highlighted the very low species diversity in all strata of the introduced *Rhizophora* mangroves compared to the other native and mixed swamp forests, with a nearly monospecific understory formed by *Rhizophora* seedlings. The absence of other understory species might be explained by the high canopy density compared to the two other swamp forest types. The low light intensity in mangrove dense forests could limit the recruitment and growth of understory species, such as the light-demanding erect fern *Acrostichum aureum* (Medina et al. 1990). The presence of this fern in other swamp forests appears to be beneficial for epiphytes and understory species as their erect stipe (up to 1.5 m tall) serve as a host structure for woody plant seedlings and ferns which are protected from brackish or salty waters. This facilitation of seed germination is also often

observed on tree ferns trunks (Gaxiola et al. 2008).

Among littoral forests, the poor diversity of the understory in *Barringtonia* forests was also noted by Whistler (2002) who observed the forest floor to be typically very open, with only sparse ground cover, due to the shady conditions caused by the dense canopy and large leaves of this tree. By contrast, the highest tree and understory diversity found in *Pandanus* forests can be explained by their intermediate position between littoral shrubland and littoral forests (Whistler 2002). Indeed, this forest type can be considered as an ecotone, that is, a transition area between two adjacent but different plant communities (Puyravaud et al. 1994).

Our study on species richness and abundance of vascular epiphytes (mostly ferns) shows their preference for swamp habitats. Ferns are particularly sensitive to humidity (Benzing 1998, Zotz and Bader 2009), which makes swamps preferential habitats for them. Their diversity is highest in the *Acrostichum-Rhizophora* mixed swamps, including *Dendrobium* spp. orchid species perhaps by the presence of new microhabitats (related to *R. stylosa* invasion) favourable to their development (Mallik et al. 2001).

### *Implications for Conservation and Restoration*

In this study conducted in Tahiti, we were faced with the difficulty of finding relatively undisturbed native littoral and swamp forests, constraining us to reduce our sampling method to three sites, with a maximum of two or three 10 × 20 m plots per forest type. Native coastal forests and lowland wetlands loss and degradation due to past and present human occupation has long been documented (Papy 1951–1954, Florence 1993, Mueller-Dombois and Fosberg 1998, Meyer 2007). There is an urgent need to conserve and restore these threatened remnant forests. As an example, the only littoral and swamp forest located on the north coast of Tahiti Iti (Faratea site) and mapped in the 1990s (Florence 1993) has been completely deforested and converted into an urbanized area

(pers. obs. 2022). Restoration of the last remnants of native habitats is now becoming a priority in many international conservation policies. IUCN has recently adopted the “Nature-Based Solutions” resolution which are actions to protect, sustainably manage, and restore natural and modified ecosystems (Cohen-Shacham et al. 2016) and the United Nations have declared in 2021 the “Decade on Ecosystem Restoration” to prevent, halt and reverse the degradation of ecosystems (United Nations 2019).

Because mangroves are known worldwide to provide regulating, provisioning and cultural ecosystem services (Singh and Odaki 2004, Webber et al. 2016), people have a positive perception of mangroves, including in French Polynesia in the Society Islands where it was introduced (Meyer et al. 2021). However, *Rhizophora stylosa* has colonized and replaced native submangroves, *Paspalum vaginatum* littoral grasslands, and the thickets formed by the large *A. aureum* ferns with negative ecological impacts (Papy 1951–1954, Iltis and Meyer 2010, Meyer et al. 2021). We believe our results will help restoration projects targeting the studied native habitats while focusing on the described native floristic composition in order to ensure their preservation.

This study provides the first quantitative baseline dataset on relict native littoral and swamp forests in Tahiti that will enable future conservation of these threatened habitats but also in other high volcanic islands of the Society archipelago. Further research is still needed to supplement our data on forest structure and composition, in particular by conducting field surveys during the dry season to see whether changes in plant cover are observed in the understory, and by increasing the number of plots on Tahiti or on its “sister island” of Moorea, if other relatively undisturbed native littoral and swamp habitat remnants are still found.

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