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Contact:

epress@unitec.ac.nz

www.unitec.ac.nz/epress/

Unitec Institute of Technology

Private Bag 92025, Victoria Street West

Auckland 1142

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Implications for selected indigenous fauna of Tiritiri Matangi of the establishment of *Austropuccinia psidii* (G. Winter) Beenken (myrtle rust) in northern New Zealand

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Abstract

Myrtle rust (*Austropuccinia psidii* (G. Winter) Beenken) was detected on the New Zealand mainland in May 2017. Myrtle rust was first described in Brazil in 1998, and since then has spread throughout the Americas, to Asia, Africa, the Pacific islands, and most recently to Australia, causing a global pandemic. *A. psidii* is a pathogen of the Myrtaceae family, and attacks young leaves, shoots, stems and flowers. Given overseas experience with the pathogen, a wide range of host species in New Zealand are expected to have the potential to be infected. In New Zealand, the optimal conditions for myrtle rust are predicted to be confined to mainly coastal and the northern areas of the North Island. In these areas, Myrtaceae species, principally pōhutukawa *Metrosideros excelsa*, kānuka *Kunzea robusta* and mānuka *Leptospermum scoparium* are common, and may dominate plant communities. The aim of this review is to consider the potential longer-term impact of myrtle rust, with a focus on the flow-on effect to indigenous New Zealand fauna, particularly the nectarivorous species that use myrtaceous flowers as a food source. This potential is explored through a case study of Tiritiri Matangi Island, an ecological restoration project in the Hauraki Gulf, northern New Zealand. Although any degradation or loss of the Myrtaceae will have long-term and potentially devastating impacts on the myrtaceous habitats and allied fauna, we suggest that niche flexibility associated with much of the New Zealand fauna bodes well for such future environmental challenges. Fauna with an obligate relationship with Myrtaceae, however, may be at greatest risk from the pathogen's establishment. Management options are suggested to mitigate the impact of myrtle rust on nectarivorous fauna.

Introduction

The disease known as myrtle, guava or eucalyptus rust is caused by the fungus *Austropuccinia psidii* (G. Winter) Beenken. This disease affects members of the Myrtaceae, attacking young leaves, shoots, stems, fruit and flowers (Glen et al., 2007; Pegg et al., 2014; Teulon et al., 2015). First symptoms are brown-to-grey spots on leaves and shoots, often surrounded by a reddish halo, followed by yellow-orange spore-containing pustules (Figure 1). This may eventually result in defoliation, galling, flower and nectar failure, and death of susceptible hosts (Coutinho et al., 1998; Glen et al., 2007; Uchida & Loope, 2009; Pegg et al., 2014; Teulon et al., 2015).

Myrtle rust was first described on guava (*Psidium guajava*) in Brazil (Coutinho et al., 1998), from where it has spread throughout Central and South America and to the continental United States (California & Florida),

Hawaii, Japan, China, South Africa, New Caledonia, Indonesia, Australia (Marlatt & Kimbrough, 1979; Uchida et al., 2006; Kawanishi et al., 2009; Carnegie et al., 2010; Zhuang & Wei, 2011; Roux et al., 2013; Buys et al., 2016) and now New Zealand, where its arrival had been predicted (Goldson et al., 2015; Teulon et al., 2015; Buys et al., 2016). Myrtle rust arrived in Australia about mid-2010 and was first identified in Gosford on the central New South Wales coast (Carnegie et al., 2010; Makinson & Conn, 2014). Unfortunately, slow identification of the pathogen delayed eradication attempts, which may have contributed to its establishment and spread throughout the eastern regions of Australia (Elith et al., 2013; Howard et al., 2015).

Although globally there are several strains of *A. psidii* affecting different hosts, only one strain is present in Australia (Loope & La Rosa, 2008; Carnegie & Cooper,



Figure 1. Myrtle rust on o'hia (*Metrosideros polymorpha*).
(Photo: © J. Friday, University of Hawai'i)

2011; Graça et al., 2013; da S. Machado et al., 2015a; da S. Machado et al., 2015b; Buys et al., 2016). This was described as *Uredo rangellii* (Simpson et al., 2006) and known as such from 2010-2011. Following genetic analysis, this was considered a biotype of *Puccinia psidii* (Makinson & Conn, 2014), but has recently been re-assigned to the *Austropuccinia* genus on the basis of a new genetic analysis (Beenken, 2017). A full overview of the taxonomy and biology of this rust species is covered by Clark (2011), Teulon et al. (2015) and Beenken (2017). Unfortunately, this strain appears to have a wide host specificity, infecting in excess of 445 species and including c.46% of genera in the Myrtaceae (Buys et al., 2016; Potts et al., 2016; Ganley, 2017).

Makinson (2014) suggests that the movement of infected material by humans has been the primary agent of long-distance dispersal in Australia, where myrtle rust can now be found from Queensland to Victoria, Tasmania and the Northern Territory (Department of the Environment and Energy, 2017). The introduction of rust fungi into New Zealand is relatively common due principally to the prevailing westerly weather patterns carrying spores across the Tasman Sea. Since 1945, more than one new rust species per year has been found in New Zealand, and most of those are of Australian origin (Mckenzie, 1998). To demonstrate the importance of wind assisted spread from Australia, Mckenzie (1998) lists 40 species of rust present in New Zealand from herbarium and disease lists in 1931, of which 22% were introduced. By 1997 this number had increased to 234 species, of which 46% were of Australian origin. It seems inevitable that spore material could arrive repeatedly in New Zealand from Australian sources (Viljanen-Rollinson & Cromey, 2002; Kim & Beresford, 2008).

Myrtle rust was first reported in New Zealand in March 2017 on Raoul Island, two months before its detection on mainland New Zealand in Kerikeri and Taranaki. These two reports, that are from approximately the same time (2 May and 17 May, respectively), were followed by three geographically separate locations: Te Puke on 13 June, Otorohanga on 8 September, and Auckland on 23 November (Department of Conservation, 2017; Ministry for Primary Industries, 2017a, 2017b, 2017c, 2017d). It is currently unclear how the fungus arrived in New Zealand or how it has been dispersed.

The life cycle of myrtle rust is not completely understood, it is either autoecious (single host), or heteroecious (requiring at least two hosts) with an unknown alternate aecial host (Morin et al., 2014). Although the establishment and effect of a heteroecious rust pathogen can depend on the presence of an alternate host to establish, it is not always the case, as climatic adaptation of the particular rust and distribution of the alternate host may also play a role. For example *Melampsora larici-populina*, which arrived in New Zealand the year after it was recorded in Australia in 1973 (Spiers 1989), virtually eradicated susceptible poplar varieties, including the Lombardy poplar (varieties of *Populus nigra*) (Spiers, 1974; Van Kraayenoord et al., 1974; Wilkinson & Spiers, 1976). In contrast, the related *Melampsora medusae*, also pathogenic to poplars, introduced to NZ from Australia at about the same time, failed to establish due to absence of its alternate host (Wilkinson, 1988). For other rusts with known alternate hosts, like *Puccinia hordei* in barley and *P. striiformis* in wheat, the uredinal cycle persists through winter and epidemics develop without the alternate host being available. Given that an alternate host for *A. psidii* has not been identified, it is unknown whether one is essential for development.

Climate modelling (Kriticos et al., 2013; Narouei-Khandan, 2014) suggests that the greatest impact of myrtle rust introduction to New Zealand will be seen in the North Island and the upper South Island (see Bebbler, 2015 for a discussion on the extended effect of climate change on this scenario). As this disease has only just been recorded in New Zealand, its impact is uncertain. It may be that its presence is driven by microclimate, leaf wetness and some degree of tolerance in the hosts (Alvares et al., 2017; Pegg, 2017; P. Cannon, personal communication, September 7, 2017).

Although knowledge of the exact susceptibility of New Zealand hosts to *A. psidii* is incomplete and dependent on ongoing investigation, the catholic nature of the Australian strain may indicate that a wide range

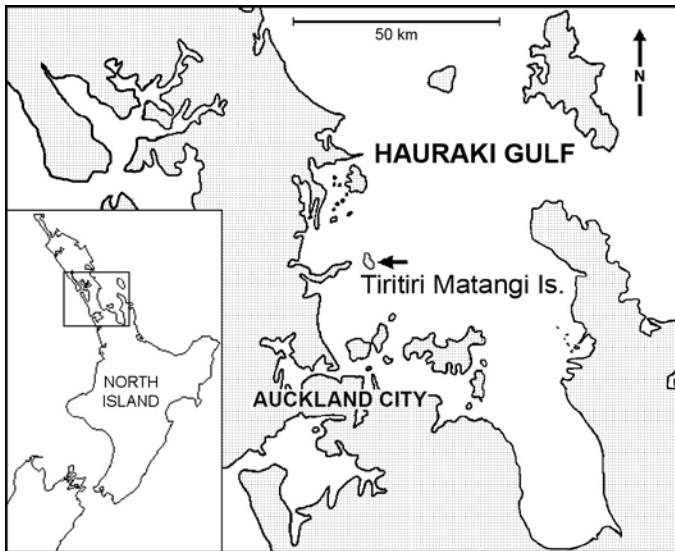


Figure 2. Location of Tiritiri Matangi Island, Hauraki Gulf, New Zealand.

of host species in New Zealand is at risk of infection (Ridley et al., 2000). Teulon et al. (2015) assessed the susceptibility of indigenous New Zealand taxa to the fungus, with special reference to Māori taonga plant species. In particular, they noted the genera *Metrosideros*, *Kunzea*, *Leptospermum*, *Syzygium*, and *Lophomyrtus* were at risk. The threat to *Metrosideros excelsa*, *M. kermadecensis* and *Lophomyrtus bullata* has also been specifically noted (Giblin & Carnegie, 2014a).

Also potentially at risk are common introduced garden species, commercial crops and tree species. Although, the susceptibility of feijoa (*Acca sellowiana*) is considered to be low (Ministry for Primary Industries, 2017e) other plants including *Eucalyptus* species are considered susceptible. (Giblin & Carnegie, 2014a, 2014b; Teulon et al., 2015; Carnegie et al., 2016). The potential commercial impact of this pathogen, including the threat to the mānuka honey industry, has been discussed (Glen et al., 2007; Teulon et al., 2015; Buys et al., 2016).

The hidden flow-on effect to the indigenous New Zealand fauna, however – in particular the species that rely on the myrtaceous elements of the flora as food sources – is less visible in the literature. An assessment of the impact on fauna is being made in Australia, including the implication of limited food sources for some species of flying foxes, lorikeets and honeyeaters (McLeish, 2016). The long term effects, however, are not known.

The aims of this review are:

1. to evaluate the existing literature and recorded field observations to make an informed assessment of

the severity of the possible impacts of myrtle rust on indigenous New Zealand fauna that are associated with the Myrtaceae;

2. to propose possible actions for management and research that can be initiated before the full impacts of myrtle rust are known;
3. to provide further evidence for the environmental benefits of managing myrtle rust.

We explore these aims through a general case study of Tiritiri Matangi Island, an ecological restoration project in the Hauraki Gulf, northern New Zealand (Figure 2).

Case study site

Modelling under a current climate scenario (Ramsfield et al., 2010; Kriticos et al., 2013; Narouei-Khandan, 2014) predicts optimal conditions for myrtle rust in New Zealand to be confined principally to coastal and northern areas of the North Island. This range would likely expand with future climate change (Hanna et al., 2011; Bebber, 2015). Tiritiri Matangi Island is located in the northern North Island, and may be considered indicative of both island and coastal ecophysiological environments in northern New Zealand. The island has:

1. remnants of pohutukawa (*Metrosideros excelsa*)-dominated forest typical of the northern New Zealand coast and islands, which are considered to be iconic (Bergin & Hosking, 2006; Galbraith & Cooper, 2013);
2. species of Myrtaceae that make a significant contribution to the biodiversity:
 - natural vegetation regrowth, covering 19% of the island, dominated in places by kānuka (*Kunzea robusta*) and mānuka (*Leptospermum scoparium*) (Cameron & Davies, 2013);
 - established planted areas, covering 64% of the island, that include extensive pohutukawa stands providing salt-resistant shelter canopies (Cameron & Davies, 2013);
3. populations of fauna, such as nectarivorous birds and reptiles (Graham et al., 2013; Supporters of Tiritiri Matangi, 2013), that have potential to be affected by any degradation of the Myrtaceae.

The habitat

As with any canopy species, Myrtaceae on Tiritiri Matangi provide a general habitat and resource for other flora and fauna. The plant surface is a substrate to support epiphytes (including lichens), the stringy bark a shelter for invertebrates, and the leaves and wood are

resources for herbivores. In a northern New Zealand context, the Myrtaceae, in particular *Metrosideros*, *Kunzea* and *Leptospermum*, may be considered keystone genera due to their influence on ecosystem functioning (Kriticos et al., 2013). This influence is evident in their role in ecological succession as pioneer species tolerant to harsh dry conditions, and with their closed canopy providing shelter for following seral stages. The habitat and ecosystem characteristics (Simpson, 1994, 2005; Bergin & Hosking, 2006; Derraik, 2008) associated with these northern New Zealand Myrtaceae species are:

Kānuka and mānuka

- form extensive communities during early stages of the ecological recovery of deforested communities, often under conditions of dry and poor soils;
- develop a deep organically-rich, fine leaf-litter;
- have entomophilous flowers (small and nectar-producing, insect pollination strategy) (Kelly et al., 2010).

Pōhutukawa

- tolerates salt, resulting in a role as the first (and often only) woody plant to colonise bare cliff faces and the coastal supra-littoral zone, and to persist to form, and often dominate, coastal forest;
- has extensive hydrotropic roots that provide habitat over bare rock/cliffs;
- develops weather-influenced, gnarled old-growth trees that provide a multitude of cavities for fauna of all sizes, from small invertebrates to cavity-nesting birds;
- has a stable and strong root system that may develop conditions suitable for burrows of nesting seabirds;
- develops a deep organically-rich, coarse leaf-litter;
- has large nectar-producing brush flowers and a pollination strategy considered to be either ornithophilous (bird pollinated) (Castro & Robertson, 1997) or generalist (pollinated by all animal groups) (Newstrom & Robertson, 2005; Pattemore & Wilcove, 2012).

Birds

The nectarivorous birds present on Tiritiri Matangi are North Island saddleback *Philesturnus rufusater* and North Island kōkako *Callaeas cinerea wilsoni* (Callaeidae), hihi *Notiomystis cincta* (Notiomystidae), bellbird *Anthornis melanura* and tūī *Prothemadera novaeseelandiae* (Meliphagidae), and silvereye *Zosterops lateralis*

(Zosteropidae). These species all have brush structures on their tongues, and generally decurved, narrow bills characteristic of nectar feeders (McCann, 1964; Mees, 1969; Paton & Collins, 1989; Driskell & Christidis, 2004). Almost all nectar sources, including flowers with ornithophilous, entomophilous or generalist pollination strategies, can be used by each nectarivorous species (Gravatt, 1970; Newstrom & Robertson, 2005; Kelly et al., 2010). All these nectarivorous birds, however, are also frugivorous and insectivorous, and use the respective resources to varying degrees (Table 1). The use of nectar resources by saddleback, kōkako and silvereye is relatively minor, thus these birds are not likely to be impacted by the arrival of myrtle rust to Tiritiri Matangi. However, tūī, bellbird and hihi have a considerably higher proportion of their diet provided by nectar.

Studies of the food sources of tūī (Merton, 1966a; Gravatt, 1971; Bergquist, 1985; O'Donnell & Dilks, 1994) have shown their diet to be predominantly nectar. Bergquist (1985) calculated 70-80% of the diet to be nectar, with male tūī being more dependent on the resource than females. Such is the drive of tūī for nectar, they have been shown to travel long distances to feed (Gravatt, 1971), including movement on and off islands on a seasonal or daily basis (Stewart & Craig, 1985). Although kānuka and mānuka flowers are entomophilous (Kelly et al., 2010; Spurr et al., 2011), tūī and bellbird have been observed visiting both species (Baker, 1992; Roper, 2012; MG personal observation), perhaps indicative of their high dependence on nectar.

Bellbird are also known to travel long distances for nectar resources (Gravatt, 1971), although their nectar consumption has been shown to be lower than that of tūī (Merton, 1966a; Gravatt, 1971; O'Donnell & Dilks, 1994). Their access to nectar resources may be restricted by dominant behaviour of tūī, particularly when nectar sources are limited (Rasch & Craig, 1988; Anderson & Craig, 2003).

Hihi also have high dependence on nectar (Gravatt, 1971), however their access to nectar sources is highly constrained by more dominant tūī and bellbird (Rasch & Craig, 1988; Anderson & Craig, 2003; Murphy & Kelly, 2003). Gravatt (1970) observed hihi to be more bound to territories for food, and tended to only access ornithophilous flowers (e.g., pohutukawa) if they were close to the territory. On Tiritiri Matangi, hihi receive supplementary food (Thorogood et al., 2013) to assist their survival in winter when competition with bellbird is most intense. Supplementary feeding stations are

Species	Average dietary proportion (annual range) (%)			References ^b
	Nectar	Fruit	Invertebrates	
tūī	50 (37-98)	4 (1-8)	16 (13-35)	(1, 2, 3)
bellbird	54 (46-81)	3 (1-8)	27 (13-53)	(1, 2, 3, 4)
hihi	66 (29-89)	12 (4-20)	18 (16-19)	(2, 3, 4)
saddleback	8 (4-19)	20 (4-45)	50 (31-86)	(5, 6, 7, 8,)
kōkako	1	44 (14-52)	8 (5-29)	(9)

Table 1. Dietary components of indigenous nectarivorous bird species recorded in northern New Zealand habitats.

a) Vegetation and unidentified foods are omitted from the table.

b(1) Merton, 1966b; (2) Gravatt, 1971; (3) Rasch & Craig, 1988; (4) Roper, 2012; (5) Atkinson, 1964; (6) Merton, 1966a; (7) Atkinson, 1966; (8) Blackburn, 1967; (9) Powesland, 1987; (10) Moeed, 1979.

positioned within a mesh cage that excludes the larger tūī from the resource.

Research on Tiritiri Matangi during the early stages of ecological restoration identified pōhutukawa as the main nectar source during the breeding season of nectarivorous birds (Rasch & Craig, 1988; Anderson & Craig, 2003). This is consistent with observations elsewhere (e.g., Gravatt, 1970) that indicate that few other plant species are visited by tūī and bellbird when the pōhutukawa is in flower. Poor flowering of such important plant species, particularly *Metrosideros*, has been suggested as having a marked effect on the survival and breeding success of nectarivores (Gravatt, 1970). This suggests that loss of pōhutukawa would increase the demand for nectar at other flowers during the December-January flowering period, and inevitably increase competition between the birds.

The Myrtaceae, however, are not the only source of nectar for fauna on Tiritiri Matangi. The revegetation of the island has resulted in an increase in diversity and abundance of angiosperms (Cameron & Davies, 2013), with nectar available all year round (Table 2a), although the quantity will vary seasonally, and depend on whether the species have an ornithophilous, entomophilous or generalist pollination strategy. Since almost all nectar sources can be used by each nectarivorous bird species (Gravatt, 1970), the loss of Myrtaceae may be offset, at least partially, by the availability of nectar from plants

in other families. Although the flowering angiosperms on the island are dominated by entomophilous and generalist forms, such flowers have been shown to be of significant value to nectarivorous birds (Castro & Robertson, 1997).

Rasch & Craig (1988) considered tūī–hihi competition to be less intense than that of bellbird–hihi. This is explained by the extensive use by hihi of small low-energy-value entomophilous flowers (Rasch & Craig, 1988; Castro & Robertson, 1997) (Figure 3a). Given the behavioural dominance of tūī and their requirement for nectar, a loss of Myrtaceae flowers may see them switch to greater use of entomophilous and generalist flowers, further increasing the intensity of competition between all nectarivorous birds. Revegetation on Tiritiri Matangi has also resulted in extensive areas of pōhutukawa, the result of an unexpectedly high survivorship rate of the planted seedlings, many of which, however, have never flowered (Forbes & Craig, 2013). This suggests that other angiosperms with largely entomophilous and generalist pollination strategies may already be providing significant nectar resources on the island (Anderson, 2003; Roper, 2012).

Another source of carbohydrates for birds is fruit, which has the potential to offset any loss of Myrtaceae nectar, particularly at times of peak demand. All nectarivorous birds take fruit, with the proportion of fruit in the hihi diet shown to be higher than that of tūī

Table 2:

Flowering (a) and fruiting (b) phenology^a of plants present on Tiritiri Matangi Island, and observed both on Tiritiri Matangi and elsewhere to be used as sources of nectar and fruit by New Zealand fauna species. Shading indicates plant abundance on the island^b.

= abundant = locally common, occasional = scarce

(a) Species ^c	Floral strategy ^d	Energetic return ^e	Winter			Spring			Summer			Autumn			References ^f	
			J	J	A	S	O	N	D	J	F	M	A	M		
Myrtaceae:																
<i>Leptospermum scoparium</i>	E	4														(1)
<i>Kunzea robusta</i>	E	4														(2, 3)
<i>Metrosideros excelsa</i>	O	1														(4, 5, 6, 7, 8)
<i>Acca sellowiana</i> *	G	2														(9)
<i>Eucalyptus saligna</i> *	E	1														(7, 8)
<i>Rhabdthamnus solandri</i>	O	4														(1, 10, 11)
<i>Rosmarinus officinalis</i> *	E	5														(3)
<i>Vitex lucens</i>	O	2														(4, 5, 6, 11, 12)
<i>Pseudopanax arboreus</i>	G	1														(4, 5, 6, 13)
<i>Dysoxylum spectabile</i>	E	2														(4, 5, 6, 10, 11)
<i>Veronica</i> spp.	E	5														(2, 4, 11, 14, 15)
<i>Clematis paniculata</i>	E	2														(8, 12)
<i>Sophora chathamica</i>	O	1														(5, 6, 13)
<i>Pittosporum crassifolium</i>	E	2														(5, 6, 19)
<i>Pittosporum umbellatum</i>	E	1														(4, 11)
<i>Erythrina x sykesii</i> *	O	1														(3, 17)
<i>Corynocarpus laevigatus</i>	E	5														(4, 10, 14)
<i>Alseuosmia macrophylla</i>	O	4														(4, 5, 6, 11)
<i>Leucopogon fasciculatus</i>	E	5														(4, 5)
<i>Phormium tenax</i>	O	1														(5, 6, 7, 13)
<i>Geniostoma ligustrifolium</i>	G	3														(9, 18, 19)
<i>Myrsine australis</i>	E	5														(14)
<i>Parsonia heterophylla</i>	E	3														(1, 14, 20)
<i>Knightia excelsa</i>	O	1														(4, 4, 5, 11)
<i>Cordylina australis</i>	E	1														(6, 13)
<i>Carmichaelia australis</i>	G	5														(8, 16)
<i>Ripogonum scandens</i>	E	2														(10)
<i>Myoporum laetum</i>	E	3														(1, 6, 20)
<i>Beilschmiedia tarairi</i>	E	5														(20)
<i>Meliccytus ramiflorus</i>	E	4														(4, 8, 18)
<i>Rhopalostylis sapida</i>	E	3														(14)
<i>Muehlenbeckia australis</i>	E	4														(9)
<i>Pseudopanax lessonii</i>	E	2														(6)
<i>Beilschmiedia tawa</i>	E	5														(6)
<i>Hoheria populnea</i>	E	3														(2, 14)
<i>Schefflera digitata</i>	E	4														(4, 14, 18, 20)
<i>Astelia banksii</i>	E	5														(14, 21)
<i>Paraserianthes lophantha</i> *	O	1														(2, 6, 22, 23)

(b) Species ^c	J	J	A	S	O	N	D	J	F	M	A	M	References ^f
<i>Coprosma</i> spp.													(15, 18, 24, 25, 26)
<i>Piper excelsum</i>													(25, 27, 28)
<i>Ripogonum scandens</i>													(10, 16, 27)
<i>Phytolacca octandra</i> *													(15, 24)
<i>Vitex lucens</i>													(4, 5, 6, 11, 12)
<i>Rhopalostylis sapida</i>													(14)
<i>Pittosporum crassifolium</i>													(5, 6, 8, 24)
<i>Pseudopanax arboreus</i>													(4, 5, 6, 13, 15)
<i>Myrsine australis</i>													(8, 14, 15, 26)
<i>Leucopogon fasciculatus</i>													(4, 5, 18, 27)
<i>Pittosporum umbellatum</i>													(4, 11)
<i>Alseuosmia macrophylla</i>													(4, 5, 6, 11, 18)
<i>Geniostoma ligustrifolium</i>													(9, 16, 18, 23)
<i>Meliccytus ramiflorus</i>													(4, 8, 15, 18, 25)
<i>Muehlenbeckia australis</i>													(9, 15, 25, 27)
<i>Coriaria arborea</i>													(8, 15, 18, 28)
<i>Cordylina australis</i>													(6, 13, 15, 26)
<i>Parsonia heterophylla</i>													(1, 14, 19)
<i>Schefflera digitata</i>													(4, 8, 13, 14, 18, 19)
<i>Dacrycarpus dacrydioides</i>													(26, 27)
<i>Pseudopanax lessonii</i>													(6, 10)
<i>Astelia banksii</i>													(14, 21)
<i>Hedycarya arborea</i>													(8)
<i>Podocarpus totara</i>													(15, 26)
<i>Myoporum laetum</i>													(1, 6, 15, 19)
<i>Dysoxylum spectabile</i>													(4, 5, 6, 10, 11)

^a Flowering & fruiting: Moore & Edgar (1970); Allan (1982); Bryant (1994); Dawson & Lucas (2000); New Zealand Plant Conservation Network (2017).

^b Abundance based on observations, M. Galbraith and H. Cooper (after Cameron & Davies 2013).

^c After Cameron & Davies (2013) and de Lange (2014). * = exotic species.

^d Pollination strategy: O = ornithophilous; E = entomophilous; G = generalist (after Castro & Robertson 1997; Spurr et al. 2011; Kelly et al. 2010).

^e Relative energetic return based on floral types: 1 = clumped rich; 2 = dispersed rich; 3 = clumped moderate; 4 = dispersed moderate;

5 = "insect" flowers (after Feinsinger & Colwell 1978; Ford & Paton 1982; Rasch & Craig 1988; Castro & Robertson 1987).

^f (1) Craig 1985; (2) Baker 1986; (3) M. Galbraith pers obs.; (4) Gravatt 1970; (5) Godley 1979; (6) Craig et al. 1981; (7) Dept. of Lands & Survey 1982; (8) O'Donnell & Dilks 1994; (9) B. Walter pers obs.; (10) Merton 1966a; (11) Rasch & Craig 1988; (12) Atkinson 1964; (13) Spurr et al. 2011; (14) Castro & Robertson 1997; (15) Baker 1999; (19) Anderson 2003; (17) Turbott 1953; (18) Perrott 1997; (20) Craig & Douglas 1984; (16) Heenan & De Lange 1999; (21) Castro 1995; (22) Hawley 1997; (23) Supporters of Tiritiri Matangi 2013; (24) Anderson & Craig 2003; (25) Dilks 2004; (26) Bergquist 1987; (27) Williams & Karl 1996; (28) Perrott & Armstrong 2000.



Figure 3. Nectarivorous birds feeding on nectar of entomophilous flowers: (a) tūī (*Prosthemadera novaeseelandiae*) feeding on karo (*Pittosporum crassifolium*), and (b) hihi (*Notiomystis cincta*) feeding on hangehange (*Geniostoma ligustrifolium*). (Photos: © Martin Sanders)

and bellbird (Table 1). The proportion of indigenous angiosperms that produce fleshy fruits is greater in the northern North Island compared to the rest of New Zealand (Kelly et al., 2010), with most fruiting between November and April, and peaking December-February (Wotton & McAlpine, 2015). The vegetation changes on Tiritiri Matangi over the past 33 years have resulted in increased diversity and abundance of understory angiosperms (Cameron & Davies, 2013) that provide fruit throughout the year (Table 2b).

A further source of energy-rich carbohydrate available in some New Zealand habitats is honeydew, a mixture of excess carbohydrates and water excreted by sap-feeding scale insects (Beggs & Wardle, 2006). Honeydew has been shown to be an important food for nectar-feeders in South Island habitats, where it provides a year-round supply of high-energy sugar (Gaze & Clout, 1983). Honeydew is present on Tiritiri Matangi Island, as evident by the presence of the sooty mould associated with the scale insects that produce honeydew (Gardner-Gee & Beegs, 2009; Supporters of Tiritiri Matangi, 2013). Bellbird have been recorded accessing this resource on the island (Roper, 2012), and both tūī and bellbird have been observed feeding on honeydew on other northern islands (Towns, 2002). Observations elsewhere of birds feeding from bark where consumption of invertebrates was not confirmed (e.g., Gravatt, 1971), may easily have been birds feeding on honeydew.

Where plant communities are dominated by Myrtaceae species, a loss of habitat as a result of myrtle rust is likely to have a significant impact on avifauna. The impact of the loss of Myrtaceae nectar,

however, may be minimal if there is sufficient diversity in plant communities to provide nectar and fruit from other plants. Nonetheless, a reduction in the availability of pōhutukawa nectar during the peak demand period, for breeding tūī in particular, may constitute high potential for impact, albeit over a short period.

On Tiritiri Matangi, supplementary feeding is currently in place for hihi, with bellbird also having access to this resource (Supporters of Tiritiri Matangi, 2013). This supplementary sugar will alleviate any increased competition in the absence of Myrtaceae, although the volume of sugar required would inevitably increase and be dependent on the availability of personnel to maintain the resource. The needs of tūī, particularly during a reduced seasonal peak of pōhutukawa nectar, may be met through supplementary feeding, though careful management of the feeding structures would be required to prevent tūī from dominating every site.

Reptiles

The Raukawa gecko (*Woodworthia maculatus*), Duvaucel's gecko (*Hoplodactylus duvaucelii*) and the elegant (green) gecko (*Naultinus elegans*) are present on numerous northern islands (McCallum & Harker, 1982; Towns & Robb, 1986; Jewell, 2008) including Tiritiri Matangi. All three species are known to feed on nectar sources as available seasonally (Figure 4a) (McCann, 1955; Whitaker, 1987; Evans et al., 2015).

Both Raukawa and Duvaucel's geckos have been observed feeding on *Metrosideros* nectar at peak flowering (Eifler, 1995; Evans et al., 2015). There is, however, strong evidence of resource partitioning



Figure 4. Raukawa gecko (*Woodworthia maculatus*) feeding on (a) flax (*Phormium tenax*) nectar (Photo: © Neil Fitzgerald), and (b) kawakawa (*Piper excelsum*) fruit (Photo: © Debra Wotton, Moa's Ark Research).

between species, with Evans et al. (2015) suggesting that, overall, flax nectar may be a more significant nectar source for Raukawa gecko, and honeydew more important for Duvaucel's gecko. The elegant gecko tends to be arboreal, and is recognised as having a strong association with mānuka (Sharrell, 1966; Forster & Forster, 1970; Lindsey & Morris, 2000; Jewell, 2008). The diet of the elegant green gecko is primarily invertebrates (McCann, 1955; Bull & Whitaker, 1975) but nectar, presumably from mānuka flowers, is also taken (McCann, 1955).

The loss of Myrtaceae habitat and nectar resources will impact on geckos, but to varying degrees depending on the species. Geckos are seasonally opportunistic, visiting a range of plant species for nectar and fruit (Olesen & Valido, 2003; Evans et al., 2015). This flexibility may offset the impact of any loss of Myrtaceae nectar for these taxa. The fruit of *Coprosma* species, kawakawa (*Piper excelsum*) (Figure 4b), pōhuehue (*Muehlenbeckia complexa*), mingimingi (*Leucopogon fasciculatus*) and inkweed (*Phytolacca octandra*), all either abundant or locally common on Tiritiri Matangi (Cameron & Davies, 2013), have been recorded in the diet of one or more of the gecko species present on the island (Whitaker, 1987; Wotton, 2002; Knox et al., 2012). Collectively, these plants provide fruit all year round. Other sources of carbohydrate-rich foods used by geckos, also present on Tiritiri Matangi and available all year round, are honeydew and flax sap (Evans et al., 2015).

The elegant gecko may be at greatest risk given its close association with mānuka, both from habitat and nectar perspectives. However, other *Naultinus* species elsewhere in New Zealand inhabit a range of plant taxa, e.g., species of *Coprosma*, *Muehlenbeckia*, *Pittosporum*

and *Olearia*, and tauhinu (*Ozothamnus leptophyllus*) (Hare et al., 2007). All of these plant taxa are present on Tiritiri Matangi, and are generally well represented in the regenerating areas alongside mānuka (Cameron & Davies, 2013).

We suggest that the niches of gecko species appear sufficiently flexible to minimise the impact of the loss or degradation of Myrtaceae.

Bats

New Zealand has two extant endemic species of bat, the long-tailed bat (*Chalinolobus tuberculatus*) and the lesser short-tailed bat (*Mystacina tuberculata*), each with a differing relationship with the Myrtaceae.

The long-tailed bat (*Chalinolobus tuberculatus*) is distributed widely throughout northern New Zealand, including a number of Hauraki Gulf islands (O'Donnell, 2001a; O'Donnell et al., 2010). The species is an aerial insectivore known to inhabit a variety of forest types (O'Donnell, 2001a), including coastal pōhutukawa forests (Arkins et al., 1999), and has been observed to feed over regenerating mānuka and kānuka shrublands (O'Donnell, 2001b). Any degradation of habitats and invertebrate resources as a result of myrtle rust may affect local populations of the long-tailed bat, but the species is likely to have sufficient ecological flexibility to avoid the impacts of such degradation. There is evidence that long-tailed bats were formerly present on Tiritiri Matangi (Supporters of Tiritiri Matangi, 2013), and the species has been identified as having potential for reintroduction. The loss of myrtaceous habitat or food resources on the island due to the effects of myrtle rust may jeopardise such a reintroduction.

Pattimore and Wilcove (2012) propose a significant pollination relationship between the short-tailed bat (*Mystacina tuberculata*) and pōhutukawa, and the brush structure of the pōhutukawa flower is consistent with chiropterophily (pollination by bats) (Newstrom & Robertson, 2005). In northern New Zealand, the lesser short-tailed bat is now restricted to Hauturu-ō-Toi/Little Barrier Island and localised populations in Northland (O'Donnell et al., 2010). The species is generally restricted to the interior of old growth forests, but will forage in coastal forests for nectar, including that of pōhutukawa (Arkins et al., 1999; Lloyd, 2001; Pattimore & Wilcove, 2012). This suggests that loss of myrtaceous nectar will have some impact on the species, particularly on Hauturu-ō-Toi. However, given the short flowering season of pōhutukawa, and the omnivorous diet of the short-tailed bat that includes nectar from a wide variety of plant taxa (Daniel, 1976; Lloyd, 2001), this impact may be minimal, at least for the Hauturu-ō-Toi population. Pattimore and Wilcove (2012) advocate the restoration of short-tailed bat populations following invasive mammal eradications, such as the removal of kiore/Pacific rat (*Rattus exulans*) from Tiritiri Matangi (Veitch, 2002), to restore a pollination function. Although the recovery plan for the short-tailed bat includes an objective to establish new populations on suitable islands (Molloy, 1995) where myrtaceous vegetation is prevalent, there are no current intentions to reintroduce populations to any island or mainland locations in northern New Zealand (C. O'Donnell, personal communication, October 25, 2017).

Invertebrates

It is expected that the coastal and replanted pōhutukawa forests such as those on Tiritiri Matangi, and the regenerating kānuka and mānuka shrub communities, will contain a diversity of invertebrates and ecological relationships (Dugdale & Hutcheson, 1997; Derraik et al., 2001; Harris et al., 2004). Although the information about such communities dominated by Myrtaceae is not strong, there is some evidence that characteristic invertebrate faunas are associated with pōhutukawa, kānuka and mānuka (Hosking & Hutcheson, 1993; Harris et al., 2004; Hood, 2016).

The names of a number of invertebrate species, mostly endemic (Bergin & Hosking, 2006), indicate a specific association with the Myrtaceae: spotted mānuka moth *Declana leptomera* (Crowe, 2002); pōhutukawa leaf miner *Neomycta rubida* (May, 1993); a weevil *Neocyba metrosideros* (Kuschel, 2003); the mānuka chafer *Pyronota festiva* (Crowe, 2002); scale insects *Eriococcus leptospermi* (Stephens et al., 2005), mānuka

giant scale *Coelostomidia wairoensis* (Morales, 2000), *Lecanochiton metrosideri* (Hodgson & Henderson, 2004) and the pōhutukawa button scale *L. actites* (Landcare Research, 2017); a gall fly (*Fergusonina metrosiderosi*) and its associated nematode (*Fergusobia pohutukawa*) (Taylor et al., 2007). Myrtaceous flowers (dish/bowl or brush) have a structure consistent with insect pollination (Newstrom & Robertson, 2005), and are accessed by a wide variety of insect taxa for nectar (Primack, 1978). This suggests that myrtaceous nectar will play a significant role in ecosystem function, and that mutualistic relationships are likely.

The honeydew produced by scale insects can be an abundant year-round resource readily available to other species. Scale insects may thus play a pivotal role in the flow of energy in communities where they are present, to the point where they fulfil a keystone species role (Beggs & Wardle, 2006). A number of scale insects have a host-specific relationship with the Myrtaceae. All four of the button scales (*Lecanochiton* spp.) are endemic to New Zealand, and are host-specific to the genus *Metrosideros* (Hodgson, 2000). Gardner-Gee & Beegs (2009) identify four further scale insect species with a close relationship with Myrtaceae: *Coelostomidia wairoensis*, *Eriococcus leptospermi*, *E. campbelli* and *E. orariensis*. These were recorded in sufficiently high infestations in kānuka and mānuka forests in the Auckland region for the forests to be considered honeydew-influenced (Gardner-Gee & Beegs, 2009). Such mutualistic relationships between scale insects and myrtaceous hosts are at risk from the effects of myrtle rust. Furthermore, since scale insects are considered to be keystone species, negative impacts have the potential to generate flow-on effects within communities.

The Myrtaceae are also common hosts of the New Zealand stick insects (Buckley et al., 2010a; Buckley et al., 2010b), and in some cases the association may be significant. As early as 1955, Salmon pointed out potential obligate relationships between stick insects and species of Myrtaceae. For example, the smooth stick insect (*Clitarchus hookeri*) may require a diet of mānuka to complete its life cycle, prickly stick insects (*Acanthoxyla* spp.) require *Metrosideros* species (in particular *M. excelsa* or *M. robusta*), whereas the New Zealand giant stick insect (*Argosarchus horridus*) appears to require ramarama (*Lophomyrtus bullata*) (Salmon, 1955). The smooth stick insect has been recorded on Tiritiri Matangi (Milton, 2016), however, little is known about its ecology on the island.

Loss or degradation of Myrtaceae habitats due

to myrtle rust will impact on associated invertebrate communities, particularly those with a mutualistic relationship with the family. However, further work assessing and recording Myrtaceae-invertebrate relationships is needed to better understand the potential impacts of myrtle rust.

Summary

As keystone species, the degradation or loss of the Myrtaceae will have long-term and potentially devastating impact on the associated habitats. The composition of communities would likely change as other plant species colonise following the release of competitive constraints. Such changes will have significant impact on faunal populations, potentially generating flow-on effects (e.g., trophic cascades) within ecological networks. Such effects on ecological relationships are hard to predict, but this uncertainty is typical of incursions of new alien species.

O'Donnell and Dilks (1994) suggest that the broad omnivorous diets of the New Zealand nectarivorous birds is a function of generalist niches associated with isolated temperate island systems. Although it is acknowledged that nectar-feeders have complex feeding strategies that include sequential specialisation from season to season, it is possible that the niche flexibility associated with the generalist ecology bodes well for future environmental challenges such as the impacts of myrtle rust. This may apply equally to reptile fauna. The greatest risk is likely to lie with invertebrates that have an obligate relationship with Myrtaceae, and thus less flexibility in their ecological niche. For these species, the impact of myrtle rust would almost certainly result in population declines, and may require refugia (such as Tiritiri Matangi) maintained through targeted management of incursions of myrtle rust, if this proves feasible.

The nectarivorous birds and geckos on Tiritiri Matangi are unlikely to experience acute impact from myrtle rust because of their ecological flexibility and the availability of alternative carbohydrate sources. If these alternative sources prove limiting, additional supplementary feeding may be required. The presence of five nectarivorous bird species on Tiritiri Matangi, however, may represent a worst-case scenario because in most locations in northern New Zealand, saddleback, hihi and bellbird are absent as are the short-tailed bat and many reptiles.

Ecological restoration of islands and mainland sanctuaries has delivered the re-establishment of

indigenous communities (Butler, 2014). The diversity of indigenous plants here may mitigate the impacts of myrtle rust over time. However, in non-restored locations where indigenous biodiversity may be considered to be most impoverished (Lee & Lee, 2014), the loss of myrtaceous nectar may still have impact through increased competition between common indigenous and exotic nectarivores, e.g., tūī, silvereye, starling (*Sturnus vulgaris*), sparrow (*Passer domesticus*), honeybee (*Apis mellifera*) and wasps (*Vespula* and *Polistes* spp.) (McCann, 1964; Godley, 1979; Butz Huryn, 1995; Clapperton, 1999). Nevertheless, in these locations, particularly on the mainland, exotic angiosperms may offer alternative sources of nectar (Godley, 1979; Spurr et al., 2011).

As with any incursion of an alien species, the full ecological impact of the arrival of myrtle rust on New Zealand ecosystems will not be known until after a period of establishment during which its distribution will be localised and its effects variable. This establishment period, however, provides the opportunity for a precautionary management approach, and to implement in advance actions to mitigate the potential impacts of the pathogen. The effects of myrtle rust may take several years (at worst, though potentially longer in the case of aged pōhutukawa) to take effect since only new growth is affected (Carnegie et al., 2016). This would afford time to implement measures to mitigate the impact. These measures could include:

1. the development of a phenology of nectar and fruit-bearing angiosperms to identify seasonal gaps in nectar/sugar availability;
2. undertaking supplementary plantings to facilitate a continuous flowering cycle, and/or specific plantings of known sugar-rich ornithophilous resources;
3. undertaking plantings of known non-Myrtaceae hosts of scale insects, e.g., *Pittosporum crassifolium*, *Myoporum laetum*;
4. consideration of whether seasonal supplementary feeding of sugar water is necessary for nectarivorous birds as a short-term measure while ecosystems readjust;
5. consideration of whether planting or retention of exotic plant species is necessary, even as an intermediate measure, to supplement seasonal nectar;
6. selection of resistant strains of Myrtaceae, if any, for propagation and ultimate revegetation;
7. support of research into obligate associations between invertebrates and the Myrtaceae to inform future conservation needs.

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Authors

Mel Galbraith, MSc Hons, is a senior lecturer in Environmental and Animal Sciences, and a member of the Biodiversity Management and Animal Welfare Research Group, Unitec Institute of Technology, Auckland, New Zealand.

Mark Large, PhD, is Associate Professor in Environmental and Animal Sciences, and a member of the Biodiversity Management and Animal Welfare Research Group, Unitec Institute of Technology.

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