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INVASIVE RODENTS ON ISLANDS

The impacts of rats on the endangered native flora of French Polynesia (Pacific Islands): drivers of plant extinction or *coup de grâce* species?

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Abstract Although rats have clearly contributed to bird extinctions on islands, their role in plant extinctions is not as clear. Paleoenvironmental studies suggest rats were responsible for the demise of several island palm species. French Polynesia's islands provide an opportunity to evaluate "modern" impacts of rats on native flora. Our study shows that 15 threatened taxa (nine families) are damaged by rats. All 12 subjected to seed predation are woody plants with large-seeded drupes. Three experience severe predation and recruitment depression (*Santalum insulare*, *Ochrosia tahitensis*, *Nesoluma nadeaudii*). Three-year monitoring of Polynesian sandalwood (*Santalum insulare*) populations in Tahiti during rat control suggested that over 99% of fruits were eaten before ripening. Seed predation on sandalwood appeared to be lower on islands without black rats *Rattus rattus*. Studies from Indo-Pacific islands document rat impact on at least 56 taxa (28 families). Certain families (Arecaceae, Elaeocarpaceae, Rubiaceae, Santalaceae, and Sapotaceae) are particularly vulnerable to seed predation. Other soft-barked trees (Araliaceae, Euphorbiaceae, and Malvaceae) suffer from stem or bark damages, especially during dry seasons. Although rats depress seedling recruitment and alter vegetation dynamics, no evidence demonstrates that they are solely responsible for current plant extinctions. Most of French Polynesia's endangered species impacted by rats occur in severely degraded habitats. We therefore suggest that rats can be viewed more as *coup de grâce* species (i.e., that give the final stroke of death), rather than as main drivers of plant extinctions. More research is needed to clarify the impacts of rat species and their importance in plant population decline or demise.

Keywords Island flora · Plant extinctions · Rats · Sandalwood · Seed predation

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Introduction

The destructive impacts of rats, mainly the black or ship rat *Rattus rattus* (L.), the Pacific or Polynesian rat *R. exulans* (Peale), and the Norway or roof rat *R. norvegicus* (Berkenhout), on native island fauna is well documented. Rats are notorious in having caused the decline of seabirds and land-birds, leading to extirpations (local extinction) or complete extinctions (see, e.g., Atkinson 1985; Tomich 1986 in Hawai'i; Towns et al. 2006 in New Zealand; Martin et al. 2000,

in the Mediterranean islands). In the tropical oceanic islands of French Polynesia (South Pacific), for instance, there is a strong relation between the arrival of the black rat and the decline followed by the extinction of monarchs *Pomarea* spp. (Monarchidae) in the Marquesas archipelago (Thibault and Meyer 2001; Thibault et al. 2002). Yet monarchs, as well as ground doves (*Gallicolumba* spp., Columbidae), coexist with the Pacific rat in the Marquesas (J.-C. Thibault, personal communication 2007). However, some seabirds are now strictly restricted to completely rat-free small islets (Thibault and Bretagnolle 2007) and others have reduced breeding success in the presence of the Pacific rat, leading to the decline of these bird populations (see, e.g., Brooke 1995; Booth et al. 1996). Both "prehistoric" (during the Polynesian period, starting ca. 1,000 years BP) and "historical" (European period, starting in the 18th century) extinctions of many endemic birds in French Polynesia, such as ground doves, parakeets *Cyanoramphus* spp., lorikeets *Vini* spp., pigeons *Ducula* spp., kingfishers *Todiramphus* spp., sandpipers *Prosobonia* spp. or rails *Gallirallus* spp., are commonly attributed to a combination of habitat destruction or modification, hunting, and predation by a set of introduced animals such as rats, dogs, pigs, and cats (Seitre and Seitre 1992; Steadman 2006). This list includes introduced raptors such as the swamp harrier *Circus approximans* (Accipitridae), present in Tahiti since 1884, and the great horned owl *Bubo virginianus* (Strigidae), in Hiva Oa (Marquesas) since 1927, which were both introduced to control rats.

The negative effects of rodents on the native island flora, especially on seedling recruitment and plant regeneration (also called "recruitment depression"), are relatively well studied (see references below). Destruction of flowers, fruits, seeds, seedlings, stems, leaves, buds, roots, and rhizomes of indigenous and endemic plants in island ecosystems is documented for the Hawaiian Islands (Stone 1985; Cuddihy and Stone 1990; Tonga (McConkey et al. 2003) and New Zealand (Allen et al. 1994; Campbell and Atkinson 1999) in the Pacific Ocean, and Mauritius (Strahm 1988) and Aldabra (Underwood 2006) in the Indian Ocean. Other observations based on rat diets (stomach contents analysis) containing plant parts are given for Hawai'i (Sugihara 1997), the island of Pohnpei (Ponape) in the Federated States of Micronesia (Storer 1962), the atoll of Eniwetok in the Marshall Islands (Fall et al. 1971), and the Galápagos Islands (Hamann 1979; Clark 1981).

Based on recent archaeological studies and paleoenvironmental data, some authors (Athens et al. 2002; Hunt 2007) suggest that rats were the main cause of past extinction (ca. 1200 AD) of several endemic palm species in Hawai'i (*Pritchardia* spp.) and in Rapa Nui (Easter Island) (*Paschalococos disperta*, closely related to *Jubaea chilensis* endemic to Chile). Stephen Athens (op. cit.) stated that "the main source of destruction of the native forests was the introduced Polynesian rat *Rattus exulans*," which causes the demise of the *Pritchardia* palm forests on the Ewa plain of Oahu (Hawai'i), and Terry Hunt (2007) argued that "rats alone are capable of widespread forest destruction" in Rapa Nui.

The ca. 120 small tropical oceanic islands of French Polynesia (South Pacific) provide an excellent opportunity to investigate the "modern" impacts of rats on the native and endemic flora because these archipelagoes are home to a high number of threatened plants, and invasive rats have been present throughout almost all the islands and habitat types for two or more centuries.

Materials and methods

The five archipelagoes of French Polynesia (namely the Australs, the Gambier, the Marquesas, the Society, and the Tuamotu) comprise ca. 120 small oceanic islands ranging from young high volcanic islands (the youngest is Mehetia, 30,000 years old) to very old low-lying coral islands or atolls (up to 60 MY old), with a total land surface of only 3,500 km^2 (Dupon et al. 1993).

In order to confirm that rats are potential drivers of plant extirpations or extinctions in French Polynesia, we listed all native and endemic plant species considered to be threatened according to World Conservation Union (IUCN) criteria (critically endangered, CR; endangered, EN; vulnerable, VU) or supposed to be extinct (EX), that are known to be impacted by rats (i.e., whose fruits, seeds, stems, barks, and leaves show clear signs of rat attack). Evidence of impacts is based on personal observations conducted during the last 15 years of field surveys in most of the islands of French Polynesia. Rat predation of seeds of the endangered endemic

sandalwood *Santalum insulare* was evaluated on the island of Tahiti (Society) during rat control experiments by poisoning. We predicted that reduction in rat numbers would result in lowered levels of seed predation that would in turn allow for subsequent collection of ripe fruits for seed germination and ex situ propagation. The data on the endangered flora of French Polynesia were compared with the available information of rat impacts on the native flora in other tropical Indo-Pacific islands. Sources for comparison include published literature, personal communications, and personal observations on the island of Wallis (Uvea) located in Western Polynesia.

Threatened plants

The primary flora of French Polynesia comprises 885 native plant species including 520 endemics, i.e., 59% endemism (Florence 2007). A total of 47 endemic plant species is considered threatened according to the IUCN red lists, and six more are designated extinct. French Polynesia has one of the most endangered floras in the Pacific Ocean, along with the large continental islands of New Caledonia (219 threatened plant species on an area of 19,100 km^2), Papua New Guinea (146 threatened species, 462,000 km^2) and Fiji (66 threatened species, 18,270 km^2), and the large oceanic islands of Hawai'i' (289 endangered plant taxa, 16,640 km^2, Hawaii Biological Survey 1995–2003). However, the IUCN database greatly underestimates the real number of threatened plants in French Polynesia. Indeed, among the 34 species whose status is considered as poorly documented (data deficient, DD) by IUCN, many are in fact critically endangered (e.g., *Ixora temehaniensis*, *Metatrophis margaretae*, *Nesoluma nadeaudii*, and *Psychotria franchetiana*, personal observation.) or endangered (e.g., *Psychotria tubuaiensis*, personal observation), and a few of them are probably extinct (e.g., *Myoporum rimatarense*, personal observation or *Psychotria adamsonii*, a species not collected since its first description in 1929, Lorence and Wagner 2005). On the other hand, some species considered EX by IUCN [e.g., *Christiana* (*Tahitia*) *vescoana*, *Ochrosia tahitensis*, and *Neisosperma brownii*] were recently rediscovered during extensive field-botanical surveys conducted in the last decade, and should be classified as CR. Moreover, many species previously considered to be threatened in the 1997 IUCN red lists (Walter and Gillett 1998) were not included in the 2007 list (e.g., the lobeliods *Apetahia* spp. and *Sclerotheca* spp., the different endemic varieties of Polynesian sandalwood *Santalum insulare,* or the different varieties of the endemic Polynesian sea almond *Terminalia glabrata*). Conservation status for plant species that are treated in the two first volumes of the Flora of French Polynesia, including newly described species, were also recently reassessed (Florence 1997, 2004). We believe that a total of 167 native and endemic plant species, legally declared protected species in French Polynesia in 2006, should be considered at high risk of extinction (Meyer 2007).

The major recognized threats to the native flora of French Polynesia are habitat destruction by humans (especially for intensive cultivation, housing development, roads and airport construction), accidental or intentional fires, browsing and trampling by introduced large feral ungulates (goats, pigs, sheep, cattle, and horses), overexploitation and harvesting of some plant species (e.g., the large native trees *Neonauclea forsteri*, Rubiaceae, and *Alphitonia* spp., Rhamnaceae, for timber, the endemic sandalwood *Santalum insulare*, Santalaceae, for its fragrant wood, or the endemic tree *Rauvolfia sachetiae*, Apocynaceae, in the Marquesas for the medicinal use of its bark) and invasion by alien plants (Meyer 2004, 2007). The loss of dispersal agents (e.g., frugivorous birds), pollinators, and other potential mutualistic plant-animal associations, as well as the introduction of plant pests (i.e., invertebrates and pathogens), might also be involved as they contribute to the decline of some endangered species on other oceanic islands, but are not well documented in French Polynesia. The detrimental role of rats (*Rattus* spp.) on endemic plants was recently brought to light during a comprehensive study on sandalwood distribution, ecology, and regeneration in French Polynesia (Butaud 2004, 2007).

Rats in French Polynesia

Pacific rats *Rattus exulans* were thought to be introduced to the "Polynesian Triangle" accidentally as stowaways or intentionally as a food source (Matisso-Smith et al. 1998) by the initial Polynesian discoverers. The islands of French Polynesia, located in Southeastern Polynesia, were settled ca. 1,000 years ago (E. Conte, personal communication,

2007). Bones of Pacific rats were found in rockshelter excavations in Tahiti dated 580 ± 60 BP (Orliac 1997). Black rats *Rattus rattus* and Norway rats *Rattus norvegicus* arrived with Europeans, who first landed in Tahiti in 1768. Because rodents initially arrived on islands lacking predators, they might have attained relatively high population densities (Athens et al. 2002).

Currently, only five islands of the ca. 120 in French Polynesia are known to be free of all rats (Table 1). They are remote and small atolls and rocky islets, less than 300 ha in area, and often uninhabited. Other small offshore islets such as Motu Hotuatua near Raivavae (Australs) or Motu Hemeni near Ua Huka (Marquesas) are suspected to be completely rat-free because of their large populations of burrowing sea-birds (Table 1). Rats are found on almost all 76 inhabited islands of French Polynesia. Only eight of them are reported to be free of black rats *Rattus rattus*, including three islands in the Australs, one in the Marquesas (Ua Huka), the atoll of Scilly in the Society Islands and at least three atolls in the Tuamotu. The islands free of black rats include the uninhabited natural reserves of Fatu Huku (or Fatu 'Uku), Hatutu (Hatuta'a), and Mohotani (Motane) in the Marquesas archipelago. The islands of Ua Huka (Marquesas) and Rimatara (Australs) are the only populated islands where endemic lorikeets (*Vini ultramarina* and *Vini kuhlii*, Psittacidae, respectively) are still surviving, and good populations of Monarchs (*Pomarea* spp., Monarchidae) are still found in Ua Huka and Mohotani.

Table 1 Islands and islets in French Polynesia free of rats

Archipelago	Island name	Island type	Area (ha)	Human presence	Source
Australs	Hotuatua[b,c]	Offshore rocky islet (Raivavae)	2	No	Personal observation (2002)
	Maria[a]	Atoll	53	No	Pierce et al. (2003)
	Raivavae[a]	High island	2,305	Yes	Thibault et al. (2002)
	Rimatara[a]	Composite island	836	Yes	Thibault personal communication (2004)
	Rapa[a,c]	High island	3,929	Yes	Thibault and Bretagnolle (1999)
	Tarakoi[b,c]	Offshore rocky islet (Rapa)	2	No	Personal observation (2002)
Gambier	Manui[b]	Rocky islet	10	No	Thibault and Bretagnolle (1999)
	Teiku[b]	Rocky islet	2	No	Thibault and Bretagnolle (1999)
Marquesas	Ua Huka[a]	High island	8,340	Yes	Thibault and Meyer (2001)
	Fatu Huku (Fatu 'Uku)[a]	High island	100	No	Seitre and Seitre (1992)
	Hatutu (Hatuta'a)[a]	High island	660	No	Thibault (1989)
	Mohotani (Motane)[a]	High island	1,280	No	Thibault and Meyer (2001)
Society	Bellingshausen (Motu One)[a]	Atoll	380	No	Seitre and Seitre (1992)
	Scilly (Manuae)[a]	Atoll	773	Yes	Seitre and Seitre (1992)
Tuamotu	Morane[b]	Atoll	224	No	Seitre and Seitre (1992), Pierce et al. (2003)
	Nukutepipi[a]	Atoll	179	Yes	Salvat et al. (1993)
	Reitoru[a]	Atoll	532	Yes	Pierce et al. (2003)
	Takapoto[a]	Atoll	57	Yes	Le Gonidec (1977)
	Tekokota[b]	Atoll	57	No	Pierce et al. (2003)
	Tenararo[b]	Atoll	272	No	Pierce et al. (2003)

[a] Free of black rat (*Rattus rattus*)

[b] Free of all rat species

[c] Absence suspected but not recently confirmed

Rats have successfully invaded almost all the habitat types in French Polynesia, from atoll to littoral forests at sea level, to dry and mesic forests at low elevation, high-elevation montane rain forest (cloud forests), and in the subalpine vegetation zone, above 2,000 m elevation (e.g., on the summit of Mt Pito Hiti, 2,110 m elevation on the island of Tahiti, personal observation).

Impacts of rats on the flora

Rodents are generally known as important seed predators, destroying seeds by gnawing them to pieces, and sometimes as seed dispersers through transport of large seeds to food caches (called husking stations) or through ingestion of fleshy fruits containing small seeds (see, e.g., Ridley 1930; McConkey and Drake 2002; Medeiros 2004). The role of rats as predators or dispersal agents depends on fruit/seed characteristics such as size, seed energy value, seed chemistry, and toxicity, but also the costs of processing and consuming (e.g., rodents usually prefer husked over unhusked seeds, the husk being the fibrous mesocarp) (Janzen 1971; Price and Jenkins 1986). Rats forage for fruits/seeds on the forest floor as well as on the vegetative parts of plants themselves (including trees). Fruiting phenology is also important (e.g., rats prefer dense seed patches/clumped seeds rather than sparse seed patches, Price and Jenkins op. cit.). Fruiting periods can contribute to sustaining high densities of rats that exert huge levels of seed predation (Cuddihy and Stone 1990).

The impacts of rats on plants in Tahiti were reported as early as 1860 by the French pharmacist G. Cuzent who wrote that "les rats et les souris dévorent de grandes quantités de fruits et empêchent ainsi les arbres de se propager de graines" ("rats and mice devoured large quantities of fruits, thus preventing trees from propagating by seeds," Cuzent 1860) without naming the rat and plant species. Black rats are well known to attack coconut fruits (*Cocos nucifera*, Arecaceae) in the Pacific Islands (Storer 1962; Jackson 1967). Coconut trees in plantations in French Polynesia have slippery metal put around the trunks to prevent rats from climbing. The presence of these metal rings in remote islands (such as Niau in the Tuamotu, Maiao in the Society) is strong anecdotal evidence that black rats might be present. Rats of unknown species have been reported to damage nonnative fruiting trees, especially seeds of the candlenut tree (*Aleurites moluccana,* Euphorbiaceae) and the Tahitian chestnut *Inocarpus fagifer*, Leguminosae (Ridley 1930; Papy 1951–1954; McConkey et al. 2003, personal observation), recognized as ancient Polynesian introductions, as well as the probably introduced tropical almond *Terminalia catappa*, Combretaceae (Ridley 1930; McConkey et al. 2003, personal observation) and the native coastal tree *Barringtonia asiatica*, Lecythidaceae (personal observation). Common native plants such as the pandanus tree *Pandanus tectorius*, Pandanaceae (McConkey et al. 2003, personal observation) and the lianescent or climbing screwpine *Freycinetia impavida* have their fruits and leaves eaten by rats (personal observation). In Pohnpei, Pacific rats were observed in the rainforest damaging the endemic trees *Parinarium glaberrimum*, Rosaceae, *Elaeocarpus carolinensis*, Elaeocarpaceae, and *Campnosperma brevipetiolata*, Anacardiaceae (Storer 1962), the fruits of the last two species being "eaten extensively by rats" (p. 55). In Tonga, fruits of 15 trees and two vines, mainly the trees *Pleiogynium timoriense*, *Neisosperma oppositifolium*, *Apocynaceae*, *Pandanus tectorius*, and *Myristica hypagyraea*, *Myristicaceae*, were eaten by rats of unknown species (McConkey et al. 2003). In the Galápagos, black rats are seed predators of at least 39 species of native and alien plants (Clark 1981).

Seed predation on Polynesian sandalwood

The Polynesian sandalwood *Santalum insulare* (Santalaceae) consists of nine botanical varieties endemic to Southeastern Polynesia, including seven varieties in French Polynesia (in ten different islands of the Marquesas, the Society, and the Australs), one in the Cook Islands (var. *mitiaro* on the island of Mitiaro) and one in the Pitcairn Islands (var. *hendersonense* on the raised atoll of Henderson) (Fosberg and Sachet 1985). These taxa are shrubs or small trees found on coralline or volcanic soil, from sea level to 2,240 m elevation (Butaud 2004). Fruits are drupes with a fleshy pulp, measuring between 1.4 and 4.8 cm in length (depending on the variety). Sandalwoods were widely and heavily exploited for their fragrant heartwood during the 19th century, leading to small remnant populations in many islands, and perhaps to local extinction in the islands of Ua

Huka (Marquesas), Makatea (Tuamotu), and Tubuai (Australs) (Butaud, loc. cit.).

In order to evaluate pre- and post-control levels of fruit/seed predation, we conducted rat control experiments (by poisoning) in two remnant populations of *Santalum insulare* var. *insulare* located on the northwest (or leeward) coast of the island of Tahiti. The Pic Vert population, at ca. 1,200 m elevation, is the largest remaining population known in Tahiti, comprising 30 mature (i.e., reproductive) trees. The Tiapa population, discovered in 2006, is composed of 15 mature trees located at ca. 500 m elevation.

Sandalwood phenology (flowering and fruiting seasons) was monitored for 3 years (July 2001–June 2004) in the Pic Vert population and for 4 months in the Tiapa population (November 2004–April 2005). Control using rodenticide (bromadiolone as anticoagulant) was implemented every 2 weeks with at least one bait under each tree. The numbers of ripe and green fruits per tree were counted during each visit in the two study sites.

Results

Threatened plants impacted by rats in French Polynesia

The impacts of rats on endemic plants were poorly known in French Polynesia until we started to report signs of rat attacks during the last 10–15 years of field surveys, especially by monitoring endangered endemic plants. Fruits/seeds of at least 12 indigenous and endemic species, considered to be threatened or previously thought to be extinct in French Polynesia, are damaged by rat predation (Table 3). They belong to six vascular plant families, including Santalaceae, with seven endemic varieties of *Santalum insulare*, Apocynaceae with four species within four different genera (*Lepinia*, *Neisosperma*, *Ochrosia* and *Rauvolfia*) and Sapotaceae with two species within two different genera (*Nesoluma* and *Planchonella*, syn. *Pouteria*). All these taxa are woody species, ranging in size from shrubs to large trees up to 20 m in height. Most of them (10 of the 12 taxa) bear drupes, i.e., fleshy fruits, containing a relatively large seed (>1 cm in length). Three of them (*Santalum insulare*, *Ochrosia tahitensis*, and *Nesoluma nadeaudii*) are severely depredated by rats and suffer from recruitment depression, characterized by the almost complete absence of seedlings despite green fruit production on trees (Table 2).

Six woody endemic taxa, including the Polynesian sandalwood, have their bark, stems or leaves attacked by rats (Table 3). It is noteworthy that most of these species are restricted to high-elevation montane rainforests (or cloud forests). The stems of the subshrubs or small shrubs *Apetahia* spp. (Campanulaceae), and the shrubs or small trees *Psychotria speciosa* (Rubiaceae) and *Meryta lanceolata* (Araliaceae) can be completely girdled, which eventually may kill the plants. We noticed that rats consume the bark of sandalwood and other small trees such as *Meryta* during seasonal drought. Rats are also reported to have a significant impact on the vegetation of small islands or atolls such as Aldabra during dry seasons (Underwood 2006).

Seed predation of Polynesian sandalwood in French Polynesia

The 3-year phenological study conducted at the Pic Vert population shows that a major fruiting peak occurs each year between April and September, just after the rainy season that occurs between November and March in Tahiti. There is a minor or secondary fruiting peak between October and January, at the onset of the rainy season. At the beginning of our experiment, before rat poisoning, 33 green fruits were counted in the Pic Vert population and 199 in the Tiapa population. Only one ripe fruit was found on the 45 monitored mature trees in the two populations, i.e., less than 1% of the total. The remains of huge numbers of rat-depredated seeds were also seen on the ground. In the Pic Vert population, the first ripe fruits were found on the trees 3 months after the beginning of the rat control (Fig. 1). Ripe fruits were available on trees except during the low fruiting seasons and when rat control was suspended for 5 weeks during July and August 2003. Approximately 2 years after the first treatment, the absence of bait consumption and the presence of newly depredated fruits/seeds suggested that bait shyness or poison aversion had occurred. The subsequent change of the bait composition once again reduced levels of seed predation and allowed for the production of ripening fruits. During this 3-year monitoring period, a total of 500 ripe fruits was harvested from the 30

Table 2 Threatened and endangered plant species damaged by rats in French Polynesia

Family	Scientific name	Habit (height in m)	Islands (archipelago)	Habitat (elevation range in m)	IUCN status (proposed current status)	Estimated number of mature individuals in the wild	Rat damage type
Apocynaceae	*Lepinia taitensis*	Shrub to small tree (2–10)	Tahiti, Moorea (Society)	Wet forest (100–600)	CR	<500	FS
	Ochrosia tahitensis	Small tree (5–10)	Tahiti (Society)	Mesic forest (200–800)	EX (CR)	<15	FS
	Neisosperma brownii	Small tree (8–10)	Nuku Hiva (Marquesas)	Mesic forest (700–800)	EX (CR)	1	FS
	Rauvolfia sachetiae	Shrub to small tree (2–10)	Nuku Hiva, Hiva Oa (Marquesas)	Dry-Mesic forests (200–600)	CR	<100	FS, BSL
Araliaceae	*Meryta* spp.	Subshrub to small (1–10)	Tahiti (Society)	Littoral-Mesic-Wet forests to Cloud forest (10–1,900)	LR, DD, VU and CR	<5,000	FS, BSL
Arecaceae (Palmae)	*Pelagodoxa henryana*	Palm tree (3–10)	Nuku Hiva (Marquesas)	Wet valley forest (50–100)	CR	11	FS
	Pritchardia pericularum	Palm (3–15)	Niau (Tuamotu)	Littoral-Mesic forests (0–10)	VU	<1,000	FS
Campanulaceae	*Apetahia longistigmata*	Subshrub to shrub (0.5–2)	Hiva Oa, Nuku Hiva, Tahuata, Ua Pou (Marquesas)	Cloud forest, summit ridges (700–1,100)	(EN)[b]	<1,000	BSL
	Apetahia raiateensis	Subshrub to shrub (0.5–2)	Raiatea (Society)	Cloud forest, shrubland communities (600–800)	CR[a]	<500	BSL
Elaeocarpaceae	*Elaeocarpus floridanus*	Tree (10–15)	Tubuai, Raivavae, Rurutu (Australs)	Mesic forest (10–400)	VU	<5,000	FS
Fabaceae (Leguminosae)	*Serianthes rurutensis*	Tree (10–15)	Tubuai, Rurutu (Australs)	Mesic forest (50–300)	CR	<100	FS
Rubiaceae	*Psychotria speciosa*	Shrub (2–5)	Tahiti (Society)	Cloud forest 7,600–1,100)	CR	<500	BSL
Santalaceae	*Santalum insulare* (7 varieties)	Subshrub to small tree (1–10)	(Australs, Marquesas, Society)	Littoral-Dry-Mesic forests to cloud forests and summit ridges (0–2,200)	LR[a], VU[a], and CR[a]	<5,000	FS, BSL

Table 2 continued

Family	Scientific name	Habit (height in m)	Islands (archipelago)	Habitat (elevation range in m)	IUCN status (proposed current status)	Estimated number of mature individuals in the wild	Rat damage type
Sapotaceae	*Nesoluma nadeaudii*	Tree (5–15)	Tahiti, Moorea (Society)	Mesic forest (400–800)	DD (CR)	<20	FS
	Planchonella tahitensis (syn. *Pouteria grayana* var. *florencei*)	Tree (10–20)	Tahiti, Moorea, Raiatea (Society)	Mesic-Wet forests (300–800)	(EN)[b]	<100	FS

FS fruit or seed predation

BSL bark, stem or leaf damages

Habit and habitat according to the Nadeaud database of the flora of French Polynesia (www.herbier-tahiti.pf) and personal observations

IUCN Status according to the IUCN (2007) and [a] Walter and Gillett (1998)

[b] No conservation status (doubtful taxa and/or native species)

(CR) proposed current status according to recent personal field observations

mature trees, and the seeds were used to set up an ex situ sandalwood population. In the Tiapa population, rat control allowed the production and harvesting of more than 100 ripe fruits.

Comparison with plants damaged by rats in other Indo-Pacific tropical islands

We listed a total of 38 taxa within 23 botanical families which are documented to have their fruits or seeds depredated by rats in several tropical islands of the Pacific Ocean (Hawai'i, Tonga, Pohnpei, Wallis) and the Indian Ocean (La Réunion, Mauritius, Seychelles). As observed for French Polynesia, all of them are woody species (subshrubs to large trees), and a great majority produce drupes with large seeds (Table 4). The taxonomic similarity between the plant foods eaten in French Polynesia and those consumed in other islands is striking. Several species belonging to the same genera are documented to be severely damaged by rats (e.g., *Pritchardia* in the Arecaceae, *Neisosperma* in the Apocynaceae, *Santalum* in the Santalaceae, *Nesoluma* and *Pouteria* in the Sapotaceae). Other rat-sensitive taxa include *Pittosporum* spp. (Pittosporaceae), also known to be heavily attacked in New Zealand (Campbell and Atkinson 1999), species in the Rubiaceae, the Elaeocarpaceae, and the Oleaceae families (e.g., *Nestegis* in Hawai'i, also reported to be damaged by rats in New Zealand).

Soft-barked shrubs and small trees belonging to the Araliaceae (*Gastonia* spp. in La Réunion and Seychelles, *Meryta* spp. in Tahiti, French Polynesia, *Pseudopanax* in New Zealand), Malvaceae (*Hibiscadelphus* sp. in Hawai'i and in *Hibiscus* in La Réunion), and Euphorbiaceae (*Acalypha* spp. in Aldabra and La Réunion, *Codiaeum* in the Galápagos, H. Jäger, personal communication, 2007) are very sensitive to damages on their vegetative parts (Table 4).

Two island taxa that are subjected to severe levels of both reproductive and vegetative rat damage are the sandalwoods and the palms. In the Hawaiian Islands, three of the four described endemic sandalwood species (*Santalum* spp., Wagner et al. 1990), have their seeds heavily depredated by rats. The few fruits of *Santalum haleakalae* that reach maturity in the island of Maui (Hawai'i) are subject to rodent predation, primarily by *Rattus rattus* (Loope and Medeiros 1990). Palms of the genus *Pritchardia* have their seeds severely affected in the Hawaiian Islands

Table 3 Fruit/seed characteristics of threatened endemic plant species and rat predation intensity

Family	Scientific name	Fruit type (size in cm)	Seed size (cm)	Predation intensity
Apocynaceae	*Lepinia taitensis*	Dry indehiscent fruit (3.2–4.8 long, 1.1–1.4 diam.)	Nearly as long as the fruit	Minor
	Ochrosia tahitensis	Drupe (2–3 × 1–1.5)	1.5–2.5 × 1–1.5	Major
	Neisosperma brownii	Drupe (4–6 × 3)	2.5 × 2	Minor
	Rauvolfia sachetiae	Drupe (1.5 diam.)	1 × 0.5 × 0.3	Medium
Araliaceae Arecaceae (Palmae)	*Meryta* spp.	Syncarp (0.7–2)		Medium
	Pelagodoxa henryana	Drupe (10–15 diam.)	8 diam.	Minor
	Pritchardia pericularum	Drupe (0.5–0.7 diam.)	0.4–0.6 diam.	Minor
Elaeocarpaceae	*Elaeocarpus floridanus*	Drupe (1.1–1.4 × 0.8–1.2)	0.7 × 0.4	Minor
Fabaceae (Leguminosae)	*Serianthes rurutensis*	Pod	1–1.6 × 0.4–0.6	Minor
Santalaceae	*Santalum insulare* (7 varieties)	Drupe (1.4–4.8 × 0.8–4.3)	0.7–3.4–0.5–3.1	Major
Sapotaceae	*Nesoluma nadeaudii*	Drupe (2.5–3 × 1.5–2)	1.5–2 × 1–1.5	Major
	Planchonella tahitensis	Drupe (2.5–4 × 1.5–3)	2.5–3.5 × 1–1.5	Minor

Fruit and seed size according to the Nadeaud database of the flora of French Polynesia (www.herbier-tahiti.pf) and personal observations

Predation intensity: minor = numerous ripe fruits on the tree and seedlings on the ground; medium = few ripe fruits and few seedlings; major = no ripe fruit and no or a few seedlings

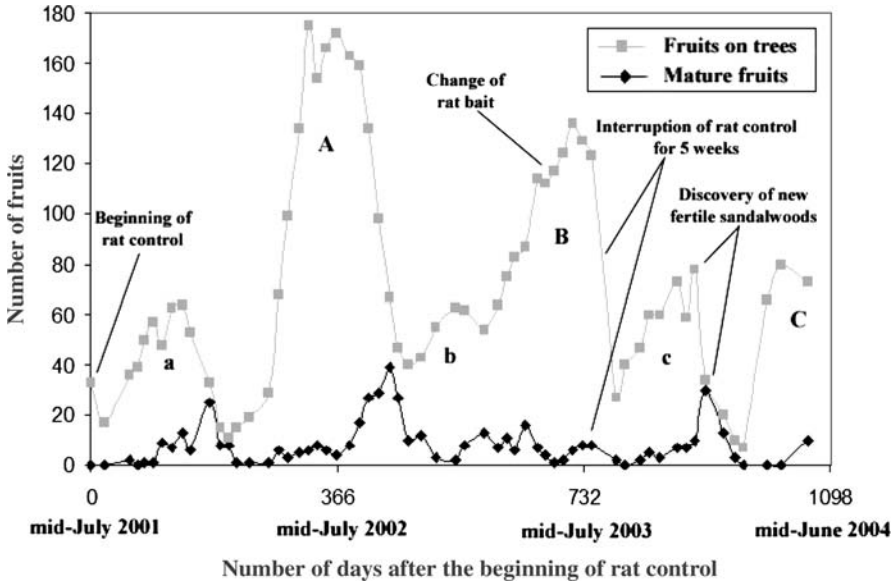

Fig. 1 Evolution of sandalwood fruit production during a 3-year rodent control experiment conducted in Tahiti (Pic Vert population, $N = 30$ mature trees). A, B, C = major fruiting peaks; a, b, c = secondary/minor fruiting peaks

(Beccari and Rock 1921–1923). Rats feed on their seedlings and damage their palm hearts (Chapin et al. 2004). The reduction or even absence of regeneration under the Fiji fan palm *Pritchardia pacifica* is also attributed to rat predation (Watling and Bennett 2005). In the Seychelles, rats damage palms of the endemic genera *Roscheria* and *Deckenia* by eating the growing tips or by chewing the base of leaves to get sap and often kill trees by gnawing through the growing heart (Anonymous 2006). In New Zealand, rats eat the leaves of young seedlings of the Nikau palm *Rhopalostylis sapida* and dig them up to eat the bulbous root base (Campbell 1978 in Campbell and Atkinson 1999). Exclosures have demonstrated that

Table 4 Rats damages on native and endemic plant species in other Indo-Pacific tropical islands (excluding New Zealand) according to published literature and personal observations

Family	Scientific name	Habit (height in m)	Fruit type (size in cm)	Island	Rat damage type	Source
Agavaceae	*Pleomele auwahiensis*	Small tree (1.5–10)	Berry (1.1–1.4 long)	Hawai'i	FS	Medeiros et al. (1986), Loope and Medeiros (1990)
Araliaceae	*Gastonia cutispongia*	Small tree (5–6)	Berry	La Réunion	BSL	Grondin and Lavergne (2006)
	Gastonia crassa	Shrub to small tree (up to 10)	Berry	Seychelles	BSL	Anonymous (2006), C. Kueffer personal communication (2007)
Arecaceae (Palmae)	*Deckenia nobilis*	Palm	Drupe	Seychelles	BSL	Anonymous (2006), C. Kueffer personal communication (2007)
	Latania lontaroides	Palm (up to 12)	Drupe (4.5 diam.)	La Réunion	FS	Lavergne et al. (2004)
	Pritchardia spp.	Palm (2–30)	Drupe (1.5–4.5 diam.)	Hawai'i	FS	Beccari and Rock (1921–1923)
	Roscheria melanochaetes	Palm	Drupe	Seychelles	BSL	Anonymous (2006), C. Kueffer personal communication (2007)
Anacardiaceae	*Campnosperma brevipetiolata*	Tree	Drupe	Pohnpei	FS	Storer (1962)
	Pleiogynium timoriense (syn. *P. solanderi*)	Tree (10)	Drupe (1.2 × 1.4)	Tonga	FS	McConkey et al. (2003)
Apocynaceae	*Neisosperma oppositifolium* (syn. *Ochrosia oppositifolia*)	Tree (9–10)	Drupe (5.7 × 7.3)	Tonga	FS	McConkey et al. (2003)
Burseraceae	*Canarium harveyi*	Tree (12)	Drupe (1.9 × 3.3)	Tonga	FS	McConkey et al. (2003)
	Protium obtusifolium	Tree (up to 20)	Drupaceous capsule (1.5–2 long)	Mauritius	FS	Strahm (1988)
Celastraceae	*Cassine orientale* (syn. *Elaeodendron orientale*)	Tree (up to 15)	Drupe	Mauritius	FS	Strahm (1988)
Chrysobalanaceae	*Parinari insularum*	Tree (5–20)	Drupe (3–6 long)	Wallis	FS	J-Y Meyer personal observation (2007)
Combretaceae	*Terminalia catappa*	Large tree	Drupe (1–7 long)	Tonga	FS	McConkey et al. (2003)
Ebenaceae	*Diospyros sandwicensis*	Small tree (2–15)	Drupe (1.2–2.6 long)	Hawai'i	FS	Medeiros et al. (1986), Cabin et al. (2000), Chimera (2004)

Table 4 continued

Family	Scientific name	Habit (height in m)	Fruit type (size in cm)	Island	Rat damage type	Source
Elaeocarpaceae	*Elaeocarpus carolinensis*	Tree	Drupe	Pohnpei	FS	Storer (1962)
	Elaeocarpus angustifolius	Tree (5–15)	Drupe (1–1.5 diam.)	Wallis	FS	J-Y Meyer personal observation (2007)
	Elaeocarpus tonganus	Tree (10)	Drupe (0.7 × 1.5)	Tonga	FS	McConkey et al. (2003)
Euphorbiaceae	*Acalypha claoxyloides*	Shrub (1–2)		Aldabra	BSL	Underwood (2006)
	Acalypha integrifolia	Subshrub		La Réunion	BSL	Ghestemme (2005)
	Croton scouleri	Shrub to small tree		Galápagos	BSL	H. Jäger personal communication (2007)
Flacourtiaceae	*Erythrospermum monticolum*	Subshrub to small tree (4–8)	Capsule (1–2 diam.)	Mauritius	FS	Strahm (1988)
Lauraceae	*Cryptocarya turbinata* (syn. *C. glaucescens*)	Small tree	Drupe (1–1.3 diam.)	Tonga	FS	McConkey et al. (2003)
Leguminosae	*Acacia koa*	Large tree (up to 35)	Pod (0.8–2.5 × 8–30)	Hawai'i	BSL	Scowcroft and Sakai (1984) in Stone (1985)
	Maniltoa grandiflora	Tree (12–18)	Pod (3.5 × 6)	Tonga	FS	McConkey et al. (2003)
	Vicia menziesii	Climbing herb (up to 2 long)	Pod (1.5–2 × 9–10)	Hawai'i	BSL	Clarke et al. in Cuddihy and Stone (1990)
Malvaceae	*Hibiscadelphus sp.*	Small tree (5–7)	Woody capsule (2–5 long)	Hawai'i	FS, BSL	Baker (1979) in Cuddihy and Stone (1990)
	Hibiscus boryanus	Shrub to small tree (up to 8)	Woody capsule	La Réunion	BSL	Ghestemme (2005)
Myristicaceae	*Myristica hypagyraea*	Small tree (up to 10)	(4–5 long)	Tonga	FS	McConkey et al. (2003)
Myrsinaceae	*Myrsine* spp.	Shrubs to small trees (0.5–8)	Drupe (0.5–1 diam.)	Hawai'i	FS	Drake (1993) in Hunt (2007)
Myrtaceae	*Syzygium clusiifolium*	Tree (5–20)	Drupe (1.5–3 diam.)	Wallis	FS	J-Y Meyer personal observation (2007)
	Syzygium glomeratum	Tree (10)	Drupe	Mauritius	FS	Strahm (1988)
Oleaceae	*Chionanthus vitiensis*	Tree	(1.7 × 4.9)	Tonga	FS	McConkey et al. (2003)
	Nestegis sandwicensis	Tree (8–25)	Drupe (1.6–2.2 long)	Hawai'i	FS, BSL	Stone (1985), Cuddihy and Stone (1990), Chimera (2004)
Pittosporaceae	*Pittosporum hosmeri*	Small tree (3–8)	Capsule (2.8–8 long)	Hawai'i	FS	Stone (1985), Cuddihy and Stone (1990)
	Pittosporum senacia	Shrub to small tree	Capsule	La Réunion	BSL	Ghestemme (2005)
	Pittosporum spp.	Shrub to small trees (2–14)	Capsule (0.9–4 long)	Hawai'i	BSL	Stone (1985)

Table 4 continued

Family	Scientific name	Habit (height in m)	Fruit type (size in cm)	Island	Rat damage type	Source
Rubiaceae	*Coprosma rhyncocarpa*	Small tree (3–15)	Drupe (0.7–1.3)	Hawai'i	BSL	Stone (1985), Cuddihy and Stone (1990)
	Psydrax odorata (syn. *Canthium odoratum*)	Shrub to, small tree (3–15)	Drupe (0.8–1 long)	Hawai'i	FS	Medeiros et al. (1986)
	Fernelia buxifolia	Subshrub to small tree (1–10)	Drupe (0.4–0.7 diam.)	Mauritius	FS	Strahm (1988)
	Myonima obovata	Subshrub to small tree (1–10)	Drupe (1.3–2 diam.)	Mauritius	FS	Strahm (1988)
	Psychotria rufipes	Shrub (1–3)	Drupe (0.7–0.9)	Galápagos	FS	Clark (1981)
Rutaceae	*Euodia obtusifolia*, *E. borbonica*	Subshrub to small tree (2–10)		La Réunion	BSL	Ghestemme (2005)
	Zanthoxylum dipetalum	Small tree (4–15)	Follicle (1–2.6 long)	Hawai'i	BSL	Cuddihy and Stone (1990)
Santalaceae	*Santalum ellipticum*	Shrub to small tree (1–5)	Drupe (0.9–1.2 long)	Hawai'i	FS	Chimera (2004)
	Santalum haleakalae	Shrub to small tree (2–4)	Drupe (1–1.5 long)	Hawai'i	FS	Loope and Medeiros (1990)
	Santalum paniculatum	Shrub to tree (3–20)	Drupe (1–1.2 long)	Hawai'i	FS	Stone (1985), Cuddihy and Stone (1990)
Sapindaceae	*Alectryon macrococcus*	Small tree (3–11)	Dry fruit (2.5–7 diam.)	Hawai'i	FS	Medeiros et al. (1986), Chimera (2004)
	Allophyllus borbonicus	Small tree (8–10)		La Réunion	BSL	Ghestemme (2005)
	Elattostachys falcata	Large tree	(0.4 × 0.6)	Tonga	FS	McConkey et al. (2003)
Sapotaceae	*Nesoluma polynesicum*	Shrub to small tree (10)	Drupe (1–2 long)	Hawai'i	FS	Chimera (2004)
	Pouteria sandwicensis	Tree (12–20)	Drupe (1.5–5 long)	Hawai'i	FS	Medeiros et al. (1986), Chimera (2004)
	Pouteria grayana (syn. *Planchonella costata* var. *vitiensis*)	Tree (up to 8)	Drupe (2–3 diam.)	Tonga	FS	McConkey et al. (2003)
Sterculiaceae	*Dombeya punctata*	Small tree		La Réunion	BSL	Ghestemme (2005)
Thymeleaceae	*Wikstroemia* sp.	Shrub to small tree (1–6)	Drupe (0.6–1.8 long)	Hawai'i	FS	Medeiros et al. (1986)

FS fruit or seed predation

BSL bark, stem or leaf damage*s*

Habit and fruit type and size according to literature (Wagner et al. 1990 for Hawai'i, Bosser et al. 1976 for Mauritius and La Réunion, Friedman 1994 for Seychelles)

Indian Ocean island Aldabra, La Réunion, Mauritius, Seychelles

Pacific Ocean islands Hawai'i, Pohnpei (Ponape), Tonga, Wallis (Uvea)

Rattus exulans strongly depress the survival of the palm seedlings.

Discussion

A relatively small number of endangered plants (14 taxa) is directly impacted by rat species in French Polynesia. Rats represent only 5% of the main threats documented on the 167 threatened and protected plant species (Fig. 2). However, two of them, strictly endemic to the island of Tahiti (*Ochrosia tahitensis* and *Nesoluma nadeaudii*), have very small remaining populations (<15–20 mature plants known in the wild) and exhibit almost complete recruitment depression in the field, and thus could be on the verge of extinction. In the ten islands of French Polynesia where Polynesian sandalwood *Santalum insulare* still occurs, we found no seedlings, only small numbers of ripe fruits on trees, and large amounts of rat-eaten seeds on the ground in most populations. The 3-year monitoring of the largest remaining *Santalum insulare* population in Tahiti indicated that, prior to rodent control, more than 99% of the fruits on trees were eaten by rats before maturation and that poisoning was very effective in protecting and obtaining viable seeds. Moreover, predation of sandalwood seeds by rats appeared to be lower on islands where black rats are absent (Table 5). The smallest sandalwood population is currently found in the island of Rapa (Australs) with only 14 individuals left in the wild. Other populations, observed by local inhabitants in the past, may have recently gone extinct on the islands of Ua Huka (Marquesas), Makatea (Tuamotu), and Tubuai (Australs). However, it is difficult to conclude whether rats are the major contributor of the decline and extirpations (i.e., local extinctions) of these species, as habitat destruction and sandalwood over-exploitation were also extensive in these three islands.

The environmental variables are too numerous to assign definitive cause and effects statements about the vegetation status entirely to rodent predation. In Hawai'i, for instance, the crucial role that rats plays in the survival or decline of a particular species has been emphasized, as dense *Pritchardia hillebrandii* populations are found on the rat-free islet of Huelo near Molokai, whereas only a single mature palm survives on the nearby Mokapu island in the presence of rats (Athens et al. 2002). However, a recent study on the conservation status of *Pritchardia* species in Hawai'i (Chapin et al. 2004) reveals that at least 12 individuals of palms were counted on Mokapu, and that the Huelo rock is not only free of rats but also from goats. According to these authors, the major contemporary threats to *Pritchardia* palms include introduced goats *Capra hircus* and deer *Axix axis* as well as pigs *Sus scrofa* that eat seedlings and destroy the habitat, and invasive plants which compete with both established trees and seedlings (Chapin et al. 2004) In the same way, despite the presence of kiore *Rattus exulans* which are depressing seedling recruitment and survival of the Nikau palm in Little Barrier Island in New Zealand, the species is still locally common, and there is "spectacular Nikau regeneration on Cuvier Island after goats were removed and while kiore remained" (Campbell and Atkinson 1999, p 283).

The two endemic *Pritchardia* palms in French Polynesia, *P. vuylstekeana* on the raised atoll of Makatea and *P. pericularum* on Niau in the Tuamotu archipelago, still have viable populations with seedling recruitment (personal observation) and thus seem to coexist with rats. The fact that their fruits and seeds have a smaller size (between 0.5 and 1 cm in diam., Meyer unpublished data) compared with their Hawaiian relatives (1.5–4.5 cm in diam., Wagner et al. 1990) might have an influence on seed predation by rats. Large seeds generally contain more energy than small ones and most rodents prefer large over small seeds (Price and Jenkins 1986). Black rats, for instance, fed on an extremely broad range of plant foods in the Galápagos islands, but they are very selective feeders and are able to discriminate among plant species and among parts of plants, such as seeds high in fats and protein (Clark 1981).

The three most endangered plant species attacked by rats in French Polynesia (*Ochrosia tahitensis*, *Santalum insulare*, and *Nesoluma nadeaudii*) are indeed trees with relatively large fleshy fruits (>1 cm in diam). Potential dispersal agents such as large frugivorous birds (e.g., *Ducula*) are now extinct in the large majority of the islands of French Polynesia (McConkey and Drake 2002; Meehan et al. 2002; Steadman 2006). The only two islands with surviving *Ducula* species are the raised atoll of Makatea (the Polynesian imperial pigeon *Ducula aurorae*) and Nuku Hiva (the Nuku Hiva imperial pigeon *Ducula galeata*).

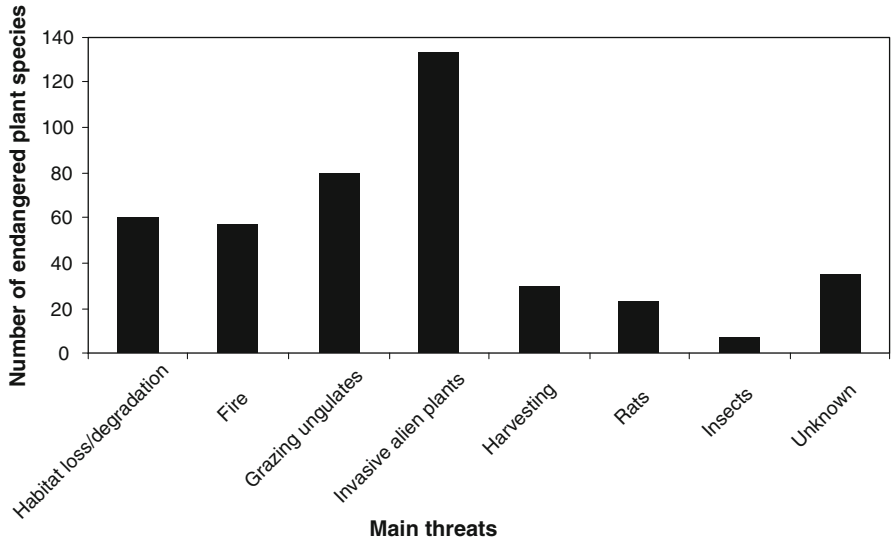

Fig. 2 The main threats to the 167 endangered and legally protected plant species in French Polynesia. For a given species, each threat may count more than once

Table 5 Abundance of sandalwood populations related to rat presence in French Polynesia according to personal field observations

Archipelago	Island	Abundance (estimated number of individuals)	*Rattus exulans*	*Rattus rattus*	Seed predation
Society	Tahiti	300–400	X	X	Complete
	Moorea	50–100	X	X	Complete
	Raiatea	200–300	X	X	Complete
Marquesas	Nuku Hiva	1,200–1,400	X	X	Complete
	Ua Pou	70–100	X	X	Complete
	Hiva Oa	150–200	X	X	Complete
	Tahuata	240–300	X	0	Partial
	Fatu Hiva	50–100	X	X	Complete
Australs	Rapa	14	X	?	Complete
	Raivavae	2,000–2,500	X	0	Partial

X = rat presence; 0 = absence of rat

Complete seed predation = no ripe fruit on the tree and no seedling on the ground

Partial seed predation = few ripe fruits and seedlings

? = unknown

Ducula aurorae was last seen in the 1970s or 1980s in the interior of the island (Holyoak and Thibault 1984; J.-C. Thibault, personal communication, 2007). Black rats, as well-known bird predators, might have been involved in the decline of these frugivorous birds in Tahiti, thus contributing indirectly to the low recruitment of these large-seeded endemic trees.

Finally, most of the endangered trees damaged by rats in French Polynesia are growing at low elevations (0–800 m elevation) in para-littoral, or dry to mesic forests, habitats with a long history of anthropogenic impacts (i.e., deforestation and land development, fire, introduction and subsequent grazing by feral ungulates such as goats, cattle, pigs, invasion by alien weeds). The importance of rats predation compared with these other environmental factors is not clear.

Conclusion

Rats as drivers of plant extinction or *coup de grâce* species?

Despite the fact that rats (mainly *Rattus exulans* and *R. rattus*) can severely depress seedling recruitment and thus alter vegetation composition, structure, and dynamics (Allen et al. 1994; Campbell and Atkinson 1999; Towns et al. 2006), we did not find any evidence in the field in French Polynesia or in the literature in other Indo-Pacific islands that rats are solely responsible for current plant extirpations or extinctions. Rats might rather be considered as the *coup de grâce* (literally that which gives the last stroke of death in French) for some plant taxa, such as sandalwoods (e.g., *Santalum insulare* in Eastern Polynesia) or large-seeded trees (e.g., as *Ochrosia tahitensis* and *Nesoluma nadeaudii* in Tahiti) that are in need of urgent conservation measures. The historical extinction of the two endemic *Ochrosia* tree species in the Marquesas (*O. nukuhivensis* and *O. fatuhivensis*), only known by the type-specimen collected in the 1920s (Brown 1935; Sachet 1975) might be attributed to the *coup de grâce* of rats.

Based on comparisons with vulnerable taxa in other tropical Indo-Pacific islands and in New Zealand, seed predation by rats on critically endangered trees in French Polynesia such as the very rare *Pittosporum raivaveense* (CR according to IUCN 2007) in the island of Raivavae, *Pisonia amplifolia* (CR according to Florence 2004) in Tubuai, *Streblus pendulinus* (EN according to Florence 1997) in Rapa, and the native tree *Nesoluma polynesicum* in the Australs (personal observation) should be more carefully considered.

The only case of a modern plant extinction caused by rats is the death of the last individual of the small endemic shrub *Robinsonia beteroi* (Asteraceae) in the Robinson Crusoe Island of the Juan Fernández archipelago; in this instance the bark at the base of the trunk was found to be seriously damaged by rats (Danton and Perrier 2005). Even so, the sole wild individual of this dioecious species was male, the last female plant having been noted as long ago as 1917.

More paleoenvironmental and "modern" ecological research studies need to be conducted to clarify the role of each rat species and their relative importance in the decline and demise of plant populations. Nonetheless, rat damage to native and endemic plant species should be taken into account or recognized in further conservation planning and actions in island ecosystems, particularly for the small tropical Indo-Pacific islands.

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