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Chapter 9

Distribution of Native Banyan fig-trees on Archaeological Remains on the island of Tahiti (Pacific Ocean): “Novel Habitat” or Past Human Cultivation?

Sébastien LARRUE
Université de Clermont-Ferrand¹

Jean-Yves MEYER
Délégation à la Recherche, Gouvernement de Polynésie française²

Abstract

The Pacific Banyan (*Ficus prolixa* var. *prolixa*, Moraceae) is a native fig-tree widely dispersed in the South Pacific islands but locally endangered on some of them. Some authors have documented the presence of the Pacific Banyan on Polynesian archaeological remains and assumed that they were planted intentionally as sacred trees on ceremonial stone platforms. We tested this hypothesis by reporting the presence or absence of Pacific Banyans on 45 prominent archaeological remains (stone platforms and stone walls) on the island of Tahiti (French Polynesia). In addition, we surveyed two semi-natural areas and noted the type of habitat where the species was naturally found. Our results show that lithosols and stone archaeological remains are the preferred habitat of the Pacific Banyan. These two similar substrates, as well as the frequency of fig-trees on stone walls, suggest that the trees have naturally colonized these pre-European ruins. Large archaeological stone remains may thus serve as an additional man-made “novel habitat” for Pacific Banyans, contributing to the protection of this species on Tahiti.

Key Words: archaeological remains, Pacific Banyan, novel habitat, French Polynesia, seed dispersal, Tahiti.

Résumé

Le banyan du Pacifique (*Ficus prolixa* var. *prolixa*, Moraceae) est un arbre indigène amplement dispersé dans les îles du Pacifique Sud mais localement menacé et

- 1 Corresponding author, Université de Clermont-Ferrand, GEOLAB UMR 6042, 63057 Clermont-Ferrand Cedex 1, France.
- 2 Délégation à la Recherche, Gouvernement de Polynésie française, B.P. 20981, Papeete, Tahiti, French Polynesia.

présentant souvent de faibles densités sur les îles. Quelques auteurs ont observé l'espèce sur des vestiges archéologiques en Polynésie française et supposent que l'arbre était jadis planté par les Polynésiens sur les plateformes lithiques cérémonielles. Nous avons testé cette hypothèse sur Tahiti (Polynésie française) en reportant (1) la présence/absence de *Ficus prolixa* sur 45 vestiges archéologiques (plateformes lithiques et vieux murs) et (2) avons reporté la fréquence de *Ficus prolixa* dans différents types d'habitat et de substrat sur une surface totale de 235,5 km². La disponibilité des habitats montre que les lithosols et les vestiges archéologiques sont des substrats plus fréquemment colonisés que les autres par *Ficus prolixa*. Les similitudes édaphiques entre les lithosols et les vestiges lithiques pré-européens, ainsi que la fréquence des banians sur les vieux murs, suggèrent que ces arbres ont colonisé les vestiges archéologiques sans intervention humaine. Ces ruines constituent un « nouvel habitat » pour *Ficus prolixa* et contribuent à la sauvegarde de l'espèce sur Tahiti.

Mots-clés : vestiges archéologiques, Banian du Pacifique, nouvel habitat, Polynésie française, dispersion des graines, Tahiti.

1. Introduction

Many studies have shown that biodiversity erosion in the Pacific Islands is caused by Polynesian pre- and post-cosmopolitan human impacts, either direct such as habitat destruction and overhunting (Kirch 2009; Pimm *et al.* 1995; Steadman 2006), or indirect such as invasion by introduced plant and animal species (*e.g.* Denslow 2003; Kueffer *et al.* 2009; Larrue 2008; Merlin and Juvik 1992; Meyer and Florence 1996; Meyer 2000; Reaser *et al.* 2007). Some native trees have also been cultivated by Polynesians through planting, layering and cuttings (Grépin and Grépin 1984; Guerin 1990; Lepofsky 1994, 2003; Nadeaud 1864, 1873). In French Polynesia, a few native tree species were cultivated close to human habitations and ceremonial stone platforms by pre-contact Polynesians in ancient times (Cuzent 1860; Henry 1928; Lavondès 1976; Lepofsky 1994; Nadeaud 1873). The most frequently cited of these include *Calophyllum inophyllum* L. (Clusiaceae), *Thespesia populnea* (L.) Solander ex Corrèa (Malvaceae), *Casuarina equisetifolia* L. (Casuarinaceae), *Fagraea berteiroana* A. Gray ex Benth. (Loganiaceae), *Terminalia glabrata* var. *brownii* Fosberg & Sachet (Combretaceae) and the native banyan *Ficus prolixa* J.G. Forster var. *prolixa* (Moraceae) (Cuzent 1860; Florence 1993; Gérard 1978; Henry 1928; Nadeaud 1873; Orliac 1984; Ottino 1996). According to fossil pollen records, some of these trees might be Polynesian introductions rather than indigenous to Southeastern Polynesia *e.g.* *Casuarina equisetifolia* (M. Prebble, pers. comm.). None of these species is considered endangered (*e.g.* on the IUCN Red List) except for the Marquesan endemic sea almond *Terminalia glabrata* var. *brownii*, now extremely rare on some islands (Florence *et al.* 2007; Meyer 1996).

Although *Ficus prolixa* var. *prolixa* is widely distributed in the Pacific Islands (Brown 1935; Corner 1963; Florence 1997; Florence *et al.* 2007), it is currently rare and locally endangered on some islands such as Tongatapu in the Tongan archipelago (Wiser *et al.* 2002) or Rarotonga and Aitutaki in the Cook Islands (Compton and McCormack 1999; Staddon *et al.* 2010). This banyan is ecologically important in the

Pacific Islands (Compton and McCormack 1999; Steadman, 1997, 2006; Staddon *et al.* 2010), and figs have long been recognized as an important food source for many vertebrate frugivores in tropical forests and are considered to be “keystone resources” (Shanahan *et al.* 2001).

In the Australs, Tuamotu, Society and Marquesas archipelagoes of French Polynesia, *Ficus prolixa* is relatively common and observed in native and human-disturbed habitats, including archaeological sites (Florence 1997; Gérard 1978; Larrue 2007; Lepofsky 1994, 2003; Ottino 1996, 2006).

In ancient times, *Ficus prolixa* was regarded as a sacred tree (“*tapu*”) by Polynesians (Brown 1935; Ottino 1996, 2006), and was intentionally planted in front of the royal houses of chiefs (Cuzent 1860) or between the boundaries of chiefdoms in the Society Islands (Rey-Lescure 1951). Therefore, the current distribution pattern in French Polynesia of the native species *Ficus prolixa* is linked to past human occupation, as well as to both natural dispersal and ecological factors (*e.g.* precipitation, temperatures, soil, etc.). The presence of *Ficus prolixa* on some archaeological remains, notably on ancient Polynesian ceremonial stone platforms, is commonly viewed as human heritage. However, banyans are also well-known colonists of old exposed substrates like walls or dwellings (Condit 1969).

In this paper, we tested if the presence of *Ficus prolixa* on the archaeological remains of Tahiti is the result of natural colonization rather than the legacy of past human cultivation. The research question is: do the Polynesian archaeological remains provide a potential “ecological refugium” for the indigenous species *Ficus prolixa* on the island of Tahiti?

2. Materials and methods

2.1 Study area

Located between 17°29'50"-17°52'32" lat. S, and 149°07'40-149°36'48" long. W, Tahiti is the largest (1,045 km² with a summit at 2,241 m) of the 14 tropical high volcanic islands that form the Society archipelago in French Polynesia (Dupon 1993). Its geological age ranges from *ca.* 300,000 years old on the peninsula of “Tahiti Iti” to *ca.* one million years on the volcano of “Tahiti Nui” (Brousse *et al.* 1985). The tropical oceanic climate of Tahiti is characterized by an average annual temperature of 26°C and two alternating “seasons”, a wet and warm one (November to April) with maximum average temperatures of 28° to 29°C and another (May to October) with lower rainfall and cooler temperatures (Laurence *et al.* 2004). As observed in many high volcanic islands in the Pacific, Tahiti has a leeward dry coast and a windward wetter side exposed to the dominant Southeastern tradewinds. Different vegetation types are found according to the substrate (limestone versus basaltic), the elevation gradient (0.6°C decrease every 100 m) and rainfall patterns (from 1,000 mm/year at sea level on the leeward coast to more than 5,000 mm/year on the windward coast and reaching 8,000 mm/year in the interior of the island) (Papy 1954; Florence 1993; Meyer 2007; Meyer and Salvat 2009).

2.2 Species studied

Ficus prolixa J.G. Forster var. *prolixa* (hereafter *F. prolixa*), commonly called the Pacific Banyan (Compton and McCormack 1999), is a large monoecious tree, 6-12 m in height (Smith 1981), reaching 25-30 m (Brown 1935; Florence 1997), with a wide-spreading crown up to 35 m in diameter. As with other strangler fig-trees, it is characterized by descending aerial roots forming a complex ‘trunk’ of diameter 2-9 m (Florence 1997). *F. prolixa* is indigenous in the Pacific region, ranging from Micronesia in the north, to Vanuatu and New Caledonia to Fiji in the west, and Samoa, the Cook islands, French Polynesia and the Pitcairn islands in the east (Florence 1997), but it is absent in the Hawaiian islands. Its island distribution ranges from coastal plains and rocky shores (Corner 1963, Smith 1981) to montane rainforests, up to 1,000 m elevation in the Marquesas, French Polynesia (Brown 1935; Florence 1997).

In the Society Islands, and in Tahiti in particular, the species occurs in different habitat types: coastal forests, low- to middle-elevation semi-dry forests (with an average annual rainfall of less than 1,500 mm), low- to middle-elevation moist or mesic forests (between 1,500 and 3,000 mm) and mid- to upper-elevation wet forests (above 3,000 mm) including valley forests and high-elevation plateaus 750-850 m (Meyer, pers. obs.). *F. prolixa* is rarely found in montane cloud forest (Florence, pers. comm. 2011; Meyer, pers. obs.).

The Pacific Banyan is pollinated by a single species of fig wasp (Wiebes 1994; Vougioukalou 2000) and its numerous small fleshy fruits, dark red to purple-black when ripe, are actively dispersed by frugivorous birds and flying foxes (Florence 1997; Staddon *et al.* 2010). *Ficus prolixa* seedlings grow best in a sunny exposure on different well-drained substrates: on the branches of host-trees, as a hemi-epiphytic parasite (Compton and McCormack 1999; Florence 1997), on cliffs in rock crevices, and on eroded slopes of valleys (Cuzent 1860; Brown 1935; Florence 1997).

2.3 Methods

A total of 45 archaeological remains formed of both Polynesian stone walls and rectangular stone platforms of medium and large size (about 10 to 360 m²), listed by the French Polynesian Department of Culture and Heritage (Marchesi and Maric 2005), were surveyed (**Fig. 1**). These archaeological remains are composed of stacked basalt stones, sometimes with a few stones of limestone. The presence of *F. prolixa* was recorded on both Polynesian stone walls and rectangular platforms, and then the distribution of stone platforms and stone walls was compared to the distribution of *F. prolixa* among these archaeological remains (**Fig. 2**). The aim was to test if the stone platforms were more frequently colonized by *F. prolixa* than the stone walls.

In addition, the preferred habitat of *F. prolixa* in Tahiti was investigated. Two surveyed areas (235.5 km²) were delineated (**Fig. 1**) and the presence of *F. prolixa* in different environments called “habitat types” was reported. Only areas approachable by inland roads and trails were surveyed. Five “habitat types” where *F. prolixa* was found were identified: (1) lowland volcanic and alluvial soils in forest (< 250 m); (2) lithosols on steep slopes and boulders (< 500 m); (3) volcanic soils in forests of plateaus and low slopes; (4) fernlands and grasslands on low slopes and plateaus; and

(5) archaeological remains.

The distribution of “habitat type” availability in the surveyed areas was estimated by using the Geographic Information System (GIS Mapinfo® Professional version 10, WGS 1984 projection). Layers were made with, respectively, (1) the soil map of Tahiti (Dupon 1993), (2) the map of archaeological sites of Tahiti, and (3) aerial photographs (April 2011) on which the forests, fernlands and grasslands were mapped. We have superposed the layers from these documents to obtain a final map and then the distribution of habitat types in the surveyed areas was calculated.

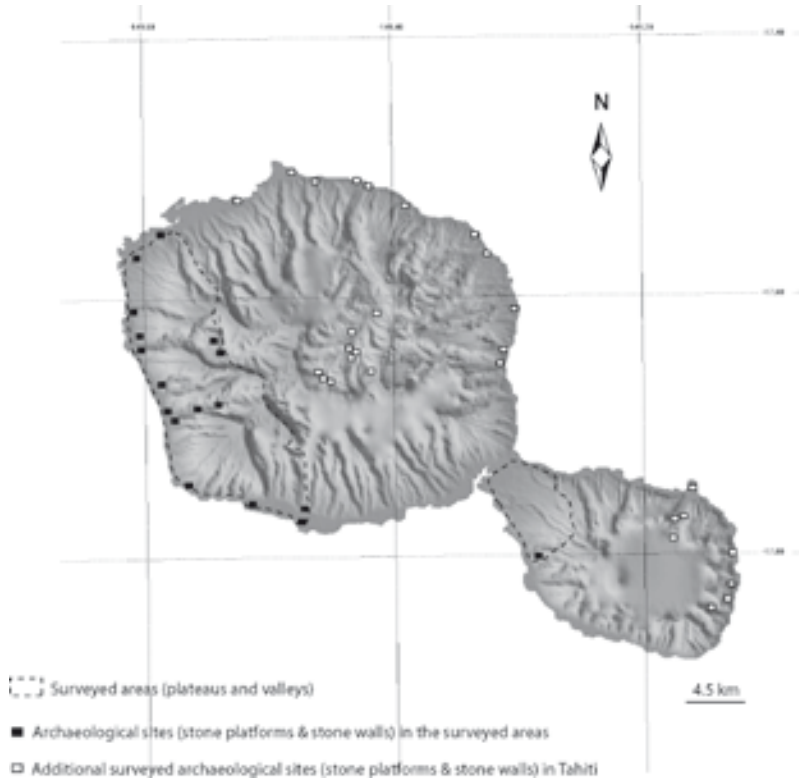


Figure 1. Surveyed areas and archaeological remains on the island of Tahiti (Society Islands, French Polynesia).

3. Results

3.1 Frequency of *Ficus prolixa* on the total surveyed archaeological remains in Tahiti

Only seven *F. prolixa* trees were recorded among the 45 stone archaeological remains surveyed in Tahiti. The maximum at any one site was one tree. According to the sample surveyed, the frequency of *F. prolixa* is thus 0.15 tree per ruin. More *F. prolixa* were recorded on stone walls than on stone platforms (**Fig. 2**).

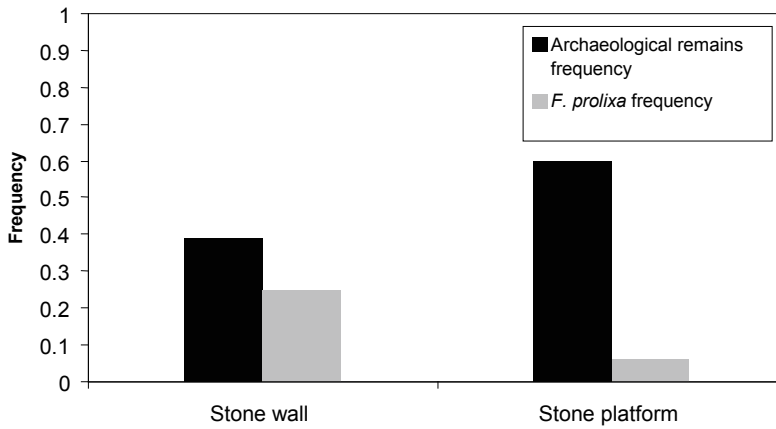


Figure 2. Distribution of *Ficus prolixa* on both stone platforms and stone walls compared to the distribution of these ruins among all the archaeological remains surveyed.

3.2 Frequency of *Ficus prolixa* in the surveyed areas and “habitat type”.

A total of 27 *F. prolixa* trees were recorded in the surveyed areas. The trees were observed in different natural habitats: 11 on steep and eroded forested slopes, growing on boulders and soil from partly weathered rock fragments usually called lithosols; 5 on archaeological stone remains; 6 on lowland volcanic soils in valley forest; 4 in open fernlands and grasslands mainly on the Taravao plateau (Tahiti Iti); and one in plateau forest in epiphytic conditions.

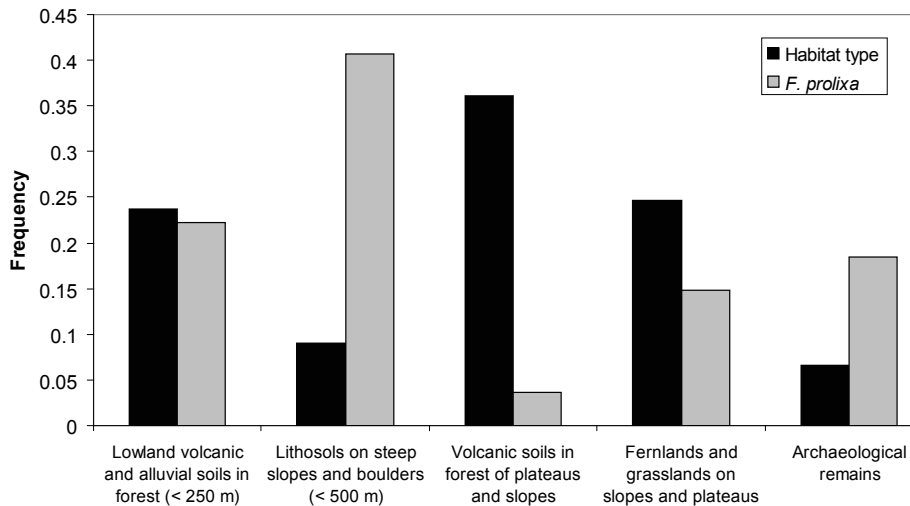


Figure 3. Distribution of *F. prolixa* according to natural “habitat type” compared to the distribution of these “habitat types” in the two surveyed areas.

4. Discussion

4.1 Natural habitats of *Ficus prolixa* in surveyed areas

The suitable environments for *F. prolixa* in the surveyed areas include lithosols and boulders, lowland volcanic soils, fernlands and grasslands, archaeological remains and epiphytic conditions. The latter result of *F. prolixa* in “epiphytic conditions” in the forests needs to be carefully interpreted. Although the epiphytic conditions were very abundant, our result shows a low frequency of *F. prolixa* in this environment (Fig. 3), which suggests it is non-preferred. However, it is difficult to target *F. prolixa* among canopy trees and some fig-trees could not be listed.

F. prolixa trees were more commonly observed on the lithosols of steep and eroded slopes and lowland volcanic soils (Fig. 3) as mentioned by Cuzent (1860) and Florence (1997) in the Society Islands.

Regarding the availability of “habitat type” (Fig. 3), our results show that lithosols and stone archaeological remains are the preferred environments of *F. prolixa*. Brown (1935:40) indicates that *F. prolixa* “is also one of the first trees to gain foothold on the unstable precipitous slopes characteristic of the Marquesas coast and ravines. In habitats of this type, the roots penetrate deeply in the rock crevices”. This observation supports our results; a rocky substrate appears to be a preferred habitat for *F. prolixa*.

In addition, other favorable rocky substrates, reported elsewhere in Polynesia, include limestones, such as on the raised atolls of Makatea in the Tuamotu archipelago (Meyer, pers. obs.), Mangaia in the Cook Islands (Compton and McCormack 1999) or Nauru where *F. prolixa* is considered one of the most important tree species recolonizing old phosphate mining sites (Manner *et al.* 1985). Merlin and Juvik (1992:616) wrote that on Nauru “the natural forest vegetation of the central plateau is dominated by *Calophyllum inophyllum* [...] and in the most severe limestone areas by *Ficus prolixa* (canopy height up to 65 ft or 20 m).”

4.2 Distribution of *Ficus prolixa* on the surveyed archaeological remains

Our results indicate that, although some *F. prolixa* were recorded on archaeological stone remains, the species is not always found on these sites. In fact, its presence was noted on only 15.5% of archaeological remains among the 45 sites surveyed in Tahiti. Thus, this distribution suggests that this banyan was not commonly planted on the stone platforms.

An alternative explanation would be the natural death of *F. prolixa* planted on the stone platforms by the Polynesians in ancient times. However, this seems unlikely because the stone remains in the Society Islands are relatively recent while *F. prolixa* is thought to be long-lived (Compton and McCormack 1999).

The dating of stone platforms ranges over a period of 140 years immediately before initial European contact in AD 1767 to AD 1780 in the Society Islands (Gérard 1974; Sharp *et al.* 2010). The pre-European sites were abandoned in the 19th century (Emory 1933; O’Reilly 1975) and thus the age of these archaeological remains is between about 383 and 230 years-old. While the life-span of *F. prolixa* is unknown,

some elements about the approximate age of *F. prolixa* in French Polynesia are available. The *F. prolixa* located close to the Government's Garden in Papeete (island of Tahiti) is thought to be around 400 years old (Babin, pers. comm.). In 1898, a large *F. prolixa* was photographed by Van den Steinen in the Hatiheu valley on the island of Nuku Hiva (Marquesas, French Polynesia). The same banyan tree covering part of the stone platform of the Kamuihei archaeological site can still be observed and does not appear senescent (Larrue, pers. obs.). In Ua Huka (Marquesas, French Polynesia), the age of an *F. prolixa* on a platform in the Vaipaee valley is estimated to be between 200 and 400 years old (Ottino 2006).

Overall, if *F. prolixa* trees had been planted on the stone platforms in Tahiti by ancient Polynesians, they should still be visible today. Furthermore, although the stone platform environments were available; our results show that *F. prolixa* trees are mainly found on ancient stone walls (Fig. 2), which cannot be the result of past human cultivation in these places.

4.3 Are the archaeological remains a “novel habitat” for *Ficus prolixa*?

The archaeological remains consisting of both Polynesian stone platforms and stone walls can be viewed as “anthropogenic lithosols and boulders” scattered in the forests. One additional observation shows that *F. prolixa* is able to colonize the ruins by itself and grows rapidly on stone remains without human cultivation.

In Tahiti, an *F. prolixa* tree was observed on the structure reported to be a stone platform of Mataoa, which was studied by Handy in the 1920s (Emory 1933). The platform measured 36 m wide and 54 m long at that time. During excavations in 2004, the remains attributed to the Mataoa platform formed a mound 15 m long and 1.5 m high surmounted by a banyan fig-tree (Maric 2005). In addition, these excavations indicated that this mound was not the remains of the platform but a recent landfill containing some stones of the Mataoa platform destroyed in 1980 by the land-owners (Maric 2005). The fig-tree of Mataoa is thus only 30 years old.

Consequently, the current presence of *F. prolixa* on the archaeological remains in Tahiti may be explained by a natural colonization of stone walls and platforms after their abandonment in the 19th and early 20th centuries.

The small fleshy fruits of *F. prolixa*, produced in large quantities, are well adapted to endozoochory. The main seed dispersers of *F. prolixa* in the Pacific Islands are frugivorous birds and flying foxes (Compton and McCormack 1999; Steadman, 1997, 2006; Staddon *et al.* 2010), especially the endemic Gray-green fruit-dove *Ptilinopus purpuratus* in the Society Islands, the Makatea fruit-dove *Ptilinopus chalcurus*, and the Polynesian-Imperial pigeon *Ducula aurorae* on the raised atoll of Makatea in the Tuamotu (Holyoak and Thibault 1984), and both the fruit-dove *Ptilinopus raro-tongensis* and the pigeon *Ducula pacifica* in the Cook Islands (Staddon *et al.* 2010).

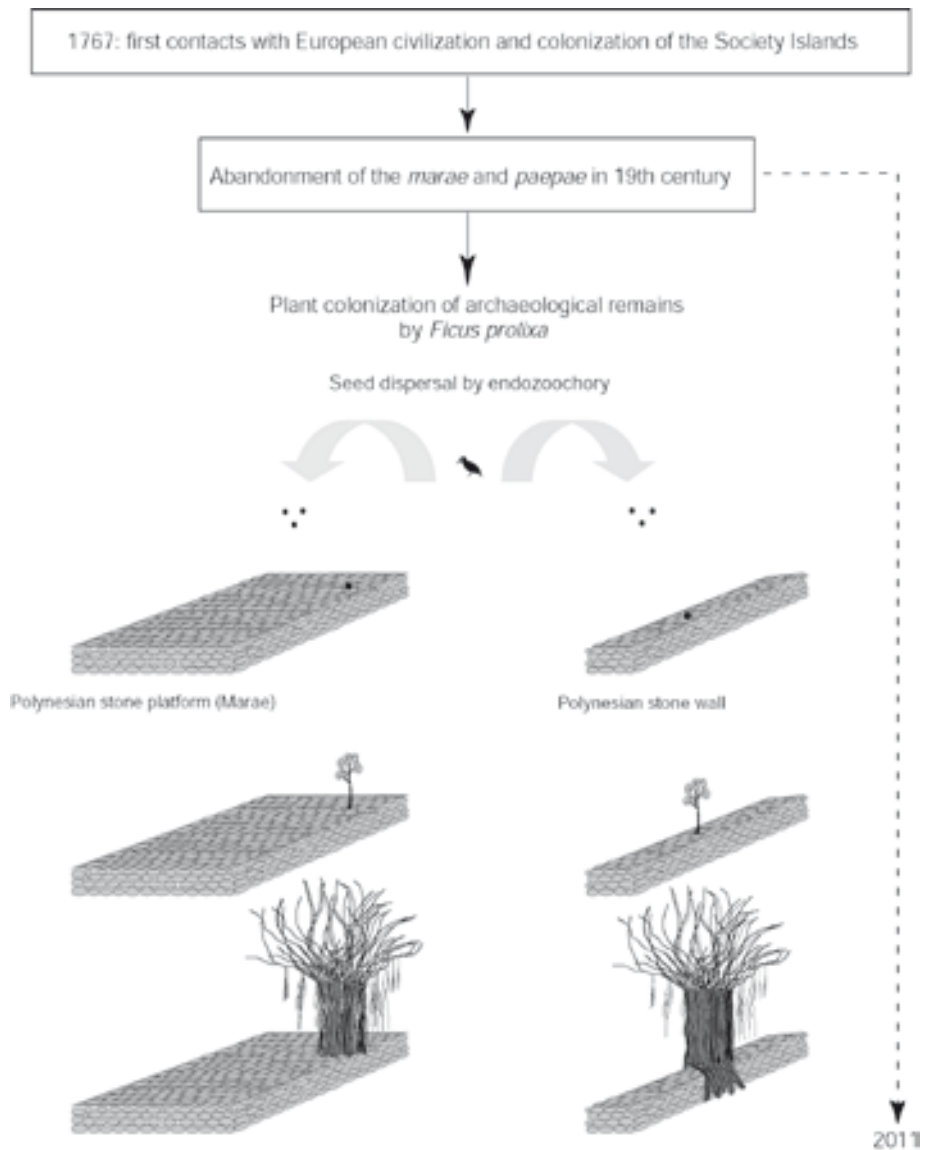


Figure 4. Illustration of the natural colonization of stone platforms and walls by *F. prolixa*.

The huge number of fruits produced by *F. prolixa* attracts many frugivorous native and alien birds even when trees are isolated (Meyer, pers. obs.); on the island of Tahuata (Marquesas), about 200 Marquesan fruit-doves *Ptilinopus dupetithouarsii* were observed in a Pacific Banyan during several days (Holyoak and Thibault 1984). The endemic Gray-green fruit-dove is still relatively common in Tahiti where it is found in forested areas from sea-level up to 800-900 m elevation (Holyoak and Thibault 1984; Meyer, pers. obs.); this fruit-dove contributes to the potential *F. prolixa* “seed-rain” on archaeological remains.

Conclusion

Whereas some plant species have shown a stronger association with archaeological sites and past human cultivation in Tahiti, such as the bamboo *Schizostachyum glaucifolium* (Ruprecht) Munro (Larrue *et al.* 2010), there is no significant link between the presence of *F. prolixa* and the archaeological remains on the island of Tahiti. Its presence on some remains and its distribution according to habitat type support the hypothesis of the natural colonization of archaeological stone remains as a preferred habitat. We can therefore assume that the presence of *F. prolixa* on archaeological remains on the island of Tahiti is the result of “ecological chance” through its seed dispersers.

Like the pattern of ‘transported landscapes’ indicating that the first Polynesians modified the distribution and spatial pattern of some species in remote Pacific islands (Kirch 1984, 1996), archaeological remains may provide “ecological refugia” for some *F. prolixa* trees in these man-made “novel” habitats, especially as the natural habitats of fig-trees are declining (Compton and McCormack 1999).

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