Threat of Invasive Alien Plants to Native Flora and Forest Vegetation of Eastern Polynesia¹

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Abstract: Eastern Polynesia, a phytogeographical subregion of Polynesia in the Pacific Ocean, comprises the archipelagoes of the Cook Islands, the Austral Islands, the Society Islands, the Tuamotu Islands, the Marquesas Islands, the Gambier Islands, the Pitcairn Islands, and Rapa Nui, which is the easternmost inhabited island of Polynesia. It consists of a total of about 140 tropical to subtropical oceanic islands that are among the most remote in the world, being over 3,000 km distant from the nearest continents. Because of this strong geographic isolation, the relatively young geological age, and small terrestrial surface (less than 4,000 km²) of these islands, the native flora of eastern Polynesia is impoverished, disharmonic, and with a relative low number of endemic genera (12). However, some high volcanic islands within these archipelagoes display a great diversity of habitats and a highly endemic flora (e.g., 50% for the vascular plants in Nuku Hiva, 45% in Tahiti) with striking cases of adaptative radiation (e.g., in the genera Bidens, Cyrtandra, Glochidion, Myrsine, and Psychotria). Most of these endemic taxa are restricted to montane rain forests and cloud forests. These upland wet forests are not directly threatened by habitat destruction by humans or disturbance by large mammals but rather by invasive alien plants. Native forests of eastern Polynesian islands are invaded by aggressive introduced species (e.g., Lantana camara and Psidium cattleianum in most island groups; Syzygium jambos in Pitcairn, Tahiti, and Nuku Hiva; Ardisia elliptica, Cestrum nocturnum, Spathodea campanulata in Tahiti and Rarotonga; Rubus rosifolius in the Society Islands, Hiva Oa, and Rapa Iti). Therefore, one of the highest priorities for the long-term conservation of the original native flora and forest vegetation of eastern Polynesia should be given to the study (invasion dynamics and ecological impacts) and control (strategy and methods) of the current invasive alien plants and to the early detection and eradication of potential plant invaders. Eastern Polynesia, with its small, diverse, and isolated oceanic islands, also offers opportunities to test hypotheses on the vulnerability of islands to invasion by alien species, with or without disturbance.

IN THIS PAPER I review the physical and vegetation characteristics of the islands of eastern Polynesia, with an emphasis on their unique flora and the importance of montane

rain forests as critical habitats. The growing threat of invasion by introduced (alien) plant species to the still relatively undisturbed native vegetation is documented, and the most important plant invaders are described. Hypotheses on the invasibility of island biotas are discussed in light of data and field observations collected in eastern Polynesia. Attention is drawn to the need to conduct more research (e.g., through the Pacific-Asia Biodiversity Transect [PABITRA] network project) and management efforts to control current and potential alien invasive plant species in the islands of eastern Polynesia.

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A Galaxy of Small, Diverse, and Remote Oceanic Islands

Polynesia is one of the largest floristic regions in the Pacific Ocean, along with Micronesia. Both areas have been included by some authors in the same "Polynesian floristic region" (Takhtajan 1986) or "Polynesian biogeographic province" (Thorne 1963) and were recently classified as one of the 25 "biodiversity hotspots" worldwide (Myers et al. 2000). Eastern Polynesia, also called South-Eastern Polynesia (Balgooy 1971), is recognized as the largest phytogeographical subregion of Polynesia, which also comprises western Polynesia, central Polynesia, and Hawai'i (Mueller-Dombois and Fosberg 1998). It comprises, from west (165° W long.) to east (109° W long.), the archipelagoes of the Cook Islands, the Society Islands, the Austral Islands (including Rapa Iti), the Tuamotu Islands (including Makatea), the Gambier Islands (including Mangareva), the Marquesas Islands, the Pitcairn Islands, and Rapa Nui (also called Easter Island), which is the easternmost inhabited island of Polynesia (Figure 1). They represent a total number of 142 tropical and subtropical oceanic islands and islets lying between 7° and 27° South latitude (Table 1), with a mean annual temperature and rainfall at sea level ranging, respectively, between 18 and 28°C and 1,300 and 3,000 mm. The coldest island is the southernmost inhabited subtropical island of Rapa Iti (absolute minimum recorded at 8.5°C), and the driest is the subtropical island of Rapa Nui (1,325 mm annual precipitation). Eastern Polynesian islands are exposed to the dominant southeast trade winds and are out of the tropical cyclone zone; thus major cyclones are infrequent compared with western Polynesia and Melanesia.

The islands of eastern Polynesia show a large variety of physiographic types (Nunn 1994, 1999) from young high volcanic islands (e.g., Pitcairn, Tahiti, Rarotonga) and rocky islets (Marotiri), through barrier-reef old volcanic islands (e.g., Bora Bora, Aitutaki), to carbonate atolls (e.g., Oeno, Rangiroa, Palmerston), coral islets, *motu* and sand cays, elevated (or raised) coral limestone islands

(e.g., Henderson, Rimatara), and composite (volcanic and limestone) islands called makatea (e.g., Atiu, Mangaia, Rurutu). Several high volcanic islands are less than 3 million vr old. The youngest is Mehetia in the Society Islands at 0.2 million yr. The oldest are the low coral atolls of the northern Cook Islands at around 100 million yr (G. MacCormack, pers. comm.). Most island groups have a northwest-southeast orientation related to their formation as the Pacific Plate has moved in a northwestern direction over heating anomalies, including "hot spots." The islands are typically in water over 3,000 m deep and have never been connected to continental landmasses in the past.

The islands of eastern Polynesia represent a total land area of less than $4,000 \text{ km}^2$ scattered over nearly 8 million km² of ocean and are among the most remote in the world, the nearest continents being from 3,000 to 6,000 km distant (Figure 1). Eastern Polynesia can thus be viewed as a galaxy of small, diverse, and isolated islands stretched over a vast ocean.

An Impoverished and Disharmonic Flora, but with High Endemism and Peculiar Floristic Affinities

Because of this strong geographic isolation, the relatively young geological age of most of the islands, and their small size (which also implies the lack of topographic and habitat diversity on most of the islands), the native flora of eastern Polynesia is impoverished or "depauperate" in terms of the number of species. There are, for example, only 105 native vascular plant species in the Pitcairn Islands and only 30 species in the easternmost island of Rapa Nui. The Society Islands have the richest native flora of all the island groups, with 575 native vascular plant species, including 495 found on the high volcanic island of Tahiti (Table 2). The number of endemic genera (12, Table 3) in eastern Polynesia is low compared with the Hawaiian Islands (with 32 endemic genera) but nearly similar to that of the Fiji Islands or Juan Fernández Islands (with 12 endemic genera [Sohmer 1990]). The native flora of eastern

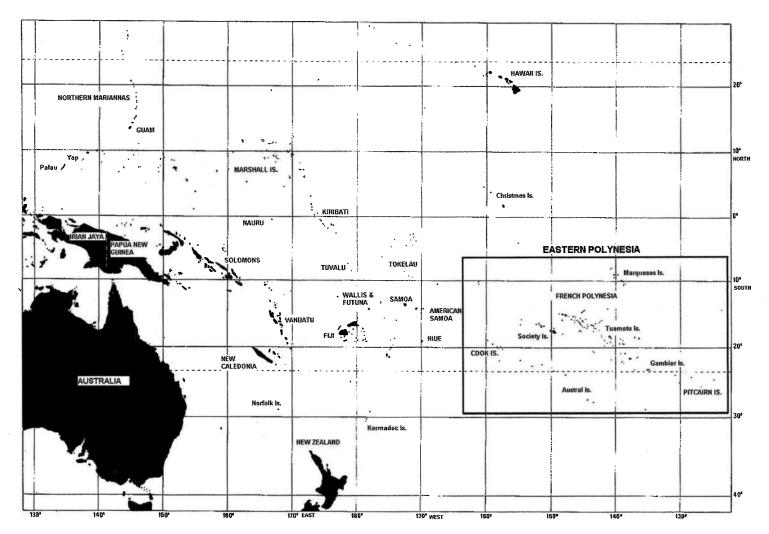


FIGURE 1. Map of the islands of eastern Polynesia in the Pacific Ocean. Distance from nearest continental landmass: Cook Islands, 3,000 km from New Zealand; Marquesas Islands, 4,850 km from Mexico; Pitcairn Islands, 4,500 km from South America; Rapa Nui, 3,750 km from Chile; Society Islands, 6,000 km from Australia.

Island Groups	Latitude/ Longitude	Surface Area (km²)	Maximum Elevation Highest Summit Name (Island Name)	Age (myr)	Atolls + Coral Islets	Raised Islands + Uplifted Atolls	High Volcanic Islands + Rock Islets	Total No. of Islands
Cook Is.	8–23° S/ 156–165° W	238	653 m Te Manga	0.7-100	10	4	1	15
Society Is.	15–18° S/ 148–154° W	1,597	(Rarotonga) 2,241 m Orohena (Tahiti)	0.2-4.5	5	0	9	14
Austral Is.	22–23° S/ 147–152° W	108	438 m Hiro (Raivavae)	4.8–28.6	2	1	3	6
Tuamotu Is. (+Makatea)	14–24° S/ 134–148° W	726	90 m Aetia (Makatea)	9.5–13.7	68	1	0	69
Gambier Is.	21–23° S/ 134–137° W	46	445 m Duff (Mangareva)	5.7-6.3	7	0	10	17
Marquesas Is.	7–10° S/ 138–140° W	1,050	1,276 m Temetiu (Hiva Oa)	1.3-5.6	1	0	11	12
Rapa Iti (+Marotiri)	27° 35′ S/ 144° W	40	650 m Perau (Rapa Iti)	3.5-5.5	0	0	4	4
Pitcairn Is.	23–24° S/ 125–130° W	45	347 m Palva (Pitcairn)	0.4–1	2	1	1	4
Rapa Nui (Easter Island)	27° S/109° W	166	511 m Terevaka	0.3-2.5	0	0	1	1
Eastern Polynesia	7–27° S/ 109–165° W	3,916	2,241 m Orohena (Tahiti)	0.2–100	96	7	38	142

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Physiographic Diversity of Eastern Polynesian Island Groups from West to East

Note: Data from various sources including Dupon (1993), Nunn (1994), Spencer (1995), and Munschy et al. (1998).

Polynesia is typically disharmonic, with an abundance of fern species and lacking some taxa such as gymnosperms, mangrove species, and plants with large seeds and limited dispersal capacities (e.g., Annonaceae, Dipterocarpaceae, Lauraceae, or Myristicaceae). However, this floristic disharmony "brings in return adaptative radiation, high local endemism, and other unusual features" (Mueller-Dombois and Fosberg 1998:387) of great phytogeographic interest.

The floristic richness of eastern Polynesia varies greatly with island types. The large dissected high volcanic islands display a greater diversity of habitats than raised limestone islands and coral atolls. Eastern Polynesia, according to Fosberg (1984:38), who studied Pacific Island floras for nearly half a century, contains "some of the most spectacular and beautiful islands, culminating in Tahiti, a magnificent, deeply dissected dead volcano 7300 feet high. Its upper slopes are clothed with montane rain forests and cloud forest of many species and a spectacular development of tree ferns." In contrast to the low-lying islands (there are no endemics on

Island Groups	Native Vascular	Endemic Vascular Plant	Native Flowering	Endemic Flowering Plant	Naturalized	
Main Island (land area)	Plant Species	Species (% Endemism)	Plant Species	Species (% Endemism)	Alien Plant Species (IS) ^a	References
Cook Is. Rarotonga (64 km²)	278 234	27 (10%) 22 (10%)	180 142	20 (11%) 16 (11%)	286 (0.97)	McCormack (1992), Royen and Davis (1995) McCormack and Künzle (1995); G. McCormack (pers. comm., 2000)
Society Is.	575	250 (43%)			420 (1.37)	Florence (1997)
Tahiti (1,045 km²)	495	224 (45%)	_		373 (1.33)	Florence (1993)
Austral Is.	185	28 (15%)	_		_	Florence (1997)
Rurutu (32 km²)	126	17 (13%)	—		157 (0.80)	Florence (1993)
Tuamotu Ís.	95	4 (4%)	80	4 (5%)	_	Florence et al. (1995)
Makatea (29 km²)	60	3 (5%)	—		102 (0.59)	Florence (1993)
Gambier Is.	80	8 (10%)	61	8 (13%)		Florence et al. (1995)
Mangareva (14 km²)	—	—			—	
Marquesas Is.	320	134 (42%)	212	117 (55%)	—	Florence and
Nuku Hiva (339 km²)	254	126 (50%)	—	—	215 (1.18)	Lorence (1997) Florence (1993)
Rapa Iti (38 km²)	189	67 (35%)	_	—		Florence (1997)
Pitcairn Is.	105	19 (18%)	80	17 (21%)	53 (1.98)	Florence et al. (1995)
Henderson (37 km ²)	63	9 (14%)	54	9 (17%)	17 (3.71)	Florence et al. (1995), Waldren et al. (1999)
Rapa Nui (166 km ²)	30	5 (17%)		—	67 (0.68)	Skottsberg (1920–1956), Zizka (1991)

TABLE 2

Floristic Diversity of Eastern Polynesian Island Groups

Note: ---, data not available.

" IS (index of secondarization) = no. of primary flora (native plant species)/no. of secondary flora (naturalized alien plant species).

the atolls of the northern Cook Islands and only a few endemic species on the Tuamotu atolls), the high islands of eastern Polynesia have a far richer flora with a relatively high degree of endemism (e.g., 45% for the native vascular plant species in the island of Tahiti [Society Islands] and up to 50% in Nuku Hiva [Marquesas Islands], Table 2). The endemism rate reaches 55% for the flowering plants of the Marquesas Islands (Florence and Lorence 1997). Mount Orohena (2241 m elevation) in Tahiti is the highest point in Polynesia outside the Hawaiian Islands and New Zealand. The rugged relief of many of the high volcanic islands, with their very steep slopes, deep valleys or gulches, narrow ridges, and spirelike peaks, sometimes associated with the difference between a wet windward side and a drier leeward side in the rain shadows, provides unique microclimates and marked isolation that may have facilitated evolutionary, and sometimes adaptative, radiation in the flora.

Striking cases of evolutionary (sometimes adaptative) species radiation are found in eastern Polynesia (e.g., *Bidens* [Asteraceae] with 19 endemic species, *Cyrtandra* [Gesneriaceae] with 27 species, *Glochidion* [Euphorbiaceae] with 22 species, *Myrsine* [Myrsinaceae] with 27 species, and *Psychotria* [Rubiaceae] with 24 described species [Table 4]). These species numbers are underesti-

Genus Name (Family)	Cook Is.	Society Is.	Austral Is.	Gambier Is.	Marquesas Is.	Rapa Iti	Pitcairn Is.	Rapa Nui	Eastern Polynesia
Apetahia (Campanulaceae)	0	1	0	0	2	1	0	0	4
Apostates (Compositae)	0	0	0	0	0	1	0	0	1
Fitchia (Compositae)	1	4	0	(1 extinct)	0	1	0	0	6 (+1 extinct)
Haroldiella (Urticaceae)	0	0	1	0	0	1	0	0	2
Lebronnecia (Malvaceae)	0	0	0	0	1	0	0	0	1
Metatrophis (Urticaceae)	0	0	0	0	0	1	0	0	1
Oparanthus (Compositae)	0	0	0	0	2	1	0	0	3
Pacifigeron (Compositae)	0	0	0	0	0	1	0	0	1
Pelagodoxa (Palmae)	0	0	0	0	1	0	0	0	1
Plakothira (Loasaceae)	0	0	0	0	3	0	0	0	3
Sclerotheca (Campanulaceae)	1	5	0	0	0	0	0	0	6
Tahitia (Tiliaceae)	0	1	0	0	0	0	0	0	1
No. of endemic genera/endemic species	2/12	4/12	1/12	(1/12)	5/12	7/12	0/12	0/12	

TABLE 3

Endemic Genera in Eastern Polynesia and the Number of Endemic Species per Island Group

mated because recent botanical explorations and field trips in the interior of the high islands of the Society and the Marquesas Islands have led to the discovery and descriptions of new *Bidens, Psychotria*, and *Melicope* species (D. Lorence, pers comm.; J. Florence, pers. comm.; unpubl. data).

Eastern Polynesia is characterized by an attenuated Indo-Malesian and Austro-Melanesian flora (Balgooy 1993), with very few New Zealand taxa (e.g., *Corokia* [Grossulariaceae] and *Hebe* [Scrophulariaceae] in Rapa Iti; *Myoporum* [Myoporaceae] in the Cook Islands and the Austral Islands), and a few American components (e.g., *Fuchsia* [Onagraceae] in Tahiti; *Plakothira* [Loasaceae] in the Marquesas Islands [Florence 1993]; *Gouania* [Rhamnaceae] in Mangareva [Fosberg 1984]; *Axonopus* [Graminae] and *Jubaea* [Palmae] in Rapa Nui [Dransfield et al.

1984, Zizka 1991]). The Marguesas Islands show some floristic affinities with Fiji as well (e.g., Trimenia [Trimeniaceae]) and the Hawaiian Islands (e.g., Cheirodendron [Araliaceae]). The southern Cook Islands and the Austral Islands also have taxa otherwise found only in the Hawaiian Islands (e.g., Charpentiera [Amaranthaceae], Ischaemum [Poaceae], and Nesoluma polynesicum [Sapotaceae] [Wagner et al. 1999]). Several indigenous species have very disjunct distribution, such as *Tetra*molopium sylvae (Asteraceae), found only on Mitiaro (Cook Islands), the Hawaiian Islands, and New Guinea (Wagner et al. 1999); Osteomeles anthyllidifolia (Rosaceae) found in the Cook Islands, Hawaiian Islands, Pitcairn Islands, and Rapa Iti (Steenis and Balgooy 1966); and Oreobolus furcatus (Cyperaceae), first described in the montane bogs of Hawai'i and more recently discovered on

TABLE 4

Most Speciose Genera of Endemic Flowering Plant Taxa in Eastern Polynesia (Rapa Nui excluded) and Comparison with Other Pacific Island Groups (Hawai'i and Fiji)

Genus Name (Family)	Cook Is."	Society Is. ^b	Austral Is.+ Rapa Iti ^b	Tuamotu + Gambier Is. ^b	Marquesas Is. ^{b,c}	Pitcairn Is. ^d	Eastern Polynesia	Hawai'i ^e	Fiji <i>f</i> ,g
Bidens (Compositae)	0	8	0	0	9	2	19	19	0
(Coprosma (Rubiaceae)	1	6	3	1	3	1	15	13	1
Cyrtandra (Gesneriaceae)	2	12	1	0	12	0	27	53	37
Glochidion (Euphorbiaceae)	1	14	3	0	3	1	22	0	18
Ixora (Rubiaceae)	1	7	3	0	3	1	15	0	0
Melicope (Rutaceae)	1	4	0	0	6	0	11	47	9
Meryta (Araliaceae)	1	6	1	0	1	1	10	0	1
Myrsine (Myrsinaceae)	1	13	3	2	6	2	27	20	3
Peperomia (Piperaceae)	3	4	2	0	4	2	15	25	23
Psychotria (Rubiaceae)	1	11	3	0	9	0	24	11	76

^a Cheeseman (1903), Wilder (1931), McCormack (1992).

^b Florence (1987, 1997).

^c Florence and Lorence (1997).

^d Florence et al. (1995).

^e Sohmer (1990), Wagner et al. (1999).

f Sohmer (1990).

g A. C. Smith (1985–1991).

the highest peak of Orohena in the island of Tahiti (Raynal 1976).

These archipelagoes also contain "Old Pacific elements" (Fosberg 1984) that have no obvious geographical connections (e.g., *Abutilon* and *Lebronnecia* [Malvaceae], *Lepinia* [Apocynaceae], *Meryta* [Araliaceae], the palms *Pritchardia* and *Pelagodoxa*, the arborescent Asteraceae *Fitchia* and *Oparanthus*, and the lobeliads *Apetahia* and *Sclerotheca* [Campanulaceae-Lobelioidae].

Finally, another principal interest of the eastern Polynesian flora is that it lies at the easternmost limit of the range of a very large number of genera in Malesia and Pacific Ocean islands, such as *Alyxia* (Apocynaceae), *Ascarina* (Chloranthaceae), *Cyrtandra* (Gesneriaceae), *Fagraea* and *Geniostoma* (Loganiaceae), *Meryta* (Araliaceae), *Metrosideros* (Myrtaceae), *Pittosporum* (Pittosporaceae), and *Pouteria* (Sapotaceae) (Steenis and Balgooy 1966, Grant et al. 1974, Balgooy 1993, Balgooy et al. 1996).

Montane Rain Forests: Small and Fragile Local Biodiversity Hot Spots

Most of the endemic taxa just cited are restricted to the native upper-elevation wet forests (montane rain forests), where the mean annual rainfall is 2,000–3,000 mm or more. Cloud forests, a subtype of montane rain forests characterized by high precipitation and a diurnal cloud cap, are generally found on the eastern Polynesian high volcanic islands above 400–500 m elevation, up to 1,200–1,800 m elevation. About 70% of the endemic plant species found on the island of Tahiti (Society Islands) are located in these montane rain forests, ca. 50% on Nuku Hiva (Marquesas Islands) (Meyer and Florence 1998), and ca. 30% on Rarotonga (Cook Islands) (data calculated after MacCormack and Künzle 1990).

The upland wet forests of eastern Polynesia are usually dominated by the native trees Weinmannia spp. (Cunoniaceae) and Metrosideros spp. (Myrtaceae), tree ferns Cyathea spp. (Cyatheaceae), and climbing lianas Freycinetia spp. (Pandanaceae), with an understory of large ferns (especially Marattiaceae such as Angiopteris spp. and Marattia spp., and Blechnaceae) and endemic shrubs or small trees such as Cyrtandra spp. (Gesneriaceae), Geniostoma spp. (Loganiaceae), Melicope spp. (Rutaceae), and Psychotria spp. (Rubiaceae). Cloud forests, also called mossy, dwarf, or elfin forests, are characterized by short, gnarled, or stunted trees covered with epiphytic ferns (especially Davalliaceae, Polypodiaceae, and Hymenophyllaceae), orchids, hepatics, and mosses that grow on their trunks and branches (Merlin and Juvik 1995, Manner et al. 1999). They contain particular floristic elements with north or south temperate biogeographic affinities, such as Astelia (Liliaceae) or Coprosma (Rubiaceae). The rare lobeliads *Sclerotheca* spp. are found almost exclusively in the wet upland (montane) rain forests of Rarotonga in the Cook Islands (S. viridiflora), of Moorea (S. forsteri) and Tahiti (S. arborea, S. jayorum, S. magdalenae Florence, and S. oreades) in the Society Islands, as well as Apetabia spp. in the high-elevation plateaus of Raiatea (A. raiateensis), and in the cloud forests of Hiva Oa and Nuku Hiva (A. longistigmata) and Fatu Hiva (A. seigelii) in the Marquesas. Eastern Polynesian montane rain forests can thus be viewed as local "biodiversity hot-spots and refugia for insular endemic species" (Merlin and Juvik 1995).

Montane rain forests have remained relatively undisturbed to date by anthropogenic impacts because of their isolated occurrence on inacessible mountain ridges and summits (Fosberg 1992). However, their highly restricted range and their small population size make these endemic plant species particularly vulnerable to extinction through habitat losses (complete destruction, fragmentation, or alteration) and interactions with introduced species, the so-called "environmental fragility or low resiliency" insular syndrome (Fosberg 1991). Cloud forests, for example, are restricted to only 3% (ca. 115 ha) of the island of Rarotonga (Cook Islands) in the interior mountain summits (MacCormack and Künzle 1990) and are found only on the highest summit of Ua Huka (Marquesas Islands), Mount Hitikau, between 750 and 870 m elevation, and on the highest summits of Rapa Iti (Austral Islands) between 550 and 650 m elevation. The larger and higher islands, such as Tahiti (Society Islands) or Nuku Hiva and Hiva Oa (Marquesas Islands) still support large areas of cloud forest habitats.

It must also be emphasized that the upperelevation rain forests and cloud forests protect the mountain watersheds of the small Polynesian islands, where limited water resources are critical for agriculture and economic development (Merlin and Juvik 1995).

The Threat of Invasive Alien Plants in Native Upland Wet Forests

There is hardly any natural vegetation left on the island of Rapa Nui today (Zizka 1991), where complete deforestation seems to have occurred after the arrival of the first Polynesian settlers. On the small and moderately elevated islands (<500 m elevation [e.g., Mangareva in the Gambier Islands; Raivavae, Tubuai, and Rurutu in the Austral Islands; Maupiti in the Society Islands]), most of the native vegetation has been grazed by introduced mammals and/or converted to agricultural land and secondary vegetation (e.g., grasslands dominated by Miscanthus floridulus or fernland dominated by Dicranopteris linearis). Thus, the most substantial areas of native vegetation lie in the montane rain forests and cloud forests of the largest high islands. The main threat to these native species is not direct habitat destruction by humans (for intensive cultivation, housing, etc.), fire, or browsing and trampling by large feral ungulates (such as pigs, goats, sheep, cattle, and horses), which are not able to thrive in that suboptimal habitat, but rather the less visible or "pernicious" invasion of alien plant species. Island ecosystems are well known to have a higher representation of alien species in their flora than do mainland ecosystems (D'Antonio and Dudley 1995). In the Austral, Cook, and Tuamotu Islands, the number of naturalized alien plants exceeds that of the native plants (Index of Secondarization [IS] <1, Table 2), and the island of Rapa Nui has the smallest IS value. The highest IS value (3.71) is found in the remote and uninhabited raised atoll of Henderson (Pitcairn Islands), which is relatively pristine.

MATERIALS AND METHODS

In this study I list and describe the most important alien invasive plant species in eastern Polynesia. It is based on personal recent (1992-2002) botanical surveys and extensive field observations I conducted in the Austral, Cook (Rarotonga), Gambier (Mangareva), Marquesas, and Society Islands, supplemented with bibliographical searches of other islands or archipelagos (Pitcairn Islands, Rapa Nui). The most important (or dominant) alien invasive species are defined as species that are widely naturalized and forming dense stands (covers, thickets, or forests) in natural (or native, primary, relatively undisturbed) and seminatural (or restored, partially disturbed, secondary) habitats. They are thus considered to have a notable ecological impact on the composition and structure of the ecosystem processes.

RESULTS

Current Alien Invasive Plants

The native vegetation of eastern Polynesian islands is impacted by a number of introduced invasive plant species, most of which occur throughout the region (Table 5).The medium-sized trees *Leucaena leucocephala* (Leguminosae) and *Psidium guajava* (Myrtaceae) form monodominant stands in the dry and mesic lowland forests of most island groups. The thorny ornamental shrub *Lantana camara* (Verbenaceae) forms impenetrable thickets in nearly all the island groups from sea level up to 1,500 m elevation in Tahiti. The fast-growing pioneer trees *Cecropia* spp. (Cecropiaceae) and the small tree *Ardisia elliptica* (Myrsinaceae), whose fruits are actively dispersed by frugivorous birds, form dense stands in the lowland and mid-elevation rain forests of Raiatea, Tahiti (Society Islands), and Rarotonga (Cook Islands) up to 500–600 m. The shrub *Cestrum nocturnum* (Verbenaceae) is also very invasive in the latter two islands and is an aggressive colonizer of trailsides, forest gaps, and landslides, up to 400 m elevation on Rarotonga and 900 m elevation in the rain forests of Tahiti (unpubl. data).

Some of the invasive alien plants are able to spread above 1,000 m elevation, choking the species-rich montane rain forests, including the cloud forests. Prevalent among these aliens are the strawberry or Chinese guava, Psidium cattleianum (Myrtaceae), in most of the island groups, especially on Rapa Iti and Tubuai (Austral Islands), where nearly all the montane summits are covered by dense monospecific forests; the Rose-apple, Syzygium jambos (Myrtaceae), a dominant invader of the wet valleys and mid-elevation slopes in the islands of Pitcairn (Pitcairn Islands) and Tahiti (Society Islands) and can be found at up to 1,100 m elevation in the cloud forests of Nuku Hiva (Marquesas Islands) (Meyer and Florence 1998); the Java plum, Syzygium cumini (Myrtaceae), in the Austral, Gambier, Society, and Marquesas Islands, where it is encroaching the cloud forest slopes and highests summits of Hiva Oa up to 1,200 m elevation; the African tulip tree, Spathodea campanulata (Bignoniaceae), a large tree up to 20 m in height whose winged seeds are wind dispersed, which dominates lowland mesic forests as well as native upland wet forests up to 1.200 m elevation in Tahiti. The thimbleberry, Rubus rosifolius (Rosaceae), thrives in cloud forest gullies, treefall gaps, forest edges, and trailsides in the Society Islands, Raivavae and Rapa Iti (Austral Islands), and Hiva Oa (Marquesas Islands), where it was introduced in the late 1980s. This prickly shrub colonized the highest peak of Tahiti, Mount Orohena, after an accidental fire that partially destroyed subalpine vegetation unique to eastern Polynesia (unpubl. data). The coco plum or icaco, Chrysobalanus icaco (Chryso-

Naturalized ^c
Cook Is.
Austral Is., Cook Is., Marquesas Is Society Is.
Marquesas Is., Society Is.
Austral Is., Marquesas Is Society Is.
Austral Is., Rap Nui
Austral Is., Gambier Is., Pitcairn Is.
Austral Is., Cook Is., Marquesas Is Society Is.
Rapa Nui
Austral Is.
Marquesas Is.

 TABLE 5

 Most Significant Alien Invasive Plants in Eastern Polynesia

Species Name (Family)	Common Name(s)	Life Form"	Habitat Type ^b	Elevation Range (m)	Invasivec	Naturalized
Mimosa diplotricha C. Wright ex Sauvalle (syn. M. invisa Martius ex Colla) (Leguminosae)	Giant sensitive plant, Spiny mimosa	Spiny shrub	Mesic	0-800	Gambier Is., Society Is.	
Paraserianthes falcataria (L.) I. Nielsen*	Molluca albizia	Large tree	Mesic	0–1,300	Society Is.	Austral Is., Cook Is., Gambier Is., Marquesas Is.
(Leguminosae) <i>Paspalum conjugatum</i> Bergius* (Gramineae)	T-grass, Sour paspalum	Grass	Mesic– Wet	10-900	Austral Is., Cook Is., Marquesas Is., Society Is.	Pitcairn Is., Rapa Nui
Passiflora maliformis L. (Passifloraceae)	Hard-shelled passion fruit	Vine	Mesic	0-300	Austral Is., Society Is.	Gambier Is., Pitcairn Is.
Passiflora rubra (Passifloraceae)	Red passion fruit	Vine	Mesic	0-300	Cook Is.	
Psidium cattleianum Sabine* (Myrtaceae)	Strawberry guava, Chinese guava	Tree	Mesic– Wet	10–1,200	Austral Is., Cook Is., Society Is., Marquesas Is.	Pitcairn Is.
<i>Psidium guajava</i> L.* (Myrtaceae)	Common guava	Tree	Dry– Mesic	0–1,200	Marquesas Is. Marquesas Is., Pitcairn Is., Society Is., Rapa Nui	Austral Is., Cook Is.
Rhodomyrtus tomentosa (Aiton) Hassk.* (Myrtaceae)	Rose myrtle, Downy myrtle	Shrub	Mesic– Wet	100-700	Society Is.	
(Rosaceae)	Thimbleberry, Roseleaf raspberry	Spiny shrub	Wet	10-2,200	Society Is., Austral Is.	Marquesas Is.
Spathodea campanulata P. Beauv.* (Bignoniaceae)	African tulip tree	Large tree	Mesic– Wet	10–1,200	Cook Is., Society Is.	Gambier Is., Marquesas Is.
(Digitofilaceae) Stachytarpheta urticifolia Sims* (Verbenaceae)	Blue rat's tail, Dark blue snakeweed	Herb	Mesic	10-300	Austral Is., Society Is.	Marquesas Is.
(verbenaceae) Syzygium cumini (L.) Skeels* (Myrtaceae)	Java plum, Jambolan	Large tree	Mesic– Wet	0–1,200	Gambier Is., Society Is., Marquesas Is.	Austral Is., Cook Is.
(Myrtaceae) Syzygium jambos (L.) Alston* (Myrtaceae)	Rose apple	Tree	Wet	10-1,100	Austral Is., Marquesas Is., Pitcairn Is., Society Is.	Cook Is., Gambier Is.
Tecoma stans (L.) Juss. ex Kunth (Bignoniaceae)	Yellow bells, Yellow elder	Small tree	Dry– Mesic	100–1,500	Austral Is., Society Is.	Cook Is., Marquesas Is., Tuamotu Is.

TABLE 5 (continued)

^a Shrub, <5 m tall; small tree, 5-20 m; tree, >20 m.
 ^b Moisture regime: dry, <1,250 mm/yr; mesic, 1,250-2,500 mm/yr; wet, >2,500 mm/yr.
 ^c Status of alien species: invasive, widely naturalized in natural or seminatural habitats and forming dense stands; naturalized, established in the wild and reproducing without direct human intervention but not yet invasive.
 * Also invasive in the Hawaiian Islands.

balanaceae), a shrub known to be highly invasive in the Seychelles Islands where it was introduced as a reforestation species (Friedmann 1994), has invaded the Temehani plateaus on the island of Raiatea (Society Islands) that support a unique dwarf cloud forest association between 600 and 700 m elevation (Meyer 1998a). Last but not least, the tree *Miconia calvescens* (Melastomataceae), a dominant invader in the Society Islands (Tahiti, Moorea, Raiatea, and Tahaa) and recently accidentally introduced in the Marquesas Islands (Nuku Hiva, Fatu Hiva) and the Austral Islands (Rurutu and Rapa Iti) with contaminated soil, is considered to be by far the worst of all invasive plants in the Pacific Island wet forests (Fosberg 1992, Meyer and Florence 1996, Mueller-Dombois and Fosberg 1998, Whittaker 1998). It forms densely shaded monospecific stands from near sea level up to 1,300 m elevation and occupies the belt between 1,500 and 2,500 mm of rainfall per year, including pristine, undisturbed cloud forest habitats (Meyer 1996).

It is noteworthy that most of the species cited here are also dominant invaders in other tropical oceanic islands such as the Hawaiian Islands (C. W. Smith 1985, Medeiros et al. 1995, Table 5), the Mascarene Islands (see, e.g., MacDonald et al. 1991, Strahm 1999), and the Galápagos Islands (Schofield 1989). Other potentially serious invasive plants in the native wet forests of eastern Polynesia are introduced ornamental plants belonging to the genera Hedychium (Zingiberaceae), especially H. flavescens on some of the highest summits of Rarotonga and in wet valleys of Rapa Iti; Passiflora (Passifloraceae); and Rubus (Rosaceae), with several species known to be dominant plant invaders in other tropical islands in the Pacific (Meyer 2000) and in the Indian Ocean.

Potential or Incipient Alien Invasive Plants

Some invasive plants currently found in a few islands of eastern Polynesia, such as the milea-minute vine, *Mikania micrantha* (Compositae), in Rarotonga (up to the highest summit at 650 m elevation), or found in the neighboring Polynesian islands, such as the African

rubber tree, Funtumia elastica (Apocynaceae), which forms monodominant forests in the lowlands and foothills on 'Upolu in the Samoa Islands (Whistler 1995), should be carefully monitored (e.g., prevention or early detection and eradication). Koster's curse, Clidemia hirta (Melastomataceae), a highly invasive shrub in the montane rain forests and cloud forests of Samoa, Fiji, Wallis and Futuna, and the Hawaiian Islands (Meyer 2000), is still absent in eastern Polynesia, and its introduction should be strongly avoided. Indeed, our most reliable predictor of plant invasiveness remains the aggressive behavior of the same species in other islands or countries with similar climatic and edaphic situations. For instance, the red quinine tree, Cinchona pubescens (syn. C. succirubra, Rubiaceae), is well known as an aggressive invader in the montane rain forests of the Galápagos Islands (MacDonald et al. 1988, Schofield 1989). It was introduced to Tahiti in the 1940s as a potential economic plant and was found naturalized in the 1970s. I recently found isolated reproductive trees, whose winged seeds are wind dispersed, in the cloud forest above 950 m elevation, with seedling carpets (unpubl. data). The octopus or umbrella tree, Schefflera actinophylla (syn. Brassaia actinophylla, Araliaceae), one of the most popular ornamental trees in the Tropics, is commonly cultivated in the urban areas of the Society Islands (Tahiti, Moorea, Raiatea) and Rarotonga (Cook Islands), although well known as being an invasive plant in Florida and the Hawaiian Islands. I recently found this species naturalized in the understory of mesic forests of Tahiti between 300 and 400 m elevation (unpubl. data).

Endemic Plants Endangered by Invasive Plants

Some rare endemic plants of eastern Polynesia have been documented to be directly theatened by alien invasive plants that are able to form dense monodominant stands (Table 6). Between 40 and 50 endemic plant species are considered directly threatened by the invasion of *Miconia calvescens* in the island of Tahiti (Meyer and Florence 1996). Most of them are understory shrubs or small trees

Species name (Family)	Island (Archipelago)	Conservation Status (IUCN Category) ^a	Main Threats/Causes of Population Decrease, Extirpation, or Extinction	Reference
<i>Acalypha wilderi</i> (Euphorbiaceae)	Rarotonga (Cook Is.)	EX?	Competition with Ardisia elliptica, Cestrum nocturnum, Mikania micrantha, and Passiflora rubra	McCormack (pers. comm., 2000)
<i>Charpenteria australis</i> (Amaranthaceae)	Tubuai, Raivavae (Austral Is.) + Rarotonga (Cook Is.)	DD	Severe invasion by <i>Psidium</i> cattleianum on Tubuai	JY.M. (unpubl. data)
<i>Cyrtandra elizabethae</i> (Gesneriaceae)	Rurutu (Austral Is.)	CR	Competition with Ocimum gratissimum	JY.M. (unpubl. data)
Glochidion pitcairnense (Euphorbiaceae)	Pitcairn (Pitcairn Is.)	VU	Invasion by Syzygium jambos	Waldren et al. (1995)
Lepinia taitensis (Apocynaceae)	Tahiti, Moorea (Society Is.)	VU	Severe invasion by Miconia calvescens	Meyer (2001)
Meryta brachypoda (Araliaceae)	Tubuai, Raivavae (Austral Is.) + Rapa Iti + Henderson (Pitcairn Is.)	CR	Severe invasion by <i>Psidium cattleianum</i> on Tubuai	JY.M. (unpubl. data)
Pilea sancti-johannis (Urticaceae)	Mangareva (Gambier Is.)	CR	Competition with Commelina diffusa	Florence (1997)
Psychotria speciosa (Rubiaceae)	Tahiti (Society Is.)	CR	Severe invasion by Miconia calvescens	Meyer and Florence (1996)

TABLE 6

Examples of Rare Endemic Plants Threatened by Alien Invasive Plants in Native Forests of Eastern Polynesian Islands

" CR, critically endangered; DD, data deficient; EX, extinct; VU, vulnerable (IUCN 1994).

that cannot survive or reproduce in the shade of a dense *Miconia calvescens* canopy. For example, endemic species of the genus *Psychotria* (Rubiaceae) show a significant decrease of flower and fruit production with the increasing density of *Miconia calvescens* in Tahiti (Meyer et al. 2003); regeneration (seedling recruitment) of *Lepinia taitensis* (Apocynaceae), measured by the percentage of seedlings (diameter at breast height [dbh] <1 cm) in plant populations, dropped from 60% in a nintact native forest in Moorea to 7% in a forest in Tahiti invaded by *Miconia calvescens* (Meyer 2001).

The strawberry or Chinese guava, *Psidium* cattleianum, which has invaded all the upland wet forests on Tubuai (Austral Islands) where it forms monodominant stands, is threatening the extremely rare *Charpenteria* australis (Amaranthaceae) and Meryta brachypoda (Araliaceae) (unpubl. data).

DISCUSSION

Several hypotheses have been involved to explain the vulnerability of island biotas to invasion by introduced species (or invasibility). They include reduced competitive ability ("aggressiveness") of island species, absence of ecological guilds or functional groups, small populations and genetic variability, relative lack of natural disturbance (especially fire), loss of resistance to consumers and diseases, and intensive exploitation by humans (Vitousek 1988, Loope and Mueller-Dombois 1989).

It has been hypothesized that species-poor communities are more susceptible to invasion. This is suggested to result in shorter food web structure, undersaturated communities, and "vacant niche space." The flora of remote oceanic islands, such as eastern Polynesia, is depauperate in terms of taxonomic types present and is called "disharmonic." However, recent studies of island communities suggest that there are few "unoccupied" or "vacant" ecological niches (Keast 1996), which implies that they are ecologically harmonious.

It is also often argued that disturbed native plant communities are more prone to invasion. However, some studies indicate that even island communities protected from human disturbance can be vulnerable to invasion by exotic species and that some plant invaders are able to penetrate apparently undisturbed forest that lacks natural, human or ungulate soil disturbance (e.g., *Psidium cattleianum* Sabine on Mauritius [Lorence and Sussman 1988]; *Tibouchina berbacea* in the Hawaiian Islands [Mueller-Dombois and Fosberg 1998]; *Ligustrum robustum* subsp. *walkeri* on La Réunion Island [Lavergne et al. 1999]).

Some already established facts and recent observations obtained in eastern Polynesia can help to test these hypotheses:

(1) The apparent persistence of the native upland forest in Rarotonga (Cook Islands) and of the native vegetation of the raised atoll of Henderson (Pitcairn Islands) is attributed to the lack of human disturbance and the absence of introduced hooved mammals such as goats, sheep, and pigs (Merlin 1985, Merlin and Juvik 1992, Waldren et al. 1995). However, I recently observed the intrusion of Cestrum nocturnum and Psidium cattleianum in the understory of relatively undisturbed native forest in Rarotonga up to 400-500 m elevation (unpubl. data). In the Society Islands, the alien trees Miconia calvescens (Meyer 1996, Meyer and Malet 1997) and Spathodea campanulata (pers. obs.) are able to penetrate into apparently pristine undisturbed forests;

(2) Feral pig activity is known to facilitate the spread of many alien plants by creating open habitats through digging and by disseminating seeds in their feces (Stone and Loope 1987), including *Psidium cattleianum* in the Hawaiian Islands (Medeiros et al. 1995). This was also observed in the cloud forests of Hiva Oa (Marquesas Islands) (unpubl. data). Cattle were found to actively disperse eaten fruits of *Psidium cattleianum* on Rapa Iti, and feral goats to passively disperse *Miconia cal*- *vescens* in high-elevation plateau native forests on Tahiti (unpubl. data);

(3) Natural disturbances such as hurricanes have caused the sudden and rapid spread of some invasive plants (e.g., the thimbleberry, *Rubus rosifolius*, in Tahiti [Society Islands] after the 1982–1983 hurricanes [Meyer 1998*a*], and the climbing vine *Cardiospermum grandiflorum* [Sapindaceae] in Rarotonga [Cook Islands] after Hurricane Sally in 1986 [Meyer 200]);

(4) Fire has promoted the spread of bunchforming fire-resistant alien grasses such as *Andropogon virginicus* and *Pennisetum setaceum* (Gramineae) in the Hawaiian Islands (D'Antonio and Vitousek 1992) and *Melinis minutiflora* in the Austral, Marquesas, and Society Islands. The population explosion of the shrub *Rhodomyrtus tomentosa* (Myrtaceae) on the island of Raiatea (Society Islands) was also the result of a fire (Meyer 1998*a*).

I propose an additional hypothesis that may explain the vulnerability of island vegetation to invasion by alien trees, in relation to their forest structure. Remote island forests are known to be structurally simple (Mueller-Dombois and Loope 1990). Multistoried tallstatured tropical rain forests (canopy >30 m in height) that are found in tropical continental countries or in large Melanesian islands are very rare (only in deep valley bottoms) in the small oceanic islands of eastern Polynesia. Native montane forests in eastern Polynesia are mainly low-statured, with a canopy between 10 and 20 m tall, and only a few strata. The simplified vegetation structure, the relatively low number of canopy species, and difference in life forms or ecological groups may favor invasion of island forests by small alien trees (Meyer and Lavergne 2001). For instance, Miconia calvescens, a late secondary successional and shade-tolerant species, is uncommon in its native range of tropical America and in Sri Lanka where it was introduced as an ornamental plant. In both areas, the species is exclusively found in small gaps, at forest edges, and on riverbanks. In the Society and Hawaiian Islands, this small tree up to 15 m in height can easily attain or overtop the canopy of the native wet forests and reproduces profusely (Meyer 1998b).

The PABITRA network, a collaborative program whose aim is to investigate the function of biodiversity and the health of ecosystems in the tropical Pacific Islands with particular emphasis on the comparative analysis of upland and inland forests of the volcanic high islands (Mueller-Dombois et al. 1999), may provide a good frame and an opportunity to test some of these hypotheses on the invasibility of island biotas of eastern Polynesia in comparison with other archipelagoes and islands (continental islands versus oceanic islands, large islands versus small islands, remote islands versus islands near continents).

CONCLUSIONS

Despite their extreme isolation and their small size, the islands of eastern Polynesia display a relatively rich and unique native flora, with great phytogeographic interest. The tropical and subtropical "moist broadleaf forests" of the South Pacific islands were recently classified as an endangered terrestrial ecoregion whose biodiversity and representative values are outstanding on a global scale (Olson and Dinerstein 1998). Most of the endemic plant species in eastern Polynesian high volcanic islands are restricted to the montane rain forests that remain relatively undisturbed because of their isolated occurrence on mountain ridges and summits that are preserved from fire, feral ungulates, and human activities.

In recent decades, introductions of alien plant species to eastern Polynesia have dramatically increased with the movement of people and intentional transportation of plants between the Pacific islands and the nearest continents, as well as among island countries. Many alien plants have now invaded native habitats, with some even able to spread into the species-rich upland wet forests.

The recent arrival of the climbing vine *Passiflora maliformis* (Passifloraceae), an aggressive invader in the Society and Austral Islands, and the weedy grass *Setaria verticillata* (Gramineae) on the raised limestone island of Henderson (Waldren et al. 1999) indicates

the increasing potential threat of alien species being deliberately or accidentally introduced, even to extremely remote islands. The recent introduction on Rapa Nui of Melinis minutiflora and Pennisetum clandestinum (Gramineae) to improve pasture, and Lantana camara (Verbenaceae) as an ornamental plant (Zizka 1991) reveals the urgent need for more information, education, and prevention for the local authorities and public in eastern Polynesia. There is now a growing concern that invasive plant species are a serious threat to the survival of the remaining and relatively well-preserved native montane rain forests in the Pacific Islands (SPREP 1999, Meyer 2000), especially those of the small, diverse, and remote islands of eastern Polynesia.

Therefore, one of the highest priorities for eastern Polynesian islands should be given to the study (invasion dynamics and ecological impacts) and control (strategy and methods) of the current invasive plants, and to the early detection and eradication of potential plant invaders. Otherwise, long-term conservation of these original native montane wet forests cannot be expected. My hope is that a coordinated effort, such as attempted through the PABITRA network, will help in conservation science and management.

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Literature Cited

- Balgooy, M. M. J. van. 1971. Plant geography of the Pacific. Blumea Suppl. 6.
 - ——. 1993. Pacific plant areas. Vol. 5. Rijksherbarium/Hortus Botanicus, Leiden University, Leiden.
- Balgooy, M. M. J. van, P. H. Hovenkamp, and P. C. van Welzen. 1996. Phytogeography of the Pacific—floristic and historical distribution patterns in plants. Pages 191–213 in A. Keast and S. E. Miller, eds. The origin and evolution of Pacific Island biotas, New Guinea to eastern Polynesia: Patterns and processes. SPB Academic Publishing, Amsterdam.
- Cheeseman, T. F. 1903. The flora of Rarotonga, the chief island of the Cook group. Trans. Linn. Soc. Lond., 2nd ser. Botany, Vol. 6.
- D'Antonio, C. M., and T. L. Dudley. 1995. Biological invasions as agents of change on islands versus mainlands. Pages 103–121 *in* P. M. Vitousek, L. L. Loope, and H. Andersen, eds. Biological diversity and ecosystem function on islands. Springer Verlag, New York.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. Annu. Rev. Ecol. Syst. 23:63–87.
- Dransfield, J., J. R. Flenley, S. M. King, D. D. Harkness, and S. Rapu. 1984. A recently extinct palm from Easter Island. Nature (Lond.) 312 (5996): 750–752.
- Dupon, J.-F., coord. 1993. Atlas de la Polynésie française. Editions de l'ORSTOM, Paris.
- Florence, J. 1987. Endémisme et évolution de la flore de la Polynésie française. Bull. Soc. Zool. Fr. 112 (3–4): 369–380.
 - ——. 1993. La végétation de quelques îles de Polynésie française. Planche 54–55 in

J.-F. Dupon, coord. Atlas de la Polynésie française. Editions de l'ORSTOM, Paris.

- ------. 1997. Flore de la Polynésie française. Vol. 1. Editions de l'ORSTOM, Paris.
- Florence, J., and D. H. Lorence. 1997. Introduction to the flora and vegetation of the Marquesas Islands. Allertonia 7 (4): 226–237.
- Florence, J., S. Waldren, and A. J. Chepstow-Lusty. 1995. The flora of the Pitcairn Islands: A review. Biol. J. Linn. Soc. 56:79–114.
- Fosberg, F. R. 1984. Phytogeographic comparison of Polynesia and Micronesia. Pages 23–44 *in* F. J. Radovsky, P. H. Raven, and S. H. Sohmer, eds. Biogeography of the tropical Pacific. Bishop Mus. Spec. Publ. 72.
- ——. 1991. Polynesian plant environments. Pages 11–23 in P. A. Cox and S. A. Banack, eds. Islands, plants and Polynesians. Dioscorides Press, Portland.
- -------. 1992. Vegetation of the Society Islands. Pac. Sci. 46:232–250.
- Friedmann, F. 1994. Flore des Seychelles. Dicotylédones. Editions de l'ORSTOM, Paris.
- Grant, M. L., F. R. Fosberg, and H. M. Smith. 1974. Partial flora of the Society Islands: Ericaceae to Apocynaceae. Smithson. Contrib. Bot. 17.
- IUCN. 1994. IUCN Red List categories. IUCN, Gland, Switzerland.
- Keast, A. 1996. Pacific biogeography: Patterns and processes. Pages 477–512 in A. Keast and S. E. Miller, eds. The origin and evolution of Pacific Island biotas. New Guinea to eastern Polynesia: Patterns and processes. SPB Academic Publishing, Amsterdam.
- Lavergne, C., J.-C. Rameau, and J. Figier. 1999. The invasive woody weed *Ligustrum robustum* subsp. *walkeri* threatens native forests on La Réunion. Biol. Invasion 1:337–392.
- Loope, L. L., and D. Mueller-Dombois. 1989. Characteristics of invaded islands, with special reference to Hawaii. Pages 257–280 *in* J. Drake, F. Di Castri, R. Groves, F. Kruger, H. Mooney, M. Rejmanek, and M. Williamson, eds. Biologi-

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cal invasions: A global perspective. John Wiley and Sons, New York.

- Lorence, D. H., and R. W. Sussman. 1988. Diversity, density, and invasion in a Mauritian wet forest. Monogr. Syst. Bot. 25:187–204.
- MacCormack, G. 1992. A preliminary report on Cook Island biodiversity. In D.
 R. Given, comp. Overviews of the biodiversity of some Pacific Islands. Global Environment Facility, The South Pacific Biodiversity Conservation Programme, South Pacific Regional Environmental Program, Apia.
- MacCormack, G., and J. Künzle. 1990. Rarotonga's cloud forest. Cook Islands Conservation Service (poster).

------. 1995. Rarotonga's mountain tracks and plants: A field guide. Cook Islands Natural Heritage Project, Rarotonga.

- MacDonald, I. A. W., L. Ortiz, J. E. Lawesson, and J. Bosco Nowak. 1988. The invasion of highlands in Galápagos by the red quinine-tree *Cinchona succirubra*. Environ. Conserv. 15 (3): 215–220.
- MacDonald, I. A. W., C. Thebaud, W. A. Strahm, and D. Strasberg. 1991. Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean). Environ. Conserv. 18 (1): 51–61.
- Manner, H. I., D. Mueller-Dombois, and M. Rapaport. 1999. Terrestrial ecosystems. Pages 93–108 in M. Rapaport, ed. The Pacific islands: Environment and society. The Bess Press, Honolulu.
- Medeiros, A. C., L. L. Loope, and R. W. Hobdy. 1995. Conservation of cloud forests in Maui County (Maui, Moloka'i, and Lana'i), Hawaiian Islands. Pages 223–233 in L. S. Hamilton, J. O. Juvik, and F. N. Scatena, eds. Tropical montane cloud forests. Ecological Studies 110. Springer Verlag, New York.
- Merlin, M. D. 1985. Woody vegetation in the upland region of Rarotonga, Cook Islands. Pac. Sci. 39:81–99.
- Merlin, M. D., and J. O. Juvik. 1992. Relationships among native and alien plants on Pacific islands with and without significant human disturbance and feral ungulates.

Pages 597–624 in C. P. Stone, C. W. Smith, and J. T. Tunison, eds. Alien plant invasions in native ecosystems of Hawaii: Management and research. University of Hawai'i Cooperative National Park Resource Studies Unit, Honolulu.

- ——. 1995. Montane cloud forest in the tropical Pacific: Some aspects of their floristics, biogeography, ecology and conservation. Pages 234–253 *in* L. S. Hamilton, J. O. Juvik, and F. N. Scatena, eds. Tropical montane cloud forests. Ecological Studies 110. Springer Verlag, New York.
- Meyer, J.-Y. 1996. Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pac. Sci. 50:66–76.
- ———. 1998a. Mécanismes et gestion des invasions biologiques par des plantes introduites dans des forêts naturelles à Hawai'i et en Polynésie française: Une étude de cas. Rapport d'étude post-doctorale, Délégation à la Recherche/University of Hawai'i at Mānoa. Available from Délégation à la Recherche, Governement of French Polynesia, Papeete.
- ——. 1998b. Observations on the reproductive biology of *Miconia calvescens* DC (Melastomataceae), an alien invasive tree on the island of Tahiti (South Pacific Ocean). Biotropica 30 (4): 609–624.
- ——. 2000. Preliminary review of the invasive plants in the Pacific islands (SPREP Member Countries). Pages 85–114 in G. Sherley, comp. Invasive species in the Pacific: A technical review and regional strategy. South Pacific Regional Environmental Program, Apia.
- 2001. Liste et statut des plantes endémiques menacées par *Miconia calvescens* à Tahiti et Moorea. Contribution à la Biodiversité de Polynésie française no. 8, Délégation à la Recherche, Papeete.
- Meyer, J.-Y., and J. Florence. 1996. Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae).
 J. Biogeogr. 23:775-781.
- ——. 1998. Mont Mauru (Tahiti, Society Islands) and Toovii ridges (Nuku Hiva, Marquesas Islands), two natural areas of ecological interest in French Polynesia,

proposed as PABITRA sites. Proceedings, 19th Pacific Science Congress, 4–9 July 1999, Sydney (abstract).

- Meyer, J.-Y., and C. Lavergne. 2001. The role of forest structure in plant invasions on tropical oceanic islands. Pages 456–458 in K. N. Ganeshaiah, R. Uma Shaanker, and K. S. Bawa, eds. Tropical ecosystems: Structure, diversity and human welfare. Proceedings of the International Conference on Tropical Ecosystems, Oxford-IBH, New Delhi.
- Meyer, J.-Y., and J.-P. Malet. 1997. Study and management of the alien invasive tree *Miconia calvescens* (Melastomataceae) in the islands of Raiatea and Tahaa (Society Islands, French Polynesia): 1992–1996. University of Hawai'i Cooperative National Park Resource Studies Unit, Tech. Rep. 111.
- Meyer, J.-Y., J. Florence, and V. Tchung. 2003. Les *Psychotria* (Rubiacées) endémiques de Tahiti (Polynésie française) menacés par l'invasion par *Miconia calvescens* (Mélastomatacées): Statut, répartition, écologie, phénologie et protection. Rev. Ecol. Terre Vie 58:161–185.
- Mueller-Dombois, D., and F. R. Fosberg. 1998. Vegetation of the tropical Pacific Islands. Springer Verlag, New York.
- Mueller-Dombois, D., and L. L. Loope. 1990. Some unique ecological aspects of oceanic island ecosystems. Monogr. Syst. Bot. 32:21–27.
- Mueller-Dombois, D., R. A. Thaman, J. O. Juvik, and K. Kitayama. 1999. The Pacific-Asia Biodiversity Transect (PABITRA): A new conservation biology initiative. Pages 13–20 in C. H. Chou, G. R. Waller, and C. Reinhardt, eds. Biodiversity and allelopathy: From organisms to ecosystems in the Pacific. Academica Sinica, Taipei.
- Munschy, M., C. Antoine, G. Guille, and H. Guillou. 1998. La croûte océanique et les points chauds de la Polynésie française (Océan Pacifique central). Geol. Fr. 3:5–13.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature (Lond.) 403:853– 858.

- Nunn, P. D. 1994. Oceanic islands. Blackwell Publishers, Oxford.
- ——. 1999. Geomorphology. Pages 43–55 in M. Rapaport, ed. The Pacific islands: Environment and society. The Bess Press, Honolulu.
- Olson, D. M., and E. Dinerstein. 1998. The Global 200: A representation approach to conserving the Earth's most biologically valuable ecoregions. Conserv. Biol. 12 (3): 502–515.
- Raynal, J. 1976. Une Lobéliacées polynésienne nouvelle. Adansonia, sér. 2, 16 (3): 379–382.
- Royen, P. van, and S. D. Davis. 1995. Regional overview: Pacific Ocean islands.
 Pages 519–555 in S. D. Davis, V. H. Heywood, and A. C. Hamilton, eds. Centres of plant diversity: A guide and strategy for their conservation. Vol. 2. Asia, Australasia and the Pacific. World Wildlife Fund for Nature/IUCN Publications Unit, Cambridge.
- Schofield, E. K. 1989. Effects of introduced plants and animals on island vegetation: Examples from the Galápagos Archipelago. Conserv. Biol. 3 (3): 227–238.
- Skottsberg, C. J. F., ed. 1920–1956. The natural history of Juan Fernández and Easter Island. Vol. 1. Almqvist & Wiksells, Uppsala.
- Smith, A. C. 1979–1991. Flora Vitiensis nova: A new flora of Fiji. National (formerly Pacific) Tropical Botanical Garden, Lāwa'i, Hawai'i. 5 vols. + comprehensive indices.
- Smith, C. W. 1985. Impact of alien plants in Hawai'i's native biota. Pages 180–250 in C. P. Stone and J. M. Scott, eds. Hawai'i's terrestrial ecosystems: Preservation and management. University of Hawai'i Cooperative National Park Resource Studies Unit, Honolulu.
- Sohmer, S. H. 1990. Elements of Pacific phytodiversity. Pages 239–304 in P. Baas, K. Kalkman, and R. Geesink, eds. The plant diversity of Malesia. Kluwer Academic Publishers, Dordrecht.
- Spencer, T. 1995. The Pitcairn Islands, South Pacific Ocean: Plate tectonic and climatic contexts. Biol. J. Linn. Soc. 56:13–42.

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- SPREP (South Pacific Regional Environmental Program). 1999. Action strategy for nature conservation in the Pacific Islands region 1999–2002. Apia.
- Steenis, C. G. G. J. van, and M. M. J. van Balgooy. 1966. Pacific plant area. Vol. 2. Blumea Suppl. 5.
- Stone, C. P., and L. L. Loope. 1987. Reducing negative effects of introduced animals on native biotas in Hawai'i: What is being done, what needs doing, and the role of national parks. Environ. Conserv. 14 (3): 246–258.
- Strahm, W. 1999. Invasive species in Mauritius: Examining the past and charting the future. Pages 325–347 in O. T. Sandlung, P. J. Schei, and A. Viken, eds. Invasive species and biodiversity management. Kluwer Academic Publishers, Dordrecht.
- Takhtajan, A. 1986. Floristic regions of the world (translated by T. J. Crovello and A. Cronquist). University of California Press, Berkeley.
- Thorne, R. F. 1963. Biotic distribution patterns in the tropical Pacific. Pages 311– 354 in J. L. Gressitt, ed. Pacific basin biogeography, a symposium. Proceedings, 10th Pacific Science Congress, 1961, Honolulu, Hawai'i. Bishop Museum Press, Honolulu.
- Vitousek, P. M. 1988. Diversity and biolog-

ical invasions of oceanic islands. Pages 181–189 in E. O. Wilson, ed. Biodiversity. National Academic Press, Washington, D.C.

- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the flowering plants of Hawai'i. Rev. ed. University of Hawai'i Press and Bishop Museum Press, Honolulu.
- Waldren, S., J. Florence, and A. J. Chepstow-Lusty. 1995. Rare and endemic vascular plants of the Pitcairn Islands, South-Central Pacific Ocean: A conservation appraisal. Biol. Conserv. 74:83–98.
- Waldren, S., M. I. Weisler, J. G. Hather, and D. Morrow. 1999. The non-native vascular plants of Henderson Island, South-Central Pacific Ocean. Atoll Res. Bull. 463.
- Whistler, A. 1995. The cloud forest of Samoa. Pages 353–362 in L. S. Hamilton, J. O. Juvik, and F. N. Scatena, eds. Tropical montane cloud forests. Ecological Studies 110. Springer Verlag, New York.
- Whittaker, R. J. 1998. Island biogeography: Ecology, evolution and conservation. Oxford University Press, Oxford.
- Wilder, G. P. 1931. Flora of Rarotonga. Bernice P. Bishop Mus. Bull. 86.
- Zizka, G. 1991. Flowering plants of Easter Island. Palmarum Hortus Francofurtensis 3, Frankfurt am Main.