

Relationships between alien plants and an alien bird species on Reunion Island

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Abstract: Many studies have shown that plant or bird invasions can be facilitated by native species, but few have demonstrated the possibility of a positive interaction between introduced species. We analysed the relationships between four invasive alien fleshy-fruited plants, *Clidemia hirta*, *Rubus alceifolius*, *Lantana camara*, *Schinus terebinthifolius*, and an invasive alien bird, the red-whiskered bulbul *Pycnonotus jocosus* introduced to Reunion Island (Indian Ocean). We compared the distribution of food items in the bulbul diet according to seasons and to abundance classes of this bird. *Pycnonotus jocosus* is mostly frugivorous and frequently eats the main alien plants (more than 80% frequency of food items). Sites with alien species, such as *Clidemia hirta*, providing fruits throughout the year supported more birds than sites providing fruits, such as *Schinus terebinthifolius*, seasonally. The birds facilitated seed germination by removing the pulp of fruit: the final per cent germination (FG) of cleaned seeds was higher than those within the fruit for three of the four plant species and in some cases passage through birds significantly increased FG (*Schinus terebinthifolius*) or Coefficient of Velocity (CV) (*Lantana camara*).

Key Words: *Clidemia hirta*, frugivorous bird, germination, invasion, mutualism, propagation, *Pycnonotus jocosus*

INTRODUCTION

Typical attributes of invasive plants, such as a short juvenile period, a short interval between large seed crops and low seed weight (Rejmánek & Richardson 1996), lead to early and consistent reproduction, and also rapid population growth. These plants, and their seeds and fruits, can produce an important resource available for birds at any given time of the year (Van Riper *et al.* 1979). On the other hand, high dispersal ability, omnivory and gregariousness are commonly believed to increase the chances of colonization and establishment of exotic birds (Ehrlich 1989, Holway & Suarez 1999). In contrast to biotic resistance, most studies of invasions ignore facilitative interactions (Richardson *et al.* 2000). Many studies of interactions between exotic and native species explain how plant or bird invasions could be facilitated by native species (Ferguson & Drake 1999, Richardson *et al.* 2000, reviewed in Levey *et al.* 2002). However, according

to Simberloff & Von Holle (1999), few studies have shown the possibility of a positive interaction between introduced species.

One of the main problems in conservation biology is the rapidity of the colonization of introduced plant species and their negative effects on the native vegetation (Gargominy *et al.* 1996, Lorence & Sussman 1986, Meyer & Florence 1996). Introduced birds also threaten biodiversity (Pratt 1994) and involve socio-economic costs (Clergeau *et al.* 2002). Reunion Island belongs to one of the world's 25 biodiversity hot spots (Myers *et al.* 2000). Many plant (MacDonald *et al.* 1991) and bird (Cheke 1987, Simberloff 1992) species have been introduced to Reunion. These include introductions of fruit plants (Strasberg 1995) and frugivorous birds (Clergeau & Mandon-Dalger 2001, Mandon-Dalger *et al.* 1999, Tassin & Rivière 2001). The recent introduction of a frugivorous bird, the red-whiskered bulbul *Pycnonotus jocosus*, in 1972, was an opportunity to examine the interactions between this species and invasive plant species introduced earlier such as *Rubus alceifolius*, *Lantana camara* and *Schinus terebinthifolius* or contemporaneously with the bulbul such as *Clidemia hirta*.

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The shrub *C. hirta* is considered to be one of the most disruptive alien plants in regions where it has been introduced, especially on islands of the tropical parts of the Pacific and Indian Oceans (Wester & Wood 1977). Native to Central and South America, this plant is a successful invader as described by Rejmánek & Richardson (1996): each fruit contains over 300 seeds (Gatti 2000), juvenile stage is short (6–10 mo), mature plants produce over 500 fruits per year and, though it is considered as a tree fall-gap specialist (Peters 2001), it has broad environmental tolerances (Wester & Wood 1977).

The red-whiskered bulbul, native to south Asia, is also a pest bird in many places where it has become established, such as California, Florida, Hawaii, Sumatra or Australia (Lever 1987, Williams & Giddings 1984). Previous studies have shown that the diet of red-whiskered bulbul includes insects, buds, and fruits of native and alien plants (Carleton & Owre 1975). Damage caused by this bird to orchards in all the regions where it has been introduced suggest also the importance of fruits in its diet. On Reunion Island, only suggestions (Lavergne *et al.* 1999, MacDonald *et al.* 1991), or unpublished works (C. Thébaud, unpubl. data) have reported that this bulbul can disperse introduced plants such as *R. alceifolius* and *Ligustrum robustum*.

The main goal of this study was to find out if the invasion of some alien plants has been facilitated by the red-whiskered bulbul, and that, as a feed-back process, eating fruits and spreading seeds of alien plants which grow easily could be a way to survive and colonize new sites on Reunion. The distribution of the red-whiskered bulbul on Reunion has been published elsewhere (Mandon-Dalger *et al.* 1999) and largely overlaps in the eastern part of the island with *C. hirta* (T. Le Bourgeois, *pers. comm.*). Although another hypothesis on co-occurrence resulting from similar habitat preferences could be considered, here we focused our analysis to examine relationships between these species: Does the red-whiskered bulbul eat alien plants? Is the red-whiskered bulbul more abundant in sites invaded by these alien plants and during their fruiting season? Does the red-whiskered bulbul facilitate germination of alien plants such as *C. hirta*, *R. alceifolius*, *L. camara* and *S. terebinthifolius*?

MATERIALS AND METHODS

Study area

Reunion Island (21° S, 55° E) is located near Mauritius in the Indian Ocean, east of Madagascar. The island, 50 km wide by 70 km long, has an area of 2512 km², and reaches a height of 3069 m (on the volcano Piton des Neiges). The climate is characterized by a warm rainy season from November to April, and a cool dry season

from May to October. The rugged relief supports marked local variations in rainfall between the windward (east) and leeward (west) sides. The leeward coast, which is in a rain shadow, receives about 1000 mm y⁻¹, whereas on the eastern windward slopes it varies from 3000–10 000 mm y⁻¹ depending on altitude.

Diet analysis

We studied the diet of the red-whiskered bulbul from October 1998 to June 2000. Following previous results (Mandon-Dalger 2002), we divided this period into three: (1) October to December, the first part of the bird breeding season, (2) January to March, the second part of the breeding season and the moulting season and (3) April to June, the first part of the non-breeding season. The second part of the non-breeding season was not studied.

Among the many methods of studying passerine diets, we chose faecal analysis because it causes minimum disturbance and is directly related to seed dispersal (Tatner 1983). We obtained bird droppings (n = 185 from 185 birds; 72 in period (1), 29 in period (2) and 84 in period (3)) using two methods. First, birds were captured with mist-nets and then were kept in cardboard boxes or clean bags (Herrera 1984) for about 1 h. Second, we used captive-decoy traps: in a part of the trap we used a captive decoy bird and in another part of the trap we baited with fruit to capture resident birds which then defecated in the trap; droppings were collected directly in a simple removable bottom. The fresh faecal samples were preserved in dilute alcohol. They were examined with a binocular microscope to identify food items with the help of reference collections or with the use of identification keys.

We conducted diet analysis in nine plots representative of the four main landscapes of the island, i.e. coastal towns (T), sugar cane plantations (C), orchards (O) and forest (F), on both windward and leeward sides of Reunion Island (Figure 1). We concentrated our study on sugar cane plantations and orchards, the main habitats of bulbuls (Mandon-Dalger 2002). More than 50 h of trapping activity were conducted with mist-nets and traps in each landscape (O) and (C). All in all, capture effort was 9845 h mist-net m⁻¹ and 253.5 trap d.

When a bird was caught and had eaten a food item, we considered that this resource was available in the plot during this season. We compared the distribution of items in the bulbul diet according to seasons. We distinguished permanent resources (P) which were consumed all year round, from seasonal resources (S) using Kruskal–Wallis χ^2 non-parametric test.

Relationships between bird abundance and alien plants

We hypothesized that availability of resources is responsible for the abundance of birds. We examined the

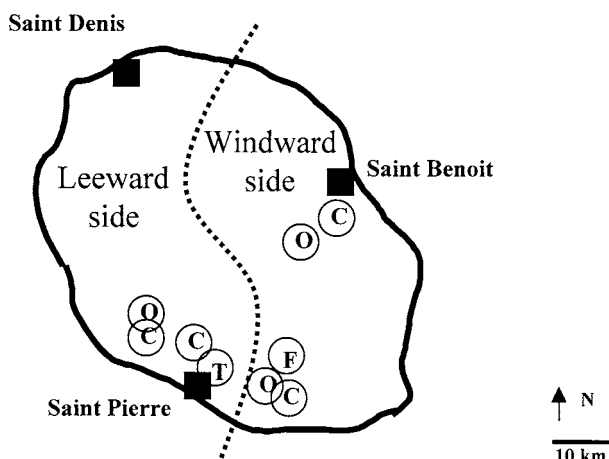


Figure 1. Distribution of the nine study plots on Reunion Island: T = in town, C = in sugar cane, O = in orchards and F = in forest.

possible effect of the presence of food items on the local abundance of red-whiskered bulbul in three steps:

(1) We determined the spatial variation of bird abundance and classified plots according to their bird abundances. We quantified abundance of red-whiskered bulbul with the IPA method (Indice Ponctuel d'Abondance, Bibby *et al.* 2000). In the nine capture plots, we recorded the number of birds seen or heard within about 140-m radius, equivalent to visibility and hearing limits. The same observer conducted all surveys throughout the study period. Each census lasted 10 min (Kwok & Corlett 1999) and was repeated three times during the same day at 6h30–10h00, 10h00–14h30 and 14h30–18h00 periods. Three census days were realized in each plot during the same month as captures. Then plots were categorized into eight classes (Sturge's rule, Scherrer 1984) with class intervals of 4.63 bird averages. Two classes were empty, so we present results on the six classes, from plots with few bulbuls to plots with many bulbuls: class 1 = 0–4.63 birds, class 2 = 4.64–9.26, class 3 = 9.27–13.89, class 4 = 13.90–18.52, class 5 = 23.15–27.78 and class 6 = 32.41–37.

(2) We studied the distribution of food items according to the abundance class of red-whiskered bulbuls in order to determine the capacity of these items to discriminate bird abundance classes. First, we used a Kruskal–Wallis χ^2 non-parametric test in order to show whether the presence of some alien plant species in the droppings

was correlated with red-whiskered bulbul abundance or not (Morse 1985). Using Bonferroni correction, we eliminated tests providing values superior to 0.0052 in order to conserve significance level at $P = 0.05$, and for those providing values superior to 0.00014 (Table 2) to conserve significance at $P = 0.001$. Second, a multivariate discriminant function analysis was used to link the distributions of the bulbul abundance classes to the food item variables. Axes were constructed from bird abundance data set along which the differences among populations of birds were maximized according to discriminating items. Pertinence of discriminant function analysis was confirmed using a permutation test (Thioulouse *et al.* 1997).

(3) We examined the proportion of discriminant alien plants and the consumption of permanent and seasonal resources in the different bird abundance classes. We took into account the distinction between seasonal and permanent resources and studied their variation according to bird abundance classes using the Kruskal–Wallis χ^2 non-parametric test.

Effect of seed ingestion on germination

Fruits of four very abundant alien fleshy-fruited plants (*R. alceifolius*, *L. camara*, *C. hirta* and *S. terebinthifolius*; characteristics in Table 1) were collected in 2000 on the basis of red-whiskered bulbul diet results and the potential threat that these plants presented (MacDonald *et al.* 1991). Fruits of each species were prepared in three ways to test the facilitation effect of fruit ingestion on their germination capacity. Batch A: intact fleshy fruits were put into germination conditions on the day after collection (intact fruit). Batch B: seeds were manually extracted and rapidly washed (cleaned seeds), also 1 d after collection, and were put into germination conditions. Batch C: fruits were fed to 10 captive red-whiskered bulbuls, seeds were collected from the droppings, rapidly washed, and were put into germination conditions on the day following the defecation (defecated seeds). Each treatment was replicated four times for each species, using 25 seeds (intact fruits, cleaned seeds, defecated seeds) for each replication.

The three batches were sown in Petri dishes on sterilized sand saturated with water. During the study period, dishes were maintained at 24 °C, with 12 h light per day

Table 1. Main characteristics of the four studied alien plants. Average data from Bosser *et al.* (1976).

	Classification of plant	Size of plant (m)	Classification of fruit	Size of fruit (mm)	Number of seeds per fruit	Size of seed (mm)
<i>Clidemia hirta</i> L.	Shrub	0.5–1.5	Berry	7–8	300–400	0.5
<i>Lantana camara</i> L.	Shrub	2–5	Drupe	3–6	1–2	1.5–3
<i>Rubus alceifolius</i> Poir.	Liana	5–6	Aggregate fruit	15–25	10–30	1.5–2
<i>Schinus terebinthifolius</i> Raddi	Small tree	3–7	Drupe	3–5	1	4

Table 2. Diet of red-whiskered bulbul on Reunion Island during the study: 1. Percentage calculated from item frequencies (n = 185), 2. Distribution test of the food items according to three seasonal periods (October–December: n = 72, January–March: n = 29, April–June: n = 84; except for *Clidemia hirta* calculated only from eastern region) and 3. Distribution test of the food items according to six abundance classes of red-whiskered bulbul (see Methods). In this last analysis, we have excluded items that represent less than 5% (noted + in 1. Item %) of occurrence in global sample. **P** = Permanent resource, **S** = Seasonal resource.

Diet items	Order/Family	Species	1. Item % Oct–June (n = 185)	2. Distribution of food items according to seasonal periods			Kind of resource (ns → P) (* → S)	3. Distribution of food items according to abundance classes of bulbul		
				χ^2	P	Significance after Bonferroni correction		χ^2	P	Significance after Bonferroni correction
Plant			98							
	Melastomataceae	<i>Clidemia hirta</i> #	25	2.12	0.346	ns	P	160	< 0.0001	***
	Verbenaceae	<i>Lantana camara</i> #	43	25.4	< 0.0001	***	S	26.7	0.0001	***
	Solanaceae	<i>Solanum</i>	11	2.33	0.310	ns	P	8.66	0.124	ns
		<i>auriculatum</i> #								
		<i>Solanum nigrum</i>	28	67.7	< 0.0001	***	S	50.2	< 0.0001	***
		<i>Nicandra physaloides</i>	+	4.98	0.083	ns				
		<i>Capsicum frutescens</i>	+	2.42	0.298	ns				
	Anacardiaceae	<i>Schinus</i>	16	41.1	< 0.0001	***	S	58.1	< 0.0001	***
		<i>terebinthifolius</i> #								
	Myrtaceae	<i>Psidium</i>	13	12.7	0.0017	*	S	14.3	0.013	ns
		<i>cattleianum</i> #								
	Rosaceae	<i>Rubus alceifolius</i> #	11	17.3	0.0002	**	S	8.26	0.142	ns
	Moraceae	<i>Morus alba</i>	6	4.2	0.122	ns	P	5.25	0.386	ns
	Lauraceae	<i>Litsea glutinosa</i> #	6	10.1	0.0064	ns	P	9.74	0.083	ns
		<i>Aphloia theiformis</i>	5	5.21	0.074	ns	P	7.05	0.217	ns
		An unidentified large seed	5	17.3	0.0002	**	S	54.3	< 0.0001	***
		Unidentified small seeds	15	1.64	0.440	ns	P	9.74	0.830	ns
		Plant fragments	17	7.46	0.024	ns	P	29.7	< 0.0001	***
Animal			46							
Arthropods										
	Coleoptera	<i>Cratopus</i> sp.	22	38.8	< 0.0001	***	S	62.3	< 0.0001	***
		others	8	3.28	0.194	ns	P	8.14	0.148	ns
	Hymenoptera		6	1.47	0.478	ns	P	3.85	0.571	ns
	Diptera		+	0.06	0.969	ns				
	Lepidoptera		+	0.44	0.803	ns				
	Orthoptera		+	0.43	0.808	ns				
	Other arthropods		24	16.4	0.0003	**	S	32.3	< 0.0001	***
	Arachnida		+	0.61	0.737	ns				
Other invertebrates										
	Gastropoda		+	3.82	0.148	ns				
	Annelida		+	1.95	0.378	ns				
Frequency of bulbuls eating permanent resources (P)							P	43.4	< 0.0001	***
Frequency of bulbuls eating seasonal resources (S)							S	2.64	0.754	ns

alien plant species.

and the moisture was controlled. Every day, dishes were examined: germinated seeds were counted and removed to reduce a possible effect on non-germinated seeds. Germination was defined as radicle emergence from seed or fruit. For each species and treatment, the final per cent germination (FG) and the coefficient of velocity (CV) were calculated (Clergeau 1992, Scott *et al.* 2000). The coefficient of velocity is calculated from $CV = 100 \left[\frac{\sum N_i}{\sum N_i T_i} \right]$, where N is the number of seeds germinated on day *i* and T is the number of days from sowing. CV increases as more seeds germinate and with a shorter germination time (Scott *et al.* 1984). Germination indexes were compared between treatments, using one-way analysis of variance (ANOVA). Proportions were angular transformed before analysis and Bonferroni's test was used to compare means.

RESULTS

Bulbul diet

Both plant and animal items were eaten (Table 2), but the diet was mostly vegetarian (98.4% total frequency of occurrence of plant items, n = 185). Plant items belonged to at least eight plant families. Animal items involved eight invertebrate orders, six of them being arthropods. No vertebrates were found.

We recorded several alien species identified as having a high importance value by MacDonald *et al.* (1991), including *C. hirta*, *L. camara*, *Solanum auriculatum*, *S. terebinthifolius*, *Psidium cattleianum*, *R. alceifolius* and *Litsea glutinosa*. These species were eaten by a large

majority of red-whiskered bulbuls (87%, $n = 185$). *Clidemia hirta* was present in 95.8% ($n = 48$) of our bird samples from the eastern part of the island, the only part where *C. hirta* was present. We have found up to 2000 seeds of *C. hirta* per dropping.

Clidemia hirta and *S. auriculatum* can be considered as permanent fruit resources (Table 2) because they were eaten throughout the study period (respectively $P = 0.346$ and $P = 0.310$). Although fruiting occurs throughout the year, *L. camara* was not found in the bulbul's diet in the same proportion in the different seasons ($P < 0.0001$) and has therefore been classified as a seasonal resource. *Schinus terebinthifolius* and *Solanum nigrum* were clearly seasonal fruit resources ($P < 0.0001$), like *P. cattleianum* and *R. alceifolius*.

Relationships between alien plant and bulbul abundance locations

If we excluded items that represent less than 5% of occurrence in the global sample, the six bird abundance classes showed significant variation in the consumption of food for 8 (with Bonferroni correction) of the 17 items (Table 2), of which three were alien invasive plant species, three were weeds or unidentified and two were arthropods. It appears that (1) some items (*L. camara*, *Solanum nigrum* and Other arthropods) were eaten in each bird abundance class; (2) some items (*C. hirta* and less significantly *Cratopus* sp.) were eaten in plots where bulbuls were abundant; and (3) some items (*S. terebinthifolius*) were eaten in areas where few birds were present. The alien invasive plant species that we have characterized as permanent fruit resources were eaten in plots where bulbuls showed a high abundance ($P < 0.0001$; Table 2). *Clidemia hirta* seemed to be the most typical of these plots.

This point was confirmed by discriminant function analysis. The analysis showed that bird abundance classes were clearly separated by the first factorial axis (permutation test, $n = 10\,000$, $P < 0.0001$; Figure 2). The two first axes represented 75% of inertia. The equation of the first factorial axis gave the higher normalized values for *Clidemia hirta* (0.971) and suggested that this plant was principally responsible for distinction of plots with few birds (classes 1, 2, 3) from other plots (classes 4, 5, 6).

Effect of seed ingestion on germination

The onset of the germination period was similar for the four species, being about 5–12 d. However germination curves differed from species to species, with many *S. terebinthifolius* seeds germinating very quickly in the first 10 d whereas *R. alceifolius*, *C. hirta* and *L. camara* seeds

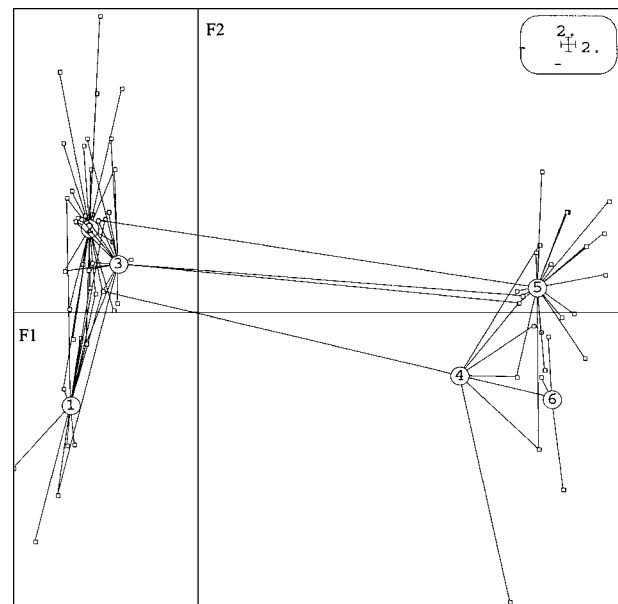


Figure 2. Representation of the two first axes of discriminant function analysis. Numbers represent centres of gravity abundance classes of red-whiskered bulbul, from class 1 with few birds to class 6 with numerous birds (see Methods). Because many birds had the same diet on the same plot, numerous faecal samples are superposed.

showed a more progressive germination curve lasting more than 100 d.

The final percentage germination FG showed significant differences between treatments for three species (Table 3). In each of these species, FG of defecated seeds (batch C) seeds was higher than FG of the fruit (batch A). However *Schinus terebinthifolius* was the only species for which FG of ingested seeds was significantly higher than that of cleaned seeds. The coefficient of velocity related to *L. camara* was higher both for cleaned and defecated seeds than for seeds within fruit. Even if the other results were not so clear, these results corroborate the action of birds on seed germination of alien plant species.

DISCUSSION

Feeding behaviour

The red-whiskered bulbul has been described as an opportunistic bird, eating fruits, buds, insects (Carleton & Owre 1975, Van Riper *et al.* 1979) and even nectar (Olesen *et al.* 1998). On Reunion Island, we confirmed that the red-whiskered bulbul was mostly frugivorous. Among the fruit species, we noted that fruits of alien species of high importance value (MacDonald *et al.* 1991), especially *Clidemia hirta*, *Psidium cattleianum*, *Rubus alceifolius*, *Lantana camara*, *Solanum auriculatum*, *Litsea glutinosa* and *Schinus terebinthifolius* were eaten by a

Table 3. Germination rates FG and velocity coefficients CV of seeds (in four replications \times 25 seeds) of four alien plant species among three treatments: A = seeds within fresh fruits, B = cleaned seeds, C = defecated seeds. -: not sown. Tests = ANOVA.

	Fruit A	Cleaned B	Defecated C	test 1 (A to C)	test 2 (B to C)
Final per cent germination FG					
<i>Clidemia hirta</i>	–	0.88 \pm 0.06	0.89 \pm 0.10		0.64ns
<i>Rubus alceifolius</i>	0.24 \pm 0.09	0.53 \pm 0.05	0.51 \pm 0.17	0.02*	0.98ns
<i>Lantana camara</i>	0.01 \pm 0.02	0.48 \pm 0.28	0.63 \pm 0.09	< 0.01**	0.47ns
<i>Schinus terebinthifolius</i>	0.22 \pm 0.11	0.68 \pm 0.05	0.97 \pm 0.06	< 0.001***	< 0.001***
Coefficient of velocity CV					
<i>Clidemia hirta</i>	–	1.02 \pm 0.06	1.08 \pm 0.03		0.09ns
<i>Rubus alceifolius</i>	1.19 \pm 0.25	1.38 \pm 0.15	1.40 \pm 0.17	0.34ns	0.99ns
<i>Lantana camara</i>	0.20 \pm 0.40	1.12 \pm 0.16	1.20 \pm 0.09	< 0.01**	< 0.01**
<i>Schinus terebinthifolius</i>	8.71 \pm 1.29	25.6 \pm 9.76	13.4 \pm 3.77	0.55ns	0.05*

large majority of bulbuls. This bird eats fruits of small seed diameter (Kitamura *et al.* 2002). Although some alien plants can be considered to constitute seasonal resources (e.g. *S. terebinthifolius* and *R. alceifolius*), we observed that others are clearly permanent resources (e.g. *C. hirta*, *S. auriculatum*).

Fruit production is less predictable than other food resources (Pérez-Tris & Telleria 2002). Opportunistic behaviour of birds allows them to exploit resources scattered in space and time, especially in the tropics where fruiting is often not synchronized (Brown & Hopkins 1996) and in montane forests where flowering and fruiting patterns depend on altitude (Kimura *et al.* 2001). We observed that sites providing fruits, such as *C. hirta*, throughout the year were characterized by more abundant red-whiskered bulbuls than sites providing seasonal fruits, such as *L. camara*. Invasive plant species with continuous fruiting could be one of the factors determining the distribution of this bird. First this permanent resource can help survival in periods of shortage or provide supplements to seasonal resources. Second it can also help in the successful colonization of the alien consumer throughout the island. Although the red-whiskered bulbul seems to be sedentary in a large part of its native range (Ali & Ripley 1971), roost behaviours and juvenile dispersal which involve birds moving away from their home range could contribute to seed dispersal. This spatial hypothesis of a positive species interaction is supported by our observation that *C. hirta* first occupied new sites in dense rows immediately below cables where bulbuls regularly perched. Experiments, for example using perches, have to be conducted to demonstrate this process more clearly.

Facilitation of plant species

These exotic plants were not only dispersed by frugivorous birds, but also had their germination facilitated by ingestion. We have corroborated that the main effect of birds on ingested seeds was pulp removal.

This confirms the result of Mayer & Poljakoff-Mayer (1989) that germination inhibitors in the pulp may prevent germination within the fruit. Defecated seeds of *S. terebinthifolius* have both a higher germination percentage and a shorter dormancy than pulp-removed seeds. In this case gut passage had a positive effect on germination.

The dispersal effects of birds are well documented (see review in Janzen 1983, Levey *et al.* 2002), but the role of birds in seed germination has been much less studied. Results obtained in Mediterranean conditions (Debussche 1985, Izhaki & Safriel 1990), in temperate conditions (Clergeau 1992, Sorensen 1981), in tropical conditions (Barnea *et al.* 1990, Tassin & Rivière 2001) and in this work, indicate that birds significantly enhance the capacity of germination: the effect is at least similar to the removal of the fruit pulp, and sometimes enhances germination rate. This later role varies according to plant species and perhaps retention time in the gut as suggested by Clergeau (1992). This is consistent with a previous study attesting the dependence of *S. terebinthifolius* recruitment to bird ingestion (Panetta & McKee 1997).

Information on seed dispersal of these alien plants (e.g. *L. camara*, *S. auriculatum*, *R. alceifolius*, *L. glutinosa*) needs more details. These last species have been widely spread in Reunion Island (Tassin & Rivière 2003) and are supposed to have reached the limits of their spatial extension.

Mutualism between animal and plant species

There is evidence that bulbuls disperse *C. hirta* and that the bird is common where this alien plant occurs. Our results suggest that the invasion of Reunion Island by *C. hirta* could be facilitated by frugivorous birds like the red-whiskered bulbul. The maintenance of high bulbul populations throughout the year in sites containing *C. hirta* can enhance local reproduction and dispersal of the alien plant, which in turn allows the bulbul to maintain and reproduce itself. This could be a mutualism

cycle in which both invasive bird and invasive plant favour each other. Watling (1978) had also suggested that the restricted distribution of *Pycnonotus cafer* in the Fiji Islands coincided with that of several weed species which constitute its main food supply and probably limit its spread.

However, the expansion of bulbul may not depend on the shrub. Climate and especially rainfall, could be an important covariant factor providing several fruiting periods over the year for other fleshy-fruited plants (Mandon-Dalger 2002). Similarly, bulbuls are obviously not the only disperser of *C. hirta*: other birds and human shoes disseminate these weeds. However multiplication of seed dispersers, including alien birds added to native birds, could provide introduced plants a way to become invasive (Richardson *et al.* 2000). As suggested by Olesen *et al.* (2002), an invader complex is constituted by introduced species interacting more frequently than expected by chance alone. *Clidemia hirta*, *L. camara*, *R. alceifolius* and *S. terebinthifolius* are obviously included in an invader complex involving more or less long-distance dispersers such as people and birds.

In accordance with Simberloff & Von Holle (1999), we observed a possible synergistic interaction between alien species and we can suggest that propagation of each alien species could be accelerated. So, modifications of habitat and impacts on native ecosystem by synergism between alien species could be greater than the sum of the impacts of the individual species and need new research in applied ecology.

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