Interactions between Plants and Avian Frugivores in the Society Archipelago, (French Polynesia)

[1]Erica N. Spotswood and [2]Jean-Yves Meyer

[1]Department of Environmental Science, Policy and Management, University of California at Berkeley CA 94720
[2]Délégation à la Recherche B.P. 20981 Papeete, Tahiti, French Polynesia
[1]espots@nature.berkeley.edu, [2]jean-yves.meyer@recherche.gov.pf

ABSTRACT

On the tropical islands of French Polynesia, many alien and native plants produce fleshy fruit that are dispersed by birds. Novel relationships between exotic and native birds and the plants they consume have the potential to influence the dynamics of the spread of invasive species and to modify plant communities. In this study, we used a combination of dietary analysis of fecal samples and observations of foraging behavior to determine the diet of three frugivorous birds on Tahiti and Moorea. In total, 25 plant species were present in the diets of birds. All birds consumed the fruit of both alien and native plants. The two exotic frugivores consumed more alien species while the native frugivore consumed more native plants. The large numbers of both exotic and native species consumed by frugivores demonstrates that multiple novel relationships between newly naturalized and native species have been established. Invasive plants and exotic birds have potential to benefit from these associations, while the consequences for native communities are likely to be negative.

Keywords

Exotic birds, invasive species, frugivory, mutualism, French Polynesia

1. INTRODUCTION

Birds and other vertebrate frugivores can alter the seed shadow, or the spatial distribution of seeds relative to parent trees. These changes in deposition of seeds can be important in structuring tropical plant communities [1, 2]. As exotic (or alien non-native) species are introduced into novel communities, new mutualisms between dispersers and plants can be established. These dispersal mutualisms are most often generalized and diffuse and can be established quickly after the arrival of new organisms [3]. Resulting communities with many exotic species are often characterized by multiple newly established dispersal relationships between exotic and native frugivores and plants [3, 5-7, 9-11]. These interactions can assist alien plants and vertebrates while disrupting native mutualisms [3, 18, 19].

On the tropical oceanic islands of French Polynesia, the introduction of many exotic plants and animals since the arrival of Polynesians has altered biotic communities in often unintended and poorly understood ways [12, 22-24]. Currently, plant and animal communities are highly modified by the presence of multiple introduced organisms [24-26]. The resulting extinctions of multiple native and endemic species and the high numbers of threatened endemic species demonstrates the degree of vulnerability intrinsic to these small island systems [27-29].

Though at several frugivorous vertebrates and fruit-bearing plants have been introduced, to date no study has characterized existing relationships between native and exotic birds and plants and the impacts of newly established mutualisms on native communities remains poorly understood. The objectives of this study were to document the diets of native and exotic frugivorous birds on Moorea and Tahiti in order to identify new and old relationships between dispersers and plants.

2. METHODS

2.1 Study Site

Tahiti and Mo'orea (17º 38'S, 149º 30'W and 17º 30'S, 149º 50'W respectively), are small tropical volcanic islands (1045 km^2 and 142 km^2 respectively) with high peaks reaching 2241 and 1207 m respectively. Their isolation from neighboring continents has restricted colonization leading to a disharmonic flora and fauna with some taxa overrepresented while others are absent or underrepresented [29-31]. Endemism is also high, reaching 62% on Tahiti for native vascular plants [31, 32]. Additionally, introduction of alien organisms has been particularly pronounced, and in both birds and plants, exotic species now comprise around half of the biodiversity on these islands [5, 33]. Field work for this study was conducted at 8 sites on Tahiti and Moorea. Three sites on Tahiti varied in elevation from 600 to 800m while 5 sites on Moorea varied from 0 to 500m. Sites also varied in the abundance of the most common invasive tree species, *Miconia calvescens* and were chosen on the basis of accessibility and the presence of viewpoints that permitted observation of avian foraging behavior.

Table 1. Percentages of 579 exotic plant species in French Polynesia that are dispersed by animals, which produce fleshy fruit, and which are considered highly invasive. (Data after Fourdriniez & Meyer 2008)

Category	Percentage of total species
Highest two categories of invasive potential (4 and 5)	10%
Produce fleshy fruit	18%
Use endochory as mode of dispersal	20%

2.2 Plant community

French Polynesia is characterized by relatively low native plant diversity which has been attributed to the young age of the islands, their small size and their strong geographic isolation [25]. Plant introductions have occurred since the arrival of Polynesians between 1500 and 2000 years ago, with numbers now surpassing

Table 2. Status, distribution, and history of the Grey-green Fruit Dove, the Red-vented Bulbul, and the Silvereye in French Polynesia

	Grey-green Fruit Dove (*Ptilinopus purpuratus)*	**Red-vented Bulbul (*Pycnonotus cafer)***	**Silvereye (*Zosterops lateralis)***
Status	Native	Exotic	Exotic
Date of introduction	-	Probably in the late 1970s	1937
Native Range	Society Islands, French Polynesia	India and Pakistan	New Zealand and Australia
Range in French Polynesia	Huahine, Raiatea, Tahiti, Moorea, Maupiti, Bora Bora, Tahaa	Tahiti, Moorea, Huahine, Raiatea, Tahaa	Tahiti, Moorea, Leeward Islands (except coral atolls), Makatea, Raivavae, Tubuai, Rurutu
Elevation range on Tahiti and Moorea	0 – 8 to 900 m	0 - 2200	0 - 2200 m
Habitat preference	Primary and secondary forest, agriculture, gardens. Absent from atolls and montane forest, prefers understory	Very common in farms, residential areas, low elevation valleys and ridge forests, gardens, orchards, less abundant in high elevation forests	Abundant in all habitat types, absent from atolls
Diet	Fruit 2 - 17mm in diameter, occasionally insects	Fruit, flower petals, insects, lizards and geckos	Fruit, nectar, insects
Group size	Most often seen singly or in pairs, but groups up to 12 sometimes gather in fruiting trees, can also be seen in small family groups of 3. Maximum group size ever recorded is 40 (MP Poulsen 1985) on Tahiti	Family groups 2 - 10 individuals	Pairs during breeding season, otherwise gregarious in groups 4 - 50 individuals
Behavior	Shy, skulking, cryptic, not territorial	Vocal, aggressive towards other species and conspecifics, territorial during breeding season	Vocal, maintains contact with group members via contact calls, gregarious, territorial during breeding season
Interactions with other species	Preyed on by Swamp Harriers (*Cirus approximans*) and cats, Competes with and is victim of agonistic interactions with Bubuls and Mynas, Mynas (*Acridotheres tristis*) and Rats prey on eggs	Preyed on by Swamp Harriers, Aggressive towards most other species and conspecifics, competes with and is aggressive towards Mynas, Fruit Doves, and occasionally silvereyes.	Probably preyed on by Swamp Harriers, victim of occasional aggression from Bulbuls and Mynas
Breeding season	All months except September	November - January in French Polynesia, coincides with monsoon in native range	Records vary, probably year round
Populations on Tahiti and Moorea	Estimated 5 - 6,000 in 1973, 2 -3 birds per hectare	Tens of thousands	Extremely abundant. Estimated hundreds of thousands (JC Thibault personal communication)
Population changes during 20th century	Very abundant in 1907. Thought to have declined since 1900, though no systematic surveys have quantified changes	Between 1980s and 1991 high densities only on west coast of Tahiti, in less than 10 years, spread to most coastal areas on Tahiti and up to 1500 m	Rare on Tahiti in 1958s, very abundant by 1970s, First noticed on Moorea in 1971. Colonized several islands Societies and probably the Australs without assistance.
References	[4-9]	[5, 12-17]	[5, 6, 8, 20, 21]

total numbers of native species [17, 33]. The total number of introduced species, estimated at 1558 is nearly double the 885 described native species across French Polynesia [33-35]. Of those introduced species, 557 have naturalized populations and 35 are classified as threatening to native biodiversity [5, 6, 8, 21, 33, 36]. Of 579 alien naturalized plant species evaluated by Fourdriniez and Meyer (2008), 10% fall into the highest two categories of invasive potential while 18% produce fleshy fruit and 20% use animal digestion as a mode of dispersal (Table 1).

2.3 Frugivorous bird Species

Though birds have better dispersal abilities than many other groups, land bird diversity is low, with only 16 species on Tahiti and 11 on Moorea [5]. Of these landbirds, only 11 and 7 species are native to Tahiti and Moorea respectively [5, 24]. Only three species of birds on Tahiti and Mo'orea regularly consume fruit; the Grey-green Fruit Dove (*Ptilinopus purpuratus*; Fruit Dove hereafter) is endemic to the Society Islands and common on both Tahiti and Moorea (Table 2). The Red-vented Bulbul *(Pycnonotus cafer)* was introduced from India in the late 1970s [37] (Table 2). The Silvereye (*Zosterops lateralis*) was introduced by an American bird fancier in 1937 [21]. The Fruit Dove is a generalist that has incorporated many introduced fruits into its diet, though the extent of its potential to disperse and spread invasive plants is unknown [38]. Though there is little evidence of the Red-vented Bulbul dispersing invasive plants either in French Polynesia or elsewhere, other species in the genus *Pycnonotus* have been found to be important to the spread of weeds. For example, the Red-whiskered Bulbul (*Pycnonotus jocosus*) is thought to be partially responsible for the spread of weeds in Florida and La Reunion [39, 40]. Some of the plant species consumed by the Red-whiskered Bulbul such as *Lantana camara* and *Schinus terebenthifolius* are also present in French Polynesia, indicating that there is a potential for the Red-vented Bulbul to consume and disperse these plants. The Silvereye is the most abundant land bird on Tahiti and Moorea [36]. It is thought to be responsible for dispersal of weeds elsewhere in the Pacific including Australia, where it has been implicated in the dispersal of the Bridal Creeper (*Asparagus asparagoides*) [41].

2.4 Plant Consumption by Birds

Birds were caught using 4 mist nets (mesh size 36mm) 2.5 meters wide and 12m long raised 50cm off the ground on poles reaching 3m in height. Mist netting was conducted on 2-9 days per month from September 2007 to November 2008. Total net hours calculated as the number of 12 m nets multiplied by the number of hours was 1048 during 42 days of mist netting. Nets were opened between 5:30 and 6:00 am and closed either after a half day at 11 am or after a full day at 6pm. Nets were closed during periods of rain or high wind to prevent injuries or hypothermia in captured birds.

Birds were placed inside thin paper envelopes in a cloth bag for up to one hour until they had produced a fecal sample. Weight, molt pattern, skull pneumatization, adult or juvenile status, wing length, reproductive status, and any other distinct features were recorded for each individual. All birds were fitted with an aluminum band before release. At some sites, fecal samples of Bulbuls were also obtained by collecting fresh samples from underneath perching sites after observing the behavior of local individuals.

Table 3. Plants consumed by birds in which S, B, and D represent Silvereye, Bulbul, and Gray-green fruit dove respectively. Status as A – Alien or N – Native and invasive status after Fourdriniez & Meyer 2008

Species	Birds	Status	Plant parts consumed	Invasive status
Cananga odorata (Annonaceae)	D	A	Fruit	1
Carica papaya (Caricaceae)	B	A	Fruit	1
Cecropia peltata (Cecropiaceae)	S,B,D	A	Fruit	5
Cyclophyllum barbatum (Rubiaceae)	D	N	Fruit	NA
Dypsis madagascariensis (Arecaceae)	B,D	A	Fruit	
Fagraea berteroana (Loganiaceae)	S,B,D	N	Fruit	NA
Ficus cf. prolixa var. prolixa(Moraceae)	S,B,D	N	Fruit	NA
Inga feuillei (Mimosaceae)	S	A	Flower	3
Ixora moorensis (Rubiaceae)	D	N	Fruit	NA
Lantana camara (Verbenaceae)	S,B,D	A	Fruit	5
Meryta lanceolata (Araliaceae)	D	N	Fruit	NA
Metrosideros collina (Myrtaceae)	S,B	A	Flower	NA
Miconia calvescens (Melastomataceae)	S,B,D	A	Fruit	5
Momordica charantia (Cucurbitaceae)	S,B	A	Fruit	3
Albizia moluccana (syn. *Paraserianthes falcataria,* Fabaceae)	S	A	Flower	4
Passiflora foetida (Passifloraceae)	B	A	Flower	4
Psidium guajava (Myrtaceae)	B,D	E	Fruit	4
Rhus taitensis (Anacardiaceae)	S,B,D	N	Fruit	NA
Rubus rosifolius (Rosaceae)	S,B	E	Fruit	5
Schefflera actinophylla (Araliaceae)	B	E	Fruit	4
Schinus terebinthifolius (Anacardiaceae)	S	E	Fruit	4
Spathodea campanulata (Bignoniaceae)	S,B	E	Flower	5
Syzygium cumini (Myrtaceae)	B	E	Fruit	5
Tarenna sambucina (Rubiaceae)	B,D	N	Fruit	NA
Wikstroemia foetida (Thymeleaceae)	B,D	N	Fruit	NA
Xylosma sauveolens (Flacourtiaceae)	D	N	Fruit	NA

Table 4. Numbers of fecal samples containing seeds by plant species for Silvereyes, Bulbuls, and Gray-green Fruit Doves.

Plant Species	Silvereye	Bulbul	Fruit Dove
Cananga odorata	0	0	2
Cecropia peltata	1	24	1
Cyclophyllum barbatum	0	0	2
Fagraea berteroana	4	1	1
Ficus cf. prolixa	1	0	1
Ixora moorensis	0	0	1
Lantana camara	10	6	1
Meryta sp	0	0	2
Miconia calvescens	165	82	42
Poaceae	2	1	0
Psidium guajava	0	0	1
Rhus taitensis	6	2	0
Rubus	22	3	0
Schinus terebinthifolius	3	0	0
Tarenna sambucina	0	0	24
Unknown seeds	8	4	6
Total Fecal samples	**386**	**96**	**52**

Each paper envelope containing a fecal sample was placed in a Ziploc bag and refrigerated for up to 3 months until they could be analyzed. All fecal material was then scraped out of the inside of envelopes into petri dishes to which several drops of water were added. A dissecting microscope was used to count and identify all seeds and other material. Each sample and fecal material was spread evenly over the surface of the dish and using a grid of 50 points spaced 1mm apart on the bottom of the petri dish, frequencies of each material in the fecal sample were determined as numbers of hits out of 50. Arthropod remains were identified to the highest taxonomic category possible. All samples were stored in 90% ethanol.

In addition to dietary records obtained from fecal samples, a list of plant species consumed by each bird species was compiled using opportunistically collected observations of birds in the field at all sites on Moorea and Tahiti.

3. RESULTS

3.1 Normal or Body Text

A total of 534 fecal samples were collected of which 96 were from Bulbuls, 386 were from Silvereyes, and 52 were from fruit doves. Birds were determined to consume the fruit, the nectar, or the flowers of 25 different species of plants (Table 3). Of these species, 16 are exotic introductions while only 8 were native. All three species of birds consumed both exotic and native plants. However, the Fruit Dove ate many more species of native plants than either the Silvereye or the Bulbul (Figure 1).

Several plant species were consumed by multiple bird species. The seed most commonly found in fecal samples was that of *Miconia calvescens* (Table 4). Other common species in bird diets were *Cecropia peltata, Rubus rosifolius,* and *Tarenna sambucina* in the diet of the Fruit Dove. Bird diets included multiple parts of plants including nectar, flower petals and seeds. Both trees and herbaceous plants were consumed. The most common weedy herbaceous plant consumed was *Rubus rosifolius*. With only two exceptions, all exotic plants consumed by birds were in the highest three categories of invasive potential (Table 3).

4. DISCUSSION

Both alien and native plants are consumed by both exotic and native birds in French Polynesia. The diets of three frugivores in this study were determined using data from all months except December during the study period in 2007 and 2008. Thus, diet estimates probably account for differences in consumption as fruiting and flowering patterns change across seasons. However, because we restricted our field sites to elevations below 800 meters on Tahiti and 500 on Moorea, it is likely that some species that are consumed by birds were not represented in our study. Because native plant communities are currently restricted to high elevations on both Tahiti and Moorea, it is likely that native plant species are underrepresented in the dietary estimates for Bulbuls and Silvereyes [30]. Lastly, though mist netting sampling effort was consistent across months and sites, not all food consumed appeared in the fecal samples of birds. We compensated for this by supplementing direct capture with observations of foraging behavior. However, our observations were opportunistic and thus are probably biased towards the most obvious species.

The high degree of overlap in the diets of all three frugivorous species indicates that, as with many other dispersal systems, these dispersal relationships are generalized and diffuse [3]. Novel relationships have emerged quickly, especially in the case of the Bulbul, which was introduced with the last 35 years. Though the arrival dates of all invasive plants are not known, several including *Miconia calvescens* were introduced during the 20th century [33].

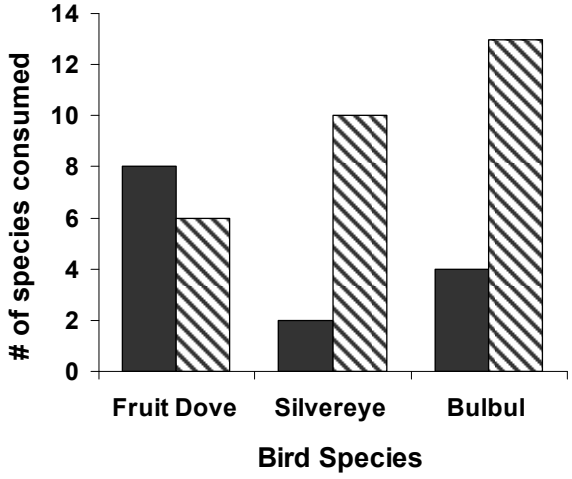

Figure 1. Numbers of plant species consumed by each bird species. Black bars indicate native while slashed bars indicate alien species. Native and alien status taken from Fourdrigniez & Meyer 2008 and Butaud *et al.* 2007.

4.1 Exotic frugivore diets

Bulbuls and Silvereyes consumed many of the same fruits. However, the silvereye consumed more insect material, and thus overall fewer seeds in fewer fecal samples than the Bulbul [42]. Both species consumed large numbers of exotic species and very few native species. The notable exceptions are *Fagraea berteroana, Tarenna sambucina,* and *Rhus taitensis* which are all common native species at mid-elevations with large fruit crops [43]. Though *Tarenna sambucina* was never found in Bulbul fecal samples, Bulbuls were observed visiting and eating the fruit of this tree on many occasions. Interestingly, the Bulbul was never observed to consume *Schinus terebinthifolius* while the Silvereye only rarely consumed the seeds of *Cecropia peltata.* Neither species is present on Moorea, and *S. terebinthifolius* is only present and naturalized at one site on Tahiti. *C. peltata* has a relatively large seed with very little flesh which may not be palatable to Silvereyes while *S. terebinthifolius* has a very strong peppery taste and very little flesh. Thus, the absence of consumption of these two species could reflect differences in preference between the two species.

Overall, both Bulbuls and Silvereyes consumed more exotic plants than native. These results reflect those of other studies which have demonstrated the positive impacts that these novel mutualisms can have for exotic frugivores and plants [3, 10, 11]. For example, dispersal of exotic seeds by birds can alter the seed shadow, recruitment patterns, and mean dispersal distance of plants, ultimately contributing to their capacity to invade novel ecosystems [10, 11]. Likewise, exotic plants which sometimes have different phenological patterns than native species can provide an important resource for exotic frugivores that may be more readily available, more abundant, or have a longer fruiting season than native plants [3]. On Tahiti and Moorea, the three plants most commonly consumed by Silvereyes and Bulbuls (*T. sambucina, R.. taitensis,* and *F. berteroana*) fruit for 6 months, 2 months and 3 months respectively whereas *C. peltata* and *M. calvescens* nearly always have fruit available (Spotswood, unpublished data).

4.2 Fruit Dove diet

Fruit Dove diet consists of many more native species than the diet of the Silvereyes or Bulbuls. This is not surprising considering it is a native frugivore that has been present in the Society archipelago for at least 1000 years [24]. The Fruit Dove also consumed fewer exotic species than the other two frugivores, with only 6 exotic species represented in its diet.

The incorporation of novel exotic fruit into the diet of native frugivores has been documented elsewhere [3]. The impact of such changes in dietary preference are predicted to alter foraging behavior, visits to native plants, and ultimately their seed recruitment patterns, though little empirical work has demonstrated the outcomes of these changes [18].

4.3 The case of Miconia calvescens

Miconia (*Miconia calvescens)* was the most frequently occurring seed in the fecal samples of all three frugivores in this study. The high rates of consumption of Miconia are also reflected in observations of frugivores which frequently visit and consume Miconia in areas where it is abundant.

Miconia is extremely abundant on both Tahiti and Moorea, covering 60 and 10% of the land surface of the islands respectively [44, 45]. Miconia is more abundant than any other species at all sites on Tahiti and at 3 of 5 sites on Moorea (Spotswood unpublished data). Thus, it is unknown whether the high consumption of Miconia by birds reflects true preferences or simply the much greater availability of Miconia relative to other species. Miconia is not only more abundant than many other species but also produces fruit nearly continuously (Spotswood, unpublished data, [46]).

Miconia is regarded as the most important threat of all invasive plants in French Polynesia due to its ability to invade undisturbed native forests at high elevations and its ability to create monotypic stands [32]. At the same time, theoretical evidence predicts that long distance dispersal by vertebrate vectors can alter the dynamics and speed of invasion of plants [47, 48]. The high frequency of consumption of Miconia by birds indicates its importance as a resource to birds, which are probably capable of spreading Miconia seeds to distances much greater than seeds would otherwise be able to travel. Thus, dispersal via avian vectors could trigger modifications in the dynamics of Miconia invasions in French Polynesia including an increase in the speed of spread and the establishment of satellite populations in remote locations [42]. Such changes in dynamics indicate the importance of dispersal agents to plant communities with high numbers of exotic species.

4.4 Conclusion

This study has documented the establishment of multiple novel relationships between exotic and native bird frugivores and plants in French Polyensia. High numbers of recently naturalized plant species in the diets of both native and exotic frugivores suggest that community wide changes are probably taking place. Further research is needed in order to quantify the impacts on regeneration of native plants, the potential for modification of invasion spread dynamics, and the importance of alien plants as resources for frugivores.

5. ACKNOWLEDGMENTS

We thank Ravahere Taputuarai, Colleen Cassidy, Carol Raydon, and Hela Tetaunui for assistance in the field and in the lab. The staff at the Richard B. Gump station contributed logistic support. James Bartolome, Jean-Claude Thibault, John Battles, Brent Mishler, Bradley Balukjian, David Hembry, and Kari Roesch Goodman gave much needed advice on methods, troubleshooting and occasional assistance in the field. The work was conducted under the UC Berkeley Animal Care and Use Committee's Master Animal Use Protocol for Research #R313-0609 and a Protocol d'Accueil administered by the Délégation à la Recherche, Polynésie française. Capture of Fruit Doves was possible under the collecting permit for protected species delivered by the Minister of the Environment, Government of French Polynesia, to the second author for a period of two years (Arrêté n°1207/PR du 17 Avril 2007). The first author received financial support from a Fulbright Advanced Student Fellowship, a PEO International Scholarship, the Cooper Ornithological Society and Berkeley Sigma Xi.

6. REFERENCES

[1] Nathan R, Muller-Landau HC (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15: 278

[2] Levine JM, Murrell DJ (2003). The community-level consequences of seed dispersal patterns. Annual Review of Ecology, Evolution and Systematics 34: 549

[3] Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmanek M (2000). Plant invasions - the role of mutualisms. Biological Reviews 75: 65

[4] Gibbs D, Barnes E, Cox J (2001) Pigeons and Doves: A Guide to the Pigeons and Doves of the World. Yale University Press, New Haven

[5] Gouni A, Zysman T (2007). Oiseaux du Fenua: Tahiti et ses Iles Tethys Editions, Papeete, French Polynesia

[6] Holyoak DT, Thibault JC (1984). Contribution à l'étude des oiseaux de Polynésie Orientale. Mémoires du Muséum National d'Histoire Naturelle Nouvelle Série 127: 62

[7] Holyoak DT (1974). Les oiseaux des îles de la Société. Oiseau & Revue française d'Ornithologie 44: 153

[8] Bruner PL (1972). The Birds of French Polynesia Pacific Science Information Center, Bishop Museum, Honolulu

[9] Seitre R, Seitre J (1992). Causes of land-bird extinctions in French Polynesia. Oryx 26: 215

[10] Gosper CR, Stansbury CD, Vivian-Smith G (2005). Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. Diversity and Distributions 11: 549

[11] Buckley YM, Anderson S, Catterall CP, Corlett RT, Engel T, Gosper CR, Nathan RAN, Richardson DM, Setter M, Spiegel ORR (2006). Management of plant invasions mediated by frugivore interactions. Journal of Applied Ecology 43: 848

[12] Thibault JC, Martin JL, Penloup A, Meyer JY (2002). Understanding the decline and extinction of monarchs (Aves) in Polynesian Islands. Biological Conservation 108: 161

[13] Monnet C, Thibault JC, Varney A (1993). Stability and changes during the twentieth century in the breeding landbirds of Tahiti (Polynesia). Bird Conservation International 3: 261

[14] Dhondt AA (1977). Breeding and postnuptial molt of the Red-Vented Bulbul in Western Samoa. Condor: 257

[15] Blanvillain C, Salducci JM, Tutururai G, Maeura M (2003). Impact of introduced birds on the recovery of the Tahiti Flycatcher (*Pomarea nigra*), a critically endangered forest bird of Tahiti. Biological Conservation 109: 197

[16] Roberts TJ (1991) The Birds of Pakistan. Oxford University Press, New York

[17] Kirch PV (2002) On the Road of the Winds: An Archaeological History of the Pacific Islands Before European contact. University of California Press, Berkeley

[18] Traveset A, Richardson DM (2006). Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution 21: 208

[19] Traveset A, Riera N (2005). Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. Conservation Biology 19: 421

[20] Higgins PJ, Peter JM, Cowling SJ (2005). Handbook of Australian, New Zealand, and Antarctic Birds: Boatbill to Starling Oxford University Press, Auckland 7

[21] Guild E (1938). Tahitian aviculture: Acclimatization of foreign birds Aviculture Magazine 5: 8

[22] Coote T, Loeve E (2003). From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme. Oryx 37: 91

[23] Clarke B, Murray J, Johnson MS (1984). The extinction of endemic species by a program of biological control. Pacific Science 38: 97

[24] Steadman DW (2006) Extinction & Biogeography of Tropical Pacific Birds. University of Chicago Press, Chicago

[25] Meyer JY (2004). Threat of invasive alien plants to native flora and forest vegetation of Eastern Polynesia. Pacific Science 58: 357

[26] Mueller-Dombois D, Fosberg FR (1998) Vegetation of the tropical Pacific Islands. Springer, New York

[27] Paulay G (1994). Biodiversity on oceanic islands: Its origin and extinction Integrative and Comparative Biology 34: 134

[28] Courchamp F, Chapuis JL, Pascal M (2003). Mammal invaders on islands: impact, control and control impact. Biological Reviews 78: 347

[29] Gillespie RG, Claridge EM, Goodacre SL (2008). Review. Biogeography of the fauna of French Polynesia: diversification within and between a series of hot spot archipelagos. Philosophical Transactions of the Royal Society B: Biological Sciences 363: 3335

[30] Florence J (1993). La végétation de quelques îles de Polynésie française. Atlas de la Polynésie française (ed. Dupon JF), pp. 54 - 55. Paris, France: ORSTOM

[31] Meyer JY, Salvat B (2009) In: Gillespie RG (ed) Encyclopedia of Islands. University of California Press, Berkeley p 332

[32] Meyer JY, Florence J (1996). Tahiti's native flora endangered by the invasion of Miconia calvescens DC (Melastomataceae). Journal of Biogeography 23: 775

[33] Fourdringniez M, Meyer JY (2008). Liste et caractéristiques des plantes introduites naturalisées et envahissantes en Polynésie française

Contribution à la Biodiversité de Polynésie française N. 17 Délégation à la Recherche, Papeete Tahiti

[34] Watling D (1983). The breeding biology of the red-vented bulbul Pycnonotus cafer in Fiji. Emu 83: 173

[35] Ali S (1955) The book of Indian birds. Printed for Mathew Collins and Francis Cossinet, London

[36] Thibault JC, Monnet C (1990). Le Zosterops à poitrine grise *Zosterops lateralis* (Latham) en Polynésie: un oiseau introduit devenu colonisateur actif L'Oiseau & Revue française d'Ornithologie 60: 233

[37] Bruner A (1979). Red-vented Bulbul now in Tahiti. Elapio 40: 92

[38] Steadman DW, Freifeld HB (1999). The food habits of Polynesian pigeons and doves: a systematic and biogeographic review. Ecotropica 5: 13

[39] Simberloff D, Von Holle B (1999). Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions 1: 21

[40] Mandon-Dalger I, Clergeau P, Tassin J, Riviere JN, Gatti S (2004). Relationships between alien plants and an alien bird species on Reunion Island. Journal of Tropical Ecology 20: 635
[41] Stansbury CD (2001). Dispersal of the environmental weed Bridal Creeper, *Asparagus asparagoides*, by Silvereyes, *Zosterops lateralis*, in south-western Australia. Emu 101: 39
[42] Spotswood E (2009). Dispersal of *Miconia calvescens* by birds in the Society Islands (French Polynesia) *In Press*. Proceedings of the Second Regional Conference on Miconia Control, Maui, Hawaii, U.S.A.
[43] Butaud JF, Gérard J, Guibal D (2008) Guide des Arbres de Polynésie française: Bois et Utilisations. Au Vent des Iles, Papeete
[44] Meyer JY (1996). Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pacific Science 50: 66
[45] Pasari J (2000). Integration of the invasive plant *Miconia calvescens* DC on Moorea, French Polynesia. Biology and Geomorphology of Tropical Islands 9: 142
[46] Meyer JY (1998). Observations on the reproductive biology of *Miconia calvescens* DC (Melastomataceae), an alien invasive tree on the island of Tahiti (South Pacific Ocean). Biotropica 30: 609
[47] Clark JS, Lewis M, Horvath L (2001). Invasion by extremes: population spread with variation in dispersal and reproduction. American Naturalist 157: 537
[48] Neubert MG, Parker IM (2004). Projecting rates of spread for invasive species. Risk Analysis 24: 817