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# **Do rats and possums reduce the reproductive capacity of large-fruited broadleaved species in Waikato hill-country forests?**

A thesis  
submitted partial fulfilment  
of the requirements for the degree  
of  
Master of Science (Research) in Ecology and Biodiversity  
at  
**The University of Waikato**  
by  
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THE UNIVERSITY OF  
**WAIKATO**  
*Te Whare Wānanga o Waikato*

2021

# Abstract

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Although brushtail possum (*Trichosurus vulpecula*) browsing can have conspicuous impacts by killing trees outright, there is also evidence of more insidious threats to regeneration of some species through depression of seed production. It is not known how widespread these more cryptic effects are. The elimination of all introduced mammals except mice (*Mus musculus*) from Sanctuary Mountain Maungatautari (herein referred to as Maungatautari) fourteen years ago, provided a valuable reference system for gauging the impacts of possums and rats (*Rattus* spp.) on seed production in very similar forest at Maungakawa where these invasive mammals are common. This study compares phenology, fruit development and seed fall of three large-fruited species in the two forests: tawa (*Beilschmiedia tawa*) and mangeao (*Litsea calicaris*) are dominant canopy trees, and pigeonwood (*Hedycarya arborea*, porokaiwhiri) is an important subcanopy species. The reproductive cycles of tawa, mangeao and pigeonwood were extended (18 to 27 months), but the extended stage was different in each species: mangeao inflorescence buds developed over a nine-month period, pollinated tawa flowers were dormant over autumn before fruit emerged during the winter and ripened during the following summer. In pigeonwood part of the fruit crop remained on the trees until anthesis the following year. Despite almost concurrent tawa and mangeao anthesis, the resulting fruit crops matured in consecutive autumns: mangeao in 2020 and tawa in 2021. In the absence of rats and possums, tawa seed fall varied significantly in consecutive years. Tawa seed fall in the first season (2020) was negligible at both forests. At Maungatautari seed fall was significantly more abundant in the second season (2021). Despite the successful pest control campaign significantly reducing possum abundance at Maungakawa in June 2020, seed fall did not increase significantly in 2021. There was evidence of green tawa fruit consumption by possums. They also consumed the flesh of ripe fruit in the trees and on the ground but discarded the seeds. Mangeao seed production was higher at Maungatautari than in the forest inhabited by rats and possums, although this effect fell short of statistical significance. Seed production at Maungatautari was abundant in 2020 with more than 4000 seeds captured in seed traps but in 2021 seed production was negligible. Seed production was reduced at Maungakawa in both years. In 2021 only two seeds were captured in each forest. The timing of mangeao's reproductive cycle leaves the swollen inflorescence buds in winter especially vulnerable to damage by possums and possibly rats when food resources are low. Elimination of the possums rather than control at low abundance may be required to restore tawa seed production to historical levels. The underlying cause of low mangeao seed production is likely to be related to loss of inflorescence buds, but the role of arboreal invasive mammals requires further investigation. There was no evidence rats and possums reduce pigeonwood fruit production or destroy the seeds. However, by discarding seeds where they feed, rats and possums may limit seed dispersal across the spatial landscape. Further

investigations are required to fully understand the extent to which the reproductive cycles of tawa, mangeao and pigeonwood are depressed and the consequences for the large-fruited species within Waikato hill-country forests. It is reassuring that abundant tawa and mangeao seed production has rebounded at Maungatautari within 15 years of eradication of invasive species. This suggests that loss of seed fall from vulnerable large-fruited species can be overcome by removal of invasive mammals.



# Preface

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Evidence of impacts rats (*Rattus* spp.) and possums (*Trichosurus vulpecula*) have on the reproductive capacity of fleshy large-fruited broadleaved forest trees is cryptic like the fruit on the tawa (*Beilschmiedia tawa*) above. During autumn 2021 seed fall was abundant. There are 13 well developed, unripe fruit in the image above. (MND December 2020)

## Keywords

rat; *Rattus rattus*; possum; *Trichosurus vulpecula*; tawa; *Beilschmiedia tawa*; mangeo; *Litsea calicaris*; pigeonwood; *Hedycarya arborea*; fleshy large-fruit; seed production;

# Acknowledgements

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First, a special thank you to my University of Waikato supervisor, Associate Professor Christopher Lusk. I have appreciated your support throughout this project: from assisting me to define the scope of my topic, identifying and measuring trees and seeds, and especially for challenging my interpretations of what I saw, measured and wrote. Thank you also to Neil Fitzgerald, Manaaki Whenua Landcare Research, for your advice and for the tracking tunnels, chew cards, seed traps and especially the wildlife cameras that gave me access to the cryptic lives of the wildlife inhabiting our forests.

Thank you to the landowners who allowed us to use their farm tracks to access the forests and their assistance. Gaining access to the matched Maungakawa and Maungatautari forest study areas has been critical to obtaining robust data. Your insights into the local areas and history of the forests have been valuable.

A huge shout out to my field assistants especially the core team; Maggie McCaughan, Dave and Judy Browning and Hugh Eccles. You stuck with me through rain and hail as well as those stunning summer days when the forest provided respite from the midday sun. Thank you for proofreading my drafts of this thesis. Your enthusiasm and support have been awesome. Your assistance with 4WD transport and advice for driving my own 4WD on the farm tracks was much appreciated. Thank you also to the many others who answered my calls when I needed additional assistance with rat and possum surveys, and to cover gaps in my field assistant calendar. My other great assistant has been Cheryl Ward, University of Waikato science librarian. Thank you for your assistance with formatting this thesis.

There are many others who have assisted. Thank you to Ngāti Korokī Kahukura, Ngāti Hauā, Raukawa and Waikato - Tainui for allowing us to access Sanctuary Mountain Maungatautari forests and to Ngāti Hauā Iwi Trust for access to Maungakawa forests, to the Department of Conservation and Waipa District Council for my research permits, to Sanctuary Mountain Maungatautari Management, Waikato District Council and Predator Free Taupo for support with this project, to Warren Agnew of Gotcha Traps for supplying the Black Trakka™ cards and Lodge Kaimanawa 426 for providing me a PLB. Thankfully we never needed to use it.

My sincere thanks to all. I hope my findings will spur your enthusiasm to rid our forests of the invasive mammals forever.

## **Dedication**

My thesis is dedicated to my late mother, Dorothy Herald, a life-long advocate for the environment. She has been with me all the way. This research has been funded from my inheritance.

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# Chapter 1

## Introduction

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### 1.1 Introduction

When humans first arrived in New Zealand (c.1280 AD) the land was predominantly forested (Wardle, 1991; Wilmshurst et al., 2008). Some trees standing in the New Zealand forests today germinated prior to human arrival in New Zealand (Bergin, 2000; Steward and Beveridge, 2010). For several million years previously, seals and bats were the only mammals present (King and Forsyth, 2021). The earliest human arrivals, Polynesians, brought kiore (*Rattus exulans*), chickens, dogs and tropical crop plants with them (Smith, 2008). European settlement in the late 18<sup>th</sup> century initiated a new wave of environmental impacts (Wyse et al., 2018; King and Forsyth, 2021). Norway rats (*R. norvegicus*) are thought to have arrived about the time Cook visited New Zealand. Ship rats (*R. rattus*) probably did not arrive until the mid-19<sup>th</sup> century (Atkinson, 1973). Brushtail possums (*Trichosurus vulpecula*) were introduced about the same time to establish a fur trade (Kean and Pracy, 1949). At the time, there was no understanding that New Zealand forests had very low resilience to possums.

The New Zealand landscape has been dramatically changed over the last 200 years by humans and the mammals we have introduced (Latham et al., 2017). Today 14 species of wild mammals are invasive within the indigenous forests and across the wider landscape (King and Forsyth, 2021). Ungulates browse the forest floor (Nugent et al., 2001) while rodents, possums and mustelids range more widely, feeding on the ground and within forest canopies (Innes and Russell, 2021). These mammals quickly adapted to new food sources in New Zealand, decimating bird populations (Innes et al., 2010a) and some plant species (Atkinson et al., 1995).

Across the central Waikato region, the original 800 000 ha forest land cover is now reduced to 9% land cover (Ewers et al., 2006) represented by the few protected unfragmented forests and approximately 5000 dispersed fragments each less than 25 ha mostly located on private land (Burns et al., 2011). The forest fragments on the hill-country fragments are classified as broadleaf-podocarp forest although today there are very few emergent podocarps. Broadleaved species, tawa (*Beilschmiedia tawa*), rewarewa (*Knightia excelsa*), pukatea (*Laurelia novae-zelandiae*) and mangeao (*Litsea calicaris*), dominate the forest canopies with occasional emergent red rata (*Metrosideros robusta*). Historically hīnau (*Elaeocarpus dentatus*) was also reportedly common (Burns et al., 2011) but they are uncommon today. Tawa, mangeao and hīnau bear fleshy large-fruit that are important food resources for endemic birds (Clout and Hay, 1989).

Possum browsing can cause mortality and even local extinction of some native species where they had previously been common (Fitzgerald, 1976; Campbell, 1990) although this is

questioned by others (Payton, 2000; Bellingham and Lee, 2006). In Orongorongo Valley several palatable species including kamahi (*Weinmannia racemosa*), red rata (*Metrosideros robusta*), native fuchsia, (*Fuchsia excorticata*), and titoki (*Alectryon excelsus*) were severely defoliated by possums and many trees died (Fitzgerald, 1976; Campbell, 1990). Kamahi and red rata were browsed throughout the year while other species were only eaten seasonally. The loss of the high canopy has changed the forest structure. Less palatable species such as pigeonwood (*Hedycarya arborea*) and tree ferns taking advantage of opened canopy gaps now dominate the canopy in Orongorongo Valley, Wellington (Campbell, 1990; Brock, 2017).

Although possum browsing can have conspicuous impacts by killing canopy trees outright, there is also evidence of more insidious threats to regeneration of some species through depression of seed production. Elements of the reproductive cycles of large-fruited broadleaved species are particularly susceptible to depression by rats (*Rattus* spp.) and/or possums. They consume flower buds, flowers, fruits, and seeds (Cowan, 1990; Clout, 2006). Cowan and Waddington (1990) attributed suppression of hīnau fruit crops in Orongorongo Valley, when crops were abundant elsewhere, to possums feeding on developing flower buds and flowers. Burns et al. (2011) attributed the loss of previously common species in Waikato fenced forest fragments to possums and rats: kohekohe (*Dysoxylum spectabile*) succumbing to sustained browsing by possums and hīnau to possums browsing the flower buds and to rats destroying the seeds (Williams et al., 2000; Wilson et al., 2003).

When foliar cover falls below a threshold level, plants lack the energy resources necessary to support seed production (Holland et al., 2013). Sweetapple et al. (2016) reported significant improvement in foliage condition of palatable species six years after possums were eradicated from Kapiti Island. Although possums are often assumed responsible for loss of foliage and the reproductive capacity of canopy trees, wider ecological factors should also be considered (Bellingham and Lee, 2006) (**Figure 1-2, Figure 1-4 and Figure 1-5**). Forsyth and Parkes (2005) found insects contribute equally to foliar browse damage of some species e.g., mahoe (*Melicactus ramiflorus*) and kamahi. Climate, site stability, soils, disease, tree age, and successional stage also exacerbate loss of canopy foliage (Holland et al., 2013). On the other hand, where accessible, pasture species may contribute 30% of possums' diet particularly during winter and spring (Dodd et al., 2006) when forest food resources are low.

Many New Zealand forest trees are reliant on birds for pollination and/or seed dispersal (Clout and Hay, 1989; Pattemore and Anderson, 2013). Where predatory mammals are present pollinating birds e.g., bellbirds (*Athornis melanura*) and stitchbirds (*Notiomystus cinerea*, hihi) that feed on nectar are rare (Kelly et al., 2010; Pattemore and Anderson, 2013). In many forests, kererū (*Hemiphaga novaeseelandiae*) is the only remaining species capable of dispersing undamaged seeds from large-fruited forest species. Kōkako (*Callaeas cinerea*) and weka (*Gallirallus australis*) also disperse large seeds but these species only remain in limited forest habitats where predation by invasive mammals is low (Carpenter et al., 2018). Invasive

mammals and non-endemic birds have not compensated for the reduction in pollination and seed dispersal by declining endemic bird populations (Kelly et al., 2006).

Local eradication of rats and possums from ecological sanctuaries has highlighted the influences they have on forest biodiversity (Binny et al., 2021; Bombaci et al., 2021). Until recently rats and possums were ubiquitous throughout New Zealand forests. Over the last 30 years they have been eradicated from 80 ecological sanctuaries, representing 1% of indigenous forest (Innes et al., 2019). More than 3500 community groups control invasive mammals in many more fragments of indigenous forest, plantation forests, pastoral and urban areas throughout the country (TrapNZ, 2021). Short term results suggest degradation of the forests can be arrested but this must happen before the invaded forests lose their “ecological memory” to support recovery (Fahey et al., 2018). Using exclosure studies, Nugent (2001) confirmed loss of browsed species is reversible only if viable seeds persist in the forest litter. The alternative is restoration seeding or planting together with continuing suppression of invasive mammals (Forbes et al., 2020).

Sanctuary Mountain Maungatautari (herein referred to as Maungatautari) and Maungakawa forests are large remnants of old-growth, *sensu* Wirth et al. (2009), broadleaf-podocarp forests in the Waikato (**Figure 1-1**) with contrasting abundance of invasive mammals. Maungatautari forest is enclosed by predator proof fencing, and all introduced mammals apart from mice (*Mus musculus*) were eradicated in 2006. This has provided a valuable reference system for gauging the impacts of rats and possums on seed production in other hill country forests of the Waikato region. Surveys indicate the forest ecosystem at Maungatautari is recovering (Byrom et al., 2016). At Maungakawa where possums and rats are abundant, their populations have only been controlled intermittently since 1999. Compared to the forest at Maungatautari, indigenous species richness was lower in 27 other fenced Waikato forest fragments (Burns et al., 2011) indicating a lack of regeneration of sub-canopy and canopy species where invasive mammals inhabit the forests.

I asked if rats and possums are reducing the reproductive capacity of tawa, mangao and pigeonwood. Key criteria for selection of these species were being codominant within the Maungatautari Ecological District hill-country forests, commonly occurring on my selected forest margins and have fleshy-fruit large enough to be individually counted on inflorescence branchlets and able to be readily identified in litter on the forest floor. Tawa, mangao and pigeonwood are considered as representatives of large-fruited broadleaved species in Waikato hill-country forests. It is very likely that ship rat is the only species of rats present in the forest at Maungakawa. As Norway rats, are largely confined to the ground and absent from most forest, they do not affect seed production however they do consume seeds found on the ground. As my methodology was not able to distinguish ship rats and Norway rats, I include the latter within the term *Rattus* spp. but they were unlikely to have been present (Foster, 2010).



## **1.2 Thesis outline**

### **Chapter 2: The forests and study locations**

This chapter establishes that Maungatautari and Maungakawa forest ecology, climate, geological origin, topography, and soils are sufficiently alike for valid investigation of the impacts of possum and rats on the reproductive capacity of tawa, mangero and pigeonwood. At each forest, three study locations were selected where abiotic factors matched, tawa, mangero and pigeonwood were codominant within the forests and sexually mature specimens were accessible on the forest margins.

### **Chapter 3: Forest structure and composition**

Forest structure and community composition were determined using point centre quarter (PCQ) methodology (Cottam and Curtis, 1956). Species were identified and their relative density and basal area were measured, and relative dominance calculated. In both forests, tawa and mangero were codominant canopy species and pigeonwood together with the smaller fruited mahoe were codominant subcanopy species.

### **Chapter 4: Contrasting wildlife presence and impacts**

This chapter confirms the single biggest difference between Maungatautari and Maungakawa forests: the absence of all introduced mammals apart from mice in Maungatautari forest which is surrounded by a predator proof fence. Surveys were undertaken to establish the relative abundance of rats and possums within the study locations at Maungakawa. Maungatautari management provided data from their on-going pest monitoring programme. I used wildlife cameras at both forests to monitor the activities of mammals and birds in the immediate vicinity of seed traps and germination cages and supplementary cameras across the wider landscape. Images of 10 introduced mammal species as well as endemic and introduced bird species confirmed their presence at Maungakawa. Only mice and birds triggered the cameras at Maungatautari. At Maungakawa, a predator control campaign was undertaken by Waikato Regional Council midway through my research period.

### **Chapter 5: Phenology of tawa, mangero and pigeonwood**

I investigated the phenology and demography of foliage, buds, flowers, and fruit; to test possible mechanisms by which rats, and possums might reduce seed output of my study species. The forest margin was used as a proxy for the forest canopy as it closely replicates canopy conditions: an environment with high light availability, but also exposed to the potential mechanical damage and drying effects of prevailing climatic conditions. Small and potentially reproductive branchlets of tawa, mangero and pigeonwood growing on forest margins were tagged. Branchlet length, inflorescence / flower bud development, anthesis, fruit development and seed fall were measured over a 13-month period. General observations of foliage condition, pollination processes and disturbances including insect attack and bird and

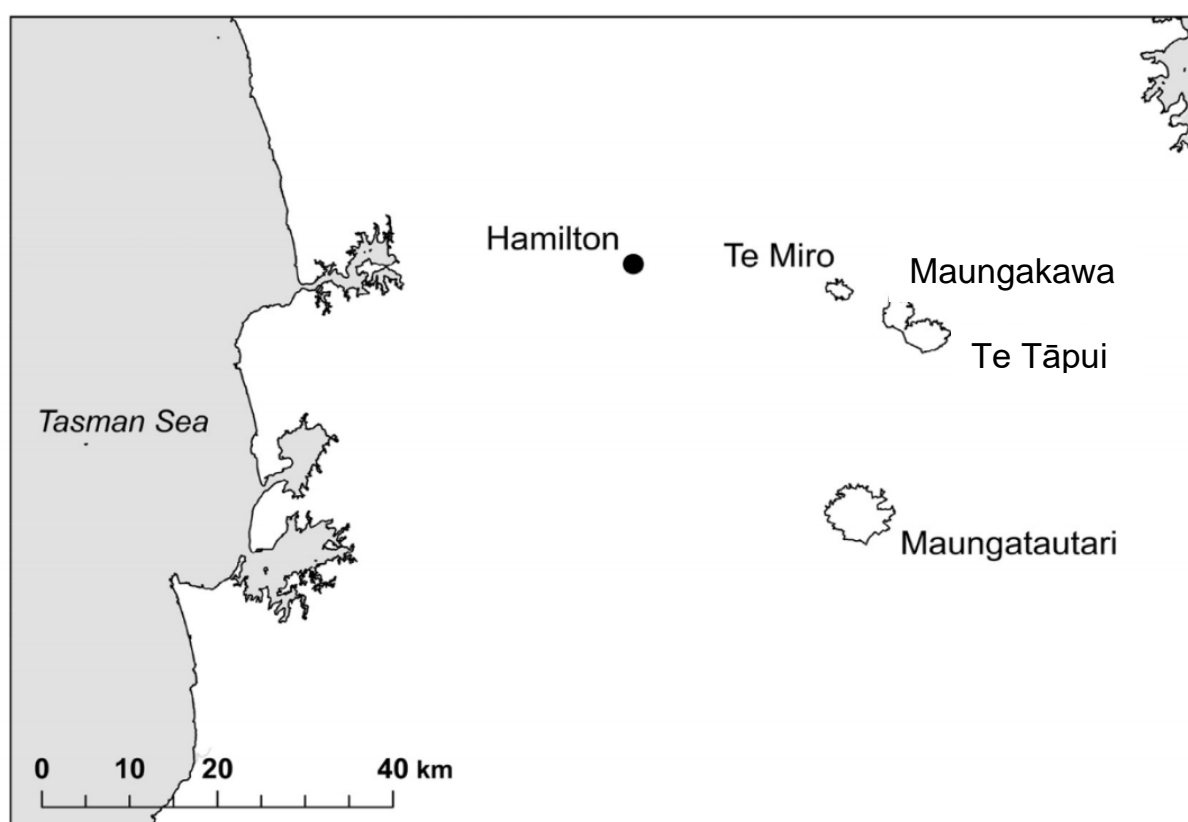
mammal browsing were also recorded. This information supports interpretation of seed fall (Chapter 6).

## **Chapter 6: Seed fall and germination**

Seeds and other material falling from the canopy were captured in seed traps along transects also used to measure rat and possum abundance and activities. Tawa, mangero and pigeonwood seeds were examined, counted, and placed on the forest floor to germinate. Half the seeds were placed within germination cages designed to exclude rodents, possums, and birds and the remaining seeds were placed on the forest floor adjacent to the cage. Total seed fall (standardized by tree basal area) at each forest and seed fall of each species was compared.

## **Chapter 7: Synthesis and conclusions**

In this chapter I synthesize my findings from the preceding chapters to assess the influence rats and possums are having on the reproductive capacity of tawa, mangero and pigeonwood. I conclude that rats and possums use elements of the reproductive cycles of tawa, mangero and pigeonwood as food resources at different times of the year. The resultant impacts on reproductive capacity are not consistent across the large-fruited species.



**Figure 1-1:** Locations of study forests south-east of Hamilton city in the Waikato district of New Zealand. Reproduced with permission from Whyte and Lusk (2019)



**Figure 1-2:** Kererū browsing large-leaf coprosma (*Coprosma autumnalis*) during winter.  
(MNR June 2020)



**Figure 1-3:** Mahoe (*Melicytus ramiflorus*) is a leaf exchanger (most of the previous year's leaves are shed as the new leaves flush in the spring). The above trees are growing where kererū are uncommon and possums have been subject to predator control for several years. Note the abundant foliage in contrast to the images below.  
(Aratiatia restoration area August 2021)





**Figure 1-4:** Browse by possums has stripped most leaves from this mahoe in the Maungakawa forest margin. Similar damage was observed in the forest canopy along the study transects. Kererū were not often observed at Maungakawa. (TTJ November 2019)



**Figure 1-5:** At Maungatautari kererū were observed browsing mahoe, large-leaf coprosma and other margin broadleaved trees and shrubs during winter and spring. Mahoe is also browsed by insects including several wētā species. (MND September 2020)



# Chapter 2

## The forests and study locations

---

### 2.1 Introduction

Recognising the influences of rats (*Rattus* spp.) and possums (*Trichosurus vulpecula*) on forest ecology requires an understanding of the similarities and differences between Maungatautari and Maungakawa forests. This research was carried out in the old-growth broadleaved forest covering the mid-slopes of the two volcanic cones: Maungakawa within Te Tāpui Scenic reserve, and Maungatautari 35 km to the south (**Appendix 1**). Variables considered when selecting study locations included forest type, previous history, accessibility, species present on the forest margins, altitude ranges, and aspect.

Phenology and seed fall were key aspects to understanding the reproductive capacity of tawa (*Beilschmiedia tawa*), mangeao (*Litsea calicaris*) and pigeonwood (*Hedycarya arborea*). Three key criteria for this species selection included the species being: endemic to New Zealand, commonly occurring in forests including the forest margins within the Maungatautari Ecological District hill-country forests and have fleshy fruit large enough to be individually counted on inflorescence branchlets and able to be readily identified in litter on the forest floor.

Phenology of each of the species growing on the forest margins was measured as a proxy for the forest canopy (Chapter 5). The margin environment provided a close replicate of canopy conditions: high light exposure and a niche for flower and fruit development, but where there was competition for space and exposure to wind as a damaging and drying agent. Seed fall from the species was measured along forest transects running into the forest from the margins (Chapter 6). Periodic visits were made to the top of the 16 m observation tower in the tawa and mangeao canopy, at Sanctuary Mountain Maungatautari southern enclosure, to record (photographs and notes) the phenological cycles of these species in the canopy. Specific measurements e.g., flower bud, flower and fruit counts were not taken. These canopy observations combined with litter composition in seed traps e.g., tawa and mangeao flower debris and fruit (Chapter 6) indicated that phenological development of canopy trees was more-or-less synchronous with that of trees on the margins.

To minimise possible abiotic influences on forest ecology, landform, aspect, and altitude were considered when identifying suitable study locations within the forests. Study locations were also defined by the criteria for forests where “transition old-growth”, *sensu* Wirth et al. (2009), broadleaved species predominate with tawa, mangeao and pigeonwood trees present in the canopy and on the forest margin. Forest areas which had been heavily cut over and now dominated by seral species or tree ferns were avoided. Trees selected for the phenology study

(Chapter 5) needed to have the potential for flowers and fruit to develop within a height range that was able to be observed, examined, and measured directly from ground level. Suitable forest margins were identified by examination of maps and reconnaissance visits.

Over a 13-month period (July 2019 to August 2020) each study location forest margin was visited on a four-week cycle. Due to Covid 19 lockdown in 2020, forest visits were curtailed from mid-March until the end of April 2020. From August 2020 forest visits to gather seed fall and seedling germination data continued but on a six-week cycle.

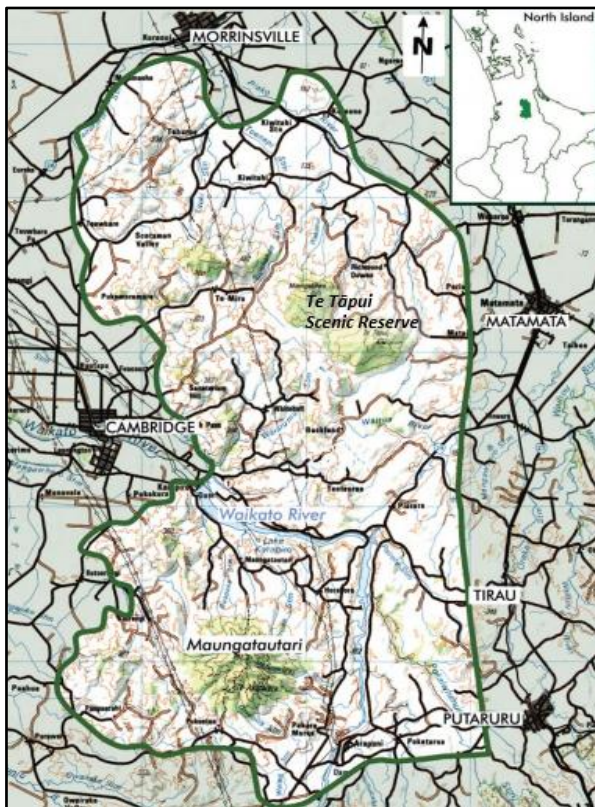
This chapter seeks to establish that Maungatautari and Maungakawa are historically, climatically, and geographically matched to enable elucidation of the impacts that rats and possums are having on the reproductive capacity of tawa, mangeao and pigeonwood. The three broadleaved species are briefly described here, and their phenologies are more fully investigated in Chapter 5.

## 2.2 Location and history

Both forests fall within the Maungatautari Ecological District (area code 11.6) (McEwen, 1987), “the hilly country surrounded by the lowland townships of Cambridge, Morrinsville, Tirau and Matamata” (**Figure 2-1**) which was covered with “old-growth conifer / broadleaved forest prior to 1840” (**Figure 2-2**). An ecological district is defined as “a local part of New Zealand where the topographical, geological, climatic, soil and biological features, including the broad cultural pattern, produce a characteristic landscape and range of biological communities” (Park et al., 1983 in McEwen (1987)).

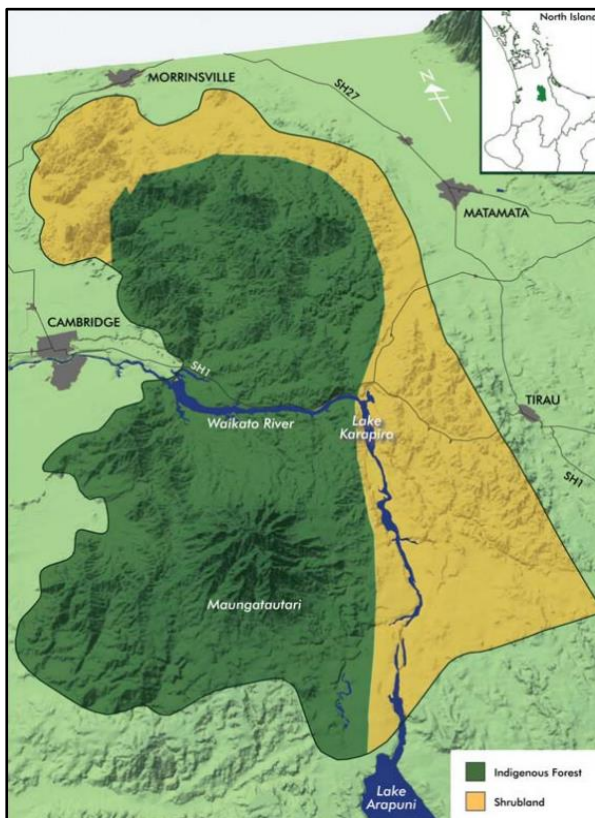
Spiritual, ancestral, cultural, customary, and historic significance are very important to Iwi with dominant mana whenua of Maungatautari and Maungakawa forests. At Maungatautari Ngāti Korokī Kahukura hold dominant mana whenua status and other Iwi (Ngāti Hauā, Raukawa and Waikato-Tainui) also have a spiritual, ancestral, cultural, customary, and historic interest in Maungatautari. Deeds of Settlement for loss of their entitlements have been settled between the Crown and Iwi, as recorded in the legislation: *Ngāti Korokī Kahukura Claims Settlement Act 2014*, *the Raukawa Claims Settlement Act 2014*, and *the Ngāti Hauā Claims Settlement Act 2014*. In 2015, 623 ha of the forested land on Maungakawa was transferred to Ngāti Hauā Iwi Trust under Sec 61 of the Ngāti Hauā Claims Settlement Act. Previously part of Te Tāpui Hunting Block A, this area reverted to its correct Māori name, Maungakawa. The settlement provides for continued integrated management by the Department of Conservation (DOC) and the *Ngāti Hauā Iwi Trust* (Ngāti Hauā Iwi Trust, 2018). This information is taken from my research permits granted by Waipa District Council (Maungatautari) and the Department of Conservation (Maungakawa).

Maungatautari Ecological Island Trust (MEIT) is the trust that governs and helps manage the funds and oversight for the Sanctuary Mountain Maungatautari project. The Board of Trustees includes Iwi with mana whenua, landowners, and community representatives.



**Figure 2-1:** Map of Maungatautari Ecological District from Environment Waikato local area planting guide series “What to plant in Maungatautari ecological district.” (Amoore and Denyer, 2019). Maungatautari and Te Tāpui Scenic Reserve are the largest remnant native forest areas. Maungakawa is the northern volcanic cone within Te Tāpui Scenic Reserve.

Credits: **Figure 2-1, Figure 2-2 and Figure 2-3** from Amoore and Denyer (2019).



**Figure 2-2:** Maungatautari ecological district native vegetation cover in 1840.



**Figure 2-3:** Maungatautari ecological district remaining native vegetation cover in 2006.

## 2.3 Biodiversity

Today the extent of remaining indigenous forests in the Waikato region is less than 10% (Amoore and Denyer, 2019) (**Figure 2-3**). Much of the remaining forest is located on the extinct volcanic cones, Maungatautari (3363 ha) and Maungakawa and Te Tāpui within Te Tāpui Scenic Reserve (2383 ha). A little under half of the forest within Te Tapui (approximately 1000 ha) is on the Maungakawa cone.

The forests on Maungakawa and Maungatautari are classified as “broadleaf-podocarp” (Leathwick, 2001). On the lower slopes of the forests where this research was carried out tawa, rewarewa (*Knightia excelsa*), pukatea (*Laurelia novae-zelandiae*) and mangeao dominate the forest canopies with scattered emergent rata (*Metrosideros robusta*). Hīnau (*Elaeocarpus dentatus*) and titoki (*Alectryon excelsus*) occur at lower densities with kohekohe (*Dysoxylum spectabile*), and kamahi (*Weinmannia racemosa*) also locally present. Dominant subcanopy species are large-leafed coprosma (*Coprosma autumnalis*), hangehange (*Geniostoma ligustrifolium*), pigeonwood (*Hedycarya arborea*), mahoe (*Melicytus ramiflorus* ssp. *Ramiflorus*), red mapou (*Myrsine australis*), kawakawa (*Piper excelsum*), patē (*Schefflera digitata*), tree ferns: ponga (*Cyathea dealbata*), mamaku (*Cyathea medullaris*) and wheki (*Dicksonia squarrosa*) and sporadically the native nikau palm (*Rhopalostylis sapida*) (Burns et al., 2011; Whyte and Lusk, 2019). Few emergent podocarps remain. Only occasional miro (*Prumnopitys ferruginea*) and rimu (*Dacrydium cupressinum*) emerging in the canopy layer, were observed during this study.

Intrusion by large herbivores and arboreal folivores and mammalian predators continues to degrade the ecosystems in most Waikato native forests (Burns et al., 2011). Sanctuary Mountain Maungatautari being within predator proof fencing, is the exception. Since completion of the predator proof fencing in 2006, a total of 14 introduced mammal species have been eliminated from the forest: brushtail possums herein referred to as “possums”, fallow deer (*Dama dama*), red deer (*Cervus elephus*), goats (*Capra hircus*), pigs (*Sus scrofa*), cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*Mustela erminea*), weasels (*Mustela nivalis vulgaris*), hares (*Lepus europaeus occidentalis*), rabbits (*Oryctolagus cuniculus cuniculus*), hedgehogs (*Erinaceus europaeus occidentalis*), Norway rats (*Rattus norvegicus*) not confirmed but known to be present in the locality, and ship rats (*R. rattus*) (Speedy et al., 2007). Only mice (*Mus musculus*) remain, with populations increasing in the absence of its previous predators (Innes et al., 2018). In recent years, control initiatives without erection of predator proof fencing are advancing with the New Zealand government “Predator Free” target to “eradicate stoats (‘stoats’ includes all three mustelid species of stoats, ferrets and weasels), rats and possums” by 2050 (Department of Conservation, 2020). Meantime, most of the above species continue to inhabit and disturb the Maungakawa forest.



## 2.4 The study locations

Three accessible forest study locations at Maungatautari and at Maungakawa were identified (**Appendix 1**). The discrete study locations were limited to an altitude range of 240 to 380 m asl (**Table 2-1**) and the forest slopes generally facing the northeast to northwest direction. The length of each study margin needed to be accessible from a single-entry point and where all planned measurements could be completed within a 10-hour period including transport to and from the forest. Permission of landowners was sought to use farm tracks to access suitable forest margins. The research locations are collectively referred to as Maungakawa with the abbreviation “TT” (derived from Te Tāpui) and Maungatautari “MN” used as the identifiers to clearly differentiate the study locations throughout this thesis (**Appendix 2** to **Appendix 7**).

Study locations on Maungatautari (MND), (MNR) and (MNG) were all located within the Maungatautari predator proof fenced forest (**Figure 2-4**). Much of Maungatautari forest became a reserve in 1912 after a wildlife service survey found the forest to be of high significance (MEIT, 2020). Prior to installation of the predator proof fencing in 2006, Maungatautari, like Maungakawa today, had only farm boundary fencing separating the forest from adjacent pastoral land (Burns et al., 2011) The fences were in various states of repair and farm livestock grazed in some areas that are now within the predator proof fencing (D. Browning, forest surveyor in 1980, pers. comm.).

At Maungakawa the understorey and forest margins contrasted markedly between forests fenced to exclude livestock and unfenced forest fragments (**Figure 2-6** and **Figure 2-7**). TTB and TTJ were within the area administered by DOC as part of Te Tāpui Scenic Reserve. TTW was mainly within the scenic reserve fenced forest, but one transect (PCQ1) was in the fenced forest remnant in an adjacent gully on privately owned farmland. All fence lines were porous (**Figure 2-5**) as evidenced by cattle dung deposits within the scenic reserve forest and TTW gully and wildlife camera footage of forest dwelling folivores and herbivores accessing and browsing / grazing pastoral land.

**Table 2-1:** Forest and location topography: latitude and longitude at the access points for each study location. Altitudes are the highest and lowest points across the location.

Sample location	Maungatautari			Maungakawa		
	MND	MNR	MNG	TTW	TTB	TTJ
Latitude	-38.0008	-38.0030	-38.0148	-37.8027	-37.7997	-37.8302
Longitude	175.5771	175.5463	175.5334	175.6167	175.6046	175.6031
Altitude (m asl) low	294	255	259	240	277	258
Altitude (m asl) high	380	346	322	364	345	300



**Figure 2-4:** Sanctuary Mountain Maungatautari: The 3400 ha Waikato hill-country broadleaf-podocarp forest is enclosed by 47 km of predator proof fencing. Emergent rewarewa, pukatea and rata tower above the predominantly tawa canopy. (MNG February 2020)



**Figure 2-5:** Maungakawa Scenic Reserve Waikato - 1000 ha hill-country broadleaf-podocarp forest separated from adjacent pastoral land by traditional eight wire boundary fencing often in a poor state of repair. The fences are not a barrier to fallow deer, possums, rats, other small, introduced mammals and occasionally farm livestock. (TTB September 2019)





**Figure 2-6:** The margin of fenced but privately owned forest at Maungakawa with verdant grass growth up to the tree line. Introduced mammals including fallow deer reside both in the forest and on the farm side of the fence. (TTW Nov 2019)

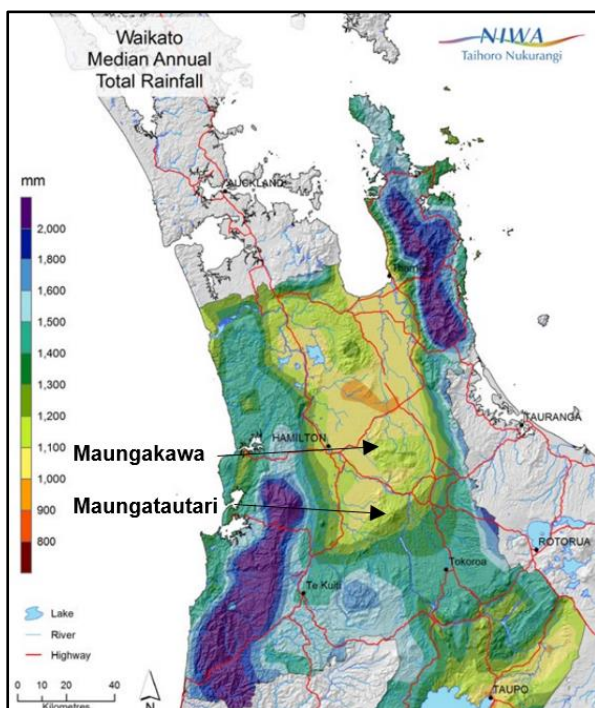


**Figure 2-7:** Undergrowth within the Te Tāpui Scenic Reserve fencing (on the left of the fence) contrasts with the adjacent unfenced forest remnant ground cover. Introduced mammals including fallow deer reside both in the forest and on the farm side of the fence. (TTB June 2020)

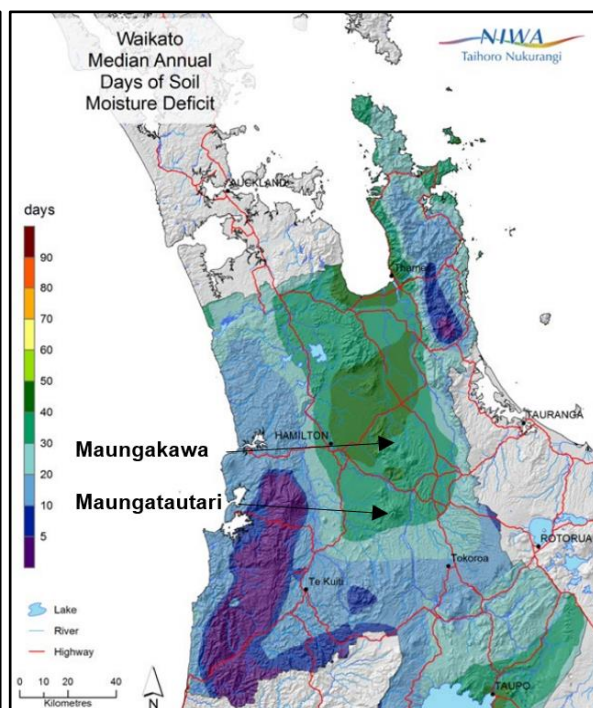
## 2.5 Climate

Climatic conditions in the forested study locations on Maungatautari and Maungakawa are similar. Median climatic data (1981 to 2010) for the Maungakawa and Maungatautari study locations which have consistent altitudes (240 to 380 m asl) was interpolated from maps published by NIWA (**Figure 2-8** to **Figure 2-13**). Details of statistical calculations (Chappell, 2014) and data are available at <https://niwa.co.nz/climate/our-services/virtual-climate-stations>. Since climate records were initiated in 1905, temperate climate conditions have prevailed; annual total rainfall 1100 to 1300 mm, annual days of soil moisture deficit 20 to 30 days, median average temperature between 12 and 14 °C, annual sunshine 1900 to 1950 hours, winter average daily minimum temperature between 4 °C and 5 °C, summer average daily maximum temperature 21 °C to 22 °C. Over the study period June 2019 to May 2021, air temperatures recorded at the nearest NIWA monitoring station, Hamilton airport, were above the historical average and rainfall was below average (**Figure 2-15**). In general cooler and wetter climates occur at higher elevations around Maungatautari peak (797 m asl) which is well above the study locations. During January and February 2020 drought conditions prevailed throughout the Waikato region (**Figure 2-14** and **Figure 2-15**) (NIWA, 2020).

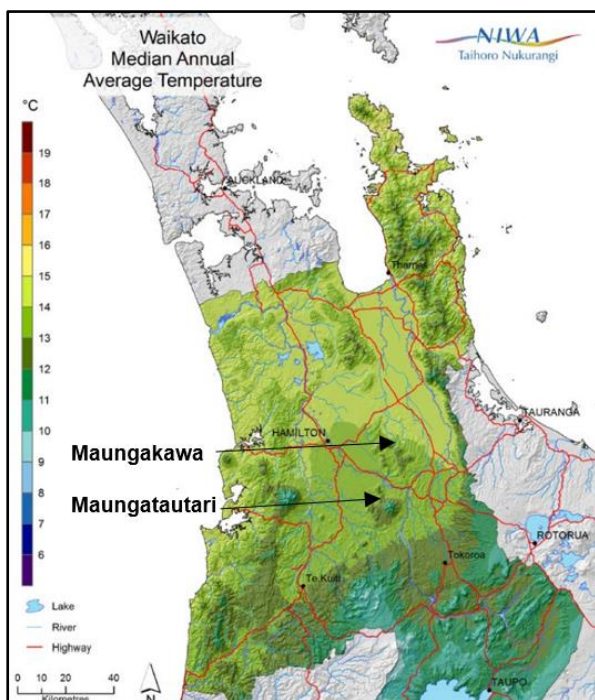
Temperature extremes within the forests were moderated. Data from a study north of Auckland (Young and Mitchell, 1994) suggests maximum air temperatures inside Maungatautari and Maungakawa forest would be 5 °C less than at Hamilton airport (**Figure 2-15**). Wildlife cameras (Chapter 4) recorded the ambient temperature on each image. Data (2020) from both forests indicated temperatures within the forest (approximately 50 m from the margin) ranged between -3 °C during the night in July to 22 °C mid-afternoon in the summer.



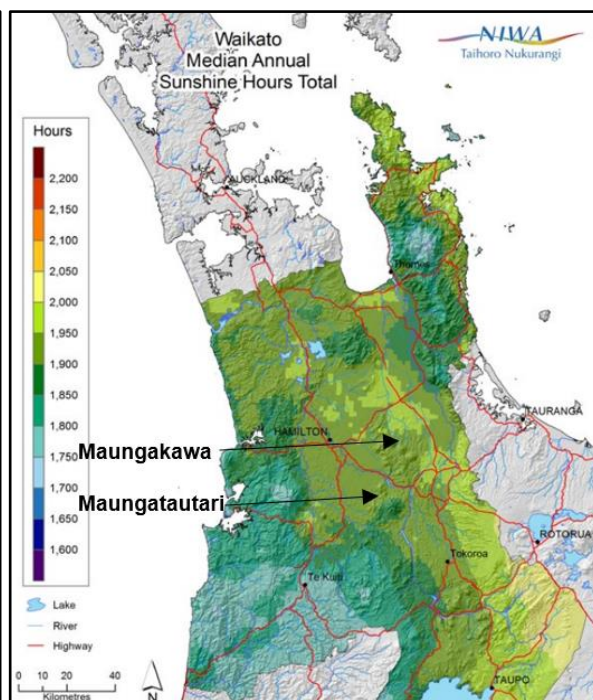
**Figure 2-8:** Waikato median annual total rainfall, 1981 to 2010.



**Figure 2-9:** Waikato median annual days of soil moisture deficit, 1981 to 2010.

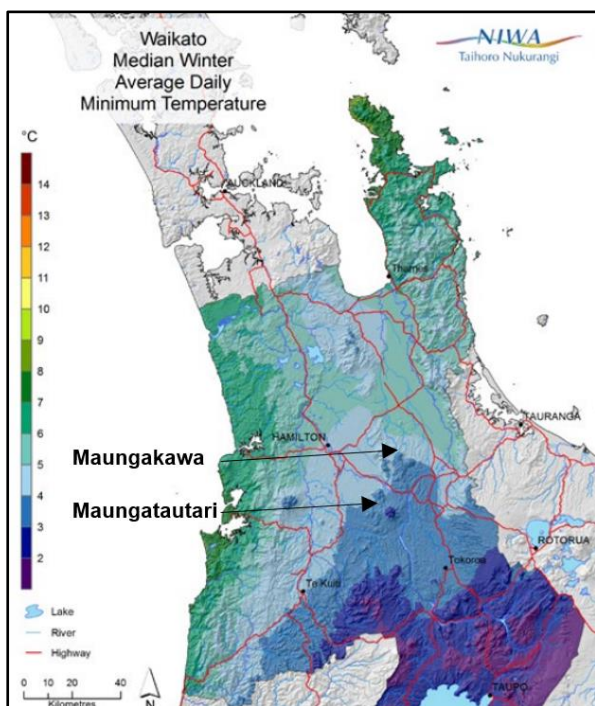


**Figure 2-10:** Waikato median annual average temperature, 1981 to 2010.

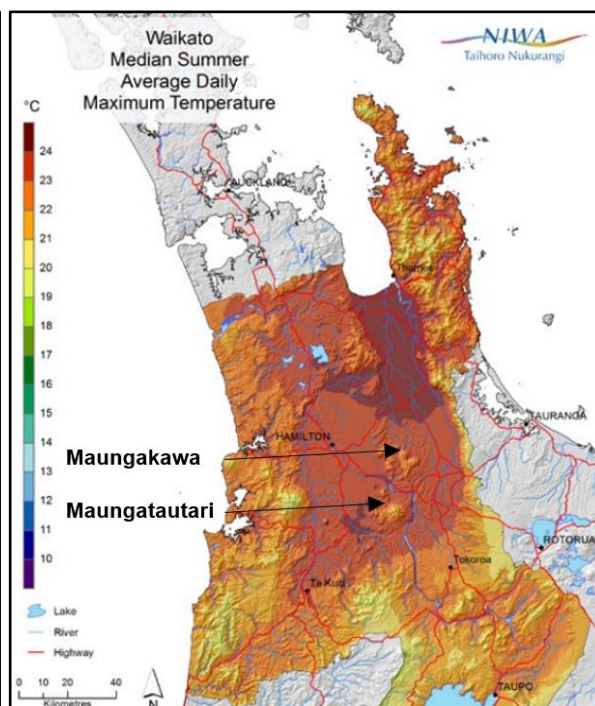


**Figure 2-11:** Waikato median annual sunshine hours total, 1981 to 2010.





**Figure 2-12:** Waikato median winter average daily minimum temperature, 1981 to 2010.

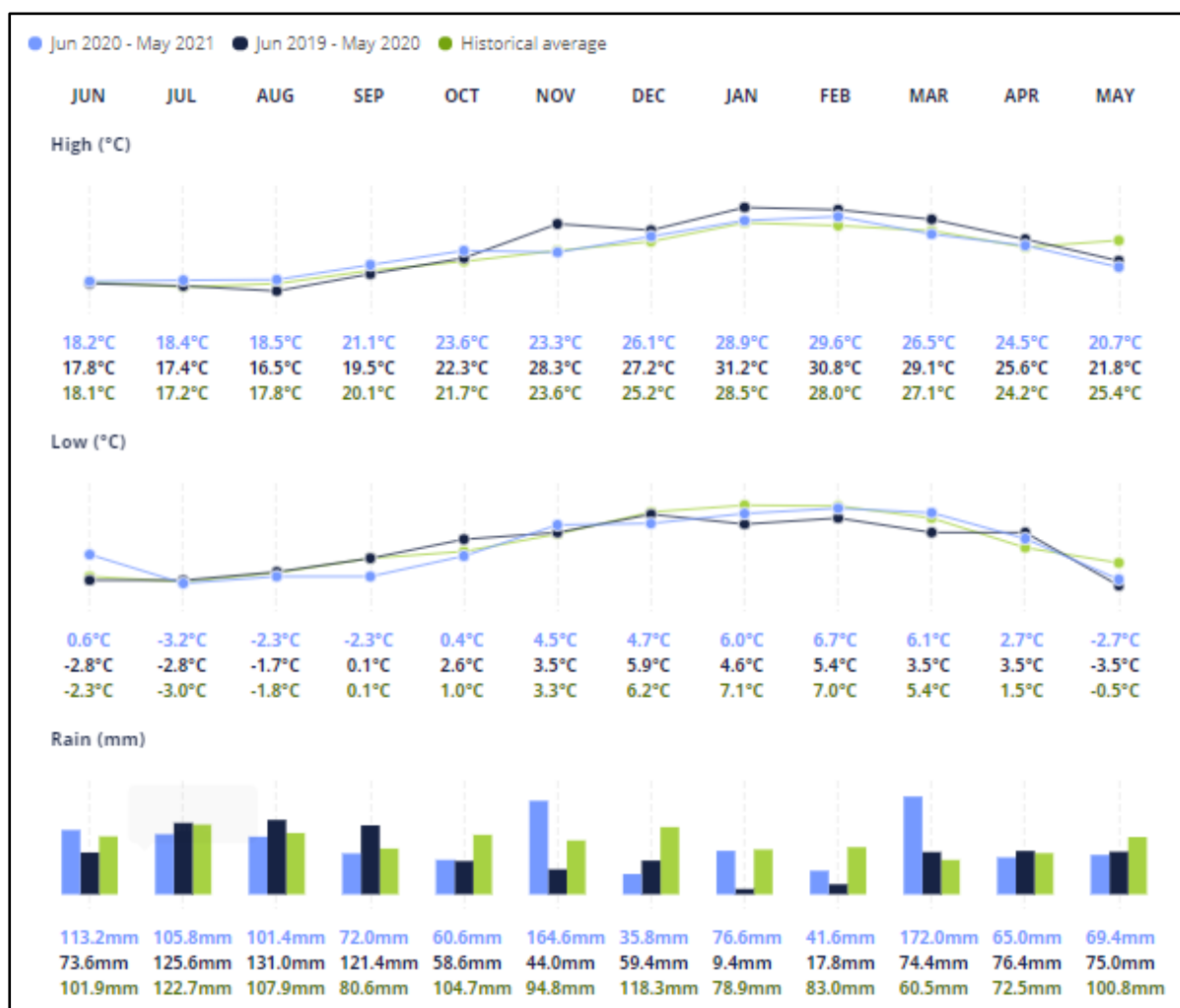


**Figure 2-13:** Waikato median summer average daily temperature maximum temperature, 1981 to 2010.

Maps (**Figure 2-8** to **Figure 2-13**) from <https://niwa.co.nz/static/Waikato%20ClimateWEB.pdf> accessed 18 Oct 2020.



**Figure 2-14:** Drought conditions prevailed in the Waikato in January and February 2020. (MNG February 2020). Photo credit: M. McCaughan.



**Figure 2-15:** Waikato temperature and rainfall during the study period (June 2019 to May 2021). The shade of the bar indicates the year or historical average. Temperature: The historical data is the extreme minimum and maximum air temperatures for the month averaged over a historical period (10 years). The data for the previous two years is the highest maximum and lowest minimum recorded for the month. Rainfall: The total rainfall that fell during the month. Observations were recorded at Hamilton Airport (AWS-93173). Data was obtained from: <https://www.metservice.com/towns-cities/locations/hamilton/past-weather> accessed 5 June 2021. This information is made freely available by MetService. Despite this, MetService is not associated with, and does not endorse, my research or have any involvement in how this information is presented.

## 2.6 Geology

Maungatautari and Maungakawa are extinct andesitic volcanic cones. The lavas at Maungatautari are derived from three distinct mantle sources. The andesitic-dacitic composite cone of Maungatautari formed around two million years (ma) ago originated in the Colville volcanic arc that extended south from Tauranga to Maungatautari (Prentice, 2017). Maungatautari lavas are thought to have resulted from partial melting of the subduction zone at a depth of 200 km (Cole, 1978). All Maungatautari study locations (MND, MNR, MNG) lie over this formation. Maungakawa on the west side of the Hauraki Depression formed around 1.8 ma (Cole, 1978; Prentice, 2017) although Black et al. (1992) date Maungakawa to



c. 5.7 ma. It is part of the 'Kiwitahi Volcanics' chain. This volcanic region is thought to have originated by partial melting of oceanic crust which had assimilated small amounts of sediment and been subducted to a depth of 150 to 200 km (Cole, 1978).

Slopes on the upper portions of Maungatautari mountain are steep ( $> 25^\circ$ ). Streams have deeply incised gullies. The forest cover has dampened water erosion and limited outcrop exposure; however, outcrops were observed within the forest particularly in the gullies. Outside the perimeter fence lower slopes are more rounded with moderate to gentle ( $6^\circ$  to  $25^\circ$ ) slopes and are covered in pasture (Prentice, 2017). Maungakawa topography resembles the lower slopes of Maungatautari.

## 2.7 Soils

Organic matter plays a major role in determining soil physical characteristics. Soils with medium to high organic matter levels would generally be expected to have good structure, moisture retention and water infiltration (Hill Laboratories, 2020). Anaerobically mineralisable nitrogen is the nitrogen component that can be readily mobilised from organic matter. Soil total nitrogen and total carbon for all forest locations fell within the medium to high value ranges for soil growing potential. Lower carbon to nitrogen ratios indicate greater nitrogen being available for potential growth. However, this is balanced by the organic component underlying optimal soil physical characteristics. An organic litter layer is present throughout the forest study locations apart from along frequently used deer tracks and occasional areas which became water courses following heavy rain.

Soils on Maungatautari and Maungakawa are brown granular clay / loam and yellow-brown loam on an andesitic base at Maungatautari, and basalt, andesite and greywacke base layers at Maungakawa (Deichmann, 2012). In the absence of published soil composition data specific to the study locations, soil samples were taken for analysis.

Soil samples were taken at each PCQ point where forest composition and structure was measured (Chapter 3) and seed traps were located (Chapter 3) (**Appendix 2 to Appendix 7**). To take each sample, an area as close as possible to the PCQ point that was free of large roots, was selected and the surface leaf litter and brown loam layers were removed. Using a hand trowel approximately 75 g of soil was collected from the darker layer at 10 to 15 cm depth and added to a forest location composite collection in a zip lock bag. Care was taken to ensure minimal organic matter (litter and root) contamination. The composited samples were sent to Hill Laboratories, Hamilton for analysis. Soil analysis included volume weight, organic matter (%), total carbon (%), total nitrogen (%) C/N ratio, anaerobically ( $AnO_2$ ) mineralisable N,  $AnO_2$  mineralisable N / Total% N Ratio and total phosphorus (mg /kg). At the laboratory samples were ground, dried and screened prior to analysis. At TTW the samples for PCQ1 and PCQ2 (**Appendix 5**) were collected on different dates and sent individually to the laboratory.

Reported results are the average for the two lines. Additional samples for each PCQ line at MND were taken later to confirm the initial analysis. Reported results (**Table 2-2**) are the overall average.

**Table 2-2:** Soil Analysis results for individual forest locations. Composited sample results are reported for Maungatautari locations (MND, MNR and MNG) and Maungakawa locations (TTW, TTB, TTJ). Samples for Maungakawa (TTW) PCQ lines 1 and 2 were collected on different dates and mean results are reported. Analysis by Hill Laboratories, Hamilton (IANZ accreditation number 365, soil chemistry)

Sample location	Units	Maungatautari			Maungakawa		
		MND	MNR	MNG	TTW	TTB	TTJ
Volume weight	g mL <sup>-1</sup>	0.70	0.66	0.72	0.79	0.67	0.70
Available nitrogen	kg ha <sup>-1</sup>	138	124	127	176	152	103
ANO2 mineralisable N	µg g <sup>-1</sup>	131	125	118	147	150	98
Organic matter	%	12.2	13.2	13.4	9.4	13.6	12.6
Total carbon	%	7.1	7.7	7.8	5.5	7.9	7.3
Total nitrogen	%	0.68	0.74	0.60	0.48	0.74	0.60
C/N ratio		10.4	10.3	12.9	11.5	10.7	12.1
AnO2 mineralisable N (N/Total% N ratio)		1.9	1.7	2.0	3.5	2.0	1.6
Total phosphorus	mg kg <sup>-1</sup>	1030	645	629	546	615	646

In general soil analysis yielded results in the medium to high soil quality ranges as published by the analytical laboratory publication; "Soils test and interpretation" (Kay and Hill, 1998). Overall, no significant differences ( $p < 0.05$ ) were found between the soils at Maungatautari (MND, MNR and MNG) and at Maungakawa (TTW, TTB and TTJ). Volume weight (previously known as bulk density) fell between peat predominantly organic content and that of clays. This was consistent with the loam composition of forest soils. At TTW PCQ1 the volume weight (15 cm depth) was 0.84 g mL<sup>-1</sup>. This was greater than on any other transect and aligned to the organic matter (9.4%), and total carbon (4.4%) being the lowest across both forests. TTW PCQ1 is within a narrow and relatively deep Maungakawa gully. The soil surface was heavily disturbed by mammal trampling, and in places heavy rainfall runoff to the stream where minimal forest litter accumulation was observed. This was consistent with increased volume weight (density) and reduced organic content.

Total phosphate concentrations in undisturbed native forest soils tend to be low compared to forests that have been subject to anthropogenic activity. Higher phosphates derived from the breakdown of organic litter tend to be retained in the upper soil layers. Across all study locations soil total phosphates at 10 to 15 cm depth (546 to 646 mg kg<sup>-1</sup> and 1033 mg kg<sup>-1</sup>) were greater than reported for a reference forest at Whatawhata, Waikato research station



(457 mg kg<sup>-1</sup> in the 0 to 10 cm soil layer and 355 mg kg<sup>-1</sup> in the 10 to 20 cm soil layer) but more closely align to pasture land concentrations (903 mg kg<sup>-1</sup> in the 0 to 10 cm soil layer and 345 mg kg<sup>-1</sup> in the 10 to 20 cm soil layer) (Stevenson, 2004). Across all study locations total phosphate concentrations possibly reflected drift from aerial superphosphate fertiliser applications (Stevenson, 2004). All PCQ lines (sampling points) were within 200 m of the forest margins. Applications of superphosphate fertiliser to adjacent pasture lands commenced in the mid-1940s (B. Garland, pers. comm.) and continues today although over the last 10 years advances in GPS and GIS have reduced poorly targeted applications and in general resulted in lower application rates.

## 2.8 My focus large-fruited broadleaved species

Despite similarities in ecological attributes and services (large-fruited broadleaved forest subcanopy / canopy trees), my focus tree species differ in their phenological development characteristics. Tawa has been the subject of a number of detailed scientific studies (Roper, 1967; Knowles and Beveridge, 1982; Morales, 2015), but published scientific details are comparatively sparse for mangeao and pigeonwood. Sampson (1969) published his PhD thesis which explored the floral morphology and gametophyte development of pigeonwood.

Tawa, mangeao and pigeonwood are codominant large, fleshy-fruited broadleaved species at Maungatautari and Maungakawa. Tawa and mangeao are Lauraceae and pigeonwood is classified in the closely related Monimiaceae family (Sampson, 1969). The conservation status of each of the species is “not threatened” (de Lange et al., 2017). The fleshy fruit of each species are favoured food for kererū (*Hemiphaga novaeseelandiae*) and smaller frugivorous birds that peck the flesh. A general description of each of the large-fruited broadleaved species is given here and their phenology was investigated (Chapter 5).

### 2.8.1 Tawa (*Beilschmiedia tawa*)

Tawa grows throughout the North Island and in the northern South Island. It is a major canopy tree, dominant in lowland and lower montane forest. It grows up to 35 m tall with a straight trunk up to 2 m diameter (**Figure 2-16**). It often develops a buttress base. Epicormic and coppice shoots can arise and persist. Multiple stems sometimes fuse back to a single trunk (Knowles and Beveridge, 1982). Tawa saplings are very shade tolerant and may live 60 to 80 years awaiting a light well opening in which to develop. Longevity is probably in the range 300 to 400 years (Ogden and West, 1981). Tawa is a monoecious species (Roper, 1967).



**Figure 2-16:** Mature tawa within both forests had tall trunks with spreading canopies. (TTJ close to PCQ2-5, November 2020)



### 2.8.2 Mangeao (*Litsea calicaris*)

Mangeao is a fairly localised tree in the top of the North Island but is more common in Waikato and Bay of Plenty forests, particularly on the deep “ash” soils and on the limestones in the western Waikato (Tane's Tree Trust, 2021). It favours high rainfall, but it is not tolerant of wet soils. The trunk is usually solitary and may have numerous suckers and epicormic shoots (Dawson et al., 2011). This dioecious (Poole and Adams, 1964) species is of intermediate shade tolerance, as seedlings and small saplings are often common in the understories but gaps are needed for them to get bigger (Smale and Kimberley, 1983; Lusk and Laughlin, 2017; Whyte and Lusk, 2019). Mangeao trees within Maungatautari and Maungakawa forests were very tall with little side branching (probably due to previous forest structure and high canopy) whereas margin trees were comparatively short and very branched (**Figure 2-17** and **Figure 2-18**). Although mangeao is not a “threatened” species, possum browse may be a problem. From time to time “mangeao die back” is reported in the media but the cause is unknown. The wood density and poorly defined growth rings hamper estimation of the longevity of mangeao (Tane's Tree Trust, 2021).



**Figure 2-17:** Mangeao trees in the margin are spreading and highly productive. (MNR January 2020)





**Figure 2-18:** Dieback was apparent in mangero at both Maungatautari and Maungakawa. Mangero with wide spreading full height canopies were only occasionally observed. (MNR January 2020)



### 2.8.3 Pigeonwood (*Hedycarya arborea*)

Pigeonwood is a common species up to 12 m tall and the trunk up to 0.5 m diameter. It is found in lowland and mid altitude forest in the North Island and in the South Island it grows at lower altitudes north of Banks Peninsula in the east and to Fiordland on the west coast. It is very shade tolerant and often found in the subcanopy. It usually occurs in moist situations such as damp gullies. (Dawson et al., 2011) Trees within the forest are usually clear of branches for the first few metres but on the forest margin where soils are moist it is a vigorous tree with vegetative growth extending from the ground to the canopy (Figure 2-19). Pigeonwood is a dioecious species (Sampson, 1969).



**Figure 2-19:** A mature pigeonwood in the margin at Maungatautari. The canopy extended from the ground to more than 8 m above and the tree fruited heavily in each year. (MNR HA5, January 2020)

# Chapter 3

## Forest structure and composition

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### 3.1 Introduction

The structure and community composition of Maungatautari and Maungakawa forests are diverging (Burns et al., 2011). Maungatautari is recovering from impacts of invasive mammals and logging over the past 200 years. Although logging no longer occurs in either forest, at Maungakawa invasive mammals continue to damage the forest. While invasive animals have only been absent from Maungatautari for a relatively short period, divergence of the forest communities are already apparent (Binny et al., 2021) particularly on the margins and in the undergrowth. However, the longevity of dominant trees can conceal gradual divergence in forest structure and composition (Smale and Kimberley, 1983; Burns et al., 2011).

In this chapter my focus was on determining the underlying forest structure and composition as well as the density and size of tawa (*Beilschmiedia tawa*), mangeao (*Litsea calicaris*) and pigeonwood (*Hedycarya arborea*) within my study locations at Maungatautari and Maungakawa. The data was used to facilitate understanding of the activities of invasive arboreal mammals i.e., rodents and possums (Chapter 5) and seed fall (Chapter 6).

A plotless point centred quarter (PCQ) technique (Cottam and Curtis, 1956) was used to establish the forest structure and composition of each forest study location. Compared to fixed plot measurements, the PCQ technique has the advantage of increased sampling efficiency. A number of authors have compared plotless measurements of forest composition with plot-based measurements (Cogbill et al., 2018). Bias in density estimates have long been recognised (Bryant et al., 2005) including specific examples from comparative studies of New Zealand indigenous forests (Franklin, 1967; Mark and Esler, 1970). Franklin, (1967) demonstrated high bias of PCQ measurements versus fully measured plot inventories in southern beech and podocarp forest but he couldn't explain the bias. A subsequent New Zealand study (Mark and Esler, 1970) revealed less bias in PCQ density estimations compared to plot-based measurements in North Island tawa forest. They did not describe the correlation for understorey / subcanopy layers of typically smaller shade tolerant species e.g., pigeonwood. As Maungatautari and Maungakawa fall within the same ecological district and apart from the last 16 years have had similar histories, I expect the bias to be similar at both forests. Therefore, for this study, PCQ is an acceptable method for measurement of species densities, basal area, and relative dominance at my study locations and forests.

## 3.2 Method

Absolute tree density and basal area for trees greater than 10 cm diameter at breast height (dbh) were measured at PCQ points. These points were located on each of two 200 m transects at each study location (**Appendix 2** to **Appendix 7**). The transects were spaced at least 100 m apart and ran at 90° to the margin on an approximately north to south orientation. PCQ points ( $n = 5$ ) were placed at random distances (between 31 and 40 m) along the transects. At Maungakawa two of the four transects previously measured for rat and possum abundance surveys were used. At Maungatautari the initial criteria for random placement of transects had to be over-ridden by health and safety concerns about steep drop offs and access causing damage to the forest. A conceptual line at right angles to the transect and radiating from the PCQ point divided the area around each point into quadrants. They were designated in anti-clockwise order: front left, back left, back right, front right. Each PCQ point was marked with labelled orange and blue flagging tape attached to the nearest reachable overhead vegetation e.g., tree or sapling branch or liane. At each point, the closest tree to the point in each of the four quarters around the point was identified and measured. For calculation of density the distance (metric) was measured, from the PCQ point to the mid-point of each identified tree's trunk(s). For calculation of the basal area a girthing tape (Forestry Supplies Inc. Jackson, MS, USA) was used to measure dbh<sub>135</sub>. The tape measured the trunk circumference but was marked in the calculated diameter (**Equation 1**). As breast height can be a very subjective measure, the height above ground level was defined to ensure consistent measurement by my field assistants. In New Zealand dbh is usually measured at 135 cm (dbh<sub>135</sub>) above the highest point at which the trunk emerges from the ground (**Figure 3-1**). The contingent forest structure and composition represents only the forest study locations bounded by the relevant forest margins and the transect penetration depth, 200 meters. Wildlife (Chapter 4) and seed fall (Chapter 6) were also measured on the transects at both forests.

Measuring the spacing of trees provided an accurate estimation of mean area each tree occupies ( $M$ ) and tree density (**Table 3-1**). This was applied to measure the total trees per area and individual species per area. The average of the four distances is equal to  $\sqrt{M}$  (Morisita, (1954) in Cottam and Curtis (1956). The mean area occupied by each tree is the reciprocal of the density. Therefore, density of trees ( $M^{-1}$ ) is calculated as trees per unit area e.g., trees  $m^{-2}$ . The mean density relates to the squared average distance of trees from each PCQ point, not the averaged space occupied by individual trees, see Cogbill et al. (2018) for discussion of point density estimators, accuracy and errors. To reduce error due to variable tree ecological responses between trees of single and mixed species, the most accurate measure of mean density is the sum of all distances over the study area divided by the number of distances (trees) measured (Cottam and Curtis, 1956).

Absolute density was reported for trees ( $\text{dbh}_{135} > 10 \text{ cm}$ ) at each study location and in each forest and for each species at each study location. Absolute tree density measurements were calculated from the mean distance of the nearest tree in each quarter at each PCQ point (**Equation 2**). The absolute density of trees in each study location and in each forest were calculated independently.

Basal area of measured trees is the sum of the cross-sectional area of tree trunks intersecting a horizontal plane at breast height (**Equation 4**). Basal area of an individual tree was obtained by measuring the diameter of the tree's trunk(s) at a standard height above ground level ( $\text{dbh}_{135}$ ) and calculating the cross-sectional area of each trunk (**Figure 3-1**). If a tree had multiple trunks (**Figure 3-3**), the basal area of each trunk was calculated before summing to obtain the basal area of the tree (**Equation 5**). Where possible the tape was placed under lianas attached to the tree or allowances were made (**Figure 3-4**). Where the trunk was swollen or had an indented contour, the tape was moved up or down the trunk to achieve the best possible estimate of  $\text{dbh}_{135}$  (Mitchell, 2010). Although tree ferns occupy canopy space (**Figure 3-2**), they did not contribute to seed fall (Chapter 6). Therefore, they were not included in measurement of the forest structure and composition.

Forest structure is represented by an estimate of tree density per unit area and the absolute basal area ( $\text{cm}^2 \text{ ha}^{-1}$ ) of the species or forest (**Equation 6**). Absolute basal area incorporates forest area through converting the sum of total measured basal area to basal area per unit area of forest per hectare (**Equation 7**). The disadvantage of this statistic is that the error in calculation of tree density becomes a source of error in comparison of the forest structures across the spatial landscape. Absolute tree density and absolute basal area statistical error calculations are not appropriate given the calculation includes values for the total area averaged distance squared. Traceable precision and accuracy of the original distance measurements are lost when mathematically manipulated. Cogbill et al. (2018) overcame this using computer simulations derived from bootstrapped data to create multiple random data sets from the original datasets. Relative dominance of each species was calculated (**Equation 8**) to ascertain the relationship of species cover within the forests.





**Figure 3-1:** Use of a girthing tape to obtain an accurate estimation of the trunk diameter. (Raukawa (*R. edgerleyi*) dbh<sub>135</sub> = 11.2 cm. TTJ PCQ2-4, back right quadrant, January 2020).



**Figure 3-2:** Radiating tree fern fronds occupy canopy space. (MNR PCQ1-4 January 2020)



**Figure 3-3:** Multi-stem tawa with all trunks dbh<sub>135</sub> > 10 cm. Note the shared root system from the base of trunks. (TTW PCQ2-4, September 2020)



**Figure 3-4:** A mature tawa with four multi-trunks of which three were dbh<sub>135</sub> > 40 cm and one trunk dbh<sub>135</sub> = 12.9 cm. The right-hand trunk had visible decay beneath the liana, but canopy foliage was still present. (TTW PCQ2-4, September 2020)

**Table 3-1:** Equations used to calculate absolute density, basal area of measured trees, absolute basal area, and relative dominance of trees and of species per area. Mathematical notation is defined in **Table 3-2**.

**Diameter of a trunk**

$$d = \frac{\pi}{c}$$

**Equation 1**

**Absolute density (trees ha<sup>-1</sup>) (transect, location or forest)**

$$\hat{\lambda} = \frac{1}{\left[ \sum_{i=1}^n \sum_{j=1}^4 (r_{ij}) \cdot (4n)^{-1} \right]^2} \times 10000$$

**Equation 2**

(Cottam and Curtis, 1956)

**Absolute density of a species (trees ha<sup>-1</sup>)**

$$\hat{\lambda}_k = \frac{\text{Qudarants with species } k}{4n} \times \hat{\lambda}$$

**Equation 3**

(Mitchell, 2010)

**Basal area of measured trees (cm<sup>2</sup>)**

$$\hat{\beta} = \sum_{i=1}^n \delta_i^2 \cdot \pi (4n)^{-1}$$

**Equation 4**

(Cottam and Curtis, 1956)

**Basal area of a multi trunk tree (cm<sup>2</sup>) (included in  $\hat{B}_{abs}$  as a “single” trunk)**

$$\hat{\beta} (\text{multi trunk tree}) = \sum_{j=1}^t \delta_j^2 \cdot \frac{\pi}{4}$$

**Equation 5**

(Mitchell, 2010)

**Absolute basal area of all trees or all trees of a species (cm<sup>2</sup> m<sup>-2</sup>)**

$$\hat{\beta}_{abs} = \hat{\lambda}_{abs} \sum_{i=1}^n \delta_i^2 \cdot \pi (4n)^{-1}$$

**Equation 6**

(Cogbill et al., 2018)

**Absolute basal area of all trees or all trees of a species (m<sup>2</sup> ha<sup>-1</sup>)**

$$\hat{\beta}_{abs} = \left( \hat{\lambda}_{abs} \sum_{i=1}^n \delta_i^2 \cdot \pi (4n)^{-1} \right) \times 10000$$

**Equation 7**

(Cogbill et al., 2018)

**Relative dominance of species *k* (%)**

$$\frac{\hat{\beta} \text{ of species } k}{\hat{\beta}_{abs} \text{ of all species}} \times 100$$

**Equation 8**

(Mitchell, 2010)

**Table 3-2:** Key to mathematical notation in PCQ formula used in this thesis.

Symbol	Value	Symbol	Value
$r_{ij}$	Distance (r) from point $i$ to the nearest tree in quadrant $j$	$n$	Number of points sampled
$\delta$	Diameter at breast height (dbh <sub>135</sub> ) of $i$ th tree (cm)	$k$	Identifier of a species
$\beta$	Basal area – cross sectional area of an individual tree at dbh <sub>135</sub>	$\pi$	3.14159
$\hat{\beta}$	Empirical estimator of basal area	abs	Absolute
$t$	Number of trunks of a multi-trunk tree	d	Diameter
$\lambda$	Absolute density – mean number of trees per unit area	c	Circumference
$\hat{\lambda}$	Empirical estimator of absolute density	rel	Relative

### 3.3 Data analysis

The structure and species composition of the study locations and the forest study areas were investigated using Statistica V13 (Tibco, Palo Alto, CA.) to analyse data. Absolute density and basal area analysis data met the assumptions of random sampling, normality and equal variance required for  $T$ -tests. For  $T$ -test statistical analysis each location and each species were independent variables.  $T$ -tests were used to determine if there was a significant difference in forest structure i.e., absolute density or absolute basal area of study locations at Maungatautari and at Maungakawa. As there were no replicates for forest absolute density and absolute basal area, this data was not able to be statistically tested. Absolute density of tawa, mangeao and pigeonwood and their basal areas within each forest were visualised using box and whisker plots (**Figure 3-5**).

Multidimensional scaling analysis (MDS) was used to investigate the species relationships (**Figure 3-6** and **Figure 3-7**): by density and by the sum of the basal area for individual species at each of the study locations. Data portrayed as ordination plots was carried out using Statistica V13 (Tibco, Palo Alto, CA) multivariate exploratory module. The MDS prerequisite pairwise Euclidean distance matrices were created for species names with absolute density and measured basal area as the independent variables. MDS rearranges objects, in this case the species, to arrive at a configuration in the form of an ordination plot that best approximates community composition rank order similarity.



## 3.4 Results

### 3.4.1 Forest structure

Forest density and absolute basal areas at Maungatautari and Maungakawa were similar (**Table 3-3**). Overall forest density at Maungatautari (465 trees ha<sup>-1</sup>) and at Maungakawa forest (484 trees ha<sup>-1</sup>) were similar (*T*-test  $p = 0.83$ ). Mean absolute basal area of Maungatautari forest study areas (50.7 m<sup>2</sup> ha<sup>-1</sup>) and Maungakawa forest (56.6 m<sup>2</sup> ha<sup>-1</sup>) were also similar (*T*-test  $p = 0.51$ ). At Maungatautari the nearest tree in each quadrant was within 10 metres of the PCQ point. At Maungakawa trees were generally more widely spaced with seven (12%) of nearest trees more than 10 metres from the PCQ point. However, at TTW increased numbers of juvenile canopy species (mainly tawa) and smaller subcanopy species (mahoe and pigeonwood) led to the increased absolute density at this study location.

**Table 3-3:** Absolute density and absolute basal area of trees (dbh<sub>135</sub> great than 10 cm) within the study locations at Maungatautari and Maungakawa and the study locations at each forest.

		Absolute density ( $\hat{\lambda}_{abs}$ ) (trees ha <sup>-1</sup> )		Absolute basal area ( $\hat{\beta}_{abs}$ ) (m <sup>2</sup> ha <sup>-1</sup> )	
	Location	Forest		Location	Forest
<b>Maungatautari</b>		465			50.7
	MND	533		39.7	
	MNR	529		59.6	
	MNG	366		51.2	
<b>Maungakawa</b>		484			56.6
	TTW	697		80.1	
	TTB	424		56.3	
	TTJ	403		41.3	

Absolute density difference between forests: *T*-test  $p = 0.83$

Absolute basal area difference between forests: *T*-test  $p = 0.51$

### 3.4.2 Forest composition

Across Maungatautari and Maungakawa forests, 15 species of endemic broadleaved species and a single endemic podocarp were identified as the nearest tree in at least one PCQ quarter (**Table 3-5** and **Table 3-6**). Tawa, mangeao, pigeonwood, mahoe (*Melicytus ramiflorus*), pukatea (*Laurelia novae-zelandiae*) and rewarewa (*Knightia excelsa*) occurred at each location. Other endemic species: heketara (*Olearia rani*), kamahi (*Weinmannia racemosa*), kawakawa (*Piper excelsum*), lancewood (*Pseudopanax crassifolius*), lemonwood (*Pittosporum eugenioides*), pate (*Schefflera digitata*), raukawa (*Raukawa edgerleyi*), red mapou (*Myrsine australis*), titoki (*Alectryon excelsus*) and rimu (*Dacrydium cupressium*)

occurred in varying numbers sporadically or occasionally. The single rimu measured, had only reached subcanopy height. There were no emergent podocarps. In the absence of the original emergent podocarp over-canopy, tawa, rewarewa, pukatea, and mangeao have become the dominant canopy layer. Some of the remaining species, usually described as subcanopy trees, reach into the canopy layer. A range of other broadleaved species e.g., kohekohe (*Dysoxylum spectabile*) and developing podocarps e.g., miro (*Prumnopitys ferruginea*) and matai (*Prumnopitys taxifolia*) were observed within the forest, but they did not occur as the nearest tree in a quarter at any PCQ point or they were less than 10 cm dbh<sub>135</sub>. Between eight and ten species were measured at all study locations except at TTB where diversity was limited to six species. Forest composition and structure in my study locations were consistent with previously reported research for these forests (as discussed in Chapter 2).

The absolute density and basal area of each of my study species, tawa, mangeao and pigeonwood, were similar at Maungatautari and Maungakawa (**Table 3-4** and **Figure 3-5**). Tawa was a dominant species in both forests (Maungatautari relative dominance = 29% and Maungakawa relative dominance = 36%) with mangeao being a codominant at Maungatautari (relative dominance = 26%) (**Table 3-5** and **Table 3-6**). Mangeao contributed 16% of basal area at Maungakawa. In both forests basal areas of both tawa and mangeao were more than five times that of pigeonwood although absolute density was within the same order of magnitude. Pigeonwood sizes were similar at both forests apart from two very large trees (basal area 1906 cm<sup>2</sup> and 2019 cm<sup>2</sup>) that were statistical outliers at Maungakawa. The tree with basal area 2019 cm<sup>2</sup> appeared to have been damaged at sapling stage. The lower trunk was almost parallel to the ground for about one meter with two side trunks each greater than 10 dbh<sub>135</sub> ascending vertically from it. The highest density of pigeonwood was on the gully transect at Maungakawa.

Multidimensional scaling analysis (MDS) based on absolute density for each species (**Figure 3-6**) reveals community composition at TTW stands apart from all other locations. TTW absolute density (697 trees ha<sup>-1</sup>) included the highest density of tawa (139 trees ha<sup>-1</sup>), pigeonwood (174 trees ha<sup>-1</sup>) and mahoe (174 trees ha<sup>-1</sup>) and the least mangeao (17 trees ha<sup>-1</sup>). All other locations had 366 to 533 trees ha<sup>-1</sup> and more homogenous species distributions. Similar MDS analysis of community composition based on basal area for each species (**Figure 3-7**) on transects at each location reveals there were more larger trees of the common species at TTB and MNG which caused them to plot at a distance from the other study locations.



**Table 3-4:** Tawa, mangeao and pigeonwood absolute density (trees ha<sup>-1</sup>) and basal area (cm<sup>2</sup>) for the forest and study locations: Maungatautari (MND, MNR, MNG) and Maungakawa (TTW, TTB, TTJ). The study location basal area data was used to calculate seed fall abundance (Chapter 6).

Location	Absolute density (trees ha <sup>-1</sup> )			Sum basal area (cm <sup>2</sup> )		
	Tawa	Mangeao	Pigeonwood	Tawa	Mangeao	Pigeonwood
<b>Maungatautari</b>						
Forest	85	81	54	37990	33909	3751
<b>Study Locations</b>						
MND	53	133	80	2881	18435	1472
MNR	66	119	40	8809	12095	872
MNG	119	18	46	26300	3380	1406
<b>Maungakawa</b>						
Forest	117	48	81	50719	21857	10039
<b>Study Locations</b>						
TTW	139	17	174	14517	531	5303
TTB	117	85	32	22928	18418	1960
TTJ	101	30	70	13275	2908	2776

**Absolute density (trees ha<sup>-1</sup>) difference between forests (*T*-test):**

Tawa:  $p = 0.16$

Mangeao:  $p = 0.33$

Pigeonwood:  $p = 0.45$

**Basal area (cm<sup>2</sup>) difference between forests (*T*-test):**

Tawa:  $p = 0.61$

Mangeao:  $p = 0.60$

Pigeonwood:  $p = 0.11$

## Absolute density (trees ha<sup>-1</sup>)

## Tree basal area (tree cm<sup>2</sup>)

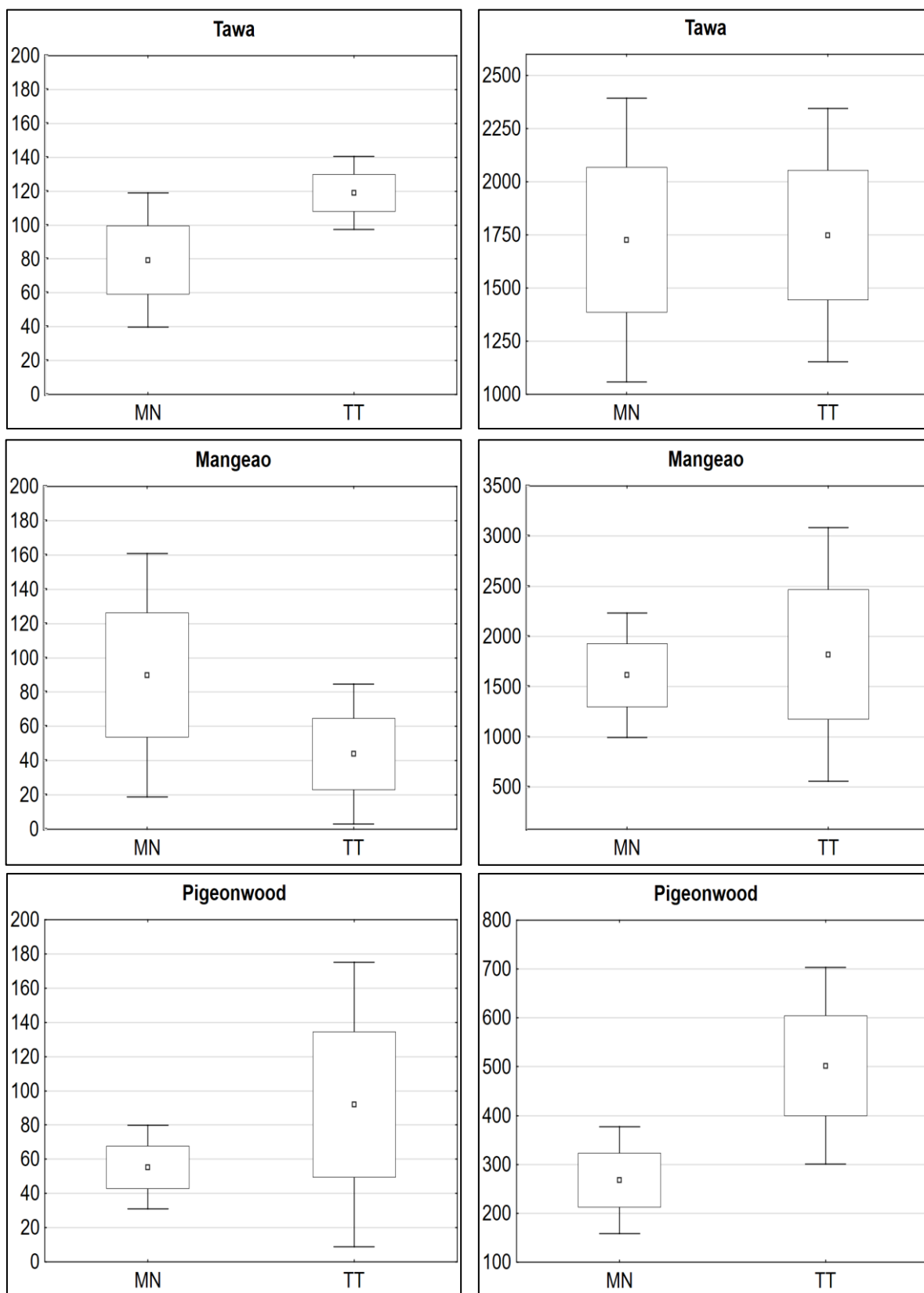
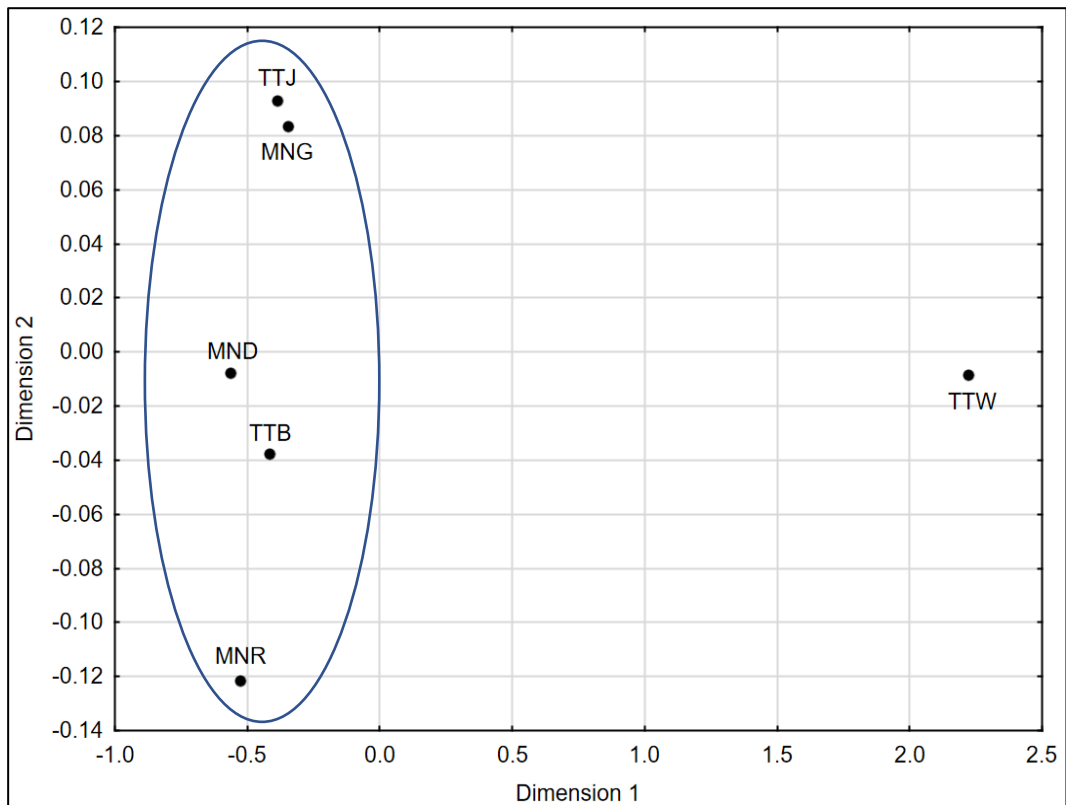
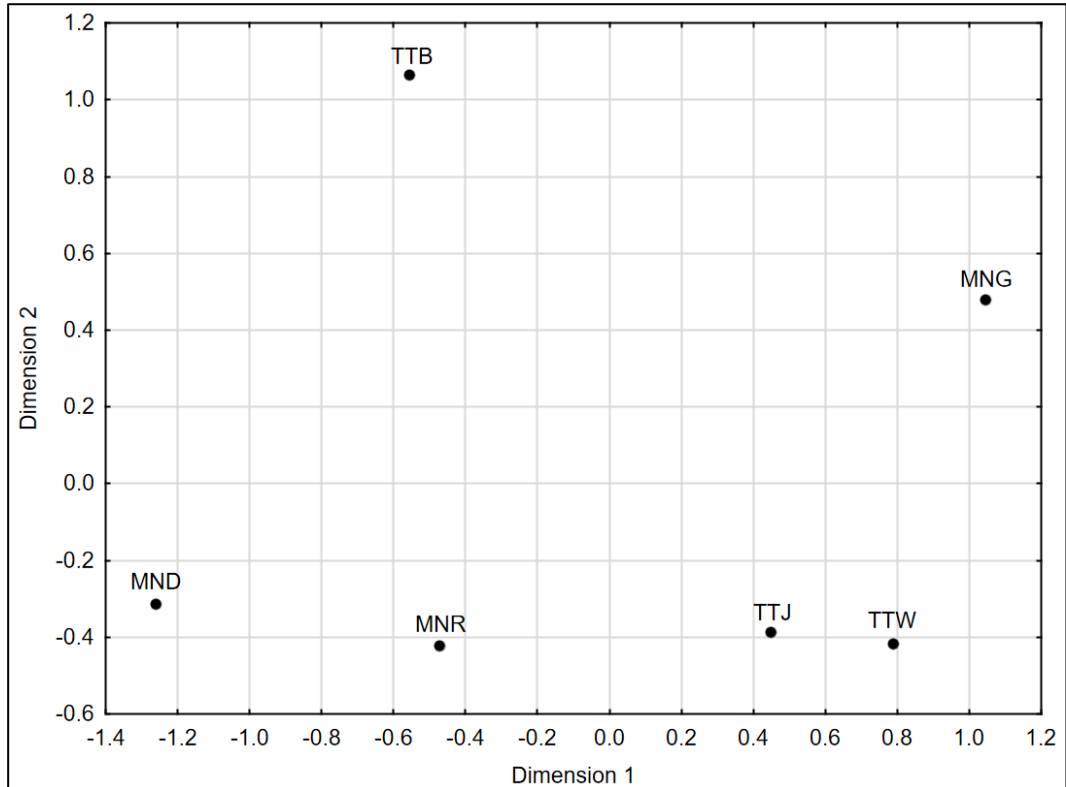


Figure 3-5: Distributions of the absolute density (trees ha<sup>-1</sup>) of tawa, mangeao and pigeonwood at each study location and the basal area (cm<sup>2</sup>) of individual trees. Notes: Basal area y axis scales are different on each plot, only trees > 10 dbh<sub>135</sub> (basal area > 80 cm<sup>2</sup>) were measured. Mean point, box  $\pm$  SE and whisker bars  $\pm 1.96$  SD. Abbreviations: Maungatautari (MN), Maungakawa (TT).



**Figure 3-6:** Relationships between absolute density of forest species (**Table 3-5** and **Table 3-6**) across locations in Maungatautari (MN) and in Maungakawa (TT) forests. Forests grouped within the blue ellipse are most similar. D-hat stress = 0.01 indicates excellent resolution



**Figure 3-7:** Relationships between mean basal area of forest species (**Table 3-5** and **Table 3-6**) across locations in Maungatautari (MN) and in Maungakawa (TT) forests. Similarity grouping was not strong. D hat stress= <0.01 indicates excellent resolution.

**Table 3-5:** Maungatautari: Species counts, absolute density, relative density, basal area and relative dominance for each forest location. NVS codes, botanical names, family, and genus, species codes and species names and vernacular names, are indexed in **Appendix 8**.

NVS Species Code	MND					MNR					MNG				
	Species count	Absolute density (trees ha <sup>-1</sup> )	Relative density (%)	PCQ points basal area (cm <sup>2</sup> )	Relative dominance (%)	Species count	Absolute density (trees ha <sup>-1</sup> )	Relative density (%)	PCQ points basal area (cm <sup>2</sup> )	Relative dominance (%)	Species count	Absolute density (trees ha <sup>-1</sup> )	Relative density (%)	PCQ points basal area (cm <sup>2</sup> )	Relative dominance (%)
ALEEXC											1	9	2.5	2489	4.5
BEITAW	4	53	10.0	2881	9.7	5	66	12.5	8809	19.6	13	119	32.5	26300	47.0
DACCUP															
HEDARB	6	80	15.0	1472	4.9	3	40	7.5	872	1.9	5	46	12.5	1406	2.5
KNIEXC	3	40	7.5	3054	10.3	5	66	12.5	7202	16.0	3	27	7.5	2309	4.1
LAUNOV	4	53	10.0	1228	4.1	3	40	7.5	5657	12.6	4	37	10.0	13357	23.9
LITCAL	10	133	25.0	18435	61.9	9	119	22.5	12095	26.8	2	18	5.0	3380	6.0
MELRAM	7	93	17.5	2030	6.8	5	66	12.5	2834	6.3	8	73	20.0	5030	9.0
MYRAUS						1	13	2.5	179	0.4					
OLERAN															
PIPEXC	5	67	12.5	598	2.0	1	13	2.5	119	0.3					
PITEUG											1	9	2.5	1276	2.3
PSECRA															
RAUEDG															
SCHDIG	1	13	2.5	88	0.3						3	27	7.5	358	0.6
WEIRAC						8	106	20.0	7279	16.2					



**Table 3-6:** Maungakawa: species counts, absolute density, relative density, basal area and relative dominance for each forest location. NVS codes, botanical names, family, and genus, species codes and species names and vernacular names, are indexed in **Appendix 8**.

NVS and Species Code	TTW					TTB					TTJ				
	Species count	Absolute density (trees ha <sup>-1</sup> )	Relative density (%)	PCQ points basal area (cm <sup>2</sup> )	Relative dominance (%)	Species count	Absolute density (trees ha <sup>-1</sup> )	Relative density (%)	PCQ points basal area (cm <sup>2</sup> )	Relative dominance (%)	Species count	Absolute density (trees ha <sup>-1</sup> )	Relative density (%)	PCQ points basal area (cm <sup>2</sup> )	Relative dominance (%)
ALEEXC	1	17	2.5	423	0.9						1	10	2.5	460	1.1
BEITAW	8	139	20.0	14517	31.5	11	117	27.5	22928	43.2	10	101	25.0	13275	32.4
DACCUP											1	10	2.5	1787	4.4
HEDARB	10	174	25.0	5303	11.5	3	32	7.5	1960	3.7	7	70	17.5	2776	6.8
KNIEXC	5	87	12.5	6033	13.1	6	64	15.0	4377	8.2	8	81	20.0	7728	18.9
LAUNOV	2	35	5.0	12659	27.5						5	50	12.5	9238	22.5
LITCAL	1	17	2.5	531	1.2	8	85	20.0	18418	34.7	3	30	7.5	2908	7.1
MELRAM	10	174	25.0	5022	10.9	9	95	22.5	5158	9.7	2	20	5.0	2506	6.1
MYRAUS															
OLERAN	1	17	2.5	1269	2.8										
PIPEXC	1	17	2.5	79	0.2	3	32	7.5	272	0.5					
PITEUG															
PSECRA	1	17	2.5	177	0.4										
RAUEDG											1	10	2.5	99	0.2
SCHDIG											2	20	5.0	206	0.5
WEIRAC															

# Chapter 4

## Contrasting wildlife presence and impacts.

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### 4.1 Introduction

Rodents and possums (*Trichosurus vulpecula*) disrupt forest ecology and biodiversity across the New Zealand landscape (Leathwick et al., 1983; Rogers and Leathwick, 1997; Craig et al., 2000). In less than 200 years, ship rat (*Rattus rattus* or black rat), Norway rat (*R. norvegicus* or brown rat) and possums have invaded almost every forest, pastoral, coastal and urban environment (King, 1984). Kiore (*R. exulans* or Pacific rat), introduced by early Polynesian settlers in the 13<sup>th</sup> century, disappeared from across most of the North and South Islands as ship rats and Norway rats spread but some remain on outlying islands (Wilmshurst and Ruscoe, 2021). Possums were first liberated into Waikato forests between 1883 and 1929 (Pracy, 1962).

The home ranges of rodents and possums are three dimensional (Atkinson, 2006). In summer 2008, ship rat abundance ( $6.5 \text{ ha}^{-1}$ ) in fenced Waikato forest fragments was higher than any previous measurements on the New Zealand mainland (Innes et al., 2010b). Cowan and Glen (2021) compiled multiple studies since the 1970s to estimate that possum density in broadleaf-podocarp forest nationally, averaged between 10 and  $12 \text{ ha}^{-1}$  (range 7 to  $24 \text{ ha}^{-1}$ ). Relative abundance surveys at Maungakawa, where no small invasive mammal control was undertaken between 2012 and June 2020, detected rats on more than 70% of measuring devices on the ground and in the forest canopy in 2015 (Innes et al., 2018). Rat abundance sometimes increases following possum control (Sweetapple and Nugent, 2007) probably reflecting reduced competition for food resources such as seeds and fruit. Possums were detected on 25% of devices on the ground and only occasionally in the canopy, while mice (*Mus musculus*) were occasionally detected only on the ground (Innes et al., 2018). At Maungatautari, predator control programmes and rigorous monitoring are used to ensure the forest remains free of invasive mammals, excepting mice. Without larger rodents present, mice have thrived and now inhabit the forest floors, shrub and subcanopy layers. They were not detected in the upper canopy (Innes et al., 2018). However, mice may perpetuate the damage caused by rats, particularly destruction of small seeds when they consume them (Williams et al., 2000).

Rodents and possums are polyphagous arboreal mammals. Possums switch between nutritionally different foods to meet their dietary needs. The vegetative component of their diet includes leaves (photosynthetic energy resource) as well as reproductive structures, flowers, fruit and seeds (Cowan and Waddington, 1990; Lord, 1999; Coomes et al., 2003). A two-year study of rat and possum diets in a North Island podocarp hardwood forest found rats' stomach contents had 26% fruit dry matter, 48% seed dry matter and 23% invertebrates, with less than

3% other foods including herbaceous and woody foliage. In contrast possum stomachs contained 38% seed dry matter, 15% fruit dry matter and 47% other foods including 33% woody foliage (Sweetapple and Nugent, 2007). Mature possums weighing 2.3 to 4.9 kg (Cowan and Glen, 2021) would be expected to consume greater volumes than rats that weigh only 120 to 300 g (Campbell and Atkinson, 2002; King and Forsyth, 2021).

The invasive mammals' food preferences are partitioned by differences in their digestive systems and food availability (Nugent et al., 2001). Rats destroy all but the smallest of the seeds they consume (Williams et al., 2000). Possums consume a wide range of fruits but when eating larger fruits including tawa (*Beilschmedia tawa*) and pigeonwood (*Hedycarya arborea*), they eat only the flesh and discard the seeds (Cowan, 1992). Possums destroy 15% of the seeds they consume and they only defaecate whole seeds less than 7.1 mm (mean) diameter (Wyman and Kelly, 2017).

Rats and possums have been found to depress seed production and/or reproduction of some large-fruited tree species in New Zealand forests with some species becoming rare where the invasive mammals are present (Fitzgerald, 1976; Campbell, 1990; Campbell and Atkinson, 2002; Burns et al., 2011). In some forest species, recovery of seed production follows release from browse damage (repeated pruning) by possums (Ramsey et al., 2002) thereby increasing food resources for rats. Rats and possums predate reproductive parts in other forest species such as hīnau (*Elaeocarpus dentatus*) buds and flowers during winter and spring when other food resources are low (Cowan, 1990). Other wildlife such as birds, insects, lizards, and bats also feed on reproductive parts.

Predator control at Maungakawa has been intermittent. Waikato Regional Council (WRC) confirmed that no small mammal predator control had been carried out between November 2011 and June 2020 (mid-way through this research study) when a campaign targeted at possum control was undertaken. Aerial pre-baiting was carried out over the entire Te Tāpui Scenic Reserve, followed by 1080 ground baiting using the existing ground-based bait station infrastructure in Maungakawa forest (Te Tāpui A block) and aerial 1080 baiting over the remaining forest (pers. comm from the contractor, EcoFX Limited). Pre and post baiting possum relative abundance were measured using leg hold traps to determine the Residual Trap Catch (RTC) data provided for my research. Areas of remnant forest outside the Scenic Reserve but included within my study locations i.e., TTW PCQ1 (**Appendix 5**), and TTJ (insert in **Appendix 7**), were not covered by the Waikato Regional Council (WRC) initiated possum control campaign. One transect (TTW PCQ1 and TL3) was within a forest remnant fenced to exclude farm stock. Margin trees on areas of unfenced forest (TTB and TTJ) were only measured as part of the phenology study (Chapter 5). At TTJ, the farm owners lay bait to control rodents and regularly control possums by shooting. Under the national TB control programme, OSPRI completed rat and possum control during summer 2019/20 across farms, adjacent to the western and southern boundaries of Te Tāpui Scenic Reserve. This campaign



included forest remnants at TTB and TTJ. Invasive mammal control within the fenced forest remnant outside of the Scenic Reserve (TTW) was limited to farm personnel occasionally shooting “possums, hares and deer”. The farmer reported shooting 15 possums in a single night in March 2021.

Multiple methods are available to measure rodent and possum density across the landscape. When areas and survey conditions are standardised over time and there is a demographically closed population, tracking tunnels and chew cards provide a standardised relative abundance index; for rodents (Gillies and Williams, 2013) (denoted herein as RTI) and for possums (Sweetapple and Nugent, 2011; NPCA, 2015) (denoted herein as CCI). The standardised protocols are designed for large-scale surveys where 500 m transects are spread at least 200 m apart. Brown et al. (1996) found a “linear relationship between rat density (estimated by extinction trapping) and rat tracking rate”, but where rodents occur at high densities, saturation of tracking cards may occur (Gillies and Williams, 2013). Utilising tracking tunnels across a grid is a simple, rapid and cost effective approach (Innes et al., 2018) suitable for comparison of the relative abundance index (RAI) of rats within small locations over an extended period and a fine spatial scale. Leaving the tunnels in place throughout the research period ensured detection parameters were replicated and hence validity of the comparative data.

Possums are attracted to rodent tunnel lures, but usually their size prevents them entering the tunnel. They may leave paw marks on the ends of cards or remove the card and/or destroy the tunnel. Residual trap catch (RTC) using leg hold traps is regarded as a reference method to determine possum population size (NPCA, 2015). Sweetapple and Nugent (2011) report chew cards appear to be as sensitive, or more so, than leg hold traps for detecting possums. Chew cards with lures attractive to possums also attract rodents, however the different species are distinguishable by characteristic bite mark patterns (Sweetapple and Nugent, 2011). Possum and rat abundance may be biased by a high rate of contra-specific interactions with the cards (Sweetapple and Nugent, 2011; Burge et al., 2017). The relative abundance index measured as the chew card index (CCI) for cards set out for three (CCI<sub>3</sub>) or seven (CCI<sub>7</sub>) nights (Gillies, 2013) have not been validated against RTC (NPCA, 2015). Forsyth et al. (2018a) have more recently demonstrated that chew card relative abundance index (CCI) and RTC are comparable when the cards are set out for only one night and “possum dough” lure is used.

Over the last 20 years camera traps (wildlife cameras with motion sensors) have been recognised as an effective and non-invasive tool for detection and surveillance of wildlife (Anton et al., 2018). Camera traps enable ecological and conservation data collection across extended spatial and temporal scales. They permit close up observation of wildlife behaviour within their natural environment. (Delisle et al., 2021). Camera traps were set up at a standardised point on each PCQ transect for 12 months to corroborate wildlife activity

(**Appendix 12**) and at supplementary locations of interest. More than 100 000 camera trap hours (CTH) (Rovero et al., 2013) were recorded.

Documenting the relative abundance of each of the invasive species, and their behaviour, informs where and how they disrupt ecology on spatial and temporal scales (Forsyth et al., 2018b). Compared to Maungatautari forest, Maungakawa forest interior lacks understorey diversity and abundance (Burns et al., 2011). At landscape level, field signs (Cowan and Glen, 2021) of possum presence and behaviour were readily observed throughout the forest and on adjacent pastures. Signs included torn leaves on species palatable to possums, horizontal teeth scars on the bark of a variety of trees and teeth indentations on fruit, the almost complete absence of a favoured food; pohuehue (*Muehlenbeckia australis*) vines (Sweetapple et al., 2013) along forest margins, as well as faecal pellets both on the ground (**Figure 4-15**) and in seed traps (Chapter 6).

Rodent and possum activity was measured along forest transects where I had also measured forest composition and structure (Chapter 3), tree phenology (Chapter 5) and concurrently measured fruit and seed fall (Chapter 6). Camera trap evidence and searching for clues dropped from the canopy above, had to substitute for direct observation of their nocturnal arboreal lifestyles.

I asked three questions:

1. What is the relative abundance of rodents and possums within the contrasting Waikato hill-country forests?
2. How active are rodents and possums at ground level?
3. Did habitat usage, and activity patterns of rats and possums change following the possum control campaign?

## 4.2 Methods

### 4.2.1 Rodent footprint surveys

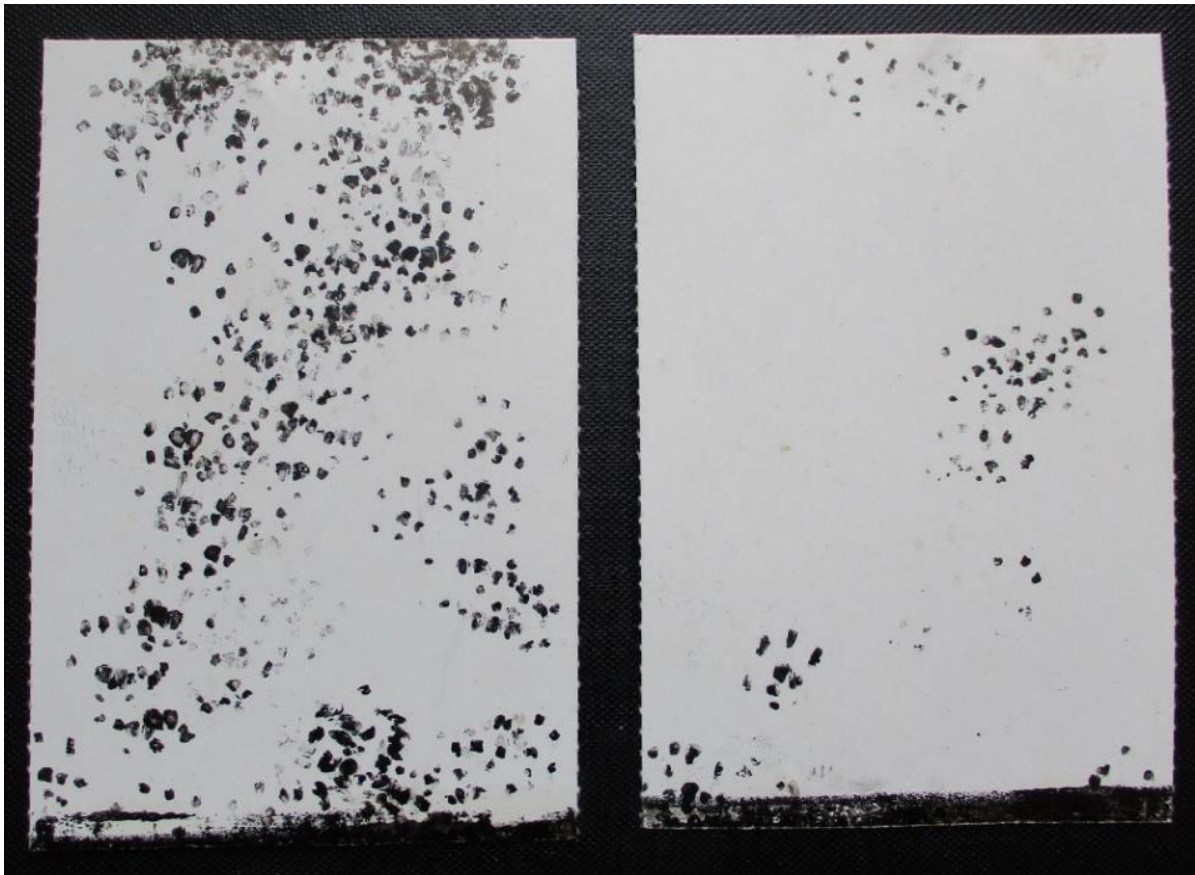
Rodent abundance (RAI) was determined using rodent tunnels with Black Trakka™ tracking cards inserted (Gotcha Traps Ltd, 2019). At Maungakawa, each study location was approximately 6 ha which is only 3% of the area considered small in the DOC guide (Gillies and Williams, 2013). This made it more appropriate to lay tunnels out on a grid (Innes et al., 2010b) although they were accessed along transects (**Appendix 2** to **Appendix 7**). At each study location, rodent tunnel line (TL) transects (4 x 200 m, each at 90° to the margin) were set out at 100 m intervals along the forest margin (400 m). On each transect, a tunnel was set out at the margin and four tunnels placed at 50 m intervals along the transect. Tunnels were placed level on the ground and secured with wire pegs. Where ground conditions or terrain topology presented increased health and safety hazards, such as steep overhangs or there was a risk of tracking cards getting wet i.e., close to streams and swampy ground, the rodent

tunnel was moved along the transect to the nearest safe position. TTJ TL4-4 was moved to the far side of swampy ground and the transect distances restarted; TTJ TL4-5 being placed a further 50 m along the transect. The transects were set in position between one and four weeks prior to the initial survey, October 2019, and remained *in situ* throughout this study. Further surveys were completed in January 2020 and in October 2020 (post possum control). All tunnel locations were mapped using GIS. The intended straight transects deviated at TTJ TL1-3 and at TTW TL1-3 where each transect veered to the north-west. These transect set outs were retained as time and resource constraints prevented further forest visits to realign the transect at least seven days prior to the first survey. The errors were unlikely to have influenced the estimation of rodent behaviour at these forest locations. On the survey dates, tracking cards with peanut butter lure, were installed in the rodent tunnels. Lure was smeared on the card centrefold and on the plastic surface inside each tunnel entrance (Innes et al., 2018). The cards were left in the field for 24 hours. Retrieved cards were examined and identification of species footprints determined with reference to Agnew (2012) (**Figure 4-1**). The cards were scored for the presence (1) or absence (0) of characteristic footprints of each species (Gillies and Williams, 2013). As recommended by Gillies (2013), cards were checked by an expert.

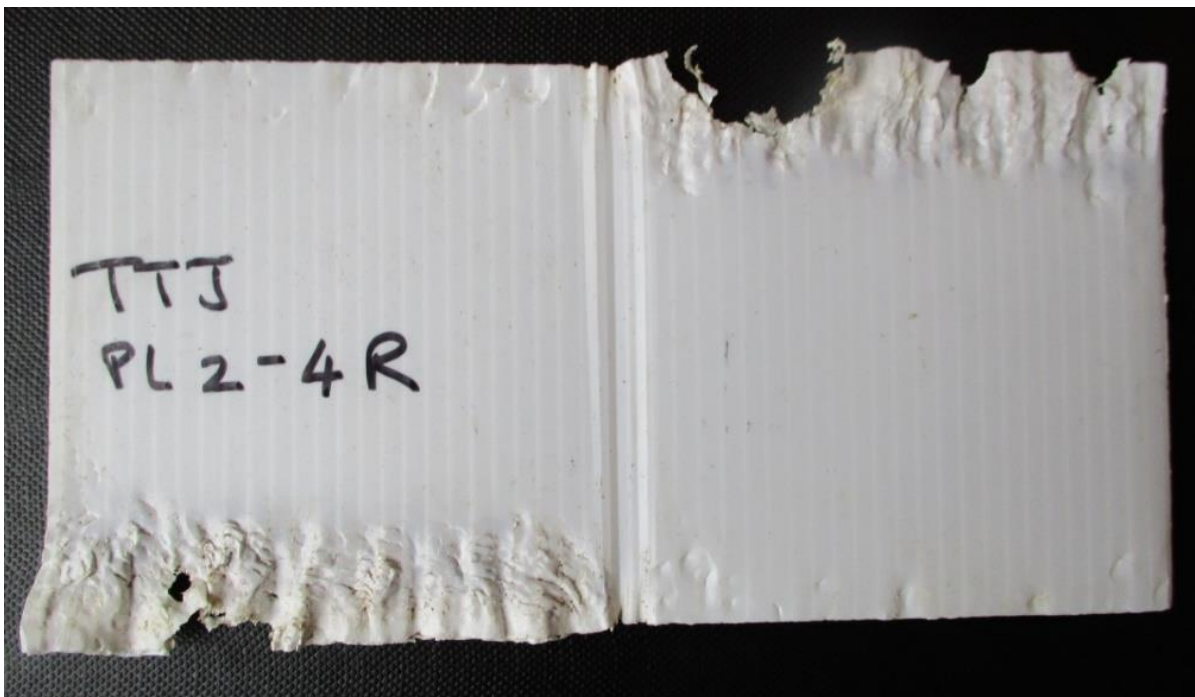
Rodent tracking tunnels with tracking cards are used for surveillance monitoring for predator incursion within the ecosanctuary by the Sanctuary Mountain Maungatautari biosecurity team. These tunnels were located at 50 m intervals along the forest margin and at 100 m intervals along selected forest tracks. The cards were set out for a period of one to three months.

#### **4.2.2 Possum surveys**

The relative abundance of possums (CCI<sub>7</sub>) was surveyed in December 2019 and again immediately prior to the possum control programme in May 2020. Lightweight plastic core-flute cards loaded with Nutella flavoured lure, but no tracking ink were used. The standard protocol (NPCA, 2015) requiring transect selection to be a minimum of 200 m apart, with cards spaced at 20 meters intervals and left *in situ* for three or seven days was implemented. The chew card transects (PL1 and PL2) were laid along two of the previously surveyed rodent tunnel lines at each study location. This resulted in transect pairing on randomly allocated pairs of tunnel lines (TTW and TTB on TLs 1 and 3, TTJ on TLs 2 and 4). Starting at the margin, 11 cards were set out at 20 m intervals along each 200 m transect. Cards were attached (tied rather than nailed) to a tree or fern trunk, 40 to 50 cm above the ground and with the folded card splayed. Cards were retrieved after seven days and were scored for presence (1) or absence (0) of possum chew markings (Sweetapple and Nugent, 2011; Ruffell et al., 2015) (**Figure 4-2**). The chew cards also detected the presence of rats and mice.



**Figure 4-1:** Scanned Black tracking card sections with rat footprints. Several sets of tracks are overlaid on the left-hand card. This may represent one or more individuals entering the tunnel. The central inked section of the card has been discarded. (TTW TL2-3 April 2020)



**Figure 4-2:** A chew card with possum marking; wide tooth indentations (wide ruffling) and rat chew; jagged edge along the missing card sections with smaller incisor tooth indentations. (TTJ PL2-4 May 2020)



### 4.2.3 Wildlife camera traps

Camera traps were used to establish the guild of introduced mammals present in the forest and to closely observe rodent and possum activity. Published literature, (Atkinson et al., 1995; Rovero et al., 2013; Anton et al., 2018; Gillies and Brady, 2018; Delisle et al., 2021) and comprehensive manufacturer's operating manuals (Bushnell, 2012, 2020) were used to guide programming and set up. All cameras had built-in passive infra-red (PIR) motion sensors and were sensitive to small differentials (Trophy Cameras 2.7 °C) between the target and the background infrared irradiance. Under sufficient daylight, colour photos or videos were recorded, and as light levels decreased, images were recorded in black and white. In very low light conditions i.e., night-time, the built-in infrared LEDs function as a flash, delivering black and white photos or videos. Motion in the monitored field of vision triggered the cameras within one second. Images were recorded according to the entered programme. At high sensitivity and at the manufacturer's recommended 2 m to 5 m target range, the smallest mammals, mice, were detected and clear imagery recorded. Fallow deer (*Dama dama*), having greater infrared irradiance surface area, triggered cameras from over 30 m even when partially obscured by vegetation. Insects, amphibia and other small ectothermic wildlife (lizards, frogs etc) did not trigger the cameras (Jarvie and Monks, 2014). Imagery was downloaded from data cards and reviewed following each forest visit. During the study period, adjustments to the position of cameras and their fields of view were necessary to minimise triggers due to seasonal changes in sunlight reflectance and false triggers caused by vegetation growth and wind movements. Cameras were well camouflaged which protected them from human interference, but wildlife very quickly discovered their presence. Possums investigated cameras resulting in violent imagery movement across multiple triggers or a series of over-exposed (white out) images when close to the camera. If cameras were not well secured the field of view was moved away from the intended target.

Camera traps were primarily used to monitor seed traps, seed germination cages and the adjacent forest floor. This was to ascertain if birds or invasive mammals were threatening the integrity of seed capture and seed germination results e.g., rodents burrowing into germination cages and consuming seeds. Bushnell Trophy cameras (n = 12) were deployed between December 2019 to December 2020. The cameras were attached to fern or tree trunks, between 0.5 to 1.0 m above ground level (**Figure 4-3**). They were programmed to operate 24 hours per day and record a series of 3 x 8 MP resolution images (Anton et al., 2018). A camera was set up at the PCQ point located approximately 75 m (PCQ1-2 or PCQ2-2) from the forest margin (**Appendix 2** to **Appendix 7**). As the abundance of sapling trunks at MNG PCQ1-2 obstructed the view of the seed trap, germination cage and the adjacent forest floor during early trials, the camera was relocated to MNG PCQ1-1, 37 m from the forest

margin. The possibility of this significantly influencing results was minimal as the species of prime interest were rats and possums, neither of which are present at Maungatautari.

Still and video imagery was used for supplementary investigations. Bushnell Trophy Cameras ( $n = 3$ ) and Bushnell Core DS No Glow Cameras ( $n = 5$ ) were deployed as supplementary camera traps to record wildlife behaviour in subcanopy trees, movement across forest margins (**Figure 4-4**), during relative abundance surveys, and rat and possum interactions with fruit and seeds on the ground during the 2021 tawa fruit-fall season. Locations are referenced in the image captions. Video resolution was generally set at high definition (1080 pixels). To minimise high trigger situations exceeding data card capacity, supplementary cameras intended to only capture images of nocturnal wildlife were programmed to only trigger during the night.

## 4.3 Data Analysis

### 4.3.1 Rodents

Cochran Q test (Statistica v12, StatSoft Inc.) was used to compare the percentage of cards marked with the characteristic footprints of rats and mice (Innes et al., 2018). Cochran Q test is a non-parametric test of equitability appropriate for a block (grid) design ( $n > 2$ ). At  $n = 2$  the test is effectively a binomial function. Although cards were set out and accessed along transects, their distribution was a  $4 \times 10$  grid across each study location. In October 2020, only one card on TTJ TL1 was retrieved within 24 hours of set out. Results on the four remaining cards were not valid. With the reduced dataset, TTJ data was not included as a separate entity in the October 2020 data for response to the possum control programme (**Table 4-2**). Cochran Q test was also used to compare effects of season (spring and summer) and the impact of possum control across all TLs within Maungakawa forest. Data from TTJ TL1 cards 2 to 5 was not available and TTW TL3 was not included in the dataset as this forest remnant was outside the Scenic Reserve and had not been subject to possum control in June 2020. Box and whisker plots for each species are used to visualise the relative abundance (RAI) and standard error for each survey date.

### 4.3.2 Possums

The relative abundance ( $CCI_7$ ) of possums at each study location and forest, for each survey date were collated. Only possum markings were statistically analysed as rat chew was present on more than 90% of the chew cards (saturation) (Forsyth et al., 2018a). Cochran Q test (Statistica v12, StatSoft Inc.) was used to compare  $CCI_7$  across the locations and for survey dates. Of the 60 chew cards set out, at retrieval one card with heavy possum markings, was found in two parts on the ground several metres from where it was originally secured to a tree trunk and two cards were not located. The two missing cards, from separate study locations

were scored as representing possum presence. Camera trap images confirmed the species presence in the vicinity as well as their destructive behaviour.

### 4.3.3 Camera Traps

Camera trap hours were used to quantify activity of wildlife on the forest floor and leaving the forests (**Figure 4-3** and **Figure 4-4**). All still images were individually viewed and scored for each set of three images, occurring more than one minute since the previous trigger. As no rats or possums were recorded during daylight hours and to simplify calculations, the camera day was entered as the 24-hour period from 1200 hrs to 1200 hours the following day. For each animal detection, the date, time, species, numbers of triggers, and behaviour of all mammals and birds present were recorded. Behaviour was classified as “still”, “foraging”, “searching the ground” or “moving” with direction of movement, if purposeful, recorded i.e., to or from the forest margin. Recorded data for all species was collated according to the visit date when data cards were changed and to align to research data for tree phenology (Chapter 5), seed net contents and germination cages (Chapter 6). Camera trap images were collated to report detections per 1000 hours (CTH) monitored for each forest visit period. For comparison of rat and possum abundance in each study location, CTH month<sup>-1</sup> was plotted (**Figure 4-8**). Multiple images were recorded with no target wildlife apparent, possibly reflecting triggering by wind movement of vegetation or mammals or birds slightly beyond the camera field of view. These images were not collated to datasets. Their impact on data veracity is unknown. Supplementary camera trap imagery was variable quality. Consequentially data was not compatible with statistical analysis. Many images contributed to understanding floral and faunal ecology, with some used to illustrate findings in this thesis.



**Figure 4-3:** Camera trap set up in the forest (TTW SNL1-5 May 2021)



**Figure 4-4:** Supplementary camera trap monitoring possums leaving the forest as in **Figure 4-13**. (TTW BT5 July 2020)

## 4.4 Maungakawa results

### 4.4.1 Rodents

Rats were detected at all study locations and in all surveys, but mice detection was patchy. In October 2019 and January 2020 rats were present at each of the study locations although the relative abundance was variable (Cochran Q  $p < 0.05$ ), (**Table 4-1** and **Figure 4-5**). Across all TLs, where the forest had been subject to the control campaign, the survey four months later (October 2020) found a significant decrease in relative abundance of rats ( $p < 0.001$ ) (**Table 4-2**). Missing data (TTJ TL2 cards 2 to 5) was unlikely to have biased this analysis. At TTW TL3 (outside the possum control campaign area) there was no change in rat relative abundance (October 2019 RAI = 20%, January 2020 RAI = 40% and October 2020 RAI = 40%) but with only five cards set out in each survey there was insufficient data for statistical analysis. Mice were not consistently detected on all survey dates at any of the study locations (**Table 4-1**). Mice were less abundant than rats but across the forest study locations mice abundance was stable ( $p < 0.24$ ) (**Table 4-2** and **Figure 4-6**). Mice were detected at each study location but across all surveys they were not detected on seven of the total 12 transects.

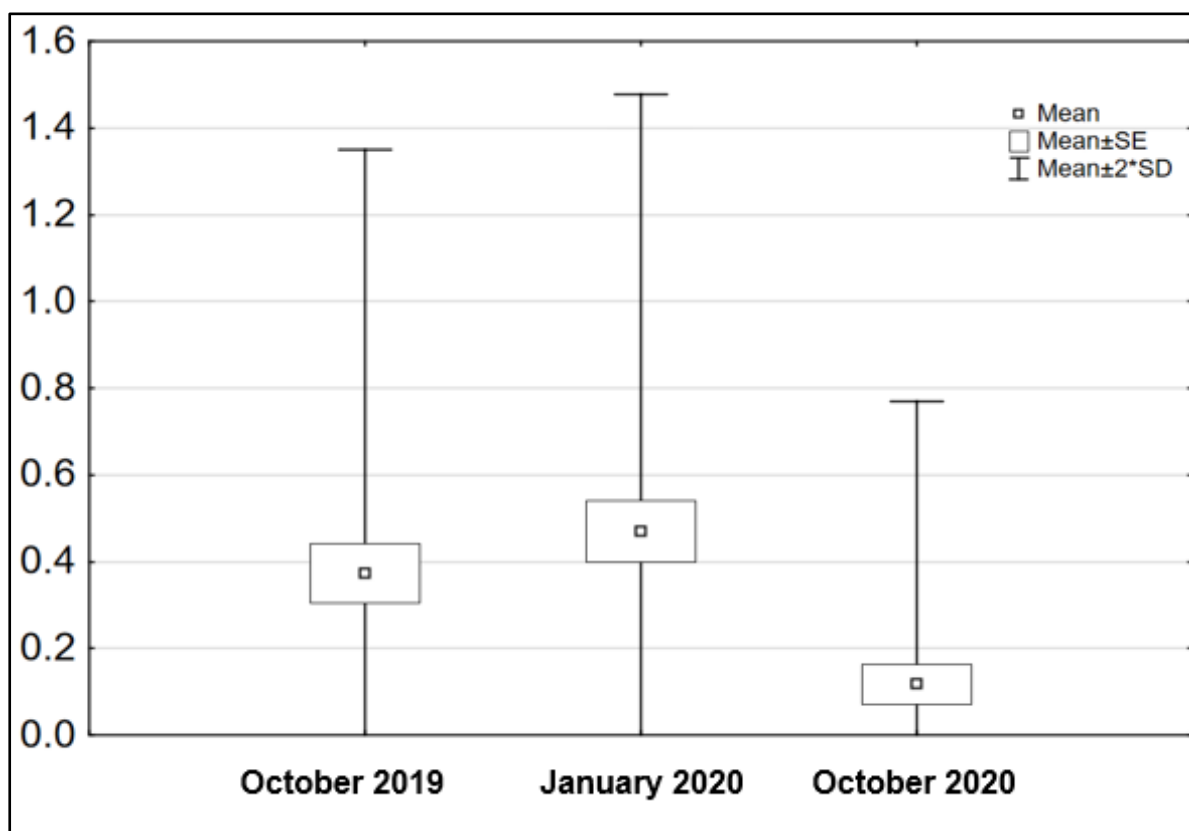
**Table 4-1:** Percentage of tracking cards marked (RAI)  $\pm$  standard error, Cochran Q and significance ( $p$ ) for rats and mice relative abundance in study locations at Maungakawa forest. Transect (TTW TL3) located in the fenced remnant but outside the possum control area is included in this dataset. The October 2020 tracking event was post June 2020 possum control. Cochran Q statistics are not presented for mice as null data violates test assumptions.

	Date	TTW	TTB	TTJ	Cochran Q	$p$
<b>Cards (n)</b>		20	20	20		
<b>Rats</b>	October 2019	55 $\pm$ 11	15 $\pm$ 8	40 $\pm$ 11	8.17	<b>&lt; 0.02</b>
	January 2020	75 $\pm$ 10	40 $\pm$ 11	40 $\pm$ 11	7.54	<b>&lt; 0.02</b>
	October 2020	35 $\pm$ 11	5 $\pm$ 11	NA	4.50	<b>&lt; 0.03</b>
<b>Mice</b>	October 2019	0	20 $\pm$ 9	10 $\pm$ 7		
	January 2020	0	10 $\pm$ 7	0		
	October 2020	5 $\pm$ 7	0	NA		

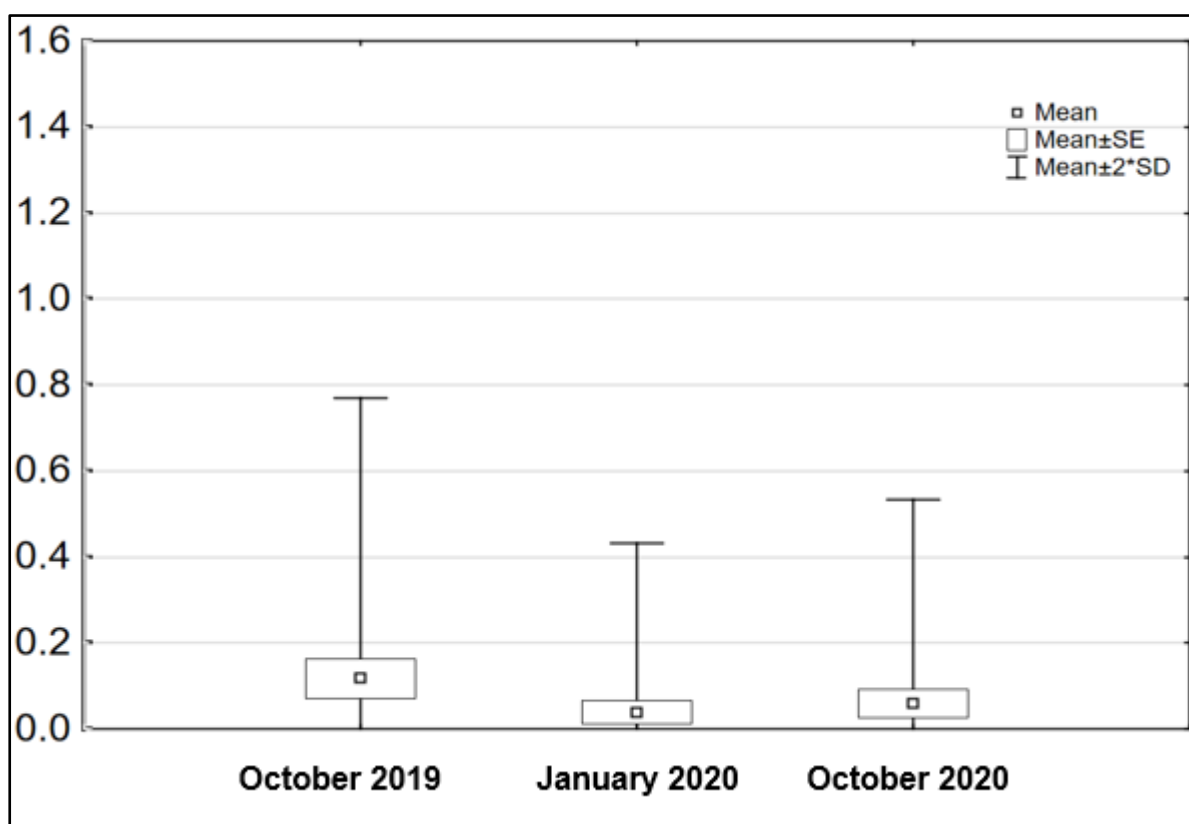
**Table 4-2:** Percentage of tracking cards marked (RAI)  $\pm$  standard error with rat and mouse footprints. Cochran Q test for survey dates pre and post the possum control campaign, across all study locations within Maungakawa Scenic Reserve fenced forest i.e., excluding TTW TL3.

	October 2019	January 2020	October 2020	Cochran Q	$p$
<b>Cards (n)</b>	51	51	51		
<b>Rats</b>	37 $\pm$ 7	47 $\pm$ 7	12 $\pm$ 5	17.23	<b>&lt; 0.001</b>
<b>Mice</b>	12 $\pm$ 5	4 $\pm$ 3	6 $\pm$ 3	2.89	<b>&lt; 0.24</b>





**Figure 4-5:** Rat relative abundance (RAI) in each survey. The y axis is notated in proportion of marked cards. Changes in RAI were significantly different (**Table 4-1**)



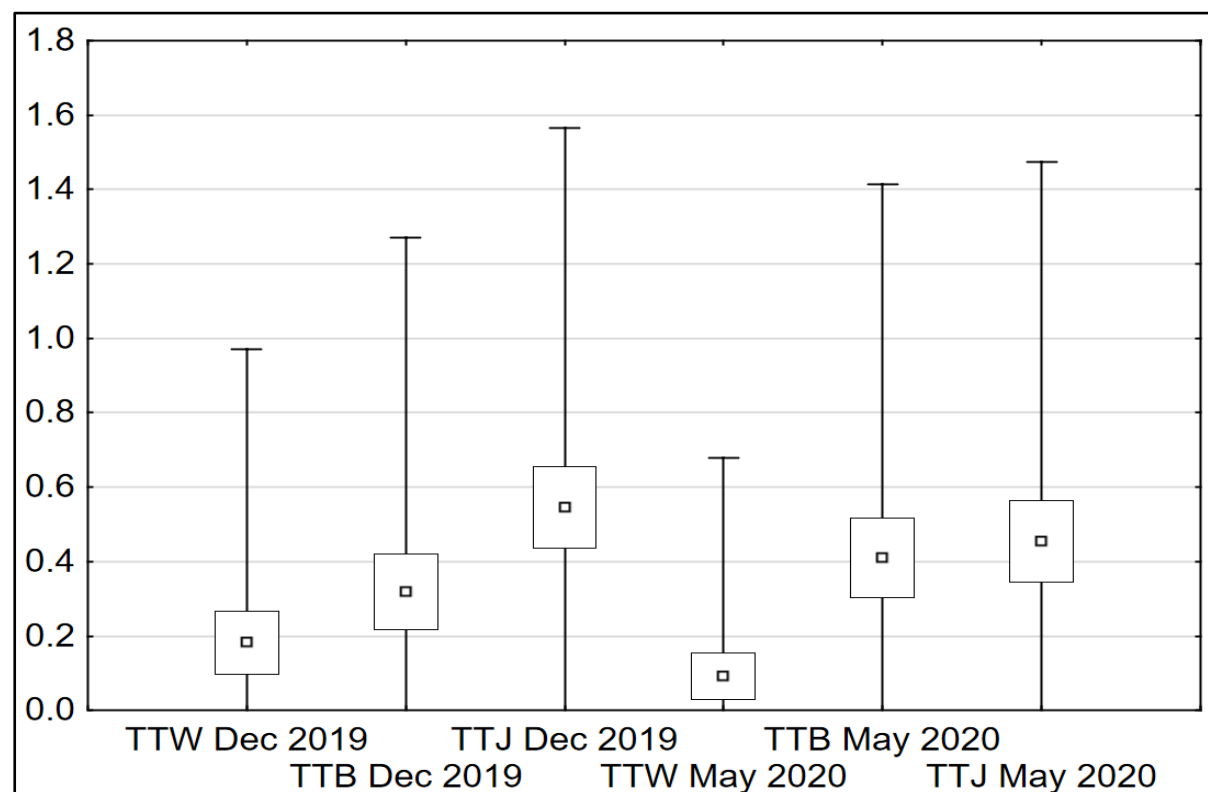
**Figure 4-6:** Mouse relative abundance (RAI) in each survey. The y axis is notated in proportion of marked cards. Changes in RAI were not significantly different (**Table 4-1**).

#### 4.4.2 Possums

Possums were detected at each of the study locations. Relative abundance ( $CCI_7$ ) was variable in December 2019 ( $p < 0.05$ ) and in May 2020 ( $p < 0.05$ ), (**Table 4-3** and **Figure 4-7**). In both surveys, relative abundance at TTW was the lowest. Across the forest landscape, the relative abundance of possums did not change between December 2019 ( $35 \pm 6$ ) and May 2020 ( $32 \pm 6$ ), ( $p < 0.59$ ). Rat tooth indentations / chew were found on greater than 90% of cards at TTW and TTB in both December 2019 and May 2020. At TTJ no cards on PCQ1 but all cards (100%) on PCQ2 were chewed. As statistical analysis is unreliable when  $CCI_7$  is greater than 70% (Sweetapple and Nugent, 2007; Ruffell et al., 2015); further analysis of rodent data was not considered.

**Table 4-3:** Possum  $CCI_7 \pm 1SE$ . In December 2019 and in May 2020 relative abundance was variable ( $p < 0.05$ ) across the study locations.

	TTW	TTB	TTJ	Cochran Q	<i>p</i>
<b>Cards (n)</b>	22	22	22		
<b>December 2019</b>	$18 \pm 8$	$32 \pm 10$	$55 \pm 11$	6.125	<b>0.028</b>
<b>May 2020</b>	$9 \pm 6$	$41 \pm 17$	$45 \pm 11$	7.125	<b>0.047</b>



**Figure 4-7:** Proportion of chew cards marked by possums at each study location in December 2019 and in May 2020. The survey in May 2020 was immediately prior to the possum control campaign. Note:  $CCI_7$  = proportion of cards  $\times 100$ . While the SE (box) indicates differences between the study locations (**Table 4-3**), data should be interpreted with caution as most  $CCI_7$  mean  $\pm 2$  SD (whisker) data ranges extend from  $< 0$  to  $> 100\%$ .

#### 4.4.3 Camera Traps

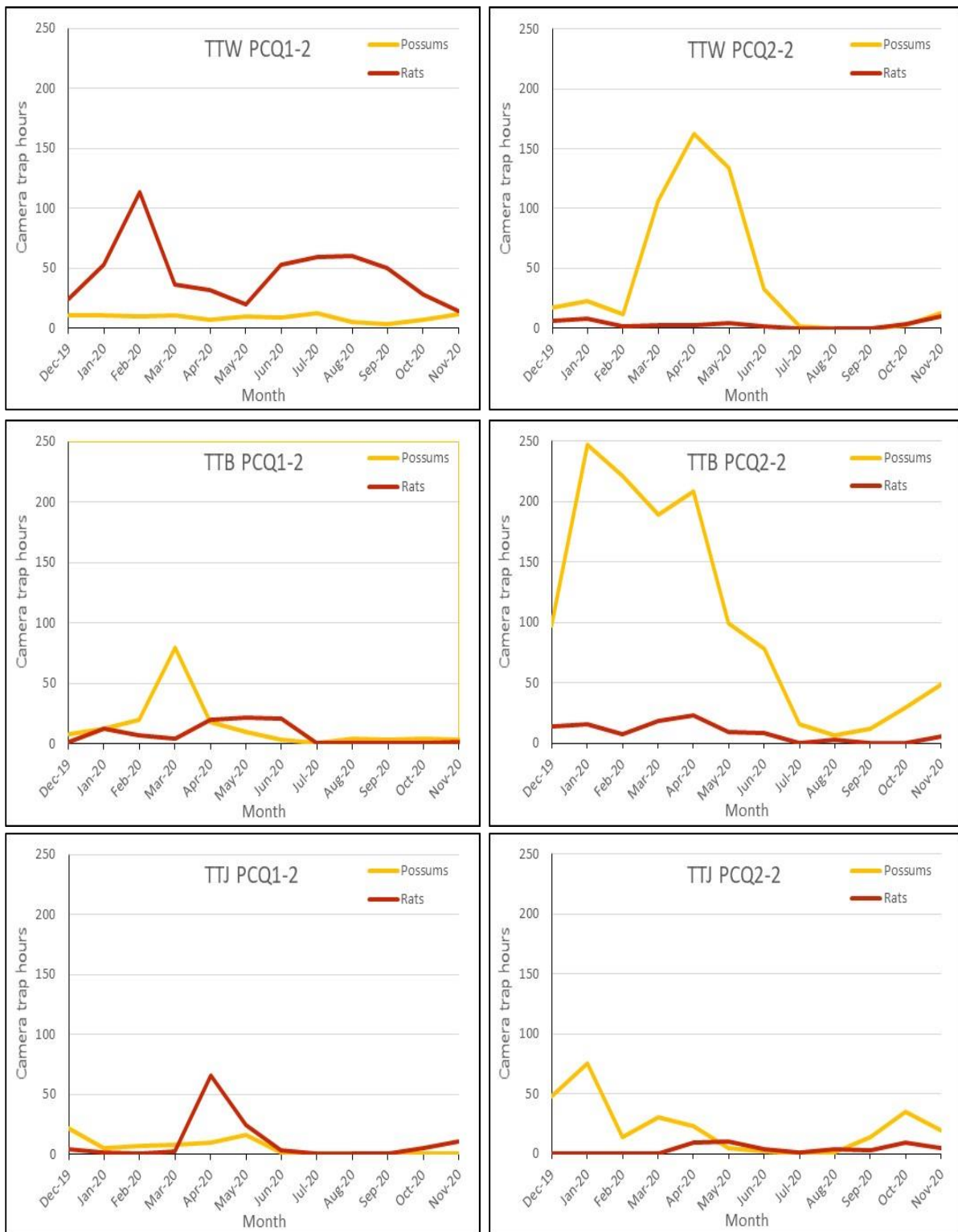
Rodents and possums were active at all locations at Maungakawa but only mice were detected at Maungatautari. Most rat and all possum detections occurred during the night. At Maungakawa rats and possums were active at ground level and in the lower branches of trees. Rats were less common (CTH) than possums on all transects apart from TTW PCQ1 (gully) (**Figure 4-8**). Although not within the possum control campaign area, rat activity on this transect (at PCQ1-2) decreased from September 2020. However, they were frequently observed on a supplementary camera at PCQ1-5 during autumn 2021. Possums were most active at TTW PCQ2-2 and TTB PCQ2-2. It appeared that these camera traps were located close to wildlife tracks leading to the forest margin.

Wildlife camera images revealed rats and possums moving with “purpose” i.e., not randomly wandering, on the forest floor but the mammals frequently stopped to investigate research equipment; cameras, rodent tunnel lines, chew cards, seed traps and germination cages as they were installed, and they were occasionally observed climbing trees. Supplementary cameras captured many images of rats and possums moving in the lower branches of trees and climbing beyond the camera range. Although some appeared to be accessing mahoe fruit, mostly their destinations or intent were not able to be determined.

All camera traps occasionally recorded rats and possums climbing the thin (< 15 mm diameter) slippery seed net support poles but they generally slipped off before reaching the wire ring supporting the net. Occasionally rodents were observed running around the top-wire, but none were observed inside a net and the captured leaf litter never appeared disturbed. Possums occasionally dislodged seed nets from a support pole (**Figure 4-10**) although they did not appear to access the contents.

Foraging behaviour by possums i.e., searching with nose to the ground while exploring the forest floor, was prevalent when ripe tawa fruit were on the ground i.e., between mid-January and late-April each year (**Figure 4-9**). After this, they reverted to moving with purpose. They did not appear to spend much time searching the ground during the rest of the year. During tawa fruit fall, images were captured of both rats (**Figure 4-11**) and possums (**Figure 4-12**) holding tawa fruit to their mouths. Possum interaction with the fruit lasted 20 seconds to over one minute. They appeared to be eating only the fruit flesh. Discarded seeds with the flesh removed were found on the ground throughout Maungakawa forest. Rats appeared to pick up ripe fruit then quickly move away. They may have also been picking up seeds, but this was not clear in camera trap images. Rats continued to search the ground for several weeks after possums had lost interest.

Possums were often observed moving to or from the forest margins and leaving the forest. Supplementary camera traps in July to December 2020 (TTW gully), and April 2021 (TTB) recorded them frequently leaving and returning to the forest (**Figure 4-13** and **Figure 4-14**). They moved under the fences to the adjacent pastures that included highly nutritious dicotyledon species e.g., clover, chicory, and plantain (**Figure 4-15** and **Figure 4-16**). Generally, they left the forest not long after dusk and returned in the early hours of the following morning.



**Figure 4-8:** Rat and possum activity (CTH) on each PCQ transect from December 2019 to the end of November 2020. TTW PCQ1-2 had a gully stream within 40 metres of the camera trap. All other locations were more than 100 metres to the nearest water. In early June 2020 possum control baits were laid at all study locations apart from TTW PQC1. Within seven days of baits being laid, possum abundance fell to zero for a short period at all study locations except TTB PCQ2-2 where it appeared one juvenile possum had survived.





**Figure 4-9:** Possum searching for tawa fruit. (TTW PCQ1-5 January 2021)



**Figure 4-10:** A possum investigating a seed trap in March 2020, but things didn't end well. Images are from a time sequence of an individual investigating a seed net apparently intent on accessing the contents but falls off and in doing so dislodges the net from one pole. The right-hand image initiated the following trigger set three minutes later. The individual was resting on top of the germination cage and then made a further attempt to access the net contents. Images are on an angle due to possum(s) previously investigating the camera. (TTW PCQ2-2, March 2020)



**Figure 4-11:** A rat placing a tawa fruit into its mouth. (TTB PCQ2-5 March 2021)

**Figure 4-12:** A possum holding a tawa fruit to its mouth. It was not clear whether the mammal was consuming the flesh or chewing the fruit and seed. (TTB PCQ2-5 March 2021)



**Figure 4-13:** Possums (n = 3) moving from the margin to the pasture crop over the ridge. A fourth possum trailed behind the possums in the image.  
(Camera trap location: TTW BT5 March 2020)



**Figure 4-14:** A possum returning to the forest (TTB). Several individuals including a female with a back rider were observed. Frequently several fallow deer also clambered under the fence at this location. (Camera trap location: TTB margin close to PCQ2 May 2021)



**Figure 4-15:** Possum scat on fresh spring clover pasture adjacent to the forest margin.  
(TTB August 2019)



**Figure 4-16:** The destination for possums leaving the forest (**Figure 4-13**). This highly nutritious pasture, adjacent to forest margins, is resown annually to provide winter forage for cattle.  
(TTW April 2021)

## 4.5 Possum control – RTC (data provided by WRC and EcoFX)

Possum abundance throughout Te Tāpui Scenic Reserve has been surveyed since 1999. Under the Priority Possum Control Areas (PPCA) initiative, WRC monitors possum residual trap catch index (RTC) to determine required possum control frequency and ensure contractors meet performance targets. All surveys were carried out as per the NPCA (2015) standard. Possum abundance (RTC) greater than 5% triggered possum focussed possum control. Initial surveys (1999) found the RTC was 4%. In 2019, abundance had increased to 14% (**Table 4-4**). Possum control was carried out in 1999, 2003, 2004, 2010, 2011, 2012 and again in 2020. The most recent surveys were in March 2019 and in October 2020 following the control campaign. Rodent surveys recorded high abundance of rats e.g., rodent tracking



index (RTI) 74% in August 2011 and substantial, but not sustained reductions, following possum control e.g., in October 2012 RTI = 1% and increasing again to 52% in June 2021. Rodent abundance has not been measured since January 2017 (RTI = 14%).

**Table 4-4:** The most recent possum RTC (March 2019) and post possum control RTC for Maungakawa forest (Te Tāpui Block A, which covers Maungakawa, n = 13 transects) and data specific to the two transects that most closely align to my study locations. A new set of randomly located transects were generated for each WRC survey (NPCA, 2015).

Date	Location	RTC (%)	SE
<b>March 2019 (pre control)</b>	Forest	14.38	5.77
	Transects (2 / 12)	6.90 / 6.78	NA
<b>October 2020 (post control)</b>	Forest	1.09	2.23
	Transects (X3 / 13)	0 / 0	NA

## 4.6 Results: Maungatautari

### 4.6.1 Invasive mammal detection

Sanctuary Mountain Maungatautari management team supplied predator surveillance data relevant to my study locations. In October / November 2019 and January 2020 there was a high relative abundance of mice, but no rats or possums were detected on the margins or within forest locations MND, MNR or MNG (**Table 4-5**). Camera trap records over the same period (> 42 000 CTH) confirmed rats and possums were not present in my study locations.

**Table 4-5:** Percentage tracking cards with mice footprint markings  $\pm$  standard error. Detection rates all exceeded 40%. Rats were not detected on any cards. The array of tunnels was located on the margins and along tracks within the forest. Cards were replaced in tunnels on the margins monthly but tunnels within the forests were surveyed on a three-month rotation. As card placement in tunnels was not consistent between October / November 2019 and January 2020 statistical comparisons between locations are not reported.

Survey date	Details	MND	MNR	MNG
<b>Oct / Nov 2019</b>	Cards (n)	85	50	53
	% cards marked	60 $\pm$ 5	40 $\pm$ 7	57 $\pm$ 7
<b>Jan 2020</b>	Cards (n)	86	41	45
	% cards marked	79 $\pm$ 4	83 $\pm$ 6	73 $\pm$ 7

## 4.7 Discussion

My results suggest the relative abundance of rats and possum at Maungakawa is comparable to the relative abundance in other Waikato broadleaved forest fragments (Innes et al., 2010b). However possum density was lower than the national average (Cowan and Glen, 2021). The initial density of rats and possums were above WRC trigger limits to instigate possum control (WRC comms.). As expected, following possum control, possum activity dropped significantly except on the transect outside the control area (**Figure 4-8**). Rat abundance decreased several weeks later although this may have reflected the natural life cycle of rats. As TTW (gully) was outside the possum control campaign boundaries it effectively became a negative control for the possum control campaign.

The density of rats within Te Tāpui Scenic Reserve corresponded to the density of rats Innes et al. (2010b) found in fenced Waikato forest fragments. Their study to compare rat markings on tracking cards to the reference method (RTI) for measuring density, found considerable variability in the relationship but they concluded the percentage of marked cards was approximately proportional to the density. The authors reported average rat density peak was  $6.6 \text{ ha}^{-1}$  (61% cards marked) in the fenced forest fragments surveyed in summer but post eradication (in autumn) that fell to  $2.9 \text{ ha}^{-1}$  (30% cards marked). I also found the relative abundance of rats increased during summer (47% SE  $\pm$  7 of cards marked) (**Table 4-2**). WRC has surveyed the relative abundance of rats in Te Tāpui Scenic Reserve intermittently since 2010, recording markings on between 13% and 71% of cards in summer. Their most recent surveys recorded markings on 21% (< 1 to 4 rats  $\text{ha}^{-1}$ ) of cards in 2016 and 14% (< 3  $\text{ha}^{-1}$ ) in 2017. I found rat relative abundance i.e. 37% (SE  $\pm$  7) of marked cards in October 2019 which decreased to 12% (SE  $\pm$  5) in October 2020, four months after the possum control campaign (**Figure 4-5**). As the grid approach deviated from the protocols required to measure rat density ( $\text{ha}^{-1}$ ) (Gillies and Williams, 2013), my results do not index density.

Relative abundance of possums (**Table 4-4**) prior to the WRC control campaign was more than twice their possum control trigger (5%) where preservation of biodiversity, mainly birds, is a priority. They generally expect possum abundance will rebound to above the 5% threshold within three to five years (WRC comms.). Rebound in possum abundance is correlated to mating opportunities and previous possum control across the wider landscape but probably not to increased food resource or den availability (Cowan and Clout, 2000; Cowan, 2016). A soft rebound is likely as very few possums escaped the control campaign, any remaining females will have a maximum two off-spring *per annum* and regular possum control is carried across the wider landscape.

Although I could not confidently identify individual possums in camera images, the span of ground-based activity for several individuals usually only extended to four or five hours each



night. This aligns with individuals only being active on the ground for 10 to 15% of their time (Cowan and Clout, 2000). Although possums are known to share dens and socialise, in general they are solitary mammals (Clout, 2006). Throughout the observation period there was minimal social interaction between individuals apart from back-riders and their mothers. These female possums appeared attentive to ensuring the wellbeing of their offspring. Following the possum control campaign initially only a single possum was observed for several weeks, then activity slowly increased but only a few individuals were observed. They didn't appear to change behaviours; they continued to move to and from the margins and search the ground.

WRC do not have trigger limits based on foliage damage for preservation of forest structure and composition however following possum control, recovery of vegetation provides possums greater dietary choices. Remaining possums are able to access favoured foods more readily (Sweetapple et al., 2013). Depressed reproductive capacity may continue when inflorescence / flower buds, flowers or seeds of these species are favoured foods.

The frequent images of possums exiting the forest at Maungakawa may reflect their exploitation of adjacent highly nutritious pastures (**Figure 4-15** and **Figure 4-16**). Evidence suggests possums preferentially feed on high quality pasture when it is accessible (Coleman et al., 1985; Bellingham and Lee, 2006; Morley, 2018). Pasture species may contribute 30% of possums' diet particularly during winter and spring (Dodd et al., 2006) when forest food resources are low. The open forest understorey that has very few palatable seedlings or saplings would have been a great incentive for the possums to use food resources outside the forest. They were most frequently observed at camera traps close to where wildlife tracks led to the forest margin (TTB PCQ2-2 and TTW PCQ2-2). In contrast, the relative abundance (CCI<sub>7</sub>) of possums was highest in the forests where secure deer fencing was a barrier to them leaving the forest (TTJ PCQ1-2 and PCQ2-2). The deer fencing, 150 mm square netting, 3 m high and with a secure bottom stay wire < 20 cm from the ground could have forced more extensive foraging within the forest and higher encounters with chew cards. At TTJ PCQ2-2 margin there was evidence of animals having pushed under a short section (approximately 10 m) of the fence where the bottom stay wire was detached.

Possums are very mobile travelling up to 1.6 kms / night to browse pasture species (Cowan and Clout, 2000; Forsyth et al., 2018b). Pastures are within 1.6 km at all points within forests on Maungakawa and within Te Tāpui Scenic Reserve. Possums cause serious damage to turnips, chou moellier and lucerne crops as well as chicory and plantain supplemented pastures particularly in the vicinity of forest margins (Spurr and Jolly, 1981). High nutrition pasture including plantain and chicory borders the forest at the TTW study location and all the listed crops were observed growing within 1.5 km of the margins of Maungakawa forest. The low relative abundance at TTW PCQ1 (gully) in the surveys may have been influenced by the

mammals' home range being on the true right of the small gully stream. The camera trap at TTW PCQ1-2 confirmed low activity of possums in the fenced forest remnant (**Figure 4-8**), but at least four possums regularly left the forest on the true right side of the stream to feed on the adjacent pasture (**Figure 4-13**). Pasture beyond the opposite gully margin was rough and steep. Although not intended by farmers, the availability of highly nutritious pastures is likely to considerably reduce possum feeding pressure within the forest or conversely support increased possum population nutrition and health and hence increased fecundity (Ramsey et al., 2002).

Ship rat populations in forests fluctuate throughout the year with juveniles being predominant in winter and spring (see discussion in Innes and Russell (2021). Their average life span is just 12 months. Populations increase from spring through to summer as juveniles mature and in response to fruit and seed food resources. Release of these food resources following possum control is a recognised driver of increasing rat abundance (Sweetapple and Nugent, 2007). I detected increasing rat activity on several transects as summer approached. It would be interesting to track rat activity in consistent fields of views in tandem with seed production over several years to establish population responses to food resources following possum control.

The interrelationship of invasive mammal species contrasted with those of introduced ground feeding birds. Throughout the study (more than 80 000 CTH), images of more than one invasive mammal species i.e., rats, possums or mice were never captured simultaneously within any three-image trigger set. However, blackbirds (*Turdus merula*) and song thrushes (*Turdus philomelos*) were frequently observed within the same image sets. More than one rat or possum was observed with others of the same species e.g., following a track (**Figure 4-13**) but apart from female possums with off-spring they didn't appear to interact with conspecifics.

Rats and possums appeared to consume the flesh of tawa fruit but it is unlikely they consumed the seeds (Grant-Hoffman and Barboza, 2010). Rats were observed picking up and placing fruit in their mouths (**Figure 4-11**), then immediately moved away. Feeding trials have demonstrated rats reject tawa seeds (Knowles and Beveridge, 1982). Possums appeared to consume only the fruit mesocarp (**Figure 4-12**). Possums do not find freshly dispersed tawa seeds palatable (Cowan, 1992) although they may consume rotting seeds (Beveridge, 1964).

Rodents extract and consume the *Cryptaspasma querula* larvae that frequently infect tawa seeds (Silberbauer, 2013), (**Figure 4-17**), (Chapter 6). Fecundity in rats appears to increase when their diet includes invertebrates including insect larvae (Sweetapple and Nugent, 2007). Small piles of damaged seeds that had contained *C. querula* larvae were found in sheltered feeding areas (**Figure 4-18**). Rather than having the expected circular larvae emergence hole, the seeds had been chewed and broken, with pieces of cotyledon scattered nearby. This suggests rats had extracted the larvae and discarded the seed case and what remained of the

cotyledons. Similar seed damage which may have been caused by mice was very occasionally observed at Maungatautari. Has the abundance of the *C. querula* larvae infestation changed due to loss of insectivorous birds? Are rodents today compensating? I ask these questions in relation to *C. querula* infestation of tawa seeds diminishing germination (Silberbauer, 2013), but these questions about the secondary impacts of rats on tawa reproductive capacity are beyond the scope of this thesis.



**Figure 4-17:** *C. querula* larva exposed when a tawa seed was broken.  
(MNG PCQ2M April 2021)



**Figure 4-18:** A pile of chewed tawa seeds which had previously been host to *C. querula* larvae.  
(TTJ April 2021)

Mice were ubiquitous but not abundant on the ground at Maungatautari. Images of mice were often captured repeatedly at specific locations such as running along the same fallen log. This suggests the camera was located close to a mouse track from a nest to a feeding source. It is likely the same population of mice were triggering the cameras, rather than mice being abundant at the location.

Released from mesopredators since 2006, mice populations at Maungatautari have increased (Wilson et al., 2018). Comparison of their population to matched study locations at Maungakawa was confounded by the extended period tracking cards were left in the field at Maungatautari. Although mice are known to consume flowers, fruit and seeds, the small populations were very unlikely to significantly reduce reproductive capacity of my focus species, tawa, mangeao or pigeonwood in either forest. Rodent tracking at Maungatautari is primarily undertaken to detect any incursion by rats.

Mice are detected less everywhere when there are rats around. This is due to both avoidance and predation (Innes et al., 2018). Mice were detected at only two of the three Maungakawa study locations and in both cases relative abundance (RAI) was less than 20%. This is consistent with Innes et al. (2018) who found mice were scarce at Maungakawa and not detected in trees there. In my study mice were observed (CTH) at all Maungatautari study locations but populations were not at eruptive abundance that can follow masting of some forest species (Ruscoe et al., 2004).

Other endothermic (warm blooded) wildlife also triggered cameras. During the rutting season (April / May) fallow deer vigorously challenged several seed traps (Chapter 6) destroying them in the process. Endemic and introduced birds were frequently recorded or visually observed on or close to the ground at Maungatautari but only introduced bird species were recorded in wildlife camera images at Maungakawa (**Appendix 13**). Kererū, tui and fantails were occasionally visually observed. Images of kiwis (*Apteryx* spp.) and moreporks (*Ninox novaeseelandiae*, ruru) were captured during hours of darkness at Maungatautari but not at Maungakawa. At both forests night flying moths were observed in infrared flash images that had been triggered in lowlight by mammals.

In addition to the well-documented fallow deer population, hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) inhabit Maungakawa forest (**Appendix 12**). Hares and rabbits were not observed browsing. However, occasionally seedlings were found with their stems nipped off at a 45° angle which is typical of hare browse. Fallow deer reduce the density of mangeao but not tawa or pigeonwood saplings in Maungakawa understorey and forest gaps (Whyte and Lusk, 2019); however occasional mangeao seedlings and saplings were observed in the forest. Fallow deer were also observed occasionally searching the ground during the tawa fruit fall season. They may have been consuming any fruit they found however it did not appear they were actively searching out the fruit. In fallow deer research trials Mouissie et al. (2005) found larger seeds were not excreted whole. This suggests any tawa fruit / seeds consumed by fallow deer were lost from the seed bank.

During daylight hours, introduced blackbirds and song thrush were observed foraging extensively on the ground at both forests (**Appendix 12**). Their direct impact through disruption of the seed bank is unclear with no published research available. They preferentially consume smaller fruits and seeds of introduced plants (Burns, 2012; MacFarlane et al., 2016) and do not appear able to disperse larger seeds. By turning over the litter and exposing germinating seeds to unfavourable abiotic conditions and rodents, song thrush and blackbird foraging behaviour is unlikely to be conducive to germination of large seeds.

## 4.8 Conclusions

Rat and possum relative abundance on the ground was initially consistent with surveys in Waikato forests reported in the literature but was probably lower than the national average. Rat and possum abundance decreased following pest control (hand laid 1080 baits) carried out in June 2020 although residual animals continued to be detected. Mice were only occasionally detected.

Direct evidence of rat and possum abundance and activities in the canopies was not obtained but the ease with which they ascended and descended the tree trunks confirmed they occupy the three-dimensional space within the forest. On the ground possums consumed the flesh of



ripe tawa fruit while rats removed the fruit from the ground. It is likely they also consumed the flesh of the fruit in “private”. Possums also frequently left the forest most likely to feed in adjacent pastures and crops.

Confirmation that there are no invasive mammals apart from mice in the forests at Maungatautari validates the use of the ecological sanctuary as the reference forest when determining the influence of rats and possums on seed fall and seedling establishment at Maungakawa.

# Chapter 5

## Phenology of tawa, mangleao and pigeonwood

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### 5.1 Introduction

Tawa (*Beilschmiedia tawa*) and mangleao (*Litsea calicaris*) which are Lauraceae and pigeonwood (*Hedycarya arborea*) a Monimiaceae, are fleshy-fruited trees common in Waikato old-growth hill-country forest. Although these species are closely related, the families have been separated for a long time and have undergone considerable evolution in different directions (Roper, 1967; Sampson, 1969). Each of the trees bears large fruit that are favoured by birds, particularly kererū (*Hemiphaga novaeseelandiae*), as well as rats (*Rattus* spp.) and possums (*Trichosurus vulpecula*) (Clout and Hay, 1989; Sweetapple and Nugent, 2007).

Regenerative processes of the broadleaved species may be inhibited by arboreal invasive species reducing vegetative productivity or consuming buds, flowers and seeds (Fitzgerald, 1976; Binny et al., 2021). Deer are known forest herbivores and impacts of deer browsing are well documented although not all researchers agree on the extent to which each of the deer species are impacting forest ecological health and integrity (Nugent et al., 2001; Smale, 2008; Wright et al., 2012). All palatable vegetation and reproductive parts within the reach of the invasive folivores and herbivores are at risk.

Flower, fruit, and seed development is not easily observed in forest canopy species. Observing and measuring trees growing on the forest margins were used as a proxy for vegetative growth, flower, fruit, and seed development in forest canopies and subcanopy layers. Tawa, mangleao and pigeonwood saplings and mature trees were part of the mosaic of species on the forest margins.

Differences between forest margin composition at Maungakawa compared to Maungatautari were observed when selecting study locations. At Maungatautari, forest composition in the external faces of the forest margin have changed substantially since removal of mammalian folivores and herbivores when the predator proof fence was completed in 2006 (Burns et al., 2011). The margin growth is now dominated by fast-growing gap-filling trees and shrubs including wineberry (*Aristotelia serrata*), coprosma (mainly *Coprosma autumnalis*), pigeonwood, mahoe (*Melicytus ramiflorus*), red mapou (*Myrsine australis*), kawakawa (*Piper excelsum*), tree ferns and lianas including *Muehlenbeckia australis* and kaihua (*Parsonia heterophylla*). These species tend to overgrow the slower growing canopy species. At Maungakawa many of the fast-growing species are favoured grazing and browsing vegetation of possums (Nugent et al., 2000) and fallow deer (*Dama dama*). Kererū also browse foliage when other food resources are low in winter and spring (Emeny et al., 2009).

This chapter focuses on the phenology of the tawa, mangero and pigeonwood. I anticipated that over a 13-month period incorporating the four seasons, disturbances attributable to wildlife and environmental factors would be evident on at least a portion of the margin trees.

### **5.1.1 Methods**

### **5.1.2 Selecting study margins**

Forest study locations (Chapter 2) were primarily selected for matched altitudes, aspect and for the presence of mature tawa, mangero and pigeonwood. Availability of trees suitable for the phenology study had determined the boundaries of the study locations. At Maungakawa the majority of tagged mangero and pigeonwood were located along the margins of the Scenic Reserve. However, only three of the 13 tagged tawa were located on forest margins within the Scenic Reserve. The remaining 10 were located on the margins of forest remnants on private farmland and within 500 metres of the fenced Scenic Reserve. One area (TTW) was fully fenced and on the other two properties (TTB and TTJ), cattle and sheep periodically graze under the mature trees. Seedlings, saplings, and other undergrowth were minimal in the latter areas. At Maungatautari all tagged trees were located within the predator proof fence, but low densities of tawa and pigeonwood made it necessary to search longer stretches of the forest margins to locate enough of these species.

### **5.1.3 Selecting and tagging study trees and branchlets**

Between three and six trees of each species that met the selection criteria were tagged at each study location (Chapter 2) giving a target of 15 trees (60 tagged branchlets) / forest. The positions of individual trees were mapped (**Appendix 2** to **Appendix 7**). Although it was necessary to tag some trees growing close to conspecifics, at each study location some of the selected trees were widely spaced along the margin.

Key criteria for selection of study trees were

- Tagged branchlets had to be directly exposed to at least an estimated 15% sky, increasing to 25% on south facing slopes.
- Branchlets had to be within reach to permit close examination and measuring.
- The apical bud had to appear healthy when the branchlet was initially tagged.
- The branchlet had to have mature leaves and the length from the node to the apical tip had to be greater than 8 cm.
- There had to be clear evidence that the tree had reached reproductive maturity i.e., evidence of flower bud, flower, or fruit development during the previous 12 months. Although mangero and pigeonwood are dioecious, gender could not be considered as a selection criterion, due to lack of flowers or fruit during the period available for tree selection. Trees were selected if at least comparable to the size (as a surrogate for

maturity) of trees with residual fruit. Tawa is monoecious and trees were selected where branchlets bearing dormant flowers, fruit or residual flowering stalks were present.

- Was the tree safe from trimming? Vegetative growth had to be accessible from the ground and not within deer browse reach. In Maungakawa forest, only branches above deer browse height, 1.5 m from the ground, were tagged. In the absence of browsing herbivores at Maungatautari, some vegetative growth less than the 1.5 m level above ground level was tagged to ensure sufficient examples for the study.

At Maungakawa cattle seemed attracted to any accessible foliage. Only branches that appeared to be safe were tagged however the reach of cattle was initially under-estimated. Some vegetation at Maungakawa was “trimmed” by livestock. Data from cattle damaged branchlets was excluded from analysis.

Vegetation is normally trimmed to maintain access along the inside of the Maungatautari predator proof fence line. By arrangement with Sanctuary Mountain Maungatautari management team, only essential trimming was carried out and trees with tags were left untrimmed. Only trees with at least a 1.5-meter gap between vegetative tips and the fence were selected. Highly visible flagging tape was attached to each tree and the adjacent fence line. Sanctuary Mountain Maungatautari management advised contractors of the research programme. Despite these precautions, branches at one Maungatautari location (MNG) were subject to unauthorised trimming.

Each tree was assigned a unique identification code and four branchlets were selected. For field identification records and reporting, species were coded tawa (BT), mangeao (LC) and pigeonwood (HA) and trees on each study location margin numbered. For example, TTB HA1 is at the Maungakawa study location accessed via farm tracks on Bodle’s property and was the first pigeonwood to be tagged. Numbering indicates the order of selection but not position along the forest margin. The gender of each tree was determined by inspection of flower reproductive parts and/or the presence of fruit.

Branchlets were also selected according to the criteria above and measured. A coloured cable tie (purple, yellow, blue, or orange) was placed on each selected branchlet, immediately in front of (apical tip side of) the first side shoot or if no side shoots were present on the shoot side of the node where the branchlet was attached to the larger branch. On each branchlet the length (cm) from the node behind the tag to the apical tip was measured and individual inflorescence or flower buds (depending on species), flowers and fruit were counted. Observations relating to phenological development including disturbances i.e., breakage and evidence of browsing, insect damage, overt disease symptoms and incidental exposure to toxic chemicals were also recorded. Photos of each branchlet were taken for later reference and a number of these images have been used to illustrate my findings.



Over the 13-month period July 2019 to August 2020, visits to the six forest locations were on a rotational basis. Usually, I visited each of the forests over a 4-week cycle although variations occurred due to the Covid 19 lockdown (2020) and to farm management requirements e.g., lambing restricting use of farm access tracks.

## **5.2 Data Analysis**

The principal objective of this phenology study was to observe and record annual (four seasons) growth, reproductive developments and herbivory. A series of measurements and counts over the four seasons of inflorescence / flower bud development, anthesis and fruit maturation were recorded. To visualise growth and reproductive cycles of each species, measurements and counts over each 4-week cycle were collated and mean values for each forest plotted against the date mid-point for each cycle. Occasionally measurements were missed e.g., on one occasion the weather deteriorated, and it was not safe to remain in the forest, or when a tag could not be found. Where possible missing data and outliers were obtained or verified from photos or the average of the previous and following visit measurement was entered. This was necessary for 45 of 14 340 data points i.e., < 0.3% of all counts and measurements. Where data could not be verified the original measurement was retained. The occurrence of many null data points for inflorescence / flower bud, flower and fruit counts precluded statistical analysis.

Branchlet counts increased then decreased through the measurement period. The number of counted branchlets increased in the second and third measurement cycles as additional trees were selected (September 2019 n= 5, October 2019 n=1) to provide, where possible, equitable sample sizes for each species at each forest. Pigeonwood trees were less common on the margins at Maungatuatari resulting in 20% less branchlets than selected at Maungakawa. If a branchlet lost its apical tip after measurements began, measurements were continued using the dominant side shoot arising from the apical bud axils. At Maungatautari MNG location 50% of tagged branchlets were lost when the trees were trimmed. At all other locations attrition rates were < 15%. Measurements up to the attrition event were included in length and count data.

## 5.3 Results

The patterns of inflorescence / flower bud development, anthesis and fruit development on each species, tawa, mangeao and pigeonwood, were different (**Appendix 9**, **Appendix 10** and **Appendix 11**). Many tawa flowers were borne on each axillary panicle, but many were shed before fruit emerged from the dormant flowers (**Figure 5-8**, **Figure 5-9** and **Figure 5-11**). A single fruit matured on some panicles. Very occasionally two mature fruit were observed on a single panicle. Mangeao inflorescence buds contained four or five flowers arranged on an umbel (**Figure 5-17**, **Figure 5-20** and **Figure 5-21**). Where trees appeared healthy during anthesis, a corresponding number of fruit (drupes) developed (**Figure 5-23** and **Figure 5-24**). Pigeonwood had the highest fruit set. Flower buds were arranged on a raceme and each flower contained up to 20 carpels (**Figure 5-40**). On branches exposed to high light on the forest margins, multiple fruit developed in tight bunches of 100 or more fruit on each raceme.

The gender of all pigeonwood trees and 85% of mangeao trees was determined (**Table 5.1**) by the gender of the flowers and the presence of fruit. At Maungakawa female pigeonwood predominated but at Maungatautari the gender ratios approximated 50%.

There was no evidence of deer browse on vegetative growth on any tagged trees along the study location margins of Maungakawa forest although there was evidence of foliage browsing on seedlings and saplings within the forest. At both forests, vegetation was damaged by insects. When measurements ceased, August 2020, leaves were often damaged by insects, fungal attack, and environmental factors e.g., wind.

**Table 5.1.** Counts of mangeao and pigeonwood male and female trees at Maungatautari and Maungakawa. The “unknowns” neither flowered nor had any fruit.

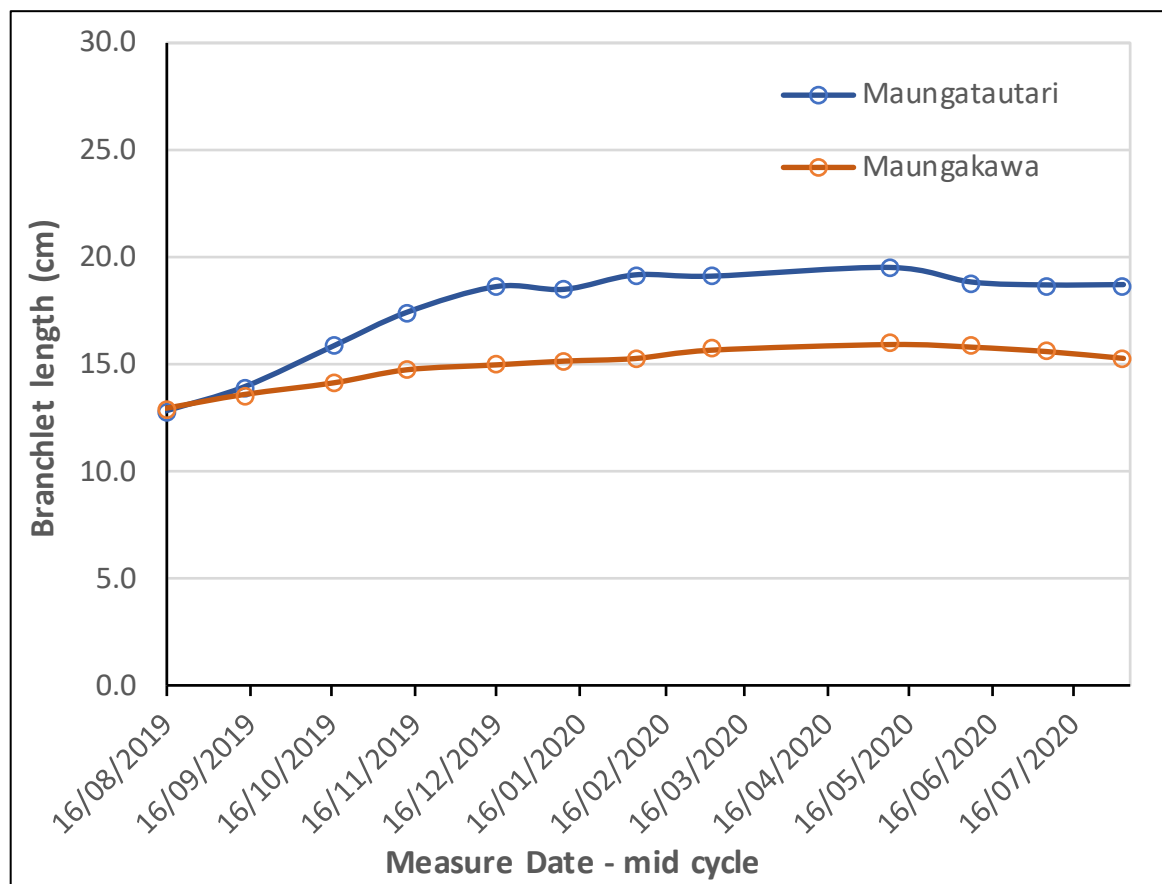
	Pigeonwood			Mangeao		
	Male	Female	Unknown	Male	Female	Unknown
Maungatautari	5	7	0	6	8	2
Maungakawa	2	13	0	7	6	2

### 5.3.1 Tawa phenology

New vegetative growth (**Figure 5-1**) was evident on tawa at the initial visits in mid-winter (July 2019). Branchlet apical buds lengthened, with new leaves and side shoots emerging (**Figure 5-2**). Elongation and lateral branching continued until early summer (December 2019). For the remainder of the 13-month study period, the mean branchlet length declined marginally due to dieback of some apical tips. When measurements ceased in August 2020, mature leaves often showed damage by insects, fungal attack, and environmental factors e.g., wind. New seasons leaves were emerging from side shoot apical buds (**Figure 5-3**).

Flower buds (**Figure 5-4**) developed concurrently with the early vegetative growth during spring (September and October 2019), (**Figure 5-5**, **Figure 5-6** and **Figure 5-7**). There was a high abscission rate for the buds with less than 20% of buds opening over summer (November 2019 to January 2020). Emerging flowers appear creamy white and gradually developed a red colouration (**Figure 5-8**). Abscission continued and by late February 2020 no flowers persisted on tagged branchlets at Maungakawa and less than 10% remained at Maungatautari (**Figure 5-7**). Occasional flowers continued to be observed on some trees along both forest margins. By March 2020 the calyx on remaining flowers appeared to have closed over (**Figure 5-9**). These dormant, *sensu* Knowles and Beveridge (1982), flowers were included in the flower count until abscission occurred or there was evidence of small green fruit emerging (May to August 2020).

Most fruit emerged from the dormant flowers in winter and ripened in late summer and autumn (**Figure 5-10**). When branchlets were tagged in July / August 2019, only very occasional developing fruit were observed on any trees in Maungatautari or Maungakawa forest margins and none were borne on tagged branchlets. In May 2020 closed over flowers ( $n = 7$ ) were observed on only one tagged branchlet (MNR BT1 orange tag). These had started to swell, and the first hint of green fruit development was visible (**Figure 5-11**). Only two developing fruit were present in August 2020 and by a follow up visit in September 2020 there were no developing fruit on this branchlet. However, by November / December 2020 developing fruit (**Figure 5-12**) were easily observed on approximately 50% of tawa growing on study location forest margins. The fruit crop was noticeably larger at Maungatautari. In February 2021 many ripe fruit were found under the trees along forest margins.



**Figure 5-1:** Tawa - length of branchlet from branch to apical tip. Over the 13-month period mean branchlet elongation at Maungatautari (mean = 5.9 cm) compared to Maungakawa (mean 2.9 cm).

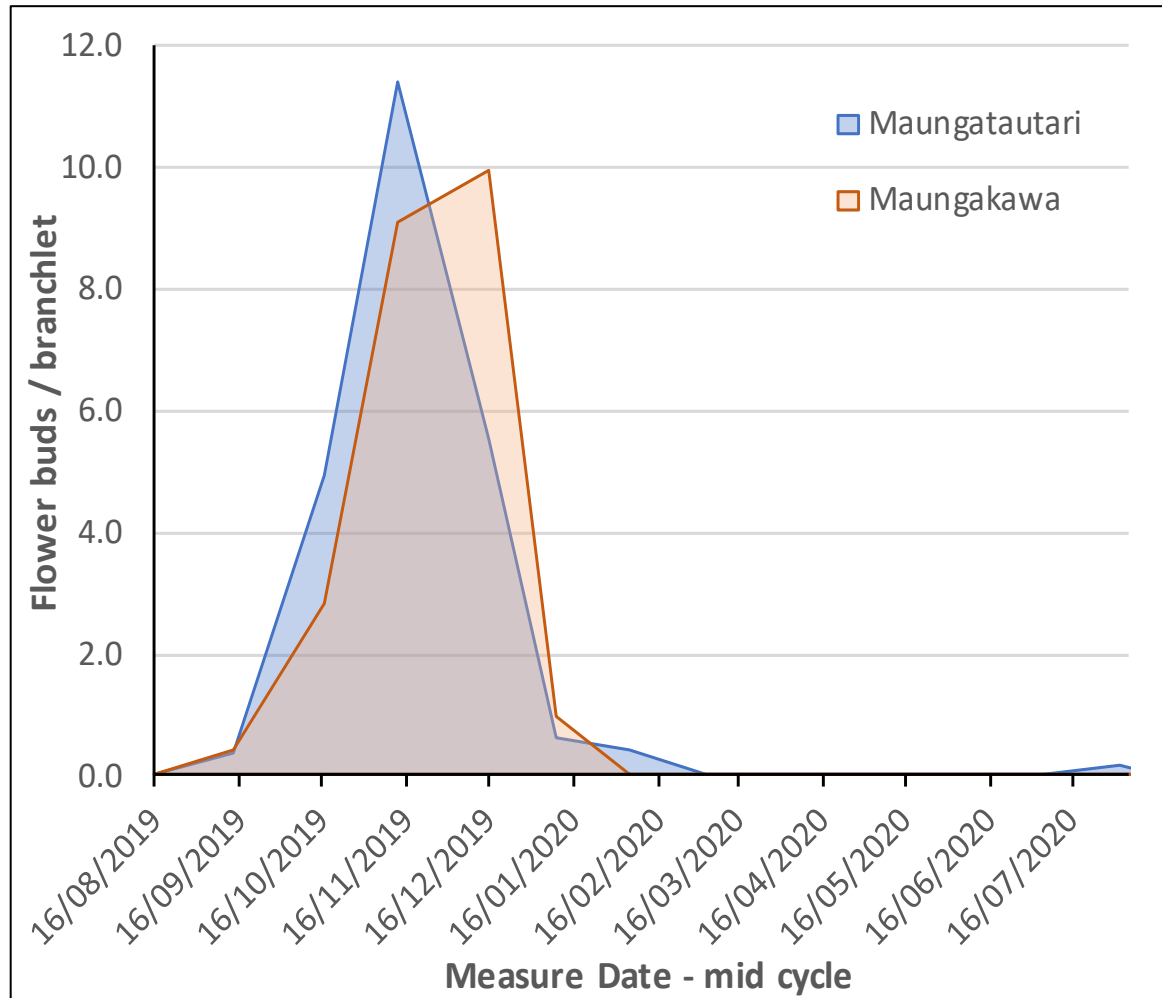


**Figure 5-2:** New leaves emerging from the apical bud. Branchlet length = 14.5 cm. (BT3 MND, August 2019)



**Figure 5-3:** New leaves emerging from the apical bud. Branchlet length = 26.0 cm. (BT3 MND, August 2020)





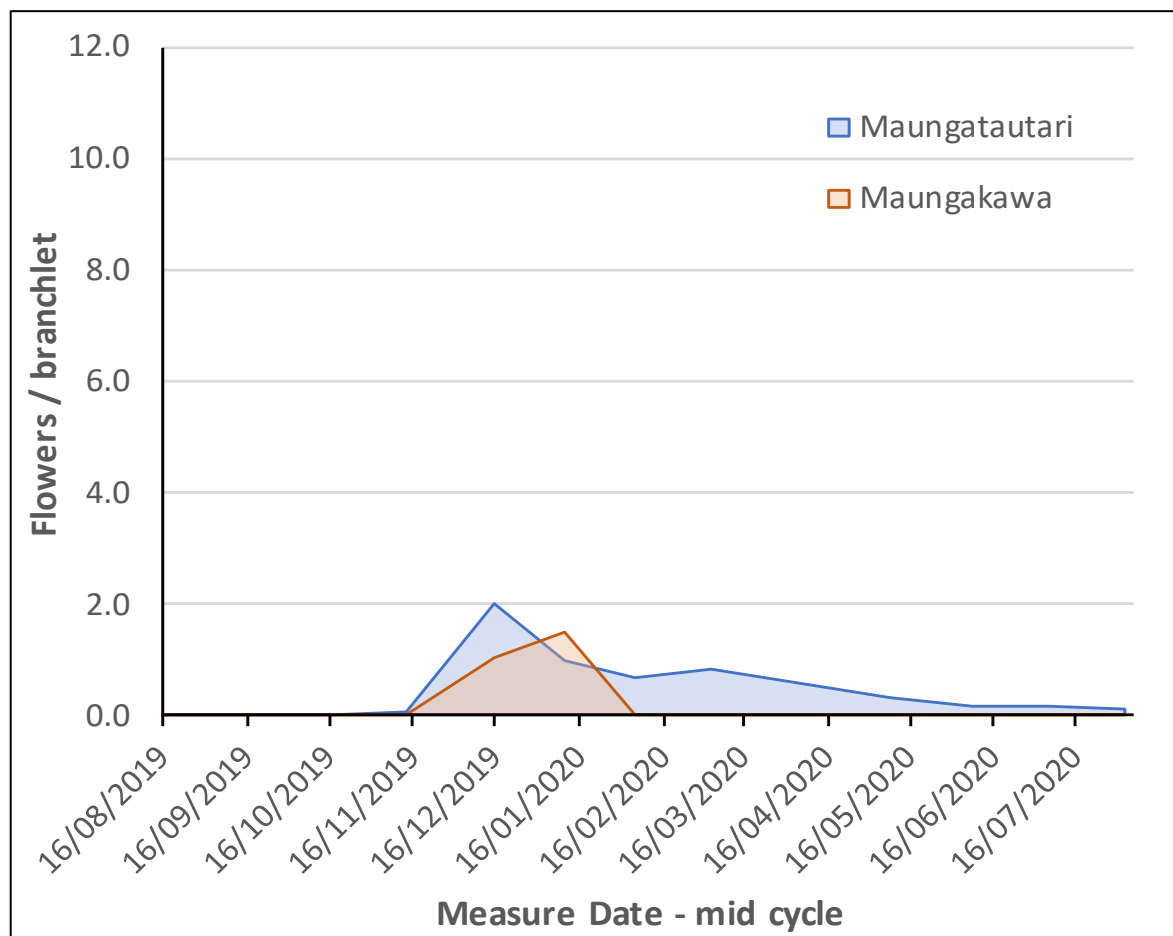
**Figure 5-4:** Tawa – flower buds / branchlet. Bud development initiated in axils of a leaf scar or developing leaves. Roper (1967) observed that the determinate inflorescence develops panicles of seven acropetal buds / flowers in whorls below the terminal flower on the primary peduncle. Generally a total of 57 flower buds develop (Roper, 1967). I observed a few panicles with more flowers and many less productive examples.



**Figure 5-5:** New flower buds developed in leaf axils. (MND BT3 September 2019)



**Figure 5-6:** Maturing flower buds on 2 inflorescences. (MNG BT6 November 2019)



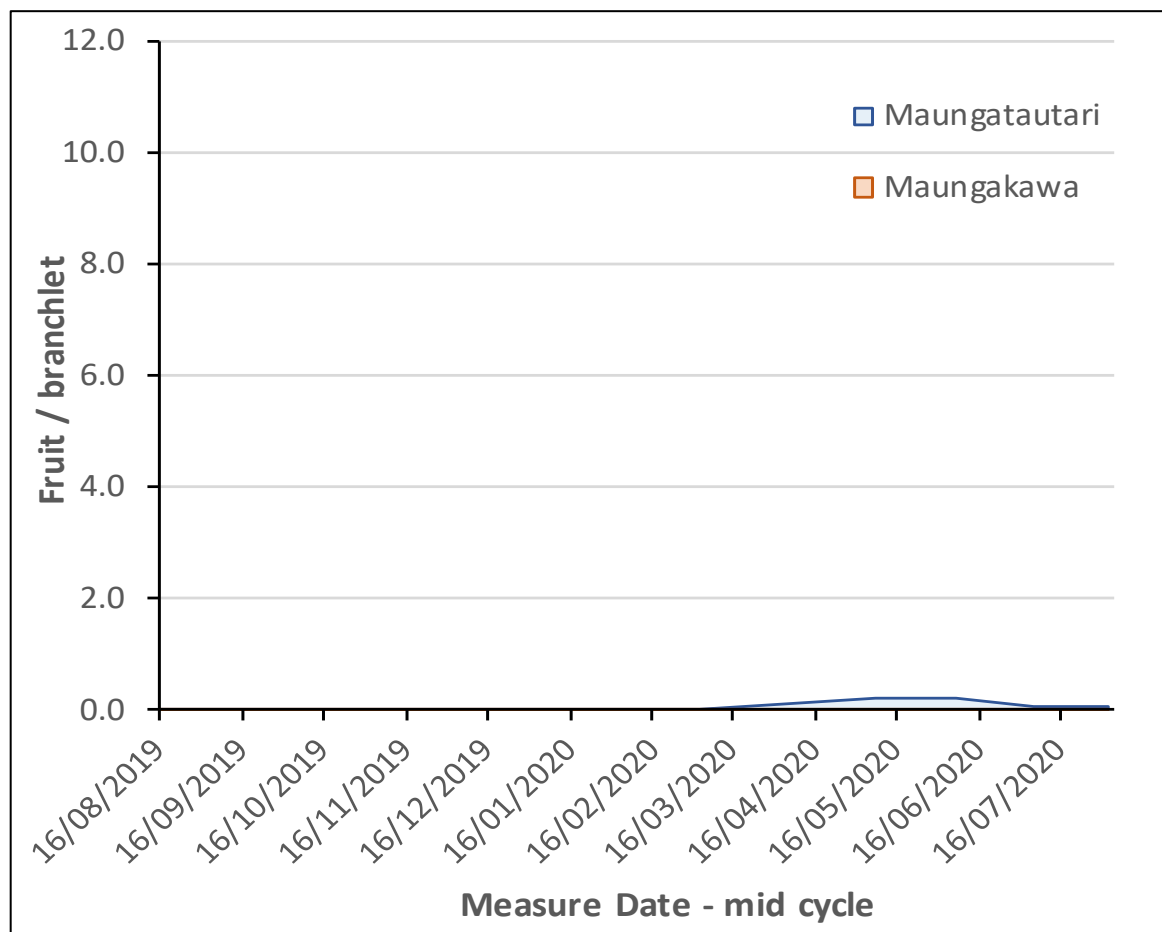
**Figure 5-7:** Tawa - flowers / branchlet. Peak anthesis appears to have occurred in early January 2020. The delayed peak measurement at Maungakawa is most likely due to an idiosyncrasy of forest visit (measurement) dates. The lack of flower persistence on tagged branchlets at Maungakawa possibly relates to the lower branches being more exposed to climatic elements i.e., they were not protected by the predator proof fencing tight gauge mesh.



**Figure 5-8:** Flowers at various stages from bud to maturity on the same branchlet. (MNG BT6 December 2019)



**Figure 5-9:** Fertilised flowers with most calyx closed over until fruit development commenced in winter. There is one early fruit developing on this panicle. (MNG BT2 March 2020)



**Figure 5-10:** Tawa - fruit / branchlet. Although some fruit was observed on approximately 50% of trees along the margins of both forests, fruit development on tagged branchlets only occurred on a single branchlet on one tree at Maungatautari. To highlight productivity relative to flower bud development, the y axis scale is consistent with each stage of the life cycle above.



**Figure 5-11:** Emerging fruit. (MNG BT3 June 2020)



**Figure 5-12:** Fruit at various stages of development: small green through to ripe purple. (MNG BT3 November 2020)



### 5.3.2 Mangeao phenology

When mangeao trees were tagged, leaf abscission scars and new growth leaf buds in leaf axils were observed but vegetative growth appeared dormant (**Figure 5-14**). Branchlet growth commenced in late September when the first inflorescence buds also began to open. The growth curves (**Figure 5-13**) for the forests were almost parallel throughout the 13-month period. Mean branchlet growth rate was 6.9 cm. Measured growth of individual branchlets ranged from 0 to 20 cm. Many branchlets had lost their apical tip but multiple side shoots had developed by the end of the study period (**Figure 5-15**).

Inflorescence buds and fruit from the previous season anthesis developed concurrently. In 2019 fewer inflorescence buds were initiated on female trees that had heavy crops of developing fruit. The bud development of this fruit crop occurred before forest visits commenced in July 2019, but the maturing buds (**Figure 5-17**) were observed during the short period prior to anthesis. Development of the following cohort of inflorescence buds was observed from December 2019 through to the conclusion of margin tree phenology measurements in July / August 2020 (**Figure 5-16**). At Maungatautari most inflorescence buds and some vegetative buds turned black and fell off the trees (January to March 2020) (**Figure 5-18**). Although fewer inflorescence buds initiated at Maungakawa, the attrition rate was lower.

Anthesis occurred between August and mid-November (**Figure 5-19**). At umbel of four or five flowers emerged from each inflorescence bud (**Figure 5-20** and **Figure 5-21**). The first flowers to emerge were observed on a male tree in a sheltered north facing location at Maungatautari on 24 August 2019. At Maungakawa anthesis commenced a few weeks later, in September and extended to mid-November. Maungakawa mean flower count per tagged branchlet was only 12% of the mean counted at Maungatautari. Tree observation notes and photographic records confirmed this difference in productivity. Anthesis, particularly on male trees, lasted only a few weeks. With the short anthesis period and counting occurring only once at each margin over the 4-week visit cycle, flower counts were snapshots rather than representative of the full extent of anthesis. Following pollination, the ovules swelled rapidly.

Fruit development took between four and seven months and ripening occurred in summer and autumn. By November 2019 small fruit (drupes) had emerged (**Figure 5-23**) but less than 25% of female flowers developed into fruit. Fruit development appeared more abundant at Maungatautari (**Figure 5-22**). At Maungakawa fruit developed on tagged branchlets on only two of the six female trees (33%), (TTJ LC1 and LC5) but at Maungatautari fruit developed on tagged branchlets on seven of the eight female trees (88%). However, many fruit aborted prior to ripening. Ripening fruit were first observed in February and March 2020 (**Figure 5-24**) but the peak occurred during the period the forest visit cycle was missed (March and April 2020). Kererū were observed feeding on ripe fruit at both forests. When observations recommenced in May 2020 most fruit had been consumed or fallen to the ground. The trees were checked

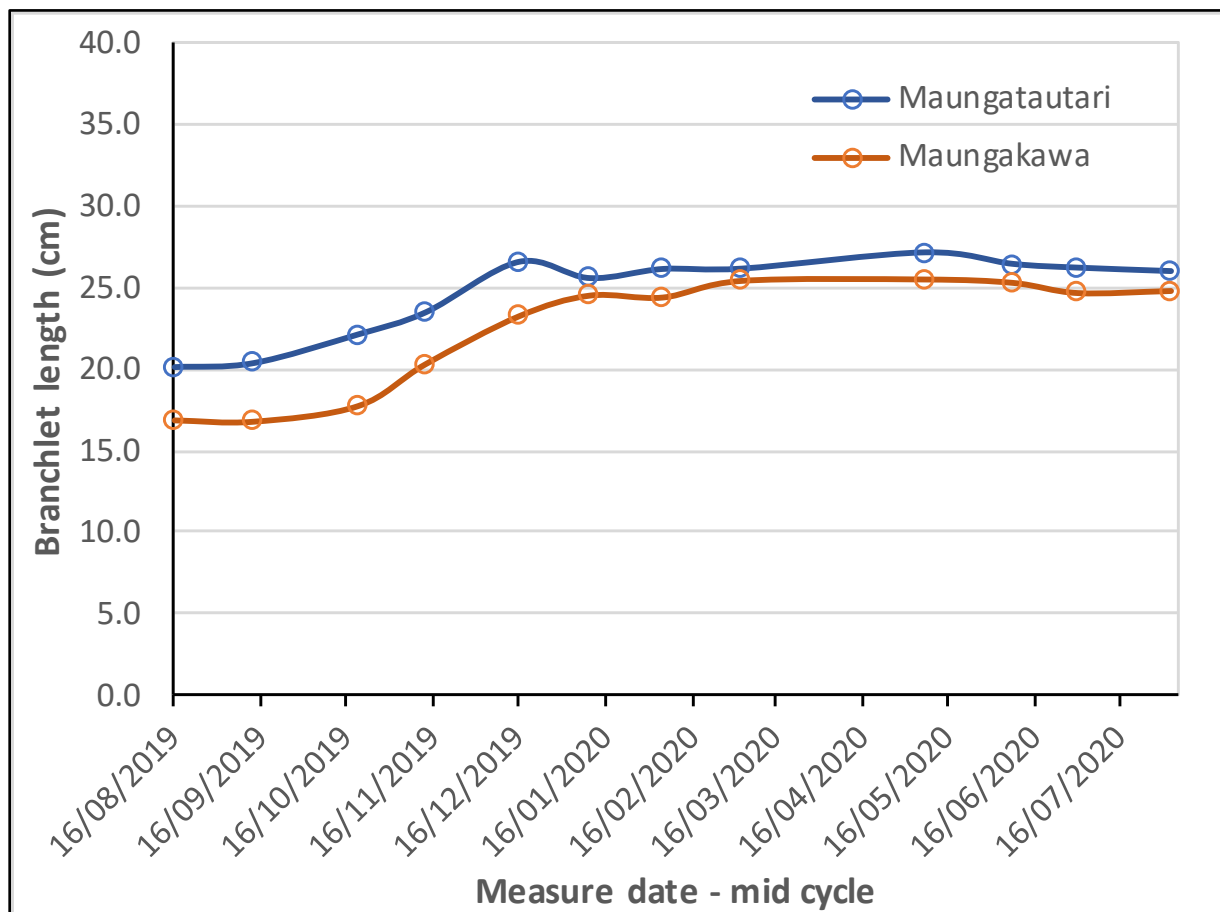
at each visit over the following six months (until February 2021). In 2021 developing fruit on female trees at Maungatauari were noticeably sparse. However new season inflorescence buds were prolific on some trees. Inflorescence bud development on trees at Maungakawa appeared similar to the previous season. At Maungatautari poor foliage condition was observed on female trees that had developed heavy fruit crops (**Figure 5-25**). This was also observed on the tree that had a moderate fruit crop at Maungakawa (TTJ LC5). Vegetative condition was good on male trees and on trees where I could not determine the gender.

At Maungatautari in 2020, when the fruit crop was abundant, the ground below the trees became littered with fruit (**Figure 5-26**). During summer 2021 dried off fruit could still be observed on the dry exposed ground inside the fence line. In damp locations these germinated during summer and autumn 2021 forming a thick carpet of seedlings. Small mangeao saplings from seed fall in previous seasons were also observed within forest margin vegetation.

Many of the more mature trees along the margins showed deterioration. A number had lost their crown, but some had developed healthy epicormic trunks from the base of the original lower trunk. In the margins, Insect damage to vegetative growth was observed on many trees (**Figure 5-29**, **Figure 5-30** and **Figure 5-31**). Note: Evidence of inflorescence bud or flower predation by birds or mammals was not recognised. However, post the fieldwork reported in this thesis, at Maungakawa in August 2021, I recognised patterns of browse and inflorescence loss that were consistent with possums or rats removing individual inflorescence buds and on lower branches deer browsing the foliage with inflorescences being collateral damage. Investigations will be continued and reported in future research papers.

In November 2019 a farmer spot-sprayed thistles on pasture adjacent to the Maungakawa Scenic Reserve (TTB). At the next visit, mid December 2020, the foliage of several nearby mangeao trees exhibited spray damage (**Figure 5-27** and **Figure 5-28**) but other nearby species (tawa, pigeonwood, titoki (*Alectryon excelsus*), red mapou, mahoe and kawakawa) and grasses were not affected.





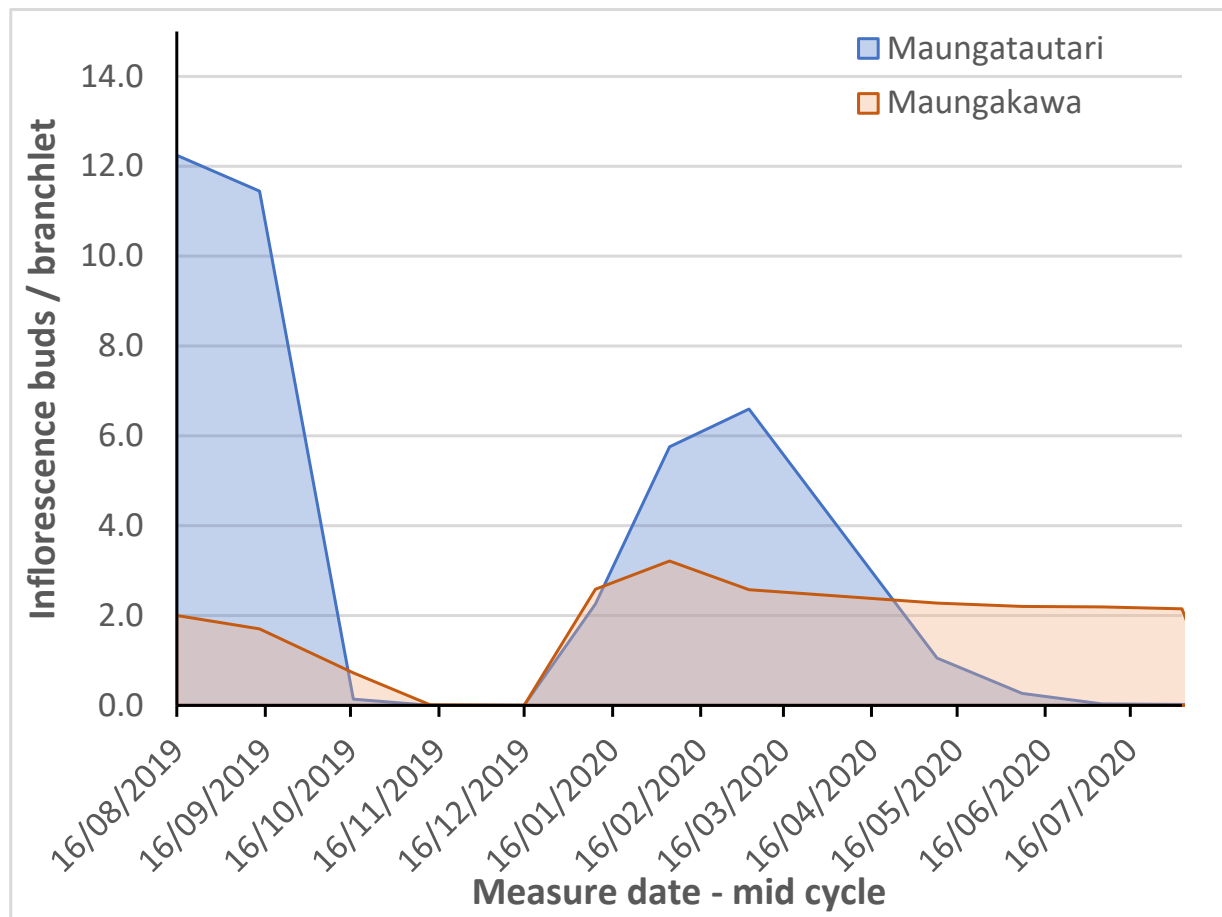
**Figure 5-13:** Mangeao - length of branchlet from branch to apical tip. The mean increase over 13 months was 6.9 cm.



**Figure 5-14:** Purple tagged branchlet = 19.0 cm. (MND LC1, July 2019)



**Figure 5-15:** Purple tagged branchlet = 30.5 cm. Many side shoots also developed over the 13-month period. (MND LC1 August 2020)



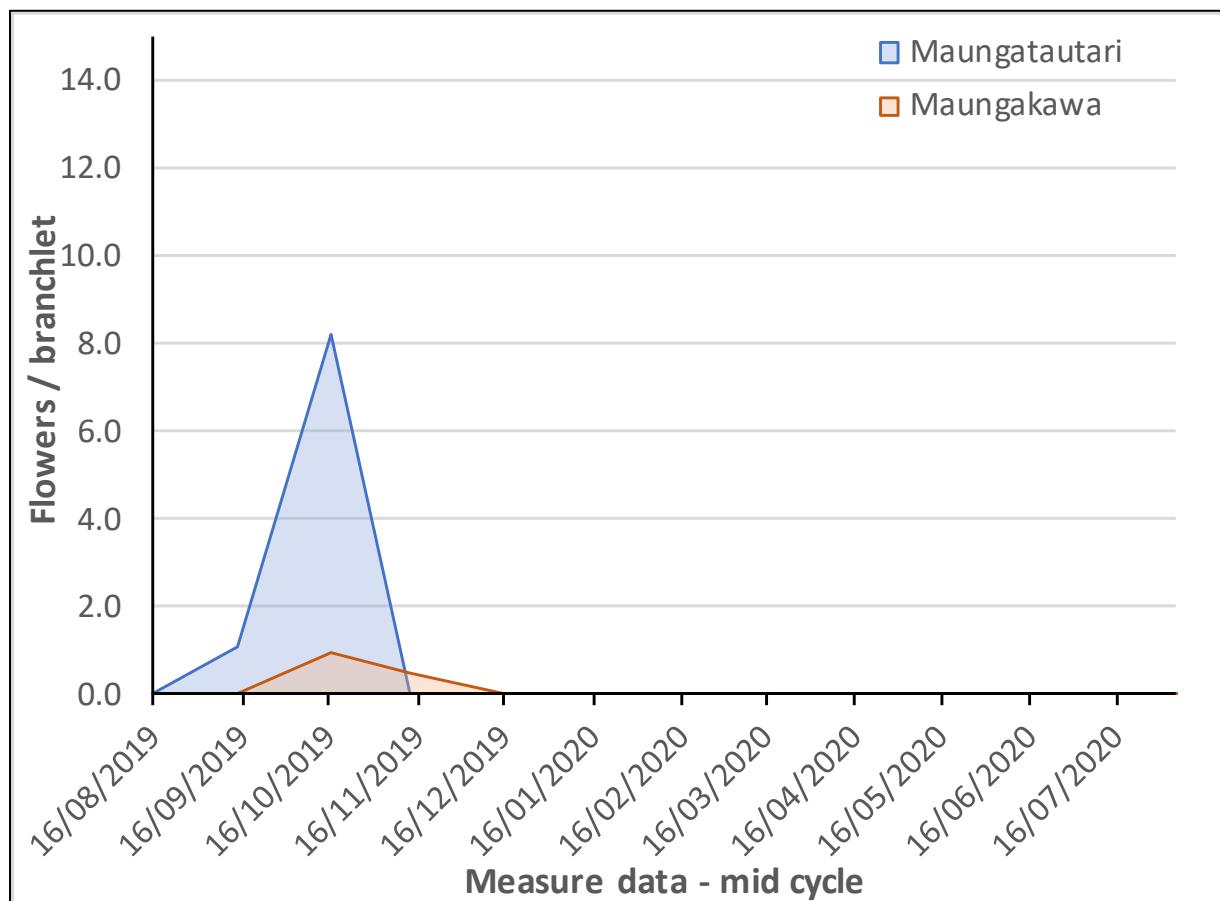
**Figure 5-16:** Mangeao – inflorescence buds / branchlet. Drought conditions prevailed during January and February 2020 (Chapter 2).



**Figure 5-17:** Inflorescence buds were developing when forest visits commenced in July / August 2019. (MNR LC1 August 2019).



**Figure 5-18:** New season inflorescence buds initiated in December 2019. Many turned black and fell off during summer drought conditions. (MNR LC1 February 2020).



**Figure 5-19:** Mangeao: flowers / branchlet. Note: One mangeao tree was not visited during peak anthesis as high winds forced me to abandon the Maungatautari forest visit (MNR, 24 Oct 2019).

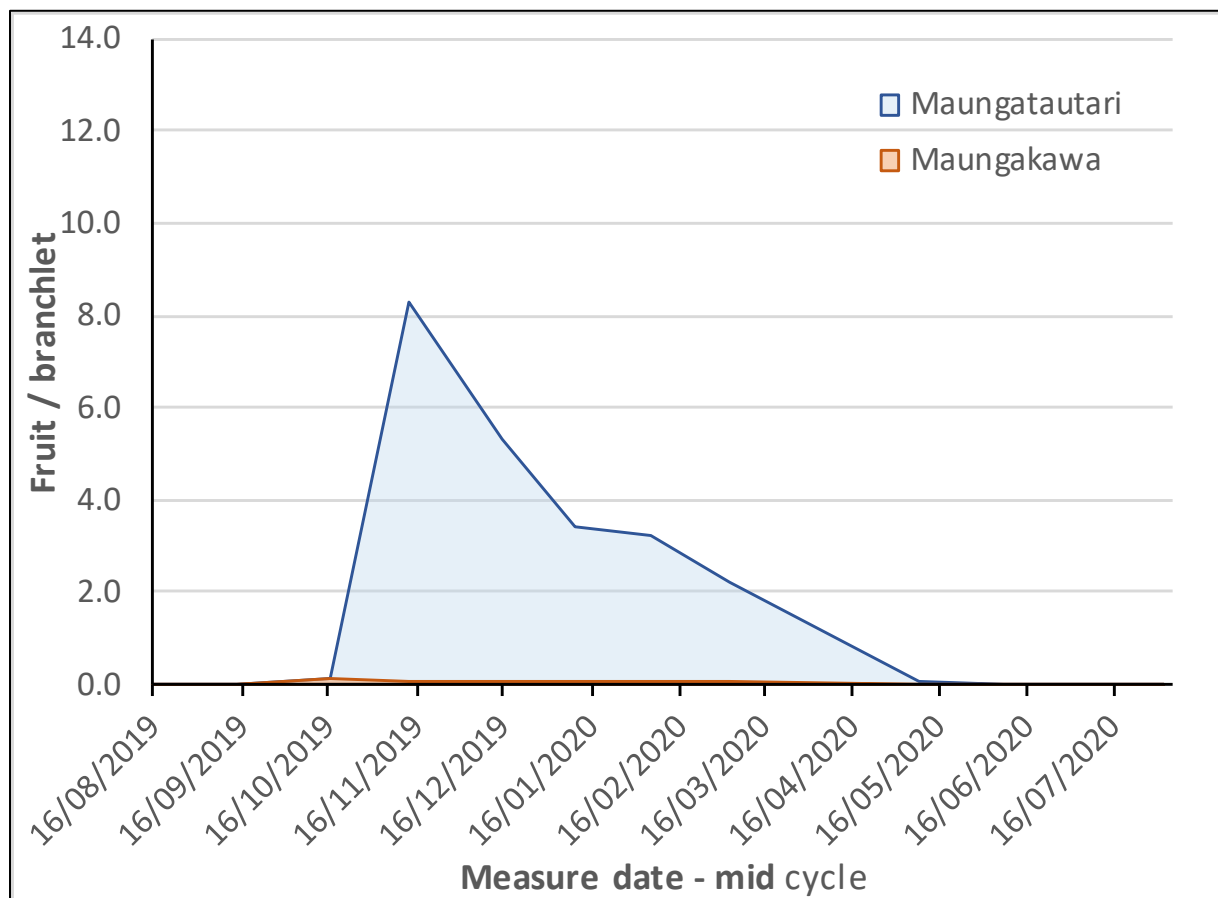


**Figure 5-20:** Mangeao: female flowers. An umbel of four or five flowers emerged from each inflorescence bud. (MND LC6 October 2019)



**Figure 5-21:** Mangeao: male flowers. An umbel of four or five flowers emerged from each inflorescence bud. (TTW LC1 October 2019)





**Figure 5-22:** Mangeao – fruit / branchlet. At Maungakawa only three fruit emerged from the flowers, but the fruit did not persist to maturity. However, on both trees (TTJ LC1 and LC5) fruit developed to maturity on branchlets that were not tagged. At both forests new season inflorescence buds were developing while fruit was on the trees (**Figure 5-16**).



**Figure 5-23:** Early fruit development. (MND LC6 November 2019)



**Figure 5-24:** A heavy crop of green and ripening fruit. Ripe fruit were a dark burgundy red colour. (MND LC6 February 2020)





**Figure 5-25:** Poor vegetative condition of female mangero following heavy fruiting. (MNR May 2020)



**Figure 5-26:** Fruit on dry ground along the fence line. Many dried fruit remained until Autumn 2021 when a few germinated and others decomposed. (MNR May 2020)



**Figure 5-27:** Curled leaves as a result of thistle spray drift that occurred mid November 2019. (TTB LC2, blue tagged branchlet, December 2019).



**Figure 5-28:** Spray damaged leaves survived on the tree. (TTB LC2, blue tagged branchlet, August 2020)





**Figure 5-29:** Kawakawa looper caterpillars (*Cleora scriptaria*) were observed chewing mangaeo leaves. (MNR LC5 December 2019)



**Figure 5-30:** Damaged mangaeo shoots caused by the unidentified caterpillar in the insert. (MND LC3 December 2019)



**Figure 5-31:** A mangaeo canopy at Maungatautari – note the insect damage. Has this been mistaken for possum chew in the past and elsewhere? The insect damage was most apparent where kawakawa grew nearby. (MNR PCQ1-4 January 2021)

### 5.3.3 Pigeonwood phenology

Pigeonwood vegetative growth over the 13-month study period was similar at both forests (**Figure 5-33**). The initial lengths of branchlets were highly variable (9.0 to 53.5 cm) and mean growth over 13 months was 5.4 cm (**Figure 5-34**). Side shoots developed on many branchlets (**Figure 5-35**). Vegetative and inflorescence buds flower buds emerged in mid-winter (July 2019 and July 2020) from leaf nodes and leaf scars. Small bud swellings were recorded as “spur development” until discreet individual buds were able to be differentiated in early spring. Inflorescence buds developed into a raceme bearing multiple flower buds. Very few inflorescences with emerging flower buds were counted on tagged branchlets. At Maungakawa only two of three male and two of the 13 female trees had flower buds on tagged branchlets in 2019. These developing flower buds disappeared as the previous season’s fruit started to ripen. At Maungatautari three of five male and one of seven female trees developed flower buds on tagged branchlets. Searching inside the foliage revealed more abundant inflorescences on older wood (**Figure 5-37** and **Figure 5-38**). As insufficient data was collected to convey quantitative flower bud, anthesis and fruiting dynamics, plots (**Figure 5-36**, **Figure 5-39** and **Figure 5-42**) were only indicative of seasonality.

Anthesis commenced (September / October 2019), concurrently with the previous year’s fruit ripening (**Figure 5-32**). The flower buds (**Figure 5-38**) and flowers were generally concealed by outer foliage. Flowers were small pale cream / green colour and had the same light spicy fragrance as the foliage. Male flowers which were only observed over a short period (September / October 2019), released a dense pollen cloud when disturbed by a sudden movement (**Figure 5-41**). The pollen could be seen rapidly dispersing in air currents. Swelling carpels attached by very short pedicels to the female receptacle were first observed from December 2019 (**Figure 5-43**). Female flowers with minimal carpel development continued to be observed until December 2019 (**Figure 5-40**). By late January these flowers appeared to have either been pollinated (carpel swelling) or were dying. Swelling carpels attached by very short pedicels to the female receptacle were first observed from December 2019 (**Figure 5-43**).

The maturing fruit (drupes) from the previous season’s anthesis had started showing hints of colour from October 2019; initially yellow and slowly increasing intensity to bright orange (November / December 2019), (**Figure 5-44**). Each fruit (a drupe) was derived from a single carpel. In contrast to the cryptic flowers, the ripe to over ripe bright orange fruit were very visible through gaps in the outer foliage and where heavy fruit laden bunches protruded through the foliage.

When this study commenced in late winter 2019, fruit was more abundant on tagged branchlets at Maungakawa than at Maungatautari, but a similar number of fruit developed from anthesis in spring 2019 at each forest (**Figure 5-42**). At Maungakawa remaining hard fruit (seeds) from 2018 anthesis were consumed or fell off as the new season’s fruit from spring 2019 anthesis emerged from the pollinated flowers. Remnants of the 2019 ripe fruit crop

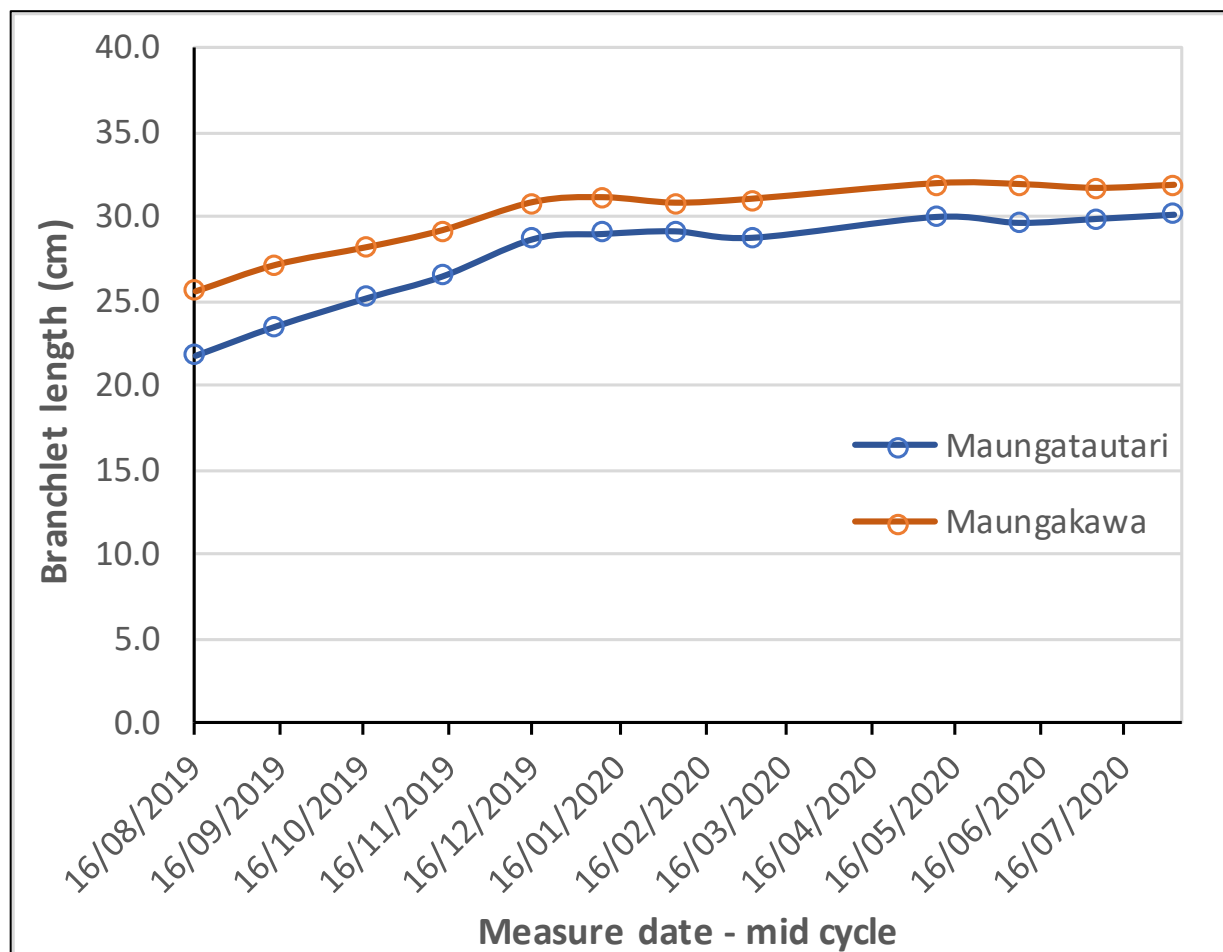
continued to be observed on the trees until anthesis in spring 2020. This contrasted with Maungatautari where none of the previous season's fruit were present when branchlets were tagged (August 2019) and only a few ripe fruit were observed on the trees throughout the study period. Most fruit disappeared from trees while still fleshy and in the early stages of colour development. By January 2020 and January 2021 remaining mature fruit were sparse.

Although a few smaller birds visited when the fruit were ripe, images of kererū frequently visiting a heavily laden margin tree (Chapter 5, MNR HA5) in October and November 2020 combined with observations of the dwindling fruit crop suggested kererū consumed most of the ripening fruit. By December only a few fruit remained on the tree and kererū visits dwindled. At both forests occasional fruit had indentations resembling the shape of a bird beak. More extensively damaged fruit were found on 66% of tagged female pigeonwood trees growing on the margins at Maungakawa (**Figure 5-45** and **Figure 5-46**). Immature fruit and fruit at various stages of ripening were also found on the ground below several of the trees. Comparable damage was not observed at Maungatautari.



**Figure 5-32:** Anthesis occurred while the previous cohort of fruit were ripening. Fruit ripened from September 2020 but by January 2020 most fruit had been consumed by birds. (MNR HA5 November 2020)





**Figure 5-33:** Pigeonwood - length of branchlet from branch to apical tip. Growth curves were similar with branchlets increasing in length steadily from mid to late winter 2019 until early summer. Average branchlet length increase over 13 months = 6.9 cm. Laterals also developed during this period.

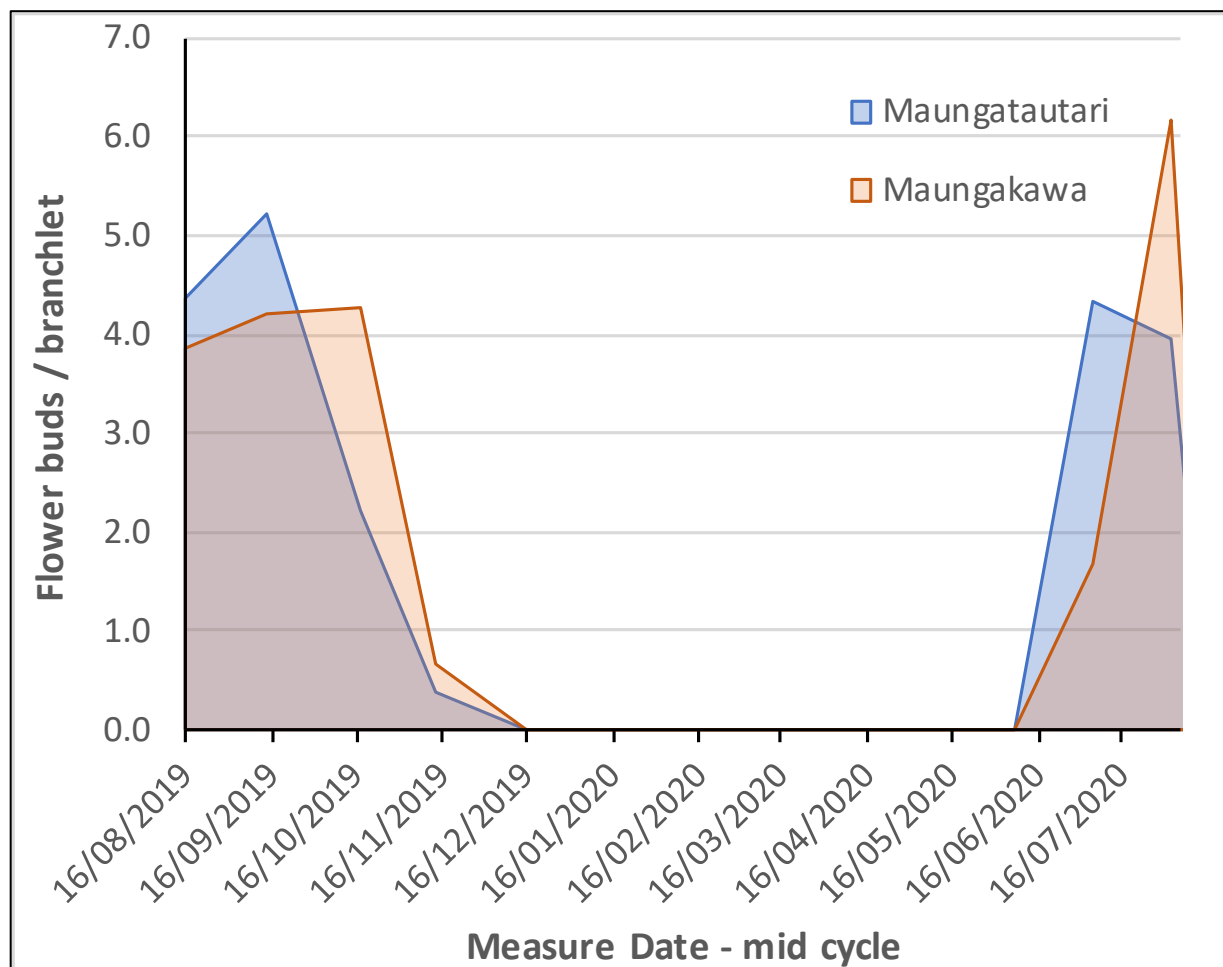


**Figure 5-34:** TTJ HA4 blue tag measured 46.0 cm in August 2019. Red arrows point to same leaf node in 2019 and in 2020 below (**Figure 5-35**).



**Figure 5-35:** TTJ HA4 blue tag measured 56.0 cm in August 2020. Note the side shoots and a developing flower bud raceme spur (yellow arrow).





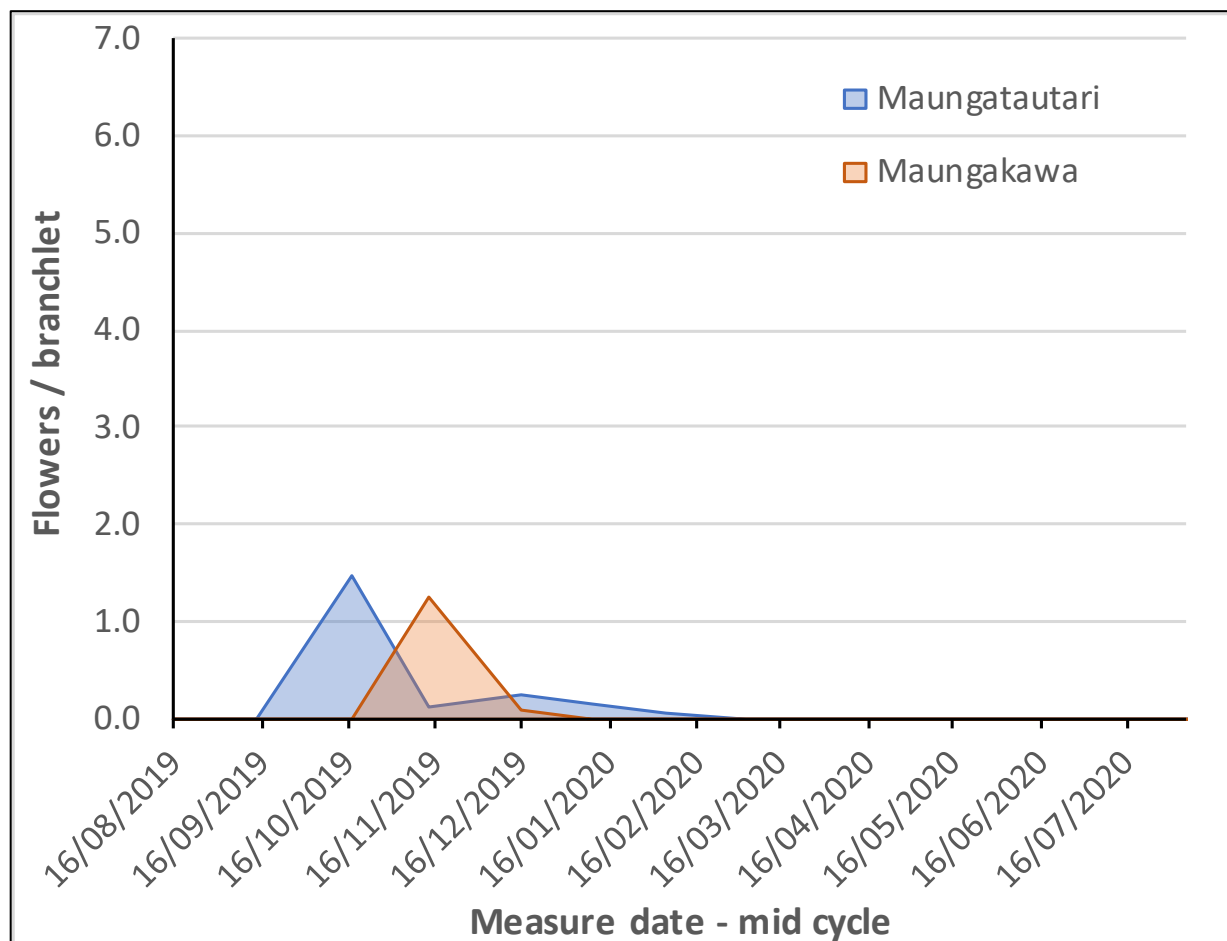
**Figure 5-36:** Pigeonwood – flower buds / branchlet. Flower bud development commenced in early winter. Although anthesis commenced in early spring, some buds didn't open until early summer.



**Figure 5-37:** A new seasons flower bud spur (red arrow) developing on a fruiting tree. (MNR HA5 July 2020)



**Figure 5-38:** Inflorescences of flower buds, arranged as a raceme, about to burst open on a female tree. (TTJ HA1 October 2019)



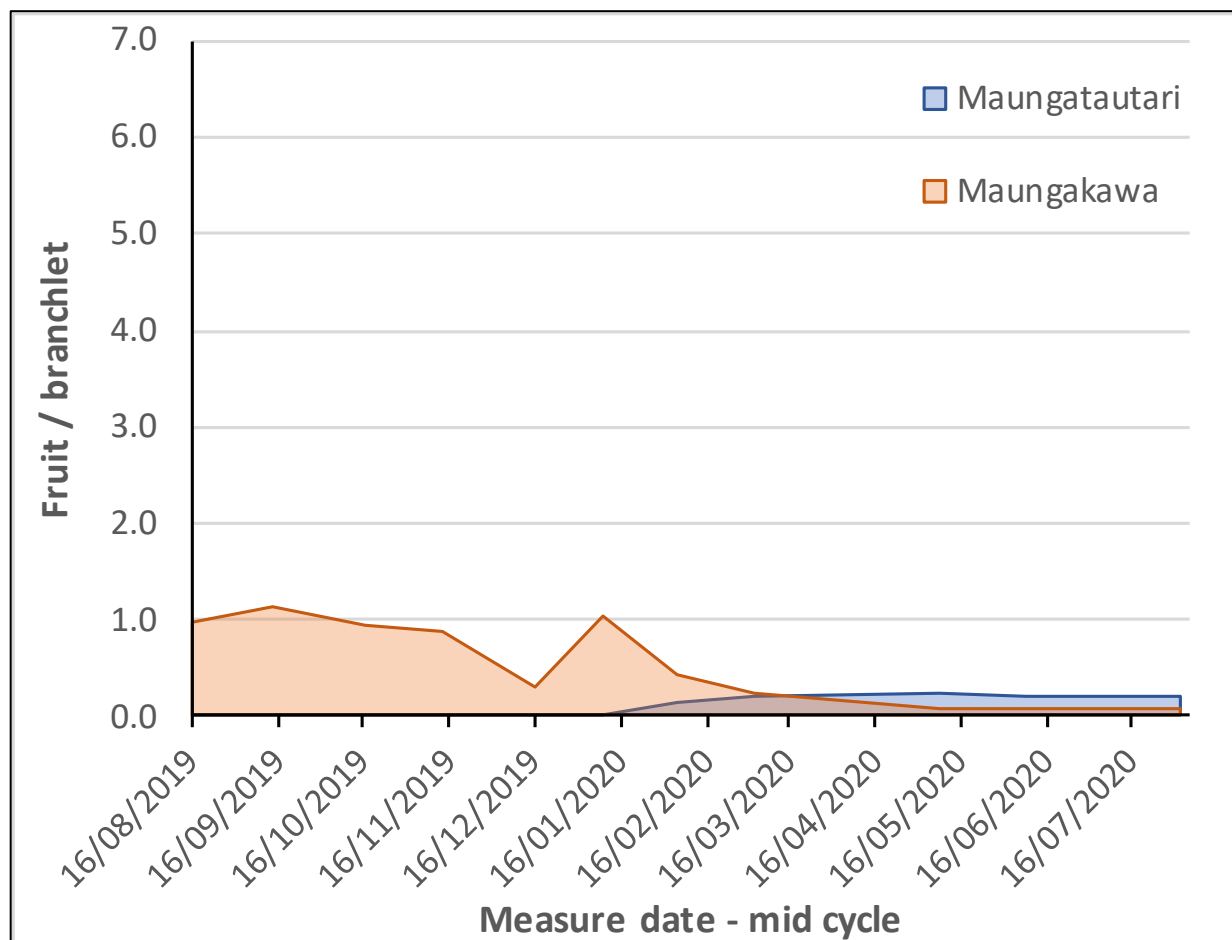
**Figure 5-39:** Pigeonwood – flowers / branchlet. Anthesis appeared to commence earlier at Maungatautari but extended for a longer period. This is likely to reflect the ratio of male to female flowers. Male trees tend to flower earlier with flowers surviving for a shorter period. Female flowers were counted as “flowers” until small emerging green fruit could be observed. A few female flowers persisted for an extended period before abscising in January and February 2020.



**Figure 5-40:** Female flowers (MNR HA5 November 2019) top right insert - male flower. (TTW HA3 November 2019)



**Figure 5-41:** Male flowers rapidly shed a pollen cloud when disturbed. (TTW HA3 November 2019)



**Figure 5-42:** Pigeonwood – fruit (drupes) / branchlet. Inflorescence bud and fruit development mainly occurred on older wood behind the tagged branchlets. At Maungatautari there was no fruit on tagged branchlets in 2019 and in 2020 very few on only one tree (MNR HA2). Review of the photos confirmed fruit development on older wood from anthesis spring 2018 and from anthesis spring 2019 (expected to ripen November 2020). At Maungakawa ripe fruit from 2018 remained on the trees concurrently with developing fruit from anthesis in 2019.



**Figure 5-43:** Early fruit development with up to 20 fruit on each receptacle. Only four immature fruit remained in the bunch when branchlet measurements were completed in July 2020. (TTJ HA1 January 2020)



**Figure 5-44:** Previous season (2018) ripening fruit (green / orange) and many bright orange fruit. Seeds became hard as the flesh dried out. (TTW HA1 November 2019)





**Figure 5-45:** Maungakawa - external damage on ripening fruit was observed on 67% of female trees. Markings on the upper fruit may be consistent with rat incisor teeth bite pattern. (TTW HA2 December 2019)



**Figure 5-46:** Maungakawa - ripening pigeonwood fruit had been removed leaving orange fleshy residues attached to the receptacle. The appearance is consistent with possum feeding habits (N. Fitzgerald, pers. comm). (TTJ HA4 October 2019)



## 5.4 Discussion

As would be expected for forests within the same ecological district and at similar elevation and aspect (Chapter 2), reproductive cycles within each species were synchronised at Maungatautari and Maungakawa. This study (July 2019 to August 2020) was undertaken in the period mangeao fruit development was high at Maungatautari but negligible at Maungakawa (Chapter 6). In this period tawa fruit development was low at both forests. The extended reproductive cycle in pigeonwood appeared similar in each year.

There were differences in the period from emergence of inflorescence and flower buds to maturation of fruit in each of the species. The negligible tawa fruit crop in autumn 2020 (**Figure 5-10**) had developed from flower buds and flowers that developed prior to the start of the study. The flower buds recorded during the study period developed into an abundant fruit crop in 2021. Similarly, mangeao fruit had developed from inflorescence buds that were well developed when the study commenced. Pigeonwood fruit developed from flower buds that were developing as the study commenced but some fruit was still on the trees in winter 2020. The fruit crops of each of these species occurred in a discrete and separate temporal space that would have contributed to the continuity of food resources for birds (Dijkgraaf, 2002) and hence continuity of seed dispersal. These varied reproductive cycles may be an adaptive attribute that underlies the competitive advantage of tawa, mangeao and pigeonwood in the forests.

The mode of pollination in tawa (Roper, 1967) and pigeonwood (Sampson, 1969) have been investigated but the mode of pollination in mangeao is not known for certain. Tawa is pollinated by small insects and may also be self-pollinating (Roper, 1967). My observations of the open structure of the pigeonwood flowers, lack of nectar in female flowers and the pollen release from male flowers are consistent with this species being wind pollinated. As this species retained brightly coloured fruit through the following flowering season, I suspect that the species has also adapted to attract pollinating birds that carry pollen on their feathers to female flowers. The mangeao flower structure suggests it is insect pollinated.

Tawa, mangeao and pigeonwood fruit potentially set from each inflorescence bud ranged over more than two orders of magnitude. Each tawa flower potentially developed into a single fruit but only one or two fruit developed on each inflorescence that may have had 50 or more flowers. A female mangeao inflorescence bud may yield five fruit and often all fruit reached maturity. One of more inflorescences developed from each leaf node or scar. As the pedicels and peduncles elongated the maturing fruit became more widely spaced (**Figure 5-23** and **Figure 5-24**). Up to 20 fruit potentially develop from each pigeonwood flower (Sampson, 1969). As many inflorescences had closely clustered flower buds, bunches of more than 100 fruit were observed on occasional trees (**Figure 5-38**, **Figure 5-40** and **Figure 5-43**). Research

into the reproductive and ecological advantages of floral arrangement has been extensively investigated over the last 50 years. Wyatt (1982) discussed flowering and fruiting cycles but in more recent years, advances in genetic research have underscored discussion of evolutionary and developmental factors (Ma et al., 2017). Floral arrangement often confers pollination and seed dispersal advantages (Webb and Kelly, 1993). The differences in floral productivity has been exploited in some domesticated species but the importance of floral arrangement and flower abundance in forest species are still not well understood.

#### **5.4.1 Tawa**

Anthesis in tawa was consistent with research at Lake Okareka (400 m asl) observed in 1970 and 1971 (Knowles and Beveridge, 1982; Leathwick, 1984) at four central North Island forests. Vegetative growth, flower bud development, anthesis and fruiting results from this study aligned to my observations of tawa canopy from the top of the tree top viewing platform at Maungatutari southern enclosure. Although (Knowles and Beveridge, 1982) found habitat conditions affect tawa vegetative growth patterns, particularly leaf size and shape, I didn't observe any differences between the canopy and study margin vegetative growth or inflorescence and flower bud to fruiting patterns. Productivity on tagged branchlets was low but appeared to be a fair representation of tree productivity.

At supplementary camera traps in lower branches on tawa trees, branches were observed moving in strong winds, swaying rapidly (at times thrashing) back and forth across and beyond the camera vision field (approximately 3 m). This thrashing movement was likely to have contributed to attrition of flower buds, flowers and developing fruit. Flexible small branches and branchlets would have been unlikely to support the weight of possums. This would have decreased their access to fruit borne on peripheral growth.

#### **5.4.2 Mangeao**

Single or interacting factors appeared to moderate productivity of the mangeao reproductive cycle. The reproductive cycle at Maungatutari was an order of magnitude more productive than on margin trees at Maungakawa in 2020 (**Figure 5-22**). The progressive reduction in potential productivity from inflorescence buds through anthesis to fruiting (**Figure 5-16**) suggests insects, rats or possums or a combination thereof, may have browsed the flower buds and flowers in late winter and spring. However direct evidence of this occurring was not obtained. If birds were responsible the effect should have been more pronounced at Maungatutari. Drought conditions (Chapter 2) could have precipitated the immature inflorescence bud loss (Stephenson, 1981) at Maungatutari during autumn 2020 but this does not explain why the buds appeared to have been more resilient at Maungakawa through to spring in 2020. Flower bud abundance was similar on female and male trees at each forest but there was insufficient data to determine if male flowers were less affected. Male trees did

not have the concurrent high energy demands of fruit development as discussed by Wheelwright (1986). At Maungatautari, the heavy fruit crop development in tandem with low soil water availability from December 2019 to April 2020 (Chapter 2) were possibly veto cues (Pearse et al., 2016) for flower bud abscission prior to anthesis. Although the drought equally affected trees at Maungakawa the female trees had not been subject to the high demands of fruit development as anthesis had been low (**Figure 5-19**).

### 5.4.3 Pigeonwood

Pigeonwood may be more productive on the forest margins than within the restricted light environment of the forest subcanopy. The light exposed margin growth of pigeonwood trees was very dense compared to growth observed under the cover of a canopy. As flower development and fruiting occurred mainly on older wood behind the tagged branchlets (**Figure 5-37**), the sampling plan was not optimal for measurement of flower and fruiting productivity of pigeonwood. The gender ratio at Maungakawa (male to female = 0.15) compared to Maungatautari (male to female ratio = 0.71) but the sample size was too small to determine the significance of this finding.

Kererū appeared to prefer the fruit when the swollen mesocarp was ripening, rather than the previous season's dry bright orange fruit. There appeared to be ample fruit for the current kererū population and what they didn't consume before the fruit dried out over summer, remained on the trees for a prolonged period. More abundant birds (Bombaci et al., 2021) to feed on the ripening fruit may account for only a few hard orange seeds remaining on the trees through until anthesis in the following spring at Maungatautari.

The remaining fruit may have been an attractant to birds during anthesis preceding the next cohort of fruit. Outwardly male and female trees appeared similar as much of the fruit developed within the canopy. Birds, including kererū, searching for ripening fruit in the trees (indiscriminately male and female) would be sufficient to initiate a pollen release cloud from male flowers (**Figure 5-41**). The pollen would coat feathers just as efficiently as it coated our hair, faces, eyes, nostrils (setting off hay fever allergy reactions) when we experimented with pollen releasing flicks. The receptive styles on female flowers are exposed across the broad floral receptacle. Birds would be likely to disperse the pollen over much longer distances than wind dispersal could in the relatively still forest subcanopy.

At Maungakawa there was evidence (**Figure 5-45** and **Figure 5-46**) that possums, and maybe rats, damaged and consumed some, but not all, the ripening pigeonwood fruit while it remained on the trees. Individual fruits and some still attached to their receptacle were also observed on the ground below these trees. The concomitant loss of flower buds from tagged branchlets during the period of observed damage to ripening fruit could have been collateral damage.

## 5.5 Conclusions

The measurement of phenology of the margin trees provided key data for understanding fruit / seed fall within the forests. As expected within a single ecological region and at similar geophysical locations, the timing of reproductive stages within each species were synchronized between study locations and across both forests.

The reproductive cycles of tawa, mangeao and pigeonwood all extend beyond 12 months with one stage of development being extended. Mangeao inflorescence buds emerged in summer but anthesis occurred nine months later in the following spring. Following anthesis pollinated tawa flowers became dormant from mid-summer until early winter when fruit emerged from the closed over calyx. In pigeonwood inflorescence and flower buds emerged in winter. Some of the previous season's fruit remained on the trees until after anthesis of the new season's flowers had been pollinated i.e., more than 12 months later. Mature tawa fruit were difficult to find on margin trees during the study period, but some fruit were observed emerging from dormant flowers from late winter 2020. These fruit did not persist to maturity. Continued observation of the tagged trees through to the conclusion of field work revealed mangeao and tawa fruit abundance were variable annually. Pigeonwood flowering, and fruit abundance appeared similar in both years. Mangeao appeared least resilient to insect attack, thistle control chemicals and adverse environmental conditions.

Rats and possums may influence fruiting in the study tree species. During the study period August 2019 to August 2020, mangeao fruit abundance appeared to be diminished where rats and possums were present. Inflorescence bud, flower, or fruit predation by rats and/or possums may have been observed but specific evidence was not obtained. There was strong evidence of possums removing fruit from pigeonwood trees. Mature tawa fruit were readily observed on margin trees at Maungatautari but to a lesser extent at Maungakawa. Where rats and possums were not present in the forest, tawa and mangeao appeared to produce plentiful fruit but in asynchronous years.

### 5.5.1 Research questions that would be worth pursuing

Do rats and/or possums browse mangeao inflorescence buds?

If rats or possums browse mangeao or pigeonwood flowers are male and female flowers equally affected?

What are the cues for successful flower development in male and female mangeao trees?

Are energy resources a factor in mangeao annual fruiting cycles?

How important are bird visits to pollination in pigeonwoods?

The high percentage of pigeonwood trees bearing fruit warrants further investigation. Do male trees develop some fruit as a mechanism to attract birds?



# Chapter 6

## Seed fall and germination

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### 6.1 Introduction

Seed fall is the culmination of inflorescence and flower bud development, anthesis, pollination, fruit, and seed development. The energy demands of the process must be met by the photosynthetic capacity of the canopy. Fleshy fruit are a valuable food resource for birds and in return birds, that can swallow the seeds whole, disperse the seeds away from the parent tree (Kelly et al., 2010). Seed fall, dispersal and subsequent species regeneration is disrupted when the reproductive processes are diminished or when predation of reproductive parts occurs (Beveridge, 1964; Campbell, 1990; Burns et al., 2011).

The drivers of fruit abundance and resultant seed fall are widely debated. Year to year variation in fruit abundance is common in New Zealand fleshy-fruited species (Knowles and Beveridge, 1982; Leathwick, 1984; Dijkgraaf, 2002). My study species: tawa (*Beilschmiedia tawa*), has variable fruit crops annually (*whakataukī* in Lyver et al. (2017)) and (Knowles and Beveridge, 1982; Dijkgraaf, 2002), but fruit abundance cycles in mangeao (*Litsea calicaris*) and pigeonwood (*Hedycarya arborea*) are not well understood. Wheelwright (1986) recognised many assumptions had been made about fruit production and seed dispersal and what is “normal” (Janzen, (1978) in Wheelwright (1986). He recognised the year-to-year variability of 22 tropical, lower montane Lauraceae (tawa and mangeao share this heritage) but found interpretation of the drivers was “not straightforward”. In recent years proximate causes (energy or nutritional resource constraints and weather cues) across extended spatial landscapes and ultimate (evolutionary benefits) of variable fruit abundance have been recognised (Pearse et al., 2016). Favourable cues may be suppressed by “veto” factors (negative influences) that limit a potentially abundant fruit crop (Bogdziewicz et al., 2018).

In many landscapes pollination and seed dispersal are the most vulnerable stages of the reproductive process (Patterson and Wilcove, 2012; Neuschulz et al., 2016). Forest fragmentation changes community composition (Young and Mitchell, 1994; Burns et al., 2011; Morales San Martin, 2015) and hence pollen abundance. Exposed edges, changed microclimates, and reduced biodiversity have reduced habitat for the endemic agents e.g., birds, lizards, insects, and bats that pollinate and disperse seeds in New Zealand forests. Disrupted pollination reduces fruit set (Aguilar et al., 2006).

Seed dispersal over the extended spatial landscape is now limited to a few bird species capable of swallowing the fruit and defecating undamaged seeds (Wyman and Kelly, 2017). Kererū and kokako (*Callaeas cinerea*) are the only endemic forest birds capable of swallowing

the larger tawa fruit (Clout and Hay, 1989). Tui (*Prosthemadera novaezelandiae*), bellbird (*Anthornis melanura*), silvereye (*Zosterops lateralis*) and tieke (*Philesturnus rufusater*) are able to swallow fruit in the range 7 to 10 mm e.g., pigeonwood, and mangeao. Another 12 species of endemic and introduced birds peck at the flesh of these fruit but fail to disperse the seeds (Kelly et al., 2010). Rodents are seed predators but may also disperse some (Cowan, 1990; Williams et al., 2000; Wyman and Kelly, 2017). Possums (*Trichosurus vulpecula*) and possibly rats (*Rattus* spp.) consume the flesh of ripe tawa and pigeonwood fruit, they do not eat the seeds (Cowan, 1992). The fate of mangeao fruit and seeds is not well documented.

The reproductive capacity of the forest or of individual trees can be measured by the abundance of seed fall from the canopy (Cottrell, 2004). The quantity of fruits and seeds captured below parent trees may underestimate the total quantity dispersed. Seeds dispersed by birds are spread below and beyond the canopy (Dijkgraaf, 2002). However, seeds consumed by birds e.g., blackbirds (*Turdus merula*) that also forage on the ground would be missed. Seed production is likely to be underestimated where rats and/or possums consume seeds within the canopy, destroy seeds when consuming them, by excreting the seeds at ground level or removing the seeds to a cache (Cowan, 1990; Williams et al., 2000).

I tested for evidence that rats and possums diminish seed fall and germination of tawa, mangeao and/or pigeonwood in Waikato hill-country forests. Seed fall and germination were measured at Maungakawa, which is inhabited by rats and possums; and at Maungatautari where they have been excluded since 2006. I placed seed traps at random surveyed points within the study locations at Maungatautari and Maungakawa forests to capture all seeds and forest litter falling from above; fruit and seeds including those dispersed by bird, inflorescence and flower buds, flowers, immature fruit, leaves, twigs, scat, insects, live and decaying epiphytes, mosses, and lichens as well as accumulated arboreal soil. This complex mixture represents the reproductive ecology of the forest canopy and provides clues to cryptic disruption of the processes. Immature fruit recovered from seed traps were included in seed counts as they represented successful flower pollination, but environmental conditions or limited energy resources have resulted in the trees shedding fruit. On the other hand, if rodents or possums had consumed the flowers, fruit development would have been curtailed, hence reducing seed abundance. If fruit had been consumed (destroyed) prior to maturation, only spilled immature fruit would be found on the ground or serendipitously in seed traps. Seed germination was tested within the context of the forest floor rather than testing seed viability in controlled conditions. This was achieved by placing captured seeds on the forest floor within cages intended to exclude both rats and possums, and on the adjacent exposed forest floor.

## 6.2 Methods

Seed traps were set up at each PCQ point (Chapter 3), to capture the natural rain of fruit and seeds. The seed traps were a funnel made of nylon 1 mm mesh fabric, hung on a wire rim 0.61 cm diameter (**Figure 6-1**). The mesh tapered to a bottom tube (diameter 15 cm) which was closed using a cable tie. A seed trap was placed within 5 m of each PCQ point. Seed traps were set up on reasonably flat ground, at least 2 m from any perceived track e.g., predator control line, or obvious animal track, and where all three support poles could be inserted to achieve a stable seed trap and a level top rim. Seed traps were placed at least 1 m from the trunk of any fern or tree greater than 10 cm dbh<sub>135</sub> to reduce “shadow” effects. The gravitational trajectory of falling fruit and seed was possibly altered by deflection by encountered vegetation but this would have been a random event occurring throughout the forests. Dead and dying vegetation falling over the seed trap was removed at each visit. To minimise analytical bias, seed traps were visited in rotation, alternating between study locations at Maungakawa and at Maungatautari. Seed fall data collection extended from November / early December 2019 to the final clearance of all traps in April / May 2021.

Seed viability and predation of seeds or germinating seedlings was determined using germination cages, intended to exclude rodents, possums, and birds. A cage was set up under each seed trap. (**Figure 6-1**). The 40 cm diameter germination cages were constructed from 10 mm welded wire mesh and pegged securely to the ground. To discourage interference by wildlife, square mesh lids protruding beyond the cage wire, were secured to prevent rodents and possums accessing fruit, seeds, or germinating seedlings. The spiky cut wire ends were left protruding from the top of the cage and edges of the lid. This approach proved effective. The enclosure cage was approximately half the area of the seed net. Seed trap installation at all PCQ points was completed in the forest visit rotation during November and early December 2019, with all germination cages installed during the following rotation. Prior to all germination cages being installed, I removed captured seeds from the forest for inspection and counting. My research permit conditions prevented me from returning them to the forest for germination trials that commenced in January 2020.

At each visit, the contents of each seed trap were examined. All collected fruit, seeds, leaves and other forest debris including insects and scat were emptied into a tray and sorted into three groups. Inflorescence buds, flower parts, fruit and seeds from tawa, pigeonwood, mangeao and other large-fruited forest species were partitioned from the leaf litter and other forest debris which included insect, rodent, and possum scat if present. Photos with the visual field standardised to the tray perimeter were taken of each sorted tray (**Figure 6-2**). Additional close-up images were taken of fruit, scat etc. All large fruit and seeds were identified, counted, and individually inspected to ascertain if they were potentially viable i.e., mature, and

undamaged. All fruit and seeds, ranging from immature to over mature, and bird dispersed seeds falling into the seed traps were included in counts as they indicate anthesis was successful and pollination processes were completed. Tawa, mangero and pigeonwood seeds defaecated by birds had a very smooth testa (for example the tawa seed in the insert on **Figure 6-4**) compared to the rough appearance of many seeds that had fallen directly into the seed trap. This is consistent with the criteria used by Kelly et al. (2010) for identifying seeds dispersed by birds when investigating the fruit dispersal capabilities of 10 bird species in New Zealand. As each fruit enclosed a potentially viable seed, and to simplify reporting, all fruit and seeds have been collectively referred to as “seeds” except where a reference specifically to the fruit is warranted.

Transfer of seeds to germination cages was initiated during the January 2020 forest visit rotation and inspection for germination initiated during the following visit rotations. All seeds more than 2 mm diameter were separated by species and transferred to the forest floor to germinate. Seeds from each species were randomly split into two groups: half were transferred to the germination cage and the remainder dropped onto the external forest floor germination zone bound by the cage and the poles (**Figure 6-1**). Fruit exocarp and mesocarp were left as found. A small amount of forest litter from the counting tray was added to the cage. This litter contained many seeds less than 2 mm that were not identified. Seed traps impeded direct fruit / seed fall from above but did not totally prevent natural fall fruit and seeds landing amongst the fruit and seeds placed in the external germination zone. At each visit, loose litter was gently removed from the exposed germination zone, taking care to avoid disturbing germinating seeds. The ground area within the cage was left undisturbed. Germinating tawa, mangero and pigeonwood seeds and seedlings were identified and counted. Individual seedlings were not tagged but could be tracked through the standardised photographic images taken through the lid of each cage. For reporting in this thesis final seed trap and germination cage inspections were from 7 April to 5 May 2021 which was prior to any expected germination of seeds that fell during autumn 2021. All infrastructure remains *in situ* as I am continuing this research over at least another two annual seed fall cycles.

Additional observations of the surrounding forest floor and up to the canopy were made to corroborate findings. Over the 13-month period from December 2019, a camera trap on the second PCQ point on each transect was used to monitor wildlife interactions (Chapter 4), and detect intrusion by rodents, particularly mice. Cages were inspected at each visit to ensure they were pegged securely. The 10 mm mesh size was marginal for preventing mice access. Only a single intrusion was detected on the camera traps when a mouse burrowed under the cage however physical evidence of burrowing under other cages was found on three occasions.





**Figure 6-1:** Seed trap and bird / mammal exclosure germination cage with a mesh lid. The cage is attached to the pole nearest the camera. The external seed germination area is indicated by yellow dashed lines. The orange and blue flagging tape attached to a liana on the tawa trunk is the PCQ surveyed position. Note: the lack of tawa fruit in the litter. Only one tawa fruit was captured in this seed trap during fruit fall in 2020 but 38 were captured during fruit fall in 2021. (TTB PCQ1-2 March 2020)





**Figure 6-2:** Sorted seed trap contents including 24 tawa seeds. The three seeds in the yellow ellipse show evidence of *Cryptaspasma querula* larvae predation. The trap also contained 14 supplejack (*Ripogonum. scandens*) seeds. The six without flesh would have been defaecated by a bird or possibly rats or possums. Several fluffy pukatea (*Laurelia novae-zelandiae*) seeds and one unopened capsule are visible adjacent to the leaves. There is one rat scat above (red arrow). The “small” litter (top left) includes tawa flower debris, and occasional insect scat. The dry leaves (on right side) include tawa, mangeao, pukatea and supplejack. (TTB PCQ1-3 May 2021)

### 6.3 Data Analysis

Seed fall ( $\text{m}^{-2}$ ) for each species was calculated for each study location (two transects each having five PCQ points). The study period encompassed two seed fall seasons for tawa, mangeao and pigeonwood: December 2019 to April / May 2020 (2020) and the matching period, December 2020 to April / May 2021 (2021). To correct for differences in forest composition, the total seed fall ( $\text{m}^{-2}$  basal area), a continuous variable, was calculated. For each study location seed fall of each species was calculated as cumulative seed fall ( $\text{m}^{-2}$  basal area) over the full study period (total seed fall) and for matched seed fall collection periods in 2020 and in 2021. For each species, the total seed fall ( $\text{m}^{-2}$  basal area) for Maungatautari and for Maungakawa study locations was plotted against the mid-point date for each forest visit rotation.

Statistica v12 software (StatSoft Inc.) was used to analyse data for total seed fall and seed fall during each of the matched collection periods (2020 and 2021). As seed fall ( $\text{m}^{-2}$  basal area) data was not linear and variability in some cases covered four orders of magnitude, data was 4<sup>th</sup> root transformed for statistical analysis.

*T*-tests and analogous non-parametric tests were used to identify if seed fall in any of the broadleaved species (tawa, mangeao or pigeonwood) was affected by growing in the forest where rats and possums were present. As differences in seed fall in each season (2020 and 2021) was a dependent variable, dependent sample (ds) *T*-tests were used to determine if temporal changes were significant. Despite 4<sup>th</sup> root transformation, pigeonwood data distribution did not meet assumptions for normality and equality of variance. Wilcoxon matched pairs test (non-parametric) was used to compare 2020 and 2021 seed fall between forests. Pigeonwood seed fall (m<sup>-2</sup> basal area) between the forests was compared using a Kuskal-Wallis ANOVA by ranks.

Other contents of seed traps, including bird dispersed seeds and mangeao inflorescence buds and flowers were also collated. Over winter 2020, inflorescence buds were easily distinguished but in other traps the mangeao buds were difficult to confidently identify as wet weather had caused much of the captured forest debris to decay. The difference in flower fall at each forest, but not flower bud fall, was tested for significance using the binomial probability distribution. The percentage of seeds that had been defaecated by birds i.e., dispersed by birds, was calculated, and reported for each species. The significance of differences (*T*-test, for independent samples) in seed dispersal (m<sup>-2</sup> basal area) by birds at each forest was determined. Observations of rodent and possum scat in seed traps was considered evidence of the species presence in the canopy but the data was not statistically analysed.

## 6.4 Results

Fleshy fruit and seeds were captured in seed traps in all months of the year. Mature tawa and mangeao fruit and seeds were predominantly found from early summer until late autumn but other species including pigeonwood, supplejack and nikau (*Rhopalostylis sapida*) were found throughout the year including over winter. Seeds of some species e.g., titoki (*Alectryon excelsus*) were only occasionally captured. Many smaller fruit and seeds e.g., mahoe (*Melicytus ramiflorus*) were also captured in some months.

Seed capture in seed traps was disrupted by several extraneous events. Seed traps at Maungakawa were destroyed by wildlife on eight occasions during seed fall periods. Camera traps recorded fallow deer (*Dama dama*) (Chapter 4 Wildlife) attacking the seed trap nets at two locations and it is likely they caused the damage in all cases. The damaged seed traps represented 7% of seed fall capture days. Most lost collection time occurred on transects where there was minimal seed fall during the collection periods immediately prior to and after the damage occurred. Possums also interacted with the seed traps but appeared to only dislodge nets from a single pole leaving the net orientation almost horizontal and able to capture falling seeds. One seed trap at Maungatautari was destroyed by a falling log and occasionally a net was found with the cable tie closure missing. This reduced the seed capture period by 2% during peak tawa seed fall. Although up to 10% of the potential tawa seed fall (2021) may not have been captured, the data loss does not change statistical interpretation. Throughout the forests up to 5% pigeonwood seeds may have been lost but mangeao seed

fall was negligible during the affected collection periods. Mangeao seeds continued to fall until June 2020. Although seed fall abundance was very light in 2021, it is possible some seed continued to fall after May 2021. This was also unlikely to change the conclusions drawn from analysed data.

#### 6.4.1 Tawa

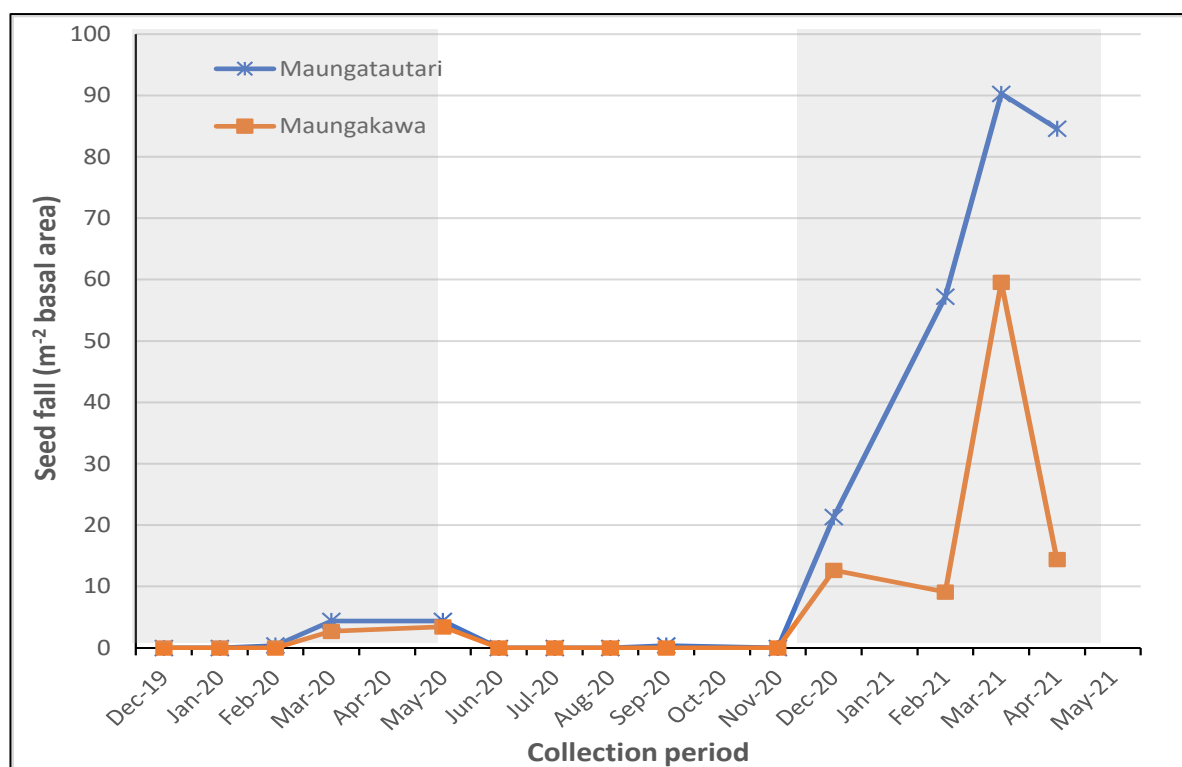
Although more seeds ( $\text{m}^{-2}$ ) were captured in seed traps at Maungakawa in both years, this changed when data was adjusted for the basal area ( $\text{m}^2$ ) of tawa in each forest (**Table 6-1**). Total tawa seed fall ( $\text{m}^{-2}$  basal area) at Maungakawa and at Maungatutari was similar ( $p = 0.40$ ) (**Table 6-2**). At both forests, peak tawa seed fall occurred in late summer and autumn; between February and June in 2020. However, in the second season, seed fall commenced in November 2020 and seeds were still dropping when the study period ended in April / May 2021 (**Figure 6-3**). Seed fall abundance ( $\text{m}^{-2}$  basal area) during the matched seed trapping periods was the same at each forest when seed fall was low in 2020 ( $T$ -test 2020  $p = 0.97$ ). In 2021 Maungatutari seed fall was significantly greater than in 2020 ( $T$ -test (ds)  $p < 0.01$ ) but Maungakawa seed fall was not significantly different to the previous season ( $T$ -test (ds)  $p = 0.16$ ) (**Table 6-1**). Birds dispersed a similar percentage of seeds in each forest ( $p = 0.50$ ) (**Table 6-2**).

The visual appearance of fruit and seeds provided evidence of the flesh being consumed and seeds being destroyed. The ripe flesh had been removed from many seeds. (**Figure 6-4** and **Figure 6-5**). Flesh remained on a greater proportion of seeds captured at Maungakawa. Seeds defaecated by birds had a very smooth testa (insert in **Figure 6-4**) compared to the rough appearance of many seeds that had fallen directly into the seed trap. Ripe fruit with possum tooth indentations (**Figure 6-8**) and seeds with freshly chewed flesh (**Figure 6-9**) were found on the ground and occasionally in seed traps during fruit fall in autumn. Green tawa seeds, and occasionally empty seed exocarps, were found on the ground at Maungakawa (TTB and TTW), (**Figure 6-6** and **Figure 6-7**) in early summer. Several had possum tooth indentations. At Maungatutari green seeds were very occasionally found on the ground and in seed traps but none had possum tooth markings.

Only a small percentage of seeds captured in seed traps had *C. querula* bore holes (**Figure 6-10**) but infestation was observed in more than 40% of fruit and seeds on the ground. Some of the seeds also appeared to have been chewed (**Figure 6-11**). Occasionally pupating larvae were recovered from seed traps in both forests (Chapter 4). Most seeds remaining on the ground for more than a few weeks had rotted.

No tawa seedlings were found in germination cages or the adjacent forest floor. However, on the final visits to the forests in May 2021, an occasional seed with the radicle emerging (**Figure 6-12**) were found in forest floor litter. Established seedlings from seed fall 2020 were observed at Maungatutari (**Figure 6-13**) but rarely at Maungakawa.





**Figure 6-3:** Tawa seed fall ( $\text{m}^{-2}$  basal area) at Maungatautari (blue line and cross markers) and Maungakawa (brown line and solid filled markers) from December 2019 to May 2021. Shaded areas indicate the two matched seed fall seasons.

**Table 6-1:** Tawa seed fall at Maungatautari and Maungakawa forests: seeds falling in January to May at each study location. Values in bold were significant ( $p < 0.05$ ). Comparison between years relates to the seed fall ( $\text{m}^{-2}$  basal area) across each forest. Seed fall in 2021 was post possum control at Maungakawa.

	Seed fall ( $\text{m}^{-2}$ )		Seed fall ( $\text{m}^{-2}$ basal area)		
	2020	2021	2020	2021	Between years
<b>Maungatautari forest</b>					<i>T</i> - test (ds) $p < 0.01$
MND	0.68	11.6	8.77	149	
MNR	0.00	7.19	0.00	23.8	
MNG	0.34	48.9	0.38	54.4	
<b>Maungakawa forest</b>					<i>T</i> - test (ds) $p = 0.16$
TTW	0.00	1.03	0.00	2.07	
TTB	0.68	81.8	0.87	84.6	
TTJ	2.05	4.11	4.52	9.04	

Seed fall ( $\text{m}^{-2}$  basal area) difference between forests in 2020: *T*-test  $p = 0.97$

Seed fall ( $\text{m}^{-2}$  basal area) difference between forests in 2021: *T*-test  $p = 0.28$

**Table 6-2:** Tawa fruit and seed ( $\text{m}^{-2}$  basal area) collected in seed traps in all months throughout the seed trapping period (Dec 2019 to May 2021) and the percentage dispersed by birds.

Maungatautari study locations			Maungakawa study locations		
	Total seeds ( $\text{m}^{-2}$ basal area)	% bird dispersed		Total seeds ( $\text{m}^{-2}$ basal area)	% bird dispersed
MND	158	25%	TTW	0	100%
MNR	23.8	24%	TTB	85.5	9%
MNG	55.1	3%	TTJ	13.6	72%

T-test seed fall ( $\text{m}^{-2}$  basal area) between forests  $p = 0.40$

T-test bird dispersed seeds ( $\text{m}^{-2}$  basal area) between forests  $p = 0.50$



**Figure 6-4:** Tawa seeds recovered from a seed trap at Maungatautari. Top left insert: A tawa seed that had been defaecated by a bird. (MNG PCQ1-2 March 2021)



**Figure 6-5:** Tawa fruit and seeds recovered from a seed trap at Maungakawa. Many seeds have fruit flesh or fibrous remnants present. (TTB PCQ1-3 March 2021)



**Figure 6-6:** Green tawa fruit were found scattered in the litter at Maungakawa. (TTW PCQ1 December 2020)



**Figure 6-7:** Tawa exocarp found on the ground at Maungakawa. Note the possum tooth mark indentations. (TTW PCQ1 December 2020)





**Figure 6-8:** Tawa fruit captured in a seed net with possum tooth marks. (TTB PCQ1-2 March 2021)



**Figure 6-9:** Flesh of some tawa fruit, captured in seed traps and found on the ground, had been chewed by possums. (TTB PCQ1-2 March 2021).



**Figure 6-10:** Tawa fruit with *C. querula* bore holes (where the larvae has entered the seed). (MNR PCQ2-1 April 2021)



**Figure 6-11:** Damage to the tawa seeds is consistent with rats or possums chewing the seed to remove almost fully developed *C. querula* larvae. (TTJ April 2021)



**Figure 6-12:** Germinating tawa seed from 2021 seed fall were found on the ground at the end of the study period. There had been rain in the previous fortnight. (MND PCQ1-3 May 2021)



**Figure 6-13:** Tawa seedlings (elongated leaves) established from 2020 seed fall at Maungatautari, but they were not common at Maungakawa. Pigeonwood seedlings (leaves with rounded ends) were observed at both forests. (MNG PCQ1-5 April 2021)

## 6.4.2 Mangeao

Mangeao seed fall abundance contrasted across seasons and forests (**Table 6-3** and **Figure 6-14**). Seed fall ( $\text{m}^{-2}$  basal area) at Maungakawa in 2020 was marginally less than at Maungatautari ( $T$ -test  $p = 0.07$ ). More than 98% of the mangeao seed fall at Maungatautari was captured at study locations MND and MNR (total > 4000 seeds). At these locations, more than 66% of the seed crop dropped as immature fruit (**Figure 6-17**). Very occasionally immature fruit were found in seed traps within the forest at MNG and at Maungakawa. Small numbers were also found in supplementary seed traps on the forest margins. In 2021 seed fall was negligible at both forests; only two seeds were captured in the seed traps in each forest.

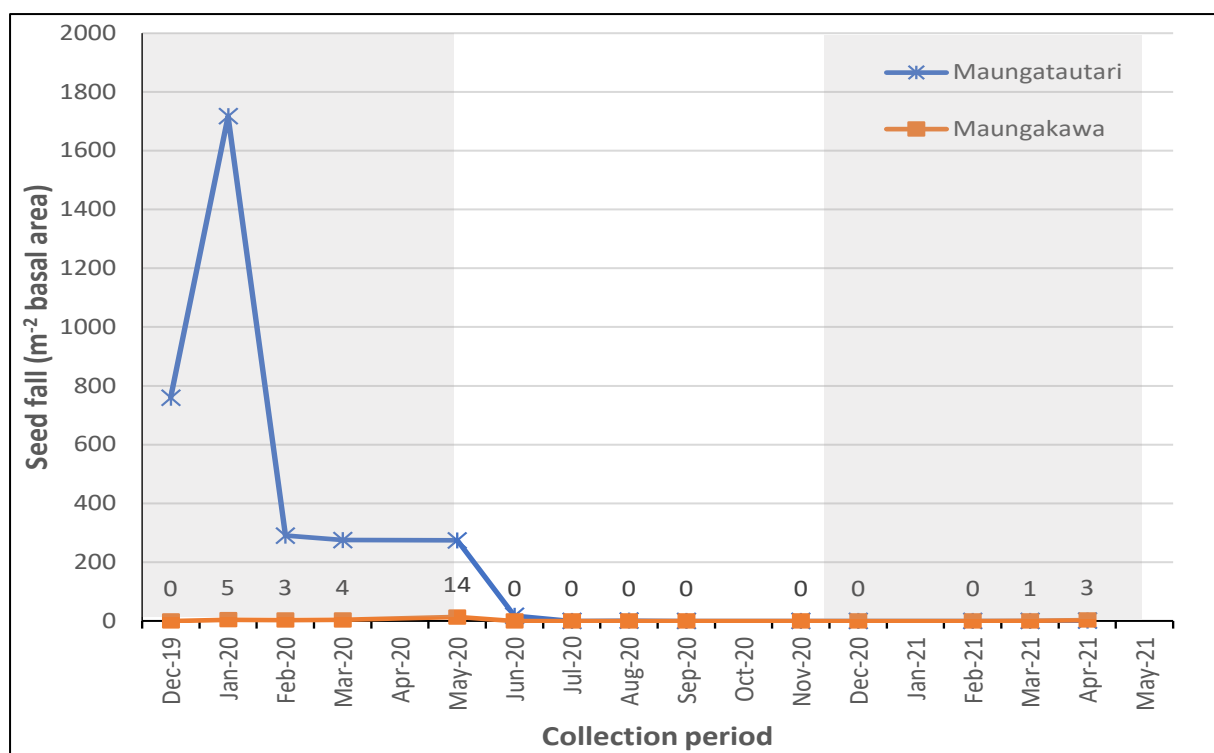
Healthy tall mature mangeao growing on the forest margin at Maungakawa had fruit crops in both years (**Figure 6-21**, **Figure 6-22** and **Figure 6-23**). Damage to the mangeao leaves captured in the margin seed trap beneath the trees, could have been caused by insects or possums (**Figure 6-24**). The fruit that fell off had not been damaged by possums or rats.

Total seeds ( $\text{m}^{-2}$  basal area) dispersed by birds (**Table 6-4**) were similar at both forests ( $p = 0.15$ ). When immature mangeao seeds were excluded from the total seeds captured at MND and MNR (prolific fruit fall), less than 5% of the seeds had been dispersed by birds. Where fruit was scarce (MNG, TTB and TTJ transects) at least 50% of seed was dispersed by birds. No bird dispersed mangeao seeds were captured in seed traps on TTW transects. In 2021 three of the four seeds captured had been dispersed by birds.

Inflorescence and flower buds and flowers were found on the ground and in seed traps. Inflorescence buds were found in seed traps at both forests during winter months. During spring flowers were found on 11 occasions in seed traps at Maungakawa but at Maungatautari they were only present once in a seed trap on the forest margin (**Table 6-5**). Many of flower parts at Maungakawa appeared chewed (**Figure 6-15** and **Figure 6-16**). Matching chew marks were also found on occasional seeds captured in seed traps (**Figure 6-19**).

Mangeao seed germination trials were hampered by the lack of seed fall at Maungakawa. At Maungatautari, in 2020, approximately 700 seeds were placed in the germination cage and a similar number on the exposed ground. Only 10% of mature seeds germinated between early spring and autumn 2021 (**Figure 6-20**) with 50% of the seedlings remaining alive at the end of the study. The dead seedlings appeared to have succumbed to the dry soil conditions. Seed fall at Maungakawa was very low in 2020 with only 12 seeds available for germination trials. The majority germinated both in the cage and on the exposed ground but at the end of the study only two seedlings remained in the cages.





**Figure 6-14:** Mangleo seed fall ( $\text{m}^2$  basal area) at Maungatautari (blue line and cross markers) and Maungakawa (brown line and solid filled markers) from December 2019 to May 2021. Data for the captured seeds at Maungakawa is entered above the plotted line. Shaded areas indicate the two matched seed fall seasons.

**Table 6-3:** Mangleo seed fall at Maungatautari and Maungakawa study locations in January to May in 2020 and in 2021. Values in bold are significant ( $p < 0.05$ ). Comparison between years relates to the seed fall ( $\text{m}^2$  basal area) across each forest. Seed fall in 2021 was post possum control at Maungakawa.

	Seed fall ( $\text{m}^2$ )		Seed fall ( $\text{m}^2$ basal area)		Between years
	2020	2021	2020	2021	
<b>Maungatautari forest</b>					<i>T</i> -test (ds) $p = 0.13$
MND	962	0.00	1525	0.00	
MNR	733	0.34	1771	0.83	
MNG	2.40	0.34	20.71	2.96	
<b>Maungakawa forest</b>					<i>T</i> -test (ds) $p = 0.27$
TTW	0.00	0.00	0.00	0.00	
TTB	1.03	0.34	1.63	0.54	
TTJ	2.40	0.34	24.07	3.44	

Seed fall ( $\text{m}^2$  basal area) difference between forests in 2020: *T*-test  $p = 0.07$

Seed fall ( $\text{m}^2$  basal area) difference between forests in 2021: *T*-test  $p = 0.98$

**Table 6-4:** Mangeao fruit and seed (m<sup>-2</sup> basal area) captured between December 2019 and May 2021. The seeds captured prior to February 2020 were immature. Seeds dispersed by birds were captured between February and June 2020. No seeds were captured between July 2020 and February 2021.

	Maungatautari			Maungakawa	
	Total seeds (m <sup>-2</sup> basal area)	% bird dispersed		Total seeds (m <sup>-2</sup> basal area)	% bird dispersed
MND	1542	1%	TTW	0.00	null
MNR	1772	2%	TTB	2.17	50%
MNG	27.5	78%	TTJ	27.5	88%

*T*-test seed fall (m<sup>-2</sup> basal area) between forests  $p = 0.09$

*T*-test bird dispersed seeds (m<sup>-2</sup> basal area) between forests  $p = 0.20$

**Table 6-5:** Seed fall traps with mangeao flower parts captured in August to November 2020. Senescent male flowers were not included in counts. Flower drop occurred post the possum control campaign at Maungakawa in June 2020 (Chapter 4).

	Maungatautari			Maungakawa		
	MND	MNR	MNG	TTW	TTB	TTJ
Total trays (n)	30	30	30	30	30	30
Trays with flower parts	1	0	0	0	8	3



**Figure 6-15:** Close up (x3) of a damaged mangeao flower. This could be due to insect chew, bird pecking or rodents. The damage is too fine to be attributed to possums. (TTB PCQ1-3 September 2020)



**Figure 6-16:** Mangeao male flower (x3). Two undamaged anthers are present at the rear of the flower (open pollen sacs) but all other anthers appear to have been chewed. (TTB SNT September 2020)



**Figure 6-17:** Many immature mangeao fruit were captured in seed traps at Maungatautari between November 2019 to February 2020. (MNR PCQ1-5 December 2019)



**Figure 6-18:** Ripe mangeao fruit in the seed sorting tray. It is likely much of this fruit (partially ripe and with attached peduncles) fell off due to the prevailing drought or was dislodged by birds feeding. (MNR SN2M March 2020).



**Figure 6-19:** A mangeao seed (magnification x3) with possible *M. musculus* gnaw marks found in a seed trap. (MND PCQ2-4 February 2021)



**Figure 6-20:** Mangeao seedlings (n = 5) germinated inside an exclosure cage. (MNR PCQ2-2 November 2020)





**Figure 6-21:** A small group of mature mangero on the forest margin at Maungakawa. Seeds were captured in the supplementary forest margin seed trap below these trees in both years. Fruit was also found on the ground below the trees each year. The reduced foliage on the tallest mangero tree was consistent with foliage loss observed in fruiting trees at Maungatautari. (TTB August 2020)



**Figure 6-22:** Fruit and seeds captured in a Maungakawa margin seed trap in February 2021 (mangero  $n = 9$  and pigeonwood  $n = 1$ ). In February 2020 four mangero seeds were captured in this trap. (TTB SNL1M February 2021).



**Figure 6-23:** Mangero fruit and seeds captured in the seed trap in March 2021 ( $n = 9$ ). The same number of seeds were captured in March 2020. The top right seed has been defaecated by a bird. (TTB SNL1M March 2021)



**Figure 6-24:** Leaves found in the seed trap. Some mangero leaves appeared to have been chewed by insects. (TTB SNL1M March 2021)

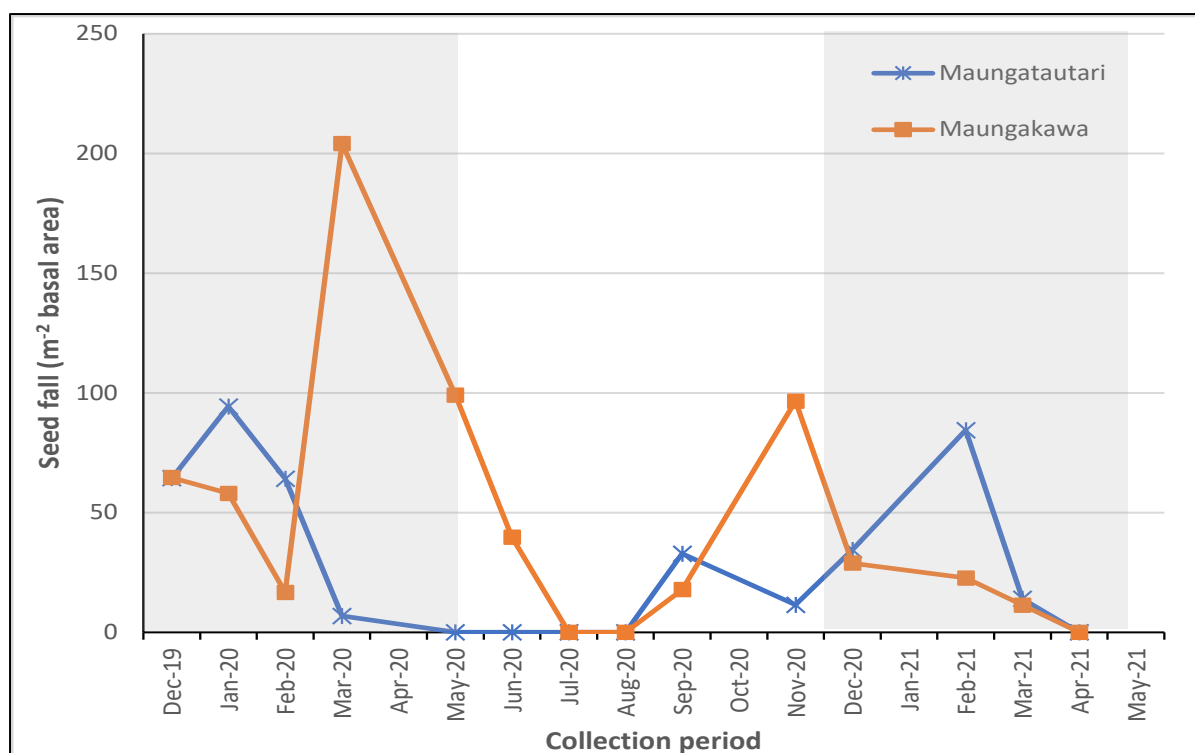


### 6.4.3 Pigeonwood

Pigeonwood fruit ripening occurred over an extended period (Chapter 5). Most of the fruit commenced ripening in the spring 12 months after anthesis but some fruit remained green until ripening in summer or autumn. The bright orange flesh of the ripe fruit only remained soft for a short period before drying to a hard outer seed coat. These hard seeds drop over the autumn, but some remained on the trees until after anthesis in the following spring.

Total seed fall was similar at each forest (**Table 6-6**) but with contrasting seed fall patterns. Pigeonwood fruit and seeds were captured in all months apart from six weeks in mid-winter 2020 (**Figure 6-25**). A peak of mature seeds was captured at Maungatautari in January to February of both years. Seed fall peaks at Maungakawa occurred in March to May 2020 and September to December 2020. Immature fruit were captured in a single Maungakawa seed trap (TTB PCQ2-4) during March to June 2020 (three visits). At Maungatautari, a few immature fruit were captured in a single supplementary seed trap (MNG PCQ2M) on the forest margin during March to June 2020 (margin seed traps were not included in seed fall data). No immature fruit were captured at either forest in 2021. Only 11 seeds ( $\text{m}^{-2}$  basal area) were captured at Maungatautari during October and early November 2020 but at Maungakawa 97 seeds ( $\text{m}^{-2}$  basal area) were captured during the same period (**Figure 6-25**). Most of these seeds had a fine coat of fibrous remains from the flesh (**Figure 6-26**). The appearance was not consistent with the smooth seed coat on seeds dispersed by birds. Bird dispersed seeds were captured between September to March. At both forests the number of seeds dispersed by birds were similar ( $T\text{-test } p = 0.99$ ), (**Table 6-7**).

Pigeonwood seed germination rates and survival at the end of the study were similar at each forest. Approximately 50% of mature seeds in the cages and on the exposed ground germinated. At the end of the study 50% of the seedlings inside the cage remained but no seedlings remained on the exposed ground outside.



**Figure 6-25:** Pigeonwood seed fall ( $\text{m}^2$  basal area) at Maungatautari (blue line and cross markers) and Maungakawa (brown line and solid filled markers) from December 2019 to May 2021. Shaded areas indicate the two matched seed fall seasons (**Table 6-6**)

**Table 6-6:** Pigeonwood seed fall at Maungatautari and Maungakawa forests. Seeds ( $\text{m}^2$  basal area) for each study location and for each forest in 2020 and 2021 seed fall seasons. Comparison between years relates to the seed fall ( $\text{m}^2$  basal area). Values in bold were significant ( $p < 0.05$ ). Comparison between years relates to the seed fall ( $\text{m}^2$  basal area) across each forest.

Seed fall season	Seed fall ( $\text{m}^2$ )		Seed fall ( $\text{m}^2$ basal area)	
	2020	2021	2020	2021
<b>Maungatautari forest</b>				
MND	4.79	1.37	95.1	27.2
MNR	2.74	1.03	91.7	34.4
MNG	2.05	3.42	42.7	71.1
<b>Maungakawa forest</b>				
TTW	8.21	6.16	45.3	33.9
TTB	21.56	0.00	321	0.00
TTJ	7.19	2.74	75.6	28.8

Difference between years: Wilcoxon matched pairs test  $p = 0.07$

Difference between forests (2020 & 2021): Kruskal-Wallis ANOVA by rank  $p = 0.63$

**Table 6-7:** Mature pigeonwood fruit and seed fall collected in seed traps and the percentage dispersed by birds throughout the seed trapping period (November 2019 to May 2021).

Maungatautari study locations			Maungakawa study locations		
	Total seeds (m <sup>-2</sup> basal area)	% bird dispersed		Total seeds (m <sup>-2</sup> basal area)	% bird dispersed
MND	122	22%	TTW	126	22%
MNR	149	46%	TTB	403	14%
MNG	135	58%	TTJ	130	69%

T-test seed fall (m<sup>-2</sup> basal area) between forests  $p = 0.43$

T-test bird dispersed seeds (m<sup>-2</sup> basal area) between forests  $p = 0.99$



**Figure 6-26:** Pigeonwood seeds ( $n = 2$ ) and possum scat amongst dried shed tawa flowers. The seeds (in red circles) were consistent with possums having consumed the flesh and dropped the seed. The peduncle remains attached on the left-hand seed. (TTB PCQ1-2 January 2020)

## 6.5 Discussion

Although there was a marginally greater mangeao seed fall at Maungatautari in 2020, all other data failed to show a significant difference between the forests. Therefore, it would be premature to conclude that rats and/or possums depress tawa, mangeao or pigeonwood reproductive capacity. However, the presence of both rat and possum scat in seed traps confirmed the arboreal invasive mammals were active in the canopy. There was also evidence of possum and rodent chew marks on fruit and seeds found in seed traps and on the ground. Both green and ripe tawa and ripe pigeonwood fruit are certainly components of the possum diets. Rodents also interacted with the fruit and seeds. I have considered the impacts of the rats and possums on tawa, mangeao and pigeonwood separately.

### 6.5.1 Tawa

Seed fall across Maungatautari and Maungakawa forests, (0 to 66 seeds  $\text{m}^{-2}$ ) was similar to the variable levels reported by Dijkgraaf (2002) in a frugivore study undertaken in the Auckland region between 1994 and 2012. However, in that study, tawa density was lower than at my study locations and the seed traps were placed directly beneath tawa trees. Knowles and Beveridge (1982) noted the extent to which tawa shed dormant flowers over the autumn. Large quantities of dormant flowers were shed in 2020 but the trees went on to have a prolific crop. As an example there were thousands of dry dormant flowers in the seed trap (TTB1-2) (**Figure 6-26**) where the most seeds ( $n = 97$ ) were captured. In the absence of drought conditions tawa seed fall may have been prolific (Pearse et al., 2016) where possums do not inhabit the forest. The most seeds in this study were 67 seeds  $\text{m}^{-2}$  whereas Knowles and Beveridge (1982) reported seed fall up to 100 seeds  $\text{m}^{-2}$  as being a heavy crop. At Maungatautari fruit abundance in 2021 was possibly in the similar quantities to those Māori elders describe occurring in their childhood (Lyver et al., 2017).

Possums were likely to have reduced seed fall at Maungakawa. Knowles and Beveridge (1982) reported “possums may destroy many immature (half-developed) seed in the tree crown by making a hole in the side or end of the fruit and extracting the soft kernel, knocking down many otherwise undamaged fruits in the process”. Fresh green fruit were found on the ground below tawa trees at Maungakawa including occasional pieces of hard green exocarp shells where the kernel had been removed (**Figure 6-6** and **Figure 6-7**). Cowan (1990) reported that possums destroyed 69% of tawa “seed” at Pureora forest in 1982 but he did not distinguish whether damage occurred to the green or to the ripe fruit. It is likely possums had consumed green fruit in the canopy at Maungakawa thus substantially reducing the crop available for ripening.

The appearance of tawa seeds defaecated by birds were distinctly different to seeds with no flesh, falling directly from the canopy (**Figure 6-4** and insert). Ripe flesh on these seeds



appeared to have been consumed by smaller birds pecking at the flesh or other fauna including insects, rodents and/or possums chewing the flesh. At Maungakawa occasional seeds defaecated by birds were captured, but seeds where the fruit flesh had been stripped by mechanical means e.g., chewing, rather than the smooth appearance resulting from chemical action within a bird's gut, were more abundant. The percentage of seeds dispersed by birds at each forest related to fruit abundance. As a percentage of total seed fall, bird dispersal was greatest where seed fall was low.

Beveridge et al. (2009) predicted that possums eating tawa fruit threatens regeneration of the species. Some ripe fruit were found on the ground at both forests in 2020 when there was low seed fall at both forests and at Maungakawa possum abundance was high. They consumed the flesh of some ripe fruit in the canopy (**Figure 6-8** and **Figure 6-9**) and were observed on the forest floor consuming the flesh of ripe and discarding the seeds. The threat to tawa regeneration due to possums, that Beveridge et al. (2009) predicted is debatable. Possums did not destroy seeds from ripe fruit, but they did limit spatial dispersion of the seeds.

Rats removed the fruit to consume "privately" but feeding trials have demonstrated they also discard the seeds (Knowles and Beveridge, 1982). The seeds were most likely lost from the viable seed bank as feeding platforms and nests are usually found in epiphyte clumps and tree hollows (Innes and Russell, 2021) where tawa seedlings are unable to establish (Wilson et al., 2003).

Tawa seeds were vulnerable to drying (Knowles and Beveridge, 1982), to *C. querula* infestation (Silberbauer, 2013) and to rotting i.e., cotyledons completely liquified. When broken open, the contents of most infested seeds had been destroyed although a few retained the embryo and part of the cotyledons. Seed rot was probably caused by a fungal pathogen *Glomerella cingulata* (Knowles and Beveridge, 1982). As small tawa seedlings were observed in Maungatautari forest in the spring 2020, some seeds from the low seed fall in 2020 must have survived larvae predation and rotting to germinate (**Figure 6-12**). Seedlings were less frequent at Maungakawa which would be expected where the seed fall was reduced. Larval infestation and rotting rather than seed predation by invasive species may be limiting tawa germination.

### **6.5.2 Mangeao**

Variable mangeao seed fall at both forests confounded the statistical interpretations analysis. Annual variability was detected in mangeao seeds captured at the two Maungatautari study locations (MND and MNR) with higher mangeao basal area however at the third location (MNG) only two mangeao trees were located at PCQ points. One was confirmed to be a male tree and the gender of the other tree was not determined. Only a single bird-dispersed seed was captured in the seed trap at that location suggesting the tree above was also a male. Similarly,

the single mangeao tree at Maungakawa TTW study location may have been a male tree. Fruiting female trees had been observed on the forest margins of MNG.

The lower seed fall ( $\text{m}^{-2}$  basal area) of mangeao at Maungakawa in 2020 was statistically only marginally significant. When mangeao seed production (capture seeds) was abundant at Maungatautari MND and MNR study locations, similar levels did not eventuate at the Maungakawa study location (TTB) where mangeao basal area exceeded that of any location in Maungatautari. Are rats and/or possums alone responsible?

There was limited circumstantial evidence to implicate rats or possums. The root cause of the diminished seed fall could have been browsing of buds, flowers or fruit (Cowan and Waddington, 1990) or loss of foliage reducing energy resources (Thomas, 2011) or a combination of both (Fitzgerald, 1981; Thomas, 2011). Throughout this study, rodent and possum scat was found in seed traps where the mammals had been active in the canopy above (as in **Figure 6-26**), however none was found in seed traps having flower parts. Minute chew marks consistent with insects chewing were observed on some flowers, but many appeared more severely damaged (**Figure 6-15** and **Figure 6-16**). Studies of ship rat diets have reported them visiting but not consuming flowers (Sweetapple and Nugent, 2007; Pattermore and Wilcove, 2012), although that does not discount them from damaging the flowers. Possums are known to eat hīnau (*Elaeocarpus dentatus*) flower buds and flowers (Fitzgerald, 1976; Cowan, 1990). Invertebrate chew on mangeao leaves was prominent on margin trees and in the canopy at both forests (Chapter 5), and on leaves captured in seed traps (**Figure 6-24**). Differences in bird species and abundance (Innes et al., 2010a) between the forests could have led to altered insect populations and ecology and hence the difference in damaged flowers.

Margin trees canopies have higher light exposure and hence potentially greater energy resource (**Figure 6-21**). Finding immature and mature fruit and seeds in some supplementary margin seed traps at both forests in 2020 and at Maungakawa in 2021 (**Figure 6-22** and **Figure 6-23**) when seed fall in all other seed traps was negligible (**Figure 6-14**) suggests possums were unable to access the inflorescence buds of the tips of the exposed outer branches and/or that energy resources were limiting factors in seed productivity. Fruiting trees at Maungatautari had appeared stressed following the heavy fruit crops in 2020. While the group of margin trees at Maungakawa had fruit in 2020, the crop was not heavy compared to crops at Maungatautari. Both possum browse of inflorescence buds and energy resources could be limiting factors in mangeao seed productivity.

Seeds were viable as they germinated (December 2020) but they did not establish in the germination cage and on the adjacent forest floor. The appearance of the drooping seedlings suggested drought was a major factor in seedling attrition.

### 6.5.3 Pigeonwood

Pigeonwood seed fall patterns diverged in autumn 2020 when immature fruit were captured at Maungakawa and in spring when fruit was ripening (**Figure 6-25**). The drought conditions that led to immature mangleo fruit fall may have also caused the abscission of immature pigeonwood in Autumn 2020. At Maungakawa immature fruit were found in a single seed trap. The location, on an upper north facing slope, did not align to pigeonwood's preferred damp habitat (Dawson et al., 2011).

The low number of pigeonwood seeds captured within Maungatautari forest in spring 2020 did not reconcile with the prolific fruit abundance observed on some margin trees. Kererū and small birds were recorded visiting fruit laden margin trees in spring 2020 (Chapter 5). Compared to the abundance of fruit on the margin trees, very few seeds were captured inside the forest, but studies have shown kererū rest in nearby trees to digest the fruit, then defaecate the seeds before flying away (Wotton and Kelly, 2012). With few alternative food resources to incentivise kererū into the forests over spring, pigeonwood seed dispersal was most likely limited to close to the most productive trees.

Traces of dried mesocarp coated seeds were captured at Maungakawa during October and November 2020. These seeds were not consistent with the smooth appearance of seeds dispersed by birds. Captured seeds appeared to have had the flesh chewed off and the seed then dropped. Cowan (1990) reported that although green pigeonwood fruit are available most of the year, possums only consumed the flesh of ripe fruit from November to March. This timing aligns with observations on the forest margin (Chapter 5) when most fruit appeared to have been plucked from a tree by possums. Dispersal appeared limited to below the possum feeding area. Not only had the invasive mammals consumed a valuable food resource for birds (Wotton and Kelly, 2011) they had also limited potential dispersal across the landscape.

Pigeonwood seeds may also be water dispersed. I noted that fallen bright orange dried fruit observed on the ground below trees was washed downhill in heavy summer rain runoff. The dried fruit / seeds are light and float. As the species preferred habitat is damp gullies it is possible the seed could be dispersed over extended distances in flowing streams.

Comparison of seeds dispersed by birds and by possums requires further investigation. This should include trapping and clearly categorising immature fruit, ripening fruit and mature dried seeds plus tracking of the dispersal mechanism of each cohort of seeds over at least two complete reproductive cycles. Statistical analysis strength would also benefit by increasing the number of seed traps at each study location.

#### 6.5.4 Seeds dispersed by birds

Kererū are now the only forest bird able to disperse large seeds (Clout and Hay, 1989) such as tawa but they are very threatened by predation by introduced mammals (Innes et al., 2010a). At Maungatautari, local farmers reported seeing flocks of kererū at some times of the year. I observed them feeding in pigeonwood and mangaeo trees at both forests although only occasionally at Maungakawa. Manaaki Whenua bird survey data (pers. Comm. N. Fitzgerald) indicates kererū abundance at Maungatautari has not increased since exclusion of predatory mammals in 2006 but this could relate to the birds leaving the forest to feed across wider spatial landscapes (Tanentzap and Lloyd, 2017) as I often observed. Kererū were often observed feeding on flowering and fruiting trees in farmhouse gardens and flying between the forest and the gardens. Tui, silvereye and tīeke can also disperse whole mangaeo and pigeonwood, but their populations in the forests were also low particularly at Maungakawa. The lack of birds able to swallow the large fruit whole and disperse the seeds (Wotton and Kelly, 2011; Bombaci et al., 2021) is likely to underlie the low percentage of tawa, mangaeo and pigeonwood seeds dispersed by birds when fruit was plentiful.

#### 6.5.5 Seed viability and germination

Seed viability is affected by resilience to drying and predation as well as suitability of the germination niche. In 2020 few tawa seeds were available for the germination trials and no seeds germinated. The period seeds remained in the seed trap prior to collection and being placed into the litter was likely to have impacted seed germination (Burrows, 1999). The delayed transfer to the germination niche; dry litter and soil, probably foiled tawa seed germination in 2020. During the tawa seed fall season (2021), captured seeds were also very dry when collected. *C. querula* seed predation was evident in both years. Freshly fallen seeds collected from the ground in 2021 commenced germinating (radicle emergence) in glass house conditions shortly after collection. An occasional seed on the ground was found germinating in May 2021 but the germination rate within the forests could not be measured prior to the research end date for this thesis. Germination trials will continue, and results will be reported in a future paper.

Pigeonwood and mangaeo seeds readily germinated in favourable conditions. Predation by invertebrates including slugs and snails (occasionally found consuming the developing leaves) and low soil moisture accounted for most losses of both species at both forests. Although seeds germinated outside the cages at Maungakawa, none survived to the end of the study period. It is likely invasive mammals consumed these seedlings.



## 6.6 Conclusions

Tawa seed falls are reported to be variable annually, but this was only evident in the forest not inhabited by rats and possums. A significant difference in annual tawa seed fall at Maungatautari was consistent with the literature reports but, at Maungakawa annual seed fall variability was muted. Visual evidence that possums consumed green fruit suggests they diminished the seed production when there was an abundant fruit crop and resultant seed fall at Maungatautari.

Mangeao exhibited variable annual seed production at Maungatautari where rats and possums do not inhabit the forest. However, statistical analysis of seed fall ( $\text{m}^{-2}$  basal area) was confounded by the patchy distribution of the dioecious mangeao trees across the study locations at both forests. Statistically seed fall was marginally less at Maungakawa in 2020. At Maungatautari depleted energy resources may have accounted for the observations of stress in female trees following abundant seed production in 2020 and negligible seed production in the following year (2021). Loss of inflorescence buds and/or flowers due to possum browsing was likely to be a significant limiting factor seed production at Maungakawa in 2020. Although these trees had not been stressed by high seed production in 2020, seed production remained low. This suggests possum and possibly rodent browsing may be the overriding factor where these arboreal mammals inhabit the forest. Consideration of seed fall alone is insufficient to elucidate the underlying mechanisms.

The complex and extended reproductive cycle of pigeonwood precluded collection of sufficient data to thoroughly compare annual seed fall. Although possums and possibly rats consumed some pigeonwood fruit, they did not destroy all the seeds. They limited seed distribution across the spatial landscape by only consuming the flesh and dropping the seeds where they fed.

When abundant, tawa and mangeao fruit crops were greater than required to satiate current kererū populations. Fruit with undamaged flesh dropped from the trees. Many of the captured seeds had only remnants of flesh indicating other wildlife including small birds and invasive mammals had also fed on the fruit. However, less than 30% of the seeds had been defaecated by birds (probably kererū).

Tawa regeneration may be depressed by loss of viable seed from the forest floor seed bank. When possums consumed the flesh of ripe tawa fruit, they did not appear to damage the seeds but by discarding the seeds *in situ* they failed to disperse the seeds across the spatial landscape. Seeds were removed from the viable seed bank on the forest floor when rats removed tawa fruit, to their feeding platforms or nests which are generally not suitable habitats for establishment of tawa seedlings. In addition to seed recalcitrance, seed infestation by *C. querula* larvae and rotting caused by *G. cingulata* further reduced potential regeneration of tawa.

My research also uncovered an asynchronous increase in tawa and mangeao fruit abundance that could have been promoted by the same climatic cue. Seed abundance however appeared to have been suppressed by cue “veto” factors: drought conditions having caused loss of dormant tawa flowers and immature mangeao fruit. Possums may also function as a cue “veto” by consuming immature tawa fruit and possibly mangeao inflorescence buds and/or flowers.

This study has assisted, but not fully resolved whether rats and possums reduce the reproductive capacity of each of the tree species. An extended study is required to determine if the complementary mangeao and tawa fruit crops in the absence of invasive mammals were coincidental in this study or are a sustained attribute of their co-dominance in Waikato hill-country forests and in the wider spatial landscape. Camera traps placed in the canopy of each of the broadleaved species, and possibly feeding trials over an extended period, are recommended for observation of which fauna interact with each stage of the reproductive cycles. Investigation of the cues to annual variation in tawa, mangeao and pigeonwood seed fall is also warranted.

# Chapter 7

## Synthesis and conclusions

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### 7.1 Introduction

My main objective was to determine if rats (*Rattus* spp.) and/or possums (*Trichosurus vulpecula*) depress the reproductive capacity of large-fruited broadleaved species in Waikato hill-country forests. In this study I compared the tree phenology, fruit development and seed fall of three codominant species in forests with contrasting rat and possum abundance. As these introduced mammals are nocturnal and mainly arboreal their lives are cryptic. My challenge was to determine if, how and when rats and possums reduce the reproductive capacity of tawa (*Beilschmiedia tawa*), mangeo (*Litsea calicaris*) and pigeonwood (*Hedycarya arborea*) within Waikato hill-country broadleaved forests. At Maungatautari, eradication of invasive mammals has changed the trajectory of diminishing biodiversity (Binny et al., 2021; Bombaci et al., 2021). I found Maungatautari was an effective reference forest to gauge the influence of rats and possums on seed production and seedling establishment at Maungakawa.

In this chapter I synthesise my key findings. Determining which invasive species consumed which foliage, buds, flowers, fruit, seeds, or germinating seedlings turned into a “whodunit” investigation drawing on subtle clues (Fitzgerald, 1981; Burns, 2004). There was evidence that seed fall from two of the tree species at mammal-free Maungatautari could be greater than at Maungakawa, where possums and rats were present. However, attributing the difference to one or other of the mammal species was not straightforward. Much of the evidence was circumstantial. At Maungakawa (TTW), there was a substantial patch of reproductive kohekohe (*Dysoxylum spectabile*) and the kohekohe seedlings spread through nearby forest were often browsed. I suspected possums until I observed peafowl (*Pavo cristatus*), browsing the leaves.

### 7.2 Synthesis

Rats and possums do not inhabit the forest at Maungatautari, but they were abundant at Maungakawa prior to the pest control campaign in June 2020. The control programme successfully reduced their abundance to low levels for several months but is unlikely to be sustained.

Forest canopy structure and composition of Maungatautari and Maungakawa were similar. Tawa was common within the forests but was not always present along the forest margins. Mangeo distribution in the forests was patchy both in the forests and along the margins. Their

preferred habitat in Maungatautari and Maungakawa forest did not include lower slopes of the gullies. Pigeonwood is a light demanding species, but it occupies the shaded subcanopy within the forests. Pigeonwood trees on the forest margins had heavy fruit crops in both years but seed fall within the forests appeared more restrained.

Seed fall data and observations within the forests indicated rats and possums potentially influence the reproductive capacity of tawa, mangeao and pigeonwood. Invasive mammals directly and indirectly functioned as a cue “veto”, *sensu* Pearse et al. (2016).

Tawa seed fall was low at both forests in 2020 and was significantly more abundant at Maungatautari in 2021. At Maungakawa immature green fruit with possum tooth indentations found on the forest floor were consistent with literature reports of possums consuming up to 50% of the immature fruit crop in the canopy (Knowles and Beveridge, 1982). The pest control campaign reduced possum activity to very low abundance within the Scenic Reserve prior to development of the 2021 fruit crop. However, seed fall was not significantly greater in 2021 than in the previous year.

Mangeao seed production was higher at Maungatautari in 2020 than at Maungakawa although this effect fell short of statistical significance. Annual variability was detected in mangeao seed production at the two Maungatautari study locations with higher mangeao basal area. This was not evident at the Maungakawa study locations with similar basal area.

The timing of mangeao’s reproductive cycle may leave inflorescence and flowers especially vulnerable to damage by possums and/or rats. When the phenology study commenced in winter 2019, well-developed buds then flowers were available on the trees during the winter and spring there were less buds on the trees at Maungakawa. Leathwick (1984) and (Cowan, 1990) reported hīnau (*Elaeocarpus dentatus*) flowers were susceptible to possum browsing as they had a long development period and anthesis occurred during winter when few other flowers were available. I found mangeao also had an extended inflorescence bud development period. This could have accounted for the reduced mangeao seed production at Maungakawa when there was abundant seed production at Maungatautari. As flower buds and flowers were found in seed traps during the winter at both forests, it is likely birds and insects also consumed some.

Pigeonwood seed fall at both forests was similar in 2020 and 2021, but periods of peak seed fall at Maungatautari and Maungakawa were not synchronised. The peak seed fall at Maungatautari occurred in summer but the peak occurred later at Maungakawa. At Maungakawa small bunches of green pigeonwood fruit plus mature seeds with fibrous flesh-remnants attached were found in seed traps during spring and summer. These seeds were not consistent with the appearance of seeds defaecated by birds. It is likely rats and/or possums had consumed the fruit but discarded the seeds.



Tawa and pigeonwood seed dispersal was compromised by rats and possums. Possums consumed the flesh of ripe fruit but dropped the seeds from where they had been feeding in the parent tree or on the ground hence limiting dispersal across the wider spatial landscape. Rats were observed removing tawa seeds from the forest floor. Innes and Russell (2021) list ripe pigeonwood fruit but not seeds as consumed by rats. As rats feed “privately” it is likely they removed ripe tawa fruit and possibly pigeonwood fruit to their feeding platforms and nests which are not suitable habitats for seedling establishment.

Bringing together the phenology and seed fall chapters revealed the reproductive cycles of tawa, mangeao and pigeonwood were extended, ranging between 18 to 27 months (**Figure 7-1**). A different life cycle stage was extended in each of the species. Mangeao inflorescence buds initiated in summer but anthesis didn’t occur until the following spring. Fruit developed over summer. Fruit fall and seed dispersal occurred in autumn. In contrast tawa flower buds emerged in late winter and anthesis occurred five months later, in early summer. The pollinated flowers were then dormant until late winter as noted by Knowles and Beveridge (1982). Fruit development occurred in the following spring. Fruit fall and seed dispersal occurred during summer and autumn. Although mangeao and tawa anthesis occurred within the same period, seed fall occurred in asynchronous years: mangeao seed fall in the summer and autumn soon after anthesis but tawa not until the following summer and autumn. Pigeonwood flower buds developed mainly on older wood inside the canopy during winter. Anthesis occurred in spring. Fruit developed slowly until ripening commenced concurrently with anthesis the following spring. Fruit continued to ripen throughout the summer and autumn and some hard ripe fruit remained on the trees until the winter, 27 months after the buds first appeared.

These findings are consistent with Cowan and Waddington (1990) who noted the extended flower development period of some large-fruited broadleaved species and the delayed (six to eight months) ripening of several other species including pigeonwood. The authors commented on the extended period for tawa anthesis to fruit ripening stages. However, the contrasting phenology of tawa and mangeao seed fall timing has not been previously reported. The limited research period for my MSc thesis, precluded replicate data collection over extended reproductive cycles for each of the broadleaved species.

Although possums may be responsible for loss of reproductive capacity of large-fruited species, wider ecological factors should also be considered (Bellingham and Lee, 2006). Energy balance is lost when a tree’s photosynthetic capacity falls below a threshold value due to loss of leaf cover (Holland et al., 2013). In mangeao this may be due to the combined effects of possum and insect browsing, disease or age related dieback (Gardner and Dick, 2002). I

consider energy resources were one of the limiting factors in mangeao seed productivity. Further investigation is required to elucidate the limiting factor(s) and their relative importance.

As the warm dry conditions in summer 2020 developed to a drought, each of the species aborted developing fruit as described by Stephenson (1981); in tawa it was the dormant pollinated flowers and in mangeao it was the developing fruit. Pigeonwood shed immature fruit where it grew in dry locations. As the drought deepened mangeao also shed some of the new season's cohort of developing inflorescence buds. Tawa fruit didn't emerge from the remaining dormant flowers until the winter by which time rain had replenished soil moisture. Loss of reproductive parts culminates in diminished seed production.

Possums frequently left the forest to feed on adjacent highly nutritious pastures (Dodd et al., 2006; Morley, 2018). Accessible highly nutritious pastures could be saving forest species from further destruction. However, the availability of replacement food resources where the forests have been depleted may also be sustaining abundance of the invasive mammals (Ramsey et al., 2002). This could exacerbate depression of seed production particularly in species with palatable inflorescence / flower buds and flowers available over winter and early spring e.g., hīnau and mangeao, when growth of pasture species is low.

### **7.3 Conclusions**

Tawa produced variable abundance of fruit annually in the absence of rats and possums; however, this variability did not occur where arboreal invasive mammals inhabited the forest. Elimination of the possums rather than control at low abundance may be required to restore tawa seed production to historical levels. There was evidence of green tawa fruit consumption by possums after the successful possum control programme reduced their abundance to very low levels. Further studies across a wider forest-landscape will be necessary to validate this perception.

Mangeao seed production was higher at Maungatautari than in the forest inhabited by rats and possums at Maungakawa, although this effect fell short of statistical significance. The underlying cause is likely to be related to loss of inflorescence buds, but the role of arboreal invasive mammals requires further investigation.

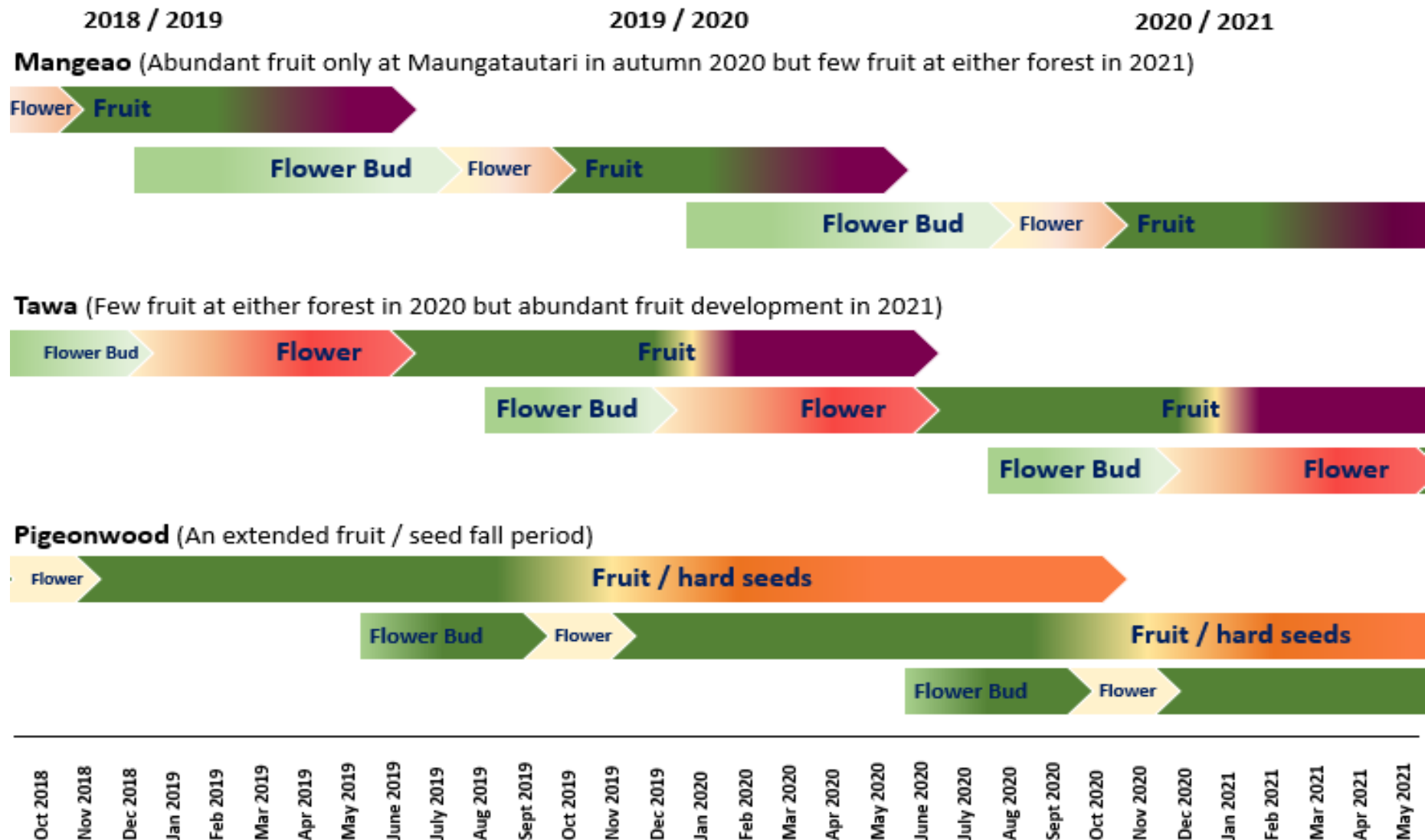
There was no evidence rats and possums reduce pigeonwood fruit production or destroy the seeds. However, by discarding seeds where they feed, rats and possums may limit seed dispersal across the spatial landscape.

This study has assisted, but not fully resolved whether rats and possums reduce the reproductive capacity of each of the three tree species. The impacts of arboreal invasive animals were not consistent across large-fruited species. More complex models will be

required to characterise the impacts rats and possums impose of the overall forest structure and composition.

Data collection over many years will be required to resolve periodicity and cyclic seed fall abundance parameters and the cues that drive these characteristics.

It is reassuring that abundant tawa and mangeao seed production has rebounded at Maungatautari within 15 years of eradication of invasive species. This suggests that loss of seed fall from vulnerable large-fruited species can be overcome by removal of invasive mammals.



**Figure 7-1:** Reproductive cycles in mangeao (extended flower bud period), tawa (flowers with an extended dormant period post pollination) and pigeonwood (extended fruit and seed fall period). Data was collated from Chapter 5 Phenology and Chapter 6 Seed fall studies.





**Cute but not welcome here!**  
(TTW PCQ1-5 January 2020)

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# Appendices

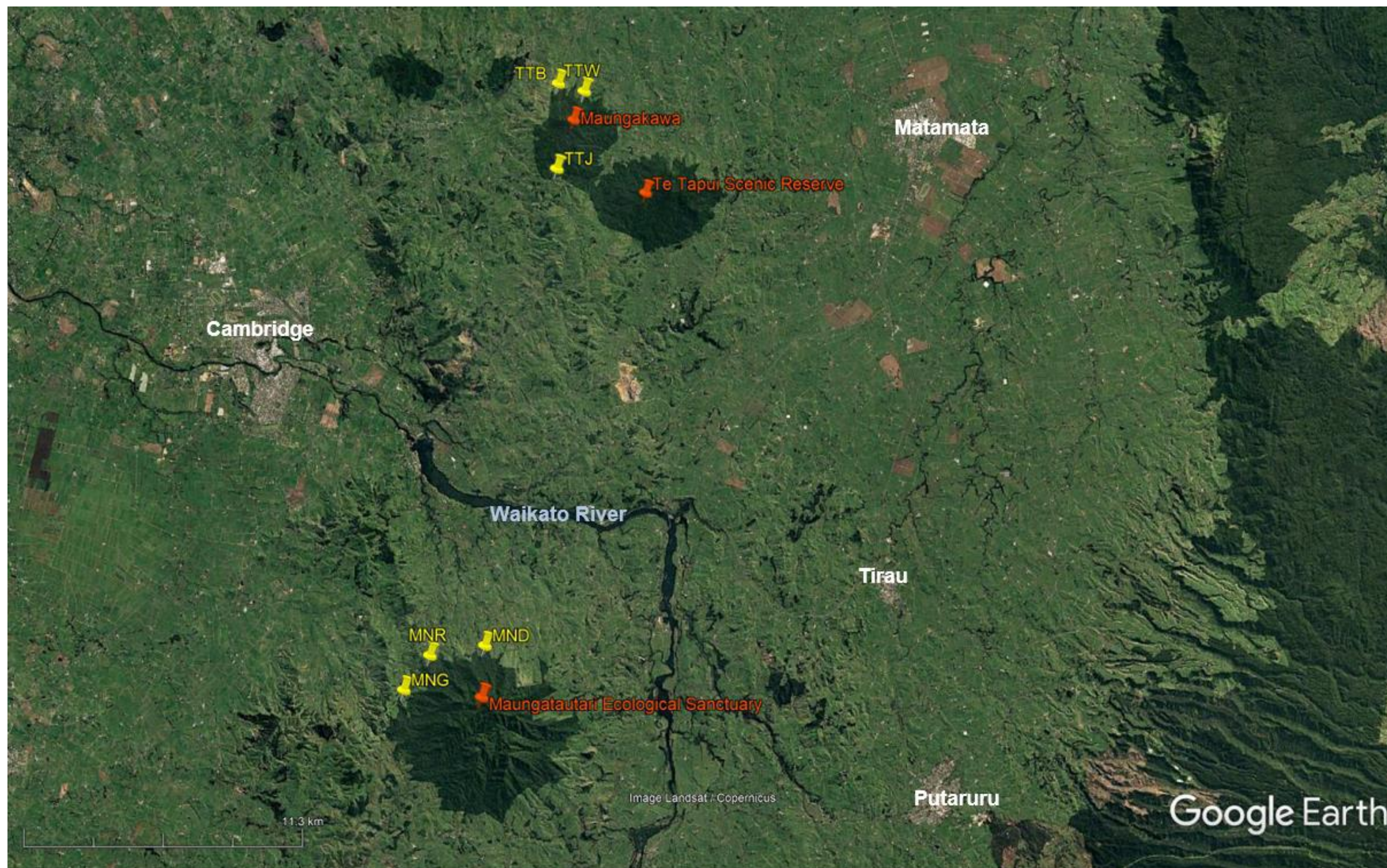
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Appendix 1: Map of the central Waikato region showing study locations within Maungatautari and Maungakawa forests.

Maungakawa is part of Te Tāpui Scenic Reserve.





## Appendix 2: Maungatautari North Study Location MND.

Accessed from Taane Road, Maungatautari. Orange pins are the PCQ points where tree structure and composition (Chapter 3), and seed fall (Chapter 6) were measured. Wildlife cams were located at PCQ points, PCQ1-2 and PCQ2-2. Blue pins are the locations of margin trees (Chapter 6). Google Earth imagery 05/02/2018.





### Appendix 3: Maungatautari Study Location MNR.

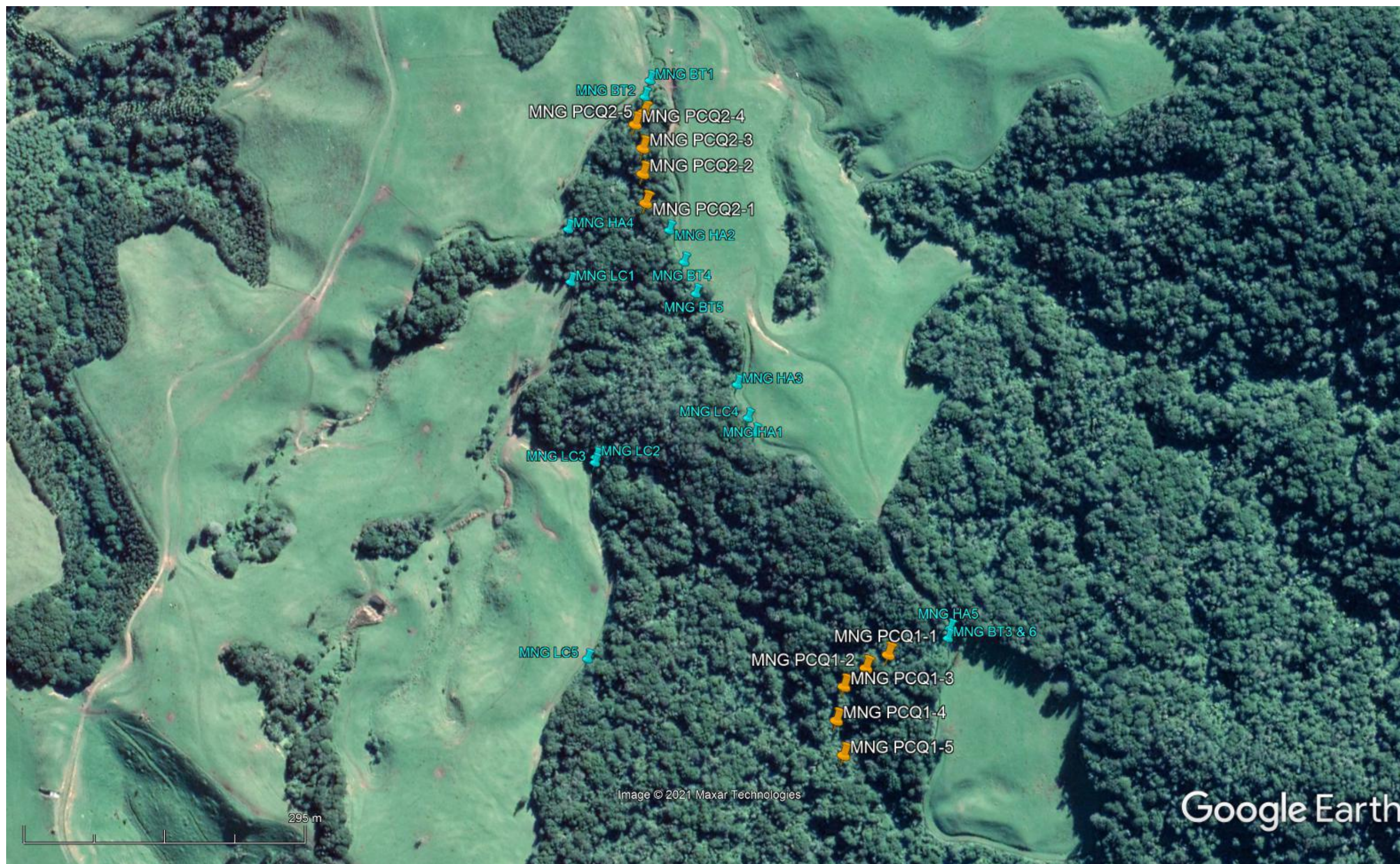
Accessed from Luck at Last Road, Maungatautari, Waikato, New Zealand. Orange pins are the PCQ points where tree structure and composition (Chapter 3), and Seed fall (Chapter 6) were measured. Wildlife cams were located at PCQ points, PCQ1-2 and PCQ2-2. Blue pins are the locations of margin trees (Chapter 6). Google Earth imagery 05/02/2018.





#### Appendix 4: Maungatautari study location MNG.

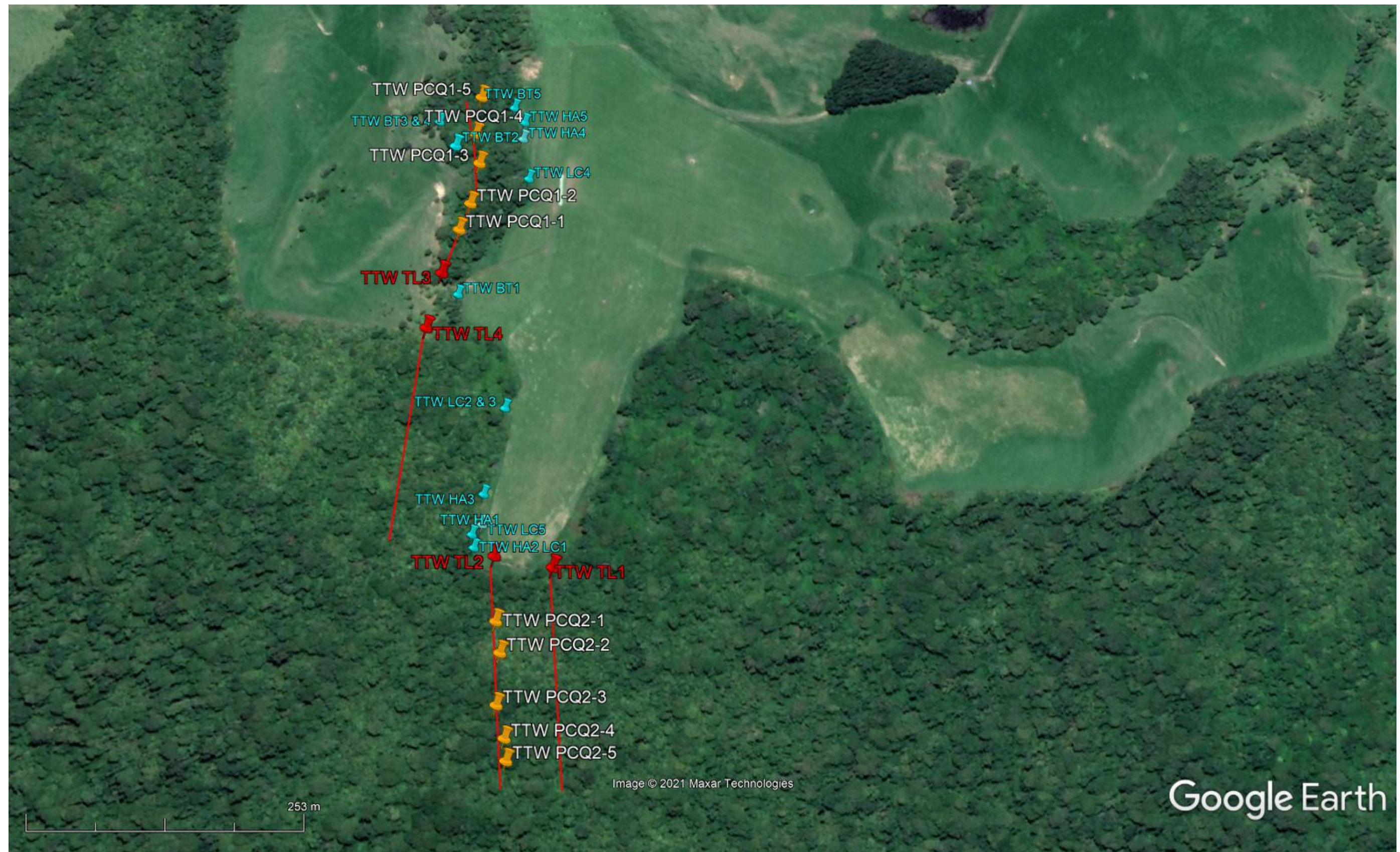
Accessed from Rahiri Road, Rotorangi, Waikato, New Zealand. Orange pins are the PCQ points where tree structure and composition (Chapter 3), and seed fall (Chapter 6) were measured. Wildlife cams were located at PCQ points, PCQ1-2 and PCQ2-1. Blue pins are the locations of margin trees (Chapter 6). Google Earth imagery 05/02/2018.





# Appendix 5: Maungakawa Study Location TTW.

This study location was accessed from Piakonui Road, Richmond Downs, Waikato, New Zealand. Rodent tracking tunnel transects are marked by redlines. Possum chew cards were laid on TL1 and TL3. TTW BT5 (blue pin) is where the camera trap recorded possums leaving the forest margin to browse on adjacent cropping pasture. Orange pins are the PCQ points where tree structure and composition (Chapter 3), and seed fall (Chapter 6) were measured. Wildlife cams were located at PCQ points, PCQ1-2 and PCQ2-2. Blue pins are the locations of margin trees (Chapter 6). Global Earth imagery date: 18/10/2018.





# Appendix 6: Maungakawa Study Location TTB.

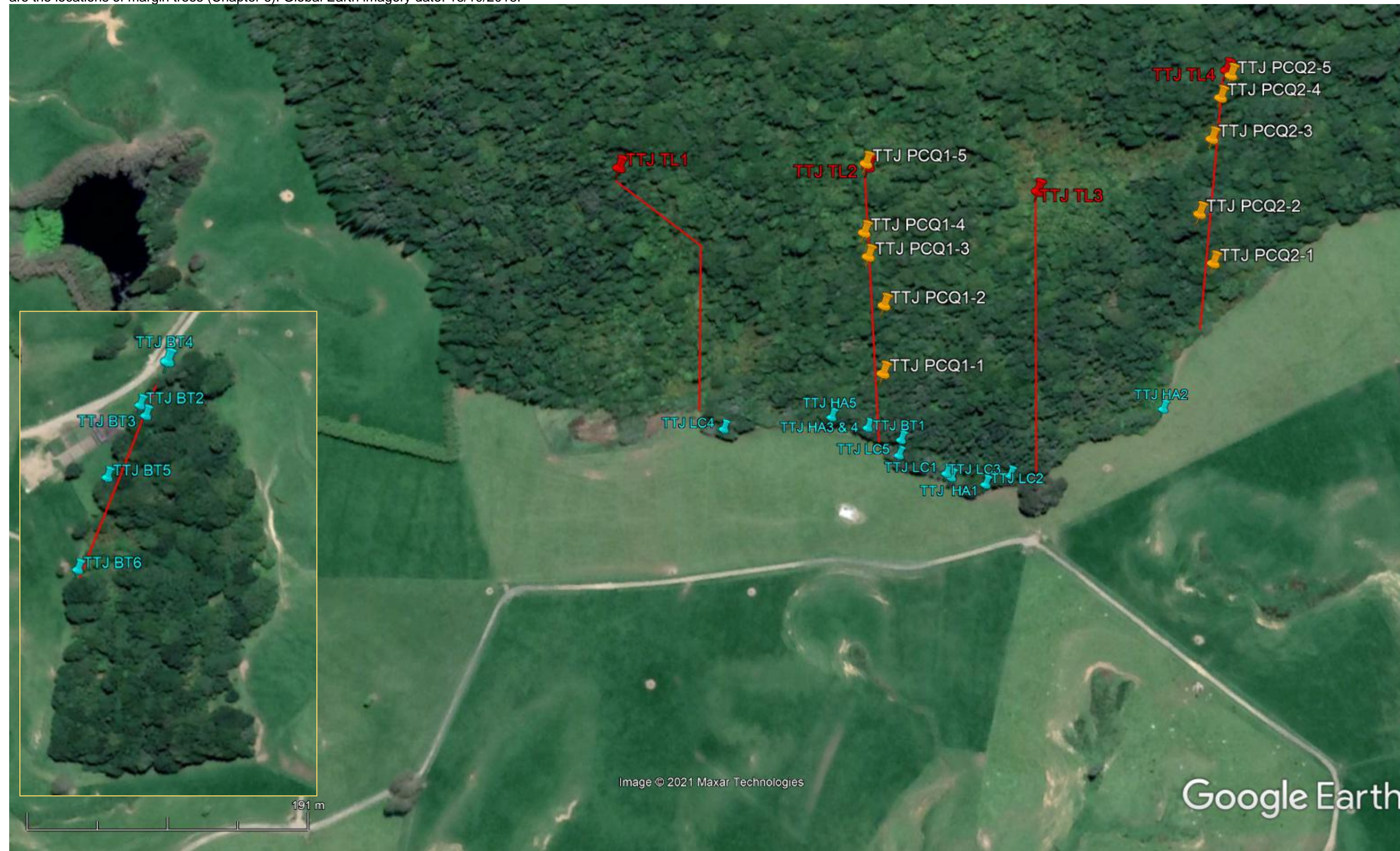
This study location was accessed from Waterworks Road, Te Miro, Waikato, New Zealand. Rodent tracking tunnel transects marked by redlines. Possum chew cards were laid on TL1 and TL3. Orange pins are the PCQ points where tree structure and composition (Chapter 3), and seed fall (Chapter 6) were measured. Wildlife cams were located at PCQ points, PCQ1-2 and PCQ2-2. Blue pins are the locations of margin trees (Chapter 6). Global Earth imagery date: 18/10/2018.





## Appendix 7: Maungakawa Study Location TTJ.

This study location was accessed from Brunskill Road, Te Miro, Waikato, New Zealand. Rodent tracking tunnel transects marked by redlines. Possum chew cards were laid on TL2 and TL4. Insert: the forest fragment approximately 500 m to the south-west of the main TTJ study location: four mature tawa trees were on the margin and an additional rodent survey transect was placed along the margin. Data from the tunnel line was not included in the rodent survey analysis (Chapter 4). Orange pins are the PCQ points where tree structure and composition (Chapter 3), and seed fall (Chapter 6) were measured. Wildlife cams were located at PCQ points, PCQ1-2 and PCQ2-2. Blue pins are the locations of margin trees (Chapter 6). Global Earth imagery date: 18/10/2018.





**Appendix 8: Trees encountered during this research project; nomenclature from de Lange (2021).**

Tree species	Māori Name	Common name	NVS code	Field code
<i>Alectryon excelsus</i>	Titoki		ALEEXC	
<i>Aristotelia serrata</i>	Makomako	Wineberry	ARISER	
<i>Beilschmiedia tawa</i>	Tawa		BEITAW	BT
<i>Brachyglottis repanda</i>	Rangiora	Bushman's toilet paper	BRAREP	
<i>Coprosma autumnalis</i>	Kanono, manono, raureka	Large-leaved coprosma	COPAUT	
<i>Coprosma robusta</i>	Karamu	Glossy karamu	COPROB	
<i>Corynocarpus laevigatus</i>	Karaka, kopi		CORLAE	
<i>Dacrydium cupressinum</i>	Rimu	Red pine	DACCUP	
<i>Dysoxylum spectabile</i>	Kohekohe	NZ mahogany	DYSSPE	
<i>Elaeocarpus dentatus</i>	Hinau		ELADEN	
<i>Fuchsia excorticata</i>	Kotukutuku	Tree fuchsia	FUCEXC	
<i>Geniostoma ligustrifolium</i>	Hangehange		GENLIG	
<i>Griselinia lucida</i>	Puka, akapuka		GRILUC	
<i>Hedycarya arborea</i>	Porokaiwhiri	Pigeonwood	HEDARB	HA
<i>Nightia excelsa</i>	Rewarewa	NZ honeysuckle	KNIEXC	
<i>Laurelia novae-zelandiae</i>	Pukatea		LAUNOV	
<i>Litsea calicaris</i>	Mangeao		LITCAL	LC
<i>Melicytus ramiflorus</i>	Mahoe, hinahina	Whitey wood	MELRAM	
<i>Myrsine australis</i>	Red mapou, red matipo, mapua	Red maple	MYRAUS	
<i>Olearia rani</i>	Heketara		OLERAN	
<i>Piper excelsum</i>	Kawakawa	Pepper tree	PIPEXC	
<i>Prumnopitys ferruginea</i>	Miro		PRUFER	
<i>Pseudopanax arboreus</i>	Whauwhaupaku	Five finger	PSEARB	
<i>Rhopalostylis sapida</i>	Nikau	Nikau palm	RHOSAP	
<i>Raukawa edgerleyi</i>	Raukawa		RAUEDG	
<i>Schefflera digitata</i>	Patete	Seven-finger	SCHDIG	
<i>Streblus heterophyllus</i>	Turepo	Small-leaved milk tree	STRHET	
<i>Weinmannia racemosa</i>	Kamahi, tawheo, tawhero, tawherowhero		WEIRAC	

**Appendix 9: Phenology data summary - Tawa at Maungatautari (MN) and Maungakawa (TT).**

mid period	Branchlets (total counted)		Branchlet length mean (cm)		Flower buds (mean / branchlet)		Flowers (mean / branchlet)		Fruit (mean / branchlet)	
	MN	TT	MN	TT	MN	TT	MN	TT	MN	TT
16/08/2019	46	44	12.8	12.9	0.0	0.0	0.0	0.0	0.0	0.0
14/09/2019	50	56	13.9	13.6	0.4	0.4	0.0	0.0	0.0	0.0
17/10/2019	50	56	15.8	14.1	4.9	2.8	0.0	0.0	0.0	0.0
13/11/2019	50	55	17.4	14.7	11.4	9.1	0.1	0.0	0.0	0.0
16/12/2019	49	55	18.6	15.0	5.6	9.9	2.0	1.0	0.0	0.0
10/01/2020	39	55	18.5	15.2	0.6	1.0	1.0	1.5	0.0	0.0
5/02/2020	33	54	19.1	15.3	0.1	0.0	1.0	0.0	0.0	0.0
4/03/2020	33	53	19.1	15.7	0.0	0.0	0.8	0.0	0.0	0.0
3/04/2020	No measurements during Covid 19 Level 4 Lockdown									
9/05/2020	33	52	19.5	16.0	0.0	0.0	0.3	0.0	0.2	0.0
8/06/2020	33	52	18.8	15.8	0.0	0.0	0.2	0.0	0.2	0.0
6/07/2020	33	50	18.7	15.6	0.0	0.0	0.2	0.0	0.1	0.0
3/08/2020	33	49	18.7	15.3	0.2	0.0	0.1	0.0	0.1	0.0

**Appendix 10: Phenology data summary - Mangeao at Maungatautari (MN) and Maungakawa (TT).**

mid period	Branchlets (total counted)		Branchlet length mean (cm)		Flower buds (mean / branchlet)		Flowers (mean / branchlet)		Fruit (mean / branchlet)	
	MN	TT	MN	TT	MN	TT	MN	TT	MN	TT
16/08/2019	58	54	20.2	16.9	12.2	2.0	0.0	0.0	0.0	0.0
14/09/2019	58	58	20.4	16.8	11.4	1.7	1.1	0.0	0.0	0.0
17/10/2019	63	58	22.2	17.8	0.1	0.7	7.7	0.9	0.1	0.1
13/11/2019	62	58	23.5	20.4	0.0	0.0	0.0	0.5	8.3	0.1
16/12/2019	62	58	26.6	23.3	0.0	0.0	0.0	0.0	5.3	0.1
10/01/2020	55	58	25.6	24.6	2.3	2.6	0.0	0.0	3.4	0.0
5/02/2020	53	55	26.2	24.5	5.8	3.2	0.0	0.0	3.1	0.0
4/03/2020	52	54	26.2	25.5	6.6	2.6	0.0	0.0	2.2	0.0
3/04/2020	No measurements during Covid 19 Level 4 Lockdown									
9/05/2020	52	53	27.2	25.6	1.1	2.3	0.0	0.0	0.0	0.0
8/06/2020	52	53	26.5	25.4	0.3	2.2	0.0	0.0	0.0	0.0
6/07/2020	52	51	26.3	24.7	0.0	2.2	0.0	0.0	0.0	0.0
3/08/2020	52	51	26.1	24.9	0.0	2.2	0.0	0.0	0.0	0.0



**Appendix 11: Phenology data summary - Pigeonwood at Maungatautari (MN) and Maungakawa (TT).**

mid period	Branchlets (total counted)		Branchlet length mean (cm)		Flower buds (mean / branchlet)		Flowers (mean / branchlet)		Fruit (mean / branchlet)	
	MN	TT	MN	TT	MN	TT	MN	TT	MN	TT
16/08/2019	44	59	21.8	25.6	4.4	3.9	0.0	0.0	0.0	1.0
13/09/2019	48	60	23.6	27.2	5.2	4.2	0.0	0.0	0.0	1.1
20/10/2019	48	60	25.3	28.2	2.2	4.3	1.5	0.0	0.0	0.9
13/11/2019	48	60	26.5	29.2	0.4	0.7	0.1	1.3	0.0	0.9
16/12/2019	48	60	28.8	30.9	0.0	0.0	0.3	0.1	0.0	0.3
10/01/2020	36	59	29.1	31.1	0.0	0.0	0.1	0.0	0.0	1.1
5/02/2020	35	57	29.2	30.8	0.0	0.0	0.1	0.0	0.1	0.4
4/03/2020	33	56	28.8	31.0	0.0	0.0	0.0	0.0	0.2	0.3
3/04/2020	No measurements during Covid 19 Level 4 Lockdown									
8/05/2020	30	54	30.1	31.9	0.0	0.0	0.0	0.0	0.2	0.1
8/06/2020	30	54	29.7	31.9	0.0	0.0	0.0	0.0	0.2	0.1
1/07/2020	30	51	30.0	31.7	4.3	1.7	0.0	0.0	0.2	0.1
3/08/2020	30	50	30.2	31.9	4.0	6.3	0.0	0.0	0.2	0.1

Appendix 12: Camera Trap Hours (trigger sets / 1000 hours) for Maungakawa Scenic Reserve study locations over 12 months (December 2019 to December 2020).

Location	Date start	Date End	Elapsed days	Total camera trap hours	<i>D. dama</i> (fallow deer)	<i>T. vulpecula</i> (Brushtail possum)	<i>Rattus spp.</i> (rats)	<i>M. musculus</i> (mouse)	<i>Leporidae spp.</i> (hare and rabbit)	<i>M. erminea</i> (stoat)	<i>E. europaeus</i> <i>occidentalis</i> (hedgehog)	<i>F. catus</i> (cat)	<i>Phasianus colchicus</i> (pheasant)	<i>Pavo cristatus</i> (peafowl)	<i>Turdus merula</i> (blackbird)	<i>Turdus philomelos</i> (song thrush)	Endemic birds	Other count (image not identified)
TTW PCQ1-2	5/12/2019	2/01/2020	28	672	3.0	10.4	31.3	0.0	1.5	0.0	1.5	0.0	0.0	0.0	3.0	0.0	0.0	3.0
TTW PCQ1-2	2/01/2020	30/01/2020	28	672	0.0	10.4	44.6	0.0	0.0	1.5	1.5	0.0	0.0	10.4	1.5	0.0	0.0	8.9
TTW PCQ1-2	30/01/2020	27/02/2020	28	672	0.0	13.4	116.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	13.4	0.0	3.0
TTW PCQ1-2	27/02/2020	29/04/2020	62	1488	0.0	8.1	35.6	8.1	0.7	0.0	0.0	0.0	0.0	0.0	11.4	18.8	0.0	1.3
TTW PCQ1-2	29/04/2020	23/05/2020	24	576	1.7	10.4	22.6	1.7	0.0	0.0	0.0	1.7	0.0	0.0	12.2	0.0	1.0	3.5
TTW PCQ1-2	23/05/2020	24/06/2020	32	768	0.0	6.5	36.5	3.9	0.0	0.0	0.0	0.0	0.0	0.0	11.7	9.1	0.0	0.0
TTW PCQ1-2	24/06/2020	20/07/2020	26	624	0.0	9.6	73.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.8	3.2	0.0	0.0
TTW PCQ1-2	20/07/2020	4/09/2020	46	1104	0.0	8.2	53.4	0.0	0.0	0.0	0.0	0.9	0.0	0.0	14.5	11.8	0.0	1.8
TTW PCQ1-2	4/09/2020	23/10/2020	49	1176	0.0	5.1	43.4	0.0	0.0	0.0	3.4	0.9	0.0	0.0	18.7	0.0	0.0	2.6
TTW PCQ1-2	23/10/2020	4/12/2020	42	1008	3.0	9.9	12.9	1.0	0.0	0.0	12.9	0.0	0.0	0.0	16.9	0.0	0.0	1.0
Blue cells = triggers / total camera trap hours at location				8760	0.7	8.8	44.7	1.9	0.1	0.1	2.2	0.3	0.0	0.8	11.4	6.7	0.0	2.3
TTW PCQ2-2	5/12/2019	2/01/2020	28	672	3.0	19.3	6.0	0.0	1.5	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TTW PCQ2-2	2/01/2020	30/01/2020	28	672	1.5	23.8	7.4	0.0	0.0	1.5	0.0	0.0	0.0	0.0	1.5	0.0	0.0	3.0
TTW PCQ2-2	30/01/2020	27/02/2020	28	672	0.0	1.5	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TTW PCQ2-2	27/02/2020	29/04/2020	62	1488	6.7	112.2	2.7	0.0	0.0	0.7	0.0	0.0	0.0	0.0	1.3	0.0	0.0	3.4
TTW PCQ2-2	29/04/2020	23/05/2020	Camera malfunction - no data						0.0									
TTW PCQ2-2	23/05/2020	24/06/2020	32	768	1.3	69.0	2.6	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	1.3
TTW PCQ2-2	24/06/2020	20/07/2020	26	624	3.2	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TTW PCQ2-2	20/07/2020	4/09/2020	46	1104	3.6	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0
TTW PCQ2-2	4/09/2020	23/10/2020	49	1176	6.8	0.9	2.6	0.0	2.6	0.0	3.4	0.0	0.0	2.6	0.0	0.0	0.0	0.0
TTW PCQ2-2	23/10/2020	4/12/2020	42	1008	7.9	9.9	6.9	0.0	0.0	0.0	5.0	0.0	0.0	3.0	7.9	0.0	0.0	0.0
Blue cells = triggers / total camera trap hours at location				8184	4.4	32.0	3.3	0.0	5.9	0.4	1.2	0.0	0.0	1.2	1.3	0.0	0.0	1.0
TTB PCQ1-2	19/11/2019	14/12/2019	25	600	0.0	15.0	1.7	5.0	1.7	3.3	1.7	0.0	0.0	0.0	26.7	65.0	0.0	1.7
TTB PCQ1-2	14/12/2019	13/01/2020	30	720	1.4	11.1	1.4	0.0	0.0	2.8	5.6	0.0	0.0	0.0	40.3	25.0	0.0	1.4
TTB PCQ1-2	13/01/2020	14/02/2020	32	768	0.0	15.6	19.5	0.0	1.3	0.0	20.8	0.0	0.0	0.0	58.6	48.2	0.0	3.9
TTB PCQ1-2	14/02/2020	10/03/2020	25	600	0.0	38.3	1.7	1.7	1.7	0.0	0.0	0.0	0.0	0.0	36.7	70.0	0.0	3.3
TTB PCQ1-2	10/03/2020	7/05/2020	58	1392	3.6	41.7	11.5	0.0	1.4	0.0	2.9	0.0	0.0	0.0	12.9	0.0	0.0	0.0
TTB PCQ1-2	7/05/2020	6/06/2020	30	720	0.0	12.5	25.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	1.4
TTB PCQ1-2	6/06/2020	2/07/2020	26	624	1.6	0.0	19.2	0.0	4.8	0.0	0.0	0.0	0.0	0.0	14.4	1.6	0.0	0.0
TTB PCQ1-2	2/07/2020	4/08/2020	33	792	0.0	1.3	0.0	0.0	5.1	0.0	0.0	0.0	0.0	0.0	8.8	2.5	0.0	0.0
TTB PCQ1-2	4/08/2020	19/09/2020	46	1104	5.4	2.7	0.0	0.0	5.4	0.0	0.9	1.8	0.9	0.0	28.1	0.0	0.0	1.8
TTB PCQ1-2	19/09/2020	2/11/2020	44	1056	1.9	3.8	0.9	0.0	6.6	0.0	12.3	0.0	2.8	0.0	35.0	0.0	0.0	0.9
TTB PCQ1-2	2/11/2020	15/12/2020	43	1032	6.8	6.8	1.9	0.0	0.0	0.0	15.5	0.0	0.0	1.0	78.5	1.0	0.0	1.0
Blue cells = triggers / total camera trap hours at location				9408	2.3	14.2	7.1	0.4	0.4	0.4	5.8	0.2	0.4	0.1	32.2	14.9	0.0	1.3
TTB PCQ2-2	14/12/2019	13/01/2020	30	720	1.4	148.6	9.7	0.0	5.6	4.2	13.9	0.0	0.0	0.0	0.0	0.0	0.0	1.4
TTB PCQ2-2	13/01/2020	14/02/2020	32	768	0.0	239.6	14.3	0.0	7.8	0.0	16.9	0.0	0.0	0.0	2.6	0.0	0.0	5.2
TTB PCQ2-2	14/02/2020	10/03/2020	25	600	0.0	190.0	10.0	0.0	8.3	0.0	40.0	1.7	0.0	1.7	0.0	0.0	0.0	1.7
TTB PCQ2-2	10/03/2020	7/05/2020	58	1392	9.3	199.7	20.8	0.0	13.6	0.0	16.5	0.0	0.7	0.0	2.2	0.0	0.0	5.0
TTB PCQ2-2	7/05/2020	6/06/2020	30	720	5.6	101.4	12.5	1.4	6.9	0.0	1.4	2.8	0.0	0.0	0.0	0.0	0.0	2.8
TTB PCQ2-2	6/06/2020	2/07/2020	26	624	8.0	75.3	6.4	0.0	6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6
TTB PCQ2-2	2/07/2020	4/08/2020	33	792	7.6	15.2	0.0	0.0	21.5	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0
TTB PCQ2-2	4/08/2020	19/09/2020	46	1104	14.5	7.2	1.8	0.0	10.9	0.0	0.0	0.0	0.9	0.0	1.8	0.0	0.0	0.9
TTB PCQ2-2	19/09/2020	2/11/2020	44	1056	13.3	28.4	0.0	0.9	12.3	0.0	25.6	0.0	0.9	0.0	0.9	0.0	0.0	4.7
TTB PCQ2-2	2/11/2020	15/12/2020	43	1032	12.6	49.4	3.9	0.0	6.8	0.0	18.4	0.0	0.0	0.0	10.7	0.0	0.0	2.9
Blue cells = triggers / total camera trap hours at location				8808	8.2	102.6	8.2	0.2	0.3	0.3	13.3	0.3	0.3	0.1	2.3	0.0	0.0	2.8
TTJ PCQ1-1	16/11/2019	26/11/2019	10	240	0.0	20.8	37.5	0.0	0.0	4.2	8.3	0.0	0.0	0.0	4.2	0.0	0.0	0.0
TTJ PCQ1-1	10/12/2019	7/01/2020	28	672	1.5	23.8	4.5	0.0	0.0	0.0	0.0	3.0	0.0	0.0	11.9	0.0	0.0	0.0
TTJ PCQ1-1	7/01/2020	3/02/2020	27	648	0.0	6.2	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
TTJ PCQ1-1	3/02/2020	2/03/2020	28	672	0.0	7.4	0.0	1.5	0.0	0.0	0.0	1.5	0.0	0.0	3.0	0.0	0.0	0.0
TTJ PCQ1-1	2/03/2020	9/05/2020	68	1632	0.0	11.6	32.5	1.2	0.0	1.2	5.5	0.0	0.0	0.0	1.8	0.0	0.0	0.0
TTJ PCQ1-1	9/05/2020	8/06/2020	30	720	0.0	13.9	25.0	0.0	5.6	1.4	1.4	0.0	0.0	0.0	2.8	0.0	0.0	0.0
TTJ PCQ1-1	8/06/2020	14/07/2020	36	864	0.0	1.2	1.2	0.0	5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TTJ PCQ1-1	14/07/2020	13/08/2020	30	720	0.0	0.0	0.0	1.4	6.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TTJ PCQ1-1	13/08/2020	2/10/2020	50	1200	0.8	0.0	0.0	0.8	3.3	0.0	0.8	0.0	0.0	0.0	6.7	0.0	0.0	0.0
TTJ PCQ1-1	2/10/2020	20/11/2020	49	1176	0.0	0.0	7.7	1.7	9.4	0.9	11.9	0.0	0.0	0.0	24.7	0.0	0.0	0.0
Blue cells = triggers / total camera trap hours at location				8544	0.2	7.0	11.0	0.8	0.6	0.6	3.2	0.4	0.0	0.0	6.3	0.0	0.0	0.0
TTJ PCQ2-2	16/11/2019	10/12/2019	24	576	15.6	1.7	3.5	0.0	0.0	0.0	12.2	1.7	0.0	0.0	6.9	0.0	0.0	0.0
TTJ PCQ2-2	10/12/2019	7/01/2020	28	672	6.0	68.5	0.0	0.0	7.4	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
TTJ PCQ2-2	7/01/2020	3/02/2020	27	648	0.0	74.1	0.0	0.0	4.6	1.5	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TTJ PCQ2-2	3/02/2020	2/03/2020	28	672	0.0	13.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	1.5
TTJ PCQ2-2	2/03/2020	9/05/2020	68	1632	3.7	25.1	4.9	1.2	0.0	0.0	1.8	0.0	0.0	0.0	6.7	0.6	0.0	0.6
TTJ PCQ2-2	9/05/2020	8/06/2020	Camera malfunction - no data						0.0									
TTJ PCQ2-2	8/06/2020	14/07/2020	36	864	1.2	1.2	2.3	2.3	5.8	0.0	0.0	0.0	0.0	0.0	5.8	0.0	0.0	0.0
TTJ PCQ2-2	14/07/2020	13/08/2020	30	720	4.2	1.4	2.8	0.0	27.8	0.0	0.0	0.0	0.0	0.0	26.4	0.0	0.0	0.0
TTJ PCQ2-2	13/08/2020	2/10/2020	50	1200	1.7	9.2	4.2	0.0	27.5	0.0	4.2	0.8	0.0	0.0	0.8	0.0	0.0	0.0
TTJ PCQ2-2	2/10/2020	20/11/2020	49	1176	2.6	28.9	6.8	0.0	9.4	0.0	15.3	1.7	0.0	0.0	6.8	0.0	0.0	1.7
Blue cells = triggers / total camera trap hours at location				8160	3.68	30.88	14.83	1.35	0.74	0.74	7.60	0.86	0.00	0.00	12.75	0.12	0.00	0.49

### Appendix 13: Endemic and introduced birds at Maungatautari and Maungakawa.

Recorded on camera traps focused on the ground and into low canopy vegetation (from low vegetation to approximately 2 m above the ground).

		Maungatautari		Maungakawa	
	Species	Ground	Low canopy	Ground	Low canopy
Chaffinch (introduced)	<i>Fringilla coelebs</i>		✓		
Eurasian blackbird (introduced)	<i>Turdus merula</i>	✓	✓	✓	✓
Fantail, pīwakawaka	<i>Rhipidura fuliginosa</i>		✓		✓
Kererū	<i>Hemiphaga novaeseelandiae</i>		✓		
Kiwi	<i>Apteryx spp.</i>	✓			
Morepork, ruru	<i>Ninox novaeseelandiae</i>	✓			
North Island robin	<i>Petroica longipes</i>	✓	✓		
North Island saddleback, tieke	<i>Philesturnus rufusater</i>	✓	✓		
Peafowl (introduced)	<i>Pavo cristatus</i>			✓	✓
Song thrush (introduced)	<i>Turdus philomelos</i>	✓	✓	✓	✓
Tomtit, ngirungiru	<i>Petroica macrocephala</i>		✓		
Whitehead, pōpokatea	<i>Mohoua albicilla</i>		✓		