# The red vented-bulbul (*Pycnonotus cafer*): invasion dynamics and ecological impacts of an introduced pest bird in New Caledonia and implications for management.



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*To Marie-Madeleine Thibault*

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**This thesis is the result of a collaboration between**



*Wildlife & Ecology Group, School of Agriculture and Environment*

**and**



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# Preface

This thesis is structured as a series of connected manuscripts. With the exception of the Introduction and final Discussion, these manuscripts have all been published, or accepted or submitted for publication, at the time of thesis submission. These manuscripts are listed below and are presented in the thesis in separate chapters.

1. Thibault, M., Vidal, E., Potter, M. A., Dyer, E., and Brescia, F. (2018). The red-vented bulbul (*Pycnonotus cafer*): serious pest or understudied invader? *Biological Invasions*, *20*(1), 121-136.
2. M. Thibault, E. Vidal, M.A. Potter, F. Masse, A. Pujapujane, B. Fogliani, G. Lannuzel, H. Jourdan, N. Robert, L. Demaret, N. Barré, and F. Brescia (*Accepted*). Invasion by the red-vented bulbul: an overview of recent studies in New Caledonia. In: C.R. Veitch, M.N. Clout, A. Martin, J. Russell and C. West (eds.) *Island Invasives: Scaling up to meet the challenge*, pp. xx-xx. Gland: IUCN.
3. Thibault, M., Vidal, E., Potter, M. A., Sanchez, T., and Brescia, F. (2018). The invasive Red-vented bulbul (*Pycnonotus cafer*) outcompetes native birds in a tropical biodiversity hotspot. *PloS one*, *13*(2), e0192249.
4. Thibault M., Masse F., Pujapujane A., Lannuzel G., Bordez L, Potter M.A., Fogliani B., Vidal E. and Brescia F. (*Accepted*). "Liaisons dangereuses": The invasive red-vented bulbul (*Pycnonotus cafer*), a disperser of exotic plant species in New Caledonia. *Ecology and Evolution*.
5. Thibault M, Brescia F. Potter M. and Barbet-Massin M. (*In prep*). Global distribution of three highly invasive bird species under climate change. Biodiversity and Distribution

All papers were intentionally prepared as stand-alone pieces of work. For this reason, there is some unavoidable repetition between chapters. For example, in the description of study species and areas. I performed the majority of the work for the papers that form this thesis. This included developing the research questions, experimental designs, data collection, statistical analysis, and writing. My supervisors Prof. Murray Potter, Dr. Fabrice Brescia and Dr. Eric Vidal contributed to the conceptualisation of research and revision of the manuscripts. The coauthors of each paper provided comments during the revision of the manuscripts. Statements of contribution are provided for each manuscript presented in this thesis (Chapter 7, **Appendix 5**).

# Acknowledgements

First, I would like to thank my supervisors. Dr. Fabrice Brescia offered me this PhD opportunity and has always defended the need for a scientific assessment of potential threats to New Caledonia from the introduced red-vented bulbul. Fabrice has always been supportive, encouraging and helpful, always managed to address my urgent needs, provided valuable feedback on draft chapters, and facilitated my participation in international conferences. Fabrice, many thanks for the trust you have placed in me all along these three years

Prof. Murray Potter was my supervisor at Massey University. He came to visit me in New Caledonia and offered me a great working environment during my stays at Massey. He defended my ideas and helped me a lot with English presentations and writing. Murray, I particularly want to thank you for having felt my stress and fears at several occasions, and for those personal conversations and trips that always helped me recovering some serenity. I hope that we'll have occasions to work together again in the future.

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I thank Bruno Fogliani, vice director of IAC, for his personal engagement in the administrative combat which spanned my PhD. He defended the PhD project from the very beginning, he played the role of main supervisor several times, and the one of main collaborator for one chapter, and he permitted my participation in conferences and my trips to Massey and has

always been direct and honest during our discussions. Without you Bruno, I think that this PhD would have probably never been done, thank you. Thanks to Laurent L'huillier and to the IAC as well for having supported this project, offered me a scholarship over the three years and an office at Port Laguerre. IAC gave me access to equipment, to several research teams with whom I developed collaborations, and to the support of several people while I was preparing my experiments; thanks to them. Thanks also to Yves Letourneur, to the Ecole "Doctoral School of the Pacific" (EDP) and the University of New Caledonia for supporting me during this PhD. I was registered at UNC for two years, benefited from their courses and had the chance to engage as a PhD student in their Doctoral committee for those first two years.

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Thanks to the people who collaborated with me for various aspects of this work and shared the authorship of the papers. Many thanks to Ellie Dyer (Zoological Society of London), Nadia Robert (IAC), Laurent Demaret (IAC), Nicolas Barré (IAC), Thierry Sanchez (SCO) and Morgane Barbet-Massin (Paris-Sud University) for sharing your experience, knowledge, data, and helping me in these projects.

People from various institutions also promoted this research program on the red-vented bulbul through collaborations, communications, or discussions. Thanks to Almudena Lorenzo (PZF), Christine Fort (CEN), Pascal Fort (FFCNC), Philipe Caplong (CA), Cendrine Meresse (PS) and Caroline Groseille (PS) for their investment in this subject as environment managers.

I also want to address a personal acknowledgement to the hunters who dedicated time voluntarily in shooting red-vented bulbuls to feed our diet study. A special thank you to Jean Yves Moreau, the main contributor, for his welcoming kindness and his participation in the TV documentary we did together in 2016.

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Finally, thanks to the people who gave me the strength to keep going and reach my PhD objective, through their love and/or unconditional friendship. The ones who deeply shared my

# Abstract

Invasive alien species are a major cause of biodiversity loss globally, especially on islands where high species richness and levels of endemism accentuate their impacts. Various international institutions have constructed lists of the most harmful invasive species to help environment managers at both global and local scales to prioritize their efforts. The red-vented bulbul (*Pycnonotus cafer*) is a passerine bird species considered among the three worst invasive birds on the planet. This species is currently spreading over the tropical archipelago of New Caledonia, one of the 36 world biodiversity hotspots. This dissertation presents the findings of a PhD study conducted in New Caledonia with two objectives: 1) to describe this introduced population, and 2) to evaluate the threats from its dispersal using both existing knowledge and new *in-situ* and *ex-situ* data and a variety of analysis techniques. From the literature, I identified three key impacts explaining the species' status: i) damage to agricultural crops, ii) noxious seed dispersal, and iii) competition with other avifauna. I estimated the local population size (approx. 140,000 individuals), its habitat use (inhabited areas), its density along an urbanization gradient (30-120 ind/km$^2$), and I produced lists of consumed plant and animal species and identified a color preference in the foraging strategy of the red-vented bulbul. Exploration of each impact category revealed i) substantial losses on fruit production (18% of tomato production), ii) impact on the abundance of nine native bird species that may be driving a spatial reassembly of the community, and iii) a short distance dispersal (77-92 m) that could promote the dispersal of introduced plant species at the expense of endemic species. Finally, through modelling, I estimated the climatic niche of the species at a global scale and identified that most island territories as suitable for the establishment of this invasive bird species. Regardless of whether the red-vented bulbul diserves its status as "world worst" species, quantitative impact assessments in its alien range such as the studies presented here are needed to prevent the dispersal and harmful impacts of this species on human activities and sensitive ecosystems. Implications for management are discussed.

# Résumé

Les espèces exotiques envahissantes sont une cause majeure de perte de biodiversité à l'échelle mondiale, en particulier sur les territoires insulaires où la richesse en espèces et les niveaux d'endémisme accentuent leurs impacts. Des listes d'espèces envahissantes parmi les plus nocives ont été conçues par des organismes internationaux pour aider les gestionnaires de l'environnement à hiérarchiser leurs efforts à l'échelle mondiale et locale. Le bulbul à ventre rouge (*Pycnonotus cafer*) est une espèce d'oiseau considérée parmi les trois pires oiseaux envahissants de la planète. Cette espèce colonise actuellement l'archipel de la Nouvelle-Calédonie, l'un des 36 hotspots mondiaux de biodiversité. Ce mémoire présente les résultats d'une thèse menée avec deux objectifs: 1) décrire la population introduite en Nouvelle-Calédonie et 2) évaluer les menaces liées à sa dispersion en utilisant les connaissances disponibles, la collecte de données *in-situ* et *ex-situ* et diverses techniques d'analyses statistiques. À partir de la littérature, j'ai identifié trois impacts clés expliquant le statut de l'espèce: i) les dégâts sur les productions agricoles, ii) la dispersion des graines de plantes envahissantes et iii) la compétition avec l'avifaune. J'ai estimé la taille de la population locale (environ 140 000 ind), son utilisation de l'habitat (zones habitées), sa densité le long d'un gradient d'urbanisation (30-120 ind / km2). J'ai dressé des listes d'espèces végétales et animales consommées et identifié une couleur préférée dans la stratégie de recherche de nourriture du bulbul à ventre rouge. L'exploration de chaque catégorie d'impact a révélé i) des pertes substantielles sur la production fruitière (18% de la production de tomate), ii) un impact sur l'abondance de 9 espèces d'oiseaux natifs, pouvant conduire à un réassemblage spatial de la communauté, et iii) une dispersion à courte distance (77-92 m) qui pourrait favoriser les espèces végétales introduites par rapport aux espèces endémiques après la digestion. J'ai finalement estimé la niche climatique de l'espèce à l'échelle mondiale et j'ai mis en évidence que la plupart des territoires insulaires sont climatiquement favorables à l'établissement de cette espèce d'oiseau envahissante. Si les efforts actuels de recherche et de gestion consacrés au bulbul à ventre rouge à l'échelle mondiale ne justifient pas son statut d'espèce parmi les «pires au monde», des évaluations quantitatives d'impact dans son aire introduite comme les études présentées ici sont nécessaires pour prévenir les impacts nocifs de l'espèce. De telles évaluations offrent également des éléments concrets aux gestionnaires de l'environnement, utilisables directement dans la conception de stratégies de gestion adaptées.

# Table of contents

# CHAPTER 1: Introduction

## Introduction

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From wildlife dispersal to biological invasions

A recent research interest

In 1958, the ecologist Charles Elton from Oxford University published the first book dealing

with Biological Invasions: "The Ecology of Invasions by Animals and Plants" (Elton 1958). By

this time, revolutionary changes were occurring in international connectivity, from boats to

the first commercial airplanes. Globalization, international trade and transportation of goods

and people fostered the transportation and dispersal of animal and plant species out of their

native distribution ranges (Hulme 2009). The rapid global increase in human activity and

habitat modification increased pressure on native biota worldwide, and the rate of recorded

species' depletion and extinction increased with the rate of species transportations (McKinney

and Lockwood 2001). Scientific concern about this increased rapidly (**Fig 1**), and in 1999 the

first Journal (*Biological Invasions*) dedicated to addressing this crisis was launched (Ricciardi

and MacIsaac 2008). A dozen years later, scientists considered biological invasions to be one

of the top three causes of biodiversity loss (Pereira et al. 2012). The international community

responded during the summit of the Convention for Biological Diversity, held in 2010 in

Nagoya (Japan), by dedicating one of the 20 biodiversity targets for 2020 to the study and

management of invasive species worldwide (Secretariat CBD 2010). The European regulation

1143/2014, ratified in January 2015, provided a set of measures to help reach this ambitious

goal. These included i) prevention of dispersal, ii) early detection of dispersal, and iii)

management of dispersal of a set of invasive species of European concern. At a wider scale,

the International Union for Conservation of Nature published the first classification of invasive

species of high-concern globally (Lowe et al. 2000). In 2018, the Invasive Species Specialist

Group of IUCN published a global register of introduced species (Pagad et al. 2018).
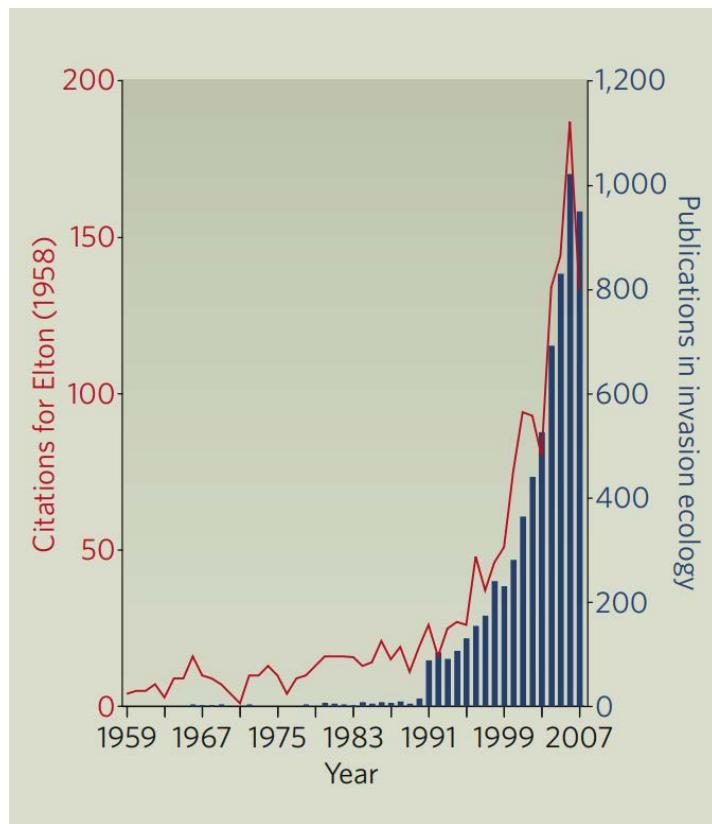
**Fig 1:** Number of publications dealing with Invasion Biology, and number of citations since Elton's 1958 book (Ricciardi and MacIsaac 2008)

## Definition: Invasive species

Defining biological invasions is not easy, as species introductions, establishment and competitive interactions occur naturally. The field of Invasion Biology was born because human activities accelerated these natural phenomena to unprecedented levels. The high frequency of long distance dispersal, the high number of transported species, the circumvention of geographic barriers, the multiplicity of transportation vectors, the global scale of the biodiversity homogenization effect, and the increase in other sources of biodiversity disturbance characterize the diversity of human effects on species introductions (Ricciardi 2007). Because of this very thin boundary between a natural phenomenon and a

"human-induced" change at a global scale, the definitions of Invasion Biology and Ecology have been a matter of considerable discussion and debate within the scientific community. Some have considered invasions to be a natural phenomenon and compared the prevention of species dispersal to a form of racism (Valéry et al. 2013). Others saw the observed impacts of alien species as an important challenge for our developing societies (Davis et al. 2011; Richardson and Ricciardi 2013; Simberloff and Vitule 2014; Blondel et al. 2014; Pereyra 2016; Russel and Blackburn 2017; Davis and Chew 2017).
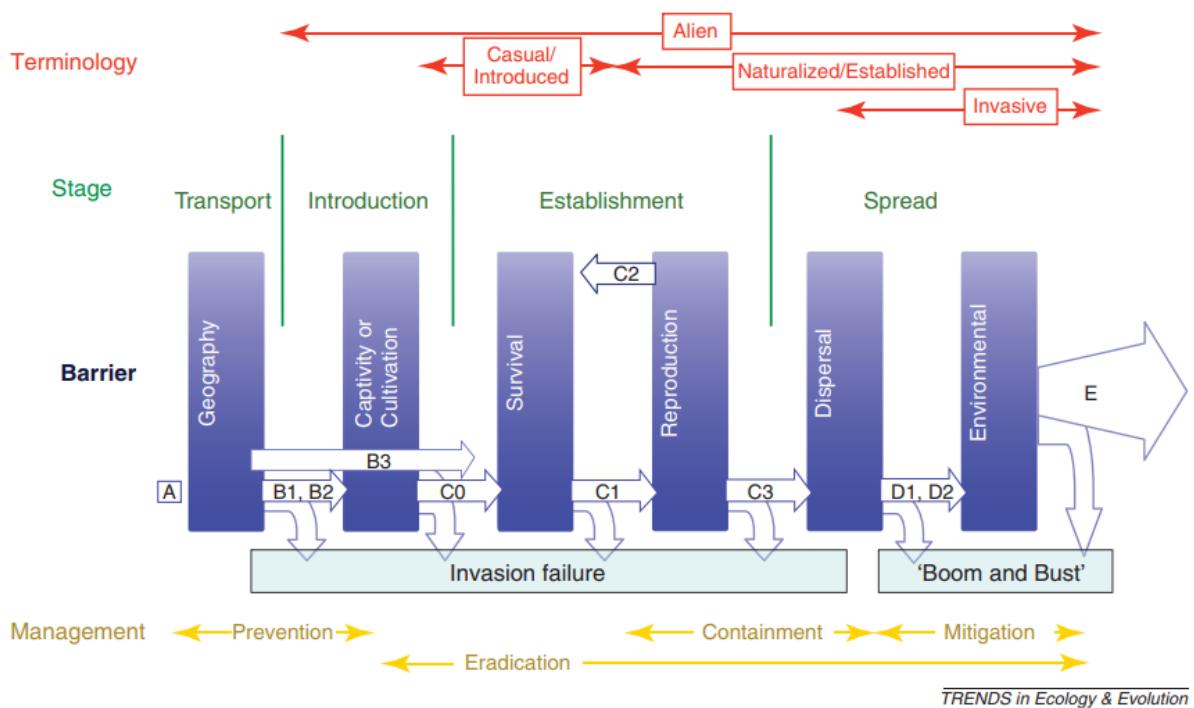


**Fig 2**: "A proposed unified framework for biological invasions" ( Blackburn et al. 2011).

The term invasion itself does not necessarily include this "human enhanced" aspect of Invasion Biology. According to the framework currently in use, a species should be considered invasive when: i) it has been introduced or spread outside of its native range, ii) it has

established, and iii) it has started to spread, resulting in significant changes in its new ecosystem (Blackburn et al. 2011; Simberloff et al. 2014). Under this framework, there is a barrier at each stage of the invasion process that a species must cross to be considered invasive (**Fig 2**). These barriers could be associated with transportation, biosecurity controls, resource availability, climate suitability, niche availability, or behavioural plasticity (Blackburn et al. 2011). From a management perspective, the most efficient strategy against an invasive species varies depending upon its invasion stage, and the formula "the sooner the better" applies to most cases of species introductions (Edelaar and Tella 2012). The conundrum is how to determine which species to fight against if waiting for observable impacts is too risky. The response has been to create lists of priority species at both global and local scales. Lists are constructed based on scientific knowledge, impact assessment studies, and social-economic factors that help identify high-risk species (Lowe et al. 2000; Pagad et al. 2018).

## Impacts of invasive Species

As a natural phenomenon, dispersal of plant and animal species can be viewed as an important process that contributes to maintaining genetic diversity (Thomas 2013). In degraded ecosystems, new arrivals can replace species, fill empty niches, and provide ecosystem services (Lugo 2004; Foster and Robinson 2007; Chiba 2010; Kaiser-Bunbury et al. 2010). Some authors highlighted a need for better consideration of potential positive effects from introduced species, which could counterbalance the negative effects (e.g. Simberloff et al. 2013; Jeschke et al. 2014). They identified a lack of pre-invasion data as a major limit to such assessments. In a sense and by definition, the domain of Invasion Biology is mostly interested in introduced species that exhibit negative effects on native biota. However, in order to better estimate, anticipate and prioritize the threats from introduced species, invasion biologists

need to understand how the addition of a new species into a native community can affect the biodiversity and ecosystem functioning, which involve very complex processes (Simberloff et al. 2013, Kumschik et al. 2015)

Through a complete range of impacts, direct or indirect, such as predation, competition, hybridization or transmission of pathogens, an introduced species may affect the diversity, richness, composition, abundance and specific interactions within its alien range (Reaser et al. 2007). Predation and competition are the mechanisms most frequently associated with impacts of invasive species (Sax and Gaines 2008). Predation alone or in combination with other impact factors is involved in 98% of current extinctions (Sax and Gaines 2008). For example, predation by the three invasive rodents (Black rat *Rattus rattus*, Pacific rat *Rattus exulans* and Norway rat *Rattus norvegicus*) are considered responsible for extinctions of birds, lizards, turtles, amphibians and even small mammals (McCallum 1986; Caut et al. 2008; Jones et al. 2008; Smith and Banks 2014; Hanna and Cardillo 2014) across a wide geographic range. Unlike predation, competition alone does not seem to have been responsible for the extinction of native species but, coupled with other impact factors, it is involved in 18% of current extinctions (Sax and Gaines 2008). Introduced ants are a good example of competitive species, affecting small to large organisms as they monopolize space and/or alimentary resources (Rowles and D'Dowd 2007; McNatty et al. 2009; Allen et al. 2017). Beyond these direct impacts, invasive species could also present indirect threats through the transmission of pathogens or by hybridization with closely related species. Transmission of pathogens often represents an additive pressure on resident species, and one that can even persist after eradication of the invasive vector (Tompkins et al. 2003; Crowl et al. 2008; Whyatt et al. 2008) including risk to public health via transmission of pathogens and diseases (Medlock et al. 2012; Juliano and Lunibos 2005). Hybridization with closely related species could threaten rare and

isolated species. Hybridization can result in genetic introgression (hybridization at a genetic or phenotype scales) by mixing native and alien genomic compositions in new hybrids (Mallet 2005; Steeves et al. 2010; Vuillaume et al. 2015). Sometimes hybridization leads to the genetic assimilation of a species by another, often the invasive one (Huxel 1999). In some cases, resulting hybrids could be sterile, resulting in a direct impact on the native population (Rhymer and Simberloff 1996; Todesco et al. 2016). Invasive species can also affect ecosystem services (Charles and Dukes 2008) and socio-economic factors (Pimentel et al. 2005) and cause behavioural changes in native species (Langkilde 2009).

Invasive species are recognized, together with climate change and habitat loss, as one of the three major components of biodiversity loss (Sala et al. 2000; Pereira et al. 2010). The detrimental effects of invasive species are particularly severe on islands where they often drive population declines or extinction of native species (Bellard et al. 2016). Indeed, the majority of documented plant and vertebrate extinctions over the last 500 years have occurred on islands (Sax and Gaines 2008; Tershy et al. 2015).

## The island paradox

Due to their isolation, islands exhibit biota and communities with often-unique characteristics, and this has always captivated the attention of Biologists and Ecologists (Warren et al. 2015). Island isolation and size often results in small population sizes and low emigration/immigration rates (MacArthur and Wilson 1967). As a result, the genetic and species-level diversities tend to be less important in island compared to continental contexts (Frankham 1997; Boessenkool et al. 2007). Isolation also favours in situ speciation mechanisms, resulting in biodiversity assemblages that are adapted to their insular

environment, with high rates of endemicity within large monophyletic groups of plants or animals (Silvertown et al. 2004; Savolainen et al. 2006). Differences between island and continental populations in reproductive strategies, behaviour, and sensitivity to environmental changes are called "Island Syndrome" (Russel et al. 2011). Interestingly, these elements contribute to explain both the uniqueness of island biota, and their extreme sensitivity to perturbations. Island ecosystems tend to be "naïve" and thus affected heavily by environmental changes and the introduction of new species, especially competitors and predators (Heavener et al. 2014). This is the paradox of island ecosystems. On one hand, islands host 19% of known bird species, 17% of rodent species, or 17% of flowering plant species in just 5.3% of the World's land (Tershy et al. 2015). On the other hand, 90% of recent bird extinctions (Steadman and Martin 2003) and more than 60% of global animal and plant extinctions (Tershy et al. 2015) have occurred on islands. Island territories host 14 times more critically endangered species (based on IUCN red-list criteria) than continental lands (Tershy et al. 2015). This concentration of species richness and conservation threat makes island territories unique model systems.

As a result, 10 islands and archipelagos were included in the list of 35 biodiversity hotspots suggested by Myers et al. (2000). Among these, New Caledonia is the smallest in area, but figures among the richest in term of floral species richness and endemicity (Kiers et al. 2009). Its unique biodiversity, shaped by its complex geological history, plus recent and increasing threats from economic development (including mining and species introductions), make this territory an excellent study site for Ecologists and Conservation Biologists (Pascal et al. 2008).

## Study Site: New Caledonia, a tropical island biodiversity hotspot

### An archipelago in the South Pacific

New Caledonia is an archipelago situated in the South Pacific Ocean (**Fig 3**), 1,453 km east of Brisbane (Austalia) and 1804 km north of Auckland (New Zealand). Its capital and largest city is Nouméa, located 22°14'8" South and 166°28'12" East according to the World Geodetic System WGS84 (Anon 2012). The territory has a total land area of 18,585 km$^2$. This comprises: i) the main island or "Grande Terre" (16,890 km$^2$), with the Belep Islands to the north and the Isle of Pines to the south; ii) the four Loyalties Islands situated northeast to the mainland (Lifou, Maré, Ouvéa, Tiga); and iii) a hundred islets spread over the surrounding lagoon (Beauvais et al. 2006).
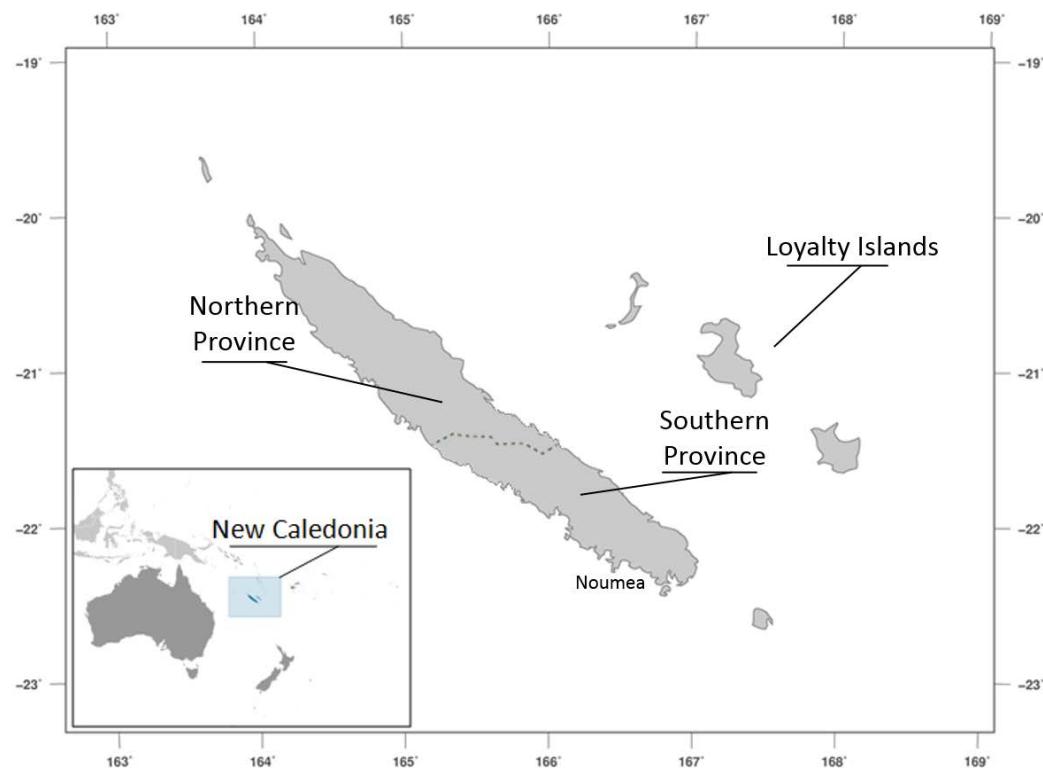


**Fig 3:** Localisation of New Caledonia, Nouméa, and the three administrative provinces of the territory (Thibault et al. 2017).

The territory was annexed by France in 1853, became a French overseas territory in 1946, and had been considered a "special collectivity" since 1999. The 2014 census reported 268,000 persons living in New Caledonia, belonging to three major communities. The original inhabitants of New Caledonia, the Kanak people, represent nearly 40% of the total population. European natives or descents account for nearly 30%, and 8% of the population is from the Wallis and Futuna Islands. Many other communities are represented within the New Caledonia society including Tahitians, Indonesians, Ni-Vanuatu, Vietnamese and people from other Asian nations.

Mountains and lagoon, subtropical weather

Grande Terre is very elongated, being 500 km long and 50 km wide (**Fig 4**; Grandcolas et al. 2008). The eastern and northern sides are separated by a central mountain range, with the highest peaks reach 1,629 m (Mont Panié) in the north, and 1,618m (Mont Colnett) in the south (Lilie and Brothers 1970). The east side of the mainland is mountainous and steep, while the western half is more open and flat (Anon 2012). A lagoon surrounds the whole of the mainland, with a maximum width of 15 km (Lillie and Brothers 1970). The lagoon is bordered by the second largest coral reef barrier of the world which extends over 23,400 km$^2$. This unique heritage was acknowledged by the World Heritage Committee of UNESCO in July 2008, with six sites being labelled World Heritage of Humanity sites.
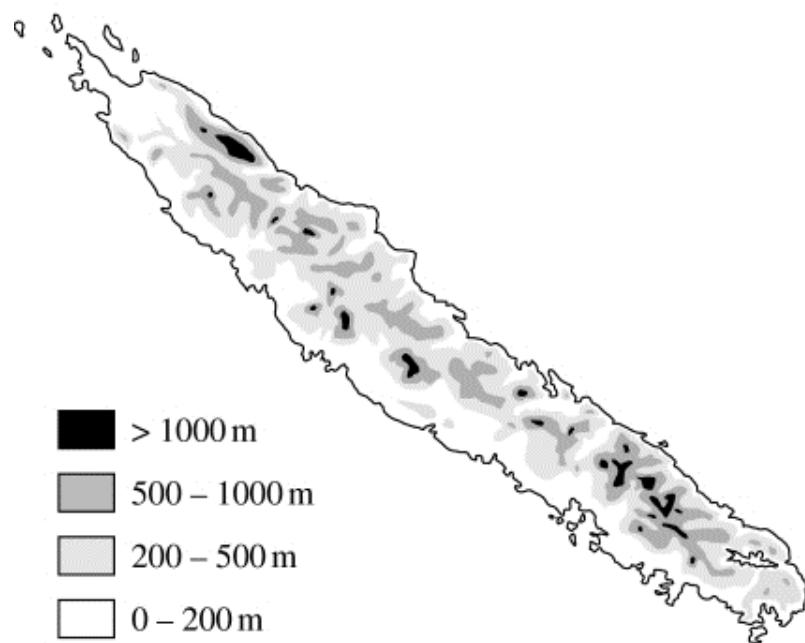
**Fig 4:** Orography in New Caledonia showing several chains of mountains, peaking at more than 1600 m in the north and south. (Adapted from Grandcolas et al. 2008).

New Caledonia has a tropical climate tempered by trade winds, with two major seasons (**Fig 5**), one hot and rainy, one cool and drier. The major driver of these seasons is annual variation in the location of the South Pacific Convergence Zone (SPCZ, Cavarero et al. 2012). Annual rainfall varies greatly by location, ranging between 300 and 4200 mm/year. The mountain range along the Grande Terre, together with dominant winds blowing from the east or southeast concentrate rainfall in the east coast and in the south of the Mainland (Caudmont and Maitrepierre 2007). The highest mean precipitation, 3,746mm, is recorded at the bottom of the Mont Panié. Maximum rainfall occurs during the rainy season, from December to February. Temperatures are warm during this period, varying between 27°C and 30°C and often higher, from November to March. Tropical influences predominate, with the weather being influenced largely by tropical depressions (Cavarero et al. 2012).

The cooler, more "temperate", season spans June to September when the SPCZ moves toward the northeast, and is marked by lower temperatures between 20°C and 23°C. These two seasons are separated by two shorter sub-seasons. From September to November, rainfall is very low and temperatures increase continuously, leading to a high risk of fires. Conversely, the temperature drops gradually from April to June while the water is still warm, resulting in an increased risk of subtropical depressions.

El Nino Southern Oscillations (ENSO) strongly influence the climate of New Caledonia. Under El Nino conditions, long droughts are expected as well as cold minimum temperatures. Conversely, La Nina often leads to more precipitation and higher minimum temperatures.
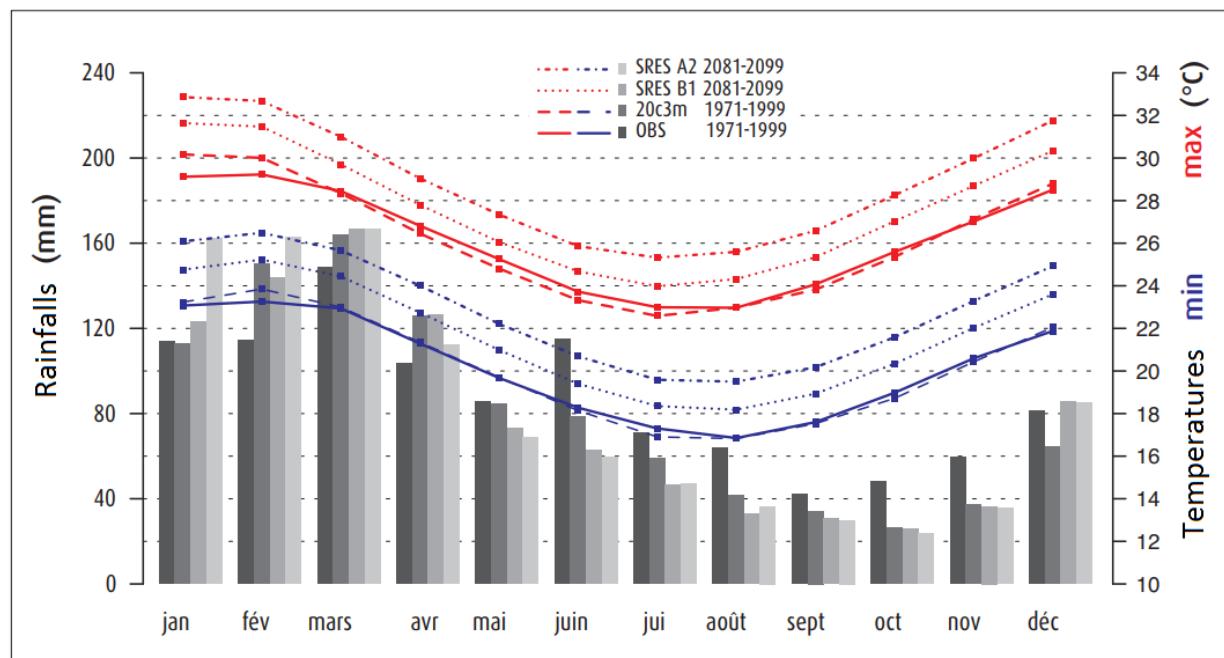


**Fig 5:** Climatograph of Nouméa, New Calédonia. (Adapted from Cavarero et al. 2012).

A swimming piece of Gondwana

The archipelago of New Caledonia has a geological history that started from the Middle Cretaceous (-120 Mya) at an active margin of the Gondwana supercontinent (Cluzel et al. 2012). Its geological history is complex and highly debated, but marked by three long major phases of tectonic, sedimentary, volcanic and accretion processes (Murienne et al. 2005).

During the first phase, from Middle Cretaceous to Early Eocene (-120 Mya to -55 Mya), the eastern margin of Gondwana was under subduction in the Tasman Sea, the Pacific plate sliding under the Australian plate. Around -88 Ma to -83Ma, a fragment of the Australian continental crust, called "Zealandia", broke off and moved to the current position of New Caledonia (Brothers and Lillie 1988; Neall and Trewick 2008). Intense tectonic and geological events such as expansions and extensions of the oceanic crust interacted to the form several fragments of continental crust (The Lord Howe wrinkle, the Norfolk Ridge and the Loyalty Arch) as well as three oceanic basins: the Tasmanian sea basin, the New Caledonia basin, and the Loyalties basin (Pelletier 2007; Maurizot and Vendé-Leclerc 2012).

Then, during the Paleocene (-65 Mya to -55 Mya), the oriental margin of Gondwana entered a period of subduction. As a result, Zealandia was deeply immersed for a long period and, due to tectonic movements, collided with the Arc of the Loyalties during the Eocene, between -55 and -34 Mya (Pelletier 2007; Maurizot and Vendé-Leclerc 2012). An abduction between the two lithospheric plates led to the deposition of an ophiolitic layer from the oceanic crust to the continental crust (Cluzel et al. 2001; Lagabrielle et al. 2005).

Following a phase of lithospheric extension, Zealandia re-emerged around -37 Mya (Cluzel et al. 1998). The re-emerging land, the northeast part of Zealandia or New Caledonia, was partly

covered with ultramafic rocks from the deep lithosphere. Ultramafic grounds are thus rich in minerals like iron, nickel, chromium, cobalt and magnesium and currently cover more than 5,500 km2 of Grande Terre.  During the Pliocene (-5 to -2.5 Mya) surrounding islands such as the Loyalties rose out of the water, and New Caledonia acquired its current form thanks to several geological events (Dubois et al. 1974). This unique geological history produced the rich and wide variety of rock types that constitute the New Caledonian archipelago.
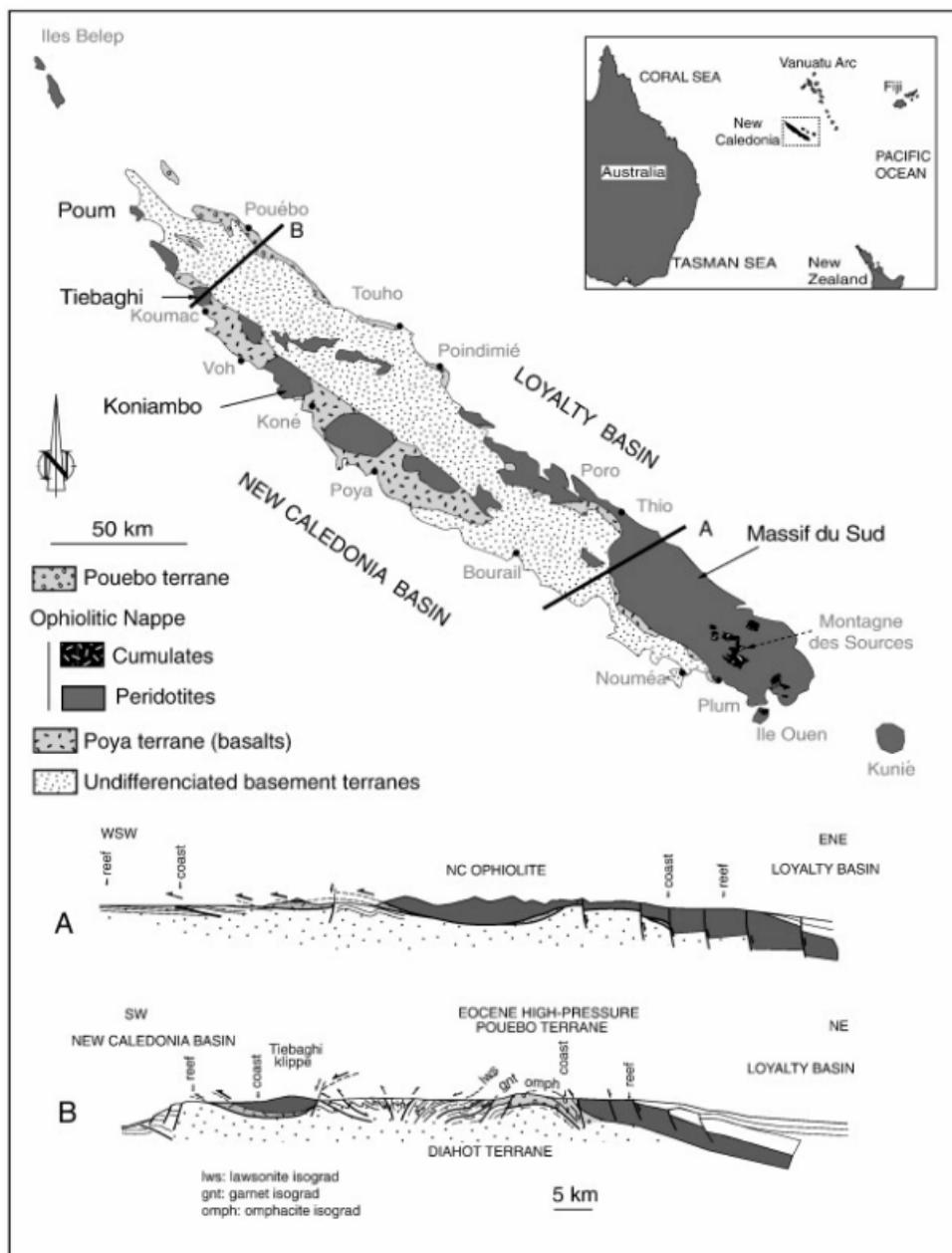


**Fig 6:** Simplified geologic map of New Caledonia. (Ulrich et al. 2010).

A biodiversity hotspot

New Caledonia's geological history suggests that New Caledonia remained underwater for about 20 Mya. This strongly influences the range of biogeographic theories that could explain the unique biodiversity found in the archipelago. Indeed, it is very unlikely that Gondwanian ancestors could have survived on the island archipelago until the present; rather, the land must have been colonized following its re-emergence from inundation (Murienne et al. 2005; Grandcolas et al. 2008; Nattier et al. 2011; Cruuaud et al. 2012; Pillon et al. 2012). Some studies suggested that a part of the Gondwanian biodiversity might have survived on emergent islands surrounding New Caledonia along the Norfolk ride (Lee et al. 2001; Head 2011). However, geological facts such as the large area covered by ultramafic soil, particularly in the south of the mainland, do not support this hypothesis (Pillon et al. 2010). The soil composition of New Caledonian soils should have been very rich in metals (Ni and Cu) and poor in nutrients on at least a third of the island. Such conditions suggest that the early biodiversity of New Caledonian, certainly coming from Australia or New Zealand, faced very high environmental constraints (Jaffré 1980; Proctor 2003; Murienne et al. 2005; Grandcolas et al. 2008).

The geological diversity, the orography of the mainland, and the East-West climatic gradient, afford New Caledonia a large diversity of landscapes and ecosystems. Six native habitat types are represented on the island: i) rainforest; ii) dry forest; iii) low and medium elevation maquis; iv) high elevation maquis; v) secondary habitats such as savannas; vi) wetlands mangroves (**Fig 7**; Jaffré et al. 1998).
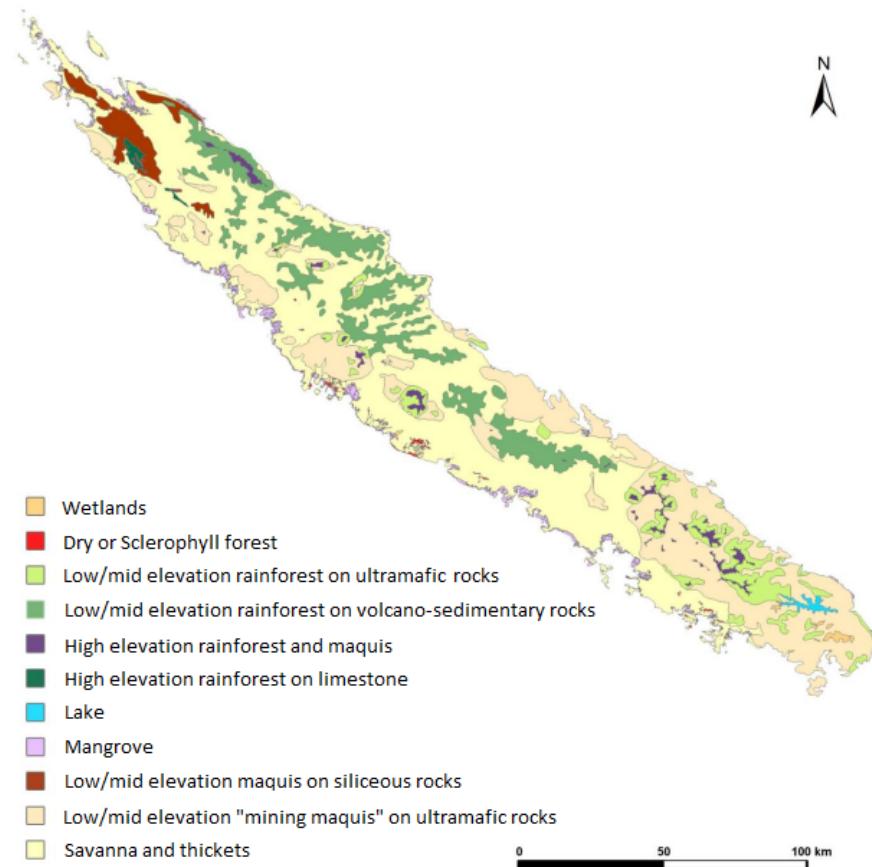
**Fig 7:** Plant formations and habitats in New Caledonia. (Adapted from Jaffre et al. 2012).

The geology and geographic isolation of New Caledonia have produced unique ecosystems and high levels of endemism (78%) (Cluzel et al. 2001; Isnard et al. 2016; Munzinger et al. 2016). The flora of New Caledonia counts 3389 vascular plant species, 74.1% of which are endemic (Munzinger et al. 2016). Flowering plants alone represent 3060 species, including an important metallophytic flora (Harrison and Rajakurana 2011). The diversity of soil types has contributed to the record level of 87.7% endemism in vascular plants in New Caledonia's rainforests (Morat et al. 2012). Among those unique species, *Amborella trichopoda* deserves special mention in being considered the sister species to all other extant angiosperms (Soltis et al. 2008). The terrestrial fauna is diverse, reflecting a history of numerous colonisation events spanning a long period, allowing evolutionary opportunities for groups to diversify in 'vacant' niches (Grandcolas et al. 2008). This has contributed to the high levels of endemism

including, for instance, the scincid and geckonid lizards that comprise 105 species (97 endemic) which are mostly monophyletic, and represent one of the highest ecological diversity of the planet in this group. Conversely, native mammals are restricted to nine Chiroptera species, among which three are endemic (Barré et al. 2012). Vertebrates are also represented by 111 taxa of nesting birds, 21 species being endemic. Most of the birdlife of New Caledonia belongs to six families (Columbidae, Psittacidae, Meliphagidae, Pachycephalidae, Campephagidae and Zosteropsidae) but the most famous species is certainly *Rhynochetos jubatus*, the cagou, which is the only representative of the Rhynochetidae and emblem to New Caledonia. Invertebrates are far less well known, and particularly those present on ultramafic substrate, even with more than 6,000 species have already been described (Chazeau 1993). However, some groups present very high endemism rates such as the cicadas (100% endemic; Delorme et al. 2015) or crickets (> 90%, Anso et al. 2016). In order to promote and protect this unique biodiversity, New Caledonia has been identified among the top ten biodiversity hotspots (Myers 1988), in the updated list of 25 (Myers et al. 2000), and amongst the 35 globe hotspots for biodiversity (Mittermeier et al. 2011).

Increasingly threatened

The biodiversity of New Caledonia is increasingly threatened by mining activities (Pascal et al. 2008; Wulff et al. 2013), natural or intentional bush fires (Ibanez 2012), and introduced species (Beauvais et al. 2006). According to Pascal et al. (2006), 16% of vertebrates recorded in New Caledonia are exotic: 17% of fish species, the only amphibian species (*Litoria aurea*), 4% of squamates, 17% of birds and 57% of mammals. Introduced vertebrates, and particularly mammals, represent a major threat to New Caledonian biodiversity, as they do not face native

competitors (Pascal et al. 2006). The most famous is certainly the rusa deer (*Cervus timorensis*), which gained a strong cultural importance but impacts the plant diversity as well as forest regeneration (de Garine-Wichatitsky et al. 2005). Among the 42 species of non-native vertebrates listed in New Caledonia, 12 are listed within the UICN-ISSG list of the "100 world's worst invasive species of the planet" (Lowe et al. 2000). The feral cat (*Felis catus*), the wild boar (*Sus scrufa*), the black rat, the Pacific rat and the Norway rat, also pose major threats to multiple biodiversity compartments (Palmas et al. 2017; Thibault et al. 2017). Regarding the invertebrates, 500 species that are now present in the archipelago are considered exotic, including the giant snail of Africa (*Achatina fulica*), the pink euglandine (*Euglandina rosea*), the whitefly (*Bemisia tabaci*), and several invasive ants (e.g. the small fire ant (*Wasmannia auropunctata*), the crazy yellow ant (*Anoplolepis gracilipes*) and the big-headed ant (*Pheidole megacephala*)) (Jourdan and Mille 2006).

## Study Species: the red-vented bulbul

### Taxonomy

*Pycnonotus cafer* Linnaeus, 1766 (Passeriformes: Pycnonotidae) is called the red-vented bulbul, common bulbul or sooty-headed bulbul. Earlier names include *Molpastes haemorrhous* J.F. Gmelin, 1789 and *Molpastes cafer* Baker, 1930. The genera *Pycnonotus* comprised 47 species (Delacourt 1943; Dickinson and Dekker 2002) including the red-vented bulbul, *Pycnonotus cafer*, which comprises eight subspecies (Dickinson et al. 2002). The Pacific sub-species is assumed to be *P. c. bengalensis,* Blyth 1845*,* originating from Himalaya and Nepal (Watling 1978).

Origin

The red-vented bulbul is native to the Indian Subcontinent, Southeast Asia and Malay Peninsula (Long 1981). Its native range extends from Eastern Pakistan to southern China and Vietnam and from Northern India to Sri Lanka. The species was historically also present in Bangladesh, Bhutan, Myanmar and Nepal (Chapter 2).

Description

The red-vented bulbul measures about 21 cm in length (Berger 1972) and its weight can vary between 26 and 45 grams (Long 1981). It may live for up to 11 years (Walker 2008). Its feathering is dark-brown. Tips of the back and breast' feathers are white and look like scales. It is easily recognizable thanks to the black crest on the top of the head (Pratt et al. 1987) and its crimson sub-caudal feathers (Berger 1981). Its rump is white, highly visible in flight, and its tail is long with a white tip. It does not show any sexual dimorphism even if the male tends to be slightly larger (Stuart and Stuart 1999). The immature bird looks like the adult, with a paler feathering and some brownish edging on feathers.

Reproduction

In its Pacific range, the breeding period of red-vented bulbuls occurs from October to February, following the beginning of the rainy season (Watling 1983). The observed number of clutches per year is one, even if a second may be possible if the first clutch fails early in the season (Watling 1983). Both sexes take part in the nest construction (Prajapati et al. 2011). The nest is cup-shaped (Vander Velde 2002) and made of plant matter, spider webs and sometimes plastic dishes. Nests are constructed about 3 m above ground (Vijayan 1980; Watling 1983), often-on forks in small bushes (Vijayan 1980; Zia et al. 2014). The nest is about

10 cm across, 6 cm height and 5 cm depth (Vijayan 1980; Watling 1983; Prajapati et al. 2011). The eggs of the red-vented bulbul are oval shaped and pinkish white with small red brown dots, and the mean clutch size is three (Zia et al. 2014). The incubation period is about 12-14 days (Berger 1981; Watling 1983; Duncan 2001). Chicks stay in the nest for approximately 12 days and remain around the nest for about two weeks following fledging. The mean number of fledglings produced per nesting attempt was estimated to be 0.33 in Fiji, with an incubation success rate of 28% and a nestling survival rate of about 50% (Watling 1983).

## Habitat

The red-vented bulbul can live in diverse habitat types. It is found in open areas, dry scrub, forest (natural or plantation) plains and cropland as well as urban areas (Vander Velde 2007). It is preferentially present in anthropogenic environments (urban areas, gardens, parks, farms), savannah areas, shrub vegetation, and more rarely on the edge of the forest (Vander Velde 2007).

## Diet

The red-vented bulbul is one of the rare animal species that cannot synthesize ascorbic acid, and is thus sensitive to scurvy (Roy and Guha 1958). This would explain why it feeds mainly on fruits and berries (Islam and Williams 2000; Brooks 2013). Consumption of flowers, buds, insects and small reptiles is also reported (Vander Velde 2002). According to Bates's (2011) study, *Red-vented bulbuls* preferred foraging substrate are branches (maybe because of its short slender legs that force it to hop from place to place). It is able to detect a new resource very quickly. It is used to foraging in the presence of some conspecifics but with only a few heterospecifics around.

Behaviour

The flight of red-vented bulbuls is quick and bouncy (Vander Velde 2002). The red-vented bulbul is often seen perched at the top of trees, foraging or calling (Brooks 2013). It is also known to be aggressive toward other birds (Watling 1983). Pairs of birds can be seen together most of the year, while flocks of three to 22 individuals can be observed after fledging or around some tree species when they are in bloom (Watling 1977). There is only one recorded observation of bulbuls catching flies (Marathe 1989).

Status

The red-vented bulbul is one of the 100 species listed by the IUCN ISSG as the world's worst invasive species (Lowe et al. 2000), together with the common Myna (*Acridotheres trists*) and the common starling (*Sturnus vulgaris*). Indeed, its global distribution and population size are believed to be increasing (Birdlife International 2016). The species is blamed i) for its aggressiveness toward other bird species, ii) for being an agricultural pest, and iii) as a disperser of noxious plant seeds. Its introduction and establishment in many Pacific Islands certainly contributes to its status as an invasive species of high-concern.

The red-vented bulbul in New Caledonia

The red-vented bulbul was introduced into Nouméa around 1983 when illegally imported caged birds were intentional released to avoid presecution (Gill et al. 1995). The first reported observation of wild red-vented bulbuls was from the district of Faubourg Blanchot just before 1983. The origin of these birds remains unknown but bird trade from Tahiti (French Polynesia) or Suva (Fiji) is highly suspected. The species quickly became locally and increasingly abundant, then its distribution increased more slowly. The first population survey was conducted in 2008

and reported red-vented bulbuls from 40 km north to 35 km south of Nouméa (Barré 2009).

These early observations suggested that the bird was spreading through the ultramafic maquis

but was absent from forests. Its presence in inhabited areas led to the first reports of harmful

effects. Several substantial impacts were reported on fruit crops, raising questions about the

economic threats posed to commercial and subsidence agricultural by the expansion in

distribution of the red-vented bulbul in New Caledonia (Metzdorf and Brescia 2008; Caplong

and Barjon 2010). There were also reports of perceived changes in the bird communities in

Nouméa's gardens and parks following establishment of red-vented bulbuls. This growing

concern from local people promoted consideration by scientists and managers in agricultural

and environmental agencies. The ongoing observed dispersal of the species appeared to be

restricted to the south of the mainland. This was quite different to the dispersal patterns of

other introduced bird species such as the common myna (*Acridotheres tristis*) which spread

throughout the main island until becoming the most common bird there. Studies of the

mechansims underlying the establishment, dispersal and impacts of red-vented bulbuls

captivated the attention of scientists and motivated them to develop tools to manage this

species, especially as demand for action grew amongst farmers and the public. Environmental

managers saw this situation as an opportunity to implement a management response,

provided that such action was justified by observable and quantifiable benefits to agriculture

and native ecosystems.

## Thesis aims and layout

The present work explores the invasive status of the red-vented bulbul through the study of

an introduced and currently expanding population present in New Caledonia. The main

objective of this research project was to describe potential threats arising from the current

dispersal of the red-vented bulbul. The study combines collection and synthesis of population-level data with investigation of fruit preference, gut transit times for seeds, and temporal movement data. These data are then used to generate models of this "in-progress" invasion to assess the ecological and economic threat posed by that this exotic invasive species, and to advise development of an effective management strategy.

This dissertation first summarizes knowledge of this species that can be extracted from literature (**Chapter 2**). I then describe the invasion as it has unfolded in New Caledonia and estimate the economic costs of the first recorded impacts on crops (**Chapter 3**). Estimations of both the effect of the establishment of red-vented bulbuls in the bird community of inhabited areas, and the seed disperser effectiveness of the invader, are presented in **Chapter 4** and **Chapter 5** respectively. In **Chapter 6** I suggest how current and future climate could shape the global distribution of the three major exotic invasive passerine species. The whole project is synthetized, and its outputs discussed in the **Chapter 7**.

**Chapter 2.** The first step of this project was to compile and summarize the knowledge available in the literature regarding the red-vented bulbul as an invasive species. I consider a range of questions including: Why is this species considered one of the three most invasive bird species on the planet? Where has the species been introduced and why? What category of impacts was it responsible for? How did the territories where the species was introduced react to the establishment of the red-vented bulbul? How is this invasive species managed in its introduced range? I searched for available information using the major search engines, extracted information from three databases, and contacted ornithologists, scientists and environment managers worldwide. Results of this synthesis are presented in the **Chapter 2** of this dissertation, and they form the academic foundation for the chapters that follow.

**Chapter 3.** In this chapter, I present the current context of the red-vented bulbul's range expansion in New Caledonia. Several studies are presented here that contribute to a better assessment of the extent of the population, the redistribution of birds within this range and the use of available habitats.  First, with help from community participation in a population survey conducted once every two years and reproduced during this project, I describe changes in the geographic distribution of the red-vented bulbul over the last 10 years, including an estimation of their dispersal speed. Second, I report on results from distance sampling that was conducted at four sites located along an urbanization gradient in order to estimate the density of birds from the introduction site to the edge of the current distribution. Third, I tried to determine if the species was able to spread into forest located close to the distribution core, using point count samplings at frontiers between occupied habitats and forests. Fourth, I tried to identify a pattern in the diet of red-vented bulbuls that could be useful for the development of a capture method. A preliminary diet study provided an assessment of the parts of plants and animals depredated by the red-vented bulbul, and suggested species that might be most seriously impacted by the species. Fifth, I tried to confirm the detected pattern through an ex-situ experiment and highlighted a colour preference in red-vented bulbuls. Finally, I conducted an open-field experiment to estimate the economic loss associated with the damage red-vented bulbuls cause to fruit species of its preferred color. Assessments presented in this chapter contributed directly to appreciate the threats posed by this species at a local scale. Most of the data presented here are usable directly by environment managers that aim to reduce or prevent the adverse effects of this bulbul on sensitive sites or species.

**Chapter 4.**  According to the results of the review, and based on examples from French Polynesia, the red-vented bulbul is expected to exhibit an aggressive behaviour toward other bird species. This behaviour, together with demographic and alimentary flexibility, is

suspected to make this bird species very competitive, inducing deleterious effects on native bird species in its alien range. This was the focus of this chapter. Thanks to a collaboration with the local Society of Ornithology, I was able to use data from a temporal monitoring of terrestrial birds to evaluate the effect of the bulbul establishment on the native bird community. This enabled me to confirm habitat preferences of red-vented bulbuls at this stage of their invasion. The chapter presents data on the effect of the red-vented bulbul presence on the abundance of 11 native and three exotic species. Results are discussed with regard to the current distribution of the species and its dispersal. This study also constitutes the first quantitative assessment of the impacts of a red-vented bulbul invasion on other bird species.

**Chapter 5.** The third adverse impact of red-vented bulbuls derived from the literature review was their contribution to dispersal of noxious plant seeds it consumes. This fifth chapter explores this hypothesis in the New Caledonia context. I first developed a collaboration with the local Federation of Hunting, to collect cadavers of red-vented bulbuls and, through gut contents analysis, determine their diet. I focused primarily on the fruit they consumed. This enabled me to confirm the fruit color preferences I identified in chapter 3, and highlighted candidate species in which to study the effectiveness of the red-vented bulbul to disperse seeds. The second part of this chapter presents the results of an ex-situ experiment aiming at estimating the gut passage time of seeds from four plant species eaten by a red-vented bulbul. For two species, I explored the effect of digestion on germination success using greenhouse trials. In the last part of this chapter, I show how tagging of a few birds with geolocators allowed estimation of the dispersal distance of seeds consumed by red-vented bulbul at source trees. The results are discussed from a conservation perspective, taking into consideration the current expansion of the species beyond inhabited areas.

**Chapter 6.** This chapter meets a broader need for an evaluation of the global potential distribution of the red-vented bulbul and two others highly-invasive passerines from the same native range. I used data from a global participative database, and latest climate data and scenarios from the International Panel on Climate Change to model the world climatic suitability for these three species. Combining high probabilities for at least two of the three species and conservation issues, I identified key locations where the prevention of invasion by these exotic passerines should be prioritized. In this section, I also suggest how expected climate changes by 2050 could shape climatic suitability and influence the geography of the establishment risk if these species spread naturally or are introduced.

**Chapter 7**. The final chapter of this dissertation i) highlights the major findings of this work, while ii) trying to present a critical assessment of the methods used. An effort is made to distinguish the elements from this thesis that could be used iii) by managers at a local scale, and iv) more widely, at regional and international scales and contexts. I finish the dissertation by highlighting priorities for future research on the introduced New Caledonian red-vented bulbul population.

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# CHAPTER 2: Literature review

## The red-vented bulbul (*Pycnonotus cafer*): serious pest or understudied invader?

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Abstract

Recently, debate has flourished about inadequacies in the simplistic "worst invasive species" approach and its global scale. Here, we investigate the status of the red-vented bulbul (*Pycnonotus cafer*), an Asian passerine bird. This species has been introduced widely across Pacific islands and is commonly blamed for its impacts on agriculture and biodiversity via dispersal of invasive plant seeds and competition with native fauna. This case study evaluates all available data on the impacts and management of this invasive species and identifies priorities for future research. We reviewed the scientific literature and information from three databases and highlight that the attention paid to this species by scientists and managers varied considerably between islands and contexts and was globally lower than the attention paid to other species on the IUCN-ISSG list. The red-vented bulbul has now established on 37 islands and in 7 continental locations outside its native range. We show that three categories of effects are associated with this species: plant damage, seed dispersal and disturbance of fauna. We compiled lists of 110 plant species consumed, 33 plant species dispersed, and 15 species of bird that this bulbul interacts with. However, these lists were mainly made of opportunistic observations rather than specific assessments. Research outputs that focus on better ways to prevent or quantify the impacts of the red-vented bulbul remain scarce. We found very few references exploring potential positive impacts of this species, and only two examples of management actions undertaken against it. The latter are required to inform management actions, especially on sensitive tropical islands where invasions and dispersal of the red-vented bulbul are ongoing. Our analysis of the literature found no clear support for considering this species to be one of the "world's worst" invasive alien species.

**Keywords:** invasive alien bird, islands, impact, biodiversity, conservation

## Résumé

Un débat est né récemment sur les limites de l'approche des « pires espèces envahissantes » à une échelle mondiale. Dans cette étude, nous nous penchons sur le statut particulier du bulbul à ventre rouge (*Pycnonotus cafer*), un passereau d'origine Asiatique. Cette espèce a été largement introduite dans les îles du Pacifique et est souvent mise en cause pour ses impacts sur l'agriculture et la biodiversité via la dispersion de graines de plantes envahissantes et la compétition avec la faune indigène. Cette étude de cas évalue toutes les données disponibles sur les impacts et la gestion de cette espèce envahissante et identifie des priorités pour les recherches futures. En examinant la littérature scientifique et les informations issues de trois bases de données, nos résultats soulignent que l'attention portée à cette espèce par les scientifiques et les gestionnaires varie considérablement entre les îles et les contextes tout en étant globalement inférieure à l'attention portée aux autres espèces de liste de l'UICN-ISSG. Le bulbul à ventre rouge est maintenant établi sur 37 îles et dans sept territoires continentaux en dehors de son aire de répartition naturelle. Nous montrons que trois catégories d'impacts sont associées à cette espèce: les dommages aux plantes, la dispersion des graines et la perturbation de la faune. Nous présentons une liste de 110 plantes consommées par le bulbul à ventre rouge, dont 33 espèces dispersées par l'oiseau, ainsi qu'une liste de 15 espèces d'oiseaux qui pourraient être impactées par ce bulbul. Cependant, ces informations sont souvent basées sur des observations opportunistes plutôt que sur des évaluations directes. Le nombre d'études scientifiques ayant pour but de prévenir ou de quantifier les impacts du bulbul à ventre rouge est assez faible. Nous avons trouvé très peu de références décrivant de potentiels effets positifs liés à l'arrivée de cette espèce, et seulement deux exemples de mesures de gestion. Pourtant, de telles informations sont nécessaires afin d'orienter les actions de gestion futures, en particulier au niveau des îles tropicales sur lesquelles le bulbul à ventre rouge est actuellement en train d'étendre sa distribution. Notre analyse de la littérature n'a pas trouvé de support clair pour considérer cette espèce comme l'une des « pires espèces exotiques envahissantes » au monde.

**Mots-clefs:** Oiseau exotique envahissant, iles, impacts, biodiversité, conservation

Introduction

Invasive alien species (IAS) are one of the main causes of biodiversity loss (Sala et al. 2000; Keane and Crawley 2002; Pereira et al. 2012; Gren et al. 2016), with associated economic impacts (Bergman et al. 2000; Pimentel 2005; Pimentel et al. 2011) and degradation of ecosystem services (Walsh et al. 2016). The highly ambitious goal of the 2010 Convention for Biological Diversity, Nagoya, Japan, was to ensure that "By 2020, IAS and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment" (Secretariat CBD 2011). Concerns about the impacts of IAS have led to the production of several lists of high priority alien species including the "100 of the World's Worst" from the IUCN Invasive Species Specialist Group (IUCN-ISSG) (Brochier et al. 2010; Burgiel and Perrault 2011; Lowe et al. 2000). Such prioritization attempts have incited intense debate among the scientific community on the definition of an invasive species (e.g. Russell and Blackburn 2017). Some considered invasion as a natural phenomenon and compared the prevention of species dispersal as a kind of racism (Valery et al. 2013). Others saw the observed impacts of alien species as an important challenge for our developing societies (Richardson and Ricciardi 2013; Simberloff and Vitule 2014; Blondel et al. 2014; Pereyra 2016). Such debate also applied to species classification methods, as prioritization attempts based on expert assessments is opposed to different classification frameworks based on data analysis and statistics (Donlan and Wilcox 2008; Kumschick et al. 2012; Blackburn et al. 2014; Kumschick et al. 2015). In this study, we consider that an alien species expanding its range in a sensitive territory deserves attention from both scientists and managers. For their part, scientists must consider the possibility that a species could be harmless in an alien territory and should produce a local assessment of potential issues associated with that species.

Of the terrestrial vertebrates in the IUCN-ISSG list, 14 are mammals, three are birds and only two are reptiles (Lowe et al. 2000). Unsurprisingly, 10 years after the publication of this "World's Worst" list, authors have commented on the imbalance in attention paid by scientists and managers to mammals in contrast to alien birds (Pysek et al. 2008; Kumschick and Nentwig 2010). Several studies have called for improvements in the way in which impact values of IAS are assessed beyond experts' "worst" lists, particularly for bird species (Strubbe et al. 2011; Ricciardi et al. 2013; Kumschick et al. 2015; Saxena 2015) and they have stressed that this is vital to better inform management decisions.

The three bird species classified as the world's worst invasive species in the IUCN-ISSG list are the common starling (*Sturnus vulgaris*), the common myna (*Acridotheres tristis*), and the red-vented bulbul (*Pycnonotus cafer*). A recent review of the impact of alien birds on native ecosystems globally (Martin-Albarracin et al. 2015) identified the three species with the highest global impact as being the mallard (*Anas platyrhynchos,* score=16), the common myna (score=13), and the red-whiskered bulbul (*Pycnonotus jocusus*, score=10) whereas the global impact score of the red-vented bulbul in this study should be only 4. Recently, Kumschick et al. (2015) identified important overlaps in the impacts associated with the common myna and the red-vented bulbul. This raises the question as to whether the red-vented bulbul should be considered as one of the three worst invasive bird species on the planet. Local farmers and environment managers need management frameworks in order to deal with the dispersal/impacts of IAS (Blackburn et al. 2011). Biosecurity protocols at frontiers were demonstrated to be the most useful techniques to prevent biological invasions (Edelaar and Tella 2012). However, controlling a newly established invasive species in a territory depends on economic, ecological and social factors and therefore on specific assessment of these factors at local scales (Mack et al. 2000). A synthesis of management programs toward an alien

species offers concrete baselines for managers, and this knowledge also helps understanding how the impacts associated with an invasive species give rise to management operations. It is urgent that we review existing assessments of impacts and management programs implemented against the red-vented bulbul.

We review invasion data to determine the nature and severity of the impacts of this species, whether its impacts are consistent throughout its alien range, whether its status as a major invasive species has led to more research and management programs at local scales, and to assess if its current acknowledged pest status is deserved. We present an updated assessment of an invasive species nearly 110 years after it was first recorded outside of its native range (Fiji in 1903, Watling 1978) and identify priorities for future research.

## Methods

### Species description

The red-vented bulbul (*Pycnonotus cafer* Linnaeus, 1766) is a passerine belonging to the family Pycnonotidae. Earlier names include *Molpastes haemorrhous* J.F. Gmelin, 1789 and *Molpastes cafer* Baker, 1930. The genus *Pycnonotus* comprises 47 species (Delacour 1943, Dickinson and Dekker 2002), among which the red-vented bulbul is represented by eight different subspecies (Dickinson et al. 2002). The Pacific sub-species is *P. c. bengalensis,* Blyth 1845 (Watling 1978)*.* The red-vented bulbul is native to the Indian Subcontinent, Southeast Asia, and Malay Peninsula (Long 1981). It occurs naturally from Eastern Pakistan to southern China and Vietnam, and from Northern India to Sri Lanka. The species also has an historic presence in Bangladesh, Bhutan, Myanmar and Nepal.

Data collection and analysis

We searched for "*Pycnonotus cafer*" and "red-vented bulbul" keywords on Google Scholar, Web of Science, ScienceDirect and SpringerLink search engines. We looked for information on impacts primarily, and collected references on pathways of invasion, establishment success, and management. We also visited the websites of the Governments, Environment Ministry, Associations and NGOs for each country where the red-vented bulbul was signaled as present. When our searches failed to find the information we sought, we made direct contact with people who had reported the presence of this species in each country. Most of the documents obtained concerned the red-vented bulbul in its alien range. Those that related to this species in its native range were used to extract information on its biology and ecology in countries of origin. We also compared the number of references obtained by searching for each of the species names listed in the IUCN "World's Worst" list in Google Scholar.

To update distribution maps, we included records from three international databases. We used the 252 quotations with references from the Global AVian Invasion Atlas Project (GAVIA, Dyer et al. 2017), 150 sightings from the Atlas of Breeding Birds of Arabia (ABBA, Ornithological Society of the Middle East, Jennings 2010) and 40,152 sightings from the participative eBird database (eBird, Sullivan et al. 2009). Maps were designed using the following R software packages: maps (Becker et al. 2015a), mapdata (Becker et al. 2015b), and mapproj (McIlroy et al. 2015) and maptools (Bivand and Lewin-Koh 2016).

We classified the reported impacts of the red-vented bulbul into three categories: 1) plant damage; 2) seed dispersal; and 3) disturbance and impact on fauna. We treated each mention of a species-specific plant or animal impact as one "report". One published article thus often contained several "reports" when listing, for example, species of plants consumed, and the

full set of documents potentially contained several reports of impacts on the same species, sometimes at the same location. We chose this index because it facilitates across-taxa comparisons and it is simple to calculate from the substantial number of references obtained. In addition, the ratio of the number of reports by the number of impacted species provides an informative insight into the attention paid to each impact-category.

## Results

### Sources of the information

We identified 112 published documents on the red-vented bulbul and obtained comments from seven ornithologists and environment managers about the bulbul from its alien range. The publications comprised 78 academic articles, 15 books, five conference proceedings, five newsletters and nine professional reports. Details about the information obtained are presented in **Fig.1**. Among the collected references, 83 addressed the red-vented bulbul in their alien range: 74 from islands and nine from continental areas. Three locations (Fiji, Hawaii and French Polynesia) were the focus of 42 documents. We used 12 references that focused on red-vented bulbul in their native range. We also used information from 17 documents dealing with biological invasions at a larger scale. These documents cover a period from 1926 to today, but we focus here on documents from 1975 onwards. The cumulative numbers of publications through time are shown in **Fig.2**. A full list of the 112 documents is given in **Online Resource 1.**

Searching for "Pycnonotus cafer" in Google Scholar produced 1,370 references. Thus, among the 100 species listed by the IUCN, the red-vented bulbul ranked 11th. In comparison, we found 4,880 references for "*Acridotheres tristis*", and 36,500 for "*Sturnus vulgaris*", the two other

bird species from the list. Searches for *"Pycnonotus jocosus"* and *"Anas platyrhynchos"* resulted 1,300 and 24,300 references respectively.
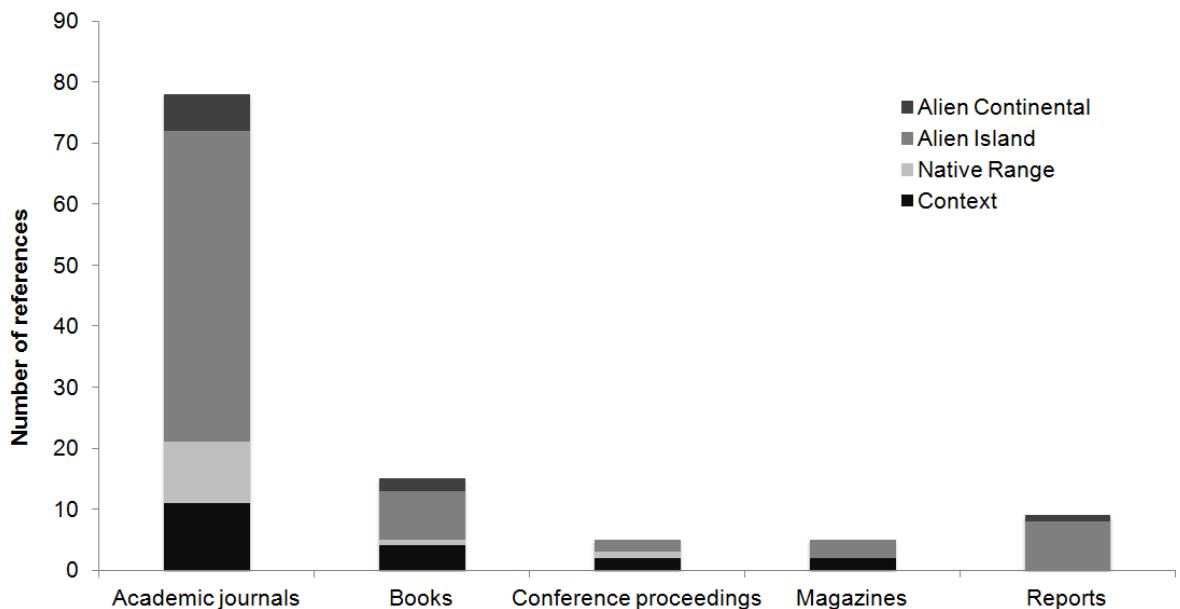


**Fig.1** Sources of the collected information. The "General information" scope refers to documents dealing with invasion biology at a global scale.
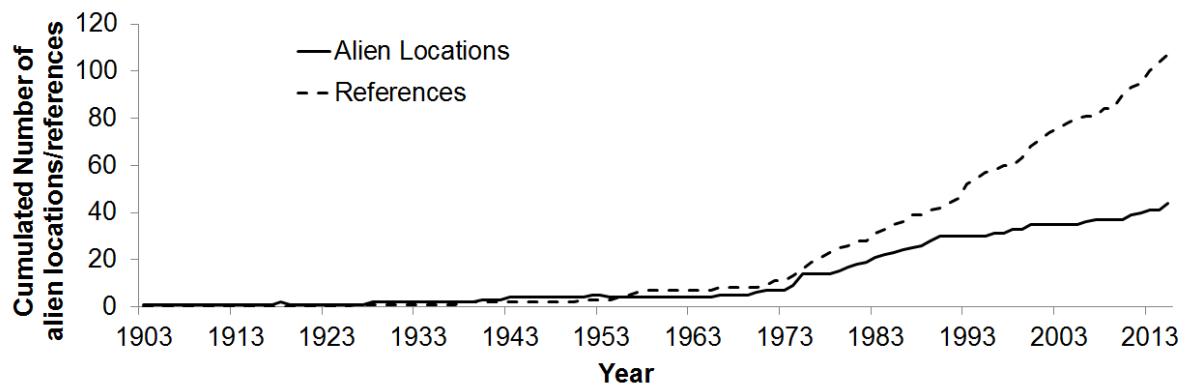


**Fig.2** Number of alien locations and published references for red-vented bulbul for the period 1903-2013.

Pathways of transport and introduction

The red-vented bulbul was first reported in Fiji in 1903 (Parham 1955), corresponding to the transportation of Indian immigrants from Calcutta harbor to Fiji in the early 1900s (Watling, 1978). This species was widely used in bird fights in India (Ali and Ripley 1971) because of its aggressive behavior. Over the following century, the red-vented bulbul was introduced into 19 countries and established in 17 of them (**Fig.3**). It is now present in at least 37 islands and seven continental locations and is anticipated to continue its range expansion in several archipelagos. The first recorded year of observation per country is presented in **Table 1**. Most introductions of the red-vented bulbul have been in the Pacific and in the Middle East, but the species was recently recorded in southern Europe (Malaga, Spain) and in North America (Houston, Texas, USA) (**Fig.3**). The exact reason for introduction is known for only three locations. The red-vented bulbul was deliberately introduced (1940s) to Tongatapu (Tonga) to control unwanted insects (Watling 1978). An American troopship re-routed to Apia took caged birds to Samoa in 1943 instead of New Caledonia that was the intended destination (Watling 1978), and the species was intentionally released in Nouméa (New Caledonia) around 1983 by bird dealers to avoid prosecution (Gill et al. 1995). For 10 other locations, bird trade is most often the suspected reason for introduction. Birds were kept in cages and transported by boat or airplane, with accidental or intentional release occurring commonly around harbours, airports and markets. For the Pacific locations, transportation of caged birds and accidental transport of free birds by boat have been the main introduction pathways, with a few records indicating that some introductions have occurred near airports. The red-vented bulbul remains abundant in Tahiti (French Polynesia) and is expanding its range in the Polynesian archipelago (T. Ghestemme *pers.comm.*). In the Middle East, land and air transport of cage

birds between markets is implicated. It is not known how the species got to Houston (Texas, USA), Malaga or Corralejo (Spain).

**Table 1** The current alien distribution of the red-vented bulbul *Pycnonotus cafer*, year of first observation (Y.F.O), number of colonized islands, current introduction success, status, range trend, and associated references. (+) Scarce (++) Common (+++) Very common

| Country | Y.F.O | Colonized Islands | Naturalization Success | Current Status | Range Trend | Number of References | Main Reference |
|---|---|---|---|---|---|---|---|
| **Island** | | | | | | | |
| Fiji | 1903 | 9 | 9 | ++ | →↗ | 10 | (1) |
| Australia | 1919 | 1 | 0 | - | - | 4 | (2) |
| Tonga | 1928 | 4 | ≥3 | ++ | | 3 | (3) |
| Western Samoa | 1943 | 1 | 1 | ++ | | 7 | (4) |
| New Zealand | 1952 | 1 | 0 | - | - | 1 | (5) |
| American Samoa | >1957 | 2 | ≥1 | | | 7 | (2) |
| United States (Hawaii) | 1966 | 6 | 1 | +++ | → | 20 | (7) |
| French Polynesia | 1979 | 9 | 9 | +++ | ↗ | 12 | (8) |
| New Caledonia | 1983 | 1 | 1 | +++ | ↗ | 5 | (9) |
| Bahrain | 1986 | 1 | 1 | | | 2 | (10) |
| Spain | 1998 | 1 | 1 | + | ↗ | 1 | (11) |
| Marshall Islands | 2000 | 2 | ≥1 | | → | 1 | (12) |
| Iran | 2007 | 1 | 1 | + | | 1 | (13) |
| | | | | | | | |
| **Continental** | | | | | | | |
| Qatar | 1971 | - | 1 | + | | 1 | (14) |
| United Arab Emirates | 1974 | - | 1 | ++ | ↗ | 3 | (15) |
| Kuwait | 1981 | - | 1 | + | ↘ | 1 | (16) |
| Oman | 1987 | - | 1 | ++ | ↗ | 0 | (17) |
| Saudi Arabia | 1980's | - | 1 | + | | 2 | (18) |
| United States (texas) | 1996 | - | 1 | + | → | 1 | (19) |
| Spain | na | - | 1 | + | ↗ | 1 | (11) |

*References*

(1) Watling 1978
(2) Lendon 1952
(3) Carlson 1974
(4) Dhondt 1976
(5) Turbott 1956
(6) Clapp and Sibley 1966

(8) Meyer 1996
(9) Gill et al. 1995
(10) Khamis 2010
(11) MAAMA 2013
(12) Vander velde 2002
(13) Azin et al. 2008

(14) Nation 1997
(15) Pederson& Aspinall 2015
(16) Gregory 2005
(17) J. Eriksen com.pers.
(18) J. Babbington com. pers
(19) Brooks 2013
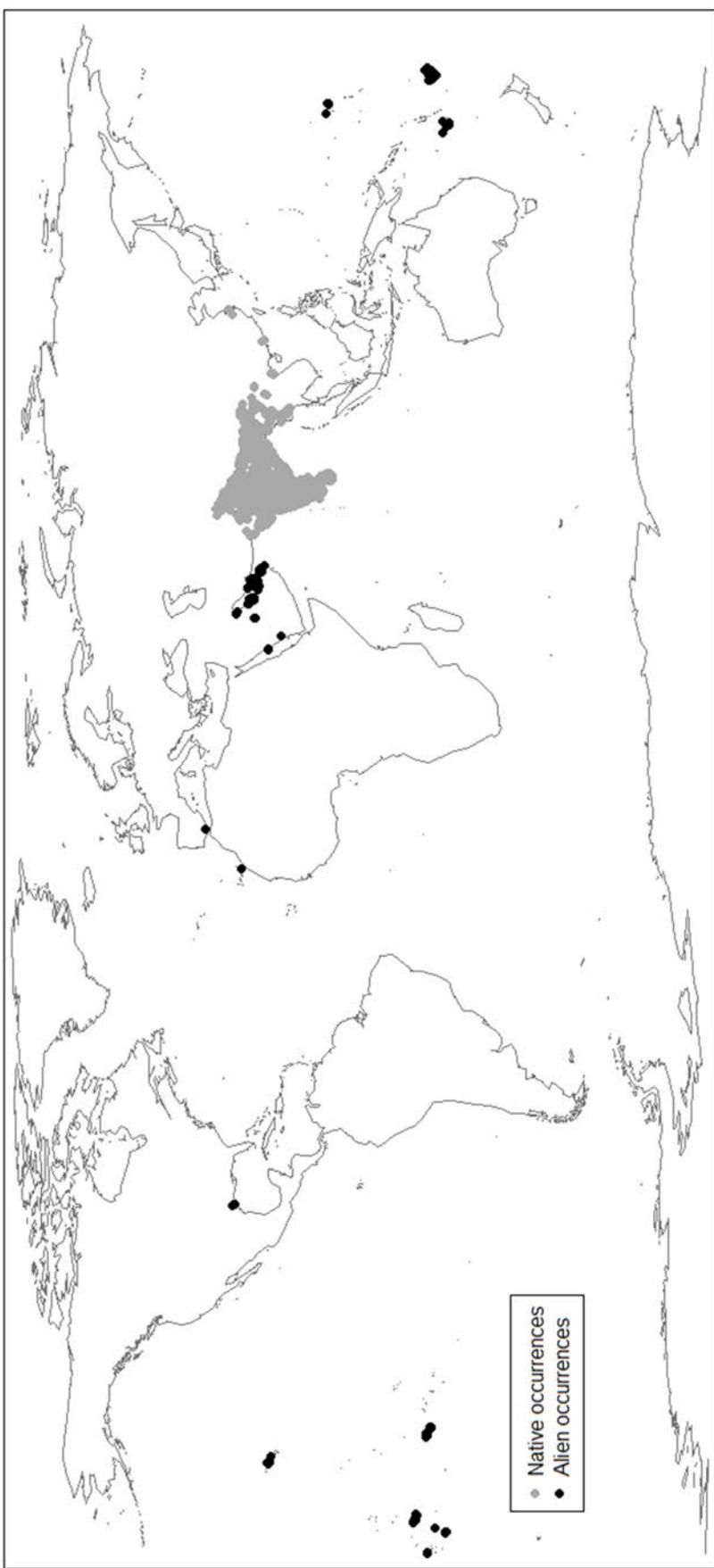
**Fig.3** Native and alien range of the red vented bulbul

Establishment success

The red vented bulbul is currently considered established in 36 of the 46 locations where it has been historically recorded. Up-to-date information is lacking for three small Pacific islands ('Eua, Savai'i and Ailinglaplap). We found mentions of red-vented bulbuls in Melbourne in 1918 and 1942 (Lendon 1952; Watling 1978), but the species has not been reported there since and it was recorded as "Eradicated" in Australia in the global invasive species database (http://www.issg.org/database). It was observed on five islands in the Hawaii archipelago between 1982 and 1989, but it seems that it failed to establish beyond Oahu (Walker 2008). It was eradicated from Auckland, New Zealand, in 1955 (Watling 1978), 3 years after the first observation in 1952 (Turbott 1956).

Recorded Impacts

The red-vented bulbul is commonly blamed for three categories of negative impacts, mostly related to its diverse diet that comprises fruits and berries (Islam and Williams 2000, Brooks 2013), and flowers, buds, insects and small reptiles (Vander velde 2002). We found 165 reports (110 species) of plants that are eaten by the red-vented bulbul. Among these, 50% concerned the degradation of cultivated plants and 35% related to seed dispersal. The remaining 17% (26 species from 17 families) were reports of consumption without consideration of the impacts. In comparison, we found 22 reports of impacts on local fauna in the bulbul's alien range.

Damage to cultivated plants is the most frequently reported impact of the red-vented bulbul in its alien range (**Fig.4**), but these studies were conducted in just four locations. In contrast, the publications reporting the red-vented bulbul to be a problematic seed disperser come from eight locations (six countries), and faunal impacts are reported for 17 species from 11 locations.
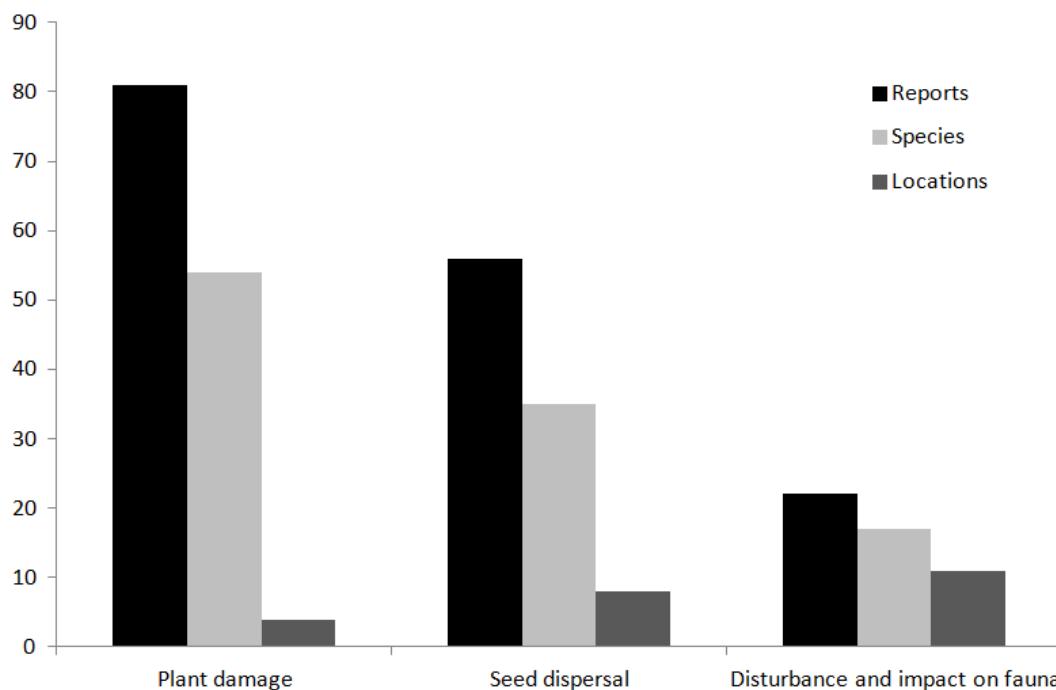
**Fig.4** Representation of the three impact categories associated with the red-vented bulbul *Pycnonotus cafer*. Each color corresponds to one category and represents the number of reports, species and location.

Plant damage

The red-vented bulbul has been reported to cause damage to at least 52 plant species (**Table 2**) belonging to 25 families with 67% (35 species) being food plants and 33% (17 species) being ornamental plant species. The full list of damaged and dispersed plant species by family and species is given in **Online Resource 2**.

**Table 2** Numbers of plant species reported as damaged, dispersed or just consumed by the red-vented bulbul *Pycnonotus cafer* in the literature and corresponding number of reports. A report corresponds to one mention in one reference. Endemic plants occurred at one location only, native plants are indigenous to the location but also present elsewhere, alien species were introduced in the corresponding location and invasive plants are alien species with negative impacts at the current location.

| Impact | Status | Species | Reports |
|---|---|---|---|
| **Damage** | | 52 | 81 |
| | Food plant | 35 | 61 |
| | Ornamental plant | 17 | 20 |
| **Seeds Dispersal** | | 33 | 56 |
| | Endemic | 1 | 1 |
| | Native | 8 | 11 |
| | Alien | 10 | 16 |
| | Invasive | 14 | 28 |
| **Consumption Only** | | 25 | 28 |
| **Total** | | 110 | 165 |

The impact of the red-vented bulbul appears to be particularly serious on Oahu (Hawaii), where Walker (2008) reported them consuming several species of fruits, vegetables and flowers, leading to considerable economic losses. The estimated value of the damage to Oahu's Orchid industry in one year (1989) was $300,000 (Fox, 2011) when the red-vented bulbul together with the Japanese white-eye (*Zosterops japonicus*) reportedly destroying up to 75% of Hawaiian orchid and anthurium plantations (Cummings et al. 1994). In New Caledonia, significant impacts have been recorded for some crops and plant nurseries (Metzdorf and Brescia 2008) with up to 35% losses (Caplong and Barjon 2010). Conversely, the red-vented bulbul is not considered an agricultural pest in Fiji (Watling 1979), nor in Houston (Texas, USA) where it was found to consume mainly introduced tropical plant species (Brooks 2013).

Seed dispersal

We found 56 mentions of problematic seed dispersal by the red-vented bulbul (**Table 2**) from

six countries inside its alien range. The red-vented bulbul can spread the seeds of at least 33

plant species from 25 families. Among these species, 30% are considered alien (10 species)

and 42% invasive (14 species) in the alien locations. We found records of only one endemic

(*Coprosma taitensis*, Tahiti) and eight native species that are spread by this bird (Spotswood

et al. 2012).

The red-vented bulbul is considered a major vector of the invasive tree *Miconia calvescens* in

Tahiti (Meyer 1996) and can potentially disperse seven other alien plant species in French

Polynesia including *Lantana camara* (Spotswood et al. 2012; 2013). Its ability to disperse

*Miconia* and *Lantana* is not unique to the red-vented bulbul, and many other species, both

alien and native, also disperse seeds of these plants, and the propensity of the red-vented

bulbul to disperse seeds of these plants varies from island to island. For example, the

introduced silvereye (*Zosterops lateralis*) also disperses these seeds in Tahiti, but in Moorea

the endemic fruit dove (*Ptilinopus purpuralis*) disperses seeds of these alien plants. In Fiji, the

red-vented bulbul contributes to the spread of primary colonist weeds (Watling 1979). In New

Caledonia, the red-vented bulbul is suspected of spreading seeds of another invasive species:

*Schinus terebinthifolius*, as it is often observed feeding on fruits (Spotswood et al. 2012;

Thouzeau-Fonseca 2013).

Disturbance and impact on fauna

The list of animal species reported to be impacted by the red-vented bulbul is presented in

**Table 3**. The list comprises 15 species of bird, one reptile and one insect. Only one study

addressed the issue of how the aggressive behavior of the red-vented bulbul affected the other bird species (Pernetta and Watling 1978).

On Oahu (Hawaii), direct predation of the monarch butterfly (*Danaus plexippus*) by the red-vented bulbul led to an induced color selection against the orange morph in the monarch (Stimson and Berman 1990). After 10 years, the same authors reported a predation transfer to the larvae, leading to an overall decline in abundance of the butterfly (Stimson and Kasuya 2000). In Tahiti, red-vented bulbuls are considered a threat to the Tahiti monarch (*Pomarea nigra*), an endemic and critically endangered passerine, through competition for nest sites and territory (Blanvillain et al. 2003).

In Fiji, several authors have reported red-vented bulbuls displaying aggressive behavior and competition for food resources towards other passerine species (Clunie 1976; Pernetta and Watling 1978; Williams 2011). However, Watling (1979) suspected that the observed confinement of native bird species to forest was mainly due to habitat loss rather than the aggressive behavior of the red-vented bulbul in Fiji. On Tutuila (American Samoa), Sherman and Fall (2010) observed that bulbuls competed for access to food resources with two passerine species. Finally, insect and skink predation by red-vented bulbuls is mentioned in several studies (Vander Velde 2002; Walker 2008; Brooks 2013). In the Middle East, cross-breeding between the exotic red-vented bulbul and the three closely related native species (white-cheeked bulbul, *P. leucogenys*; the white-eared bulbul (*P. leucotis*) and the yellow-vented bulbul, *P. xanthopygos*) is often reported as a potential threat for native bulbuls (Khan 1993; Nation et al. 1997; Gregory 2005; Azin et al. 2008; Khamis 2010).

**Table 3** List of animal species reported as being impacted by the red-vented bulbul *Pycnonotus cafer*, with associated locations, inter-specific relationship, reported impact, method and references. **H**=Hawaii; **PF**=French Polynesia; **FJ**=Fiji; **AS**=American Samoa; **AE**=United Arab Emirates; **BH**=Bahrain; **KW**=Kuwait; **QA**=Quatar; **IR**=Iran; **NC**=New Caledonia

| Species | Countries | Islands | Inter-specific relationship | Reported Impact | Method | References |
|---|---|---|---|---|---|---|
| **Insects** | | | | | | |
| *Danaus plexippus* | H | O'ahu | Predation | Decline | Indirect Obs. | (1) |
| **Birds** | | | | | | |
| *Pomarea nigra* | PF | Tahiti | Competition | Decline | Direct Obs. | (2) |
| *Lamprolia victoriae* | FJ | Vanua Levu | Competition | Decline | Hypothesis | (3) |
| *Myiagra vanikorensis* | FJ | Viti Levu | Aggressivity/competition | Nest parasitism | Monitoring | (4); (5) |
| *Lalage maculosa* | FJ | Viti Levu | Aggressivity | NA | Monitoring | (5) |
| *Acridotheres tristis* | FJ | Viti Levu | Aggressivity | NA | Monitoring | (5) |
| *Acridotheres fuscus* | FJ | Viti Levu | Aggressivity | NA | Monitoring | (5) |
| *Zosterops lateralis* | FJ | Viti Levu | Aggressivity | NA | Monitoring | (5) |
| *Amandava amandava* | FJ | Viti Levu | Aggressivity | NA | Monitoring | (5) |
| *Streptopelia chinensis* | FJ | Viti Levu | Aggressivity | NA | Monitoring | (5) |
| *Foulehaio carnunculata* | FJ; AS | Viti Levu; Tutuila | Aggressivity/competition | NA | Monitoring | (5); (6) |
| *Myzomela cardinalis* | AS | Tutuila | Aggressivity/competition | NA | Direct Obs. | (6) |
| *Pycnonotus leucogenys* | AE; BH | | Cross-breeding | Setrile hybrids | Obs. /Hypothesis | (7); (8) |
| *Pycnonotus leucotis* | KW; QA; IR | Kish Island | Cross-breeding | NA | Obs. /Hypothesis | (9); (10); (11) |
| *Pycnonotus xanthopygos* | UAE | | Cross-breeding | NA | Obs. /Hypothesis | (8) |
| *Zosterops xantochroa* | NC | Grande-Terre | Competition | NA | Hypothesis | (12) |
| **Reptile** | | | | | | |
| *Hemidactylus frenatus* | NC | Grande-Terre | Predation | NA | Direct. Obs | *Pers. Obs.* |

*References*

(1) Stimson and Berman 1990

(2) Thibault et al 2002

(3) Williams 2011

(4) Clunie 1976

(5) Pernetta and Watling 1978

(6) Sherman and Fall 2010

(7) Khamis 2010

(8) Khan 1993

(9) Azin et al 2008

(10) Gregory 2005

(11) Nation et al 1997

(12) Hannecart and Letocart 1980

Dispersal of neither endo- nor ecto-parasites by red-vented bulbul is well documented in its alien range (**Table 4**). In its native range, the red-vented bulbul is known to host *Isospora* spp. (Boughton et al. 1938), *Menacanthus eurysternus* (Price, 1975), *Bruelia guldum and Sturnidoecus guldum* (Ansari 1957) and *Pteroherpus pycnonoti* (Constantinescu et al. *unpublished*).

**Table 4** Reported parasite loads of the red-vented bulbul *Pycnonotus cafer*. Ecto-(Ectoparasites) corresponds to parasites living outside of the animal body. Conversely, Endo-(Endoparasites) corresponds to parasites living inside the animal body.

| Type | Species | Host | References |
|------|---------|------|------------|
| **Ecto-** | *Isospora sp.* | yes | (1) |
| | *Menacanthus Eurysternus* | yes | (2) |
| | *Bruelia guldum* | yes | (3) |
| | *Sturnidoecus guldum* | yes | (3) |
| | | | |
| **Endo-** | *Plasmodium sp.* | no | (4);(5) |
| | *Trypanosoma sp.* | no | (4) |
| | *Atoxoplasma sp.* | no | (4) |
| | *Chlamydia sp.* | yes | (6) |

| *References* | |
|---|---|
| *(1) Boughton et al. 1938* | *(4) Atkinson et al. 2006* |
| *(2) Price 1975* | *(5) Jarvi et al 2003* |
| *(3) Ansari 1957* | *(6) Blainvillain et al 2013* |

In 1996, Jarvi et al. (2003) detected no avian malaria (*Plasmodium* spp.) in blood smears, and Atkinson et al. (2006) found no evidence of *Plasmodium*, *Trypanosoma*, *Atoxoplasma* or microfilaria. Red-vented bulbuls in Tahiti, however, have been found to carry the zoonotic disease *Chlamydia* sp. (Blanvillain et al. 2013).

Positive impacts

Red vented bulbuls feed on a variety of native plant species (Trail 1994; Sherman and Fall 2010), and dispersal of native seeds is the only service that has been explored in the bulbul's alien range (Spotswood et al. 2012). Interestingly, in a village-scale survey led by Daigneault and Brown (2013) in Viti Levu (Fiji), 47% of the respondents reported that the red-vented bulbul was good for their community and highlighted three main reasons. First, the bulbul was effective at insect control. Second, the bulbul reduced mongoose attacks on chickens. Third, village focus groups responded that red-vented bulbuls were occasionally eaten by villagers.

Management

The red-vented bulbul is considered an invasive species and environmental pest under the law in Australia (Tasmanian government 2010), Fiji (Minister of Primary Industries 1985), French Polynesia (Direction de l'environnement de la Polynésie Française 2016), Hawaii (Division of Forestry and Wildlife 2013), New Caledonia (Direction du Développement Economique et de l'Environnement 2008, Direction de l'ENVironnement de la Province Sud 2016), New Zealand (Ministry of Primary Industries 2017), South Africa (Department of Environmental Affairs 2016) and Spain (Ministerio de Agricultura, Alimentacion y Medio Ambiante 2013). In these countries, transportation, trade or possession of this species is forbidden, and hunting is authorized. We found no mention of this species as a pest or invasive species in other countries.

We found only three examples of management action taken against the red-vented bulbul in its alien range. The first one is the successful eradication program implemented in New Zealand between 1952 and 1955 (Turbott 1956). This program allowed the early detection and shooting of bulbuls thanks to a reward associated with a call for information and led to

an announcement of eradication in 1955 (Watling 1978). This management strategy remains in place in New Zealand and it helped prevent establishment following two more recent introduction events (September 2006 and February 2013).

Second, a cage test conducted in Hawaii on bird repellant showed that Ziram, Methiocarb and Methyl anthranilate reduced the consumption of treated papaya mash by red-vented bulbuls (Cummings et al. 1994). In an open-field test, the same authors showed that Methiocarb significantly reduced damages on orchids.

The third location where management actions have been implemented against the red-vented bubul is the island of Tahiti in French Polynesia. In Tahiti, a management program that was not focused on red-vented bulbul management specifically, but rather on Tahiti monarch conservation, aimed to control alien birds. Pilot control campaigns were implemented twice, in 2012 and 2013 (Saavedra 2012; 2013), against the red vented-bulbul and the common myna. These actions resulted in 1,035 red-vented bulbuls being trapped in 2012, and 849 in 2013 and led to an increase in the breeding success of the Tahiti monarch (Saavedra 2013). Elsewhere in the French Polynesia archipelago, bulbul removal programs are in progress in Bora-Bora, Makatea and Nuku Hiva, three islands where the species is still rare but that are located near uninvaded parts of the archipelago.

In Fiji, a recent cost-benefit analysis of controlling the red-vented bulbul recommended "taking no action against the bulbul until such time as other benefits and or means of control have been field tested" (Daigneault and Brown 2013).

Discussion

The red-vented bulbul is still expanding its range into islands and continental areas across a wide geographic range between latitudes 22°N and 36°S. The number of references associated with this species outside its native range is also growing but remains low compared to other species listed in the IUCN "100 world's worst list". As an example, searching for "*Acridotheres tristis*" in Google Scholar results in a four times larger output than the keywords "*Pycnonotus cafer*". Based on this metric, the mallard and the red-whiskered bulbul could have been included in the IUCN list in the same way as suggested in Martin-Albarracin et al. (2015). This reflects the heterogeneity in the attention paid to this "world's worst invasive species". In fact, more than half of the information we obtained came from just three island locations: Fiji, where the species was first transported; Hawaii, where it was responsible for huge economic losses; and French Polynesia, where it was considered to contribute to pressures on endemic biodiversity. Dispersal of the red-vented bulbul is strongly linked to human activities, as is the case for other bird species (Cassey et al. 2015). In Assam in the north-east of India, bulbul fights were part of a traditional and religious annual celebration until this was banned in January 2016. Wild bulbuls were trapped, kept in cages and prepared for the fights, and finally released if they won (Shalet 2016). The long and close relationship with humans led to the transportation of caged birds across the Pacific Ocean by Indian migrants from the early 20th century, first by boat, and then by airplane from the 1950s, certainly fostered the bulbul expansion (Hulme 2009). This was also a key period for invasion biology, with the publication of the Elton's book (1958) marking the start of an increasing scientific interest in this field. While we found just eight references to this species between 1926 and 1966, 15 were published between 1967 and 1978. This species is still sold in local markets in several countries

of the Arabic Peninsula (J. Babbington *pers.com.*), and bird trade remains the suspected principal vector of red-vented bulbul in this region.

Precise historical data are lacking regarding the propagule pressure, exact pathways of introduction, and dates associated with each introduction event, and we found very few records of this species being introduced but failing to establish. Globally, the establishment success recorded from Pacific islands to the USA or Europe suggests a better latitudinal plasticity of this species toward climate than expected when looking at the native distribution only. Moreover, its populations are self-sustaining or increasing in most of the tropical islands to which it has been introduced. Conversely, in most of the alien continental areas, population trends are considered steady or decreasing (ABBA database, Jennings 2004). This global pattern is consistent with the finding of Cassey et al. (2004) who showed that without consideration of the propagule pressure, islands are significantly associated with introduction success and increased geographical range in birds.

Interest in introduced red-vented bulbuls grew rapidly in response to the considerable damage it caused on orchid production on Oahu, Hawaii, following its arrival in 1966. However, except for a few mentions of the cost associated with this issue (Cummings et al. 2014; Fox et al. 2011), all references that reported damage to plant production referred only to species lists, inducing a lack in quantitative data on this impact category (Martin-Albarracin et al. 2015). Impact scores attributed to the red-vented bulbul in the study of Martin-Albarracin et al. (2015) were based on the two other impact categories. Seeds dispersal was demonstrated in three studies that explored the dispersal pattern of invasive plants such as *M. calvescence*. But these studies were all conducted in French Polynesia and concluded that seed dispersal networks are complex and the interactions between native and alien plants and

birds depend on both the frugivore community and on the relative abundance of available fruit (Spotswood et al. 2012). Negative impacts through competition also gain mention in three studies. Particularly, the aggressive behavior of red-vented bulbul was reported in Fiji and French Polynesia. In Tahiti, its aggressiveness toward adults of Tahiti monarchs (*P. nigra*) combined with predation by black rats (*Rattus rattus*) has contributed substantially to the decline in abundance of the critically endangered monarch species (Thibault et al. 2002). However, the same author reported that the main cause of the Tahiti monarch decline was predation by the black rat. The red-vented bulbul was blamed as a strong competitor because of its aggressive behavior, but rats, cats, and other bird species such as the common myna are also recognized as chick predators or nest competitors (Blanvillain et al. 2003; Ghestemme 2011). According to Saavedra (2012), the combined effects of the myna and red-vented bulbul were responsible for 35% of the nest failing of the Tahiti Monarch in 2012. Except for observed hybridization with its native cousins from the Pycnonotidae family in the Middle-East (Kahn 1993; Nation et al. 1997), there are no reported impacts of red-vented bulbuls in continental areas (Khamis 2010; Brooks 2013). However, we reported some other potential impacts of the red-vented bulbul such as predation, hybridization, and dispersal of ecto- and endoparasites that were not included in any previous impact scoring attempts. This highlights a large knowledge gap about how the inter-specific behavior of the red-vented bulbul impacts other species. Therefore, we believe that the role of the red-vented bulbul in the decline of plant or animal species is still to be demonstrated, or at least quantified, as has been done for other major invasive bird species such as the common myna (Lowe et al. 2011).

Moreover, positive effects or ecosystem services brought by introduced red-vented bulbuls have been poorly studied in its alien range but may compensate to some degree for noxious impacts at the local scale (Daigneault and Brown 2013). Studies conducted in the bulbul native

range confirmed part of this assessment. For example, it was shown that the bulbul was effective at insect control, including eating the widespread and highly polyphagous agricultural pest *Helicoverpa armigera* (Rana et al. 2014; 2016). By doing so, they improved curd and seed yields of cauliflower. The bulbul was also found to be an efficient pollinator of *Erythrina variegata* in India (Raju et al. 2004). Finally, an anti-predator response strategy that relies on eavesdropping of the bulbul's alarm call may also benefit other species such as *Emoia cyanurea,* a species of skink that is widespread throughout Pacific islands (Fuong et al. 2014). These few examples suggest that positive impacts may partly counterbalance the three categories of negative impacts attributed to the red-vented bulbul depending on the environment where the species occur.

For this reason, local-scale surveys led by Daigneault and Brown (2013) are crucial to inform local farmers and environment managers. We found few published studies dealing with the local management of the red-vented bulbul in its alien range. One is the biosecurity protocol currently in place in New Zealand (Watling 1978) that illustrates the efficiency of locally preventing alien species introductions on reducing their dispersal (Edelaar and Tella 2012). A test of bird repellents on Hawaiian orchids and papaya production demonstrated the efficiency of three chemicals (Cummings et al. 2014). In their study exploring the efficiency of bird repellent methods in the bulbul native range, Patyal and Rana (2005) highlighted nets as the most efficient methods although it can be costly to implement on large orchards. In their overview of birds impacts on Indian agriculture, Kale et al. (2012) reviewed the existing repellant techniques used against birds including the red-vented bulbul, and underlined two main limits to their use being i) social and ecological issues associated with killing birds and ii) danger of most chemical repellants for the biodiversity. This suggest that preventing damages of the red-vented bulbul on plants is feasible and that the investment intensity and the

method used mostly depends on local communities. On the other hand, preventing impacts on seed dispersal and native fauna will rely on bird control programs and we found no feedbacks of such operations from the red-vented bulbul alien range yet. Results of the control programs currently in course in French Polynesia will certainly contribute to fill this gap (Saavedra 2013). In comparison, 13 eradication programs were conducted on islands against the common Myna and two against the red-whiskered bulbul that were mostly successful (DIISE 2015). Thus, more research is needed in the countries were the bulbul was introduced to evaluate threats associated with this species and guide adapted management strategies. Priority should be given to captive and field assessments of its diet and foraging ecology in its alien range. This would allow more accurate determination of the range of resources it uses and its prey (Bhatt and Kumar 2001), its role in seed dispersal (Spotswood et al. 2012), and its interspecific relationships (Bates 2014).

Management strategies often rely on rigorous expert assessment and are mostly "restricted only to species for which there is already some suspicion of a threat, often an agricultural one" (Simberloff 2003). Even for suspected pests, risk assessment is often based on "anecdotal observations relating to small areas only" rather than direct scientific research (Strubbe et al. 2011). The alien range of the red-vented bulbul, mostly consisting of tropical islands, could have also contributed to the negative reputation of the bird as island ecosystems are especially sensitive to the arrival of alien species (Sax and Gaines 2008; Tershy et al. 2015). The high endemicity and naivety of insular species accentuates their vulnerability (Gerard et al. 2016; Walsh et al. 2012). This sensitivity of tropical islands towards alien species may also be reinforced with the risk that a newly established population becomes a stepping stone for further introduction events through short-distance colonization (Gillespie et al. 2012). The information we present here supports this claim, with most reported impacts of

red-vented bulbul on biodiversity and plant production being from tropical islands, but even here the bulbul's reported impacts are heterogeneous and typically non-specific. This work reveal that the red-vented bulbul remains highly understudied considering its invasive and pest status. The species' long and close associations with people in its native range and subsequent transportation around the world as a cage-bird, coupled with its competitive foraging behavior (Sherman and Fall 2010), have surely contributed to its presence among the UICN-ISSG list of the world's worst invasive species, but this may well be overstated. Detailed and specific knowledge of this bulbul's impacts and the threats it poses is essential, and Kumschick et al. (2015) recently insisted on the need for such information to inform the construction of global prioritization lists. In comparison, the red-whiskered bulbul or the mallard, for example, apparently attracted a more attention from both scientists and managers.

In conclusion, we found few references on the red-vented bulbul, reflecting a less attention paid by scientists to this species compared to the other world's worst invasive species. The consideration of its negative impacts is largely influenced by few island locations whereas it is considered elsewhere as harmless, which prevent us from considering the bulbul as an absolute pest. Negative impacts led to the implementation of management programs in only one country and crop protection methods exist but are not necessarily used by local communities. Therefore, we suggest that the red-vented may not always be a dangerous pest.

## Acknowledgements

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## Appendices

**Appendix OR.1** List of the 112 documents relative to the red-vented bulbul that were used in this study

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**Appendix OR.2** List of plant species reported as being impacted by the red-vented bulbul *Pycnonotus cafer*, with associated country, location, status, associated impact and references. **H**=*Hawaii*; **PF**=*French Polynesia*; **FJ**=*Fiji*; **AS**=*American Samoa*; **NC**=*New Caledonia*; **US**=*United-States of America*

| Family | Species | Country | Location | Status | Impact | References |
|---|---|---|---|---|---|---|
| **Amaranthaceae** | *Spinacia oleracea* | H;NC | Oahu; Grande-terre | NA | Production | (10), (3) |
| **Anacardiaceae** | *Rhus taitensis* | PF | Tahiti; Moorea | Native | Dispersion | (7) |
| | *Schinus terebinthifolius* | NC; PF | Grande-Terre; Tahiti | Exotic Invasive | Dispersion | (7), (8) |
| | *Mangifera indica* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| **Apocynaceae** | *Thevetia peruviana* | NC | Grande-Terre | Exotic | NA | (8) |
| **Aquifoliaceae** | *Ilex vomitoria* | US | Houston | Native | NA | (2) |
| **Araceae** | *Anthurium sp* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| **Araliaceae** | *Schefflera actinophylla* | NC; H | Grande-Terre; Oahu | Exotic; Invasive | Dispersion | (10); (8) |
| | *Brassaia actinophylla* | NC | Grande-Terre | Exotic | NA | (3) |
| **Arecaceae** | *Roystonea princeps* | NC | Grande-Terre | Exotic | NA | (8) |
| | *Washingtonia robusta* | US | Houston | Exotic | NA | (2) |
| | *Chamaedorea elegans* | US | Houston | Exotic | Production | (2) |
| | *Phoenix dactylifera* | NC | Grande-Terre | Exotic | Production | (3) |
| **Asparagaceae** | *Hesperaloe parviflora* | US | Houston | Exotic | Dispersion | (2) |
| **Asteraceae** | *Lactuca sativa spp* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| **Berberidaceae** | *Nandina domestica* | US | Houston | Exotic Invasive | Dispersion | (2) |
| **Bignoniaceae** | *Spathodea campanulata* | NC | Grande-Terre | Exotic Invasive | NA | (8) |
| **Bombacaceae** | *Bombax ceiba* | NC | Grande-Terre | Exotic | NA | (3) |
| **Cactaceae** | *Hylocereus undatus* | NC | Grande-Terre | Exotic | Production | (8) |
| **Caricaceae** | *Carica papaya* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3); (8) |
| **Caryophyllaceae** | *Dianthus sp.* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| **Clusiaceae** | *Clusia rosea* | NC; H | Grande-Terre; Oahu | Exotic Invasive | Dispersion | (10); (3) |
| **Cucurbitaceae** | *Coccinia grandis* | H | Oahu | Exotic Invasive | Dispersion | (4) |
| | *Coccinia indica* | NC | Grande-Terre | NA | Dispersion | (3) |
| | *Cucumis sativus* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Cucurbita pepo* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Momordica charantia* | AS | Tutuila | Exotic | Production | (11) |
| **Elaeocarpaceae** | *Elaeocarpus rotundifolius* | NC | Grande-Terre | Endemic | NA | (8) |
| **Fabaceae** | *Erythrina variegata* | AS | Tutuila | Native | NA | (6) |
| | *Medicago sativa* | NC | Grande-Terre | Exotic | NA | (3) |
| | *Bauhinia sp* | US | Houston | Exotic | Production | (2) |
| | *Erythrina crista-galli* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |

| Family | Species | | | | | |
|---|---|---|---|---|---|---|
| **Fabaceae** | *Erythrina variegata* | AS | Tutuila | Native | NA | (6) |
| | *Medicago sativa* | NC | Grande-Terre | Exotic | NA | (3) |
| | *Bauhinia sp* | US | Houston | Exotic | Production | (2) |
| | *Erythrina crista-galli* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Erythrina herbacea* | US | Houston | Native | Production | (2) |
| | *Phaseolus vulgaris* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Pisum sativum spp* | NC; H | Grande-Terre; Oahu | NA | Production | (10); (3) |
| **Gentianaceae** | *Fagraea berteriana* | PF | Moorea | Native | Dispersion | (7) |
| **Lamiaceae** | *Clerodendrum infortunatum* | NC | Grande-Terre | Exotic | NA | (3) |
| **Lauraceae** | *Cinnamomum camphora* | US | Houston | Exotic | Production | (2) |
| | *Persea americana* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| **Lythraceae** | *Lagerstroemia indica* | US | Houston | Exotic | Production | (2) |
| **Magnoliaceae** | *Magnolia sp* | US | Houston | Exotic | Production | (2) |
| **Malvaceae** | *Commersonia bartramia* | NC | Grande-Terre | Exotic | Dispersion | (8) |
| | *Hibiscus paramutabilis* | US | Houston | Exotic | Production | (2) |
| | *Hibiscus rosa* | US | Houston | Exotic | Production | (2) |
| | *Malvaviscus drummondii* | US | Houston | Native | Production | (2) |
| **Melastomataceae** | *Clidemia hirta* | FJ | Viti Levu | Exotic Invasive | Dispersion | (12) |
| | *Clidemia sp* | NC; H | Grande-Terre; Oahu | Exotic Invasive | Dispersion | (10); (3) (5); (4); |
| | *Miconia calvescens* | PF | Tahiti; Moorea | Exotic Invasive | Dispersion | (7) |
| **Meliaceae** | *Melia azedarach* | NC | Grande-Terre | Exotic | Dispersion | (8) |
| | *Azadirachta indica* | NC | Grande-Terre | Exotic | NA | (3) |
| | *Dysoxylum maota* | AS | Tutuila | Endemic | NA | (6) |
| | *Dysoxylum samoensis* | AS | Tutuila | Endemic | NA | (6) |
| **Menispermaceae** | *Cocculus carolinus* | US | Houston | Native | Dispersion | (2) |
| **Moraceae** | *Ficus benghalensis* | H | Oahu | Exotic | Dispersion | (1), (10) (9); (3); |
| | *Ficus prolixa* | PF; AS; NC | Tahiti; Tutuila; Grande-Terre | Native | Dispersion | (7) |
| | *Ficus carica* | US; H | Houston; Oahu | Exotic | NA | (10); (2) |
| | *Ficus microcarpa* | NC | Grande-Terre | Native | NA | (3) |
| | *Ficus obliqua* | AS | Tutuila | Native | NA | (9) |
| | *Morus sp.* | NC | Grande-Terre | NA | Production | (8) |
| **Musaceae** | *Musa spp* | NC; H | Grande-Terre; Oahu | Hybrid | Production | (10); (3); (8) |

| Family | Species | | | | | |
|---|---|---|---|---|---|---|
| **Myrtaceae** | *Callistemon sp* | NC; H | Grande-Terre; Oahu | Exotic | NA | (1), (10); (3) |
| | *Eugenia uniflora* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Melaleuca quinquenervia* | NC | Grande-Terre | Native | NA | (8) |
| | *Psidium cattleianum* | H | Oahu | Exotic | Production | (10) |
| | *Psidium guajava* | NC; H; FJ; PF | Grande-Terre; Oahu; Viti Levu; Tahiti | Exotic | Production; Production | (1), (10); (3) |
| | *Syzygium cumini* | NC; H | Grande-Terre; Oahu | Exotic | Dispersion | (10); (3) |
| | *Syzygium malaccense* | H | Oahu | Exotic | Production | (10) |
| **Orchidaceae** | *Dendrobium sp.* | NC; H | Grande-Terre; Oahu | Native; Exotic | Production | (10); (3) |
| | *Vanda sp.* | H | Oahu | NA | Production | (4) |
| **Oxalidaceae** | *Oxalis corniculata* | PF | Tahiti | Exotic | Dispersion | (7) |
| **Pandanaceae** | *Freycinetia impavida* | PF | Moorea | Native | Dispersion | (7) |
| **Passifloraceae** | *Passiflora foetida* | FJ | Viti Levu | Exotic Invasive | Dispersion | (11) |
| | *Passiflora suberosa* | PF; NC | Moorea; Tahiti; Grande-Terre | Exotic Invasive | Dispersion | (7); (8) |
| **Phyllanthaceae** | *Flueggea flexuosa* | AS | Tutuila | Native | Dispersion | (9) |
| **Piperaceae** | *Piper aduncum* | FJ | Viti Levu | Exotic Invasive | Dispersion | (11) |
| **Rhamnaceae** | *Ziziphus jujuba* | NC | Grande-Terre | Exotic | NA | (3) |
| **Rosaceae** | *Rubus rosifolius* | PF | Moorea; Tahiti | Exotic Invasive | Dispersion | (7) |
| | *Pyracantha sp* | US | Houston | Exotic | NA | (2) |
| | *Eriobotrya japonica* | NC | Grande-Terre | Exotic | Production | (3) |
| | *Fragaria sp.* | NC; H | Grande-Terre; Oahu | NA | Production | (10); (3) |
| | *Prunus domestica ssp* | NC; H | Grande-Terre; Oahu | NA | Production | (10); (3) |
| | *Prunus persica* | NC; H | Grande-Terre; Oahu | NA | Production | (10); (3) |
| | *Pyrus sp.* | US | Houston | Exotic | Production | (2) |
| | *Rubus sp* | H | Oahu | NA | Production | (10) |
| **Rubiaceae** | *Coprosma taitensis* | PF | Tahiti | Endemic | Dispersion | (7) |
| | *Cyclophyllum barbatum* | PF | Moorea | Native | Dispersion | (7) |
| | *Tarenna sambucina* | PF | Moorea | Native | Dispersion | (7) |
| | *Morinda citrifolia* | AS | Tutuila | Exotic | Production | (9) |

| Family | Species | Location | Island | Status | Type | References |
|---|---|---|---|---|---|---|
| **Rutaceae** | *Citrus latifolia* | NC | Grande-Terre | Hybrid | Production | (3) |
| | *Citrus limon* | NC | Grande-Terre | Hybrid | Production | (3) |
| | *Citrus sinensis* | NC; H | Grande-Terre; Oahu | Hybrid | Production | (10); (3) |
| | *Citrus sp* | H | Oahu | Hybrid | Production | (10) |
| | *Citrus tangerina* | NC; H | Grande-Terre; Oahu | Hybrid | Production | (10); (3) |
| | *Murraya exotica* | NC | Grande-Terre | Exotic | Dispersion | (8) |
| | *Murraya paniculata* | NC; H | Grande-Terre; Oahu | Exotic | Dispersion | (10); (3) |
| **Sapindaceae** | *Litchi chinensis* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Pometia pinnata* | AS | Tutuila | Exotic | Production | (9) |
| **Scrophulariaceae** | *Myoporum sandwicense* | H | Oahu | Endemic | NA | (10) |
| **Solanaceae** | *Physalis angulata* | FJ | Viti Levu | Exotic | Dispersion | (4) |
| | *Solanum torvum* | FJ; NC | Viti Levu; Grande-Terre | Exotic; Invasive | Dispersion | (4); (8) |
| | *Capsicum annuum* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Capsicum sp* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| | *Solanum lycopersicum* | US; NC; H | Houston; Grande-Terre; Oahu | Exotic | Production | (10); (3); (2) |
| | *Solanum melongena* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |
| **Urticaceae** | *Cecropia peltata* | PF | Moorea; Tahiti | Exotic | Dispersion | (7) |
| | *Pipturus argenteus lanosus* | AS | Tutuila | Native | NA | (9) |
| **Verbenaceae** | *Lantana camara* | FJ; PF; US | Viti Levu; Moorea; Tahiti; Houston | Exotic Invasive | Dispersion | (4); (7); (2) |
| | *Callicarpa americana* | US | Houston | Native | NA | (2) |
| **Vitaceae** | *Vitis spp.* | NC | Grande-Terre | NA | Production | (3) |
| **Zingiberaceae** | *Zingiber officinale* | NC; H | Grande-Terre; Oahu | Exotic | Production | (10); (3) |

References

(1) *Bhatt&Kumar 2001*
(2) *Brooks et al. 2013*
(3) *Caplong 2010*
(4) *Fox 2011*
(5) *Meyer 1993*
(6) *Sherman and Fall 2010*
(7) *Spostwood et al. 2012*
(8) *Thouzeau A. 2013*
(9) *Trail 1994*
(10) *Walker R. 2008*
(11) *Watling 1979*
(12) *Wood et al. 1926*

## CHAPTER 3: Invasion in New Caledonia

### Invasion by the red-vented bulbul: an overview of recent studies in New Caledonia

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## Abstract

New Caledonia is a tropical archipelago of the South-Pacific Ocean, considered among the 36 world biodiversity hotspots. However, its unique biodiversity is increasingly threatened by habitat fragmentation and introduction of invasive alien species. Among these invaders, the red-vented bulbul (*Pycnonotus cafer*) is currently expanding toward the north of the main island. This passerine figure in the IUCN-ISSG list of the 100 world worst invasive species because of impacts caused by its diet. 35 years after its historical introduction, we present an overview of data from recent studies conducted in New Caledonia to describe the local status of the red-vented bulbul, its range expansion and potential impacts on both the local biodiversity and agriculture. A bi-annual monitoring of the distribution coupled with prospection at the edges of native forest highlighted a tight association of the bulbul with man-modified habitats. Using a distance sampling method, we estimated bulbul densities from a peak 200 ind/km$^2$ in the main city of Noumea, where the species has been introduced, to 30 ind/ km$^2$ in rural habitats located 50 km away from the distribution core. We conducted a diet analysis on 40 cadavers and found that 82% and 55% of individuals had consumed plant and animal items respectively. We highlight plant and insect species that may be considered in the exploration of the seed dispersal and predation by the red-vented bulbul. Finally, a food color selection experiment and an open field test showed that the red-vented bulbul had a significant preference for red and sweet fruits among other fruits. We estimated the loss caused by bulbuls to a tomato grower and discuss the result with regards of the development of an adapted management strategy, to prevent further impacts of the red-vented bulbul on the biodiversity and agriculture in the tropical island hotspot of New Caledonia.

**Keywords:** Invasive bird, *Pycnonotus cafer*, distribution, density, diet, impacts

Résumé

La Nouvelle-Calédonie est un archipel de l'océan Pacifique Sud, considéré comme l'un des 36 hotspots mondiaux de biodiversité. La biodiversité unique qu'il abrite est de plus en plus menacée par la fragmentation des habitats et l'introduction d'espèces exotiques envahissantes. Parmi ces envahisseurs, le bulbul à ventre rouge (*Pycnonotus cafer*) est en cours d'expansion. Ce passereau figure sur la liste des 100 espèces les plus envahissantes du monde de l'UICN-ISSG, en raison des impacts qu'il cause par son régime alimentaire. Trente cinq ans après son introduction, nous présentons un aperçu des études récentes menées en Nouvelle-Calédonie pour décrire la propagation du bulbul à ventre rouge et ses impacts potentiels sur la biodiversité et l'agriculture locales. Un suivi bisannuel de la distribution, couplé à des prospections en bordure de forêt native, ont mis en évidence une occupation préférentielle des habitats urbanisés. La technique du distance sampling nous a permis d'estimer des densités allant de 200 ind/ km$^2$ dans Nouméa, où l'espèce a été introduite, à 30 ind/km$^2$ dans les habitats ruraux situés 50 km au Nord. Notre analyse du régime alimentaire de 40 cadavres révèle que 82% des individus avaient consommé des végétaux, contre 55% pour les restes animaux. Nous mettons en évidence certaines espèces de plantes et d'insectes dont la dispersion ou la prédation par le bulbul à ventre rouge pourrait avoir un impact négatif. Enfin, une expérience de sélection des couleurs et un test en plein champ ont montré que l'espèce avait une préférence marquée pour les fruits rouges et sucrés parmi d'autres fruits. Nous proposons une estimation des pertes causées aux cultures de tomates et discutons nos résultats en regard de l'élaboration d'une stratégie de gestion, afin d'anticiper de futurs impacts du bulbul à ventre rouge sur la biodiversité et l'agriculture en Nouvelle-Calédonie.

**Mots-clefs:** Oiseaux invasif, *Pycnonotus cafer,* distribution, densité, régime alimentaire, impacts

## Introduction

New Caledonia is a tropical archipelago located to the east of Australia, in the South-Pacific Ocean. The archipelago has been classified as one of the world's 36 biodiversity hotspots because of its elevated levels of endemism in such a small territory (Williams et al. 2011). Among notable features of local biodiversity in New Caledonia, Myers et al. (2000) highlighted five endemic families and 112 endemic genera of plants, and one endemic family and three endemic genera of birds. However, a significant proportion of this biological richness is increasingly threatened by human activities and global changes, as is the case for most of the world's biodiversity hotspots (Bellard et al. 2014). Among factors that foster these changes, habitat fragmentation and climate change are widely recognized (Garcia et al. 2014; Haddad et al. 2015), while the best response from scientists and managers to species' introductions is still a matter of debate (Russel and Blackburn 2017; Davis and Chew 2017).

The effects of invasive species have been widely documented (Early et al. 2016). Impacts are accentuated in island ecosystems (Russell et al. 2017), often because on the naïvety of insular species (Gerard et al. 2016) and environmental, ecological and evolutionary factors associated with geographic isolation (Cabral et al. 2017). Man plays a key role in the transportation of plant and animal species worldwide (Ricciardi et al. 2017). Trade in animals (Cardador et al. 2017; Su et al. 2016) and the release or escape of cage birds are frequently identified as the main mechanisms for alien bird introductions and the dispersal of wild birds outside of their native ranges (Dyer et al. 2017).

Tropical bird species, particularly those from Southeast Asia, occupy a prominent place in global bird trade (Nijman 2010), with bulbuls, starlings, mynas and robins figuring amongst the most traded species from this region (Harris et al. 2015). As a result, two out of three

species considered in the IUCN-ISSG list of 100 worst invasive species are native to Southern Asia: the red-vented bulbul (*Pycnonotus cafer*) and the common myna (*Acridotheres tristis*) (Lowe et al. 2000). These two species historically were widely transported from India to Pacific Islands (Watling 1978) and both are now established in New Caledonia (Brochier et al. 2010). Our global review on the impact and management of alien red-vented bulbuls identified 37 islands in the alien distribution of this species (Thibault et al. 2018a). This study also highlighted the lack of quantitative data and evidence-based assessments of the impacts associated with this invasive species. The red-vented bulbul was introduced into New Caledonia around 1983 (Gill et al. 1995) and its local distribution range is currently expanding from Nouméa toward the north and south of the main island. For 25 years following its introduction into Nouméa, no studies were conducted to investigate the ecology, distribution or impacts of the species at a local scale. This lack of information has precluded any detailed assessment of the threats posed by the establishment of the red-vented bulbul in New Caledonia. Consequently, it has not thus far been possible to implement an evidence-based management strategy.

The goal of this paper is to present an overview of data from recent studies conducted in New Caledonia to describe the local status of the red-vented bulbul, its range expansion, and potential impacts on both the local biodiversity and agriculture. We first report the local distribution range of the species, the rate and nature of its range expansion, and its habitat selection and densities in different habitats. We then use diet analysis to explore potential negative effects of the red-vented bulbul on natural and agricultural systems. We present original data on an ongoing invasion process in a tropical island biodiversity hotspot and highlight priority areas for local red-vented bulbul research and risk management.

## Methods

### Red-vented bulbul range expansion

Red-vented bulbul dispersal was monitored over time using static 10-min point counts combined with 2-min playback of recorded calls to increase detection probability (Ralph et al. 1995). Points were sampled within the 4 hours following sunrise, between November and December in 2008, 2012, 2014 and 2016. Each point was geo-referenced, and the observers accounted for seen and heard individuals. In 2008, 136 points were sampled that covered Nouméa and suburbs as well as borders of the two main roads going to the north and south. Random points were also located in major urban areas along these roads to search for potential pioneering individuals. The method was replicated in 2012, 2014 and 2016, covering 203, 96 and 99 points respectively. Data were compiled and plotted in Qgis software version 2.18.1 (Quantum GIS Development Team 2016).

In April 2016, we selected six additional sites across native and man-modified habitats to explore the future establishment of the red-vented bulbul in forests. We chose three sites across urban and dry forest habitats, and three across urban and wet forest habitats. These sites were located close to the core of the distribution range, where red-vented bulbul densities were highest. We placed 10 points spaced at least 250 m apart at each site (five points per habitat) and counted red-vented bulbul individuals seen and heard. The method used was the same as for distribution monitoring. Data were compiled in Qgis software version 2.18.1 (Quantum GIS Development Team 2016) and plotted in R software version 3.4.0 (R Core Team 2017).

### Red-vented bulbul densities

Red-vented bulbul density was measured using a distance sampling method (Thomas et al. 2010) in four sites located within the core of the red-vented bulbul distribution range. This method relies on three key assumptions: i) individuals at 0 meters distance are detected with certainty, ii) individuals are detected once and at their initial location, and iii) distance measurements are exact. Sites were selected in man-modified habitats, along a distance gradient from Nouméa to Tomo, a village located about 50 km farther north. Three transects of 1 km were established at each site and sampled between October and December 2015. A pair of observers walked along each transect for 30 min and counted the number of individuals seen on both sides. The distance of observed individuals from each transect was recorded with a laser telemeter. Transects were sampled three times between 5 and 9 am and data from the three sessions were used independently and pooled to prevent a potential bias due to time of day. Data were analysed with the "Distance" package (Miller 2016) using R software version 3.4.0 (R Core Team 2017). This method considers potential missed observations in the estimated bird densities thanks to the calculation of a detection probability curve. We first estimated the bird density at each site using data from the three sessions separately. Then, we estimated densities at each site using data of the three sessions together, considering the nine transects at each site as independent. Finally, we chose to present the estimates from the pooled dataset as it provided a smoothed estimation of densities regarding the influence of time of day on bird detection.

### Red-vented bulbul diet analysis

Gut content analysis was conducted on 40 dead red-vented bulbuls provided by local hunters. There is no morphological dimorphism between male and female red-vented bulbul, so we were only able to determine the sex of sexually mature individuals, using anatomical analysis.

Gastrointestinal tracts were excised, and the contents removed and washed with tap water through a 0.2 mm sieve. The retained contents were placed in a Petri dish filled with 70% alcohol and examined under a dissecting microscope at 10 x magnification (Olympus SZ61). Items were photographed (Toupcam UCMOS camera and Toupview software) for subsequent identification (Lopes et al. 2013).

## Fruit colour selection

According to the literature, damage to cultivated plants is the most frequently reported impact of the red-vented bulbul in its alien range (Thibault et al. 2018a). This is also the impact category most often reported locally both by professionals (Caplong and Barjon 2010) and non-professionals. We tackled this issue through two distinct experiments, a colour preference test and an open-field test.

We conducted an experiment on fruit colour selection to test whether the red-vented bulbul was attracted by some fruit colours more than others. We trapped eight adult individuals, maintained them in an aviary for at least a month, and in individual cages for three days. We created false-coloured fruits of four distinct colours, following the method presented in Duan, et al. (2013). Artificial fruits were made of banana, chicken grain and water, and three quarters of the fruits were coloured with red, green and yellow food colouring. Ten fruits of each colour were placed in four different petri dishes in cages with bulbuls held individually and observed for 25 minutes from a hidden position. Each bird was tested once during five consecutive days, following either two hours or six hours of fasting. For each repetition, the colour of the first fruit eaten as well as the total number of fruit eaten per colour were recorded. ANOVA tests were conducted in R software version 3.4.0 (R Core Team 2017) with hypothesis H0 being that each fruit colour had the same probability of being eaten first.

## Damage to crops

In 2016, we conducted an open field test to explore the range of damages caused by red-vented bulbuls to tomato crops. We planted eight tomato plants inside each of 20 square plots spaced by 1 meter, and randomly covered half of the plots with bird netting during the flowering stage. During the fruiting period in August and September, each plot was monitored twice a week. Ripe and damaged fruit were harvested and separated in three categories; i) marketable; ii) pecked fruits; and iii) other damage. For each category, the colour, size, and sugar levels (in Brix degrees, Bates 1942) of fruit were recorded. Tomatoes that were pecked by the birds were easily recognizable by beak marks, and the mark's size together with direct observations were used to determine the fruits that were damaged by red-vented bulbuls. The relative economic loss in marketable tomatoes due to bulbul damages was then calculated as the total weight of pecked tomatoes divided by the total weight of tomatoes harvested in 'unprotected plots'. This percentage was then extrapolated to the national production recorded during the month of our experiment. Data were analysed with the "nlme" package (Pinheiro et al. 2012) using in R software version 3.4.0 (R Core Team 2017).

## Results

### Red-vented bulbul range expansion

The 2008-2016 red-vented bulbul bi-annual distribution map (**Fig 1**) shows a continuous increase in the distribution range occupied by the red-vented bulbul in New Caledonia. Coloured polygons contain all points where red-vented bulbul individuals were observed in 2008, 2012, 2014 and 2016. Conversely, green dots represent all points counts where red-vented bulbul were not detected either during point-counts or during playback calls.
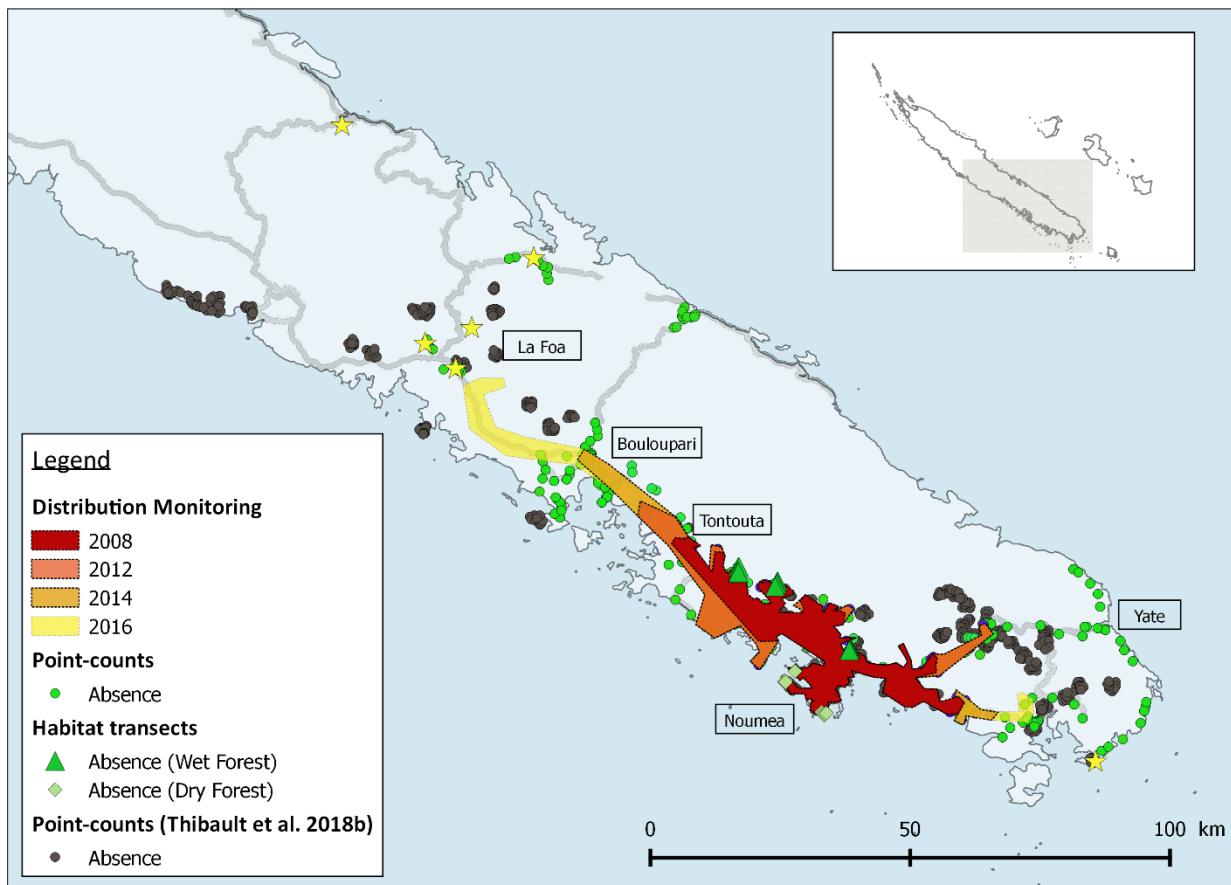
**Fig 1** Map of the expanding distribution of the red-vented bulbul between 2008 and 2016 according to the bi-annual monitoring. Stars represent observation testimonies from local people. Green dots represent point absence data (point counts) from the distribution monitoring. Green triangles and diamonds represent absence data (point counts along transects) in natural forests surrounding the distribution core. Grey dots show absence data (point counts) from another study (Thibault et al. 20108b).

The green triangles and diamonds represent respectively absence point located in natural dry forest patches located within the city of Nouméa, and in humid forest, which represent the northern border of the capital and its suburbs. This absence data suggests that the species is not yet spreading into natural forest. Indeed, over the 60 point counts conducted at frontiers between urban and forest habitats, we detected red-vented bulbul individuals at 16 points located in urban habitats and one point in dry forest habitat. We also received testimonies from local people about red-vented bulbul sightings. These testimonies were rarely confirmed by further observations but sometimes led to new detection. **Fig 1** shows a continuous

distribution of the red-vented bulbuls with range expansion particularly along main roads. **Fig 1** also presents absence data from another study (Thibault et al. 2018b) which are consistent with this hypothesis. The two road axes from Nouméa to La Foa (100 km north) and Yaté (95 km south) appeared as the main dispersal pathways. In 2012, 25 years after its introduction in the city of Nouméa, the red-vented bulbul had reached Tontouta, 42 kilometres north. From 2012 to 2016 the species travelled 35 kilometres north (**Fig 2**). Nowadays the red-vented bulbul occupies at least 1350 km$^2$ (8% of the New Caledonia territory), mostly restricted to the west coast of the southern province.
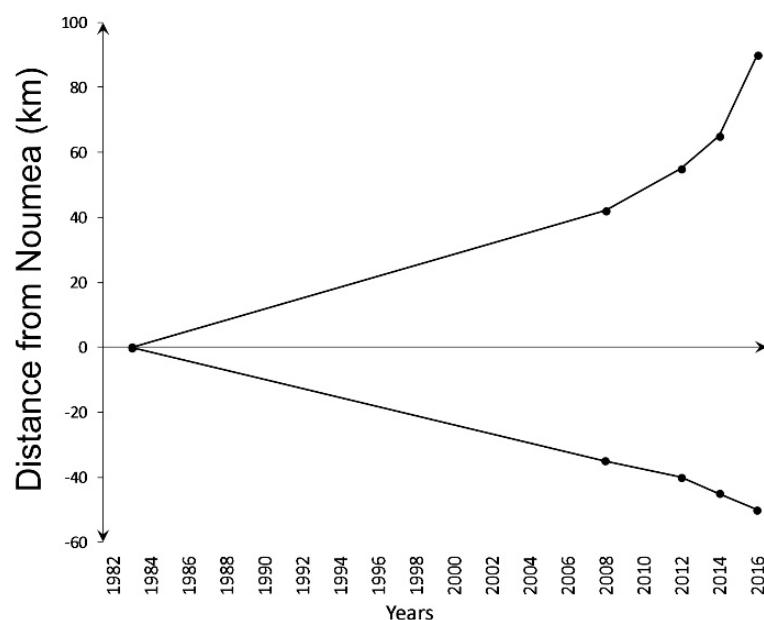


**Fig 2** Evolution of the red-vented bulbul dispersal toward the North and South of Nouméa.

Red-vented bulbul densities

Most birds were both heard and seen during our sampling sessions in inhabited areas. We fitted our data to a half-normal distribution (Thomas et al. 2010) to calculate the detection function (**Fig 3**).
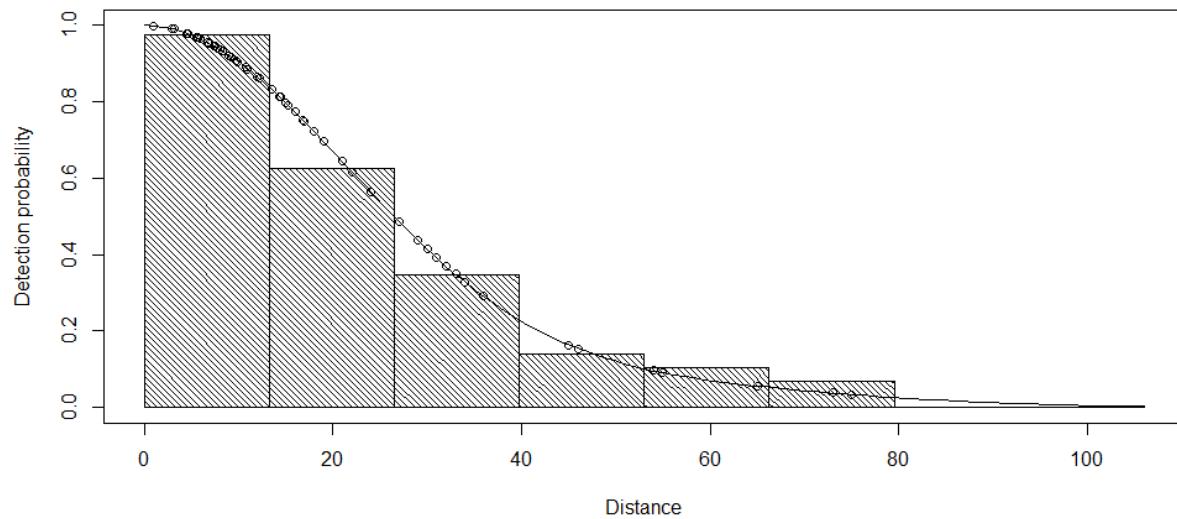
**Fig 3** Probability of detecting a red-vented bulbul individual as a function of distance from the transect in inhabited areas.
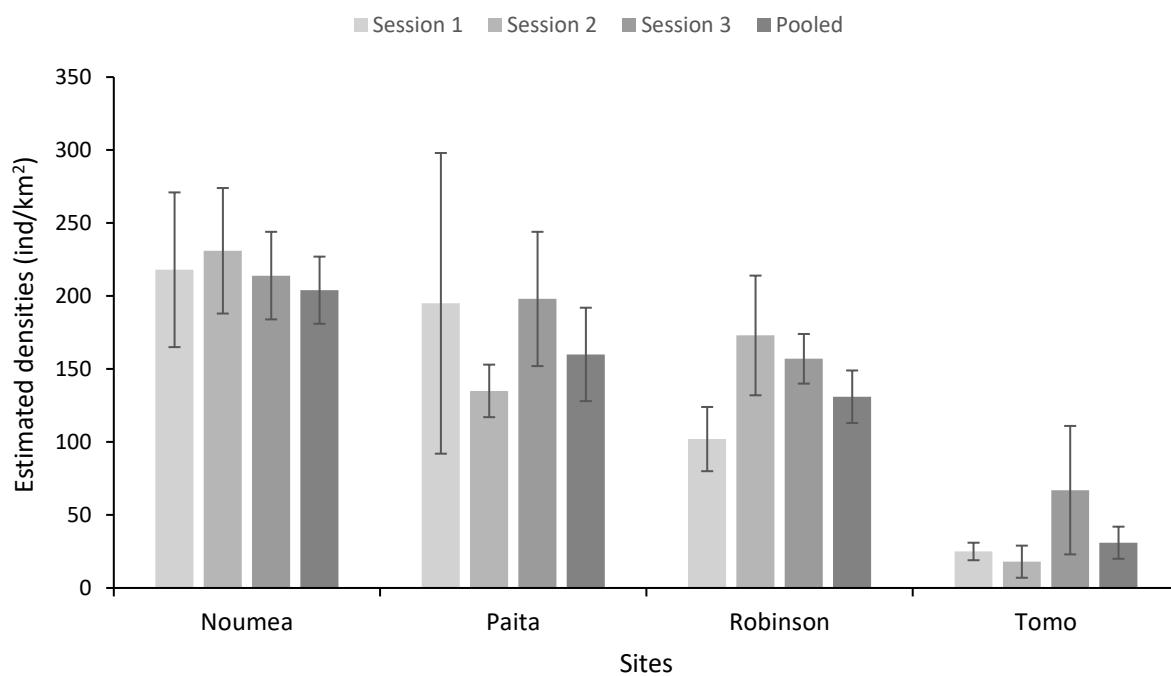


**Fig 4** Densities of red-vented bulbuls at each site calculated from the three sampling sessions, and from the pooled dataset.

Density estimates from the three sessions and from the pooled data set are presented in **Fig 4**. Red-vented bulbul estimated density was six times higher in the city of Nouméa (*d*: 204 ± 23 ind/km$^2$) than in the village of Tomo which is located 50 kilometres north (*d*: 31 ± 11 ind/km$^2$, **Table 1**). Estimates from the two suburban areas, Robinson and Paita, were almost identical (*d*: 160 ± 32 ind/km$^2$ and *d*: 131 ± 18 ind/km$^2$ respectively). The density estimates are corrected by a detection function curve which represents the probability of an observer to detect a red-vented bulbul depending on its distance from the transect. In the four urban habitats we sampled, the average probability of detecting a red-vented bulbul was 50% when the bird was approximately 25 metres from the observer.

**Table 1** Sampling statistics and density estimates at four urban sites within the current distribution range of the red-vented bulbuls according to distance from the introduction point. (n) Total number of individuals over the three sessions.

| Site | Distance (km) | Habitat | Area (m2) | n | Density estimate (ind/km$^2$) | Standard error |
|------|---------------|---------|-----------|---|-------------------------------|----------------|
| Nouméa | 0 | urban | 787.3 | 117 | 204 | ± 23 |
| Paita | 10 | suburban | 816.3 | 66 | 160 | ± 32 |
| Robinson | 25 | suburban | 492.8 | 65 | 131 | ± 18 |
| Tomo | 50 | rural | 993.3 | 15 | 31 | ± 11 |

Red-vented bulbul diet analysis

We extracted and analysed the gut content of 40 red-vented bulbuls. Results of the diet study are presented in **Table 2**. Mean weight of mature individuals was 38.3 ± 4.9 g for females and 44.1 ± 5.6 g for males. We found plant remains in the gut content of 33 individuals (82.5%) and animal items in 22 (55%). Among plant items, seeds (55%) and fruit flesh (42.5%) were

the most frequent. The most frequent plant family was Myrtaceae (20 individuals), and most consumed insect orders were Hemiptera (13 individuals) and Coleoptera (8 individuals). Remains identification highlighted the consumption of one endemic plant species (*Myrtastrum rufopunctatum*), two cultivated species (*Syzygium cumini* and *Lichi chinensis*) and two invasive alien species (*Passiflora foetida* and *Solanum torvum).* Exoskeleton parts from cicadae individuals were frequent in this sample (*F*=32.5%). No vertebrate remains were found during this analysis.

**Table 2** Occurrences (n) and frequency (%) of food items identified in the gut content of 40 bulbul individuals.

|  | | n | F (n=40) |
|---|---|---|---|
| **Fruit parts** | | | |
| | Whole fruit | 16 | 40 |
| | Seeds | 22 | 55 |
| | Fruit skin | 7 | 17.5 |
| | Fruit flesh | 17 | 42.5 |
| **Plant families** | | 33 | 82.5 |
| | *Myrtaceae* | 20 | 50 |
| | *Passifloraceae* | 1 | 2.5 |
| | *Sapindaceae* | 2 | 5 |
| | *Solanaceae* | 4 | 10 |
| **Insects** | | 22 | 55 |
| | *Coleoptera* | 8 | 20 |
| | *Diptera* | 1 | 2.5 |
| | *Hemiptera* | 13 | 32.5 |
| | *Hymenoptera* | 3 | 7.5 |
| | *Odonata* | 1 | 2.5 |

Fruit colour selection

Colour selection tests were replicated 102 times. The first pecked fruit was red in 77% of samples, followed by green (10% of samples). The average number of consumed fruits per colour is presented in **Fig 5**. Red fruits were the most often consumed (5 ± 0.3), and yellow ones were consumed five times less often (0.9 ± 0.16). Colour contributed to explain the consumption of fruits significantly (ANOVA: *F*: 8.3; *p*<0.001). In our analysis, fasting period did not contribute to explain the choice of coloured fruits (ANOVA: *F*: 2.7; *p*=0.1).
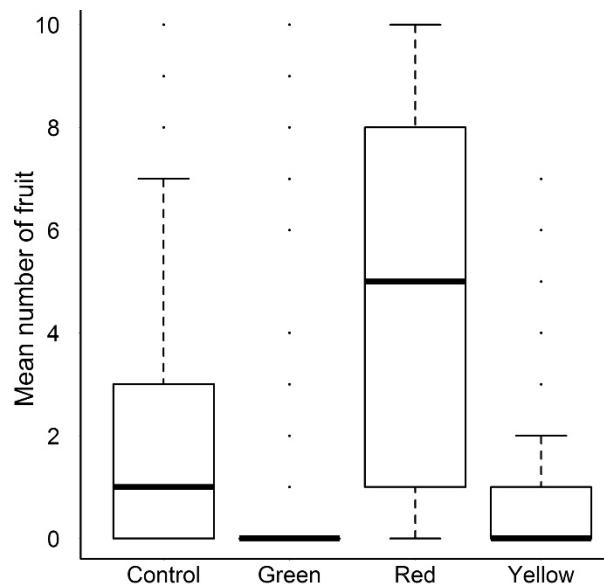


**Fig 5** Result of 102 colour preference tests with red-vented bulbuls. The y-axis represents the average number of fruits consumed by tested individuals during one session.

Damages on crops

On our 20 plots, we produced a total of 2310 tomatoes (345.5 kg). Unfortunately, three plots with nets were damaged by feral dogs just before the beginning of the fruiting season, and were thus considered as unprotected. Red-vented bulbuls were the only birds that fed on tomato fruit during the experiment. Results are presented in **Fig 6**.
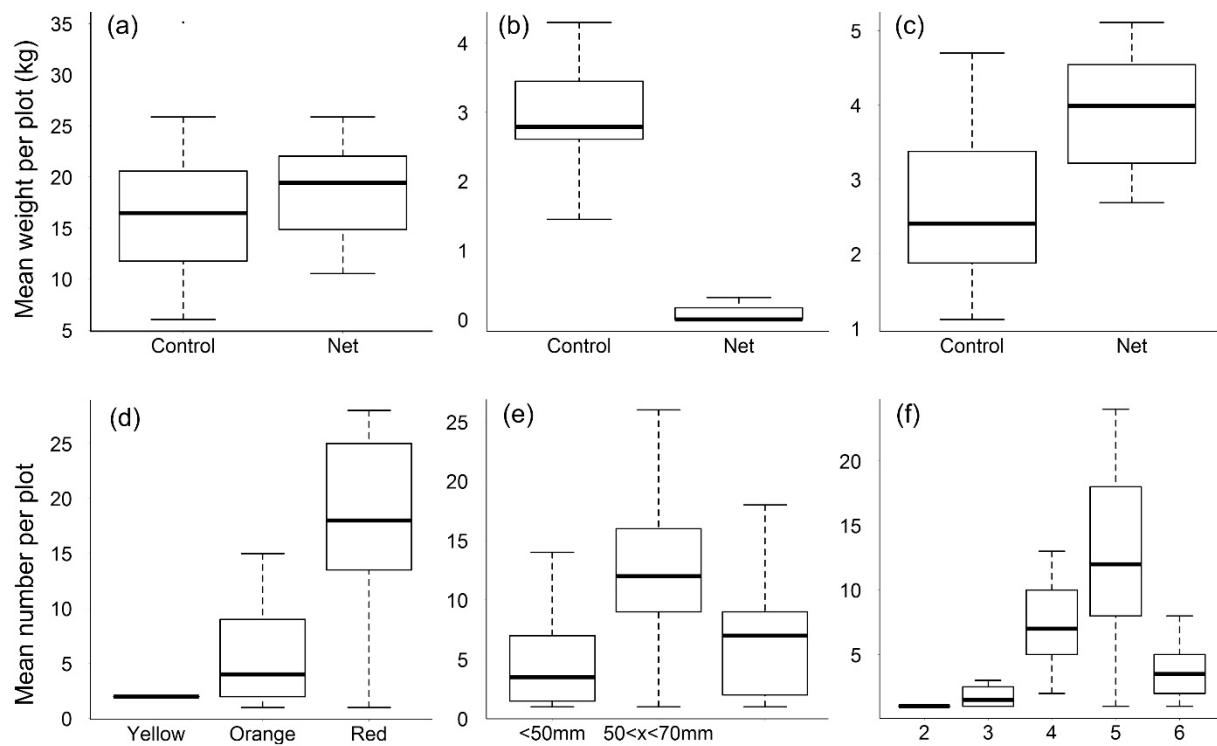
**Fig 6** Result of the open field test conducted with tomato plants. (a) Represents the global production weights for "net-protected" and "unprotected" treatments, (b) and (c) represent the mean weight of fruit damaged per plot by birds and other pests. (d), (e) and (f) represent the average number of damaged fruit depending on fruit colour, size, and sugar content, respectively.

On average, production per plot was homogenous in net-protected pots (18.5 ± 2.1 kg) compared to 'unprotected' ones (16.6 ± 2.3 kg). Losses due to bird damage were recorded almost exclusively in 'unprotected' plots and corresponded to 2.95 ± 0.24 kg per plot (17.5%), as only three tomatoes were pecked at the edge of protected plots (0.5% in weight). These losses were similar to those caused by other pests: 2.63 ± 0.3 kg in unprotected plots, and 3.9 ± 0.3 kg in protected plots. Pecked fruits were mainly red (ANOVA F: 7.6; p=0.009), between 50 and 70 mm in size and with high sugar levels (5°Bx, ANOVA: 5.95; p=0.016). Considering that 34 tons of tomato were sold at 3.18 USD/kg in September 2016 in New Caledonia, the

17.5% loss we recorded because of bird damages would have corresponded to an economic loss of approximately $18,355 USD for September 2016 alone.

## Discussion

### Dispersal along urban corridors

The red-vented bulbul has continuously increased its distribution range in New Caledonia since its introduction 25 years ago. The distribution map suggests that roads and urban habitats are the main dispersal pathways for the species. The dispersal rates we estimated were different depending on the direction. One reason for this may be differences in habitat to the north and south of Nouméa. The south of the main island of New Caledonia is dominated by ultramafic soils and the dominant vegetation type is the "maquis minier", a shrubland characterised by xerophytic plants (Jaffré et al. 2003; Jaffré et al. 2004) which may be less attractive in term of food source for red-vented bulbuls. Considering the dispersal speed, we know that the red-vented bulbul's range expanded 40 kilometres toward the north of its introduction point in 25 years. Its range expansion then increased more quickly, extending a further 35 kilometres in just four years. This is consistent with findings of Aagard and Lockwood (2014) on growth lag in alien bird populations, and suggests that this range expansion could continue to accelerate. Our observation of a lagged expansion in the red-vented bulbul could thus be explained both by a demographic time-lag, inter-specific relationships, or by the carrying capacity of the different habitats.

Study of red-vented bulbul occurrence at the frontiers between urban and forest habitats confirmed the association of the species with man-modified habitats. Our results suggest that the red-vented bulbul is not spreading from invaded urban areas either into dry forest patches or into native rainforests. This is consistent with previous observations of Watling (1979) in

Fiji. However, in Tahiti (French Polynesia) the red-vented bulbul can colonize native tropical forests with major impacts on native avifauna (Blanvillain et al. 2003). Further monitoring of the distribution is thus crucial to anticipate potential shifts in the habitat occupancy and resulting threats on forest bird communities. A specific effort could be dedicated by managers to prevent future establishment of pioneer individuals out of the current range, toward the north, the Loyalty Islands or specific areas of high conservation/agricultural value. Quick detection coupled with control actions at the edges of the red-vented bulbul range will reduce the colonization speed and prevent future negative effects.

## Density gradient

Dispersal of bird species are partly related to population densities (Matthysen 2005), so the anticipation of future dispersal events may be facilitated by the knowledge of bird density in specific locations. Our density estimates showed a density gradient in the red-vented bulbul, depending on the urbanisation level and the distance from the introduction point. This was frequently observed in alien bird populations (Chace and Walsh 2006). The density level we estimated in the rural village of Tomo were similar to those reported by Radhakrishanan and Asokan (2015) in two villages of the Cauvery delta region in Southern India, to which the red-vented bulbul is native. However, our estimates for the centre of Nouméa and suburbs are similar to those found for common bird species in European/American urban centres (Clergeau et al. 1998). High bird densities in urban habitats are often associated with low bird-community species richness (Matthysen 2005). Regarding its density, the red-vented bulbul is already one predominant species in Nouméa. Monitoring the change in red-vented bulbul densities over time will contribute to a better understanding of the species' dynamics. It will also allow the estimation of the density-impact relationship in further management programmes (Yokomizo et al. 2009), as management of invasive alien species populations

often relies on abundance/density reductions (Genovesi 2005; Simberloff et al. 2005). For example, control operations could be feasible at low densities, whereas mitigation of specific impacts could be more money-efficient at high-density levels.

## Predation and frugivory

Results of the diet analysis were consistent with previous observations elsewhere in both the alien and native range of the species (Watling et al. 1978; Bhatt and Kumar 2001; Brooks 2013; Bates et al. 2014). The diet comprised mostly, fruits, and a significant part of animal remains. We observed several red-vented bulbul individuals feeding on house geckos (*Hemidactylus frenatus*) and skinks in the field, but we did not find any reptile or gastropod remains in the gut contents we analysed. Such food items have been reported in the red-vented bulbul native range (Bhatt and Kumar 2001). Much of the gut contents we analysed (n=13, F=32.5%) contained remains from cicadas. Considering the periodic lifecycle of these insects (May 1974), this observation suggests that red-vented bulbuls can adapt their diet to this temporary resource. Levels of endemism are high in New-Caledonia, with approximately 92% of reptiles and nearly 100% of cicadas (Smith et al. 2007; Grandcolas et al. 2008; Delorme et al. 2016) being endemic. Predation by alien species such as the red-vented bulbul could thus represent an additional threat for these species of high conservation value.

Seeds and whole fruits were found in 50% of individuals. This observation emphasizes the red-vented bulbul's capacity to participate in seed dispersal, particularly in association with invasive alien plant species like *Miconia calvescens* or *Lantana camara* (Meyer 1996; Spotswood et al. 2012; Spotswood et al. 2013). In our diet study, we identified several candidates to a red-vented bulbul-mediated dispersal. Most of them were invasive or cultivated species, but we also identified one endemic (*Myrtastumrufo punctatum*) that is used for mining-site restoration (Lemay et al. 2009). Consumption of native species by the

red-vented bulbul could result in a service, by improving the dispersal capacity of some species (Kawakami et al. 2009). However, it can also lead to competitive interactions with native avifauna (Sherman and Fall 2010; Thibault et al. 2018b) which can turn into a conservation issue (Blanvillain et al. 2003). New Caledonia is considered as a biodiversity hotspot (Myers et al. 2000) thanks to its plant diversity, with 3060 species of flowering plants recorded (78% endemic, Munzinger et al. 2016). Exploring variations in the red-vented bulbul diet over different habitat, seasons and maturity stages will contribute to the better prediction of the dispersal of both alien and native plants as well as potential negative interactions with endemic species. At a wider scale, such quantitative and qualitative data will contribute to the assessment of impacts caused by red-vented bulbuls (Thibault et al. 2018a).

## Colour selection and damages on crops

Diet and preference for specific resources plays a key role in impacts caused by vertebrate pest species (Herrero et al. 2006; Gebhardt 2011). Sometimes, these preferences can be strong enough to aid bait selection for both hunters and environment managers. In our experiment, the red-vented bulbul preferred red, consistent with colour preference in the red-whiskered bulbul (*Pycnonotus jocosus*) (Duan et al. 2013). In a French Polynesian study, authors concluded that preference may sometimes be stronger than abundance in fruit selection by birds, including the red-vented bulbul (Spotswood et al. 2013).

Such preference for specific fruits implies that red-vented bulbuls are likely to disperse or damage some species of fruit more than others, and that predictions can be made about species that are likely to be most vulnerable. Observations made during our open field experiment were consistent with this hypothesis, with red tomatoes being damaged more than orange or yellow ones. In unprotected plots, damage caused by birds was equivalent to that of all the parasites and corresponded to 17.5% loss in weight of marketable fruit. This

corresponds to the average losses presented in Oerke (2006) in their global estimation of economic losses due to animal pests over 11 production types including tomato, between 2001 and 2003. In this study, recorded losses attributed to animal species and other pathogens on unprotected crops were of 18% and 15% respectively. Oerke suggested that pest control operations allowed a 39% reduction in losses due to animal pest. Here we showed that net protection on tomato plants efficiently protected 99% of fruits, reducing by 97% the loss in weight of marketable fruit. This early assessment of colour selection and damage on production suggests that red and sweet fruit/flower productions could be more sensitive to red-vented bulbul damages. Such information is already used in the development of trapping systems dedicated to this species. Indeed, fruit and fresh vegetables represented 5115 and 6292 tons of production in New Caledonia in 2012, corresponding to 25% and 30% of the total plant production that year (ISEE 2012). The red-vented bulbul is currently restricted to suburban areas in a limited range, but up to 35% loss has already been recorded on fruit production there (Caplong and Barjon 2010). Future establishment of the species in cultivated areas of the main island could thus represent an additional risk to plant productions.

## Conclusion

The global distribution and population trends of red-vented bulbul have been poorly reported relative to many other tropical invasive birds. The potential overlap in the impacts associated with tropical passerine species from south Asia, suggested by Kumschick et al. (2015), has not been explored either. Authors claimed that introduced populations of red-vented bulbuls were harmless (Watling 1979), while in other locations its role in noxious seed dispersal (Meyer et al. 1996), competition with native birds (Blanvillain et al. 2003; Thibault et al. 2018b) and damages on crops (Walker 2008) were suggested. New Caledonia must deal with the current dispersal of this species on its territory with only a few quantitative data available

from the literature (Thibault et al. 2018a). However, the establishment, on-going dispersal, and impacts of the red-vented bulbul deserve attention from conservation biologists, environment managers and local people. Perceptions of this invasive species differ across groups of people (Fisher et al. 2014), but a coordinated joint effort is required to improve our knowledge of invasion mechanisms for the red-vented bulbul in the New Caledonia archipelago. New Caledonia recently produced a list of priority invasive species for management actions, and the studies we presented here contributed to the consideration of the red-vented bulbul among the six species of this list.

## Acknowledgments

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# CHAPTER 4: Interspecific competition

## The invasive red-vented bulbul (P*ycnonotus cafer*) outcompetes native birds in a tropical biodiversity hotspot

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## Abstract

Invasive alien species are a major cause of biodiversity loss globally, but especially on islands where high species richness and levels of endemism accentuate their impacts. The Red vented bulbul (*Pycnonotus cafer*), a tropical passerine bird that has been introduced widely across locations of high conservation value, is considered an extreme pest. It is currently expanding its range in New Caledonia, one of the world's biodiversity hotspots. Decisive recommendations on management strategies are required urgently to inform local managers and policy makers, but they should be based on quantitative local evidence, not just on expert opinion. The Red-vented bulbul is widely blamed for its impacts on biodiversity, especially through competition. We used data from 2,472 point counts to explore the abundance relationships between the Red-vented bulbul and 14 other species of bird. Our results revealed a negative relationship between the occurrence of the bulbul and the mean abundance of nine species, all native (or endemic, n=3) to the New Caledonia archipelago. In contrast, the abundance of other introduced species such as *Acridotheres tristis* (Common myna), *Passer domesticus* (House sparrow) and *Spilopelia chinensis* (Spotted dove) were not affected by the Red-vented bulbul. Moreover, temporal trends in the abundance of impacted species suggest that the Red-vented bulbul may cause niche contractions rather than mortality for native species in man-modified habitats. Monitoring and control of the Red-vented bulbul is recommended to prevent on-going impacts on native bird communities throughout New Caledonia, and its impact on native bird communities elsewhere should be quantified.

**Keywords:** invasion; birds; conservation ecology; interspecific-relationships; abundance; biodiversity hotspot

## Résumé

Les espèces envahissantes sont une des causes majeures de l'érosion de la biodiversité à l'échelle mondiale, particulièrement sur les îles où la richesse spécifique et les taux d'endémisme accentuent leurs impacts. Le bulbul à ventre rouge (*Pycnonotus cafer*), un passereau introduit largement dans des territoires à haute valeur de conservation, est aujourd'hui considéré comme un envahisseur majeur. Or, cette espèce est actuellement en pleine expansion dans l'archipel de Nouvelle-Calédonie, un des 36 hotspots mondiaux de biodiversité. Des recommandations sur les stratégies de gestion adaptées sont nécessaires pour informer les gestionnaires locaux et les décideurs, mais elles doivent être fondées sur des preuves quantitatives, et pas seulement sur l'opinion d'experts. Le bulbul à ventre rouge est réputé pour ses impacts sur la biodiversité, notamment à travers la compétition. Ici, nous avons utilisé des données de 2 472 points d'écoute afin de décrire les relations d'abondance entre le bulbul à ventre rouge et 14 espèces d'oiseaux. Nos résultats révèlent une relation négative entre la présence du bulbul et l'abondance moyenne de neuf espèces, toutes natives (ou endémiques, n = 3) de Nouvelle-Calédonie. En revanche, l'abondance d'espèces introduites telles que *Acridotheres tristis* (merles des Moluques), *Passer domesticus* (moineau domestique) et *Spilopelia chinensis* (tourterelle tigrine) n'était pas affectée par sa présence. De plus, l'évolution temporelle de l'abondance des espèces touchées suggèrent que le bulbul à ventre rouge pourrait provoquer une contraction de niche plutôt que la disparition des espèces natives dans les habitats urbanisés. La surveillance et la gestion du bulbul à ventre rouge sont recommandées pour prévenir les impacts sur les communautés d'oiseaux natifs. Son impact sur d'autres communautés d'oiseaux natifs dans le Pacifique devrait être quantifié.

**Mots-clefs :** Invasion, oiseaux, écologie de la conservation, relations interspécifiques, hotspot de biodiversité

## Introduction

Exotic species play a major role in the decline of native species globally, but especially on islands with high species richness, high levels of endemism, and naivety towards novel predators and competitors (Tershy et al. 2015; Bellard et al. 2016; Gerard et al. 2016; Gren et al. 2016; Walsh et al. 2012). Defining the appropriate attitude to hold toward introduced species is a matter of debate (Davis et al. 2011; Simberloff et al. 2011; Russel and Blackburn 2017; Davis and Chew 2017). However, the continuous increase in numbers of alien species across diverse habitats is a reality (Seebens et al. 2017), and there appears to be consensus that field studies and local assessment of their negative impacts are essential to design better responses to biological invasions (Kumschick et al. 2015; Saxena 2015). Recent models suggest that 16% of biodiversity hotspots are highly vulnerable to invasive species (Lowe et al. 2000; Bellard et al. 2014; Early et al. 2016), because of various pressures on native biodiversity through predation, competition, disease transmission, hybridization and ecosystem perturbation (David et al. 2017; Rogers et al. 2017; Young et al. 2017). Most data on animal invasions have been derived from studies on established and stable alien populations, often from a macro-ecological perspective (Strayer et al. 2006), and interest from researchers and managers has been biased towards some invasive taxa such as mammals (Pyšek et al. 2008). For invasive birds particularly, more data are needed on early-stage dispersal processes and impacts to help predict, prevent, and manage harmful impacts (Strubbe et al. 2011; Evans et al. 2014).

The Red-vented bulbul, *Pycnonotus cafer* Linnaeus, 1766, is a good example of a species that is currently considered to be a major invasive species (Lowe et al. 2000), more through expert opinion than through scientific assessment of its impacts (Martin-Albarracin et al. 2015;

Thibault et al. 2018). This species is a tropical passerine from southern Asia that was widely transported as a caged bird from the early 1900s onwards (Watling 1978). Several release and escape events led to its successful establishment in at least 36 locations out of 46 where it was introduced, including 27 islands, two continental islands and seven continental areas (Thibault et al. 2018). Its diet of fruits (Brooks 2013) and its aggressive interspecific behavior (Sherman and Fall 2010) are blamed for the damage it causes to crops (Walker 2008) and its ability to out compete native avifauna (Thibault et al. 2002). Moreover, its impacts are thought to overlap considerably with other widespread invasive species such as the Common myna (*Acridotheres tristis*) or the Black rat (*Rattus rattus*), and could represent an additive pressure on species of high conservation values (Kumschick et al. 2015; Blanvillain et al. 2003). Direct assessment of local impacts and invasion mechanisms for the red-vented bulbul are scarce (Martin-Albarracin et al. 2015). Some authors have claimed that alien populations of the red-vented bulbul in tropical islands are harmless (Fiji; Gill et al. 1995) whereas others claim that this species should be at the top of invasive species priority lists (Thibault et al. 2002; Blanvillain et al. 2003).

In New Caledonia, some caged red-vented bulbuls were released in the capital (Nouméa) around 1983 (Gill et al. 1995) and the species is now in the "spread" phase (Blackburn et al. 2011; Simberloff et al. 2013). The rate of the species range expansion in the main island has increased progressively since its introduction and its range now extends nearly 100 km beyond its initial release site. New Caledonia is a biodiversity hotspot (Myers et al. 2000), with nearly 60% of its 90 species of terrestrial breeding birds being endemic (Barré et al. 2009). With increasing urbanization and habitat transformation, along with the deleterious consequences of mining activities, the additive pressures from invasive species may impact severely upon the conservation of already weakened native bird communities. Therefore, concern amongst

managers and scientists about the spread of the red-vented bulbul has increased over the last decade and the red-vented bulbul is now considered in law to be a priority pest species in the two provinces of the main island (DDEE 2008; DEPS 2016). Of particular concern is its supposed contribution to the local decline in some native passerine species in man-modified habitats, but no robust evidence exists that could corroborate or refute this concern.

Here, we studied the impacts of ongoing range expansion of the red-vented bulbul on terrestrial birds in New Caledonia. The objectives were to i) describe how anthropized habitats shape the early dispersal of this introduced species, ii) identify bird species that may decrease in abundance following the arrival of the red-vented bulbul, and iii) determine whether an increase in local abundances of the red-vented bulbul contribute to a decline in native bird species. The results are of relevance to managers at both local and global scales, providing insight into the risks associated with this invasive species. Implications for adapted management strategies are discussed.

## Methods

### Temporal Monitoring of Terrestrial Birds

Point-count data, as classically used for the temporal monitoring of terrestrial birds (Ralph et al. 1995), were collected on the Grande Terre island from 97 monitoring stations corresponding to 2,478 point counts over six consecutive years (**Fig.1**, *samplings per year are detailed in next section*). Observers were responsible for the monitoring of a station (2 km$^2$) that was covered with 10 randomly distributed listening points spaced a minimum of 250 m apart. The 10 points were monitored in a single day, annually, between October and December. Point counts started 30 minutes after sunrise (range 05.30-06.00 h) and ended at 10.00 h. At each point, the observer waited 3 minutes to avoid any impact of their arrival on

bird detection, and then counted every bird heard or seen during a 5-minute period (Ralph et al. 1995).
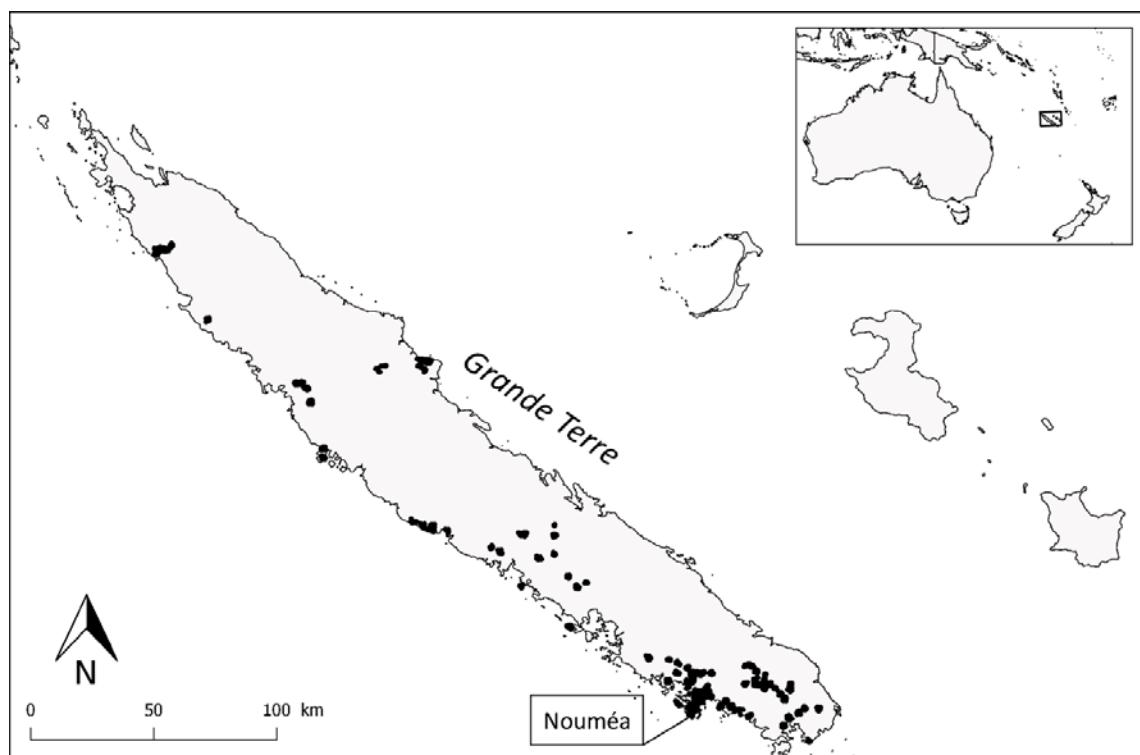


**Fig 1.** Distribution of stations considered in the monitoring of terrestrial breeding birds in New Caledonia. Points represent sampling stations and correspond to 10 point counts.

Because part of the data came from participative monitoring, and because the location of some points evolved together with habitat perturbations, the sampling effort was not homogeneous over the monitoring period. We started the monitoring with 77 points in 2010, sampled 309 and 391 points in 2011 and 2012 respectively, and reached more than 610 points in 2013 and 2014 before a small decrease in 2015 to 470 sampled points. However, the year of sampling was not found to be a significant source of variation for bird abundance in any regression or generalized mixed models' analysis. Most of the sampled sites were located within or next to the current distribution range of the red-vented bulbul.

Point count data were extracted for 15 bird species including the red-vented bulbul. Ten species were selected because they were passeriforms of comparable size to the red-vented bulbul (less than 20 cm in height) and shared the same habitat (sparse secondary forest, scrub, orchards and gardens). We considered the Fan-tailed gerygone (*Gerygone flavolateralis*)*,* the Long-tailed triller (*Lalage leucopyga*)*,* the Grey-eared honeyeater (*Lichmera incana*)*,* the Melanesian flycatcher (*Myiagra caledonica*)*,* the New Caledonian myzomela (*Myzomela caledonica*)*,* the Rufous whistler (*Pachycephala rufiventris*), the House sparrow (*Passer domesticus*)*,* the Grey fantail (*Rhipidura albiscapa*), and two silvereyes species (*Zosterops xanthochroa and Z. lateralis*). The two silvereyes species are difficult to distinguish in the field, so were considered here as a single taxon. Two species of a larger size were frequently observed feeding on the same tree species as the red-vented bulbul: the Spotted dove (*Spilopelia chinensis*) and the Coconut lorikeet (*Trichoglossus haematodus*), and were also considered in our analysis. We added two larger species with restricted distribution status that often responded to red-vented bulbul calls, the New Caledonian crow (*Corvus moneduloides*) and the New Caledonian friarbird (*Philemon diemensis*). Finally, the Common myna (*Acridotheres tristis*) was included to test for potential confounding effects of the red-vented bulbul and this other widespread and abundant invasive species. Eleven of the selected species were native to New Caledonia; the other three were introduced species. The full species list and their corresponding origin and conservation status are given in **S1 Table**.

**Environmental data**

On each sampling occasion the GPS location, date, and habitat type were recorded. Habitat was characterized by two factors. First, by one of six pre-selected macro-habitat types: 1) aquatic; 2) forest; 3) mining maquis; 4) shrubland; 5) agricultural areas; and 6) inhabited areas; second, four-to-six more precise descriptors of the habitat. The full list of habitats considered

is presented in S2 Table. Mapping of the presence of the red-vented bulbul in this dataset revealed that this species was concentrated in man-modified areas (around 40% of sampled points) and was very scarce in other habitats (<10% of points each). We therefore focused our analyses on the 579 point counts located in inhabited habitat (category 6) to avoid spatial autocorrelation. Determination of the impacts of the red-vented bulbul on other species required 'control' locations from which the red-vented bulbul is currently absent. For these, we selected man-modified locations outside of the red-vented bulbul's current range but where the other 15 targeted species were present (11<N<329; depending on the species). Using GPS data, we calculated the distance between each sampling point and the location in Nouméa where red-vented bulbuls are supposed to have been originally released (Gill et al. 1995).

**Data analysis**

All statistical analyzes were conducted using the R software, version 3.3.2 (R Core Team 2016). To describe the early dispersal of the red-vented bulbul, we ran a generalized linear mixed effect model with the red-vented bulbul' abundance as a quantitative variable explained by habitat, year and distance to introduction point. Then, we explored the relationships between the red-vented bulbul' presence and abundances of local birds through pairwise T-tests of their mean abundance, depending on whether the red-vented bulbul was present or not. In the last step we selected four native species that lived sympatrically with the red-vented bulbul (present at the same point during the same sampling session) and used model selection and model averaging techniques to explore red-vented bulbul abundance as an explanatory variable of the abundances of these native species. Relationships were considered significant when p_values were <0.01.

To test which environmental factors affected red-vented bulbul abundance, we used a generalized linear mixed model from the package "lme4" v.1.1-7 (Bates et al. 2014) that considered 'site' as a random factor. We used a subset of the data that considered only the points located inside the red-vented bulbul's current range. In this model, distance to the introduction point was used as a fixed effect corresponding to the density gradient. Macro-Habitat (**S2 Table**) was used as a factor to account for the red-vented bulbul's tight association with man-modified areas, and year was also used as a numeric fixed effect to account for an expected increase in red-vented bulbul abundance over the invasion process. Bootstrapped confidence intervals were set at 98% of confidence level. Confidence intervals were calculated from 500 parametric bootstrap simulations.

We compared the mean abundance of the 15 bird species in the presence or absence of the red-vented bulbul using a series of parametric Students t.test. This test allows a comparison between two subgroups from a quantitative variable. We compared the abundance of each species when the red-vented bulbul was present or not, by running 14 tests using the 14 data subsets corresponding to each target species. To conduct adapted analyzes for each targeted species, we calculated the range overlap between each of these and that of the red-vented bulbul. For this we first plotted the Maximum Convex Polygone (MCP) including all presence points for each of the 15 species, using the package "adehabitatHR" (Calenge 2006), and then calculated the percentage of overlap using "rgeos" (Bivand and Rundel 2017). The number of co-occurrence points was calculated and used as an index of mixed model "feasibility" for further analyzes.

To explore the mechanisms leading to a decrease in the abundance of bird species, we selected "impacted" species that were observed 30 times or more in sympatry with the red-

vented bulbul. The relationships between abundance of these birds and red-vented bulbul abundance, abundance of *A. tristis*, sub-habitat, and year were investigated using a Poisson Log generalized linear mixed model (Bolker et al. 2009), which included 'site' as a random effect. Abundance of the red-vented bulbul and sub level of "inhabited areas" habitat were the main explanatory variables. Abundance of the introduced *A. tristis* was used as a fixed effect in full models to account for any habitat partitioning with the red-vented bulbul (Bivand and Rundel 2017). Year was used as a fixed effect to account for a potential temporal autocorrelation in our dataset. Usefulness of the random effect was tested via ANOVA between full models. We modeled the abundance of the species using the package "lme4" v.1.1-7 (Bates et al. 2015) and checked graphically the correctness of the error variance (Zuur et al. 2010). We then performed a model selection using a dredging procedure, selecting and averaging all models that were within two AICc units of the most parsimonious model (i.e., the lowest AICc). This was done using the package "MuMIN" (Barton 2016). The MuMIn package does not allow random effect averaging (Barton 2016), so estimates and confidence intervals for random effects were calculated from the best model only. We controlled for the potential influence of time in the abundance of bird species by plotting the abundance of the main species over the monitoring period in man-modified habitats. Results are given in estimate per factor and bootstrapped confidence intervals at 98% of confidence level. Confidence intervals were calculated from 200 parametric bootstrap simulations.

# Results

## Red vented bulbul's distribution

The red-vented bulbul was detected and counted at 346 points, mainly concentrated around Nouméa (the initial introduction location). In 2015 the red-vented bulbul was commonly present in all sites within 30 km of the original introduction site in Nouméa. Based on all point counts available from this area (N=1139), we found that the red-vented bulbul mean abundance did not vary significantly across years (**S3 Table**). The average numbers of red-vented bulbuls per point were 1.02 ± 0.17 ($n$ = 58) and 0.42 ± 0.07 ($n$ =184) in 2010 and 2015 respectively. The mean number of red-vented bulbuls was significantly higher in man-modified habitats (1.19 ± 0.09; $n$ =216) and lower in forest habitats (0.14 ± 0.04; $n$ = 444). We also found a negative relationship between red-vented bulbul abundance and distance from the historic introduction site (-0.08 ± 0.02; P< 0.001; **Fig.2**).
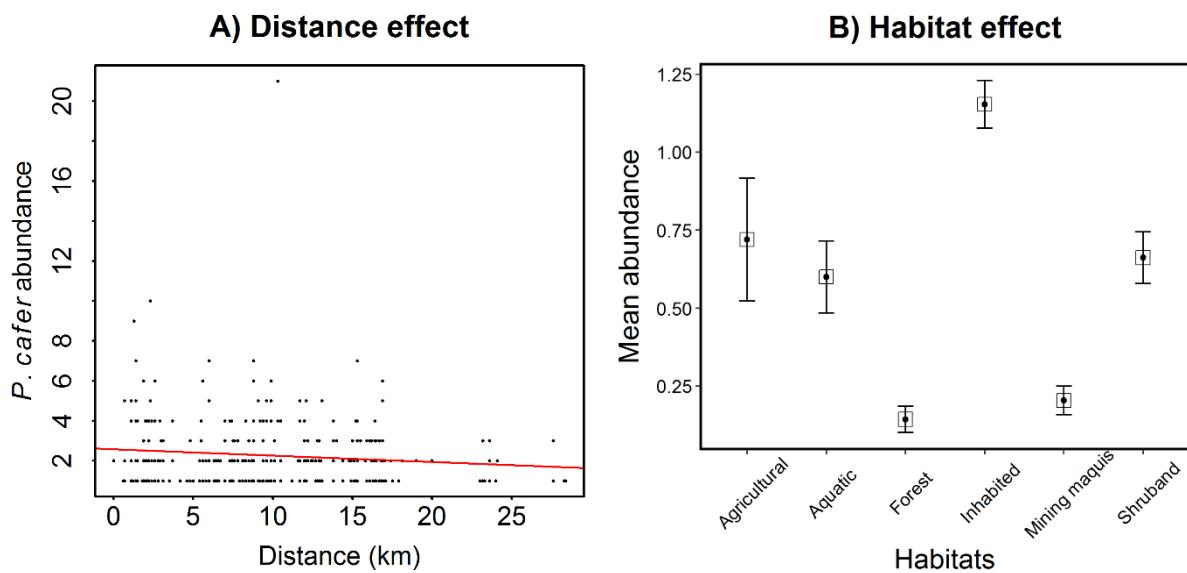


**Fig 2.** Relationship between the abundance of the red-vented bulbul and a) the distance from the introduction point in Nouméa and b) the category of habitat sampled. Bars in the Fig 2b represent the standard errors of the means.

**Impact of Red-vented bulbul presence on the abundance of other bird species**

We found a negative relationship between the presence of the red-vented bulbul and the abundance of nine of the 14 bird species considered in man-modified habitats (**Fig.3**), namely the *C. Moneduloides*, *G. flavolateralis, L. leucopyga, M. caledonica M. caledonica P. rufiventris*, *P. diemensis*, *R. albiscapa*, and *T. hematodus*. The distribution of each of the 14 bird species overlapped with at least 65% of the current distribution range of the red-vented bulbul (**S4 Table**). The abundance of only one species, the spotted dove, appeared to be higher when the red-vented bulbul was present (t: 2.84; *p* = 0.0048; S4 Table). The mean abundances of two introduced species, *A. tristis* and *P. domesticus* did not differ significantly when the red-vented bulbul was present (4.4 ± 0.36 and 6.61 ± 0.77; *n* =215) or absent from the point (4.72 ± 0.36; *n* = 261 and 7.99 ± 0.82; *n* =144, S4 Table). There was also no significant effect of whether red-vented bulbuls were present or absent on *L. incana* or the silvereyes at the 0.01 threshold (t: 1.73; *p* = 0.083 and t:  -1.7; *p* = 0.088).
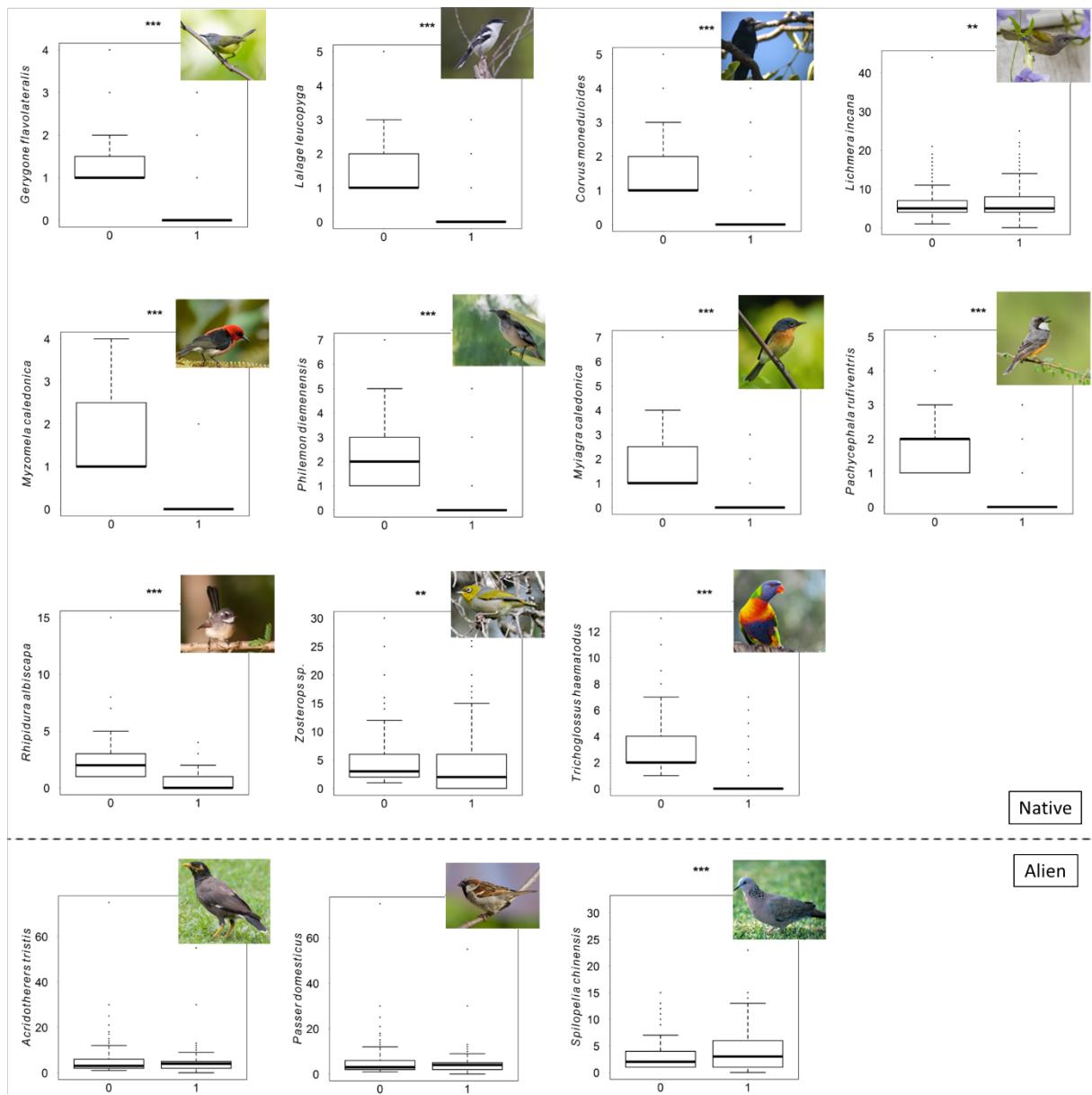
**Fig 3.** Mean abundance of 14 bird species in man-modified habitats depending on the presence of the red-vented bulbul. Mean abundance: average number of individuals per point. Significant tests are marked with *** (99% confidence) and ** (95% confidence). *0 = absence; 1= presence*

**Effect of Red-vented bulbul abundance on the reduction of local bird populations**

Among the nine bird species that were less abundant when co-occurring with the red-vented bulbul, four species (*R. albiscapa*, *Z. spp*, *P. rufiventris* and *T. haematodus*) shared more than 30 locations with the red-vented bulbul (**S4 Table**). Table 1 presents the estimates and confidence intervals for each parameter that was kept through the model selection process. Results of model selection and averaging for the abundance are detailed in **S5 Table**. Time (year) was never associated with a decrease in bird abundances but contributed significantly to explain an overall increasing abundance of silvereyes in urban habitats (**Fig.4**). Different degrees of urbanization contributed to explain the abundance of the *R. albiscapa* and *P. rufiventris* (**Table 1**), with more individuals of these species being counted in rural habitats (2.37 ± 0.27; *n* = 71 and 1.54 ± 0.18; *n* = 54) than in urban habitats (0.44 ± 0.06; *n* = 155 and 0.26 ± 0.06; *n* = 141). We found a negative relationship between the abundance of the red-vented bulbul in man-modified habitats and that of the four species (**Fig.5**). The abundance of *A. tristis* did not contribute to explain variations in the abundance of the four species.

**Table 1.** Parameter estimates and confidence intervals of the averaged models explaining the abundance of four bird species in man-modified habitats. Mean abundance: average number of individuals per point. Significant parameters are in bold.

| | *Rhipidura albiscapa* Estimates [98% CI] | *Zosterops*     *spp.* Estimates [98% CI] | *Pachycephala rufiventris* Estimates [98% CI] | *Trichoglossus haematodus* Estimates [98% CI] |
|---|---|---|---|---|
| Random effect | | | | |
| $\sigma_{(Site)}$ | 0.14[0.13;0.53] | 0.36[0.41;0.77] | 0.13[1.57E-5; 0.54] | 0.71[0.49;1.14] |
| Fixed effects | | | | |
| *Intercept* | -0.26[-0.73;0.21] | **0.67[0.30;1.04]** | -0.76[-1.48;-0.05] | 0.05[-0.57;0.68] |
| *Actri* | -0.03[-0.07;0.01] | 0.01[00.04 E-1;0.02] | -0.03[-0.08;0.02] | -0.05[-0.16;0.07] |
| *sHabitat[suburban]* | **0.84[0.39;1.28]** | -0.21[-0.46;0.04] | **1.10[0.50;1.70]** | -- |
| *sHabitat[rural]* | **1.10[0.62;1.59]** | -0.24[-0.60;0.12] | **1.29[0.69;1.90]** | -- |
| *sHabitat[tribal]* | **1.01[0.39;1.62]** | -0.01[-0.50;0.47] | **1.12[0.37;1.88]** | -- |
| *Pycaf* | **-0.28[-0.39;-0.16]** | **-0.08[-0.12;-0.04]** | **-0.43[-0.61;-0.25]** | **-0.27[-0.38;-0.16]** |
| *Year* | 0.02[-0.07;0.11] | **0.10[0.06;0.15]** | 0.06[-0.07;0.18] | 0.08[-0.02;0.17] |
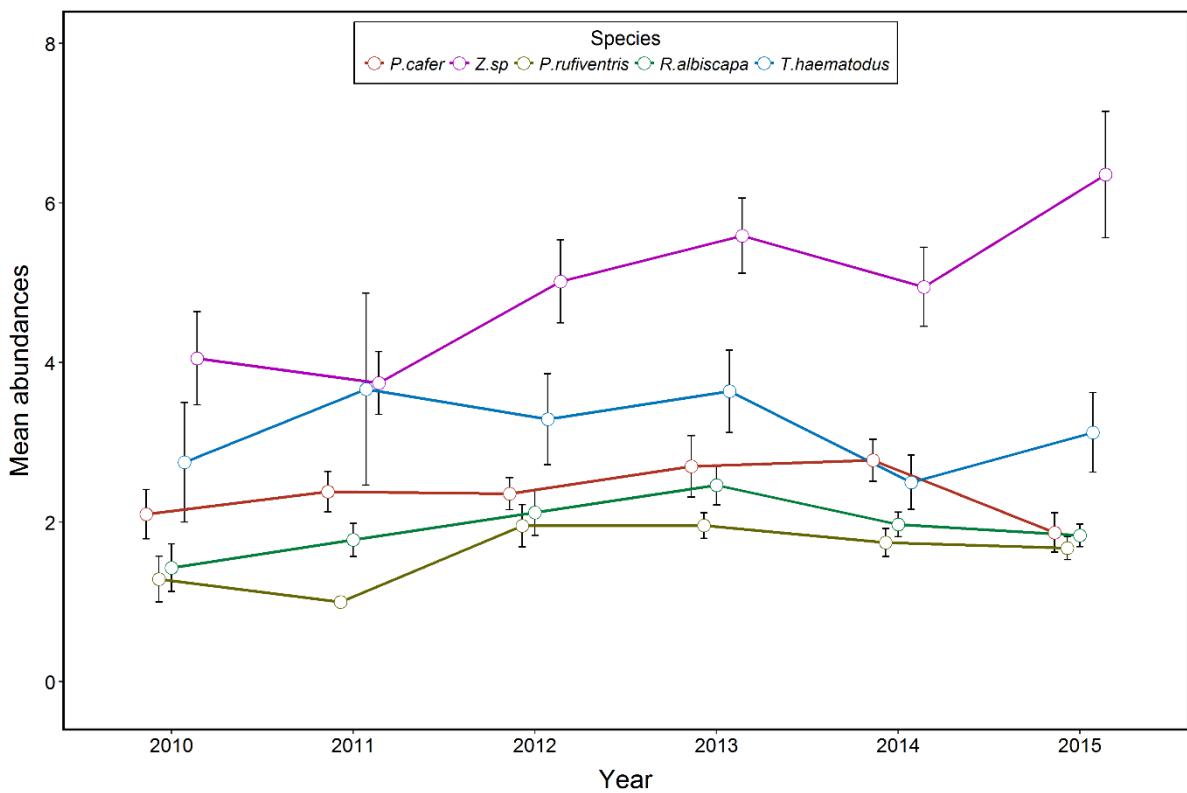
**Fig 4.** Trends through time in the abundance of *Pycnonotus cafer*, *Zosterops* spp*.,* *Pachycephala rufiventris*, *Rhipidura albiscapa* and *Trichoglossus haematodus* in man-modified habitat over time during the monitoring of terrestrial breeding birds. Mean abundance: average number of individuals per point. The increase in the abundance of *Zosterops* spp. is significant (see Table 1).
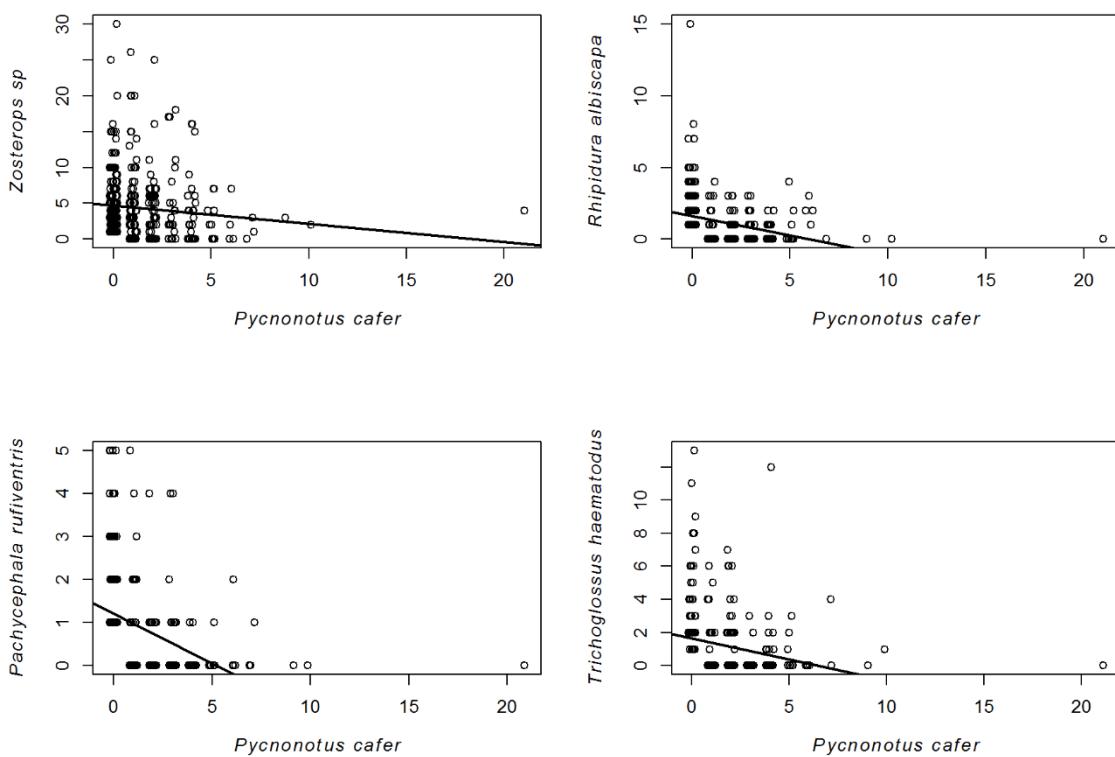
**Fig 5**. Abundance relationship between the red-vented bulbul and four bird species in man-modified habitats. Mean abundance: average number of individuals per point.

## Discussion

The red-vented bulbul is currently expanding its range over the main island of New Caledonia, so an abundance gradient from the point of first introduction outwards was expected (Blackburn et al. 2011). Alien species introductions in capital cities such as Nouméa is common in island territories (Hulme 2009) and it may favor alien species that are able to cope with close proximity to humans (Old et al. 2014; Moller et al. 2015). Because of traffic, cities are suspected to foster the invasion process toward rural habitats (Von der lippe and Kowarik 2008). This is exactly what we found here, with red-vented bulbuls being most predominant

in man-modified habitats. The red-vented bulbul is often located along roads and in gardens where plant species from its native range are present (Brooks 2013).

Our analysis indicates that nine of the 14 bird species monitored in man-modified habitats were less abundant when the red-vented bulbul was present. The response of local birds to the spread of the red-vented bulbul is therefore of great concern since 55 of the 90 breeding species of terrestrial birds in New Caledonia are strictly endemic (Barré et al. 2009). Fifty-four of them are legally protected in the Southern Province (DEPS 2016). Eight of the species that declined in abundance in the presence of the red-vented bulbul were passeriform and one was a Psittaciformes. The other species were significantly less abundant at sample points occupied by the red-vented bulbul and shared more than 30 locations with the invader. The abundance of only two native bird species appeared to be unaffected by the presence of the red-vented bulbul. *L. incana* remains very common in man-modified habitats and field observations suggest that this species is undisturbed in the presence of the red-vented bulbuls or their calls. It is a very active, noisy, gregarious honeyeater (Dutson 2011). The second unaffected native taxon was *Zosterops spp*.

Our abundance models confirmed most of the findings from the first analysis and provided additional details on interspecific competitive relationships. Interestingly, abundance models detected a negative effect of the red-vented bulbul on *Zosterops spp* in man-modified habitats that our point-sampling data had failed to detect. The GLM analyses identified an increase in the mean abundance of *Zosterops spp* in human modified habitats through time, which appeared to be independent of the presence or absence of the red-vented bulbul. This likely obscured detection of a negative impact of the red-vented bulbul on silvereyes in our point-count dataset.

We found negative abundance relationships between the red-vented bulbul and the three other species that we tested. Abundance of *R. albiscapa* and *P. rufiventris* also showed an urbanization gradient, with more birds detected in rural than in urban and suburban habitats. Conversely, abundance of the red-vented bulbul was the main factor explaining variations in the mean abundance of *T. haematodus*. The three passerine species share several life history traits with the red-vented bulbul including similar length (approx. 16 cm), nesting height (2-3 m), nest structure (cup-like shape), incubation period (14 days) or clutch size (3±1) (del Hoyo et al. 2017). On the other hand, *R. albiscapa* and *P. rufiventris* are considered mainly insectivorous (Powlesland 1982) and should not compete with the red-vented bulbul for food, as the red-vented bulbul diet comprises mainly fruit (Islam and Williams 2000). We believe that native passerine species may suffer from the foraging behavior of the red-vented bulbul, which is known to be active and aggressive toward other species in its preferred forage trees (Sherman and Fall 2010; Blanvillain et al. 2003; Gorman 1972). Such negative interaction due to aggressive behavior has already been demonstrated in the Noisy minor *Minorina melanocephala* (Grey et al. 1998). *T. haematodus* is a generalist bird that feeds mostly on fleshy fruits, nectar and pollen (Shukuroglou and Mccarth 2006). Like the red-vented bulbul, it is highly mobile and able to forage over a large area. Thus, our result could reflect a shift in forage tree selection by *T. haematodus* when too many red-vented bulbuls are present.

None of the alien species considered in this study (*A. tristis*, *P. domesticus*, *S. chinensis*) were less abundant when the red-vented bulbul was present. This is partly consistent with the finding of Bates et al. (2014) on the foraging relationship between the red-vented bulbul and *A. tristis* in Moorea, French Polynesia. Those authors suggested that the two invasive species were able to coexist in the same habitat without competing for food resources thanks to different foraging strategies. Such partitioning could also apply to *P. domesticus* and *S.*

*chinensis*, as the two species are more granivorous and ground-foraging than the red-vented bulbul (Martin and Fitzgerald 2005; Firake et al. 2016). Moreover, the three species were widely introduced and are abundant in cities worldwide (Summers-Smith 2003; Corlett 2005; Peacock et al. 2007). Time partitioning in the use of the same resource could allow an alien population of red-vented bulbul to expand, even in locations occupied by other invasive bird species (Bates et al. 2014). Such neutral interaction between sympatric invasive species is the basis for additive impacts on resources and native competitors that can lead to major conservation issues (Blackburn et al. 2005).

From a conservation perspective, our data raise concerns about the negative effects of red-vented bulbul establishment on the abundance of native birds. Our results do not reflect a temporal trend in bird abundance, as none of the native species considered here showed a decline in abundance over the monitoring period in man-modified habitats. We believe that the red-vented bulbul may drive a reassembly of native species toward sub-optimal locations along an urban-rural gradient, as suggested in the niche reduction hypothesis (Scheele et al. 2017). This is consistent with recent assessments on the effects of urbanization on the distribution of several other bird species (Møller et al. 2012). These authors suggest that urbanization promotes the establishment and development of species that can cope with human activities. These species are often generalists and more competitive in urban habitats (Møller et al. 2015; Møller 2009). Urbanization tends to drive a reassembly of bird species along an urbanization gradient through competitive interactions, with native species being more competitive in rural habitats and alien bird species more successful in urban centers (Barnagaud et al. 2009). In 1979, Watling suggested this process as an explanation for the habitat shift in native birds of Fiji following the establishment of the red-vented bulbul there (Watling 1979). Our results confirm that the red-vented bulbul appears able to coexist with

other alien birds in man-modified habitats via habitat partitioning (Bates et al. 2014). However, despite this partitioning, the red-vented bulbul may negatively affect the distribution and abundance of native birds in urban habitats through its aggressive interspecific behavior enabling it to out-compete native species and dominate access to food resources.

An increase in mean abundance of the red-vented bulbul was expected over the course of our study due to the population expansion process, but this was not significant in our models. This suggests that time may not be a major driver of red-vented bulbul abundance at a specific location, and that habitat characteristics and distance to the core of the local range are of greater importance. Establishment of the red-vented bulbul in New Caledonia is recent and we conducted this study at an early dispersal stage. The temporal monitoring of terrestrial birds of New Caledonia has started in 2010, and data on birdabundance in the current range of the red-vented bulbul before its establishment are lacking. So, it is very difficult to conclude on a temporal pattern in the effect of red-vented bulbul on the abundance of native bird species. However, invasion by the red-vented bulbul is still ongoing in New Caledonia. Here, we suggest benefitting from this original context by using spatial patterns as proxies of temporal ones, using inhabited areas that have not been invaded as background data. The hypothesis we formulated should be confirmed by measuring directly changes in bird abundances at sites that became invaded after 2010. However, since long-term temporal monitoring of birds is time consuming, required funding and consequent human resources, such data are often lacking in small territories. Where background data are lacking, we believe that the method used here could be of value while assessing threats from introduced species. When trying to implement this kind of long-term monitoring, involvement of volunteer citizens has been demonstrated to be a powerful and efficient tool (Jiguet et al. 2012).

Because we focused on a potential effect of the presence of red-vented bulbuls rather than population estimates, we did not calculate the detection probability of the bird species we studied. This could have led to an overestimation of the impact of the red-vented bulbul on the abundance of local birds if some species called less because of the presence of bulbuls. However, we believe this potential bias to be less important in the inhabited areas we sampled, as there, birds were detected through visual locations more than acoustic ones compared to other habitat contexts. Furthermore, fewer bird calls in the presence of the red-vented bulbul could also be considered as a negative impact, and the behavioral pressure of introduced red-vented bulbul on native birds could contribute to explain a reassembly of the bird community along an urbanization gradient. The respective contribution of competition for trophic resources and behavioral competition could be the subject of further studies on the ecological mechanisms that shape impacts of introduced species.

In New Caledonia, the red-vented bulbul is currently recorded exclusively in man-modified habitats that are most suitable and favor its dispersal. In its native range, the red-vented bulbul is abundant in open habitats but is rarely found in mature forest (Vijayan 1975). However, changes in red-vented bulbul abundance and distribution in Tahiti over a 10-year period have shown that the species can establish in native habitats after an initial population lag-phase in man-modified habitats (Blanvillain et al. 2003; Saavedra 2013). Therefore, if nothing is done to slow down or stop its dispersal in New Caledonia, the red-vented bulbul will likely continue its expansion across the New Caledonia archipelago. The negative effects of the red-vented bulbul at comparatively low densities on native New Caledonian bird species raise concern about escalating impacts as the red-vented bulbul's range expands and its densities increase into more native and natural habitats. New Caledonian forests host an important endemic biodiversity of not just birds but also insects and reptiles (Smith et al. 2007;

Grandcolas et al. 2008; Delorme et al. 2016) that may be impacted negatively through interaction with the red-vented bulbul (Thibault et al. 2018). Predation upon, or competition with, these species could be more damaging than the ones we have identified here because native species living in less disturbed habitats are often particularly predator-naïve and sensitive to perturbation (Byers 2002; Soh et al. 2006).

There is an urgent need for dedicated monitoring of the range expansion of the red-vented bulbul in New Caledonia, and design and implementation of an effective management plan based on research experiments such as exclusion tests. Depending on both social and financial support, eradication programs could be implemented that would minimize further conservation impacts of the red-vented bulbul in New Caledonia, such as has been achieved through control of invasive *A. tristis* in the Seychelles (Cannings 2011; Feare et al. 2017). The impact of the red-vented bulbul elsewhere has been profound, such as its competitive pressure upon the Tahiti monarch, *Pomarea nigra*, in French Polynesia (Thibault et al. 2002), but shooting, trapping and poisoning of red-vented bulbuls and *A. tristis* has been efficient in reducing the impacts of these species on endemic species of birds there (Saavedra 2013). Thoughtful consideration of similar intervention to confine and control the red-vented bulbul in New Caledonia is required, and its impact on native species throughout its exotic range should be quantified.

## Conclusions

This study generated quantitative data on the impact of invasive Red-vented bulbul on both native and other exotic species of birds in New Caledonia. Competition with native avifauna is one of the three serious impact categories associated with the red-vented bulbul (Thibault et al. 2018); the other two being damages to plants (Walker 2008) and dispersal of noxious plant

seeds (Spotswood et al. 2013). This is the first quantitative assessment of the impacts of a red-vented bulbul invasion on other bird species. Our data indicate that this tropical passerine is better adapted to human-induced ongoing habitat modification on a tropical island than are the native bird species studied here. Presence of the red-vented bulbul was associated with lower abundances of most native bird species in habitats where it established. This suggests that establishment of the red-vented bulbul could accentuate the negative impacts of urbanization on native birds around Nouméa and that dispersal of the red-vented bulbul along urban corridors in New Caledonia may already be causing a shift in the distribution of several native passerine species from the center to the edges of man-modified habitats. Enhanced monitoring of the range expansion of the red-vented bulbul in New Caledonia and implementation of an effective management plan is required urgently. Whether the red-vented bulbul is having similar impact on native species elsewhere in its exotic range should be investigated.

## Acknowledgements

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## Appendices

**Appendix S1 Table.** List of bird species considered in the study. The order, Family and species names are given for each studied bird species, as well as the authority reference. The origin of each species is provided regarding their presence in New Caledonia. Local conservation status, based on the Code de l'environnement de la Province Sud (DEPS, 2016), indicates if these species are protected or considered as pest in the Current range of the red-vented bulbul.

| Order | Family | Species | Authority | Origin | Local Conservation Status[1] |
|---|---|---|---|---|---|
| **Columbiforms** | Columbidae | Spilopelia chinensis | Scopoli, 1786 | Alien | Not Evaluated |
| **Passeriforms** | Acanthizidae | Gerygone flavolateralis flavolateralis | Gray, 1859 | Native | Protected |
| | Campephagidae | Lalage leucopyga montrosieri | Verreaux and Des Murs, 1860 | Native | Protected |
| | Corvidae | Corvus moneduloides | Lesson, 1831 | Native | Endemic |
| | Meliphagidae | Lichmera incana incana | Latham, 1790 | Native | Protected |
| | | Myzomela caledonica | Forbes, 1879 | Native | Endemic |
| | | Philemon diemenensis | Lesson, 1831 | Native | Endemic |
| | Monarchidae | Myiagra caledonica caledonica | Bonaparte, 1857 | Native | Protected |
| | Pachycephalidae | Pachycephala rufiventris xanthetraea | Latham 1801 | Native | Protected |
| | Passeridae | Passer domesticus | Linnaeus, 1758 | Alien | Not Evaluated |
| | Pycnonotidae | Pycnonotus cafer | Linnaeus, 1766 | Alien | Invasive |
| | Rhipiduridae | Rhipidura albiscapa bulgeri | Sparrman, 1787 | Native | Protected |
| | Sturnidae | Acridotheres tristis | Linnaeus, 1766 | Alien | Potentially harmful |
| | Zosteropidae | Zosterops sp[2] | Vigors and Horsfield, 1827 | Native | Protected |
| **Psittaciforms** | Psitaccidae | Trichoglossus haematodus | Linnaeus, 1771 | Native | Potentially harmful |

1: Endemic species are protected
2: lateralis griseonata + xantrochroa

**Appendix S2 Table.** Full list of habitats considered in the point counts monitoring.

| Macro-habitats | sub-levels |
|---|---|
| 1) **Aquatic** | |
| | i. Fresh water |
| | ii. Sea water |
| | iii. Brackish water |
| | iv. Mangroves |
| | v. Marsh |
| 2) **Forest** | |
| | i. Dense rainforest |
| | ii. Dense rainforest on mining soil |
| | iii. Rainforest on limestone |
| | iv. Sclerophyll forest |
| | v. Other |
| 3) **Mining maquis** | |
| | i. Bare ground |
| | ii. Sparse vegetation |
| | iii. Ligno-herbaceous maquis |
| | iv. Para-forest maquis |
| 4) **Thickets, Savannah** | |
| | i. Sparse vegetation |
| | ii. Grassland |
| | iii. Thickets |
| | iv. Littoral vegetation |
| | v. Niaouli savannah |
| | vi. Niaouli forest |
| 5) **Agroforest areas** | |
| | i. Bare ground |
| | ii. Cultivated area |
| | iii. Orchard |
| | iv. Forestry plantation |
| 6) **Inhabited areas** | |
| | i. Urban (city) |
| | ii. Suburban (village) |
| | iii. Rural |
| | iv. Tribal |

**Appendix S3 Table.** Parameter estimates and confidence intervals from the linear mixed model investigating the distribution of the red-vented bulbul abundance within its current range. Significant parameters are in bold.

| Sources of variation | Estimates | 98% CIs |
|---|---|---|
| **Random effect** | | |
| $\sigma_{(Site)}$ | 0,88 | [0,58;1,26] |
| **Fixed effects** | | |
| *Intercept* | -0,07 | [1,16; 0,63] |
| *Distance to origin* | **-0,08** | **[-0,13;-0,02]** |
| *Habitat[Forest]* | **-0,82** | **[-1,43;-0,36]** |
| *Habitat[Inhabited]* | **0,61** | **[0,21;1,07]** |
| *Habitat[maquis]* | -0,57 | [-1,54;0,24] |
| *Habitat[shrubland]* | 0,07 | [-0,37;0,67] |
| *Habitat[agricultural]* | 0,21 | [-1,29;1,11] |
| *Year* | -0,04 | [-0,11;0,03] |

**Appendix S4 Table.** Mean abundance of 14 bird species in man-modified habitats depending on the presence of the red-vented bulbul. The "RVB overlap" column represent the percentage of the current range of the bulbul where each species is considered present. Sympatry corresponds to the number of sampling points at which the species as been recorded together with the bulbul during the same sampling session. Results of Student t tests between the abundance of 14 bird species and the presence of the red-vented bulbul are provided. The "Effect" column indicates if presence of the bulbul affect the abundance of the species in a positive or negative way. Significant results are in bold.

| Species | RVB overlap | Sympatry (n) | Bulbul absence mean ± se (n) | Bulbul presence mean ± se (n) | Effect | Student t | P value |
|---|---|---|---|---|---|---|---|
| *Acridotheres tristis*[A] | 100% | 188 | 4,72 ± 0,36 (261) | 4,4 ± 0,36 (215) | | 0,63 | 0,53 |
| *Corvus moneduloides* | 65% | 8 | 1,76 ± 0,16 (42) | 0,07 ± 0,03 (215) | - | **-10,47** | **1,70E-13** |
| *Gerygone flavolateralis flavolateralis* | 99% | 14 | 1,36 ± 0,09 (59) | 0,11 ± 0,03 (215) | - | **-12,57** | **< 2,2E-16** |
| *Lalage leucopyga montrosieri* | 99% | 9 | 1,57 ± 0,18 (30) | 0,07 ± 0,02 (215) | - | **-8,39** | **2,28E-09** |
| *Lichmera incana incana* | 100% | 209 | 5,8 ± 0,22 (329) | 6,43 ± 0,29 (215) | | 1,73 | 0,083 |
| *Myiagra caledonica caledonica* | 96% | 5 | 1,96 ± 0,3 (23) | 0,04 ± 0,02 (215) | - | **-6,43** | **1,76E-06** |
| *Myzomela caledonica* | 89% | 1 | 1,81 ± 0,33 (11) | 0,01 ± 0,01 (215) | - | **-5,56** | **0,00024** |
| *Pachycephala rufiventris xanthetraea* | 99% | 39 | 1,83 ± 0,09 (118) | 0,29 ± 0,05 (215) | - | **-13,95** | **< 2,2E-16** |
| *Passer domesticus*[A] | 87% | 158 | 7,99 ± 0,82 (144) | 6,61 ± 0,77 (215) | | -1,27 | 0,21 |
| *Philemon diemenensis* | 66% | 9 | 2,1 ± 0,18 (62) | 0,07 ± 0,03 (215) | - | **-11,3** | **< 2,2E-16** |
| *Rhipidura albiscapa bulgeri* | 99% | 58 | 2,15 ± 0,12 (181) | 0,12 ± 0,06 (215) | - | **-12,43** | **< 2,2E-16** |
| *Spilopelia chinensis*[A] | 93% | 170 | 3,01 ± 0,17 (206) | 3,94 ± 0,28 (215) | + | **2,84** | **0,0048** |
| *Trichoglossus haematodus* | 100% | 43 | 3,49 ± 0,37 (51) | 0,59 ± 0,1 (215) | - | **-7,54** | **3,58E-10** |
| *Zosterops sp* | 100% | 146 | 4,74 ± 0,29 (201) | 3,98 ± 0,34 (215) | | -1,7 | 0,088 |

[A] *Indicates alien species.*

**Appendix S5 Table.** Model selection and averaging on the mean abundance of four species of native New Caledonian birds. Pycaf and actri represent the abundance of *Pycnonotus cafer* and *Acridotheres tristis* respectively. sHab represents sub-habitats. Model selection and averaging was conducted with the abundance of four species as explained variables. Characteristics of models considered in the averaging are described according the four indexes: 1) **K** is number of degree of freedom, 2) **-LL** is the log-likelihood score 3) **AICc** is the corrected Akaike criterion score and 4) **ω** is the weight of each model.

| Models | R. albiscapa | | | | Z. sp | | | | P.rufiventris | | | | T. haematodus | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | K | -LL | AICc | ω$_i$ | K | -LL | AICc | ω$_i$ | K | -LL | AICc | ω$_i$ | K | -LL | AICc | ω$_i$ |
| Full : pycaf + actri + year + shab | 8 | 509 | 1034,3 | 0,172 | 8 | 1126,3 | 2268,9 | 0,403 | 8 | 329,94 | 676,32 | 0,2 | - | - | - | - |
| pycaf + actri + shab | 7 | 509,1 | 1032,6 | 0,415 | - | - | - | - | 7 | 330,6 | 675,57 | 0,29 | - | - | - | - |
| pycaf + actri + year | - | - | - | - | 5 | 1129 | 2268,2 | 0,576 | - | - | - | - | 5 | 409,2 | 828,6 | 0,17 |
| pycaf + shab + year | - | - | - | - | - | - | - | - | 7 | 331 | 676,43 | 0,19 | - | - | - | - |
| pycaf + actri | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 410,5 | 829,09 | 0,13 |
| pycaf + shab | 6 | 510,5 | 1033,2 | 0,299 | - | - | - | - | 6 | 331,5 | 675,34 | 0,32 | - | - | - | - |
| pycaf + year | - | - | - | - | - | - | - | - | - | - | - | - | 4 | 409,5 | 827,05 | 0,37 |
| pycaf | - | - | - | - | - | - | - | - | - | - | - | - | 3 | 410,6 | 827,33 | 0,32 |

# CHAPTER 5: Seed dispersal

## "Liaisons dangereuses": The invasive red-vented bulbul (*Pycnonotus cafer*), a disperser of exotic plant species in New Caledonia

*Under review at Ecology and Evolution*

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## Abstract

The biodiversity hotspot of New Caledonia hosts high levels of endemism (78% of flora) that is threatened increasingly by climate change, habitat reduction, and invasive species. The fruit-eating red-vented bulbul (*Pycnonotus cafer*) is currently invading the main island of the archipelago and its recent dispersal out of urbanized habitats raises questions about its potential to disperse noxious plant seeds along urban corridors and beyond. Indeed, the red-vented bulbul is considered a vector of several introduced plant species in its alien range including *Miconia calvescens*, *Lantana camara*, and *Shinus terebinthifolius*. We conducted a quantitative assessment of the bulbul's fruits consumption by analysing the gut contents of shot birds. We estimated gut passage times for four species of fruit found in gut contents (*S. terebinthifolius*, *Myrtastrum rufopunctatum*, *Passiflora suberosa* and *Ficus prolixa*), and tested the effects of bird digestion on seed germination rates for two species. Finally, we monitored the movements of individual VHF-radio-tagged red-vented bulbuls. All the consumed fruit species we identified here have red fleshy diaspore, including fruit of the shrub *M. rufopunctatum* that occurred frequently (9.6%) in bulbul gut samples. Median gut passages times were short (15-41 min), corresponding to short distance seed transportation (77-92 m). The effect of gut passage was positive for the germination of the invasive *S. terebinthifolius* and negative for the endemic *M. rufopunctatum*, suggesting a potential bias in the contribution to the dispersal toward alien species. This study provides the first integrated assessment of mechanisms involved in the seed dispersal effectiveness of this high-concern invasive bird species that is expected to face similar plant communities in most of its alien range in tropical islands. More generally, our results enhance knowledge of synergies between non-native frugivores and plant species dispersal.

**Keywords:** conservation, invasive bird, plant community, island, seed dispersal effectiveness

Résumé

Le hotspot de biodiversité de la Nouvelle-Calédonie abrite des taux d'endémisme importants (78% de la flore), menacés par le changement climatique, la réduction des habitats et les espèces envahissantes. Le bulbul à ventre rouge (*Pycnonotus cafer*) envahit actuellement l'île principale de l'archipel, et son expansion récente soulève des questions sur sa capacité à disperser les graines de plantes nuisibles le long des corridors urbains et au-delà. En effet, le bulbul à ventre rouge est considéré comme un disséminateur de plusieurs espèces végétales envahissantes dans son aire introduite, comme *Miconia calvescens*, *Lantana camara* ou *Shinus terebinthifolius.* Dans cette étude, nous avons évalué de façon quantitative la consommation de fruits par le bulbul à ventre rouge en analysant les contenus digestifs d'oiseaux abattus. Nous avons estimé les temps de transit de quatre espèces de fruits trouvés dans les contenus digestifs (*S. terebinthifolius*, *Myrtastrum rufopunctatum*, *Passiflora suberosa* et *Ficus prolixa)*, et testé les effets de la digestion sur la germination des graines de deux de ces espèces. Enfin, nous avons suivi les mouvements d'individus équipés de balises VHF. Les résultats suggèrent une préférence pour des plantes introduites aux fruits rougeâtres. Les durées médianes de transit étaient courtes (15-41 min), correspondant au transport de graines sur de faibles distances (77-92 m). L'effet de la digestion était variable et suggère un biais potentiel dans la contribution à la dispersion en faveur des espèces exotiques. Cette étude fournit la première évaluation des mécanismes impliqués dans l'efficacité de la dispersion des graines de cette espèce envahissante préoccupante, et améliore la connaissance des synergies entre les frugivores introduits et la dispersion des espèces végétales.

**Mots-clefs :** conservation, oiseaux envahissants, communautés de plantes, ile, efficacité de dispersion

## Introduction

Construction, transportation, trade and other human activities modify landscape structure, change plant and animal communities, drive changes in distribution patterns, and accelerate the rate of non-native species dispersal leading to increasing biological invasions (Richardson et al. 2000; Gosper et al. 2005; Kokko and López-Sepulcre, 2006; Smart et al. 2006; McConkey et al. 2012; Hulme 2009; Haddad et al. 2015; Ramaswami et al. 2016). Dispersal of human cultures, together with animals and plants, is a key factor contributing to the current world biodiversity crisis (Cebalos et al. 2015). Thereby, dispersal has been explored from a variety of perspectives including its relevance to conservation biology (Primack and Miao 1992; Levey et al. 2002; Trackhtenbrot et al. 2005), restoration ecology (Bakker et al. 1996; Ribeiro da Silva et al. 2015) and landscape ecology (Bacles et al. 2006; Carlo and Morales 2008).

An increasing number of studies investigate potential impacts of non-native frugivorous species on plant dispersal in newly colonized ecosystems. Interactions between non-native and native species are complex, but so are interactions among introduced species (Parker et al. 2006; Relva et al. 2010). This is encapsulated in Simberloff and Von Holle's (1999) "invasional meltdown" hypothesis that postulates that mutualistic interactions between invaders can facilitate secondary invasions (Green et al. 2011). This phenomenon has been demonstrated widely in island territories (Bourgeois et al. 2005; Traveset and Richardson 2006; Davis et al. 2009), with positive interactions having been reported between introduced plants and birds (MacFarlane et al. 2012; Traveset and Richardson 2014).

How a frugivorous species contributes to the dispersal of plant species can be explored in a variety of ways. Direct observations help determine species' diets and identify apparent close

interactions between animal and plant species (Sherman and Fall 2010), and excreta or gut content analysis can provide quantitative data to confirm observational assessments (Spotswood et al. 2012). Gut passage times can be used to predict dispersal distances and are often used in associated with radio-tracking or Global Positioning System (GPS) data (Weir and Corlett 2007), and germination tests can be used to determine how seed viability is enhanced or reduced by passage through a gut (Samuels and Levey 2005; Mokotjomela et al. 2015). To predict the migration rates of plants along fragmented habitats, particularly those depending on few frugivore vectors, information on seed dispersal distance could be very useful (Pearson and Dawson 2005).

Aslan and Rejmanek (2012) suggested that non-native plant species that exhibit characters of native plants might outcompete native plants for attracting dispersers. They backed this up with reference to case studies where native dispersers preferred native plant-of-original characteristics, while non-native birds such as the common starling (*Sturnus vulgaris*) preferred fruits of non-native plant species. Preference for non-native plant species has also been postulated for the introduced red-vented bulbul (*Pycnonotus cafer*) in French Polynesia (Spotswood et al. 2013). Preferential seed dispersal of non-native plant species by invasive passerines highlights an urgent need for quantitative assessments of the dispersal capacity of non-native frugivorous species, especially in areas of high conservation value such as the world's biodiversity hotspots (Mittermeier et al. 2011).

New Caledonia is a tropical archipelago located in the South Pacific Ocean. Its geology and geographic isolation have produced unique ecosystems and high levels of endemism (78% for flora) (Cluzel et al. 2001; Isnard et al. 2016; Munzinger et al. 2016). New Caledonia hosts 3060 species of flowering plants, including an important metallophytic flora (Harrison and

Rajakurana 2011), making the archipelago a terrestrial biodiversity hotspot (Myers, 2003). Its unique biodiversity is increasingly threatened by climate change, habitat fragmentation and destruction, and invasive species (Pascal et al. 2008). One invasive species of particular concern is the red-vented bulbul, which is currently expanding its range out of the urbanized areas around Nouméa (the capital) where it was first introduced and where, until recently, it was restricted (Thibault et al. 2018b). Concerns about the range expansion of this species derive from its ability to disperse non-native plant seeds more than native ones. It feeds predominantly on fruits (Islam and Williams 2000; Brooks, 2013) and can consume leaves, flowers and fruit of a large variety of species (Thibault et al. 2018a), leading to significant impacts on agriculture and horticulture (Cummings et al. 1994; Vander Velde 2002; Walker 2008). In its alien range, it has displayed a preference for numerous non-native plant species (Sherman and Fall 2010; Spotswood et al. 2013), and it is able to defend preferred food resources from other frugivorous avifauna (Thibault et al. 2002). Its recent dispersal out of urbanized habitats raises questions about its potential to disperse seeds of noxious plant species along urban corridors and beyond.

Here, we combined a suite of methods to characterize the association between the red-vented bulbul and non-native plant species of New Caledonia, and to assess the capacity of the red-vented bulbul to disperse viable seeds from peri-urban habitats. We conducted gut contents analysis of shot and trapped birds to assess quantitatively the varieties of fruit consumed by the bulbuls. We then determined gut passage times for favored fruits and tested, for two species, the effects of ingestion on seed germination rates. Finally, we radio-tracked red-vented bulbuls and used those data to predict median and maximum dispersal distances based on how far the birds flew during periods equivalent to gut transit times. Results are discussed with regard to the current range expansion of the red-vented bulbul, and their relevance to a

broader understanding of the mechanisms and impacts of seed dispersal by non-native avian frugivores.

## Methods

### Gut content analysis

Due to their pest status, both shooting and trapping of red-vented bulbuls is authorized under New Caledonian Southern Provence law (DEPS, 2016). In June 2016, we distributed a "call for participation" to the local hunting federation to collect bulbul cadavers from various locations within its local range. Each cadaver was frozen and labeled with the date it was shot and location details.

Gut content analysis was conducted on 139 dead bulbuls from 14 peri-urban habitats over 10 months around Nouméa to check for fruit and seed remains. Gastrointestinal tracts were excised, and the contents removed and washed with tap water through a 0.2 mm sieve. The retained contents were placed in a Petri dish filled with 70% alcohol and examined under a dissecting microscope at 10x magnification (Olympus SZ61). Each new item was photographed (Toupcam UCMOS camera and Toupview software) for subsequent identification, and preserved in a reference collection (Lopes et al. 2013).

Fruit and seed species identifications were made by reference to specimens in the New Caledonian Agronomic Institute's (I.A.C) seed bank, and by expert botanists when matching samples were not available. Numbers of occurrences were counted, and frequency of occurrence was calculated for each different item. The frequency of occurrence corresponded to the number of samples that contained the item divided by the total number of samples. We then related these frequencies to the plant distribution status and use, to determine potential impacts of their consumption by the red-vented bulbul.

Gut transit time experiment

We used bulbul individuals that were trapped between January and May 2016 and kept in an aviary. For our experiment, we randomly selected 16 individuals that were placed in numbered individual bird cages. Each cage had the same volume of approximately 0.25 m³, and was equipped with a perch and water dispenser (Linnebjerg et al. 2009). Bulbuls were fed *ad libitum* with a mix of chicken grain, nectar powder and water. To avoid any bias in the measurement of retention times due to birds' stress in confinement conditions (Afik and Karasov 1995), birds were maintained in individual cages for two weeks before initiating the experiment.

The usual supply of food was removed from each cage at least 3 h before each experimental session. At the beginning of each test, a variety of fruit (see below) was placed in a petri dish inside four bulbul cages. We conducted our seed retention experiments with four types of fruit from four different plant species with different distributions. Plant species were selected based on i) direct observations of consumption, data from the literature, and results of the diet study, ii) their conservation value, and iii) their seasonal availability and morphological characteristics (small red fruit being preferred). We used berries of the endemic shrub *Myrtastrum rufopunctatum* (Pancher ex Brongn. and Gris), fruit of the native tree *Ficus prolixa* G.Forst., berries of the introduced vine *Passiflora suberosa* L., and berries of the invasive shrub *Schinus terebinthifolius* Raddi (**SM1**). We did not select *Solanum torvum* and *Syzygium cuminin,* two of the most consumed species*,* because they were not available in sufficient numbers in the field at the time of the experiment. Each bulbul was tested with a different fruit species and four bulbuls were tested simultaneously, so that four fruit species were tested simultaneously. Two observers, hidden behind a bulkhead, noted the time and number of items consumed and defecated for 60 min (Schabacker and Curio 2000). Defecated seeds

were then collected and stored for a maximum of 24 h in empty Eppendorf tubes until planting, to avoid any modification of the germination capacity.

We first controlled for the equivalent palatability of the four fruit species for the bulbuls. To do so, we calculated the mean reaction time for each fruit species. This is the time between introduction of the fruit and first fruit consumption by each individual bulbul. Reaction times are presented as mean time (s) ± standard error. We then calculated the mean gut passage time for each of the fruit species, to explore potential variations in the retention time due to specific fruit properties. In order to evaluate the dispersal capacity of the red-vented bulbul, we also calculated the gut passage time depending on whether a fruit contained one or several seeds, following the method presented in Weir and Corlett (2007). This method suits the estimation of dispersal capacity, as it allows the estimation of three thresholds in the passage time of seeds through the gut. We calculated the median time for i) the first defecation of multi-seeded fruits, ii) the defecation of one-seeded fruits and, iii) the last defecation of multi-seeded fruits.

Germination test

We explored potential effects of passage through a bulbul's gut on the seed coat or endocarp of two fruit species following the approach of Samuels and Levey (2005). We compared the germination speed (time of each germination) and rate (percentage of seeds that germinated) of control-extracted plant seeds versus defecated seeds of the two plant species that had the longest gut passage time, *Myrtastrum rufopunctatum* and *S. terebinthifolius*. In a context of resource constraints, we chose these species to avoid a potential underestimation of the dispersal distance by the red-vented bulbul. Both the control and treatment samples comprised 160 seeds extracted from fruit from an individual plant. The germination substrate

contained 60% planting mold (Dalton's premium seed mix) and 40% vermiculite (Ausperl grade 2, 2-4 mm). We placed 35 planting cells, each one sowed with two seeds, on trays that were placed on warming tables (24°C) inside a greenhouse, with normal daylight conditions (approx. 11 h of sunlight per day) and regular water supply. Cells were checked every day and seedlings were counted and removed as soon as the hypocotyl was more than 1 mm in length. We stopped the monitoring 50 days after the last germination was recorded. Differences in germination rates between the two treatments were explored through $\chi^2$ test of independence in R version 3.4.0 (R Development Core Team 2017).

## Spatial activity of bulbuls

We estimated the spatial activity of bulbuls according to the method described in Weir and Corlett (2007). This method uses three periods for activity monitoring: 1) the minimum retention time of multi-seeded fruits; 2) the median retention time of one-seeded fruits; and 3) the maximum retention time for multi-seeded fruits. We calculated these three periods from the seed-retention experiment and estimated the movements of bulbuls for each period. Monitoring was carried out between July 2016 and September 2016, corresponding to the cool, dry, and non-breeding season for this species.

Adult red-vented bulbuls were trapped using a decoy bird in an aviary trap, fitted with VHF transmitters (Titley Scientific, LT6-337), and then released. Bird position and movements were monitored following the method described in Raim (1978). The transmitters weighted 470 mg and transmitted a pulsed signal at 150 MHz. We tracked the VHF signal with a numeric receiver (Titley Scientific, Australis 26k), equipped with a flexible 3-elements Yagi antenna from Titley Scientific. Observations started 24 h after release, allowing each bird time to acclimate to the

tag. When a tagged bird was located, the observer followed the individual at a 20 m distance and monitored its activity. Birds were observed with binoculars, and their positions recorded using a GPS unit, at the start of each monitoring period and at each new location visited by the tagged bird during the monitoring session. The duration of a session varied from a few minutes to an hour, depending on the topography and bird activity.

Data were compiled in QGIS software (QGIS Desktop v.2.18.1; QGIS Development Team 2017). Each displacement was calculated from a $T_0$ location, as i) the median of distances from the T0 location to all the locations visited by the bird and ii) as the largest of these distances. We did this calculation for the three "retention" periods and at every 10-min interval. When the monitoring session was long enough, we considered the locations occupied after the studied periods as independent $T_0$. Constraints that justify this approximation are presented in Weir and Corlett (2007). These authors also discussed potential biases and why they are unlikely to have much impact on the estimates of median movements.

## Results

### Plant consumption

We found food remains in 115 out of 139 gut contents examined, and plant items were found in 93% (n=107) of samples (**Table 1**). Seeds and fruits represented about 80% of the plant remains we found in the bulbul guts: seeds represented nearly 37% of plant items, whereas entire fruits and fruit flesh accounted for 25 and 20% of plant items respectively (**SM 2**). The remaining 20% consisted of fruit skins (13%), leaf parts (1.8%) and flowers (0.5%). We were able to identify a minimum of 14 plant families that were eaten by the red-vented bulbul in the Southern Province of New Caledonia (**Table 1**). Among these plant families, *Myrtaceae*

**Table 1** Percent frequency of occurrence of plant remains present in 107 digestive tracts of red-vented bulbuls (*P. cafer*). *Distribution status according to the Department of Environment of the Southern Province (2016).

| Family Species | Frequency of occurence (%) | (n) | Distribution status |
|---|---|---|---|
| Plantae | **93.0** | 107 | |
| **Anacardiaceae** | | | |
| *Schinus terebinthifolius* | 0.9 | 1 | Non-native |
| **Annonaceae** | 1.7 | 2 | |
| *Annona muricata* | 0.9 | 1 | Non-native |
| *Annona squamosa* | 0.9 | 1 | Non-native |
| **Araliaceae** | | | |
| *Schefflera actinophylla* | 2.6 | 3 | Non-native |
| **Arecaceae** | | | |
| spp. | 2.6 | 3 | |
| **Asparagaceae** | | | |
| *Cordyline fruticosa* | 0.9 | 1 | Native |
| **Meliaceae** | | | |
| *Melia azedarach* | **8.7** | **10** | Non-native |
| **Moraceae** | | | |
| *Ficus* sp. | 5.2 | 6 | Native |
| **Myrtaceae** | 25.2 | 29 | |
| *Myrtastrum rufopunctatum* | **9.6** | **11** | Native |
| *Psidium guajava* | 5.2 | 6 | Non-native |
| *Syzygium cumini* | **10.4** | **12** | Non-native |
| spp. | 0.9 | 1 | |
| **Passifloraceae** | 6.1 | 7 | |
| *Passiflora foetida* | 0.9 | 1 | Non-native |
| *Passiflora suberosa* | 5.2 | 6 | Non-native |
| **Petiveriaceae** | | | |
| *Rivina humilis* | 1.7 | 2 | Non-native |
| **Rubiaceae** | | | |
| spp. | 1.7 | 2 | |
| **Rutaceae** | | | |
| *Murraya paniculata* | 4.3 | 5 | Non-native |
| spp | 0.9 | 1 | |
| **Sapindaceae** | | | |
| *Litchi chinensis* | 2.6 | 3 | Non-native |
| **Solanaceae** | 12.2 | 14 | |
| *Solanum torvum* | **9.6** | **11** | Non-native |
| *Solanum lycopersicum* | 0.9 | 1 | Non-native |
| spp. | 1.7 | 2 | |

and *Solanaceae* were the most frequent in bulbuls' guts, corresponding to 25.2% (n=29) and 12.2% (n=14) of occurrence respectively. Some remains were more intact than others, allowing the identification of 16 different items at a species level, and one to genus. Most identified taxa were non-native (14 species); five of these are considered invasive in New Caledonia. Among these invasive species, the most important were the Turkey berry (*Solanum torvum*; 9.5%), the Persian lilac (*Melia azedarach*; 8.6%), the Guava (*Psidium guava*; 5.2%), and the Corkystem Passionflower (*Passiflora suberosa*; 5.2%).

The Brazilian peppertree (*S. terebinthifolius*) was also consumed. This pioneer evergreen shrub is listed as one of the 100 world's worst invasive species by the IUCN (Lowe et al. 2000). The most frequently consumed plant species were the non-native Java Plum (*Syzygium cumini*; 10.3%) and *Myrtastrum rufopunctatum* (9.5%), the only endemic species identified in the diet of New Caledonian bulbuls. Of the 16 plant species identified in the bulbuls' diet, eight species are cultivated as foodplants and six as ornamentals. All of these species have red, orange or dark purple fleshy diaspora; the berries of the Brazilian peppertree being the less fleshy. The largest seed (8 mm long) that we found intact in a bulbul stomach was from *Litchi chinensis*.

## Seed retention times

There were no significant differences in the palatability of the four fruit species. Mean reaction time varied from 56 ± 34 min for *P. suberosa*, to 155 ± 66 min for *S. terebinthifolius.* On average, individual bulbuls started feeding on *M. rufopunctatum* and *F. prolixa* after 123 ± 47 min and 77 ± 25 min respectively. Mean gut passage times of the four plant species are presented in **Fig 1**. During our experiment, minimum and maximum retention times were of 7 and 65 min respectively. Fruits of *P. suberosa* and *F. prolixa* were digested in 23 ± 1.13 min and 26 ± 1.35 min on average, a little faster than those of *S. terebinthifolius* (31 ± 1.45 min)

and *M. rufopunctatum* (33 ± 1.83min). Gut passage time was significantly different between

the four species (ANOVA *F*= 11.1; *df* = 3; *p* = 6.185e$^{-07}$). In our experiment, *M. rufopunctatum*

and *S. terebinthifolius* had longer gut passage times that *F. prolixa* and *P. suberosa* (see

pairwise t tests in **SM3**).
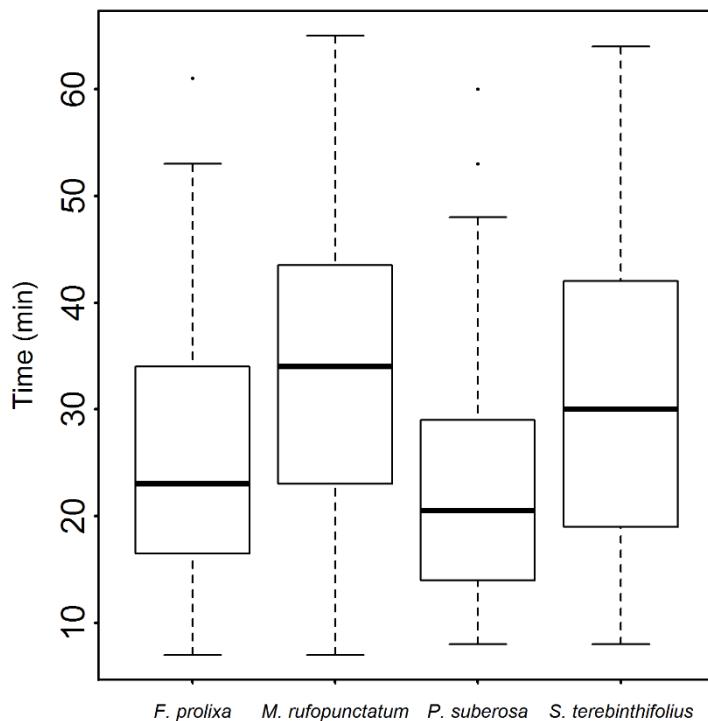


**Fig.1** Mean digestive retention times by the red-vented bulbul of *Ficus prolixa. Myrtastrum rufopunctatum. Passiflora prolixa* and *Schinus terebinthifolius* seeds.

The three gut passage thresholds estimated for the red-vented bulbul in New Caledonia are

summarized in **Table 2**. We conducted 49 measures of gut passage time for multi-seed fruits.

The first seeds took between 7 and 41 min to be dropped, with a median of 14 min. The last

seeds were dropped after 13 to 65 min with a median of 41 min. We replicated the test 93

times using berries of *S. terebinthifolius*, and recorded median gut passage time of 30 min,

with minimum and maximum times corresponding to 8 and 64 min respectively.

**Table 2** Gut passage times in minutes for seeds in single- and many-seeded fruits consumed by the red-vented bulbul in New Caledonia. Many-seeded fruits: *Myrtastrum rufopunctatum*. *Passiflora suberosa*. *Ficus prolixa*. One-seed fruit: *Schinus terebinthifolius*.

| First seed, many-seeded fruits | | | Single-seeded fruits | | | Last seed, many-seeded fruits | | |
|---|---|---|---|---|---|---|---|---|
| Median | Range | n | Median | Range | n | Median | Range | n |
| 14 | 7-41 | 49 | 30 | 8-64 | 93 | 41 | 13-65 | 49 |

Effect of passage through the gut on germination

Results of the germination tests are presented in **Fig 2**. Control seeds of the endemic shrub *M. rufopunctatum* reached the maximum germination rate (37% in 80 days). In comparison, only 25% of *M. rufopunctatum* seeds that passed through the gut of red-vented bulbuls germinated. Thus, consumption by the red-vented bulbul significantly reduced the germination rate of seeds of *M. rufopunctatum* by a factor 1.5 ($\chi^2$ = 4,71, *df* = 1, *p* = 0,03). Furthermore, germination of the digested seeds of this species was slightly delayed (40-89 days) compared with control seeds (35-81 days; *t* =-3.59, *p* = 0.0006). The germination success of the seeds of the invasive shrub *S. terebinthifolius*, were very low in our experiment. Digested seeds germinated between days 7 and 17, reaching a success rate of 10% only. Germination of control seeds started a few days later (10-20 days) and only 7% of planted seeds germinated successfully, although the difference between the two treatments was not significant ($\chi^2$ = 1,01, *df* = 1, *p* = 0,31).
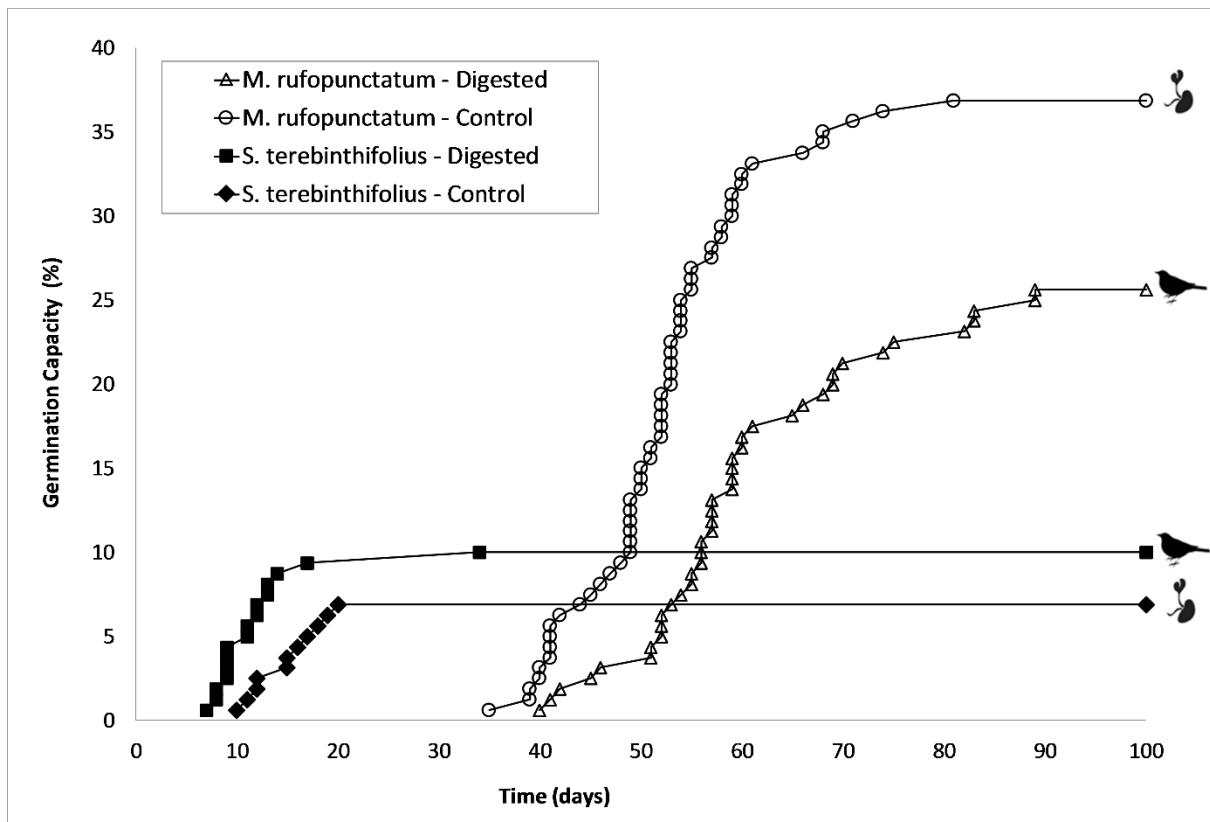
**Fig.2** The influence of passage through the gut of a re-vented bulbul on germination rates of *Myrtastrum rufopunctatum* and *Schinus terebinthifolius* seeds.

Dispersal capacity

We conducted 11 monitoring sessions of three bulbul individuals' movements. Median distance and maximum distance travelled are presented as a function of consecutive 10 min periods, giving an overview of dispersal capacity of the red-vented bulbul from the feeding time to the last dropping (**Fig. 3**). This figure suggests that, when foraging, movements of the red-vented bulbul are restricted to a radius of 100 m around a resource tree. On average, the birds covered this distance within 30 min after feeding on a specific tree. Maximum movements recorded suggest that red-vented bulbuls can cover up to 100 m in 20 min, and up to 200 meters in the 50 min following a food intake.
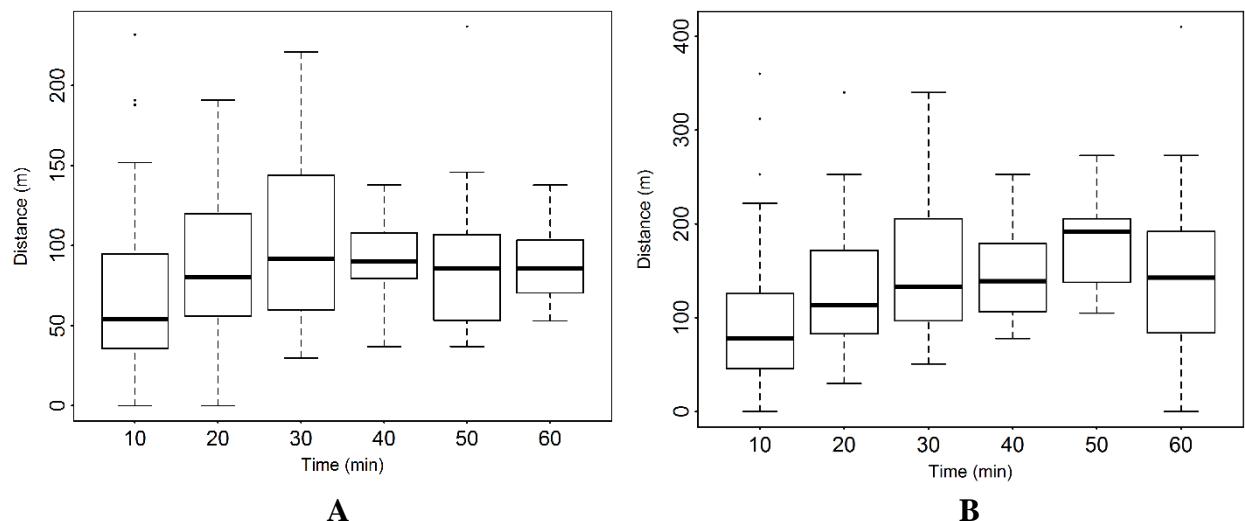
**Fig.3** Graph of the distance travelled as a function of time for the red-vented bulbul. Distances travelled from arbitrary starting points were determined at 10 intervals. A) Median distance covered as a function of time. B) Maximum distance covered as a function of time.

The median distance traveled by individual bulbuls during the three periods corresponding to our three defined gut passage times are shown in **Table 3**. Our results suggest that the median distance covered by red-vented bulbuls in 14 min was approx. 70 m (n=44), and it was 92 m after 41 min (n=11). The median distance covered within 30 min was of 92 m (n=23). According to the minimum and maximum distance we observed, we estimate that a bulbul is able to spread the seeds of multi-seeded fruit over distances of up to 273 m from the source tree. However, for these fruits the estimated median dispersal distances were 70-92 m. For single-seeded fruit, we estimated the median dispersal distance by the red-vented bulbul to be 92 m from the source tree (range 30 to 221 m).

**Table 3** Displacements (m) of bulbul individuals from arbitrary starting points during the gut passage times (GPT) for seeds (*i.e*: 14 min; 30 min; 41 min; *see Table 2*).

| Displacement during the minimum GPT (m) | | | Displacement during the median GPT (m) | | Displacement during the maximum GPTa (m) | | |
|---|---|---|---|---|---|---|---|
| Median | *n* | Lowest | Median | *n* | Median | *n* | Highest |
| 77 | 44 | 0 | 92 | 23 | 92 | 11 | 273 |

## Discussion

### Preference for non-native fruits

For now, the red-vented bulbul remains restricted to man-modified habitats in New Caledonia (Thibault et al. 2018b) where ornamental plant species are often disproportionally composed of non-native plant species (Smith et al. 2006). The diversity of plant material found in the intestines we analyzed confirmed that the red-vented bulbul feeds on a large variety of plant structures and species (Walker 2008). We also confirmed an expected association between the bulbul and a community of non-native plant species, with more than 80% of the consumed plant species identified being exotic to New Caledonia. This suggests that consumption of introduced plant species fairly meets the daily energetic requirement of the red-vented bulbuls, as demonstrated in a South African bulbul species (Jordaan et al. 2011). We confirmed that red-vented bulbuls consume the fruit of the invasive *S. terebinthifolius*, although the frequency of occurrence in the gut samples was low. The bulbuls' contribution to the dispersal of *S. terebinthifolius* along roads and urban corridors might thus rely on other factors such as fruit phenology and availability (Leck 1972). Their diet within their natural range suggests that the bulbuls may prefer fleshier fruits (Patyal and Rana 2003; Rana et al. 2005). Our data suggest that the bulbuls contribute to the dispersal of two other exotic species, *R. humilis* and *P. suberosa*. Fruits of these species are small, round, and fleshy, and are red/dark-purple in

color. These appear to be characteristics of preferred fruit for the red-vented bulbul (Spotswood et al. 2013). All of the consumed fruit species we identified here have red fleshy diaspore, including fruit of the shrub *M. rufopunctatum* that occurred frequently in bulbul gut samples. *M. rufopunctatum* is endemic to New Caledonia and promoted as an ornamental and revegetation plant (Gâteblé 2016), so this may be one native species that might benefit from consumption by the red-vented bulbul if it remains viable following passage through the gut. Our germination data (discussed below) indicated that this was not the case, with passage through the gut of the red-vented bulbul significantly reducing germination rates of *M. rufopunctatum* seeds. We included *M. rufopunctatum*, along with the invasive *S. terebinthifolius*, the introduced *P. suberosa* and the native *F. prolixa, in* the gut passage-time analysis.

## Rapid gut passage times

Passage through the gut of an animal plays a crucial role in seed dispersal and potential dispersal distance (Proctor 1968; Fukui 1996), but seeds can be affected differently depending on which species consume and digest it (Nogales et al. 2005). For example, in New Caledonia, native flying foxes and pigeons are far better small and medium-sized seed dispersal agents than introduced rodents, with rodents nibbled the seeds whereas pigeons and flying foxes swallowed them whole, resulting in significantly higher germination success (Duron et al. 2017). However, the chemical or mechanical impacts of digestion by two different bird species, although taxonomically close, can produced opposite effects on seeds germination success (Bartuszevige and Gorchov 2006). According to the gut retention time hypothesis, secondary metabolites of passerine-mediated fruits species could act as laxatives, leading to rapid passage times (Cipollini 2000). This phenomenon is expected to increase the rate of food intake by the bird.

In designing our experimental conditions for determination of gut passage times, we avoided potential complications with fruit palatability, bird stress, and degree of hunger by supplying the birds with fruits they are known to eat, providing an acclimation period, and removing their normal food for a set period before each trial (Levey and Karasov 1992). All individual bulbuls that ate during the experiment started pecking fruits within the first minute of the experiment, allowing direct comparisons of the results obtained with different fruits and across individuals. The gut passage times we measured for the red-vented bulbuls were consistent with results of a previous study conducted with 11 fruit species digested by the white-spectacled bulbul, *P. xanthopygos,* in Israel (Barnea et al. 1991). Gut passage times ranged from 7 to 65 min, with averaged values of 23 to 32 min depending on the fruit species. Barnea et al. (1991) reported gut passage times of 9 to 33 min depending on the fruit species. Linnebjerg et al. (2009) reported slightly shorter values in red-whiskered bulbuls, *P. jocosus*, of Mauritius with gut passage times around 15 min. Such differences in gut passage times are related in part to the specific characteristics of each fruit (Traveset 1998). This held true for our experiment, as we selected fruit from different species but with very similar characteristics and found small but significant differences in their mean retention times. These differences can be partly explained by the digestion physiology of the bird (Afik and Karasov 1995) and the flesh structure (Levey 1986), with juicy fruits (*P. suberosa*, *F. prolixa*) being digested more rapidly than firm fruits (*S. terebinthifolius*). Our measurements of median retention times for single versus multi-seeded fruits were comparable to the results Weir and Corlett (2007) obtained for the light vented bulbul, *P. sinensis*, and for the red-whiskered bulbul, in tropical landscapes of China.

Non-homogeneous impacts on germination

The impact of passage through the gut of a red-vented bulbul on germination rates differed between the two fruit species we tested, with germination success of *M. rufopunctatum* seeds being significantly lower when they were collected from bulbul droppings compared with control seeds that had been extracted from their fruits, but the reverse was true for *S. terebinthifolius*. Negative effects of gut passage are typically due to damage caused to the seed coat or exocarp (Samuels and Levey 2005), and our data imply that the red-vented bulbul is not an effective disperser of *M. rufopunctatum* seeds. Whether the negative effect observed here for *M. rufopunctatum* seeds is indicative of the effects of passage through the gut on germination rates of other native species should be investigated, ideally in a comparative study that also assesses the effects of passage through the intestinal tract of native bird species.

In contrast to the negative effects of passage through the gut of a red-vented bulbul on germination rates of *M. rufopunctatum* seeds, germination success of *S. terebinthifolius* seeds did not differ significantly between treatment and control seeds for which exocarp had been removed. Panetta and McKee (1997) obtained similar results with 22 other bird species. Seeds digested by red-vented bulbuls had a slightly higher germination rate and speed compared with control seeds. However, the success of germination for this species under greenhouse conditions (approx. 10%), even if consistent with results of Nilsen and Muller (1980), did not allow a statistical test of these differences. Dormancy lifting mechanisms such as chemical scarification is known to enhance the germination of *S. terebinthifolius* (Ewel et al. 1982). Here we showed that the digestion of *S. terebinthifolius* by the red-vented bulbul had a similar effect on seeds germination as removal of the exocarp. From previous studies we know that removal of the exocarp of *S. terebinthifolius* by frugivores promotes germination (*Zosterops*

*lateralis;* Panetta and McKee 1997). Therefore, we suggest that consumption by the red-vented bulbul also promote the germination success of *S. terebinthifolius.* Once again, this observation is consistent with the hypothesis of a strong mutualistic relationship between introduced red-vented bulbuls and non-native plant communities. Benefits from the fruit consumption by the bird, and from the dispersal by the fruit, could favor the expansion of both non-native species.

## Short distance dispersal

By combining gut transit time data with bird movement data, we predict that the maximum distances that red-vented bulbuls would likely distribute these fruits from source trees is 150 m. Similar seed dispersal distances have been reported for adults re-whiskered bulbuls (Weir and Corlett 2007) and white-spectacled bulbuls (*P. xanthopygos*; Spiegel and Nathan 2007). Our results were also consistent with Jordano et al.'s (2007) that small passerine species are predominant short distance (<250m) seed dispersers, although differences in species, habitat and season-dependent resource availability prevent direct comparisons across studies. Laver and Kelly (2008) rightly warned about the risks associated with such comparison, using the case of estimations of home range size in different studies. Nevertheless, we believe that the similarities between the ranges of our results and those of previous studies on pycnonotid species add confidence to our assessment of the small distance dispersal capacity of the red-vented bulbul in peri urban habitats. Exploring the contribution of biological factors such as bird maturity, sex, reproductive status, habitat, resources availability, and distance from the invasion front could help improve estimation of the seed dispersal capabilities of the red-vented bulbul.

Seed dispersal effectiveness of the red-vented bulbul

Even given the red-vented bulbul's apparently short-distance seed dispersal capabilities, the widespread planting of some of its preferred non-native fruit species in peri-urban environments may aid its range expansion north and south of Nouméa, and further disperse the seeds of these exotic plants, potentially driving an "invasional meltdown". The study highlights the need for further research on the effects that consumption by red-vented bulbuls has on germination rates of other fruit-bearing plants species, both native and invasive, and how its seed dispersal capabilities compare with those of native frugivorous birds. Particular attention should be paid to the bulbul's feeding seasonality and intensity on native and non-native plants species, including *Miconia calvescens* (Meyer 1996). This will aid the design appropriate and effective conservation actions throughout the red-vented bulbul's alien distribution.

Conclusion

We present an overview of various context-dependent and distance-dependent mechanisms that contribute to the seed dispersal capabilities of the invasive red-vented bulbul. These bulbuls showed preference for non-native fruits species in the study areas. This, combined with enhanced germination rates following gut transit of seeds of the highly invasive *S. terebinthifolius,* could represent an example of "invasional meltdown". Such a mutualistic relationship could lead to major conservation issues, particularly in ecosystems that host a large number of endemic plant species such as the ultramafic maquis of New Caledonia. Therefore, we suggest that the population of red-vented bulbuls should be confined to its current distribution range in man-modified habitats of the Southern-Province until a dedicated country scale management strategy is designed. Similarly, the small population of *M. calvescens* should be confined and/or eradicated, and substantial survey effort should be

dedicated to preventing any overlap between this invasive plant and red-vented bulbuls. Finally, there is an urgent need for research programs dedicated to describing dispersal of seeds by native frugivores in New Caledonia to prevent both future threats on endemic species by introduced frugivores and prevent the dispersal of non-native plants out of inhabited areas.

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## Appendices

**Appendix SM1.** Overview of the main characteristics of the four fruit species used in the study.

|  | *S. terebintifolius* | *M. rufopunctatum* | *P. suberosa* | *F. prolixa* |
|---|---|---|---|---|
| Type | berry | berry | berry | figs |
| Color | red | purple | purple | red-orange |
| Shape | spherical | egg-shaped | spherical | spherical |
| Diameter (cm) | 0.4-0.5 | 1 | 0.6-1.9 | 1 |
| Seeds (n) | 1 | > 30 | >20 | >100 |
| Plant type | shrub | shrub | liana | tree |
| Habitat | generalist | maquis* | drained | coasts, forests |
| Conservation | invasive | endemic | introduced | native |
| Fructification | Apr-Jun | Aug-Dec | May-Dec | May-Jun |
| Uses | ornamental food, medicinal | ornamental revegetation | medicinal | Wood, latex |
| Reference | *GEE. 2012* | *Gâteblé. 2006* | *GEE. 2012* | *Suprin. 2011* |

*maquis: shrubby vegetation growing on ultramafic outcrops*

**Appendix SM2**. Number and frequency of the different plant parts found in the digestive tracts of 115 red-vented bulbuls.
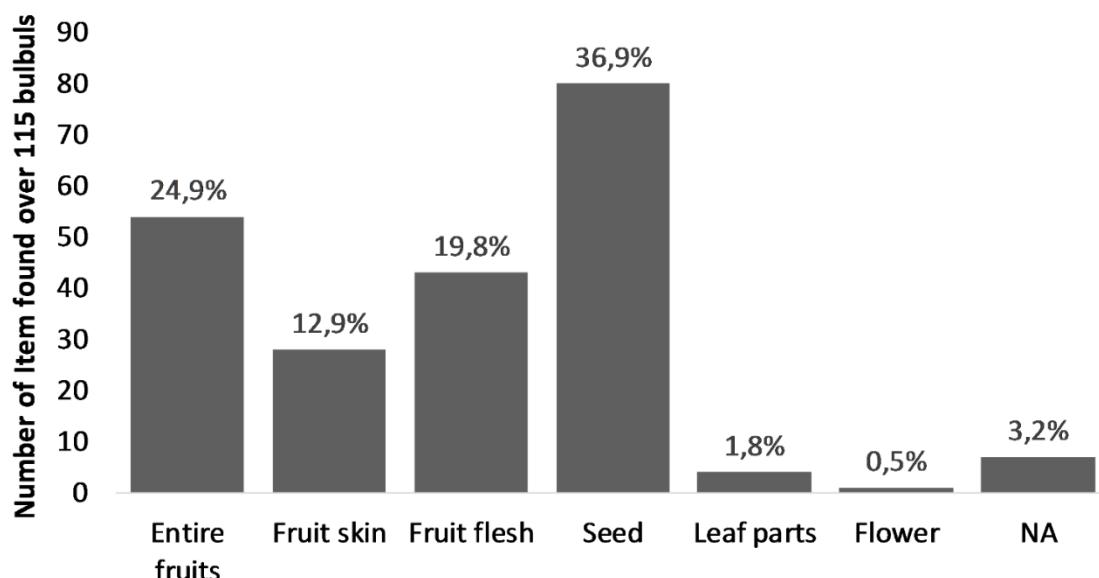
**Appendix SM3**. P values of pairwise Student's t-tests exploring the differences in gut passage times of *Ficus prolixa. Myrtastrum rufopunctatum. Passiflora prolixa* and *Schinus terebinthifolius*.

|  | *F. prolixa* | *M. rufopunctatum* | *P. suberosa* |
|---|---|---|---|
| *M. rufopunctatum* | 0.0043 | - | - |
| *P. suberosa* | 0.1774 | 7.30 E-06 | - |
| *S. terebinthifolius* | 0.0238 | 0.3728 | 5.00 E-05 |

# CHAPTER 6: Global distribution range

## Global distributions of three highly invasive bird species under climate change

*In prep* for The Condor

Co-authors: **Murray A. Potter, Fabrice Brescia, Morgane Barbet-Massin**
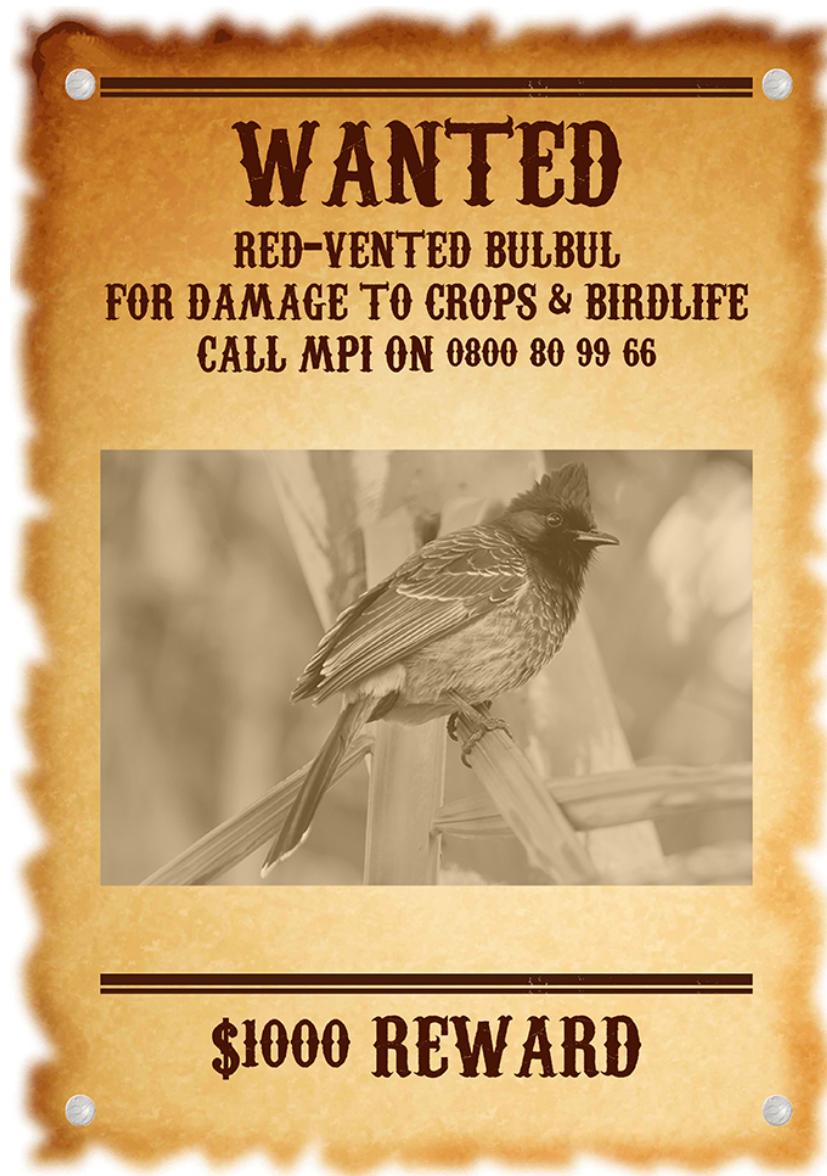
# Abstract

The red-vented bulbul (*Pycnonotus cafer*), the common myna (*Acridotheres tristis*) and the red-whiskered bulbul (*Pycnonotus jocosus*) are passerine bird species native to the Indian subcontinent. All three species were transported widely during the early 1900s as caged birds for trade. They are now considered invasive – occupying diverse habitats, feeding on and damaging a wide range of fruit, and out-compete native fauna. Predicting the current potential global distribution of these species is important to help identify locations where introduction-prevention should be prioritized. Of equal importance is an assessment of how climate change might alter their potential invasive ranges. Here, we used presence data from both their native and alien ranges and eight species distribution model (SDM) algorithms to predict their potential current ranges. We then used five global circulation models and four representative concentration pathways to predict their potential future ranges under climate change. Our results suggest that there is considerable overlap in the potential climatically suitable ranges of the three species, with the common myna having the widest potential range. Many islands, and particularly Mayotte, Madagascar, and the Indian Ocean Islands, appear to be climatically suitable for invasion. Our future projections highlight three locations (Guinea gulf, South America, and Gulf of Mexico) that could be climatically suitable for further invasion by these invasive species, and predict potential shifts in the distribution of alien populations in four main geographical areas (Middle East, Australia, and South Africa). We believe that application of SDMs for invasive bird species under climate change scenarios, as used here, can offer managers a useful tool to generate potential-range distribution maps to assess and compare invasion risk at both local and global scales.

**Keywords:** Biological Invasions, Birds, Climate, Islands, Species Distribution Modeling.

## Résumé

Le bulbul à ventre rouge (*Pycnonotus cafer*), le merle des Moluques (*Acridotheres tristis*) et le bulbul orphée (*Pycnonotus jocosus*) sont des passereaux originaires du sous-continent indien. Les trois espèces ont été largement transportées au début des années 1900 comme oiseaux d'ornement. Ils sont maintenant considérés comme envahissants - occupant divers habitats, consommant une large gamme de fruits, et menacant la faune native. Prédire la distribution de ces espèces est important pour aider à identifier les territoires prioritaires pour la prévention des invasions. Par ailleurs, évaluer l'influence des changements climatiques sur leur niche climatique mondiale semble crucial. Ici, nous avons utilisé des données de présence natives et introduites, huit variables climatiques actuelles ainsi que huit types de modèles de distribution d'espèces (SDM) pour estimer leur niche climatique mondiale. Nous avons ensuite utilisé 20 scénarios de changement climatiques pour prédire l'évolution potentielle de ces niches climatiques d'ici 2050. Nos résultats suggèrent un chevauchement considérable dans les niches climatiques des trois espèces, le merle des Moluques ayant la niche la plus large. De nombreuses îles, et en particulier Mayotte, Madagascar et les îles de l'océan Indien, semblent climatiquement favorables à l'invasion par ces espèces. Nos projections mettent en évidence trois localités (Golfe de Guinée, Amérique du Sud et Golfe du Mexique) qui pourraient être climatiquement favorables à des invasions futures, et prédisent des changements de niches climatiques dans quatre zones géographiques (Moyen-Orient, Australie et Afrique du Sud). L'application présentée ici des SDM aux espèces d'oiseaux envahissantes selon des scénarios de changement climatique pourrait offrir aux gestionnaires un outil supplémentaire pour générer des cartes de risque d'invasion aux échelles locale et mondiale.

**Mots-clefs :** Invasions biologiques, oiseaux, climat, iles, modèles de distribution d'espèces

## Introduction

The ability to describe and predict the distribution ranges of plant and animal species is crucial to a variety of research fields including conservation programs and management of invasive species (Ocampo-Penuala and Pimm 2014; Pecl et al. 2017; Weterings and Vette, 2017). Knowledge of species' distributions can aid assessment of the likelihood of a species invading a new area or going extinct, and the potential impacts of climate change on community structure (Chen et al. 2011; Barbet-Massin al. 2013). Statistical approaches such as species distribution models (SDMs) apply ecological theory to field observations and sets of environmental predictors to generate multi-scale projections of the probability of a species being present in a geographic region (Guisan and Thuiller 2005). These models are commonly used to estimate the potential distribution of native or non-native species (Jimenez-Valverde et al. 2011b; Ofori et al. 2017), and can aid management decisions (Guisan et al. 2013). Ecosystem perturbations associated with human activity will likely continue to increase during the 21st Century (Pimm et al. 2014), so exploring the influence of global changes on species' distributions is crucial, particularly for known invasive species (Hulme 2009).

The red-vented bulbul (*Pycnonotus cafer,* Linnaeus 1766; red-vented bulbul), the common myna (*Acridotheres tristis*, Linnaeus 1766; CM) and the red-whiskered bulbul (*Pycnonotus jocosus,* Linnaeus 1758; RWB) are three passerine bird species native to the Indian subcontinent. All three were transported and sold as caged birds from the early 1900s. Once established in new areas, their plasticity in diets and competitive foraging behaviors have often resulted in them becoming pests (Martin-Albarracin et al. 2015). The red-vented bulbul and the RWB are mostly frugivorous but also prey on small arthropods and skinks (Islam and Williams 2000). The common myna feeds mostly on arthropods, but also on plants (Sengupta

1976). All three can damage fruit and vegetable crops (Cummings et al. 1994; Linnebjerg et al. 2010; Peacock et al. 2007) and they are often associated with alien plant species that they can help disperse (Mandon-Dalger et al. 2004; Holzapfel et al. 2006; Spotswood et al. 2012). The two bulbuls are suspected contributors to the dispersal of highly invasive plants such as *Miconia calvescens, Shinus terebinthifolius, Lantana camara, Cecropia peltata* and *Clidemia hirta* (Mandon-Dalger et al. 2004; Linnebjerg et al. 2010; Staddon et al. 2010; Spotswood et al. 2012; Spotswood et al. 2013), all of which are listed among the UICN-ISSG's "100 world's worst invasive species" (Lowe et al. 2000). Moreover, all three bird species are believed to compete with native avifauna. The red-vented bulbul competes for food with the Polynesian starling, *Aplonis tabuensis* and the wattled honeyeater*, Foulehaio carunculate*, and lowers the reproductive output of the Tahiti monarch, *Pomaea nigra* (Blanvillain et al. 2003; Jones 1996; Sherman and Fall 2010). The CM has also contributed to the decline of the Tahiti monarch and is a significant competitor of the Seychelles Magpie-Robin, *Copsychus sechellarum* (Baker et al. 2014). The CM and red-vented bulbul are both listed in the IUCN's list of the 100 world's worst invasive species (Lowe et al. 2000), and are considered two of the three worst invasive bird species in terms of their impact on native ecosystems globally (Martin-Albarracin et al. 2015). Such status necessitates their close monitoring and management, and every effort to prevent their further introduction into climatically suitable areas. This, in turn, requires reliable prediction of climatically suitable areas.

Kumschick et al. (2016) recently highlighted important overlaps between the mechanisms that lead to negative impacts of invasive bird species in general, and the red-vented bulbul and CM in particular. They suggested that effort should be directed at identifying negative effects of these two species to clarify their rankings in international priority lists. Linked to this, a recent study on the red-vented bulbul and CM in French Polynesia suggests that habitat partitioning

might allow these species to coexist without intense competition in alien island locations (Bates et al. 2014). Authors who have tried to attribute standardized impact scores to invasive species have often called for improvements in the way in which impact values for invasive birds are assessed (Strubbe et al. 2011; Kumschick et al. 2016). Given that the CM, red-vented bulbul and RWB can and do live sympatrically, we believe that it is important to consider the three species simultaneously to manage their impacts at a global scale. Surprisingly, neither the potential distributions of these major invasive species nor the potential impact of climate change on their potential ranges have yet been investigated. The current alien ranges of the three species include several tropical islands and archipelagos (Clergeau and Mandon-Dalger 2001; Feare et al. 2015; Watling, 1978). Special attention should be paid to assessing the suitability of as-yet uninvaded islands of high-conservation status for potential establishment of these species. Indeed, the higher endemicity and naivety of insular species (Gerard et al. 2016; Walsh et al. 2012) reinforce their sensitivity to biological invasions (Sax and Gaines 2008; Tershy et al. 2015). Establishment of invasive species on islands could also increase the risk of short-distance dispersal to other near-by islands or larger land masses (Gillespie et al. 2012).

Here, we predict the worldwide potential current and future climatically suitable ranges of the CM, red-vented bulbul and RWB and produce current and forward-projected risk and climate suitability maps for each of these three species. We used native and alien presence data from a global participative database of bird observations (Ebird, Sullivan et al. 2009) within an ensemble forecast made of eight different modeling techniques (Thuiller et al. 2009) to estimate the current potential distributions of the red-vented bulbul, RWB and CM worldwide. Future potential distributions were obtained by projecting the models using IPCC fifth assessment future climatic scenarios for 2050 (IPCC 2014). More precisely, we used five

general circulation models (GCMs) and four representative concentration pathways (RCPs).

Within this framework, we produced current and future (2050) climatic suitability maps for

the red-vented bulbul, CM and RWB. This allowed us to pinpoint areas predicted to be

climatically suitable for these three Asian passerines. By comparing current and future

predicted distributions, we highlighted locations where changes in the climate suitability for

these species are expected. Finally, we highlighted locations where current and expected

future climate could be suitable for the three species. Our results help to characterize the

status and risk associated with these species at both local and global scales

## Methods

### Presence data from the native and invaded ranges

We used sightings from the Ebird database (Ebird, Sullivan et al. 2009) as presence data. This

participative database comprises bird point counts and sightings worldwide, with associated

GPS coordinates. In 2016, the database contained 40,152 sightings of the red-vented bulbul

from 25 countries, 72,526 sightings of the red-whiskered bulbul within 25 countries and

243,395 sightings within 72 countries for the common myna.

### Climatic variables

Predictions of global distributions of birds are strongly influenced by climate factors at a global

scale (Luoto et al. 2007; Jimenez-Valverde et al. 2011a; Barbet-Massin and Jetz 2014). We thus

extracted eight climatic variables from the BIOCLIM database as 10 arc-min grids

(http://www.worldclim.org/; Hijmans et al. 2005). We considered: (1) Bio1: annual mean

temperature, (2) Bio5: maximum temperature of the warmest month, (3) Bio6: minimum

temperature of the coldest month, (4) Bio4: temperature seasonality, (5) Bio12: annual

precipitation, (6) Bio13: precipitation of the wettest month, (7) Bio14: precipitation of the

driest month, and (8) Bio15: precipitation seasonality. The seasonality is the coefficient of variation of the monthly means. These variables have previously been used for niche modeling (Barbet-Massin et al. 2009).

Future climate projections (for 2050) were derived from five general circulation models (GCMS; CCSM4, HadGEM2-ES, IPSL-CM5A-LR, MIROC5 and NorESMMI-M) down-scaled at 10 arc-min resolution and four representative concentration pathways (RCPs; 2.6, 4.5, 6.0, 8.5). The four RCP scenarios represent four levels of radiative forcing (from +2.6 to +8.5 W/m$^2$) considered in the fifth IPCC assessment report (IPCC, AR5 2014; http://www.ipcc-data.org/, IPCC 2014). We thus used 20 future climate projections for each of the three species.

## Distribution modeling under current climatic conditions

The potential distribution of each of the three bird species (CM, red-vented bulbul and RWB) was modeled by running eight different niche-based modeling techniques using the BIOMOD2 package with R (Thuiller et al. 2016). These models were: (1) generalized linear model (GLM); (2) generalized boosting model (GBM); (3) generalized additive model (GAM); (4) classification tree analysis (CTA); (5) artificial neural networks (ANN); (6) multivariate adaptive regression splines (MARS); (7) mixture discriminant analysis (MDA) and (8) Random Forest (RF). All of these modeling techniques require presence / absence data, so virtual absences (pseudo-absences) were used as surrogates for absence data. We used 50,000 pseudo-absences, with the total weight of presences (the sum of all presence weights) being equal to the total weight of pseudo-absences (the sum of all pseudo-absence weights) (Barbet-Massin et al. 2009). Selection of pseudo-absences was repeated three times for each species.

The performance of current models was measured with two accuracy measures: the TSS (True Skill Statistic) and the AUC (Area Under this Curve). The TSS is the threshold value maximizing

the sensitivity and specificity (Allouche et al. 2006). The sensitivity corresponds to the proportions of actual presence that are predicted as such, and the specificity measures the proportions of negatives that are correctly predicted. A ROC plot is obtained by plotting true positive (sensitivity) against false positive (1-specificity) values, producing a ROC curve. The AUC is used as a measure of the overall accuracy. Models with an AUC higher than 0.9 and TSS higher than 0.8 are usually considered very accurate (Fielding and Bell 1997). We used a random subset of 70% of the data to calibrate every model, and the remaining 30% to evaluate the predictive performance of each species distribution model. All models were further projected worldwide.

Ensemble forecasts and modeling under future climatic conditions

To obtain a consensus distribution under current climatic conditions, we used an ensemble forecast technique that aims to determine the central tendency of all modeling techniques (Araújo and New 2007). This technique allows the calculation of a probability-weighted mean model using the evaluation scores obtained for the different modeling techniques. The predicted accuracy of each model, represented by the TSS score, was used to calculate the relative weight of each model when model-stacking (Thuiller et al. 2009).

We computed the distributions under three different pseudo-absence data combinations. After calculating the ensemble forecast for each of the three runs, we calculated the median probability distribution of the three runs. Models were also projected under future climatic scenarios (five GCMs and four RCPs) expected by 2050. The consensus future distribution was obtained by calculating the mean distributions across the 20 climate change projections.

## Binary distributions

To underline priority locations for consideration of the invasion risk associated with red-vented bulbul, RWB and CM, we converted the potential current and future climate suitability maps into binary distributions. To maximize the accuracy of the transformation, for each species we calculated the threshold value that maximized the TSS score of the model. This threshold was then applied to transform current and future continuous distributions into binary distributions (Jiménez-Valverde and Lobo 2007).

# Results

## Current climate suitability

Considerable overlap existed in the predicted current climate suitability distributions for the three species, with locations of high current suitability values falling between 40°N and 40°S for the two bulbul species, and the potential climatic envelope for the CM including this range but extending to 52°N (**Fig.1**). Climate is particularly suitable for all three species in five geographical areas. The largest suitable area corresponds to their native range (extending east), including continental countries such as China, Burma, Vietnam and Laos, and island nations such as the Philippines, Malaysia and Taiwan. Four large non-native areas were also predicted as climatically suitable for these invasive passerines: the northern parts of Western Australia, Northern Territory and Queensland; both continental and insular countries that boarder the coasts of the Mozambique Channel (e.g. Madagascar, Mozambique, Comoros, Mayotte, The Seychelles); countries of the Guinea gulf including the southern parts of Mali, and Niger; and countries in the south of the Gulf of Mexico.
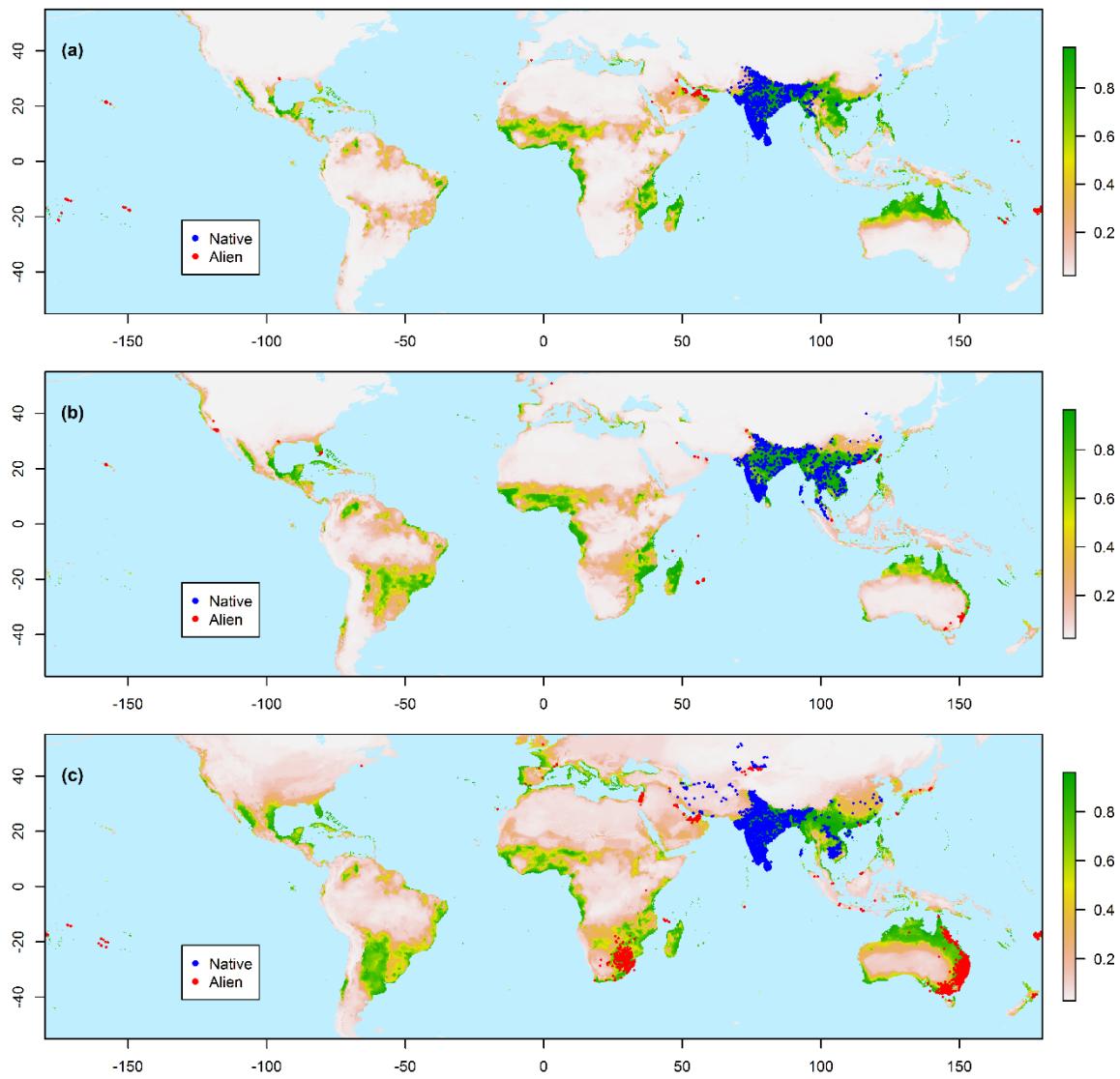
**Figure 1.** Current climate suitability for (a) *Pycnonotus cafer*, (b) *Pycnonotus jocosus* and (c) A*cridotheres tristis* estimated with all occurrences. Presence data in the native distribution range are colored in blue; presence data located outside of the native range are colored in red.

Islands and coastal locations are well represented within these predicted ranges but, because of their small size, predicting the climate suitability for the three species in the Marshall Islands, Pitcairn Island and Tokelau was not possible. Among these territories, 25 islands are already occupied by at least one of the three species, and nine by two of them (**Fig.2**). The

results presented in the **Fig.2** suggest that 62 of the 75 island territories that lie between 50°N and 50°S are climatically suitable for at least one of the three species (details are given in **Appendix S1** in Supporting Information). Moreover, 44 of these islands could be suitable for all three species if they were introduced there. The only discrepancy between a predicted climatically unsuitable location and actual occupancy by one of the three focus species was for Saint Helena, which has an established population of common myna despite the model predicting that this would be unlikely.

*The red-vented bulbul*

For the red-vented bulbul, the mean TSS and AUC scores were 0.83 and 0.96 respectively. For this species, highest current suitability values fall between 40°N and 36°S latitude (**Fig.1a**). Our modeling of the current potential distribution of the red-vented bulbul also highlighted smaller climatically suitable areas: the coasts of the Persian Gulf; Southern Islands of Greece; Archipelagos of the South Pacific; and the easternmost coast of Brazil. Interestingly, the red-vented bulbul has been reported 3080 times in five countries of the Persian Gulf since 1971 when it was first detected in Qatar. Also, it has been recorded 6,100 times in eight Pacific archipelagos since first being reported in Fiji in 1903.
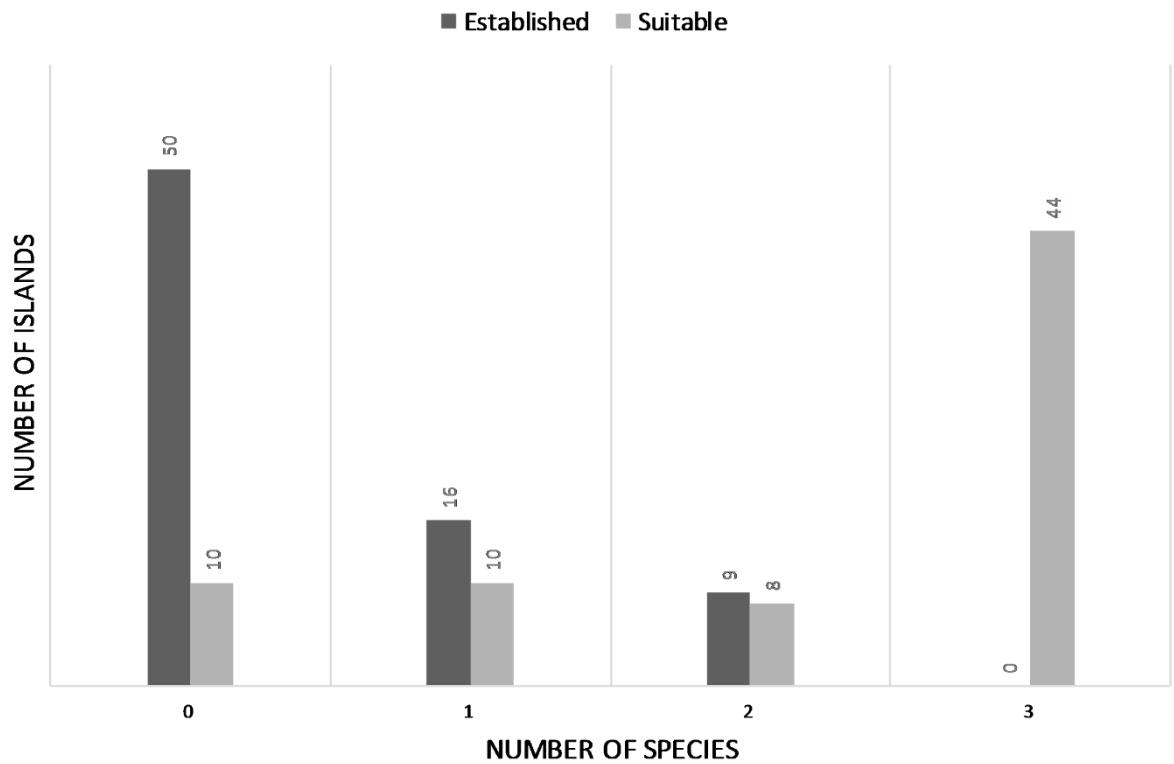
**Figure 2.** Current occupation and current climate suitability of islands located within 50°N and 50°S for the red-vented bulbul, the red-whiskered bulbul and the common myna.

*The red-whiskered bulbul*

Models that predicted the current potential distribution of the RWB had a mean TSS score of

0.81 and a mean AUC score of 0.95. The potential distribution of the red-whiskered bulbul is

very similar to the values obtained for the red-vented bulbul (**Fig.1b**). The latitudinal extent of

the climatically suitable range for the RWB was from approx. 40°N in North Spain to 40°S in

Chile. Differences between the predicted potential distributions of the red-vented bulbul and

RWB appeared at the finer scale. In particular, there was one additional climatically suitable

area for the RWB in South America, located between Brazil, Paraguay and Argentina. The

south-west coast of Australia, around Perth, appeared suitable for the RWB. Conversely, the climate in the Middle-East predicted a very low suitability for this species.

*The Common myna*

The mean TSS and AUC scores for the Common myna predictions were 0.77 and 0.93 respectively. The current predicted potential distribution of the CM (**Fig.1c**) highlights a wider potential latitudinal range than for the two bulbuls, falling approximately between 50°N and 40°S. The climatically suitable areas for the CM extend to areas in Argentina, South Africa, Western Europe including the Atlantic and Mediterranean coasts, and South Australia.

*Current invasion "risk" for the three species*

The world maps presented in **Fig.3** summarize areas where the climate is suitable for one to three of the focal species. Among the locations where the current climate is suitable for the invasion by two or three of the species, at least five macro-areas located outside of the native distribution range of the three species can be identified: the South West of the Pacific Ocean; the South West of the Indian Ocean; the Guinea gulf; South America; and the Caribbean Sea (including the southern parts of the Mexican gulf). Some countries belonging to these areas already host one or even two species of Indian-native invasive birds, except for the coasts of the Guinea gulf that are currently free of these species. Other smaller areas appear to be currently climatically suitable for several of the studied species. For example, the eastern coasts of the Mediterranean Sea (Greece, Lebanon) and several locations in the South American continent (Coasts of Brazil, Colombia, Venezuela, Bolivia, Paraguay, and Argentina).
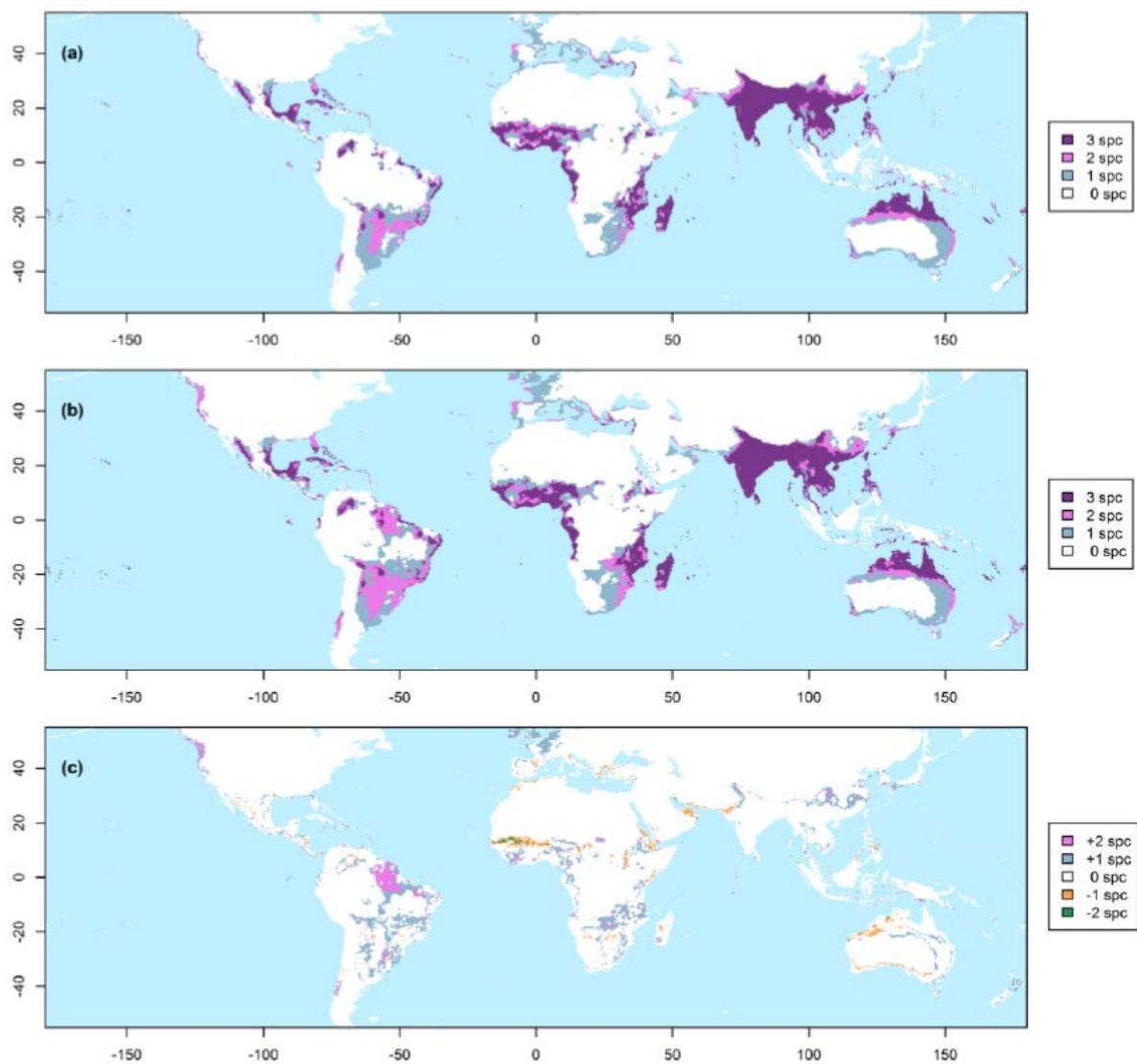
**Figure 3.** Current (a), future (b) and differences (c) in the binary climatic "risk" for the three species.

## Potential impact of climate change by 2050

*Predicted suitability for the three species*

According to our predictions, the climatic suitability of the three tropical bird species will increase massively by 2050 (**Fig.4**). The main predicted changes are located in continental areas.
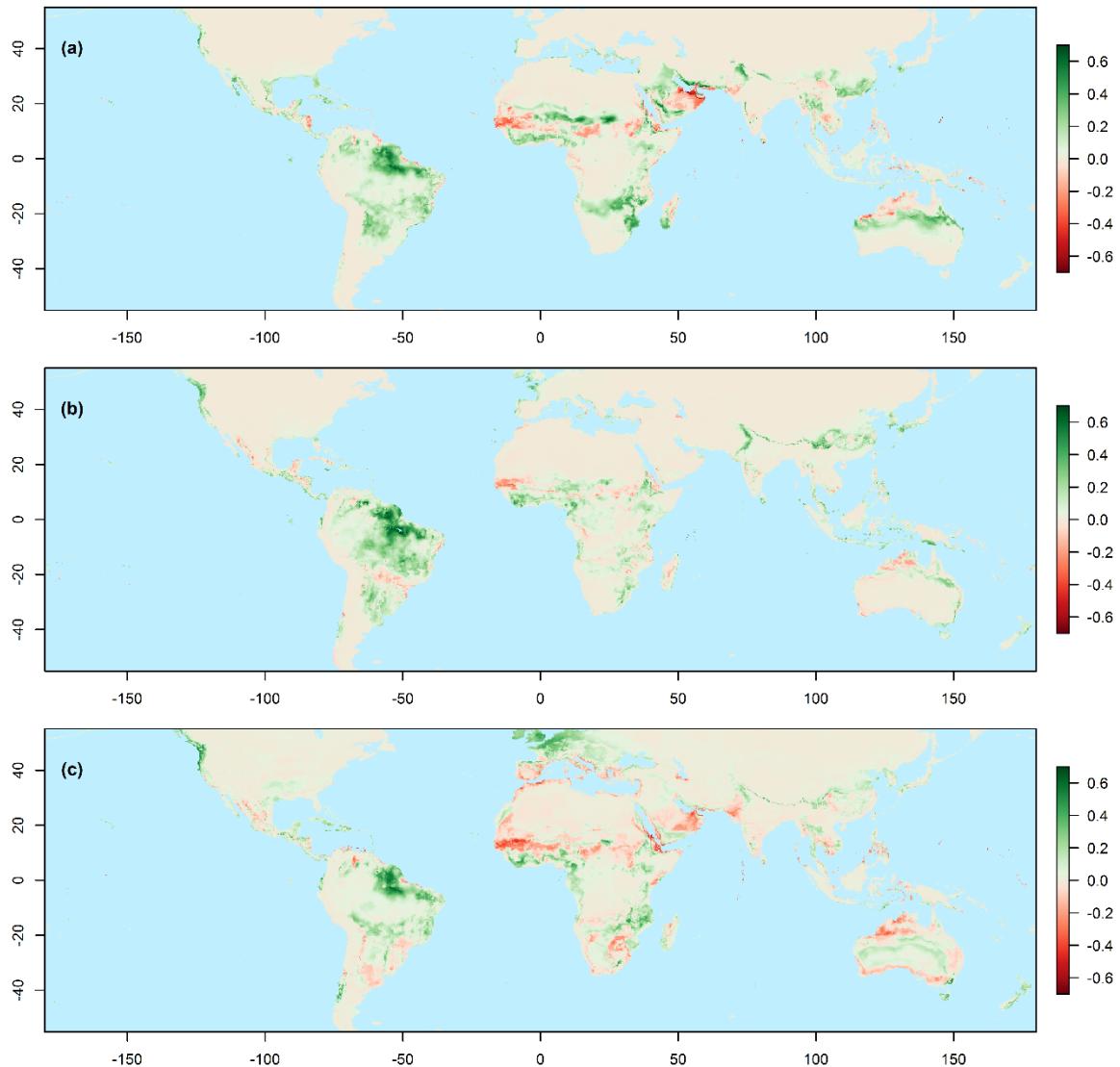


**Figure 4.** Differences between the climate suitability expected by 2050 and the current climate suitability for (a) *Pycnonotus cafer*, (b) *Pycnonotus jocosus* and (c) *Acridotheres tristis*.

For the red-vented bulbul (**Fig.4a**), climate is expected to become increasingly suitable in two principal areas. The first and most obvious one is North-Eastern South America, particularly Northern Brazil, Suriname and French Guyana. The second is located around the Mozambique Channel and includes the South East of Madagascar, and an area that covers South Mozambique, Zimbabwe, Botswana and the North-East of South Africa. In Northern Australia, coasts of the Guinea Gulf and in the Middle East, climate suitability is expected to decrease in locations that are currently highly suitable for the red-vented bulbul (Senegal, South of Mali). On the other hand, climate at the edges of these areas is expected to become more suitable by 2050. Climate suitability in most of the tropical/subtropical archipelagos is expected to remain steadily suitable, except in the Indian Ocean where it is predicted to become less suitable.

The predicted changes in climate suitability for the RWB (**Fig.4b**) are very similar to the ones for the red-vented bulbul. The main exception is in South America, where the expected increase in climate suitability could extend further south to the Amazon River. The other difference between the two bulbuls is the absence of a change in suitability in the Middle East for the RWB, but this area is not included in the current climatic range of the RWB. Also, predicted changes in climate suitability are weaker for the RWB than for the red-vented bulbul. In particular, the climate suitability is not expected to increase in the middle part of Australia or in the northernmost limit of sub-Saharan Africa (Niger, Tchad) for the RWB.

The predicted changes in climate suitability for the CM (**Fig.4c**) show some similarities with the predictions for the two bulbuls. Among them, an increase in climate suitability is expected in the North of Brazil, in the coastal countries of the Guinea Gulf, in the north of Mozambique, and to a lesser extent in the middle of Australia. Also, the climate suitability for the CM is

expected to decrease in the North of Australia, in the Middle East, and in some West African countries (Senegal, South of Mali). Predicted changes for the CM also show some differences to the bulbuls. For example, climate suitability for the CM is expected to decrease in Mediterranean coasts, in South Africa, in the southern coast of Australia and in Argentina, but increase in Western Europe (France, United-Kingdom, Germany, and the Netherland). Climate suitability for the CM in most tropical archipelago is expected to change similarly to the two bulbuls.

*Evolution of the invasion "risk" for the three species*

When focusing on the projections under future climate scenarios, we can infer that climate change is mainly expected to increase the invasion "risk" of these species. Indeed, climate is expected to become suitable for one or two more species in the North of South America (Brazil, Guyana, Suriname), in the West Coast of the North America (US and Canada), in small areas of Africa (Botswana, Zimbabwe, Ivory Coast), and in Europe (France, United Kingdom). Also, climate change could lead to a northward displacement of the northern edge of the native range of one or two species. In comparison, very few locations are expected to be at risk of invasion by fewer species. The most important one is located in western Africa, across the North of Senegal and the South of Mali. The same pattern brings out in Djibouti and Western Ethiopia, as well as in the North West of Australia.

## Discussion

Our results identify considerable overlap in the current potential climatically suitable ranges for the red-vented bulbul, the red-whiskered bulbul and the common myna, but the current potential latitudinal range is larger for CM than for the bulbuls. The current ranges of these three invasive species have been shaped by their individual introduction histories. The CM

was introduced widely and intentionally to control a range of insect pests including locusts (Jones 1996; Grarock et al. 2012; Rana et al. 2017). The red-vented bulbul and RWB, in contrast, were transported as cage birds and then accidentally or intentionally released somewhat randomly (Watling 1978; Jones 1996). All three species are still expanding their ranges which has the potential to result in underestimation of their overall potential climatic niches and hence their predicted potential distributions. This is a common issue with invasive species (Gallien et al. 2012), but it does mean that our SDM projections are likely to be conservative. Overall, our worldwide projections confirm that the climate suitability of the three species correspond to an equatorial climate according to the Kopper-Geigen classification (Kottek et al. 2006).

Our SDM projections identify numerous climatically suitable countries outside of the current species' ranges, and most island nations appear to be climatically suitable for invasion by one or more of these species. Mayotte appears to be particularly climatically suitable for invasion. CM has already established in this archipelago and the RWB and the CM have established in La Reunion, Mauritius, Seychelles. Madagascar and the Indian Ocean Islands appear to be climatically suitable for further establishment of the three alien species. This region is listed amongst 35 world biodiversity hotspots, and considerable concern has been expressed about likely impacts and management challenges should CM and RWB establish more widely in this region (Clergeau and Mandon-Dalger 2001; Feare 2010; Feare et al. 2015, 2017; Linnebjerg et al. 2010).

The majority of documented plant and vertebrate extinctions over the last 500 years have occurred on islands (Sax and Gaines 2008; Tershy et al. 2015). Island biota are especially sensitive to the impacts of invasive exotic species (Bellard et al. 2016a; Bellard et al. 2016b)

because of high levels of endemicity and naivety of island species (Tershy et al. 2015; Gerard et al. 2016). On the positive side, invasive species control and eradication tends to be more achievable on islands than on continents (Myers et al. 2000; McGeoch et al. 2016).

The increased difficulty of eradication from continents means that it is vital to restrict the further introduction of the red-vented bulbul, RWB and CM into countries around the Guinea Gulf, as coastal areas of Guinean, Ivory Coast, Liberia and Sierra Leone are world biodiversity hotspots and these countries host the westernmost rainforest of Africa where native bird communities are already threatened by land-use changes and bird trade (Beier et al. 2002; Norris et al. 2010; Arcilla et al. 2015; Atuo and O'Connell 2015). Recent projections suggested significant shifts in avian communities are likely there under short-term climate change scenarios (Baker et al. 2015). Adding additional invasive species will make matters worse. Similarly, countries that border the Caribbean Sea and Gulf of Mexico are currently climatically suitable for the red-vented bulbul, RWB and CM, and our prediction is that this will remain the case under projected climate change scenarios through until 2050. None of the three focal species have yet established in Mesoamerica or in the Caribbean, two biodiversity hotspots, though alien populations of the two bulbuls has established north of this area, in Florida and Texas. Dispersal of the bulbuls into the Mexican gulf and then the Caribbean Sea could easily be facilitated by human activities and stepwise dispersal of the species along islands in the east, and along inhabited corridors on the western continental side (Minor and Urban 2007).

Our modeling under future climate projections further highlights three areas where climate parameters could become increasingly suitable for the three invasive species: the North-East of the South American continent; the islands and coastal countries around the Guinea Gulf; and the Caribbean Sea and Gulf of Mexico. Considering that none of the three species have

yet established in South America or in Western Africa yet, we believe that these regions need to prioritize efforts to prevent any introduction, especially as their climates are predicted to become increasingly suitable for the red-vented bulbul, RWB and CM. In the South-East Pacific Ocean, in the South East Indian Ocean, and in the Caribbean Sea and Mexican gulf, the risk of multiple invasions is very real and border control and biosecurity should be given highest priority, as alien populations of these species are already present and sympatric in some of these areas.

Increasing risk of multiple invasions by these species could lead to additive impacts that should be considered seriously by scientists and managers at regional, country and/or local scales. The red-vented bulbul, RWB, and CM have very similar biology and ecology, and we showed an important overlap in their climate tolerance. The three species are already sympatric in five locations outside of their native ranges (US, Hawaii, Oman, Kuwait and United Arab Emirates). We therefore consider that the presence of one or two species does not preclude invasion by a second or third, and we recommend that invasion prevention strategies and development of management plans for dealing with new invasions or existing populations of the three species should be considered simultaneously. Indeed, controlling one of these species only could favor the establishment of the others (Russel et al. 2014).

Our modeling also highlighted potential shifts in the future distributions of the red-vented bulbul and the CM on the Arabic Peninsula. Our predication of declining climate suitability there is consistent with recent findings of Thibault et al. (2017). That review reports an absence of monitoring and management programs for the red-vented bulbul in several countries of the Peninsula (UAS, Qatar, Oman), with population trends being considered either 'steady' or 'declining'. This reinforces the need to consider climate as a key factor driving bird

distributions at a global scale (Barbet-Massin and Jetz 2014; Stephens et al. 2016). Indeed, climate could have contributed to spontaneous declines that have been observed in 68 exotic bird populations in Hawaii, Puerto Rico, Los Angeles and Miami (Aagaard and Lockwood 2016).

Our assessment of invasion risk for the three species relies on climate variables only. However, we know that other factors such as propagule pressure or tolerance to urbanization can also be key factors that influence establishment probabilities for invasive species (Blackburn et al. 2015; Møller et al. 2015). Our predictions could thus likely be improved and refined by considering such additional factors. However, it remains very difficult to determine a hierarchy between these factors (Moulton and Cropper 2015). At a global-scale, predictions of species' distributions could be improved through consideration of global trade routes (Carrete and Tella 2008) or country-scale biosecurity policies (Simberloff et al. 2013). At a smaller scale, including land areas the size of tropical islands, consideration of demographic variables (Zurell et al. 2016), habitat factors (Barbet-Massin et al. 2013), or resources availability associated with local species diversity (Tilman 2004) could improve assessment of suitable areas for novel invaders (Alexander et al. 2017).

Bird trade is suspected to have played a key role in exotic bird invasions (Carrete and Tella 2008), and a recent study highlighted the effectiveness of a regional trade ban on the risk of invasion by birds, particularly passerines (Reino et al. 2017). An historic and on-going bird trade market in the Middle East has likely contributed to the establishment of the CM and the red-vented bulbul in this area (Soorae et al. 2008; Eid et al. 2011). Preventing future introduction events at the local scale is still the most efficient way to minimize the dispersal of invasive species and their associated harmful impacts (Edelaar and Tella 2012; Simberloff et al. 2013). This is particularly true in tropical archipelagos where the climate is particularly

suitable for our three focal species and where short-distances between islands could aid the dispersal of newly established populations (Gillespie et al. 2012). Small territories like islands and archipelagos could benefit from regional collaboration in the management of invasive species. Development of policies at regional scales is likely to favor knowledge sharing, wide scale sensitization, fund raising, wide scale sensitization, and action efficiency (Latombe et al. 2017).

Long-term biosecurity operations successfully prevented the establishment of the red-vented bulbul in New Zealand (Turbott 1956). In 1954, two years after the first sighting, a dedicated committee was created under governmental supervision. Public awareness campaigns, coupled with the systematic shooting of sighted bulbuls, eliminated them from Auckland during 1955 (Watling 1978). The red-vented bulbul was detected and eradicated again in 2006 and 2013, thanks to a combination of biosecurity and rapid reaction programs coupled with the offering of a substantial reward for killed bulbuls. The last wild red-vented bulbul was killed in New Zealand in May 2016, and a phone line dedicated to new sightings is still available (Ministry of Primary Industries 2017). This example shows that preventing bird invasions early is possible through a collaborative network of monitoring and control strategies and continuous vigilance. Considering management of established populations, Saavedra (2013) used trapping, poisoning and shooting as methods of control for the red-vented bulbul and the CM in Tahiti and, through doing so, successfully increased the reproductive outputs of the Tahiti Monarch. Recent eradications of the RWB (Bunbury et al. 2013) and the CM (Canning 2011; Beaver and Mougal 2009) in the Seychelles confirmed the feasibility of management programs and provided feedback for further action against these species (DIISE 2015). Rapid investment, long term funding and support of local people are necessary for such programs to be efficient (Mack et al. 2000). However, the delay between alien species introduction and

first reported impacts (Simberloff et al. 2013; Aagaard and Lockwood 2014), and persistent criticism that compared the prevention of alien species introductions to xenophobia, certainly did not promote strong biosecurity responses from managers (Ricciardi et al. 2017).

Conclusion

We used a common species distribution modeling technique to explore potential overlap of the climate suitability for three highly invasive bird species from the Indian sub-continent. We describe the world climatic suitable distributions of the red-vented bulbul, the red-whiskered bulbul and the common myna, and highlight macro areas that could be at high risk of establishment of these invasive species. Projected areas of climate suitability for these three species are concentrated in coastal locations with equatorial climates. Islands with such climate appear to be highly suitable for the establishment of these species and this would precipitate major conservation issues. In the short term, the three species could establish simultaneously in several islands of the Indian and Pacific Oceans. Our results show that forecast climate changes through to 2050 could increase the overlap in the distribution of these birds, and favor multi-invasions in at least four macro-areas. By 2050, our projections highlight significant increases in climate suitability in three uninvaded areas that could strengthen existing climatic pathways to South America, Western Africa and the Caribbean. Finally, climate is expected to remain suitable in most of the species' current ranges through until 2050 with exceptions being the Middle East and semiarid regions of West Africa and north Australia where climate is expected to become less suitable. In light of these predictions, there is an urgent need to study the invasion dynamics and impacts of the red-vented bulbul, RWB and CM, and to development innovative management techniques for all three species, especially on islands (Ackerman et al. 2017; Patiño et al. 2017; Stanbury et al. 2017; Thibault et al. 2017).

## Acknowledgements

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# Appendices

**Appendix Table S1** List of the 75 island territories located between 50°N and 50°S, their current degree of invasion and current suitability for the three species. red-vented bulbul= red-vented bulbul; RWB= red-whiskered bulbul; CM= Common myna. The three columns headed with the species name abbreviations indicate whether the species is already present in the territory or not.

| Insular Countries | Current status | Established | RVB | RWB | CM | Suitability | Suitable species |
|---|---|---|---|---|---|---|---|
| American Samoa | multi-invaded | 2 | x | | x | 1 | RVB |
| Anguilla | free | 0 | | | | 3 | RVB + RWB + CM |
| Antigua and Barbuda | free | 0 | | | | 3 | RVB + RWB + CM |
| Aruba | free | 0 | | | | 1 | CM |
| Bahamas | free | 0 | | | | 3 | RVB + RWB + CM |
| Barbados | free | 0 | | | | 0 | |
| Bermuda | free | 0 | | | | 3 | RVB + RWB + CM |
| British Indian Ocean Territory | Invaded | 1 | | | x | 3 | RVB + RWB + CM |
| British Virgin Islands | free | 0 | | | | 3 | RVB + RWB + CM |
| Cayman Islands | free | 0 | | | | 3 | RVB + RWB + CM |
| Christmas Island | free | 0 | | | | 3 | RVB + RWB + CM |
| Cocos (Keeling) Islands | free | 0 | | | | 2 | RVB + CM |
| Comoros | Invaded | 1 | | | x | 3 | RVB + RWB + CM |
| Cook Islands | Invaded | 1 | | | x | 3 | RVB + RWB + CM |
| Cuba | free | 0 | | | | 3 | RVB + RWB + CM |
| Cyprus | free | 0 | | | | 3 | RVB + RWB + CM |
| Dominica | free | 0 | | | | 1 | RVB |
| Dominican Republic | free | 0 | | | | 3 | RVB + RWB + CM |
| Fiji | multi-invaded | 2 | x | | x | 3 | RVB + RWB + CM |
| French Polynesia | multi-invaded | 2 | x | | x | 3 | RVB + RWB + CM |
| Greece | free | 0 | | | | 3 | RVB + RWB + CM |
| Grenada | free | 0 | | | | 0 | |
| Guadeloupe | free | 0 | | | | 3 | RVB + RWB + CM |
| Guam | free | 0 | | | | 2 | RVB + CM |

| | | | | | | |
|---|---|---|---|---|---|---|
| Guernsey | free | 0 | | | 1 | CM |
| Haiti | free | 0 | | | 3 | RVB + RWB + CM |
| Indonesia | Invaded | 1 | | x | 3 | RVB + RWB + CM |
| Isle of Man | free | 0 | | | 0 | |
| Jamaica | free | 0 | | | 3 | RVB + RWB + CM |
| Japan | Invaded | 1 | | x | 3 | RVB + RWB + CM |
| Jersey | free | 0 | | | 1 | CM |
| Madagascar | free | 0 | | | 3 | RVB + RWB + CM |
| Maldives | Invaded | 1 | | x | 3 | RVB + RWB + CM |
| Malta | free | 0 | | | 1 | CM |
| Martinique | free | 0 | | | 2 | RVB + CM |
| Mauritius | multi-invaded | 2 | x | x | 3 | RVB + RWB + CM |
| Mayotte | Invaded | 1 | | x | 3 | RVB + RWB + CM |
| Micronesia, Federated States of | free | 0 | | | 0 | |
| Nauru | free | 0 | | | 0 | |
| Netherlands Antilles | free | 0 | | | 2 | RVB + CM |
| New Caledonia | multi-invaded | 2 | x | x | 3 | RVB + RWB + CM |
| New Zealand | Invaded | 1 | | x | 2 | RWB + CM |
| Niue | free | 0 | | | 3 | RVB + RWB + CM |
| Norfolk Island | free | 0 | | | 2 | RVB + CM |
| Northern Mariana Islands | free | 0 | | | 3 | RVB + RWB + CM |
| Palau | free | 0 | | | 0 | |
| Papua New Guinea | free | 0 | | | 3 | RVB + RWB + CM |
| Philippines | free | 0 | | | 3 | RVB + RWB + CM |
| Puerto Rico | free | 0 | | | 1 | CM |
| Reunion | multi-invaded | 2 | x | x | 3 | RVB + RWB + CM |
| Saint Barthelemy | free | 0 | | | 3 | RVB + RWB + CM |
| Saint Helena | Invaded | 1 | | x | 0 | |
| Saint Kitts and Nevis | free | 0 | | | 3 | RVB + RWB + CM |
| Saint Lucia | free | 0 | | | 2 | RVB + CM |
| Saint Martin | free | 0 | | | 3 | RVB + RWB + CM |
| Saint Pierre and Miquelon | free | 0 | | | 0 | |
| Saint Vincent and the Grenadines | free | 0 | | | 1 | RVB |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Samoa | Invaded | 1 | x | | | 2 | RVB + CM |
| Sao Tome and Principe | free | 0 | | | | 3 | RVB + RWB + CM |
| Seychelles | multi-invaded | 2 | | x | x | 3 | RVB + RWB + CM |
| Solomon Islands | Invaded | 1 | | | x | 1 | RVB |
| Sri Lanka | Native | 2 | x | | x | 3 | RVB + RWB + CM |
| Taiwan | multi-invaded | 2 | | x | x | 3 | RVB + RWB + CM |
| Timor-Leste | free | 0 | | | | 3 | RVB + RWB + CM |
| Tonga | Invaded | 1 | x | | | 3 | RVB + RWB + CM |
| Trinidad and Tobago | free | 0 | | | | 0 | |
| Turks and Caicos Islands | free | 0 | | | | 3 | RVB + RWB + CM |
| Tuvalu | free | 0 | | | | 0 | |
| United States Minor Outlying Islands | Invaded | 1 | | | x | 3 | RVB + RWB + CM |
| United States Virgin Islands | free | 0 | | | | 3 | RVB + RWB + CM |
| Vanuatu | Invaded | 1 | | | x | 3 | RVB + RWB + CM |
| Wallis and Futuna Islands | Invaded | 1 | | | x | 1 | RVB |
| Tokelau | free | 0 | | | | NA | |
| Pitcairn Islands | free | 0 | | | | NA | |
| Marshall Islands | Invaded | 1 | x | | | NA | |

# CHAPTER 7: Synthesis

## Synthesis

## Introduction

The red-vented bulbul was first observed in Nouméa, New Caledonia, in the 1980s but no national management strategy has yet been developed. Concerns about the negative effects of this species on crops and native flora and fauna outside its native range are widely publicised internationally, and the establishment and expansion of this invasive species in an archipelago that is listed as a world biodiversity hotspot is deeply concerning. The first public notifications about the potential impacts of this species were released in the early 2000s following concern over the species' range expansion in the south province.

In November 2009, a management method inspired by the example of red-whiskered bulbul control in La Réunion, was suggested to reduce the increasing levels of crop damage (mainly to red fruit crops) reported by farmers and other locals. The method consisted of using magpie-type traps and decoys to capture bulbuls. A dedicated group was established in 2010 to discuss and find solutions to the increasing range expansion of the species and its early impacts on agricultural outputs. The group remained inactive for several years. In October 2011, the invasion by the red-vented bulbul became a research priority for the two New Caledonian government institutions in charge of environment and agriculture but they failed to agree on a strategy. In 2012, the New Caledonian Institute for Agriculture (IAC) took the initiative and established a dedicated committee with representation from both the agriculture and environment departments and finally launched a research program that included support for the research presented in this thesis.

Meanwhile, New Zealand eradicated the species three times (1955, 2006 and 2013) thanks to a combination of early detection, sensitization and systematic shooting coordinated by a dedicated committee hosted by the Ministry of Primary industries (Ministry of Primary Industries 2017). In French Polynesia, depletion of the endemic Tahiti monarch (*Pomarea nigra*), partly due to competition with invasive bird species, justified implementation of an experimental management program against the red-vented bulbul and the common myna. This proved to be successful locally, with the reproductive success of the monarch subsequently increasing (Blanvillain et al. 2003; Saavedra 2013). The extremely slow reaction to this in New Caledonia could be partly explained by the need for environment and agriculture managers and decision makers to wait for quantifiable impacts before investing in the management of an introduced species; akin to "presumption of innocence" in a legal context.

In this thesis, I tried to draw a portrait of an introduced species under range expansion in a tropical island hotspot of biodiversity.  To do so, I focused on the ecology of the species rather than describing its biology, which was described in some detail by Dick Watling forty years ago in Fiji. Using the available knowledge, developing both local and international collaborations, and performing several experiments, I explored the early-stage effects of red-vented bulbul invasion on crops, weeds, and native flora and fauna. This final chapter of my dissertation summarizes the key findings of my work, identifying limitations, and implications for management of the species at both the local scale and more broadly. I finish with suggestions for future research that could contribute to a better understanding of the mechanisms that underlie the impacts of this species, and that could shape management strategies for the red-vented bulbul in New Caledonia and elsewhere.

## Empirical findings

**The red-vented bulbul is so understudied that it cannot, at this time, absolutely be considered a pest**

The literature review set the foundation for the thesis in helping to determine the shape and foci of the other chapters. An important outcome from the review was an updated world distribution map for the red-vented bulbul. While the bulbul's native range was known, the introduced range of the species had never been reported in detail before (Birdlife International and handbook of the birds of the world 2016; GISD 2018).

From the literature, I identified three categories of impact associated with the red-vented bulbul in its alien range: damage to plants, seed dispersal, and impacts on native fauna. This assessment shaped the design of the experiments presented in the Chapters 3, 4 and 5, with one chapter dedicated to each impact category. I used published reports to produce a small database of 52 plant species consumed by the red-vented bulbul, and I reported whether consumption of each species was known to cause economic losses or seed dispersal. I listed examples of potential positive effects from the arrival of this species in new ecosystems that could, to some degree, potentially counterbalance some negative effects as discussed.

Finally, I reported all the management methods that have been trialled against the red-vented bulbul. A major finding of this first chapter was identification of the discrepancy that exists between the status of the red-vented bulbul and the attention paid by scientists and managers to this species in its alien range, resulting in the poor number of references found in comparison to other species. Island territories host very rich and original biodiversities (Warren et al. 2015), and developing island states are often characterized by a kind of

economic "vulnerability" (Briguglio 1995). Therefore, prioritization and strategic investment in the management of introduced species in these territories should rely on concrete assessments of their impacts and underlying ecological mechanisms. The lack of such scientific assessment could contribute to the rarity of programs dedicated to the management of red-vented bulbul, as managers often need observable impacts or concrete assessments to allocate financial supports in the management of a species (Mack et al. 2000). Moreover, controlling the efficiency of a management program relies on knowledge of both the demographic status of the target species and the extent of its economic or environmental impacts. Based on these findings, I chose to dedicate the following chapter to the production of data on the red-vented population in New Caledonia, from demographic traits to early estimates of the most publicised impact category on plant productions.

**The introduced population of red-vented bulbuls in New Caledonia is currently expanding along urban corridors**

The second chapter allowed the production of an updated invasion map. The map presented there highlights the current "continuous" distribution range of the bulbul, its evolution from 2008, and testimonies from many local people about sightings of this bird. Moreover, this geographical representation of the New Caledonian population of red-vented bulbul was accompanied by three key findings.

First, the species is currently restricted to inhabited areas and is suspected to use urban corridors as major dispersal pathways. This assessment was made from three complementary approaches including the dedicated monitoring at the edge of the distribution, data from the

temporal monitoring of terrestrial birds of New Caledonia (STOT-NC) and a survey conducted at frontiers between occupied areas and natural forests.

Second, there is an important density gradient in the population from Nouméa (historical introduction) and rural habitats at the edge of the distribution. Red-vented bulbul are extremely abundant in Nouméa (>200 ind/km$^2$) and present in much lower densities (30 ind/km$^2$) 50 km away. Together with these estimates of bird densities at different distances from Nouméa, a detection probability curve is presented for the red-vented bulbul in inhabited contexts. This curve shows that the probability of detecting a red-vented bulbul falls to 50% when the individual is 25 meters from the observer.

Third, the compilation of past monitoring session with the ones I conducted in 2014 and 2016 suggested that the dispersal of red-vented bulbuls toward the north of the mainland is accelerating.

## Damages on crops could be important, and result in substantial economic losses

The production of quantitative assessments of the threats from the red-vented bulbul population on human activities and on the biodiversity of New Caledonia was the second main objective of my thesis. As one of the conclusions from the Chapter 1 was the relationship between the diet of the red-vented bulbul and its recorded impacts, I started this assessment by compiling a list of food items that have been reported for the bulbuls in New Caledonia. From my assessment of results of published studies and observations and testimonials from local people, I hypothesised that they appeared to prefer red-coloured fruits. I confirmed this using an *ex-situ* experiment and analysis of the gut contents of birds that had been shot. This

preference for red fruits is quite common in tropical fruit-eating birds from central Asia (Stanley et al. 2002; Duan et al. 2014), and was useful to help identify fruit species that might be more sensitive to consumption by introduced red-vented bulbuls.

I thus searched for a red fruit species that was grown commercially within the current red-vented bulbul's range and for which losses caused by bird damage could be evaluated. Tomato was the ideal model species and an open-field experiment was set-up in a suburb of Nouméa. It revealed that red-vented bulbuls can damage up to 17% of tomatoes produced under classical harvesting conditions. Extrapolating to the total tomato production recorded in New Caledonia for September 2016 alone, such damage would correspond to an economic loss of approximately NZD $25,250.

## The red-vented bulbul is a short-distance seed disperser that prefers introduced fruits

The gut contents analysis confirmed the preference for reddish fruits. One key finding from this work was the very close association between the red-vented bulbul and a community of introduced plant species using fleshy fruits as diaspore (80% of identified fruit species). From the list of consumed species identified in the gut of 139 red-vented bulbuls, I selected four species to estimate a median Gut Passage Time that was of approx. 30 minutes for single-seeded fruits and 14-41 minutes for many-seeded fruits. These times corresponds to dispersal distances of 92m and 70-92m respectively, based on data I collected on the movement characteristics of the bulbuls.

A second key finding arose from the germination tests of seeds that were digested by red-vented bulbuls compared to control seeds. Results of this experiment suggest that the passage

though the gut of red-vented bulbuls lowers the rate and speed of germination of the endemic *Myrtastrum rufopunctatum*, a plant that grows on the ultramafic maquis and that is used for habitat restoration purposes. Conversely, germination rate and speed of digested seeds of the highly invasive *Schinus terebinthifolius* were almost identical compared to fruits from which the epicarp had been removed, implying an enhancement of both the germination rate and speed after digestion by the invasive bird. As discussed in the Chapter 5, this could represent an example of "invasional meltdown" that can lead to major conservation issues in the ultramafic maquis of New Caledonia (Simberloff and Von Holle 1999).

## The red-vented bulbul outcompetes native birds, without endangering their populations

The third impact category identified in the Chapter 1 was the impacts on native fauna. As most of the reports I found in the literature concerned competitive interactions with native bird species, I decided to test this hypothesis. To do so, I contacted the Caledonian Society of Ornithology and offered them to share our point count data to test the hypothesis. Of the 15 candidate species present in inhabited habitats that I tested, nine native species were significantly less abundant at locations where the red-vented bulbul was present. None of the three introduced species presented the same pattern.

I also tried to explain the abundance of four native species with both environmental and biotic parameters. My models suggest that the abundance of the red-vented bulbul significantly contributed to explain the lowest abundances of these four species (Grey Fantail, Silvereye sp., Rufous whistler and Rainbow lorikeet). However, when I looked at the mean abundance of these native bird species in inhabited habitats, I found no decrease over time.

Thereby, this piece of work led to two key findings. First, when established in inhabited areas, the red-vented bulbul outcompetes most native bird species that, therefore, become less abundant. Results of linear models suggest that the abundance of red-vented bulbuls contributes to this effect. On the other hand, the temporal population trends did not indicate any depletion of these native species in man-modified habitats. Thereby, I suggest that this observation could apply to the niche reduction hypothesis, with competition with the red-vented bulbul leading to a reassembly of some native bird species along an urban-rural gradient (Scheele et al. 2017).

## Climate in 56 islands territories is favourable to the Red-vented bulbul

To efficiently prevent dispersal of the red-vented bulbul at a global scale, modelling the potential global distribution of the species is important. That is what I aimed to do in the final chapter of this thesis, using current climate parameters and climate change scenarios from the latest IPCC assessment report (IPCC, 2014). According to their close phylogeny, their similar native distribution range, somewhat overlapping alien ranges, their transportation as cage birds and their status of invasive, the red-vented bulbul, the red-whiskered bulbul and the common myna share several key characteristics. This is partly why Kumschick et al. (2016) suggested that a significant overlap exists in the extent and consideration of impacts from the red-vented bulbul and the common myna.

Based on these observations, I decided to model the potential global distributions of the three species together to identify priority locations for consideration of the invasion risk posed by these species. The main finding from the use of current climatic factors was the high climate

suitability of 44 islands (out of 75 islands tested), located between 50°N and 50°S, for establishment of the three species. Combining the climatic suitability of the three species, results identified five macro-areas of high invasion "risk": the South West of the Pacific Ocean; the South West of the Indian Ocean; the Guinea gulf; South America; and the Caribbean Sea.

The application of climate change scenarios to these models provided interesting estimates of the potential evolution of the global distribution of the red-vented bulbul and the two other species. Results suggest an increase of the overlap in the distribution of these birds is likely, favoring multi-invasions in at least four macro-areas. Except for the Middle-East and semiarid regions of West Africa and north Australia where climate is expected to become less suitable, projections out to 2050 suggest that climate will remain suitable in most of the species' current ranges. Areas suitable for the three species could even increase in continental areas and at three locations that could represent invasion pathways to South America, the Caribbean and Western Africa

## Limitations of the study

### Number of publications depends on country size

Reviewing the knowledge associated with an invasive species provides a useful overview of both its impacts and the way it is managed in its alien range (Linz et al. 2007). However, reviews are based on the synthesis of published data, leading to potential biases in access to information. A significant part of the information collected here (≈ 25%) did not came from academic journals, and information found only in magazines and project reports suggests that more information could have been missed in this 'grey literature'. Another potential bias could

be a geographic one, as I failed to find any published references for some countries within the alien range of the red-vented bulbul. This lack of published information for some locations is likely explained by the country's size, its population size, and its governance and wealth (Meijaard et al. 2015; Clarke et al. 2017). To avoid this bias and collect as much information as possible, I made direct contact with the environment managers and ornithologists of those countries.

## Potential bias from roadside sampling

One big question regarding the current dispersal of the red-vented bulbul in New Caledonia is the capacity of the species to establish in natural habitats such as dry or wet forests. Indeed, examples from Tahiti (French Polynesia) revealed that the species was present in native forests and at high elevations, and posing a threat to native avifauna (Blanvillain et al. 2003). The monitoring of the expanding distribution of the red-vented bulbul allowed production of the map presented in the Chapter 3. However, looking at this map, one might think that the assessment of the distribution could be biased by the location of sampling sites along roads, a common issue in bird surveys (Harris and Haskell 2007). One bias associated with bird surveys along roads is the range of different habitats that are sampled, with roads being mostly built in urban/suburban habitats. In this study, I believe that this bias is not of significant importance for at least three reasons. First, the survey was focused on a single species rather than on the whole bird community, and the geographic area occupied by this species is mainly covered by inhabited areas. Second, six sampling routes were monitored at frontiers between inhabited areas and forests to control for this potential bias. This sampling targeted forest patches near areas where the species was present at high density, and which

are thus more likely to be invaded. Finally, I confirmed my assessment through comparison with data collected during the temporal monitoring of the terrestrial birds of New Caledonia inititiative. This database includes 23 sampling points in natural forests that are located less than 30 km away from the center of Nouméa. Only one bulbul has been observed at one point, at the edge of a dry forest patch in a peninsula of Nouméa, next to the garden of a house where fruits are growing. Thereby, I am confident with this assessment at this stage of the invasion.

## Impacts of native birds on crops are unknown.

Resources for this study were limited in both time and people, so I was not able to control for the total absence of native birds feeding on tomatoes during the open-field experiment. Two technicians plus a trainee oversaw the experiment, and they all reported that the red-vented bulbul was the only bird species they saw feeding on tomatoes. I decided to accept this approximation because bulbuls were expected to be very attracted by ripe tomatoes and known to defend its resource aggressively from other fruit-eating birds (Sherman and Fall 2010). Further, I conducted 10 minutes point counts around the crop and counted only red-vented bulbuls myself. At a local scale, important bird damage to fruits is exclusively attributed to red-vented bulbuls (Metzdorf and Brescia 2008; Caplong and Barjon 2010), and personal communications collected at IAC reported groups of red-vented bulbuls destroying crops, including even some growing within greenhouses.  However, even if no other species of bird fed on our tomatoes, no data are available on the damage caused to crops by other species of fruit-eating birds that could be used in comparisons with our findings for red-vented bulbuls. Thanks to their strong beak, red-vented bulbuls can peck hard-skinned fruits. This capacity

could enhance damage from other bird species that could get access to fruit-flesh through the aperture made by red-vented bulbuls. Silvereye birds, for example, are fruit-eating birds that also prefer reddish fruits and can contribute to crop damage (Duan et al. 2013).

## The dark side of participative data collection

Description of the diet of red-vented bulbuls in New Caledonia relied on both field observations and gut content analysis. The first method is very useful for a qualitative description of the diet (Galetti and Pizzo 1996), while gut content analysis allows for quantitative assessments through the calculation of frequencies of consumption (Pietersen and Symes 2010). As many field observations of feeding red-vented bulbul had been done previously in New Caledonia (Thouzeau-Fonseca 2013), I wanted to produce quantitative data on this diet. Rather than analysing regurgitations (Lopes et al. 2013) or droppings (Spotswood et al. 2012) of birds, and because the red-vented bulbul is considered an invasive species, I chose dissections in laboratory as my preferred method. The choice of this method relied on the collection of red-vented bulbul cadavers, so I suggested a collaboration with the local hunting federation combined with advertisments in local newspapers and relevant websites for a "call for participation" (**Appendix 1**). This participative initiative was successful as I collected approx. 140 cadavers. However, nearly 70% of these came from three locations (in the suburbs of Nouméa), and were shot predominantly during two periods that corresponded to the two peaks of activity in the birds' annual reproductive cycle (Jan-Fev and Jun-Aug). Because of the variability in location and season, only limited evaluation of seasonal and spatial variation in the diet was possible. However, the amount of data collected allowed an overview of the diet of the red-vented bulbul throughout a year.

Impact on native birds might change as invasion progresses

The in-progress invasion by the red-vented bulbul offered a unique opportunity to assess the effects this invasion was having on native avifauna, but it also presented some challenges. As the species is present almost exclusively in inhabited areas in the Southern Province, the dataset was limited. Furthermore, data were not available from before the establishment of the red-vented bulbul in Nouméa and its Northward dispersal. In order to avoid spatial autocorrelation, I focused the analysis on a subset of the data that included inhabited habitats only. To compare the mean abundance of other species in the presence and absence of the red-vented bulbul, I chose to use the the restricted distribution of red-vented bulbuls as a temporal surrogate. This decision has implications for what can be concluded from this study. First, impacts presented in the Chapter 4 could change as the invasion progressed. Elsewhere, it has been shown that some drastic changes can happen in populations of introduced birds for potentially decades after invasion of a territory (Aagaard and Lockwood 2016). Resilience in native bird species, for example, could reverse the competition relationship when naïve native species adapt to the invader (Strauss et al. 2006). In the context of a reassembly of native species along an urban-rural gradient, the spread of the red-vented bulbul in different habitats, or its increase in density in rural habitat, could induce evolutionary and/or behavioural pressures on native bird species. Second, direct effects of the establishment of red-vented bulbul in newly invaded locations should be monitored to describe the competition mechanisms more precisely.

### Distribution modelling and local forecasting

When I started thinking about modelling the potential global distribution of the red-vented bulbul, I thought about applying those same techniques at the local scale of the New Caledonian Archipelago. Such techniques are now used to anticipate the distribution of invasive organisms at national scales (Fournier et al. 2017). However, such forecasting applied to the red-vented bulbul population in New Caledonia did not make sense for several reasons. First, the current expansion of the species' distribution is mostly restricted to inhabited areas. Using this distribution in the Species Distribution Modelling framework would have produced high vulnerability predictions for cities and villages without any real interest for local-scale management. Because of potential biotic interactions and the current absence of red-vented bulbuls from natural forests, it is very difficult to anticipate the future distribution of the invader based on examples from other countries. Finally, at a local scale, climatic gradients may not be strong enough to shape the distribution of the red-vented bulbul.

## Management implications

### From ornament bird to noxious invader

The review of the literature provided a more detailed assessment of the species than that portrayed by either its IUCN status or the local-scale public view, and resulted in the publication and dissemination to local communities of a summary information sheet by IAC together as well as placement of a news article in the main newspaper (**Appendices 2, 3**). Lists of plant and animal species that are already known to be affected by invasive red-vented bulbuls could be used in New Caledonia to identify locations, crops or species that may be

particularly sensitive to red-vented bulbuls. Finally, the literature review helped to place the present project in the regional context of invasive species on Pacific islands and provided opportunities to develop collaboration with the wider scientific community involved in projects dealing with the red-vented bulbul (e.g. in French Polynesia and Fiji).

## The bright side of participative data collection

Some of the results and descriptive data presented in Chapter 2 contributed directly to the development of a management strategy for the red-vented bulbul in New Caledonia. First, the collaboration that I initiated with the local hunting federation while attempting to collect bulbul cadavers has endured over time. Several local hunters were identified during that study who were very sensitive to the attention paid to this invasive species. The collaboration was efficient on both sides, with both television and newspaper coverage of this collaboration (**Appendix 3**). An easy decision was made to include the hunting federation in the Technical Group dedicated to the red-vented bulbul.  Meanwhile, a red-vented bulbul was located at "La Foa", the current northern edge of their distribution. I went there to conduct several point counts and detected a couple of individuals near the IAC campus where the reports had originated. I reported the information and after several discussions, the hunting federation was requested by the Southern Province (service of environment) to visit the area and to kill the birds. Our team provided the hunters with mp3 recordings of bulbul calls that they used to attract the birds and both of the two red-vented bulbuls were shot. This was the very first official control action organized in New Caledonia against the red-vented bulbul. Following this, a collaboration was established between several institutions to implement a "quick reaction" protocol that aims to locate and shoot red-vented bulbuls that are observed near or

beyond the current edge of the continuous distribution range. The distribution map presented

in Chapter 2 provides the basis for this protocol. A 'hot line' phone number was set up and

advertised to encourage community input for sightings of red-vented bulbuls beyond their

range as presented in the map. The local Conservatory for Natural Spaces (CEN) is in charge

of collecting reports. When a person calls, they are asked for the location of the bird. If this

falls outside of the known distribution range, the Hunting Federation is called and replicates

the method presented above. In every case, the person is asked to fill in a standardized form

and an information sheet is send to them that contains a summary of the information

presented in Chapter 1. A similar approach, accompanied with a substantial reward, allowed

the New Zealand Ministry of Primary Industries to eradicate introduced red-vented bulbuls on

several occsions from that country (Turbott 1978; Ministry of Primary Industries 2017).

Involvment of local people is crucial to the success of any attempt to manage an invasive

animal species, and particularly a bird species that favours urban habitats. Thereby, collection

from local people on bulbul sightings and their impacts on flora and fauna from should

continue in New Caledonia as part of an early detection protocol.


## Call for a territory-scale management strategy

Data provided on the population density, dispersal speed, occupation of habitat and impacts

will shape development of a wider, territory-scale, management strategy for this species.

During my PhD, the red-vented bulbul was included in a list of seven priority invasive species

that should be managed in New Caledonia. This list is a starting point to convince public

institutions of the urgent need to invest in the management of these invasive species. Efficient

and effective methods to control red-vented bulbul populations have been identified by

earlier programs, and a combination of shooting, poisoning and trapping is certainly the most efficient control strategy (Saavedra 2012; 2013). However, implementation of such a strategy relies on i) clear objectives, ii) substantial resources, and iii) background data against which the success of control efforts can be assessed (Mack et al. 2000).

This dissertation has presented a synthesis of the main impacts associated with the red-vented bulbul in its alien range, offering a basis to define a management objective. Each of the three-impact category was assessed locally and results were presented in the Chapters 3, 4 and 5. I found that consumption of reddish fruits could lead to substantial economic losses for producers. Thereby, security of crop production could be the objective of a management strategy. My experiment demonstrated the usefulness of protecting plants with bird nets. However, covering large crops with bird nets may not be technically feasible or may be too expensive, and direct control of red-vented bulbuls through trapping, shooting or poisoning may be a better solution. Direct control of birds at sensitive sites may be another management objective. Effort should focus on controlling red-vented bulbuls close to areas occupied by key endemic bird species (e.g. *Myzomela caledonica*), endemic insect species (e.g. cicadas) or highly invasive plant species (e.g. *Miconia calvescens*). Another objective should be to prevent dispersal of the red-vented bulbuls to of the mainland. These examples are all associated with controlling red-vented bulbul at specific locations, but one could think about the full eradication of the species from the mainland.

Thanks to the data I produced, we can estimate a minimum population size of approx. 150,000 red-vented bulbuls distributed over almost 1,500 km$^2$. Considering that these birds are concentrated in urban habitats (180,000 people in Nouméa and suburbs), a complete eradication of the species would be the first attempt at eradicating a species on this scale and

would require intense investment from managers and considerable financial commitment; as a result, it is thus very unlikely to be implemented. The largest successful eradication program against an invasive bird species occurred on Isabela Island (Galapagos). This is a 4,739 km$^2$ island with a population of fewer than 10,000 people. Hunting was the primary method of eradication for the rock Dove (*Columba livia*). Apart from this example, only three eradications have been successful on islands larger than 1,000 km$^2$ with more than 10,000 people (DIISE 2015). Implementation of a smaller-scale trial eradication would be the most efficient way to assess the feasibility of a full-scale operation and its likely benefit for native avifauna. A cost/benefit analysis as presented by Daignealt & Brown in Fiji (2013) should be conducted with inclusion of an assessment of the benefits of involvement of local people. Meanwhile, confinement of the existing population within its current distribution range through use of the outlined early detection/shooting protocol is crucial. In parallel, quantitative assessments of impacts on other plant and animal species should be undertaken to better define the potential benefits and risks associated with a large-scale management action.

## What choice regarding control methods?

In New Caledonia, poisoning is widely used to control invasive species such as rodents on islets, but not against birds because of the rich local avifauna (Barré et al. 2009). The non-selectivity of most poisons would pose a risk for non-targeted species that is not acceptable. Conversely, hunting is popular throughout the archipelago and we saw that a collaborative and participative management approach could be developed that could constitute a part of a management strategy. A major constraint to this method is the current distribution of the red-vented bulbul in inhabited areas, where shooting is forbidden. This explains why current

control actions are conducted in rural areas at the edge of the distribution range. I think that partnership with the local hunting federation provides surety that weapons are used safely, and their involvement should be increased in efforts to restrict further dispersal of the red-vented bulbul toward the north and south of the mainland. Trapping is also a viable method for control as traps can be set safely in urban areas, villages, and forests. Previous research (Thouzeau-Fonseca 2013) has demonstrated the usefulness of the use of decoy birds associated with baits in trapping red-vented bulbuls. Results of Chapter 3 confirmed that reddish fruit baits might attract red-vented bulbul efficiently. The trapping method should vary according to the context. In areas where intensive local trapping is needed (nearby sensitive area, extensive crop productions), aviary-type traps would probably be the most useful, allowing for multiple bird capture with minimal servicing of each trap. At locations where a light and movable trap is needed (invasion front, control in cities), magpie-type traps would be better. The use of a decoy bird is essential to enhance trapping success but should be avoided when trapping birds at the edge of the distribution range to prevent any accidental release. Finally, trapping success will vary seasonally, with trapping success being highest when birds are searching for partners (spring) and when juveniles form flocks (late summer).

Regardless of the chosen control method, the usefulness of a management strategy partly relies on the capacity to monitor and evaluate its efficiency. The data provided in Chapter 3 addressed this objective. Estimation of the bird abundance and density before and after the implementation of a management action would remain the easiest way to evaluate the action's efficiency.

## Theoretical implications

### Literature review: both status overview and feedback on prioritization

As presented in Chapter 1, the red-vented bulbul illustrates perfectly the weakness highlighted by Kumschick et al. (2015) in defining the priority status of invasive species. Beyond the opinions of experts, very few studies have assessed directly the impacts and threats from some invasive species. This presents challenges for managers at the local scale in deciding how much effort to dedicate to management of poorly quantified threats. The review paper produced the first overview of the invasion history, distribution, impacts and management of the red-vented bulbul, and I believe that this work will contribute to a better assessment of the species' status. Moreover, results of this review also contribute to assessment of the consequences of considering an invasive species an international priority in the face of limited data (**Appendix 4**). Despite the bulbul's status as a highly invasive species that could cause major impacts, quantitative assessments of its impacts were available at two locations only, and the species is still sold as a cage bird in the Middle East and Southwest Asia.

### Quantitative clues of harmfulness

The impact assessment presented in this dissertation provides quantitative data on early effects of introduced red-vented bulbuls on agricultural production, seed dispersal, and competition with other avifauna. To the best of my knowledge such assessment has been rare in the literature since the PhD of Dick Watling in Fiji (Watling 1977), and would be useful at

both local and global scales to define the risks associated with introduced red-vented bulbuls.

Quantitative data are crucial to compare impacts from several species, evaluate long-term threats, but also to communicate efficiently about invasive species. For example, estimations of economic losses are among the most powerful arguments to convince managers of the need of investing money on the management of an invasive species (Olsen 2006).

Combination of local harmfulness and geographical extent of threats

Modelling of the potential global distribution of the three highly invasive bird species considered in Chapter 6 offers a geographic view of the risk associated with these species. I think that such an approach is very complementary to the description of impacts themselves. Indeed, constructing maps of global hotspots of invasion risk helps identify territories that should be interested in the prevention of this invasion risk. Furthermore, consideration of the richness of the biodiversity at high-risk locations and the threats already acting on this biodiversity would improve determination of the true magnitude of threat posed by an invasive species. For the red-vented bulbuls, the high climatic suitability of island territories for its establishment suggests a very high risk from its dispersal, as discussed in Chapters 2 and 6. I believe that the approach I took in Chapter 6 of considering the impacts of global climate change on three invasive species simultaneously is unique and could be more widely applied, although the analysis would benefit from inclusion of additional environmental layers. Kumschick et al. (2016) highlighted a likely overlap in the impact of these species, so I guess that additive impacts are likely to be reported in multi-invaded areas. Such an approach would certainly be very informative if used in the determination of global hotspots of invasion risk.

## Collaborative and participative approach

Another theoretical insight from this work was the efficiency of a collaborative approach while studying an invasive species. Aiming for collaborative data collection serendipitously enabled me to build the foundation for collaborative management. The partnership with the local hunting federation was a remarkable success as it allowed increase in environmental awareness of an important community of people. It had a concrete impact through the systematic shooting of birds by volunteer hunters, and cadavers where of direct value to quantification of the diet of red-vented bulbuls in New Caledonia. Feedback on the results of this experiment was presented to the hunting federation. This strengthened the partnership and the involvement of hunters in this program. This collaboration was even the subject of a TV show in New Caledonia where I was a key invitee, and of a TV documentary that was broadcaste widely. Such communication tools are certainly among the most efficient, and media interest in such a successful collaboration between scientists and community groups is a powerful way to disseminate knowledge.

## Multidisciplinary study

Finally, there is one characteristic of this work that makes it original. I personally think that Invasion Ecology is not a research field in itself, but rather a combination of several research fields. This is what stimulated my interest the most, and what a tried to develop during my thesis; a multidisciplinary approach. In conducting the present work, I had to dig into the literature of invasion framework, population biology, agricultural production, animal behaviour, seed dispersal and recruitment, bird-plant interactions, inversional meltdown,

interspecific competition, insular syndrome, bird survey methods, participative science, species distribution modelling, climate scenarios, global changes, and management science. While limits to the validity of assessments based on the opinions of experts have been highlighted, I think that a multi-field approach is needed in order to better evaluate and prevent harmful effects of invasive species.

## Recommendations for future research

As in many situations, answering a few questions has given rise to many more hypotheses. Hereafter, here is a list of suggestions for future research related to the red-vented bulbul that would complement the findings presented in this dissertation.

### Complete the diet description

I decided to focus my description of the diet of the red-vented bulbul on plants consumed. I did this because the frugivorous part of the species' diet was the most reported source of impact in the literature. However, the red-vented bulbul is an opportunistic species, which is partly predator and has already been reported preying on some insects (Stimson and Berman 1990). From personal observations, I know that the red-vented bulbul can prey upon gecko and skink species. Insects and squamates are species rich in New Caledonia with high levels of endemism, and predation on some taxa could lead to conservation issues. As an example, one batch of red-vented bulbul gut samples contained remains of many cicadas, 100% of which are endemic to New Claedonia. Cicadas have a long reproduction cycle that could be sensitive to intense predation when reproductive adults emerge.  No skink or gecko remains were found in the gut content of red-vented bulbuls that were analysed, but personal observations

and testimonies of skink or lizard predation would justify a deeper exploration of predation on these animals by red-vented bulbuls.

Characterization of the diet of red-vented bulbuls would also benefit from a collection of more samples at specific locations. Particularly, a study could be dedicated to the characterisation of both seasonality and geographic patterns in the species' diet. Early analysis from the collected data suggested increased predation in late summer, while adults are raising young. This could be explained by protein needs of chicks and would provided valuable information in the seasonality of threats on fauna, but this hypothesis needs to be tested. Exploring the differences in the diet of adults and juveniles, as well as between sexes would help answer this hypothesis. A geographic pattern could also exist in the pressure on fruits or insects in New Caledonia, depending on habitat and soil composition. A more detailed description of such patterns could also contribute to a local mapping of threats, to a better anticipation of the species' dispersal, and to the development of an adapted management strategy.

Impacts on productions: going beyond tomatoes

In Chapter 3, I suggested an estimated cost from losses caused by red-vented bulbuls on tomato crops. Damage to fruit crops may be the most costly and visible impact from red-vented bulbuls at this stage of their invasion in New Caledonia. Lists of impacted fruit species were suggested (Caplong and Barjon 2010) on which estimation of losses could be conducted to attract the attention of environment managers. A focus could be made either on reddish fruit species or on species predominantly produced in the territory. Candidate species would include strawberry, mango, banana, papaya, and litchi. These species represented a

substantial part of fruit production in 2016 (D.A.V.A.R 2017). A collaborative collection of crop-loss data could be designed in partnership with producers.

In my trial, impacts from red-bented bulbuls was equivalent to that of all other losses caused by phytoparasites species. Replicatation of such a comparison applied to other plant crops will also contribute to a better appreciation of the extent of damage caused by red-vented bulbuls on fruit production. Another source of improvement would come from comparison between impacts induced by red-vented bulbuls versus other bird pests. For example, the western swamphen (*Porphyrio porphyrio*) is blamed for important losses on corn, banana and seedlings of several plants (Brun and Chazeau 1980). More generally, comparisons should be made with the effects of native fruit-eating species on both plant production and seed dispersal.

## Frugivory and seed dispersal: call for studies on the dispersal of native plant seeds

In many cases, frugivory leads to seed dispersal in bird species. Here, my assessment of the seed dispersal effectiveness of the red-vented bulbul faced an important lack of available data on native fruit-eating species in New Caledonia. If the diet of native bird species is well known, almost no data are available on the contribution of fruit-eating species to seed dispersal networks. Unfortunately, this lack of data makes assessment of the potential negative effects of the red-vented bulbul on the dispersal of plant seeds difficult. In Chapter 4, I provided some clues suggesting that digestion by red-vented bulbuls may affect the germination of the seeds of two species differently. In this case, germination of the endemic *M. rufopunctatum* was reduced after digestion by the birds, while seeds of the invasive *S. terebinthifolius* benefited from digestion. This observation suggest that the red-vented bulbul could promote the

dispersal of introduced plant species better than native of endemic ones. This could represent a case of "invasional meltdown", a phenomenon that could lead to important conservation issues. However, the only way to test this hypothesis would be to replicate my study framework on native fruit-eating species, and native plant species. Enhancement of the germination capacity of the invasive *S. terebinthifolius* has been documented for dozens of bird species (Panetta and McKee 1997). On the other hand, seed dispersal of endemic plant species such as *M. rufopunctatum* remain unknown.

## Interspecific competition: what is the role of behaviour?

Based on variations in the abundance of native and introduced bird species, results presented in Chapter 4 suggest a negative effect of red-vented bulbuls on native bird species. This assessment should be confirmed by monitoring the abundance of native species directly before and after establishment of the red-vented bulbul. Such monitoring could be conducted in villages like Boulouparis, where the species was absent when the distribution monitoring started in 2008. No red-vented bulbuls were counted more than 30 km away from Nouméa during the first year of the temporal monitoring of terrestrial birds of New Caledonia that started in 2010. Thereby, monitoring the establishment of red-vented bulbuls at locations located further than 30 km from Nouméa, and effects on the abundance of other bird species should confirm the findings of this study.

Because of the limited distribution of red-vented bulbuls in New Caledonia, and to avoid any major bias in the statistical analysis, I had to work on a sub-dataset. Focusing on locations where either the red-vented bulbul or the target species was present could have hidden a potential effect of the common Myna, another highly invasive species, on the abundance of

local bird species. Even if the two introduced birds do not share the same ecological niche (Bates et al. 2014), overlap has been identified in the impact the two species have on native bird species in French Polynesia (Blanvillain et al. 2003). Therefore, it would be interesting to replicate the analysis of abundance relationships with the common myna to explore potential additive effects in the pressure of the two introduced bird on native avifauna. As the common myna has already spread throughout the mainland, even into natural forests, description of potential impacts of this species depending on habitat could also contribute to a mapping of the risk on native birds from the dispersal of the red-vented bulbul.

Finally, beyond the observable effects on native bird abundance, underlying mechanisms remain unclear. The aggressiveness of red-vented bulbuls toward other bird species has been reported from several locations (Pernetta and Watling 1978; Sherman and Fall 2010), and this observation gained credit with the traditional use of the species as a fighting bird in India. However, no study has explored the hypothesis of aggression as a shared personality trait in red-vented bulbul individuals compared to other bird species. Yet, this behavioural characteristic could contribute to explaining the successfulness of the red-vented bulbul as a strong competitor, beyond demographic or ecological traits.

Behavioural traits could also partly explain why the red-vented bulbuls have spread into natural forest of French Polynesia, but apparently failed to enter these habitats in New Caledonia. From personal observation, I believe that the differences in native forest bird communities between the two territories could be part of the answer. When I conducted the transect surveys across peri-urban habitats and natural forests, I recorded strong reactions of two bird species to the diffusion of bulbul calls. Grey-eared honeyeaters and New Caledonian crows reacted very rapidly and flew toward the tree at the bottom of which I had placed the

speaker. When present near the sampling point those two-species started calling very quickly and loudly until I stopped broadcasting the calls, which is a very similar behaviour to the one of red-vented bulbuls defending their resource. The grey-eared honeyeater is a widespread bird species in New Caledonia and was the only bird species that did not appear to be affected by the red-vented bulbul in the study presented in Chapter 4. Its common presence in the ultramafic maquis in the south of the mainland could partly explain the lower progress of spread of red-vented bulbuls in this habitat. The endemic New Caledonian crow is mainly present in forest habitats. It has only been recorded in eight locations within inhabited areas, and often close to the forest edge. Habitat partitioning between the two species could contribute to explain the current restriction of red-vented bulbuls into inhabited areas, in contrast with the situation in French Polynesia where the corvid is absent. The New Caledonian crow is known as a very intelligent bird species (McGrew 2013). Thereby the above hypothesis would be a very original example of behaviour resistance of an endemic species to a competitive invader, which would be worthy of a dedicated study.

## Improve the accuracy of the distribution modelling

Modelling the potential global distribution of invasive species could be helpful in defining global hotspots of invasion risk (Thuiller et al. 2005). However, while climate is known to shape the distribution of bird species at a global scale (Barbet-Massin et al. 2009), the use of other environmental filters could improve the quality and accuracy of predictions. The use of habitat layers is expected to improve the resolution of distribution models for species using a broad range of habitats (Fournier et al. 2017). For invasive species like the red-vented bulbul, it is likely that consideration of anthropogenic variables would produce more precise estimates as

such factors may counterbalance a climatic/habitat unsuitability, which could also vary under climate change scenarios (Roura-Pascal et al. 2011).

## Conclusion

I showed that the current research and management effort dedicated to the red-vented bulbul at a global scale does not justify its status of "world worst" species. Moreover, its harmful effects on agrosystems and native fauna could be highly context-dependant. However, while it still has a restricted but on-going expansion, the introduced population in New Caledonia should be confined to its current distribution range. My thesis confirmed that substantial crop losses are to be expected from the consumption of reddish fruits by red-vented bulbuls. Colonization of damaged or inhabited areas by introduced plant species would probably be fostered by this new seed disperser. The native avifauna, which has already suffered increasing habitat fragmentation and urbanization, is facing niche reduction in areas where the red-vented bulbul has established. The early impacts assessment I presented here should justify a significant acceleration in the development of a local-scale management strategy, which relies on the investment from both local people and public institutions. General methods for managing introduced bird species are known and feedback from control and eradications programs are available. My study has provided background data on the local population (extent, size, densities, and habitat use) as well as quantitative assessments of the three categories of impacts associated with this species. It is now up to the relevant institutions to define their management objectives, from which a better strategy will arise, and to start concrete action against the invasive red-vented bulbul in New Caledonia. As shown by the recent detection of individuals in Farino and Bourail (45 and 88 km north to the current range), time is already pressing.

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## Appendices

**Appendix 1.** Call for the participation of volunteer hunters to collect red-vented bubul cadavers. This call was disseminated via local newspapers and on several public institution websites.

**Appendix 2:** Information sheet based on the results of the Chapter 2. This was sent to any person interested in the management of the red-vented bulbul. The Sheet is also freely downloadable off the IAC and CEN websites.



## PESTES ENVIRONNEMENTALES ET RAVAGEURS DE CULTURES — 01

### BULBUL A VENTRE ROUGE
*Pycnonotus cafer*
Linnaeus 1766,
Espèce Exotique Envahissante

Classe : Oiseaux
Ordre : Passériformes
Famille : **Pycnonotidae**
Genre : *Pycnonotus*
Espèce : *cafer*
Nom commun : **Bulbul à ventre rouge**
Statut UICN : **LC (Least Concern)**

[1.1] – Bulbul à ventre rouge

### Description

Le bulbul à ventre rouge est un passereau sombre d'environ 20 cm de longueur. Il est facilement reconnaissable à sa crête noire sur le dessus de la tête et **ses plumes sous caudales de couleur rouge vif** [1.1]. Il a le corps brun foncé avec des motifs plus clairs rappelant la forme d'écailles. La tête est plus foncée voire noire, la croupe est blanche et les rectrices sont noires avec des tâches blanches aux extrémités. Il ne présente **pas de dimorphisme sexuel** (mâles et femelles identiques), mais les individus immatures ont un plumage plus clair.

### Distribution

• **Mondiale**
Originaire d'Asie du Sud-Est, son aire native s'étend d'Inde au Sri Lanka, jusqu'en Birmanie et au sud-ouest de la Chine. Il a été introduit dans de nombreuses îles du Pacifique (Fidji, Hawaii, Nouvelle-Calédonie, Samoa et Tonga), et s'est installé dans certaines régions de Dubaï (Watling 1978). Il a été éradiqué à son arrivée en Nouvelle-Zélande, et ne semble pas s'être maintenu en Australie.

• **Locale**
Le bulbul à ventre rouge a été introduit dans les années 1980 en Nouvelle-Calédonie, comme oiseau d'ornement. Il a été observé en liberté à Nouméa dès 1983. Depuis, son aire de distribution ne cesse de s'agrandir. En 2008, le bulbul était présent de Tontouta au Nord, à la rive nord de la Rivière des Pirogues au Sud. En 2012, il s'était étendu un peu plus au Nord à Tomo et s'étirait au Sud à l'entrée de la Rivière Bleue. En 2014 son aire de répartition s'étendait de **Boulouparis au col de Ngo** [1.2].

[1.2] – Distribution du bulbul à ventre rouge en Nouvelle-Calédonie et signalements recueillis

Membres fondateurs de l'IAC

www.iac.nc

## Habitat

Dans son aire native, le bulbul est un oiseau des broussailles sèches, des forêts, des plaines et des terres cultivées. En Nouvelle-Calédonie, il est observable principalement dans les milieux anthropisés (près de l'Homme) et ouverts, près des lotissements dans les **zones urbanisées ou périurbaines**. De fortes densités ont également été rapportées dans les exploitations maraîchères et fruitières où il cause des dégâts importants.

## Comportement

Il est connu pour être **agressif** vis-à-vis des autres espèces d'oiseaux. Il est souvent observé **perché** en couple à la cime des arbres et se déplace rarement au sol contrairement au Merle des Moluques (*Acridotheres tristis*, Linnaeus, 1766).

## Alimentation

Principalement frugivore, *P.cafer* se nourrit de fruits mais également d'insectes et plus occasionnellement de petits reptiles. Il semble avoir une **attirance particulière pour les fruits rouges** (letchis, piments, tomates…). Il est connu pour les dégâts occasionnés aux cultures (Watling, D. 2002).

## Reproduction

Le Bulbul à ventre rouge s'accouple et pond de septembre à décembre au moins. Il est capable d'avoir plusieurs couvées par an. Les jeunes se regroupent par nombre de 8 à 12 individus avant l'émancipation, puis sont observés le plus souvent par couples ou petits groupes de 2 à 5 individus. Ils construisent un nid en couple où la femelle pond en moyenne 3 œufs.

## Statut

Le Bulbul à ventre rouge, *Pycnonotus cafer*, figure **parmi les 100 espèces les plus envahissantes au monde selon l'UICN**. Sa commercialisation en Nouvelle-Calédonie est interdite ainsi que son transport et sa détention (Codes de l'environnement des provinces Nord et Sud). Il fait parti des 6 espèces prioritaires de la stratégie de lutte contre les espèces envahissantes des espaces naturels de la Nouvelle-Calédonie (CEN 2016).

## Impacts

### • Agriculture

Au moins 36 types de productions agricoles différentes ont été observés comme faisant partie du régime alimentaire de l'oiseau (Vander Velde, 2002). Dans son aire d'origine et dans certaines îles du Pacifique, le bulbul à ventre rouge est responsable **d'impacts forts au niveau de l'agriculture et de l'horticulture**.

Le bulbul à ventre rouge est également considéré comme un **vecteur d'espèces végétales envahissantes**, comme *Miconia calvescens* (DC., 1828) en Polynésie Française (Meyer 1996) ou *Shinus terebinthifolius* (Raddi, 1820) en Nouvelle-Calédonie.



### • Biodiversité native

De part son régime alimentaire, le bulbul peut entrer en compétition directe avec d'autres espèces d'oiseaux indigènes frugivores. Le bulbul n'apparaît pas être un oiseau territorial mais son comportement agressif envers les autres espèces lors de sa quête de nourriture (Thibault et al., 2002; Blanvillain et al., 2003) peut devenir une **menace pour le reste de l'avifaune**. A Tahiti, son statut de compétiteur contribue à menacer le monarque de Tahiti *(Pomarea nigra)*, (Sparrman, 1986), un oiseau en danger critique d'extinction (Thibault et al., 2002; Blanvillain et al., 2003).

### • Régulation

Depuis 2012, l'IAC étudie l'écologie de cet oiseau et teste des méthodes de capture afin de participer à la régulation de l'oiseau [1.3]. Un groupe technique bulbul a été créé en 2009 et regroupe différents partenaires (Gouvernement de la Nouvelle-Calédonie, provinces Sud et Nord, CANC, Arbofruits, CEN, SCO et IAC).



[1.3] - Test de préférence alimentaire

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263

**Appendix 3**: List of newspaper articles, TV documentaries and reports done during this thesis that helped inform the public about the results of this project and gain their participation.

## Newspaper articles

- « Avis de recherche contre le bulbul à ventre rouge » (2016). Les Nouvelles Calédoniennes, 11 Juin 2016

- « Une invasion à vol d'oiseau » (2017). L'oeil magazine, Juillet 2017

- « Si charmant et pourtant si redoutable bulbul » (2017). Les Nouvelles Calédoniennes, Aout 2017

- « Le bulbul à ventre rouge, un oiseau sous surveillance » (2017). La Calédonie Agricole n°156, Mai 2017

- « Les impacts du bulbul à ventre rouge enfin documentés » (2017). La Calédonie Agricole n°158, Octobre 2017

## TV documentaries and shows

- **Invited** in the TV show « Hashtag le lien ». TV channel « NC 1ere». 14 september 2017

- **Interviewed** in the TV documentary « Bienvenue dans la bande ». TV channel « Caledonia ». 30 november 2017

- **Interviewed** in the TV documentary « Carnet de chasses insolites en Nouvelle-Caledonie ». TV channel « Seasons ». 8 december 2017

**Appendix 4:** List of conference talks given during this study

- Thibault, M., Vidal, E., Potter, M., Dyer, E., and Brescia, F. (2016). The red-vented bulbul, extreme pest or extreme prejudice ? *Island Biology 2016 : 2nd conference on island evolution, ecology and conservation*. 18-22 July 2016. University of the Azores, Angra de Heroismo, Acores, Portugal

- Thibault, M., Vidal, E., Potter, M., Sanchez, T., and Brescia, F. (2017). Effects of a recent invader, the red-vented bulbul, on bird commuities in a tropical island biodiversity hotspot. *Island Invasives 2017 : scaling up to meet the challenge*. University of Dundee, Dundee, Scotland

- Thibault, M., Masse F., Pujapujane A., Lannuzel G., Bordez L, Potter M.A., Fogliani B., Vidal E. and Brescia F. (2018). "Liaisons dangereuses": the invasive red-vented bulbul (*Pycnonotus cafer*) and introduced plant species in New Caledonia. *SCBO meeting 2018: Conservation in a changing world*. Te papa Museum, Wellington, New Zealand

**Appendix 5:** Statements of Contributions for the accepted articles presented in Chapters 2, 3, 4 and 5.

## MASSEY UNIVERSITY
### GRADUATE RESEARCH SCHOOL

## STATEMENT OF CONTRIBUTION
## TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

**Name of Candidate:** Martin THIBAULT

**Name/Title of Principal Supervisor:** Prof. Murray Potter

**Name of Published Research Output and full reference:**

Thibault, M., Vidal, E., Potter, M. A., Dyer, E., & Brescia, F. (2018). The red-vented bulbul (Pycnonotus cafer): serious pest or understudied invader?. Biological Invasions, 20(1), 121-136.

**In which Chapter is the Published Work:** Chapter 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: 80%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  I collected the data, and performed the synthesis. I selected the presented results and wrote the article with assistance from collaborators who are co-authors of the article.

THIBAULT

_____
Candidate's Signature

28/03/2018

_____
Date

Murray Potter

_____
Principal Supervisor's signature

28/03/2018

_____
Date

## MASSEY UNIVERSITY
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## STATEMENT OF CONTRIBUTION
## TO DOCTORAL THESIS CONTAINING PUBLICATIONS

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We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

**Name of Candidate:** Martin THIBAULT

**Name/Title of Principal Supervisor:** Prof. Murray Potter

**Name of Published Research Output and full reference:**

2. M. Thibault, E. Vidal, M.A. Potter, F. Masse, A. Pujapujane, B. Fogliani, G. Lannuzel, H. Jourdan, N. Robert, L. Demaret, N. Barré, & F. Brescia (2018). Invasion by the red-vented bulbul: an overview of recent studies in New Caledonia. In: C.R. Veitch, M.N. Clout, A. Martin, J. Russell and C. West (eds.) Island Invasives: Scaling up to meet the challenge, pp. xx-xx. Gland: IUCN.

**In which Chapter is the Published Work:** Chapter 3

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: 75%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  I designed the study, conducted a substantial part of the field/lab work and coordinated the remnant part and conducted all the analyses. I wrote the paper with assistance from my supervisors and most of the co-authors of the article

THIBAULT
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28/03/2018
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**MASSEY UNIVERSITY**
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## STATEMENT OF CONTRIBUTION
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(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

**Name of Candidate:** Martin THIBAULT

**Name/Title of Principal Supervisor:** Prof. Murray Potter

**Name of Published Research Output and full reference:**

3. Thibault, M., Vidal, E., Potter, M. A., Sanchez, T., and Brescia, F. (2018). The invasive Red-vented bulbul (Pycnonotus cafer) outcompetes native birds in a tropical biodiversity hotspot. PloS one, 13(2), e0192249.

**In which Chapter is the Published Work:** Chapter 4

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: 85%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  I designed the study, collected much of the data, performed the analyses and wrote the article with assistance from collaborators who are co-authors of the article.

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268

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(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

**Name of Candidate:** Martin THIBAULT

**Name/Title of Principal Supervisor:** Prof. Murray Potter

**Name of Published Research Output and full reference:**

Thibault M., Masse F., Pujapujane A., Lannuzel G., Bordez L, Potter M.A., Fogliani B., Vidal E. & Brescia F. (Accepted). "Liaisons dangereuses": The invasive red-vented bulbul (Pycnonotus cafer), a disperser of exotic plant species in New Caledonia. Ecology & Evolution.

**In which Chapter is the Published Work:** Chapter 5

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: 75%

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  I designed the study, coordinated the field/lab work and conducted a part myself, I conducted all the analyses. I wrote the article with assistance from most of collaborators who are co-authors of the article.

THIBAULT

Candidate's Signature

28/03/2018

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