



FLORA AND VEGETATION OF CLIPPERTON (LA PASSION)
ATOLL, NORTH-EASTERN PACIFIC OCEAN: THREE CENTURIES
OF CHANGES AND RECENT PLANT DYNAMICS

*Xenia Jost, Christian H. Jost,
and Jean-Yves Meyer*



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FLORA AND VEGETATION OF CLIPPERTON (LA PASSION) ATOLL, NORTH-EASTERN PACIFIC OCEAN: THREE CENTURIES OF CHANGES AND RECENT PLANT DYNAMICS

XENIA JOST¹, CHRISTIAN H. JOST^{2,3} and JEAN-YVES MEYER⁴

ABSTRACT

The terrestrial flora and vegetation of Clipperton (La Passion) atoll, a very remote and small (170 ha of land) French island located in the North-Eastern Pacific Ocean, at ca. 1,000 km west of the Mexican coast, have dramatically changed during the past three centuries. This paper, based on historical testimonies, previously published floristic studies, and an extensive plant inventory conducted during the “International Scientific Expedition PASSION 2015”, show that the atoll has experienced particularly active and rapid vegetation dynamics with alternating plant cover expansion and regression phases. Our results provide the first comprehensive assessment of vegetation cover and vascular plant species distribution based on georeferenced data and mapped with GIS software, as well as the first record of two newly established non-native weeds. The current composition and abundance of native and alien vascular plant communities (15 species including only 4 native taxa) appear to depend not only on abiotic factors (e.g. substrate and climatic events) but also on biotic interactions with animal communities (e.g. native seabirds and crabs). Anthropogenic activities and disturbances (e.g. coconut palm, pig, rat and weed introductions) that have occurred in the past 100 years have also played an important role in explaining the past and current floristic changes.

INTRODUCTION

The atoll of Clipperton, a French territory also called La Passion⁵, is located in the Tropical North-Eastern Pacific Ocean at 109°12' W and 10°17' N (**Figure 1**), 1,080 km West of the nearest continental land (Mexican coast), 3,980 km from the Marquesas Islands (French Polynesia), the nearest land being Socorro Island in the Revillagigedo Archipelago (Mexico) 945 km away. The total surface of the atoll with its lagoon is 9 sq. km, with 170 ha of emergent coral ring, including six tiny inner lagoon islets. Clipperton is unique because of the presence of a volcanic rock (called “Le Rocher” or “The Rock”) rising at 29 m, and a completely closed lagoon (**Figure 2**). It is the smallest of the 11 French Overseas tropical island territories (comprising French Polynesia, New Caledonia and Wallis et Futuna in the Pacific Ocean) and is considered one of the most isolated uninhabited islands in the world. Despite its small land area, Clipperton affords France sovereignty over 435 600 sq. km of ocean (Economic Exclusive Zone).

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⁵ A text adopted by the French Assembly in November 24th, 2016 indicates that the names of *La Passion* or *La Passion- Clipperton* can also be used.



Figure 1. Location of Clipperton (La Passion) atoll in the Tropical North-Eastern Pacific Ocean

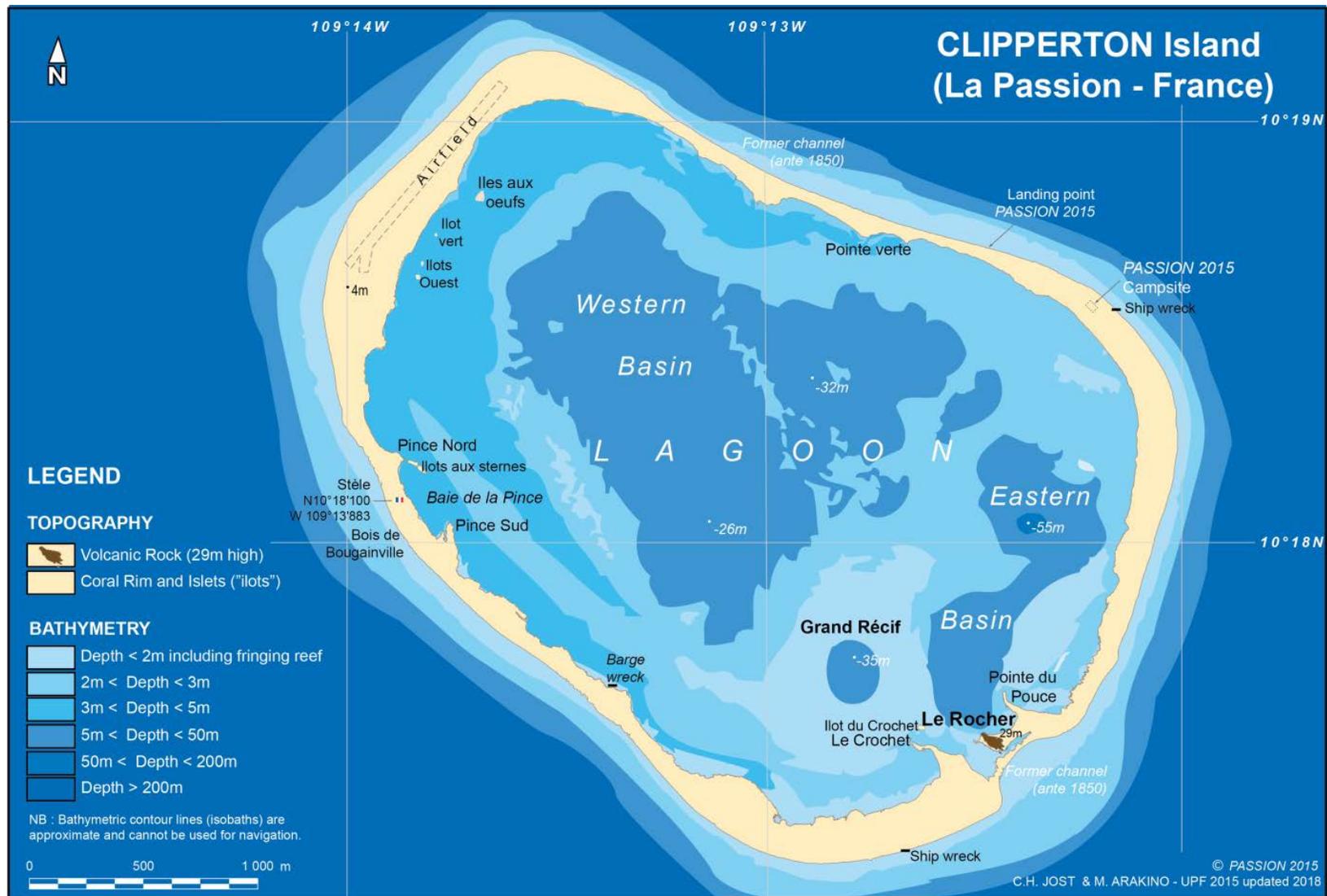


Figure 2. Description of the atoll with the main area toponyms including the location of “Le Rocher” and the six inner lagoon islets

A Brief History of Past Visits and Scientific Surveys

Clipperton was first discovered and named “La Passion” in 1711 by the French Captain Michel Dubocage en route to China on his vessel “La Découverte” (Briot and Briot, 2010). During the past three centuries, the island went through periods of strong interest, alternating with long periods of forgetfulness. In 1858, Lieutenant Le Coat de Kerveguen took official possession of Clipperton for France, but in 1892, a US citizen, Frédéric Permien, reclaim the island on behalf of the USA, relying on the “Guano Islands Act”. He created the Oceanic Phosphate Company to exploit the guano. In 1897 the Mexicans landed a military garrison and guano workers stayed on the island until 1917.

Although the next visits on this very remote island were sparse, the number of scientific and report papers are numerous, exceeding 500 (Jost, 2005a), allowing comparative studies of the natural environmental of the atoll, both in the lagoon and on land. The French Army and the Oceanographic and Hydrographic Service (SHOM) established the first map of reference in 1935. One of the first and most important scientific surveys was conducted in 1958 by the Scripps Institution of Oceanography based in California, with 13 scientists including the French botanist Marie-Hélène Sachet. The French Army occupied the island through continuous trips called “Missions Bougainville” from 1966 to 1969 (Ehrhardt and Niaussat, 1970). The famous French oceanographer, researcher, filmmaker, and undersea explorer, Jacques-Yves Cousteau visited the atoll in 1980 with a small French-Canadian-American scientific team. A Mexican-French scientific expedition “SURPACLIP” was organized in November 1997 directed by Dra Solis-Weiss (Universidad Nacional Autónoma de México) with the participation of the second author (then based at the University of New Caledonia) who later organized the “PASSION 2001” expedition with scientists from IRD (Institut de Recherche pour le Développement) and the help of the French Navy. A large scientific expedition was organized by the French explorer Jean-Louis Etienne between December 2004 and April 2005 with 30 French scientists rotating every two weeks (Charpy, 2009). The “PASSION 2013” expedition was again organized by the second author (then based at the University of French Polynesia). Throughout these expeditions, detailed observations and data were gathered on plant and animal communities in the lagoon and on land (Jost and Andréfouët, 2006).

The “International Scientific Expedition PASSION 2015”, organized and directed by the second author and involving 14 scientists, took place in April 2015. It was held under the high patronage of M. François Hollande, former president of France, sponsored by several French Ministries and Agencies, and with the logistical assistance of the French Navy and Army. Its main goals were to continue the inventories of coral reef biota and land fauna and flora, as well as an assessment of coastal dynamics and erosion.

Historical Documentation of The Vegetation

The description of the natural environment of Clipperton (La Passion) and more specifically of its vegetation and flora, come from episodic short-term visits and stays since the 18th century (**Table 1**). Visitors (sailors then scientists) described drastic changes in the vegetation from almost no plant cover (in 1871 and 1897) to dense vegetation cover (in 1934 and 1958), followed by a decline in the 1980-1990s, then a new increase of plant cover starting in 2005.

The most detailed description of the vegetation and flora was provided by French botanist M.-H. Sachet during her two and a half weeks spent on the island in 1958 (Sachet, 1959). The low vegetation was then covering almost 80% of the land (Sachet, 1962). Noticing the presence of 58 feral pigs with dramatic impacts on seabirds and their eggs, decision was taken to eradicate them by shooting. The number of land crabs *Johngarthia planata* Stimpson 1860 (syn. *Gecarcinus planata*, Gecarcinidae) then increased up to 11 million in 1968 (Ehrhardt and Niaussat, 1970), suggesting that pigs were regulating the crab population. As a result, the vegetation cover declined to become totally absent on the coral rim as

described by Jost in 1997 and 2001, except for coconut trees, and six plant species found on five inner lagoon islets not reachable by crabs (Jost, 2003).

The black rat *Rattus rattus* was accidentally introduced between 1997 and 2001, probably by a ship stranding (Lorvelec and Pascal, 2009). In 2005 a new census of the crab population showed that they decreased significantly to 1.25 million, suggesting high predation by rats (Bouchard and Poupin, 2009). C.H. Jost suggested that, despite the observation of remains of up to 20 crabs in each rat's nest, the rodent population, estimated at less than a 1000 in 2013, appeared insufficient to explain the strong decline of crabs (Jost, 2013). The crab population might have reached its demographic optimum, and possibly the island's carrying capacity, then declined because of the scarcity of food resources. During the 2005 expedition, only a few patches of vegetation, mainly composed of the vine *Ipomoea pes-caprae* (Convolvulaceae), were observed (Couté and Garrouste, 2009), while in 2013, vegetation was covering one third of the atoll land surface (Jost, 2013).

The main purpose of this paper is to give a precise assessment of the current terrestrial vascular flora and vegetation of the atoll. It updates the last plant inventory conducted 10 years earlier, and provides the first georeferenced inventory of the vegetation cover, using the Quantum GIS software.

METHOD

Field-Work Constraints

Scientific surveys and field work on Clipperton (La Passion) are constrained by the strong geographic isolation and remoteness of the island, the difficulty in accessing the closed atoll by boat, and by the lack of housing infrastructure. Indeed, three to four days navigation are necessary to reach the island from the closest land, i.e., the east coast of Mexico, and seven to eight days from the Marquesas islands (French Polynesia) to the Southwest. The landing, and above all the re-boarding are always dangerous due to the lack of channel to reach the lagoon. Moreover, the atoll is located in the tropical Northeastern Pacific zone of cyclone formation which lasts from mid-May till the end of November.

During the "PASSION 2015" expedition conducted around and on the atoll, weather conditions were fairly good during most of the 16 days spent on land except for two severely stormy days with heavy rains.

Plant Collection and Identification

Two fertile (i.e., with fruits and/or flowers) samples of each plant species observed during the 16 days of field-survey were collected by the first author. Plant specimens were labelled (with the date of collection, the location, and a collection number), pressed in newspapers, and dried in full sun. The plant collection was preserved in plastic bags with a small amount of 90% alcohol during the boat trip back to Tahiti, and species identification was confirmed or completed by the third author.

This plant collection is temporarily stored at the "Délégation à la Recherche" in Tahiti (French Polynesia) and will be permanently deposited in the main herbaria of Paris ([P]) and the Musée de Tahiti et des Îles in Tahiti [PAP]).

A few samples of plant material were also dried in silica gel for further genetic analysis and phylogeographic studies. Some seeds and fruits found on the ground in the intertidal zone ("drift propagules") were also collected.

Coconut Counting

Coconut palms (*Cocos nucifera*, Arecaceae) were counted, following a method used during past surveys (2001 and 2013) on 10 m × 10 m squared plots in all coconut groves found on the atoll, with the

assistance of the French Navy and Army. Their height was visually assessed from the ground to the top of the stipe (or trunk). Dead coconut trees (i.e., without leaves) were counted in 2001 and 2013, and distinguished from those cut by people, often at a man's height.

Vegetation Mapping

The different vegetation zones were identified, characterized and located by repeated and cross-observations made by two observers and using two indexes: the relative plant cover rate of each species in a specific area and the level of aggregation of each species (aggregated or scattered).

Areas which appeared to be homogeneous (either mono-specific, i.e., dominated by one species, or by an association of two species and up to six) were delimited and called hereafter "vegetation zones."

In order to survey the whole land area of the atoll in a relative short period of time, quadrats and transects were not set up. The cover rate of each species and of the bare soil (uncovered land) of the different vegetation zones were evaluated in relation to the surface of the study area, using the Braun-Blanquet method (Braun-Blanquet, 1928). This approach consists of using a constancy class that is the percentage of occurrences within the sampled zone: 0-5% (rare constancy), 5.1-25% (low constancy), 25.1%-50% (intermediate constancy), 50.1-75% (moderately high constancy), and 75.1-100% (high constancy).

The delimitation of these zones was realised with a GPS (Garmin Etrex 10 GPS) in the WGS84-coordinate system. These data collected in the field were imported into the Geographic Information System (GIS) software Quantum (2.2.0 version Valmiera). The base map used was from a Worldview geo-referenced satellite image dated 18 Sept. 2014.

In addition to the plant cover index, we used the specific richness, which is the number of species occurring in a vegetation zone. For each zone, each species has been identified, and a map of the species density was realised. When only one species was present, vegetation zone is considered as mono-specific.

Maps of the different vegetation zones, including plant cover rates, species number, vegetation types (according to species life forms), dominant species in each zone, were produced. These geo-referenced maps represent also a zero-reference state that will ensure a temporal and spatial comparability between the different indicators (plant cover percentage, abundance/dominance, and expansion/recession dynamics).

RESULTS

Plant Diversity

List of Species

Fifteen species of terrestrial vascular plants, all phanerogams and angiosperms (no pteridophyte nor gymnosperm was observed), belonging to 11 different families were recorded in April 2015 (**Table 2**), as well as three aquatic plant species.

By comparison, a total of 27 terrestrial plant species were reported in 1958 (Sachet, 1962), 11 species in 2005 (Couté and Garrouste, 2009) and only nine in 2013 (Jost, 2013). Four aquatic plant species were recorded in 1958 (Sachet, 1962) but only two in 2005 (Couté and Garrouste, 2009) (**Table 3**).

Biogeographic Status

The geographic origin of some of the species is sometimes difficult to assess, especially for plants with a current pantropical distribution. Species of uncertain status (sometimes classified as "cryptogenic", Carlton, 1996) on Clipperton, known as "weeds" in the Pacific Ocean but considered native in the Caribbean islands and tropical America, were considered as accidental or intentional introductions. They include for instance *Cenchrus echinatus* (Asteraceae), *Corchorus aestuans* (Malvaceae), *Ipomoea triloba* (Convolvulaceae), *Phyllanthus amarus* (Phyllanthaceae), *Portulaca oleracea* (Portulacaceae) and *Sida*

rhombofolia (Malvaceae), all recorded since 1958 (Sachet, 1962). The tree tobacco *Nicotiana glauca* was also probably intentionally introduced as a useful plant (Sachet, *op. cit.*).

We considered four species as native or indigenous: two of American/Caribbean origin (*Heliotropium curassavicum* and *Eleocharis mutata*), and two from an American or Asian origin (*Ipomoea pes-caprae* subsp. *brasiliensis* and *Eleocharis geniculata*). It is noteworthy that *Eleocharis geniculata*, *E. mutata*, and *Ipomoea pes-caprae* subsp. *brasiliensis* are considered as introduced taxa on Clipperton by the “Inventaire National du Patrimoine Naturel” (INPN) taxonomic database⁶. We have considered *Achyranthes aspera* var. *aspera* (Amaranthaceae) and *Salvia occidentalis* (Lamiaceae) as human introductions as they were noted only recently.

Among the 15 recorded species, 11 are considered as “introduced” species, i.e., 74% of the total, and four are considered “native”, i.e., 26% (**Table 4**). No endemic species are recorded on the atoll.

Newly recorded Plant Species

Two introduced and naturalized species were newly discovered: *Achyranthes aspera* var. *aspera* (Amaranthaceae), an erect or shrubby herb with a pantropical distribution, and *Salvia occidentalis* (Lamiaceae), an annual herb or sub-shrub native to Mexico, South America and the Caribbean islands.

Achyranthes aspera var. *aspera*, is considered as a “weed” in the Pacific islands and was probably introduced to Clipperton by visitors because of its seeds with spiny bracts that adhere to animals and clothing. In 2015, this species was seen in almost all vegetated areas, demonstrating a relatively high rate of dispersal (probably by seabirds) and high colonizing capacities. *Salvia occidentalis* was only found at one location, southwest of the airstrip forming a relatively dense mat (**Photo A, cf. Appendix**).

Species Not Found

Between 1958 and 2005, 17 species of terrestrial phanerogams have disappeared from the atoll (**Table 3**). Most of the missing species appear to be introduced weedy plants, and more than 70% of them are herbaceous. Between 2005 and 2013 two additional species were missing, including the small tree *Hibiscus tiliaceus* (Malvaceae) only recorded in 2005 as a single individual (Couté and Garrouste, 2009), and the creeping vine *Canavalia rosea* (Fabaceae).

Four species observed in 1958, and not mentioned in 2005 and 2013, were observed again in 2015: *Phyllanthus amarus*, *Eragrostis ciliaris* (Poaceae), *Cenchrus echinatus* and *Nicotiana glauca*. They were either dormant (as seeds in the soil seed bank), or too rare to be noticed, or accidentally reintroduced between 2013 and 2015. We also found drift seeds of the vine *Mucuna* sp. (Fabaceae) which was only recorded in 1958 as living plants.

It is interesting to note that the number of introduced “weedy” species is higher during the periods of relatively important plant cover (in 1958 and 2015), compared to the periods of sparse plant cover (in 1997, 2001 and 2005), suggesting that native species appear to be better adapted or more resilient to harsher ecological conditions.

Drift Propagules

Seeds and fruits were searched and collected on the entire shoreline in the intertidal zone. They belong to several different taxa, but only four could be identified: *Mucuna* sp. (Fabaceae), *Entada gigas* (Fabaceae) and *Dioclea* sp. (Fabaceae) which were already reported in previous studies (Sachet, 1962), and a newly recorded species, *Lagenaria* sp. (Cucurbitaceae), with several large fruits, some of them containing seeds.

⁶ <https://inpn.mnhn.fr/accueil/index>

Coconut Palms

Coconut palms expansion started in 1897 with the introduction of the two first individuals by the guano workers. In 1958, M.-H. Sachet noticed that “*there appear to be two main varieties of coconut palms on the island: some have more oval, green nuts, and the rachis of the young frond leaf is also green; others have a bright orange young rachis, and rounder large orange nuts*” (Sachet, 1962). These two varieties were observed in 2015, but their distribution could not be precisely mapped due to lack of time. However, 847 coconut trees over 1 m were counted in 2015 (**Table 5**). The orange nut variety is much less common than the green one, and more abundant on the Eastern coast. There is a regular increase ($r^2=0.9259$) of the number of coconut palms during the past 120 years (**Figure 3**) which does not distinguish the two varieties.

We noticed that the number of dead, headed and cut coconut trees was less than during previous visits. The combined total was 85 in 2015 (of which 62 were topped and 23 cut), compared with 91 topped or cut in 2013 and 168 in 2001 (no distinction between topped and cut palms). In 2015, the trunks without leaves were numerous (53) on the South coast in the old palm grove of Bougainville which seems to be reaching the end of its life. The topping seems to be related to age and weather events. Cut stems, obviously with a machete or an axe (presence of cutting lines at human height), are, on the other hand, a large majority on the North-East coast (21 out of 23), which is more frequented by humans, where landings are reported more numerous, but also where helicopter drops (purse seiners in operation) have been recorded.

Despite an increase in the total population of palms, living trunks (above 1 m in height) have diminished in the “Bois de Bougainville” from 479 in 2001, to only 305 in 2013. We also noticed in 2013 and in 2015 a total lack of undergrowth in this dense coconut grove (**Photo B, cf. Appendix**). This could be explained by the age of the grove, which corresponds to the first two specimens planted in 1897 (a coconut tree gives fruits for ca. 70 years and can live around 100 years) but also partly by the cleaning of the undergrowth for the installation of the camp of the “Jean-Louis Etienne expedition” in 2005. The other (younger) groves, located mainly on East and North coast, are rapidly expanding and have dense undergrowths of young palms.

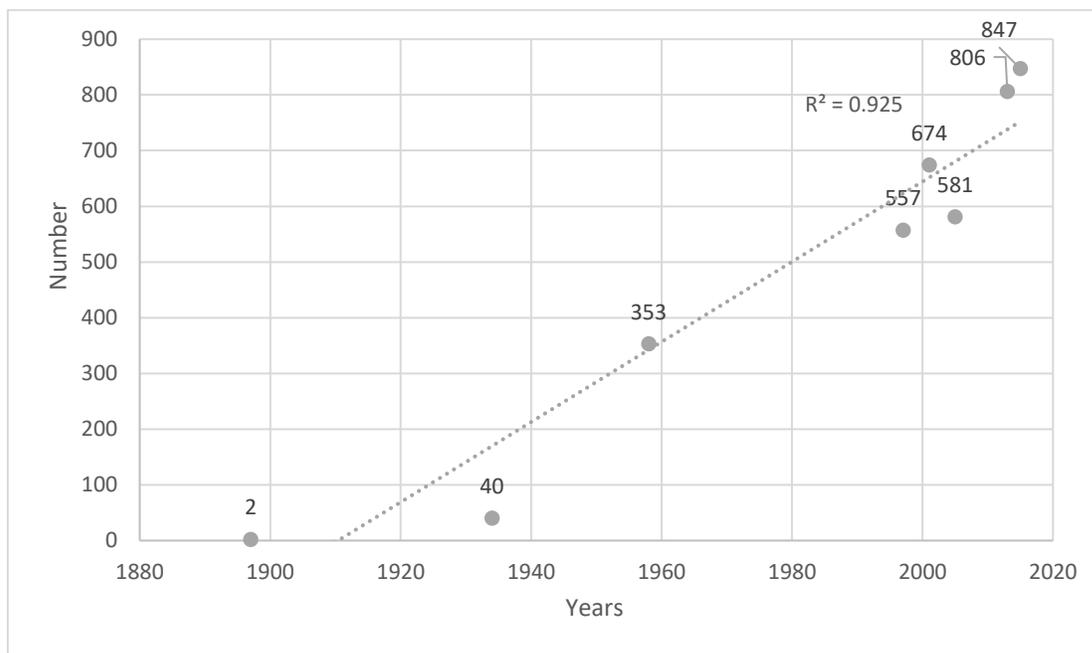


Figure 3. Increase of coconut trees between 1897 and 2015

Mapping and Implementing Data Into GPS

After processing the GPS data, various maps were developed using Quantum GIS. **Figure 4** provides information on the percentage of plant cover over the entire atoll ring, that is, the cover of all plant species by vegetation zone. A total of 68 vegetation zones were identified. As described in the methodology, the percentage of cover of each species is given as well as the percentage of bare soil. As an example, the vegetation zone named "3C" located near the "Bois de Bougainville" is composed of *Heliotropium curassavicum* (30%), *Achyranthes aspera* (5%), *Portulaca oleracea* (15%), and the bare soil represents 50% of the surface of the zone.

The entire cover extension of vegetation delimited represents a total of 79 ha (46.5%). Most of the vegetation zones (68 in total) are dense, comprising between 50 and 100% of plant cover. Zones with a cover above 75.1% and up to 100% represent 46.7 ha, those with a cover between 50.1-75% represent 27.3 ha, and only one zone has a plant cover between 5.1-25%, representing 0.11 ha. **Figure 5** illustrates the different vegetation zones (in hectares) related to the percentage of bare soil within a zone.

The zones whose coverage is 75.1% to 100% are located along the West and East parts of the atoll. Those with a 100% cover are mainly composed of *Ipomoea* spp. native and introduced vines and the native tufted sedge *Eleocharis geniculata* located near the lagoon, on the East coast and on the West coast beside the airfield, and at the Southern side of the "Bois de Bougainville".

Figure 6 presents the specific richness for each zone. An average of three to four species are found in closed association. Several zones have six associated plant species, two of which are very extensive: one located in the North-West and the second in the South, both with a vegetation zone of more than 11 hectares. Monospecific zones are mainly represented by *Ipomoea* spp. vines, but also by species such as *Heliotropium curassavicum* and *E. geniculata* mainly at the edge of the lagoon.

The three species are present in the largest number of zones: the native erect herb *Heliotropium curassavicum* with 29 out of 68 zones (43%), the introduced erect herb *Corchorus aestuans* (22 zones or 32%) and the native sedge *Eleocharis geniculata* (22 zones, 32%). These three species are present on almost the entire ring. In contrast, species such as *Nicotiana glauca* and *Salvia occidentalis* are only found at one location, e.g., on the ring at the Southern tip of the island for the tree tobacco with 16 stems of more than a meter high (**Photo C, cf. Appendix**).

Four main vegetation types can be distinguished on the atoll, namely sub-shrub stands, herbaceous stands (erect or prostrate herbs), creeping vines stands, and coconut groves, but with different plant composition and abundance according to geographic areas (**Figure 7**).

Description of the Vegetation in the Different Areas

"Le Rocher" Area – *Heliotropium curassavicum* is particularly abundant, associated with small areas of *Corchorus*, *Portulaca oleracea* and *Sida rhombifolia*. On the East side of "Le Rocher" two groups of *Ipomoea* spp. vines are competing with each other (**Photo D, cf. Appendix**), *I. pes-caprae* in the South and *I. triloba* in the North (**Photo E, cf. Appendix**). Some patches of both species of *Eleocharis* (*E. geniculata* and *E. mutata*) are also found in contact with the lagoon at the base of "Le Rocher".

Southern End Of The Atoll – A large stand of *Eleocharis mutata* surrounded by *Eleocharis geniculata* (**Photo F, cf. Appendix**) is found at the Southern end of the atoll, near "Le Crochet". Going Westward from this tip, vegetation consists mostly of erect and tufted herbaceous plants dominated by *Heliotropium curassavicum*, *Corchorus aestuans*, *Portulaca oleracea*, and *Eleocharis geniculata*. The latter forms a monospecific stand bordering the shoreline of the lagoon side up to "Le Crochet" peninsula. In the immediate vicinity of *Eleocharis* another monospecific stand of *Ipomoea triloba* is found. Shrub stands with *Sida rhombifolia* and *Achyranthes aspera* are observed in the Western part of this area, parallel to the shoreline and located in depressions of probably former phosphate mining areas (**Figure 8**).



Figure 4. Spatial distribution of vegetation zones according to plant cover

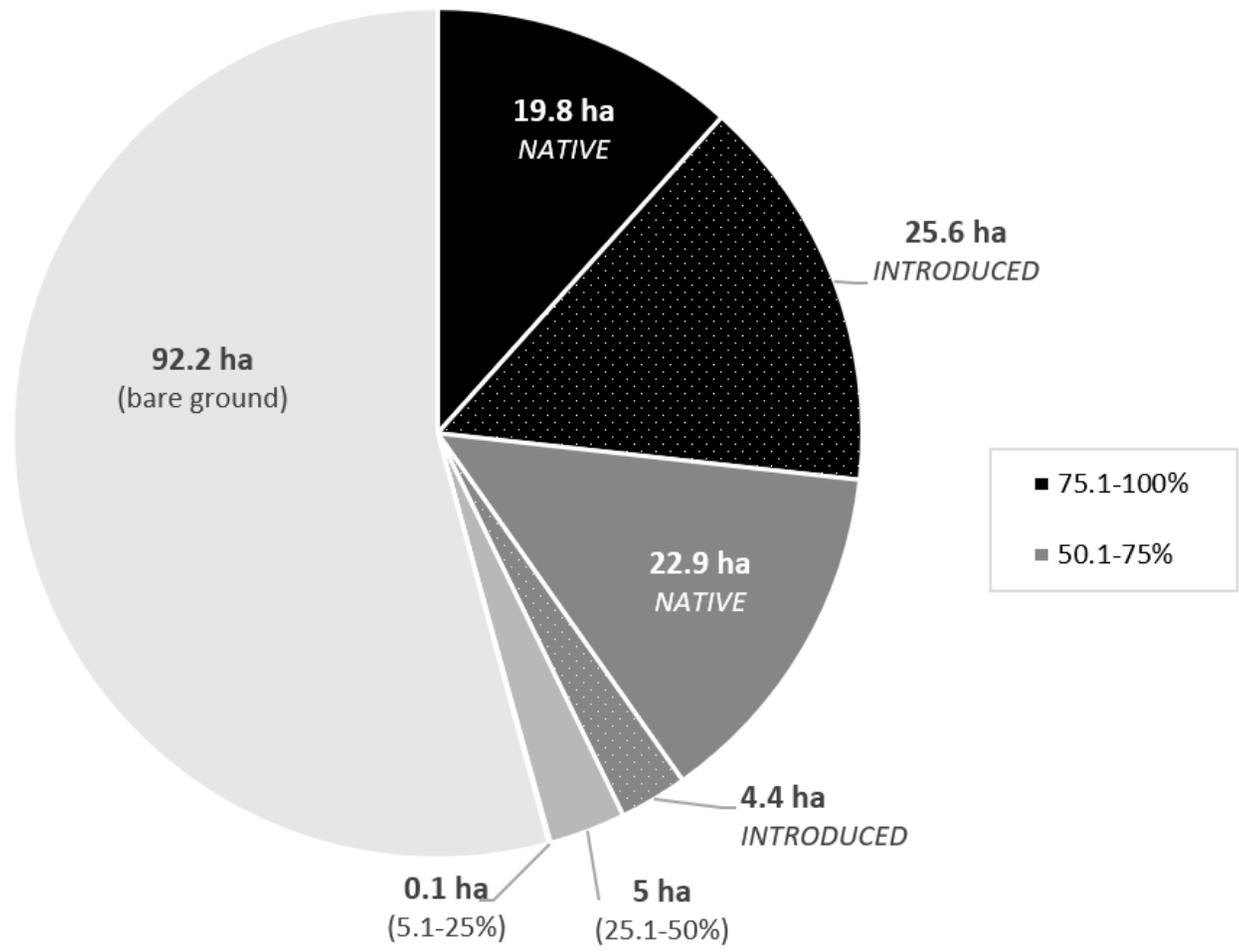


Figure 5. Areas (ha) of all vegetation zones (N=68) according to plant cover (in %) and species status (native or introduced)



Figure 6. Spatial distribution of plant species richness

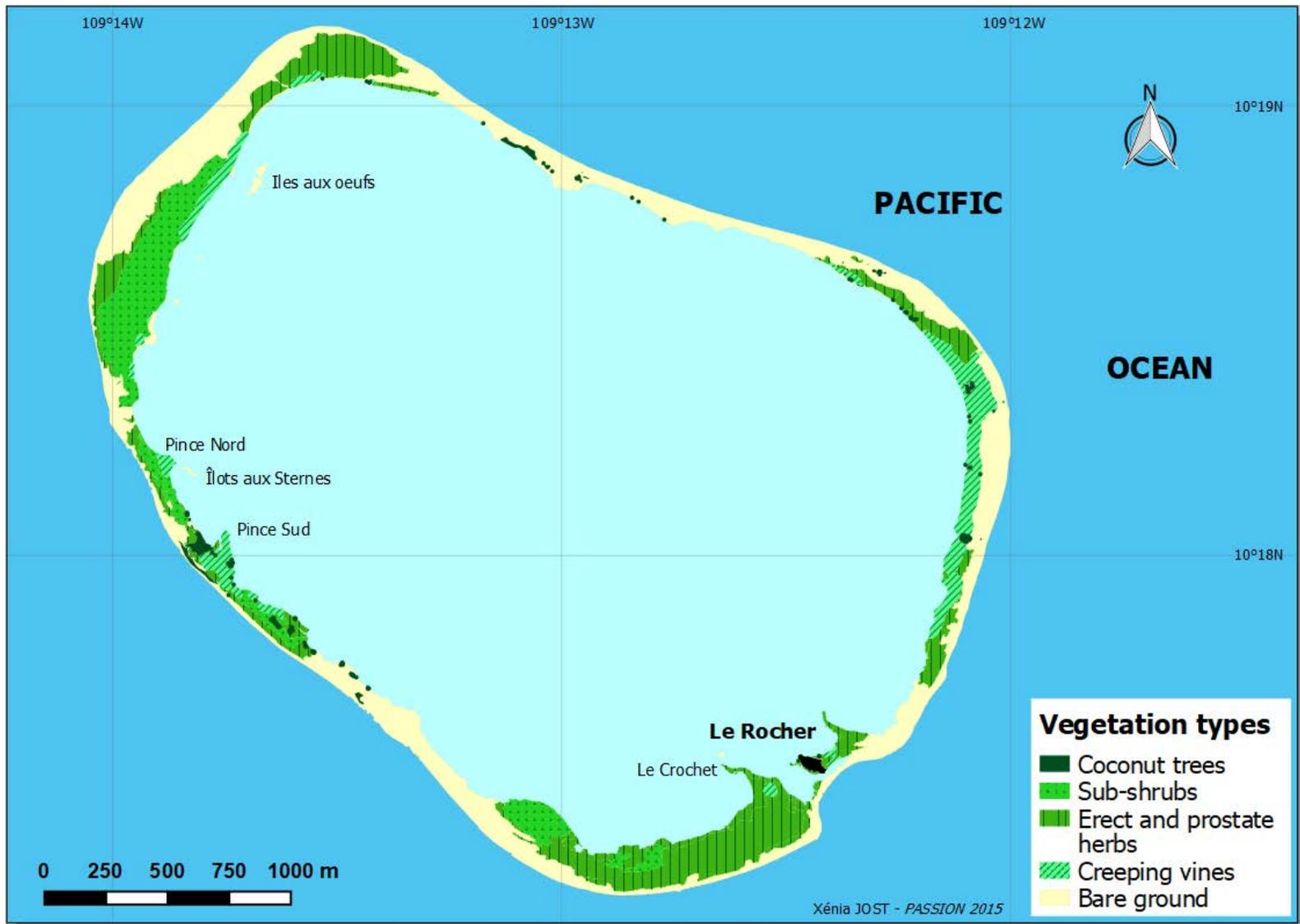


Figure 7. Spatial distribution of the four main vegetation types

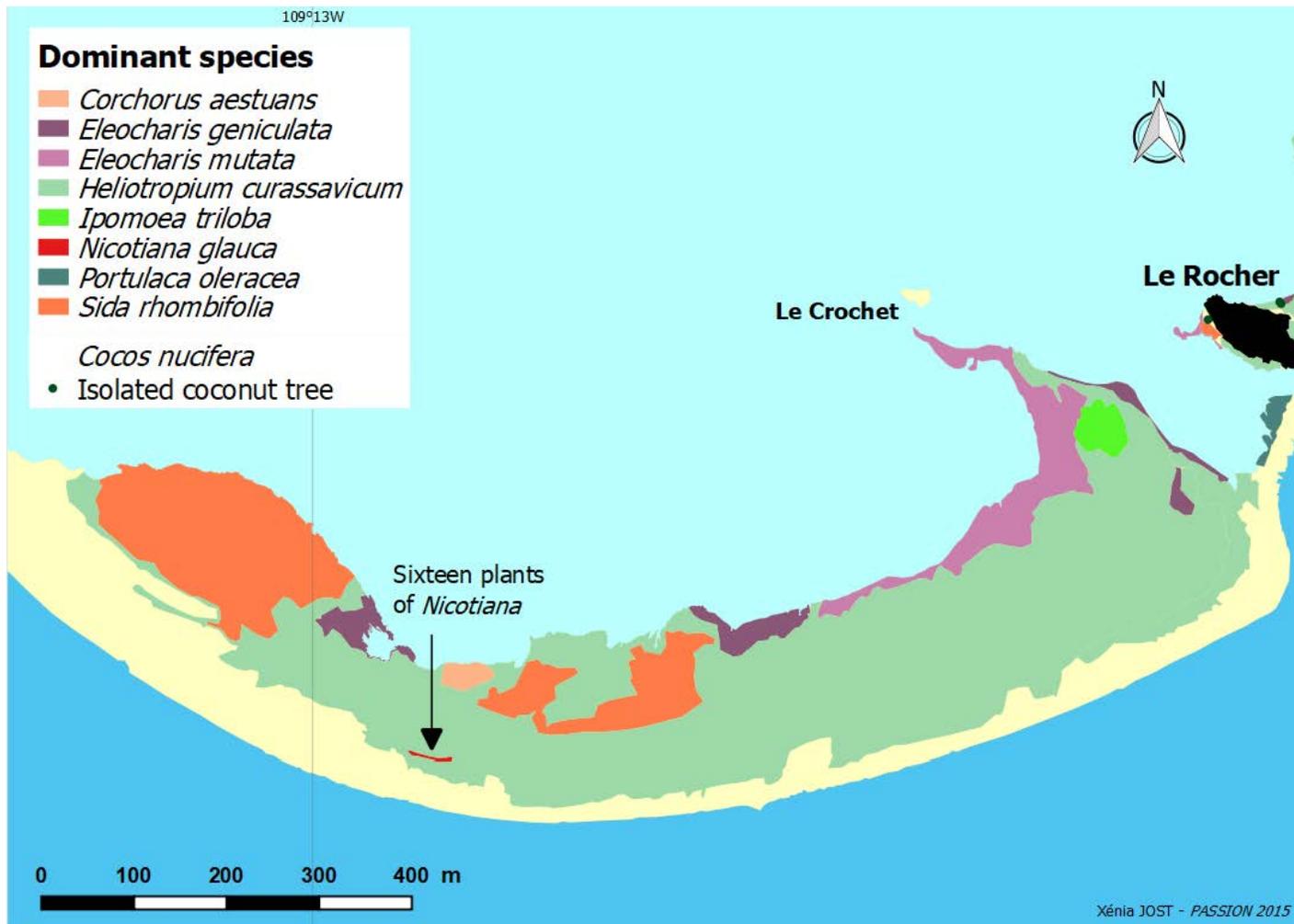


Figure 8. Spatial distribution of the dominant species on the Southern end part of the atoll

“Bois De Bougainville” Area Including “Pince Sud” And “Pince Nord” – The “Pince Sud” is entirely covered by *Ipomoea* vines (80% of *Ipomoea triloba* and 20% of *Ipomoea pes-caprae*) (**Photo G, cf. Appendix**). Couté and Garrouste (2009) have noted in 2005 that *Ipomoea pes-caprae* forms "an almost continuous cover [...] along the Pince Sud [...]". On the small peninsula facing the “Pince Sud” on its West side, a continuous and dense stand of *Eleocharis mutata* is found growing in the water Southeast of the “Pince Sud”, two other patches of *Ipomoea triloba* are found beside the lagoon while *Ipomoea* is replaced Southward by a cover of *Achyranthes aspera* in the middle part of the ring (**Figure 9**). In 2005 only two patches of *Ipomoea* were present nearby the lagoon. A strip of *Ipomoea* is found in association with the shrub *Sida rhombifolia*. *Heliotropium curassavicum* is abundant in the vicinity of the lagoon but much more widely spread all along the shore, associated with other plants such as *Portulaca oleracea* and *Corchorus aestuans*. In the Northern area of the “Bois de Bougainville” (**Figure 10**), the “Pince Nord” is covered with *Ipomoea pes-caprae* vines, largely predominant and covering some *Ipomoea triloba* (**Photo H, cf. Appendix**). The presence of *Ipomoea* was not recorded in 2005 but instead “a herbaceous vegetation with *Heliotropium* and *Portulaca*, along with some spots of *Corchorus aestuans*” (Couté and Garrouste, 2009).

On the edge of the “Pince Nord”, up to the French monument (called “Stèle” on the map) a shrubby strip of *Achyranthes aspera* and *Sida rhombifolia* 50 to 70 cm in height, associated with other erect herbaceous plants, totally covers the ground.

West And North-Western Area – On the West and largest part of the atoll (300–400 m wide), the most abundant plants are *Sida rhombifolia*, *Cenchrus echinatus* and *Corchorus aestuans*, a plant formation also highlighted in 1958 by M.-H. Sachet. They make up a shrub cover of 30–50 cm high. Low vegetation formed by *Heliotropium curassavicum* is found on the edge of this vast and homogenous bushy area on the upper part of the ring and more exposed to salt spray, while patches of *Ipomoea triloba* are found close to the lagoon (**Figure 11**). The most extensive *Ipomoea triloba* stand is mixed with the *Ipomoea pes-caprae*. To the North, at the edge of the lagoon, other small patches of *Ipomoea* spp. are observed, including a monospecific patch of *Ipomoea pes-caprae*. The herbaceous *Heliotropium* associated with *Corchorus* are forming a low and sparse cover.

North-Eastern Area – On the West side of the base camp of the “PASSION 2015” expedition. The vine stands are mostly composed of *Ipomoea triloba*, but in association with *Ipomoea pes-caprae* on the side of the lagoon.

Around the camp, the vegetation is very low and sparse (**Figure 12**), dominated by *Heliotropium curassavicum* with *Portulaca oleracea* and also *Corchorus aestuans* stretched on a long strip from West to East of the middle low part of the ring. A dense herbaceous cover hardly exceeding 15 cm high mainly composed of *Phyllanthus amarus* is found down the camp site towards the lagoon. It is the largest and almost only patch of this species on the island. At the time of Sachet’s expedition, this small herb was found at the Northwest of the island and also on the East coast. A monospecific stand of *Eleocharis geniculata* develops along the shoreline of the lagoon.

From the camp towards “Le Rocher” three groves of coconut trees (*C. nucifera*) are found, surrounded by large stretches of *Ipomoea* spp. (**Figure 13**). The first and second stands of *Ipomoea*, up to the first grove, are mostly *I. triloba*, while *I. pes-caprae* is in the background at the edge of the lagoon (**Photo I, cf. Appendix**). From the second grove of coconut palms we find again a mixture of the two *Ipomoea* species but dominated by *I. pes-caprae* (**Photo J, cf. Appendix**). The Southernmost *Ipomoea* stand is the herbaceous tuft *Eleocharis geniculata* that grows around the lagoon. The *Heliotropium curassavicum* cover that grows in the center of the ring from North to South is associated with *Portulaca oleracea* which forms patches within the zone.

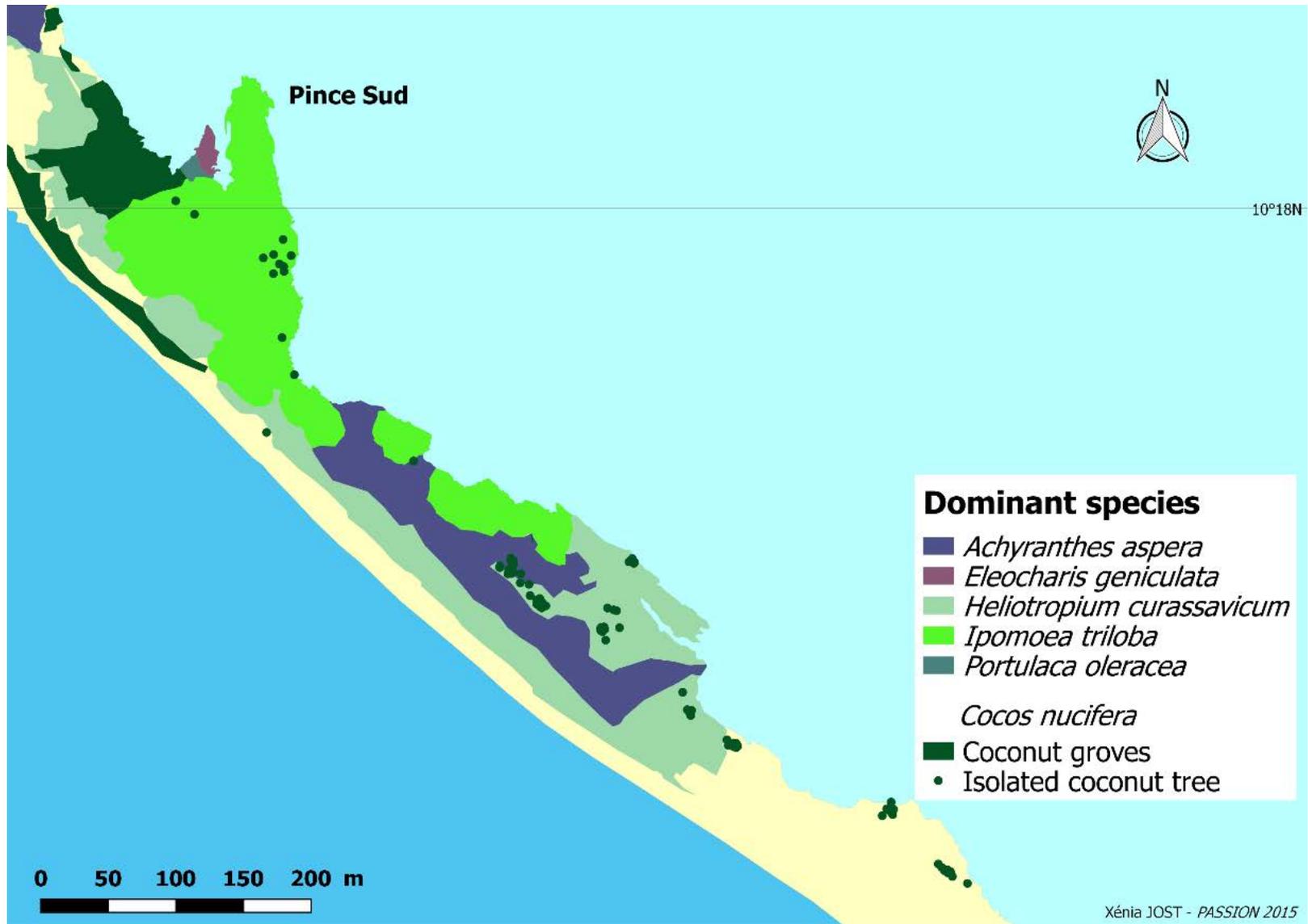


Figure 9. Spatial distribution of the dominant species on the Southern area of « Bois de Bougainville »

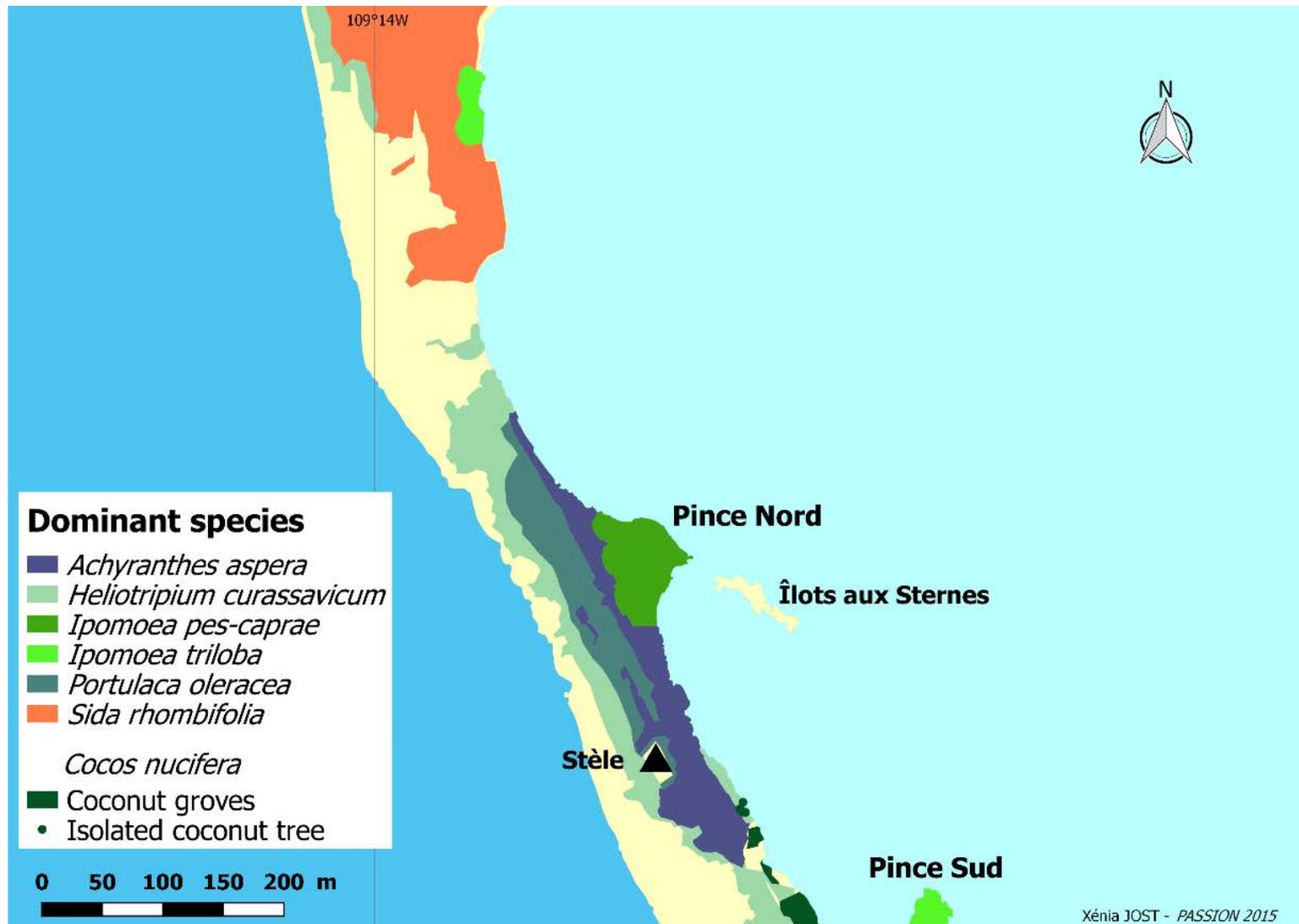


Figure 10. Spatial distribution of the dominant species on the Northern area of « Bois de Bougainville »

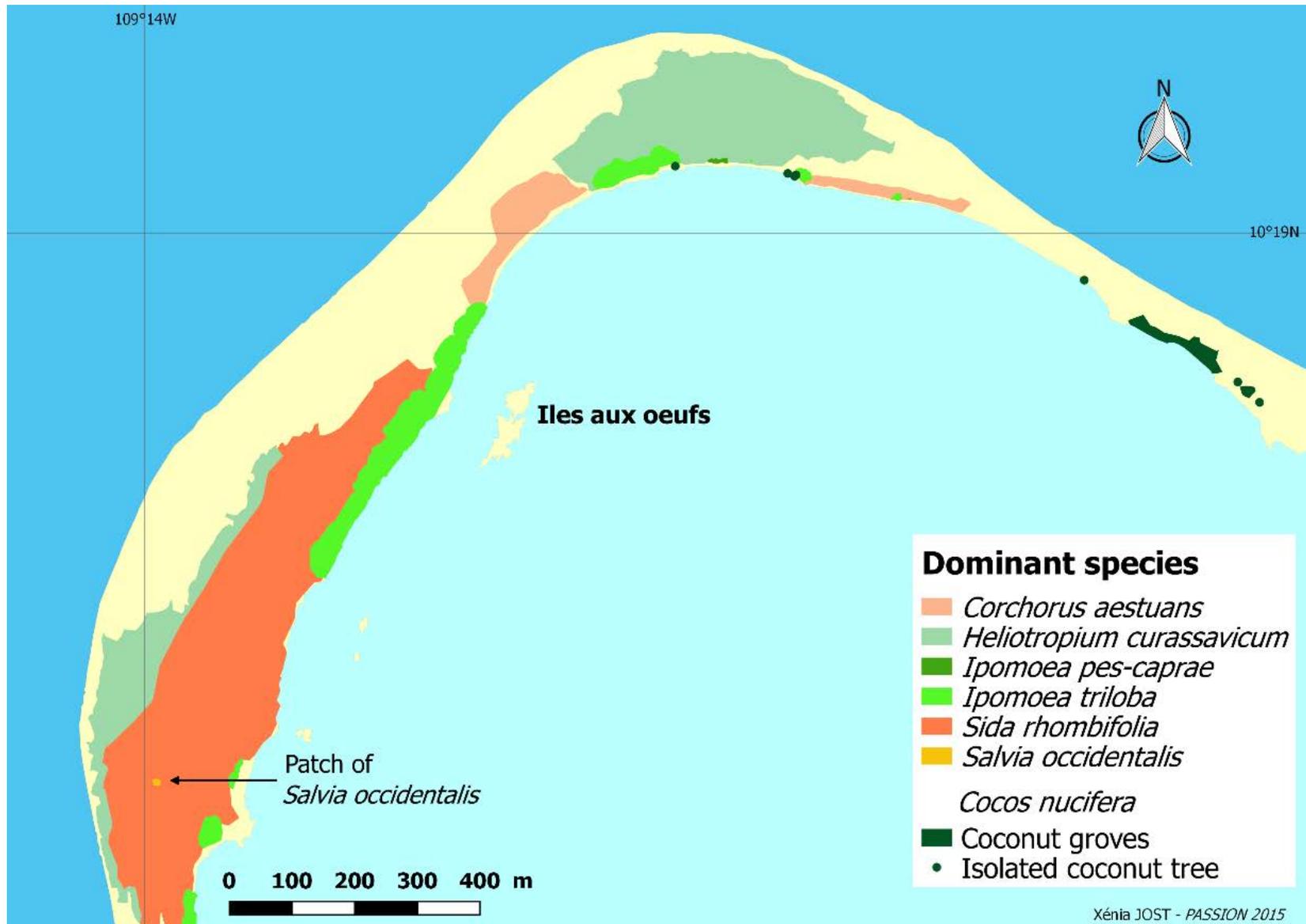


Figure 11. Spatial distribution of the dominant species on the West and Northern area

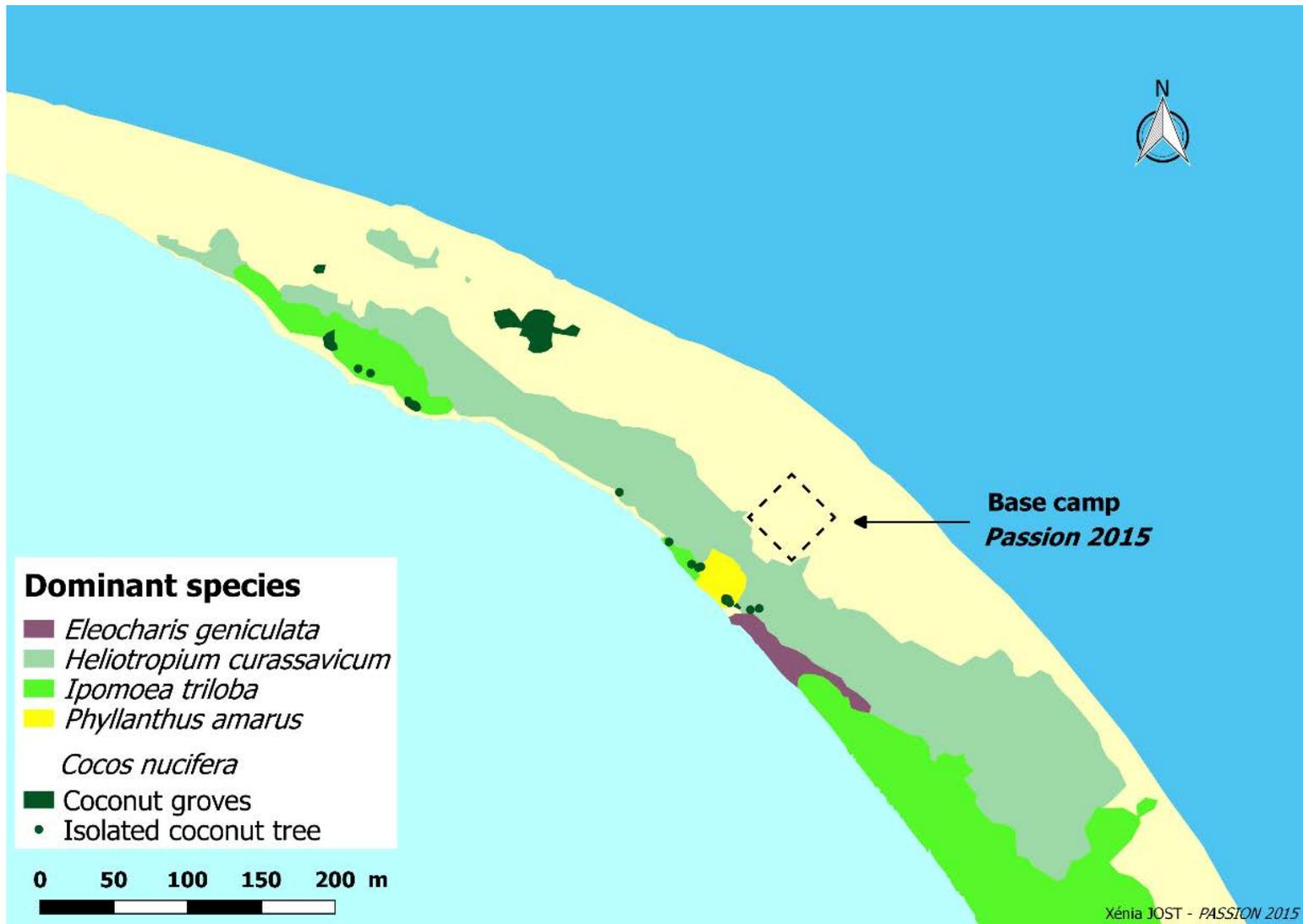


Figure 12. Spatial distribution of the dominant species on the Northeastern area

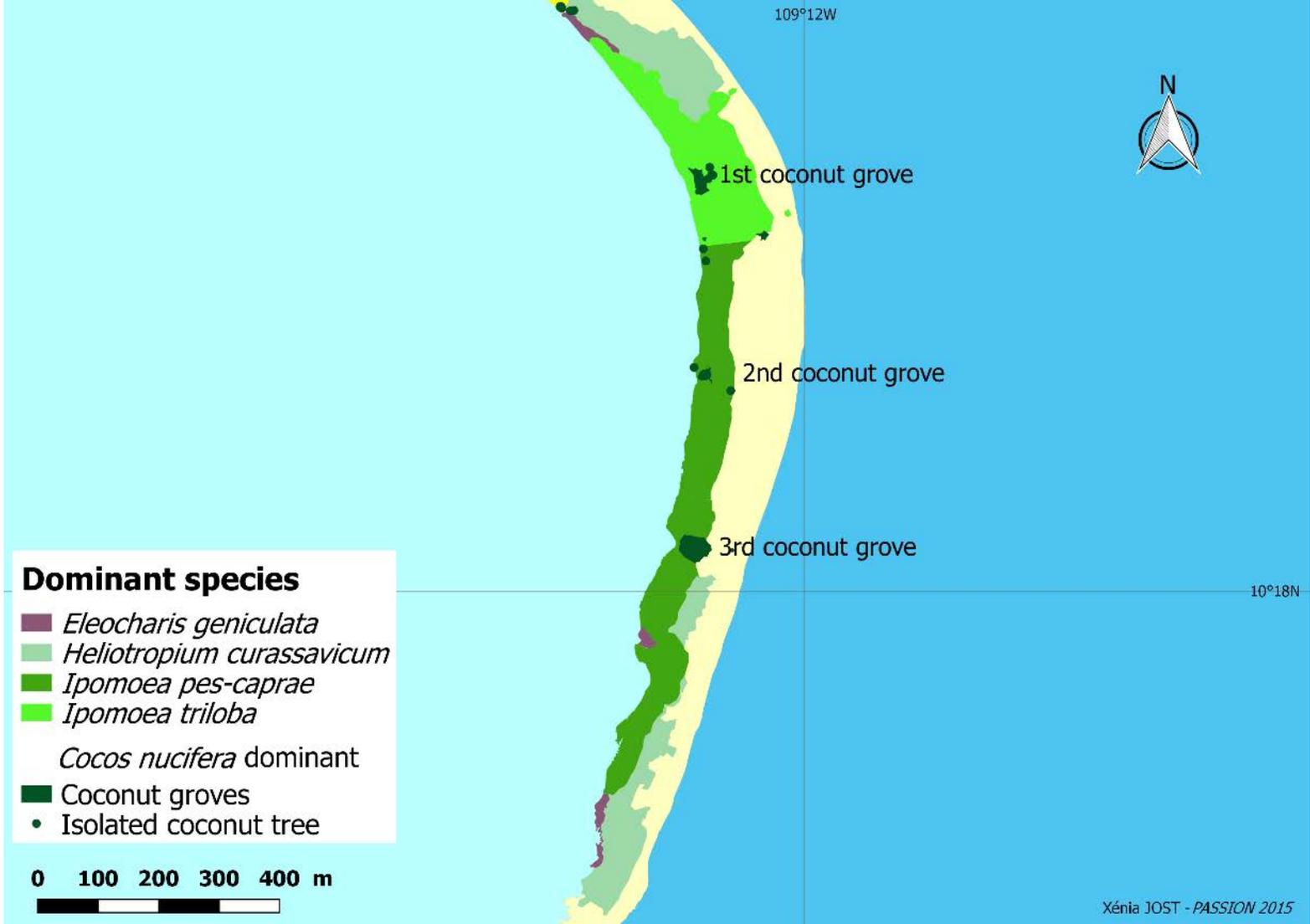


Figure 13. Spatial distribution of the dominant species on the Eastern area with three main coconut groves

DISCUSSION

A Very Depauperate Flora and Important Species Turn Over

Due to its extreme isolation, ca. 1,000 km from the nearest continent (Central America) and 945 km from the first land, Socorro island Northward (Mexico), and because of its very small land surface (170 ha) with harsh ecological conditions, Clipperton (La Passion) atoll shows a very low plant diversity. The vascular flora, which comprised 27 species including 9 native taxa in 1958 (Sachet 1962), is currently composed of 15 species including only five native taxa. These last species are particularly well adapted to the dry tropical environments of atolls characterized by nutrient poor calcareous soils with a small amount of organic matter and high salt concentrations, low rainfall, high temperatures, and periodic strong winds and heavy tropical rains during cyclones. Some of them have developed succulent and/or small leaves to reduce respiration and water loss, including the newly recorded alien subshrubs *Achyranthes aspera* var. *aspera* and *Sida rhombifolia*. Some introduced species, on the other hand, are more sensitive to these harsh ecological conditions and do not survive, such as the weed *Erigeron bonariensis* only recorded in 1958 or *Hibiscus tiliaceus* present in 2005 but not in 2015.

In 1958, according to M.-H. Sachet, the most common plants found in the atoll were the weeds *Cenchrus echinatus*, *Sida rhombifolia*, *Corchorus aestuans* and *Solanum americanum*, and "other less abundant plants locally mixed with this vegetation" (Sachet 1962) including *Heliotropium curassavicum* and the weed *Erigeron bonariensis*. In 2015, the shrub *Sida rhombifolia*, was among the most abundant plants, with *Heliotropium* and *Ipomoea triloba*, whereas *Cochorus aestuans* was one of the least common plants. In 60 years, the plant composition has dramatically changed, and some community trends have almost been reversed.

The plant density ranges between 8.8 (15 species) and 15.9 (27 species) per sq. km. In comparison, the flora of other atolls in French Polynesia varies between 11.5 for the small (4 sq. km) uninhabited atoll of Taiaro in the Tuamotu (Niva and Taputuarai, 2013) and 22.7 species per sq. km for the very isolated and uninhabited atoll of Maria (150 ha) in the Austral Islands (Meyer, 2013) but with 25 and 24 native species respectively. The floristic diversity of Clipperton is similar to the small (100 ha) island of Tromelin (Iles Eparses, South-West Indian Ocean), an upraised atoll, with 20 plant species including seven native species (Boullet *et al.*, 2018).

No tree species is found on the atoll, except for the introduced coconut palms (which are not trees botanically speaking). The absence of the small tree *Heliotropium foertherianum* (syn. *Tournefortia argentea*, Boraginaceae) and *Sophora tomentosa* (Fabaceae) or the shrubs *Suriana maritima* (Surianaceae) and *Pemphis acidula* (Lythraceae) is noteworthy, as these coastal woody species are commonly found on almost all the atolls and low sandy islands in the Pacific Ocean (Mueller-Dombois and Fosberg 1998). *S. tomentosa* is also known from the Revillagigedo Islands (Johnston, 1931), the nearest land at 945 km East of Clipperton.

Dramatic Changes in Vegetation Cover

The vegetation cover of Clipperton (La Passion) atoll has dramatically changed during the past three centuries. The atoll was described as almost a desert between 1858 and 1897, and densely covered by vegetation in the 1960's. A minimum cover was again reached between 1997 and 2001 with not a single species observed on the main land, and only six plant species found in five inner lagoon islets.

It was previously noted that expansion and diversification of the flora were correlative to the demographic growth of pigs from 1897 to 1958 (when pig population was eradicated during the Scripps Institution expedition). However, a few pigs, said to be less than six, escaped the slaughter and were finally killed in 1966 by the French Army during the "Missions Bougainville". Despite the fact that land crabs (*Johngarthia planata*, syn. *Gecarcinus planatus*), were already described as an "extremely dense

population” by Sachet (1962), it seems that their number kept increasing, reaching the spectacular number of more than 11 million in 1967 (Niaussat and Ehrhardt, 1970).

All the studies and observations following the 1958 plant inventory by M.-H. Sachet (Ehrhardt, 1968; Taxit and Ehrhardt, 1981; Jost, 1997, 2001) show a drastic reduction of the plant cover until the disappearance of the grass layer noted for the first time in 1997 (Jost, 1997). Considering this as a process of a rhexistasic period, one can assume that a species introduced by man, the pig, had for once a positive impact at least on the vegetation cover by allowing diversity and extension to develop. Indeed, pigs were observed eating not only bird eggs but also *Gecarcinidae* crabs whose shells were found in pig feces (Ehrhardt, 1972). The elimination of pigs allowed the multiplication of crabs which consume not only eggs and coconuts, but also the grass cover. The elimination of pigs had a very positive effect on the bird population which exploded between the 1960s and the 2000s from 150 masked boobies (*Sula dactylatra*) (Sachet 1962) to ca. 100,000 in 2001 and 2005 (Jost, 2003; Jost and Andréfoüët, 2006; Weimerskirch, 2009) becoming the world’s most important colony.

However, in 2005 the reappearance and extension of few patches of the herbs, vines and subshrubs was observed (Couté and Garrouste, 2009). This evolution, in correlation with the reduction of the number of crabs, was confirmed in 2013, then in 2015 (Jost, 2013, 2015).

The situations in 2001 and 2005 are difficult to compare since in 1997 and 2001 the only living plants, beside coconut trees, were located in the five inner lagoon islets (Jost 1997, 2005b), unreachable by the land crabs which were confined on main land.

If the factors which can explain these changes were still hypothetical 20 years ago, the recent and more frequent visits and studies confirm that the extension and reduction of the vegetation cover in Clipperton, mostly like on other atolls, are closely linked to two groups of factors. One group is related to weather and sea conditions, while the other is dependant from the fauna dynamics to be linked, positively or negatively, to human impacts.

The first and main factor, i.e., which has the fastest and strongest impact by being capable of destroying or burying in few hours the whole or part of the plant cover, is submerging waves loaded with sediments. In certain circumstances, they can cover the entire atoll ring. High waves of more than two meters are produced either by major hurricanes or by tsunamis. Since hurricanes are frequent in the region and may have a diameter of 500-1,000 kilometres, the fauna and flora are often directly impacted. For example, during a storm with strong swell and waves in April 2015, we observed fresh sand and gravel deposited by submerging waves in a strip several tens of meters long on the Eastern and Northern ring.

Another cause of vegetation changes is introduced plant or animal species and a demographic explosion of one or another community. Introduction of pigs was followed by the recovery of vegetation until their elimination in 1958 after which plant cover and diversity declined for forty years, followed by a new period of expansion until today. This last period is marked by the decline of the crab population but also the appearance of a new predator, the black rat *Rattus rattus*, accidentally introduced with one of the two boat wreckages between 1997 and 2001. If the crab demographic decline can be explained by the lack of food after having eaten most of the plant cover, it is also partly linked to the rats which consume crabs and occupy their burrows.

The 2015 inventory has demonstrated that the atoll can be quickly recolonized by vegetation, from a few patches to almost half of the island in only 10 years. However, it will be important to monitor plant dynamics with the increasing presence of rats, known for their deleterious impacts on island native biota (Shiels *et al.*, 2014), and more specifically to plant diversity and composition (Wolf *et al.* 2018).

CONCLUSION

Because of its geographical location, at the crossroad between the Pacific and American biogeographic regions, its extreme isolation, small size, particular geomorphology (with a closed lagoon),

climate (on cyclone paths) and human history, the atoll of Clipperton (La Passion) is a unique natural laboratory of global scientific interest.

The observed changes in native and alien plant cover and species composition for the past three centuries are probably due to abiotic factors and natural disturbances (substrate, climate including cyclonic events) but also to biotic factors (native seabirds and crabs) and anthropogenic impacts, including the past introduction of pigs, rats and weeds. The vegetation dynamics seem to follow more or less 50-year cycles tightly linked to human presence and activities. Thus, the alternating phases of plant abundance could be divided into a “pig phase” between 1897 and the 1950’s with a high plant cover, followed by a “crab and seabird phase” between the 1960’s and 2000 with a low plant cover, almost absent in 2001 and 2005, and the “rat phase” since 2005 with a new increase of the vegetation (Jost *et al.* 2015). These ecological cycles also demonstrate the resilience of the atoll ecosystem with the rapid recruitment of most of the vascular plants after natural and anthropogenic disturbances. However, the regular increase of coconut palms and the recent (accidental) introductions of alien species (e.g. the weeds *Achyranthes aspera* var. *aspera* and *Salvia occidentalis*) may profoundly alter the ecological balance of this small island ecosystem. Strict biosecurity measures should be set up during the future visits on the atoll, including scientific expeditions, to avoid new accidental plant and animal introductions.

Further research studies will include molecular analyses conducted on the native and alien plants and drift propagules, in order to construct phylogenies and assess the origin of all plant taxa found in the atoll (Pacific Islands *versus* Tropical America), as well as the assessment of the potential impacts of sea-level rise on the island biota. Long-term surveys will be necessary to confirm these ecological cycles, including plant dynamics, especially in the context of global changes.

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Table 1. Past description of the vegetation of Clipperton (La Passion) atoll and its evolution between the 18th and 20th centuries.

Period or year of observation	Author	Description	Documents (Reference)
1711	French discoverer Michel Dubocage	<i>“Some brushwood and one dry tree on the Northeast point [...] The Western side appeared to us with few small bushes ”</i>	Sketch of the island (Dubocage, 1711)
1825	American Captain Benjamin Morrell	<i>“Little shrubbery and some coarse grass, among which, I think, fresh water might be found by digging. Among the few plant productions of this island, we found a plant resembling sarsaparilla⁷, which badly poisoned several of the crew who handled it”</i>	(Morell, 1832)
1839	British Admiral Sir Edward Belcher	<i>“Very-dangerous low lagoon island, destitute of trees; North: appears to be clothed with something like grass ”</i>	Map (Belcher 1843)
1858	French Lieutenant Le Coat de Kerveguen	<i>« The land is only covered with guano. The lagoon is totally closed and its water is salted »</i>	Map (Le Coat de Kerveguen, 1858)
1861	American Lieutenant Griswold	<i>“I did not find the least sign of plant life upon the island. The only plant seen grew in considerable quantities in the lagoon”</i>	(cited in Pease, 1868)
1897	French Lieutenant Terrier	<i>“There is no vegetation on the island apart from two young coconut trees grown in crates ”</i>	(Terrier, 1897)
1934	French Navy vessel “Jeanne d’Arc”	Vegetation was described as <i>“covering a big part of the land”</i>	Map, pictures and aerial photos (Report, 1935)
1938	“US President Roosevelt” cruise	Important vegetation cover on photographs	Aerial photos (Taylor, 1939)
1958	French botanist M.-H. Sachet	Abundant low vegetation covering almost 80% of the land	Map (Sachet, 1962)
1968	French « Missions Bougainville »	Vegetation cover decrease on map	Map (Ehrhardt and Niaussat, 1970)
1980	French Cdt J.-Y. Cousteau	Vegetation continues to decline to scarce patches	Map and movie
1997	French geographer C. Jost	Vegetation totally absent of the coral rim, except 674 coconut trees	Map (Jost, 1997)
2005	French explorer J.-L. Etienne	Patches of herbaceous and subshrub vegetation in a few restricted zones	Map (Couté and Garrouste 2009)

⁷ Refers to a creeping vine of the genus *Smilax* (Smilacaceae), more probably *Ipomoea pes-caprae*

Table 2. List of the 15 terrestrial vascular plant species observed in 2015 on Clipperton (La Passion) atoll with their biological characteristics and proposed biogeographical and naturalization status.

Family	Scientific name	Life form	Dispersal mode	Native range	First obs.	Biogeographical status	Naturalization status
MONOCOTYLEDONS							
Arecaceae (Palmae)	<i>Cocos nucifera</i> L.	tree (palm)	hydrochory		1897	introduced (intentional)	cultivated, naturalized
Cyperaceae	<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	erect herb (sedge)	epizoochory or endozoochory	Caribbean, South America, Western Polynesia	1897	native	naturalized
	<i>Eleocharis mutata</i> (L.) Roem. & Schult.	erect herb (sedge)	epizoochory or endozoochory	Caribbean, South America	1897	native	naturalized
Poaceae (Graminae)	<i>Cenchrus echinatus</i> L.	erect herb (grass)	epizoochory	Caribbean, South America	1958	introduced (accidental)	« weed »
	<i>Eragrostis ciliaris</i> (L.) R.Br.	erect herb (grass)	endozoochory	Caribbean	1958	introduced (accidental)	« weed »
DICOTYLEDONS							
Amaranthaceae	<i>Achyranthes aspera</i> var. <i>aspera</i> L.	erect (woody) herb	epizoochory	Asia	2015	introduced (accidental)	« weed »
Boraginaceae	<i>Heliotropium curassavicum</i> L.	erect (woody) herb	hydrochory, endozoochory	Caribbean, South America, Australia, Hawaii	1958	native	naturalized
Convolvulaceae	<i>Ipomoea pes-caprae</i> subsp. <i>brasiliensis</i> (L.) Ooststr.	creeping vine	hydrochory	Pantropical	1897	native	naturalized
	<i>Ipomoea triloba</i> L.	creeping vine	hydrochory	Caribbean, South America	1897	introduced (accidental)?	naturalized
Lamiaceae	<i>Salvia occidentalis</i> Sw.	sub-shrub	epizoochory	Caribbean	2015	introduced (accidental)	« weed »
Malvaceae	<i>Corchorus aestuans</i> L.	erect herb	anemochory	Caribbean	1958	introduced (accidental)?	« weed »
	<i>Sida rhombifolia</i> L.	sub-shrub	epizoochory	Caribbean, South America	1958	introduced (accidental)?	« weed »
Phyllanthaceae	<i>Phyllanthus amarus</i> Schumach. & Tonn.	erect herb	endozoochory	Caribbean	1958	introduced (accidental)?	« weed »
Portulacaceae	<i>Portulaca oleracea</i> L.	prostrate herb	anemochory, epizoochory	Caribbean	1958	introduced (accidental)?	« weed »
Solanaceae	<i>Nicotiana glauca</i> Graham	sub-shrub	endozoochory, epizoochory	South America	1905	introduced (intentional)	« weed »

Table 3. Changes in plant species composition on Clipperton (La Passion) atoll.

Family	Scientific name	Life form	Status	1958	2005	2015
Amaranthaceae	<i>Achyranthes aspera</i> var. <i>aspera</i> L.	herb	introduced			X
Arecaceae (Palmae)	<i>Cocos nucifera</i> L.	tree	introduced	X	X	X
Asteraceae (Compositae)	<i>Erigeron bonariensis</i> L. (syn. <i>Conyza bonariensis</i>)	herb	introduced	X		
	<i>Eclipta prostrata</i> (L.) L. (syn. <i>Eclipta alba</i>)	herb	introduced	X		
Boraginaceae	<i>Heliotropium curassavicum</i> L.	erect herb	native	X	X	X
Brassicaceae	<i>Brassica juncea</i> (L.) Czern.	herb	introduced	X		
Convolvulaceae	<i>Ipomoea pes-caprae</i> subsp. <i>brasiliensis</i> (L.) Ooststr.	creeping vine	native	X	X	X
	<i>Ipomoea triloba</i> L.	creeping vine	introduced	X	X	X
Cyperaceae	<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	sedge	native	X	X	X
	<i>Eleocharis mutata</i> (L.) Roem. & Schult.	sedge	native	X	X	X
	<i>Cyperus subsquarrosus</i> (Muhl.) Bauters (syn. <i>Hemicarpha micrantha</i>)	sedge	native	X		
	<i>Schoenoplectus acutus</i> var. <i>occidentalis</i> (Muhl. Ex Bigelow) A.Löve & D.Löve (syn. <i>Scirpus rubiginosus</i>)	sedge	native	X		
Fabaceae (Leguminosae)	<i>Caesalpinia</i> sp.	shrub	native	X		
	<i>Canavalia cf. rosea</i> (Sw.) DC.	vine	native	X	X	
	<i>Mucuna sloanei</i> Fawc. & Rendle	liana	native	X		(drift seed)
	<i>Leptospron adenanthum</i> (G.Mey.) A.Delgado (syn. <i>Phaseolus adenanthus</i>)	creeper	introduced	X		
Lamiaceae	<i>Salvia occidentalis</i> Sw.	shrub	introduced			X
Malvaceae	<i>Corchorus aestuans</i> L.	erect herb	introduced	X	X	X
	<i>Hibiscus tiliaceus</i> L.	tree	introduced		X	
	<i>Sida rhombifolia</i> L.	shrub	introduced	X	X	X
	<i>Waltheria indica</i> L.	erect herb	introduced	X		
Phyllanthaceae	<i>Phyllanthus amarus</i> Schumach. & Thonn.	herb	introduced	X		X
Poaceae (Gramineae)	<i>Cenchrus echinatus</i> L.	grass	introduced	X		X
	<i>Dactyloctenium aegyptium</i> (L.) Willd.	grass	introduced	X		
	<i>Eragrostis amabilis</i> (L.) Wight & Arn. ex Nees	grass	introduced	X		
	<i>Eragrostis ciliaris</i> (L.) R.Br.	grass	introduced	X		X ?
Portulacaceae	<i>Portulaca oleracea</i> L.	prostrate herb	introduced	X	X	X
Sapindaceae	<i>Sapindus saponaria</i> L.	tree	native	X		
Solanaceae	<i>Nicotiana glauca</i> Graham	shrub	introduced	X		X
	<i>Solanum americanum</i> Mill. (syn. <i>Solanum nigrum</i> var. <i>americanum</i>)	herb	introduced	X		
TOTAL				27	11	15

Table 4. Evolution in species richness on Clipperton (La Passion) atoll.

Year	1958	2005	2015
Total number of species	27	11	15
Number of introduced species	20	6	11
Number of native species	7	5	4
Newly discovered species since 1958	-	1	2
Number of species not found in-between each scientific expedition	-	17	0
Number of species not found since 1958	-	17	14

Table 5. Evolution in the number of living coconut palms on Clipperton (La Passion) atoll.

Year	1897	1934	1958	1997	2001	2005	2013	2015
Size				>1 m	>1 m	>1.50 m	>1 m	>1 m
Number	2	40	353	557	674	581	806	847
Size						<1.50 m		<1 m
Number						3083		1395

APPENDIX

Photographs of some particular plant species and vegetation zones (credit: Xénia JOST).

Photo A. Small patch of the recently introduced weed *Salvia occidentalis* (inside the red circle) within a dense stand of *Sida rhombifolia*

Photo B. Dense coconut palms grove in “Bois de Bougainville” with almost no plant undergrowth

Photo C. Tree tobacco *Nicotiana glauca*, a subshrub first observed in 1958 and rediscovered in 2015

Photo D. A view of dense stands of the creeping vine *Ipomoea pes-caprae* (on the right: South side) and the introduced *I. triloba* (on the left: North side) from "Le Rocher"

Photo E. Dense stand of *Ipomoea triloba* with the lagoon visible on the right side

Photo F. Dense stand of the native tufted sedge *Eleocharis mutata* near “Le Crochet”

Photo G. A view of the "Bois de Bougainville" area with a dense stand of *Ipomoea triloba* in the foreground and coconut groves in the background

Photo H. A view of the "Pince Nord" area with the "Stèle" on a tumulus in the right background, and dense stand of *Ipomoea triloba* with a patch of *Eleocharis mutata* on the foreground

Photo I. A view of the Eastern coast with an expanding pure stand of *Ipomoea triloba* surrounding boobies nesting sites

Photo J. A view between the 3rd coconut grove and “Le Rocher” in the background (southward): *Ipomoea pes-caprae* on the left foreground and patches of *Eleocharis geniculata* elsewhere

