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Feral pigs in a temperate rainforest ecosystem: ecological impacts and management

Cheryl Rebecca Krull

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Abstract

Feral pigs (*Sus scrofa*) have negative impacts on ecosystems globally and are increasingly perceived as a problem in New Zealand. However, there is a lack of scientific evidence of the impacts of pigs in New Zealand, and no evidence-based management strategies to mitigate these impacts. This thesis determines the impacts of feral pigs in a temperate rainforest, describes the relationship between disturbance and pig density, and explores disturbance thresholds. The negative impacts of pigs on ecosystem processes, vegetation composition and structure were investigated using exclosures during a 21-month study in a podocarp-broadleaf forest in the Waitakere Ranges, Auckland. The negative impact of plant disease transmission was also assessed, by testing soil collected from feral pigs for *Phytophthora* Taxon *Agathis* (PTA), a disease attacking kauri (*Agathis australis*). The relationship between ground disturbance and pig density was explored using empirical data from ground disturbance monitoring transects and pig culls conducted in the Waitakere Ranges, which was then used in a model to simulate management scenarios and explore impact mitigation through the use of disturbance thresholds. Feral pigs were found to significantly increase litter decomposition rates and soil nutrient concentration, reduce seedling density and change plant species richness and composition. Feral pigs also vectored a large number of plant pathogens. No PTA was found in the soil associated with pigs, although this is likely due to detectability issues and pigs may still be implicated in the spread of the disease. Pig culling in the Waitakere Ranges failed to reduce pig numbers below maximum productivity, although a reduction in ground disturbance was still observed. Model simulations demonstrated the use of disturbance thresholds in maintaining disturbance at an acceptable level, although at a higher cost than fixed frequency culling regimes. The overall conclusion of this research is that feral pigs should be managed as an invasive species in New Zealand. Repeated disturbance by pigs could increase the risk of plant disease spread and may have long-term impacts on seedling recruitment and composition. This research demonstrates the capability to reduce pig ground disturbance without large reductions in pig populations and provides management recommendations advocating disturbance thresholds.

Thank you to my husband David.
I couldn’t have done this without your support.
Elephant shoes.

There was once an invasive pig
Whose trotters were awfully big
He trampled biota
‘Til hunted for quota
And now he’s a spit roast pig

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Chapter 1 – General Introduction

1.1 Overview

Invasions of species into habitats outside their natural range have had major impacts across the globe and particularly in New Zealand (Myers et al. 2000, Clout and Williams 2009). Preventing the arrival of these species is the best protection for native ecosystems, but once introduction and spread have taken place, effective and efficient management of entrenched species will be the goal. However, sound management decisions rely on detailed information on the invasive population, the type and degree of impacts caused, and the science-based strategic application of control. Feral pigs (*Sus scrofa*) are increasingly seen as a problem in New Zealand although there is a lack of sound scientific evidence about the ecological impacts of this invasive species and appropriate strategies for mitigating impacts. Therefore this study aims to investigate the impacts of feral pigs and provide managers with the detailed information needed to make evidence-based management decisions.

1.2 Invasion biology

There has been much debate over terminology referring to non-native species (Pysěk 1995, Schwartz 1996, Falk-Petersen et al. 2006). Synonymous words are often used, such as 'alien', 'introduced' and 'non-indigenous' (Colautti and MacIsaac 2004), and the greatest confusion surrounds the term 'invasive' and its definition. Falk-Petersen et al. (2006) define an invasive species as 'an alien organism that has established in a new area and is expanding its range' (Falk-Petersen et al. 2006), which is the definition I will use in this thesis.

Lockwood et al. (2007) split the invasion process into four stages, the first stage involves transport of the invader to a new location, the second stage involves invader establishment and the third stage involves population increase and geographical spread, after which the impact of the invader is perceived, which is the fourth stage (Fig. 1.1).

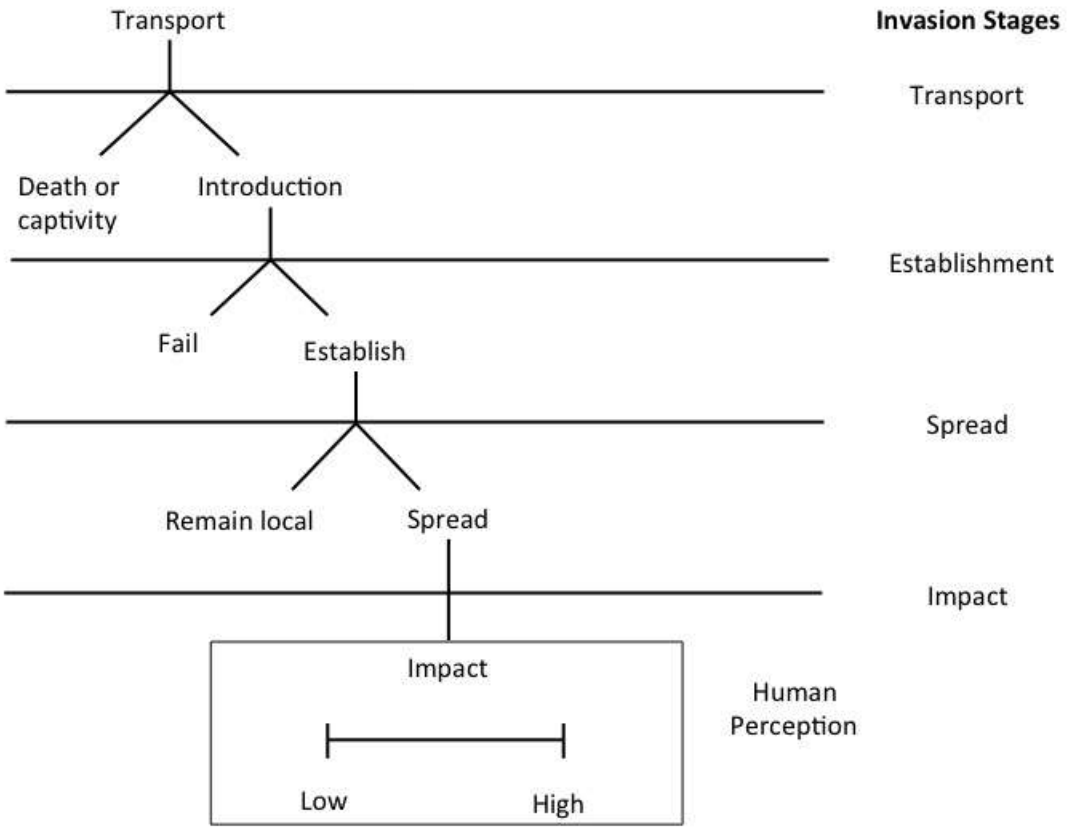

Figure 1.1 Invasion process model from Lockwood et al. (2007) showing the discrete stages of an invasion.

The New Zealand government spent US$44 million on biosecurity in 2000-2001 (Mumford 2002) in an attempt to mitigate the establishment of unwanted organisms, as eradicating and managing invasive species can be much more costly. Preventing the arrival and establishment of new organisms is not always possible, and in many cases, controlling the spread and impacts of invasive species becomes the overall management goal. The management of feral mammals in New Zealand is determined by three Acts of legislation, the Conservation Act 1987, the Wild Animal Control Act 1977 and the Biosecurity Act 1993 (Parkes and Murphy 2003). The Conservation Act determines introduced mammals as pests and warrants control when indigenous biota and ecosystems are adversely affected. The purpose of the Wild Animal Control Act is to control harmful species of introduced wild animals and regulate the operations of recreational and commercial hunters, to achieve effective wild animal control. However the recent establishment of the 'Game Animal Council' may allow commercial and recreational hunters' consultation on matters concerning the control and management of game animals of special interest. The Biosecurity Act requires that an invasive species must first be nominated on a regional pest management strategy and then the benefits of control must outweigh the costs for

any concerted action to take place (Parkes and Murphy 2003). Therefore impact (both real and perceived) whether control is implemented, particularly for feral mammals, which can be seen as a valued resource by a sector of the community.

Invasive species may have many perceived impacts on their new environment, including impacts that affect individual species or populations, such as hybridization, behavioural and morphological shifts and changes in density and distribution resulting from competitive exclusion (Falk-Petersen et al., 2006). Invasive species may also impact on wider communities by reducing species diversity, changing environmental conditions and altering ecological processes (Chapin III et al. 2000). Furthermore, invasive species are seen as one of the biggest threats to ecosystems, due to biodiversity loss, habit alteration and ecosystem degradation (Gurevitch and Padilla 2004). They are also a huge threat to island ecosystems, such as New Zealand, as species here have evolved in isolation, precluding the development of defences to protect against invaders such as mammalian predators and ungulates (Lee et al. 2006). Feral pigs are one such invader and have many impacts in their introduced range, including predation and habitat disturbance (Thomson and Challies 1988, Aplet et al. 1991, Pavlov et al. 1992, Mitchell et al. 2007).

1.3 Feral pigs In New Zealand

Using Lockwood et al's (2007) invasion model, the invasion of the feral pig in New Zealand can be tracked. There is no archaeological evidence that indicates pigs were present in New Zealand before the arrival of Europeans (Davidson 1984); although Tipene (1980) suggests that kunekune pigs were kept by Māori before the arrival of the Europeans as the name 'kunekune' is similar to that used by Polynesians. The first record of pigs being transported to New Zealand is of Captain Cook presenting domestic pigs to the Māori people on his second and third voyages to the country in 1773 and 1777, and also releasing some onto the mainland (Clarke and Dzieciolowski 1991). The adaptable diet of the pig (Baubet et al. 2004) and the lack of defensive mechanisms to ungulate grazing in New Zealand native plants would have aided the establishment of a feral pig population in New Zealand. Thomson and Challies (1988) highlighted the availability of food resources in the New Zealand forest for pigs. They discovered from examining the stomach contents of pigs living in podocarp-tawa forest that the highest percentage of feral pig food was obtained by foraging on the ground and over 70% of this food was plant material, although invertebrate species and geckos were also found. The spread of feral pigs throughout the country was aided by various feral pig releases by European expeditions as well as releases by Māori settlers (Challies 1975). Choquenot et al. (1996) suggest that pig spread throughout the country occurred predominately by unrestrained domestic stock wandering away or by restrained stock

escaping. McIlroy (2001) suggests that while feral pig range extensions have sometimes been due to natural spread, they are more often due to illegal liberations for hunting purposes. The most recent estimates (based on DOC and council reports) suggest feral pigs occupy about 93 000 km^2 of New Zealand land area (Fraser et al. 2000). This survey also indicated that pigs had increased their range since the previous surveys in 1971 and 1983 (Fraser et al. 2000), mainly extending their range into Otago, Southland and the West Coast of the South Island. This expansion is probably associated with changes in land use (McIlroy 1990, Clarke and Dzieciolowski 1991, McIlroy 2001). The total number of feral pigs in New Zealand is difficult to estimate, although Nugent et al. (1996) suggested that there could be approximately 110 000 individuals at an average density of 1.2 per km^2. McIlroy (1989) suggests that in lightly hunted areas, with abundant food and cover their density may be 12–43 per km^2. These estimates combined with Fraser et al.'s (2000) estimation of range would equate to a an estimated population size of 1.1 million– 4.0 million feral pigs in New Zealand.

Despite the presence of feral pigs in New Zealand for >200 years, the impact of this invasive species on New Zealand ecosystems has not been appropriately quantified. Consequently this species has generally not been considered a high priority for eradication or control efforts. Although there is a lack of scientific evidence for impacts, the perceived environmental impacts of feral pigs are often high. Most perceptions of pig damage focus on the ground disturbance pigs cause when foraging for food, possibly because of the extent of disturbance patches, which can range from $1.4m^2$ to $150m^2$ (Pavlov and Edwards 1995). Although many New Zealanders now view pigs as a resource rather than a pest. Māori, in particular, view pigs as a cultural resource and recreational pig hunting throughout New Zealand is widely practiced (Nugent et al. 1996). Feral pigs also have a commercial value for their meat and as a target for professional hunting guides (Nugent et al. 1996). Therefore to mitigate conflict with communities, land managers require evidence of the negative impacts of feral pigs to justify their decision to manage feral pigs as a pest, rather than a resource, in high value conservation areas.

1.4 Impacts

As the impacts of invasive species can be so widespread and perceived impacts can vary depending on the criteria being assessed, impacts can be difficult to measure. To make cost-effective management and budget decisions, managers need to be able to assess impacts and use these assessments to prioritise invasive species control. Parker et al. (1999) suggest an equation to measure overall impact of a species that is comparable across taxa and geographic space. This equation is: $I=R \times A \times E$

where *I* is the overall impact of a species, *R* is the range that the species occupies, *A* is the species' average abundance and *E* is the per capita effect. Whilst this equation is useful, it presents some problems. Defining a species range can be difficult and is seldom accurately measured. Abundance data for a species can be patchy and inaccurate if the species is cryptic. The per capita effect of an invader is the most difficult to measure, especially across different taxa and ecosystems and among different ecological levels (individuals, populations and ecosystems). To resolve this problem Parker et al. (1999) call for studies to measure impact/effect at multiple ecological levels, and the development of impact modelling that combines community or population data with the tracking of ecosystem functions. In this thesis, I will be attempting to provide some of this information for feral pigs inhabiting a temperate rainforest ecosystem.

Feral pigs have a wide range of direct and indirect impacts on indigenous plants and animals globally. The direct impacts of feral pigs in New Zealand mainly involve herbivory and predation. A study in the Urewera Ranges (podocarp-tawa forest), found that over a third of the pig's diet was comprised of the fruits of tawa (*Beilschmiedia tawa*), hinau (*Elaeocarpus dentatus*) and supplejack (*Ripogonum scandens*), all native plant species (Thompson and Challies 1988). Animal material formed twenty-eight per cent of the pig's diet, most of which were the carcasses of brushtail possums (*Trichosurus vulpecula*) (scavenged from trap lines) (Thompson and Challies 1988). Another study found that on D'Urville Island feral pigs were a potential cause of the decline of *Powelliphanta hochstetteri* (an indigenous, giant land snail), due to their consumption of the snail (Coleman et al. 2001). Pigs have also been implicated in the decline of some populations of vulnerable plants through habitat destruction and herbivory, such as *Astelia grandis* and *Lepidium banksii* in the Nelson region, and low altitude tussock on the Auckland Islands (NPCA 2009). Feral pigs have also contributed to the decline of breeding colonies of the New Zealand white-capped mollymawk (*Diomedea cauta steadi*) on main Auckland Island (Flux 2002). Evidence of pigs consuming yellow-eyed penguin (*Megadyptes antipodes*), Auckland Island prion (*Pachyptila desolata*) and Auckland Island shag (*Leucocarbo colensoi*) has also been recorded on the Auckland Islands (Challies 1975). The requirement for protein, especially for breeding and growth (McIlroy 1990), may be what drives predation of animals by feral pigs. Frogs may also be a food item for pigs in some areas, as Baber et al. (2006) state that feral pigs can destroy the habitat of the endemic Hochstetter's frog (*Leiopelma hochstetteri*) by trampling and foraging on the edge of streams, and are also likely to opportunistically kill Hochstetter's frogs. There are also records of feral pigs consuming macrofungi (Baron 1982, Thomson and Challies 1988), but no studies have been conducted on the effects of mycophagy by pigs.

Feral pigs can have indirect effects on ecosystems through ground disturbance (rooting). Several studies have found that pig rooting and disturbance have indirect effects on the plant

assemblages in tropical rainforests in Australia and Hawaii (Aplet et al. 1991, Pavlov et al. 1992, Mitchell et al. 2007), deciduous forests in the U.S (Singer et al. 1984, Siemann et al. 2009) and grasslands, also in the U.S (Cushman et al. 2004, Tierney and Cushman 2006). The indirect effects of the disturbance caused by feral pig rooting have not been studied in a temperate rainforest, such as that found in New Zealand.

Rooting caused by pigs may indirectly alter indigenous ecosystem disturbance regimes, resulting in compositional and structural shifts in vegetation (Bratton 1975, Hone and Martin 1998, Hone 2002, Tierney and Cushman 2006, Siemann et al. 2009), and may encourage the growth of weed species (disturbance specialists) (Singer et al. 1984, Aplet 1990, Cushman et al. 2004). Feral pig rooting has also been shown to modify ecosystem processes. For example, rooting was shown to cause an increase in carbon to nitrogen ratios in a number of studies (Aplet 1990, Frank and Evans 1997, Siemann et al. 2009), and may alter the nitrogen cycle (Siemann et al. 2009). Pigs may have other indirect negative effects on the environment by vectoring weeds or pathogens from one area to another. There is growing evidence that feral pigs aid dispersal of the rootrot fungus, *Phytophthora cinnamomi*, responsible for the dieback disease in native vegetation in Australia and Hawaii (Brown 1976, Kliejunas and Ko 1976, Tisdell 1982, Li et al. 2010). A new *Phytophthora* species (*Phytophthora* 'taxon *Agathis*') has been found to cause severe damage and death to kauri (*Agathis australis*) in some parts of northern New Zealand, including dense kauri stands in the Waitakere Ranges (Beever et al. 2009), and feral pigs are implicated in the spread of this disease.

The potential impacts of invasive feral pigs in New Zealand are wide-ranging and an impact assessment of the indirect effects on vegetation and ecosystem processes is required to determine if this is a priority pest species that necessitates a management response, and whether that response should be local eradication and exclusion, or on-going control.

1.5 Feral pig management

There are management tools to intercept and control invasive species at each stage of the invasion process (Clout and Williams 2009). However, eradication is generally only possible prior to the spread stage (Grice 2009). Containment or control then becomes the overall management goal when populations are large and extensive. Grice (2009) states that deciding whether to implement control will depend on three factors:

1. The importance of the perceived impacts of the invasive species relative to the cost of control

2. Which stage of the invasion process the species has progressed to
3. The availability of control methods

Preferred control methods for feral pigs are highly variable and dependent on habitat structure. Helicopter shooting is particularly effective in the Australian rangelands (Choquenot et al. 1999), although this method's efficiency declines where vegetation cover becomes taller and more dense as it provides a refuge for pigs from shooting (Choquenot et al. 1999). Therefore in forested habitats other methods must be employed. Trapping has been used in a number of different studies in forest ecosystems, in Malaya (Diong 1973), the United States (Barrett 1978), Hawaii (Anderson and Stone 1993) and Australia (Saunders et al. 1993). However, trapping can have limited effectiveness against some sections of a pig population as females and juveniles are trapped more easily (Giles 1980, Choquenot et al. 1993) and establishing traps in rugged terrain with little or no vehicle access is expensive (NPCA 2009). A particularly efficient eradication program on Santa Cruz Island used a combination of trapping, aerial shooting, Judas pigs (radio-collared pigs used to locate groups of pigs for removal) and ground-based hunting with dogs, and demonstrated the benefit of using several concurrent techniques (Parkes et al. 2010). Ground-based hunting with dogs is the most common approach to pig control in New Zealand because no toxin is currently registered for use against feral pigs (NPCA 2009). Therefore, ground-based hunting with dogs fits Grice's (2009) decision rules around control implementation using a readily available control tool to manage the invasive feral pig in New Zealand. However, the question remains as to whether the impacts of the feral pig in New Zealand warrant the cost of their control.

1.6 Effective impact mitigation

Effective and efficient management of invasive species must include the definition of a clear management goal. However, to do so requires knowledge about the scale and consequences of the problems caused by the species. In particular the flow-on effects for biodiversity and ecological relationships, but also knowledge of the appropriate control techniques and strategies required to reduce a population and maintain it at an acceptable level. Conservation management in New Zealand is generally focused on reducing the impact of invasive species on key indigenous species or ecosystems (Choquenot and Parkes 2001). Budgets are constrained and control operations are only sensible where they are seen to have the most ecological benefit. If invasive species density can be related to levels of impacts on indigenous species, the relationship can be used to set thresholds for invasive species control (Choquenot and Parkes 2001). Moller (1989) introduced the idea of an 'ecological damage threshold' (similar to the

'economic damage threshold' used in Integrated Pest Management), which involves a threshold level of invasive species density, above which ecological damage is unacceptable or undesirable. When the invasive density threshold is exceeded, the observed impacts will be great and control will be warranted, conversely if the invasive species density remains below this threshold further control will accrue unwarranted cost (Choquenot and Parkes 2001). A number of different models have been proposed to explore the relationship between pest density and the resources that they affect (Caughley 1977, Hone 1994, Beggs and Rees 1999, Choquenot and Parkes 2005). However, for feral pigs, Choquenot and Parkes (2005) developed a model that relates ground disturbance by pigs to pig population abundance, to explore the relationship between pig density and the extent of disturbance. This model will be developed further in this thesis to provide a framework for managers that links conservation of indigenous ecological communities to control inputs through their effect on ground disturbance. The framework allows managers to identify cost effective solutions for feral pig management.

1.7 Research questions and thesis layout

There has been little measurement of the impacts of feral pigs in temperate rainforests, particularly in regards to how impacts might relate to pig population density. More specifically, there has been little work published on whether ground disturbance by pigs causes significant changes in vegetation communities and ecosystem processes in New Zealand forests. The aim of this thesis is to determine the ecological impacts associated with feral pigs in a New Zealand temperate rainforest.

The study area used to assess the population and impacts of feral pigs is the Waitakere Ranges, Auckland. Impact was assessed across different ecological levels (as suggested by Parker et al. (1999)) including, individual plants, plant species and ecosystem processes. The relevance of the results to management was also explored to provide advice for management of feral pigs in this area of New Zealand.

The overall aim was achieved by investigating the following research questions:

1) What impacts does ground disturbance by feral pigs have on vegetation, ecosystem processes and plant pathogen transmission in a temperate rainforest?

2) What is the relationship between feral pig density and ground disturbance?

3) Can threshold levels for pig management be identified through the use of a model linking control activity to pig density and ground disturbance?

This thesis is presented in a series of self-contained Chapters following the research questions above, first addressing pig impacts (Chapters 2 and 3) and subsequently, the relationship between ground disturbance and pig density and resulting management recommendations (Chapters 4 and 5). Chapter two investigates the impact of feral pigs on nutrient availability, litter decomposition and seedling recruitment (species abundance, diversity and composition). Chapter three examines the evidence for feral pigs as vectors of the root rot disease *Phytophthora* 'taxon *Agathis*'. Chapter four determines the relationship between pig ground disturbance and pig density in the Waitakere Ranges and determines if ground disturbance is associated with certain environmental variables (i.e., do pigs preferentially root in certain locations in forests?). Ground disturbance and pig kill data are then used to predict pig population densities. Chapter five compares and contrasts different strategies for feral pig management in the Waitakere Ranges by modelling the relationship between ground disturbance and pig population density, and modelling the effect of different management interventions, particularly the timing of intervention. The general discussion (Chapter six) provides a synthesis of the previous Chapters and includes management and research recommendations for feral pigs in New Zealand based on findings from the Waitakere Ranges. The references are presented at the end of each Chapter for the reader's convenience.

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Chapter 2 – Feral pig ground disturbance and recovery: ecosystem engineering in a temperate rainforest

Abstract

Invasive species can act as ecosystem engineers by changing ecosystem processes. Feral pigs (*Sus scrofa*) are a widespread invasive species, and cause biotic disturbance. This study evaluated the impacts associated with ground disturbance by pigs in the North Island of New Zealand, by excluding pigs from previously disturbed areas. Exclosure cages were erected over pig-disturbed ground and undisturbed ground (the latter as controls). Over a 21-month period, soil nutrient levels and decomposition rates were examined in these plots, and seedling recruitment (abundance, species composition and richness) was monitored. Significantly more plant-available nitrate and higher rates of litter decomposition were found in disturbed plots. Total seedling density was halved after feral pig ground disturbance but returned to undisturbed densities after 3 months. Plant species richness declined after ground disturbance but recovered after 9 months. Changes in species composition occurred at disturbed sites, with a distinct assemblage of species increasing in density after ground disturbance by pigs. This study shows that ground disturbance directly affects plant communities through direct removal of vegetation, but also has indirect effects via modification of soil characteristics and increasing decomposition rates. Seedling abundance and species richness can recover if allowed, although pigs are known to repeatedly return to previously disturbed areas, causing prolonged disturbance. If left unprotected, these areas may remain in a constantly disturbed state. Through continued disturbance and mineralization of nitrogen, ecosystem changes are likely to occur, especially in characteristically nutrient-poor environments.

2.1 Introduction

Impacts of invasive species on their recipient environment include those that affect individual species and populations, such as hybridization, behavioural and morphological shifts, and changes in density and distribution resulting from competitive exclusion (Falk-Petersen et al. 2006). Invasive species may also impact on wider communities by reducing species diversity, changing environmental conditions and altering ecological processes (Chapin III et al. 2000). Vitousek et al. (1996) state that an invasive species is most likely to change the properties of an ecosystem when it introduces a novel biological process. This type of invasive species can also be classed as an ecosystem engineer, which may directly or indirectly modify, maintain or create habitats through the modulation of resources and physical state changes in biotic or abiotic material (Jones et al. 1994, Crooks 2002, Gutierrez and Jones 2006, Wright and Jones 2006). Crooks (2002) recognizes ecosystem engineering as a major means by which invasive species affect ecosystems and calls these species 'exotic engineers'. Ecosystem engineers can be autogenic, in which the organisms themselves are part of the engineered habitat, or allogenic, where the organism is altering biotic or abiotic materials from one state to another e.g. creating disturbance.

Disturbance is often recognized as an important factor in determining ecosystem composition and structure (Sousa 1984, Pickett and White 1985, Tierney and Cushman 2006). Connell (1978) described the intermediate disturbance hypothesis in which species diversity can be maximized with an optimum level of disturbance. However, an increase in disturbance regime could result in the loss of species diversity and also promote the spread of invasive weeds (D'Antonio et al. 1999, Cushman et al. 2004). Some ecosystems have evolved with biotic disturbance agents (mainly native mammals) present (Singer et al. 1984, Sherrod and Seastedt 2001, Cushman et al. 2004) that are integral to the structure and function of these ecosystems. Other ecosystems have suffered the introduction of these disturbance agents in the form of invasive mammals that establish feral populations and alter the disturbance regime in the recipient ecosystem (D'Antonio et al. 1999). The best known examples of species introducing new forms of disturbance, or enhancing or suppressing existing forms of disturbance (Cushman et al. 2004), come from feral populations of domesticated mammals, such as: feral goats (*Capra hircus*) and sheep (*Ovis aries*) (Mueller-Dombois and Spatz 1975, Van Vuren and Coblentz 1987); many species of deer (*Cervidae*) (Mark et al. 1991); feral pigs (*Sus scrofa*) (Hone 1995, Cushman et al. 2004); and horses (*Equus caballus*) (Beever and Brussard 2000).

Feral pigs physically change their local environment through disturbance, by rooting for food and destroying the surrounding vegetation and forest floor (Hone and Robards 1980, Engeman et al. 2005). The damage caused by pigs may be direct (Thomson and Challies 1988), although Tierney and Cushman (2006) have also found that ground disturbance has indirect effects on the plant assemblages in grassland ecosystems. Hone (2002) showed similar results in a montane and sub-alpine ecosystem. Indirect effects of ground disturbance by pigs include changes in the composition and structure of the ecosystem through changes in species richness and diversity, facilitating weed growth and reducing the biomass of native species (Aplet et al. 1991, Hone 2002, Cushman et al. 2004, Tierney and Cushman 2006, Siemann et al. 2009). Feral pigs have also been shown to increase carbon to nitrogen ratios in the soil in a number of studies leading to further changes in the surrounding vegetation, including higher plant productivity, increased alien plant assemblages, and increased microhabitat diversity (Aplet 1990, Frank and Evans 1997, Arrington et al. 1999, Siemann et al. 2009).

Previous studies have highlighted the impacts feral pigs have on tropical, grassland and temperate deciduous ecosystems. The majority of these studies have been conducted in places with native mammalian biotic disturbance agents. This study examines the impacts of feral pigs in a temperate rainforest ecosystem that has evolved in the absence of ground-dwelling mammals. Pre-human New Zealand was home to a number of large ground-dwelling birds, including moa (McGlone 1989) that may have performed some scarification of the soil whilst searching for food. Burrowing seabirds were more abundant on the mainland in pre-human times (McGlone 1989) and are associated with seedling disturbance and soil nutrient changes (Mulder and Keall 2001, Roberts et al. 2007), however, the disturbance caused by both large ground-dwelling birds and burrowing seabirds is fundamentally different to the turning over of soil (likened to a rotary hoe) associated with disturbance by feral pigs. The New Zealand feral pig (*Sus scrofa*), is descended from domestic pigs released in New Zealand by the European settlers in the 18th century (King 2005), which subsequently became established and widespread. They currently occupy approximately 93 000 km^2 or 35% of the country (King 2005). The ground disturbance created by feral pigs presents a novel biological process in the New Zealand forest, and, as no native species currently disturb soils to this degree or over similar scales, feral pigs consequently occupy a vacant niche. As a result feral pigs are predicted to have an impact on the ecosystem by changing ecological processes (Vitousek et al. 1996, Shea and Chesson 2002).

This study aimed to determine the effects of pig ground disturbance on seedling recruitment (including abundance, species richness and composition), soil nutrient availability, litter cover, decomposition and weed establishment, by comparing ground disturbance sites with undisturbed

controls. It is hypothesised that feral pigs will alter soil nutrients and decomposition, which will have long-term effects on plant successional processes.

2.2 Methods

2.2.1 Study site

The Waitakere Ranges in Auckland, New Zealand is a regional park of over 16 000 ha, which extends from 36.53 to 37.03°S and from 174.27 to 174.34°E (0–474 m above sea level). In this area of podocarp/broadleaf dominated temperate rainforest pigs are present in substantial, but un-quantified numbers. No other mammalian ungulates are present.

2.2.2 Experimental design

To study the impacts of feral pig ground disturbance and ecosystem recovery, areas of pig-disturbed ground and undisturbed controls were fenced off to exclude pigs. These exclosures were established at 18 disturbance sites across the Waitakere Ranges. Six areas of the ranges were targeted for the establishment of disturbance sites as previous work had highlighted high pig activity in these locations (174.566168°E -36.973304°S, 174.534936°E -36.956433°S, 174.511679°E -36.976471°S, 174.511967°E -37.035867°S, 174.568177°E -36.932140°S, 174.597557°E -36.997024°S). At each location the surrounding area was traversed, searching for ground disturbance (mainly following pig tracks). At the disturbance site, exclosures were established in the centre of a patch of fresh ground disturbance (fresh disturbance was classified as any disturbance that contained little or no plant litter and the unearthed soil was still visibly moist). An exclosure was also erected 1 m from the edge of the ground disturbance and 10 m from the edge of the ground disturbance (Fig. 2.1). Plots of ground with an equal area to the exclosure were also marked using a central flagged stake (60 cm), placed in the ground; these were designated as control plots. Therefore, for each of the three exclosure plots (centre, 1 m, 10 m) at each disturbance site (n = 18), there were three paired control plots (n = 9 at each disturbance site) each spaced at least 50 cm from one another and the three exclosure plots. The disturbance sites were established in June 2009 and were monitored for 21 months or until the ground disturbance was no longer discernable to the naked eye.

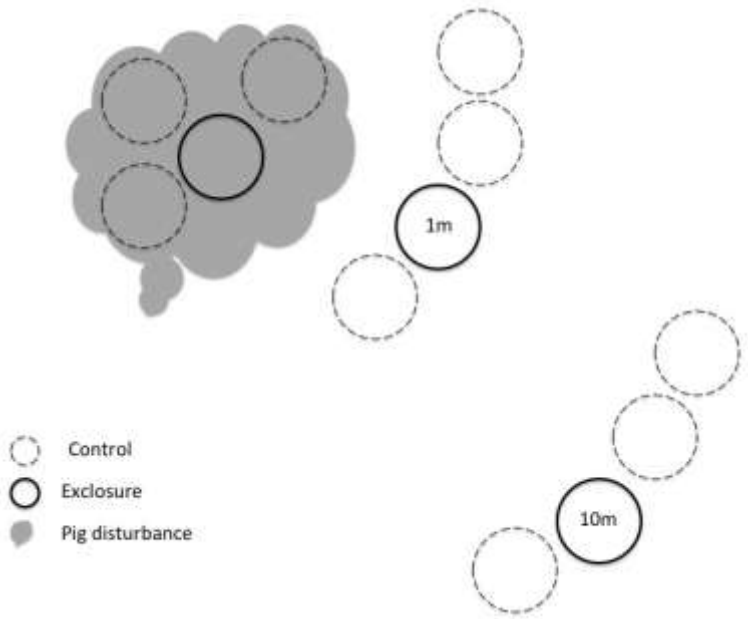

Figure 2.1 Diagram of a disturbance site showing the area of pig ground disturbance, exclosure plots and control plots.

2.2.3 Exclosure design

A pilot study on 10 disturbed sites indicated that the effects of ground disturbance on litter cover and seedling abundance did not extend beyond the edge of the disturbance site (Krull unpubl. data). Consequently, it was only necessary for exclosures to include the disturbed area itself, and not the surrounding area. On this basis, exclosures 98 cm in diameter were used, representing a single seedling monitoring area. Smaller exclosures were beneficial for ease of movement, and cost effectiveness. The exclosures were built using a 325 cm section of weld mesh (50 x 50 mm mesh hole size and 1.5 m in height). The mesh was secured into a cylindrical shape (with a 98 cm diameter) by overlapping approximately 15 cm at the ends of the length of weld mesh and securing this with cable ties on either side of the overlap. The cylinder was secured to the ground by three garden stakes hammered approximately 15 cm into the ground. The garden stakes were then attached to the weld mesh via cable ties. Lastly the weld mesh was secured to the ground using steel weed mat pins, one pin between each of the stakes.

At each exclosure and control plot the canopy density was measured with a densiometer, soil moisture with a 'Campbell Hydrosense CS620' soil moisture meter, and aspect measurements taken with a compass. Soil nutrient availability was also measured using ion exchange resin (IER) bags (Binkley and Matson 1983, Binkley 1984). Nylon resin bags were made from pantyhose and filled with approximately 5 g of BDH resin Amberlite MB6113. Each resin bag was labelled with a metal tag on a 20 cm long nylon string. One resin bag was then buried to a depth of 10 cm in the

soil in each exclosure and one randomly chosen, paired control plot. The resin bags were unearthed and taken back to the lab after 12 months. In the lab the resin bags were rinsed individually with de-ionized water to remove any soil and then spun dry to remove excess water. Samples were then extracted using 30 ml of 2M KCl per sample, shaken in an orbital shaker for 30 minutes (100 rpm), and the resulting liquid was used to determine the concentrations of NH_4-N, NO_x-N (where NO_x indicates NO_2 and NO_3) and PO_4-P in an auto-analyser.

Litter cover and decomposition, and seedling recruitment were measured every 3 months for 21 months in both exclosures and control plots, to monitor changes over time. Percentage litter cover was estimated to the nearest 5%. Litter decomposition was assessed using the litter bag technique (Crossley Jr. and Hoglund 1962) and dry weight loss was measured. The leaves of pigeon wood (*Hedycarya arborea*) were used as the litter inside the mesh bags, as this species is the most common sub-canopy species in the Waitakere Ranges. Fresh leaf material was collected and oven dried (60°C for 48 h) before placement of 5–8 g of litter into nylon mesh (5 mm) litter bags (10 x 20 cm). For each litter bag, the weight of oven dried leaf litter placed into the bag was recorded. Inside each exclosure and one randomly chosen paired control plot, three litter bags were pinned to the ground using weed mat pins. One litter bag from each exclosure and control plot was collected after 8, 16 and 32 weeks in the field. Upon return to the laboratory the leaf material was removed from each of the bags and oven dried at 60°C for 48 h in a paper bag, then reweighed.

To measure seedling recruitment, the understory subplot method was used (Hurst and Allen 2007). A circular plot with a 49 cm radius was marked by pulling a 49 cm piece of string around a central peg (this was the entire exclosure plot area). Woody seedlings within this plot were identified to species and recorded as a count within each of the following height tiers: <15 cm, 16–45 cm, 46–75 cm, 76–105 cm and 106–135 cm. Seedlings that forked visibly above or at ground level were considered the same plant. Weed species were estimated as percentage cover at each exclosure and control plot at 21 months after ground disturbance by pigs.

2.2.4 Statistical analysis

All graphs and statistical tests were performed using the statistical program R (version 2.8.1). Resin bag data could not be transformed to normality, therefore non-parametric Kruskal-Wallis tests were used to analyse these data. All means are shown with their standard errors ($x \pm$ SE).

Litter cover was averaged over the disturbed plots and then the undisturbed plots (10 m plots only). These means were used to create a ratio of disturbed to undisturbed litter cover score. This was achieved by dividing the mean litter cover in disturbed plots by the mean litter cover in

undisturbed plots; therefore a score of 100% would indicate litter cover in the disturbed plots had returned to undisturbed levels.

To examine litter bag decomposition, dry weights of the reweighed leaf material (retrieved from the field) were subtracted from the initial dry weight. Relative loss was then calculated by dividing mass lost by original weight, this was then converted to mass remaining using the calculation: 1 – relative loss. The data did not conform to normality and was transformed using a Box Cox transformation. The data were then tested for normality using a Shapiro-Wilk test (W = 0.99 P = 0.11); Levene's tests were also conducted to ensure homogeneity of variance within factors. Differences in decomposition between disturbed and undisturbed sites were tested using a 2-way ANOVA including site as the second factor. Tukey's Honestly Significant Difference was used post hoc to determine which treatments differed.

The same analysis used for the litter cover data was also used for the seedling abundance and species richness data. As these data did not conform to normality, Kruskal-Wallis tests were performed to determine if there were significant differences between disturbed and undisturbed plots overall and for each time period.

The composition of the most abundant seedling species (top 95%) in the disturbed and undisturbed plots at the sites with a podocarp broadleaf canopy (n = 10) was analysed using non-metric multidimensional scaling (nMDS) in PRIMER v6.0 software, using a Bray–Curtis similarity matrix (square root transformation) from 100 runs (Clarke and Warwick 2005). Analysis of Similarities (ANOSIM) routine was used, with 999 permutations, to analyse differences between the 10 sites, time periods and disturbance treatment. ANOSIM creates an overall test statistic (R) that indicates if differences between habitat types exist. As R approaches 1, there is more dissimilarity between sites. For ANOSIM, Clarke & Warwick (2005) use the following definitions: well-separated R > 0.75, clearly different R > 0.5, and barely separable R < 0.25. In addition, SIMPER analyses were used to examine which taxa contributed the most to the differences between disturbed and undisturbed sites (Clarke & Warwick, 2005). A distance-based test for homogeneity of multivariate dispersions (PERMDISP) was also used to test for differences in the dispersion of the disturbed and undisturbed data.

2.3 Results

2.3.1 Nutrient availability

There was no effect of distance from ground disturbance on levels of ammonium or phosphate absorbed by IER bags (Table 2.1). However, there was a significant difference between plant available nitrates (NO_x-N) levels at differing distances from ground disturbance (P = 0.046).

Table 2.1 Results (P values) of the Kruskal-Wallis tests for the distance from disturbance, *significant at the 0.05 level.

Ion	Distance from disturbance	
	X^2-value	p-value
Ammonium	2.89	0.236
NO_x-N	6.15	0.046*
Phosphate	1.28	0.527

Post hoc tests revealed that only the disturbed and 10 m distances differed significantly from one another (Kruskal-Wallis, X^2 = 5.10, df = 1, P = 0.025) in levels of NO_x-N, indicating that there may be an 'apron' effect (*sensu* Merret et al. 2000) from ground disturbance extending up to 1 m away from the disturbance in terms of nitrate availability (Fig. 2.2).

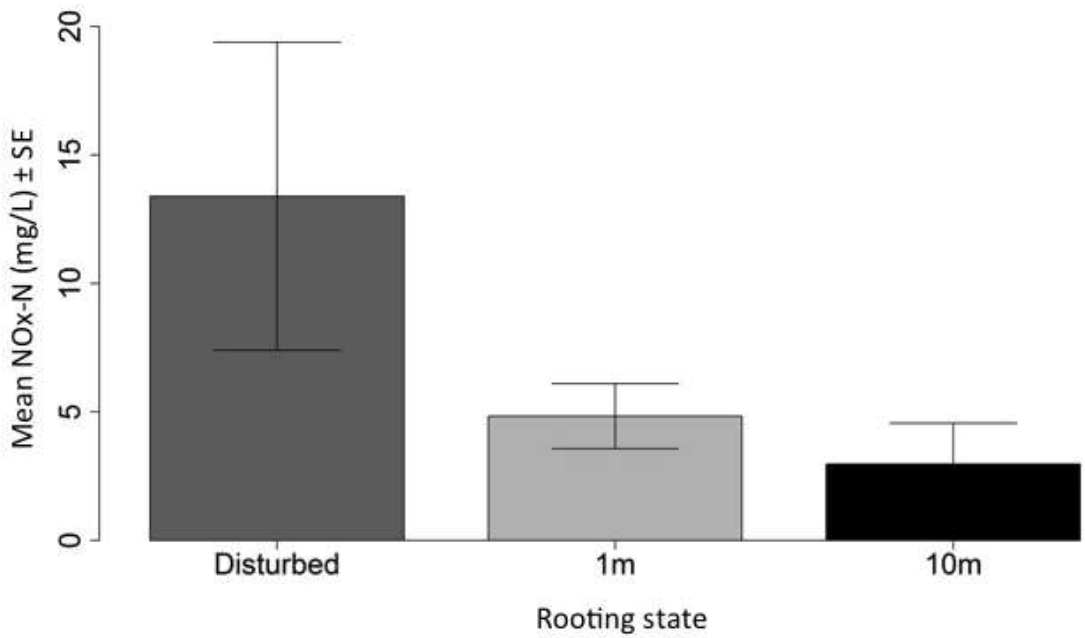

Figure 2.2 Average milligrams per litre of NO_x-N in disturbed, 1 m and 10 m plots.

2.3.2 Litter cover

The percentage of litter cover was significantly lower in disturbed plots compared to undisturbed plots (Fig. 2.3). Litter cover did not recover to undisturbed levels in the course of this study.

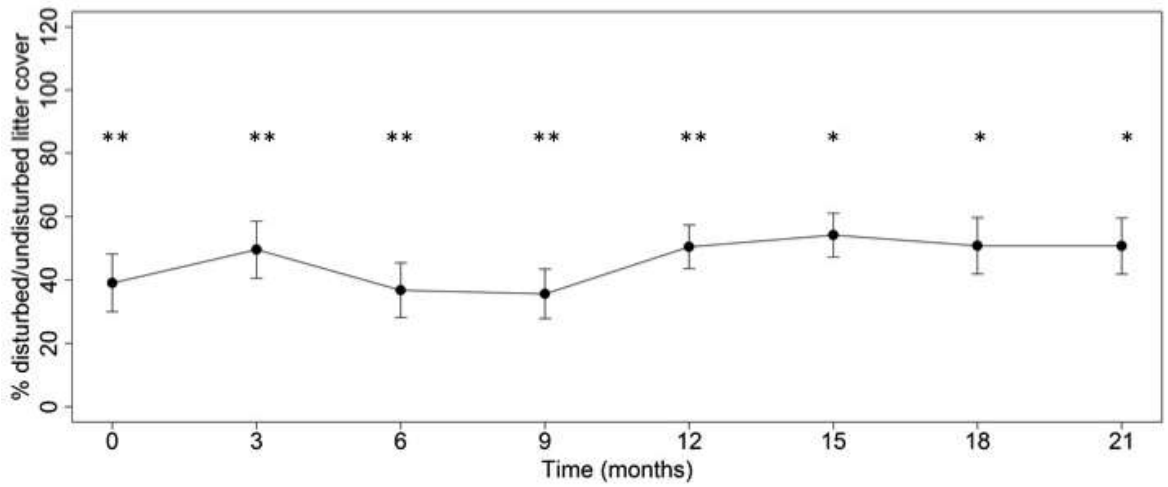

Figure 2.3 Litter cover in the disturbed plots relative to the undisturbed (100%) over time after ground disturbance by pigs. * $P < 0.05$, ** $P < 0.001$.

2.3.3 Litter decomposition

Preliminary analysis of the litter bag data showed a significant difference between sites (F = 15.31, df = 17, P = <0.001). It was determined that six of the sites had a different forest canopy and leaf litter to the remaining twelve sites, and therefore excluded from subsequent analyses. Twelve of the sites were podocarp/broadleaf or broadleaf dominated forest; although, three of the sites had a high proportion of introduced pine and the remaining three sites a native palm canopy. Distance from disturbance (disturbed, 1 m away or 10 m away) was found to significantly affect decomposition rates of plant matter in litter bags (F = 5.08, df = 2, P = 0.007). There was no interaction between the factors distance from disturbance and site (F = 0.62, df = 10, P = 0.620). Post hoc tests using the distance data determined that only the 1 m and 10 m data differed significantly with slower rates of decomposition at the 10 m plots indicating that there may again be an 'apron' effect from ground disturbance by pigs up to 1 m away, similar to the nutrient availability data (Fig. 2.4). Based on these results, and to negate any impact gradient, all subsequent analyses were conducted using the disturbed and 10 m plots (now called undisturbed) only.

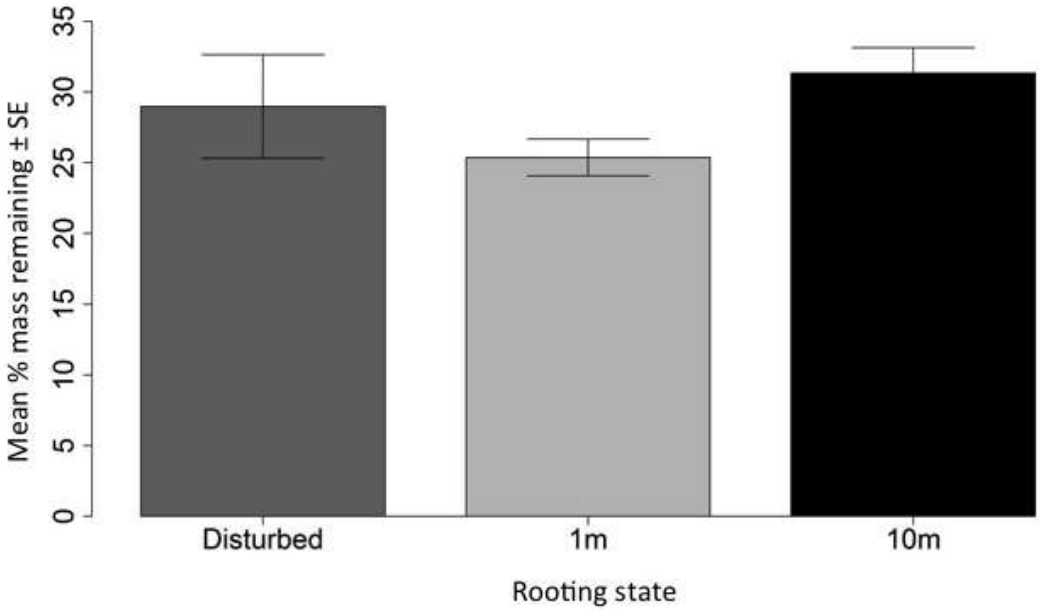

Figure 2.4 Percentage of litter biomass remaining at the disturbed, 1 m and 10 m plots.

2.3.4 Seedling recruitment

Seedling density was reduced to below 50% after pig ground disturbance, when compared to undisturbed densities but recovered to a similar density after more than 3 months (Fig. 2.5).

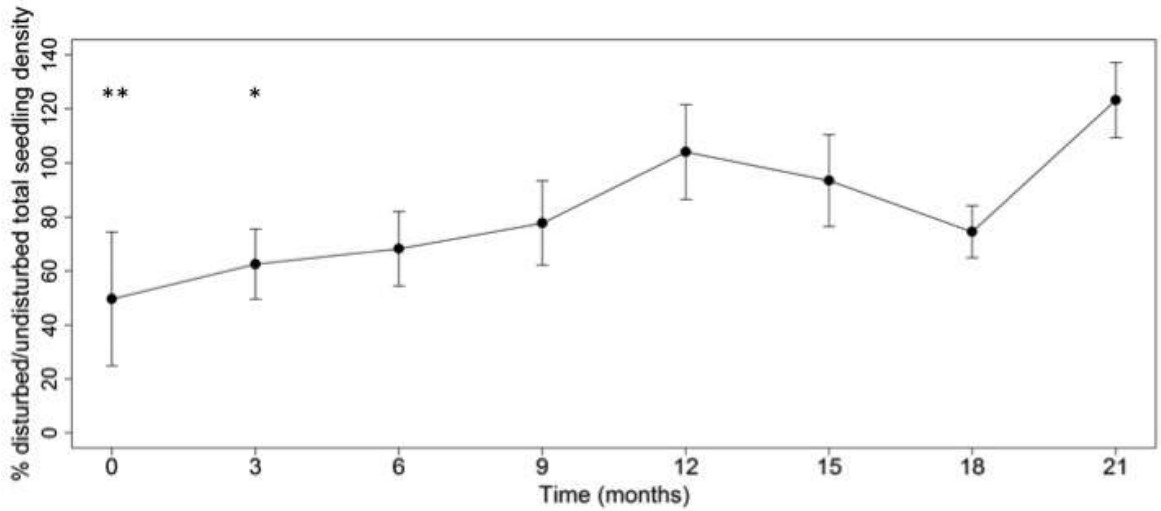

Figure 2.5 Seedling density in the disturbed plots relative to the undisturbed (100%) over time following ground disturbance by pigs. * $P < 0.05$, ** $P < 0.001$.

Seedling density between disturbed and undisturbed plots differed depending on the size class of the seedlings (Fig. 2.5). Ephemeral seedlings (<15 cm) only differed significantly until 3 months after pig ground disturbance (Fig. 2.5), whereas established seedlings (16–45 cm and 46–75 cm) were recorded at densities significantly lower in the disturbed plots until 18 months after disturbance. There were too few seedlings in the size classes 76–105 cm and 106–135 cm to perform any valid analysis.

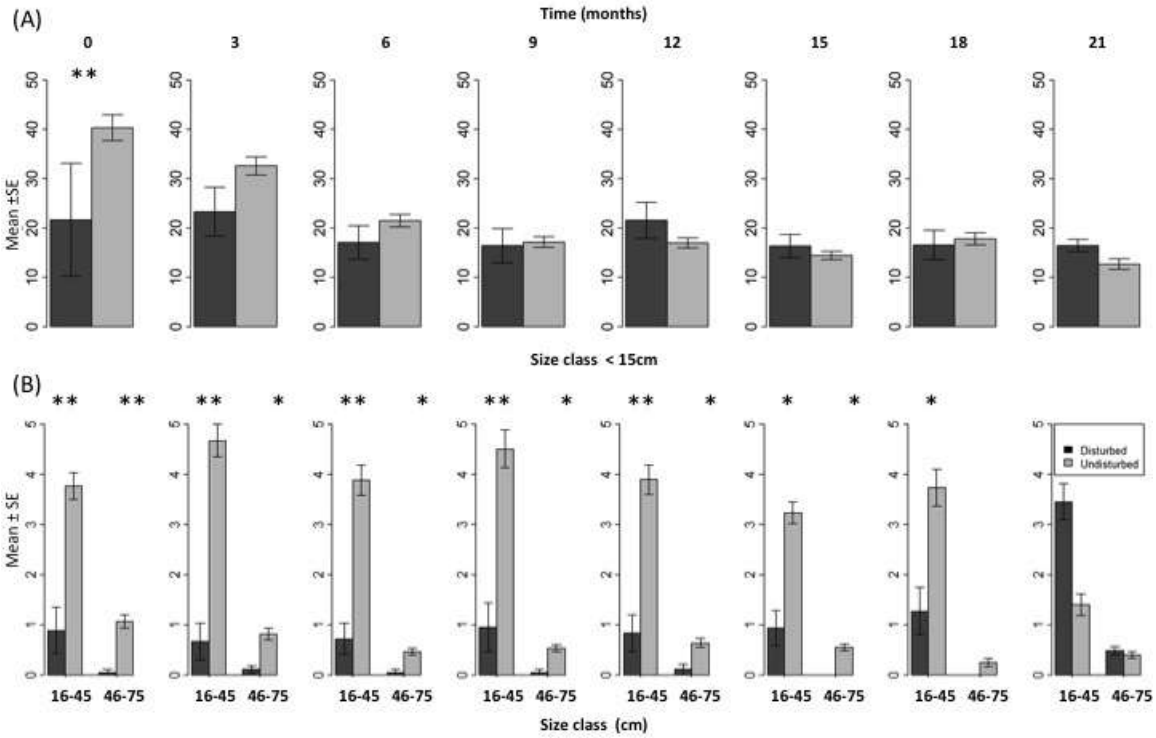

Figure 2.6 Mean ± SE abundance of (A) ephemeral seedlings (<15 cm in height) and (B) established seedlings (>15 cm) over time after ground disturbance by pigs. * $P < 0.05$, ** $P < 0.001$.

Species richness of seedlings found in the disturbed plots was significantly lower until 12 months after disturbance (Fig. 2.6), after which time disturbed plots increased to similar species richness as the undisturbed plots. There was no significant difference in weed cover in the disturbed plots when compared to the undisturbed ($X^2 = 0.69$, df = 1, $P = 0.41$), although weed numbers were low in all plots. Mean weed cover in the disturbed plots was 0.67% ± 0.56% (n = 3 species), compared with 0.54% ± 0.37% in the undisturbed plots (n = 3 species). Self heal (*Prunella vulgaris*) was present in both disturbed and undisturbed plots, African club moss (*Selaginella kraussiana*) and purple top vervain (*Verbena bonariensis*) were found in the disturbed plots only, and needle bush (*Hakea sericea*) and arum lily (*Zantedeschia aethiopica*) were found in the undisturbed plots only.

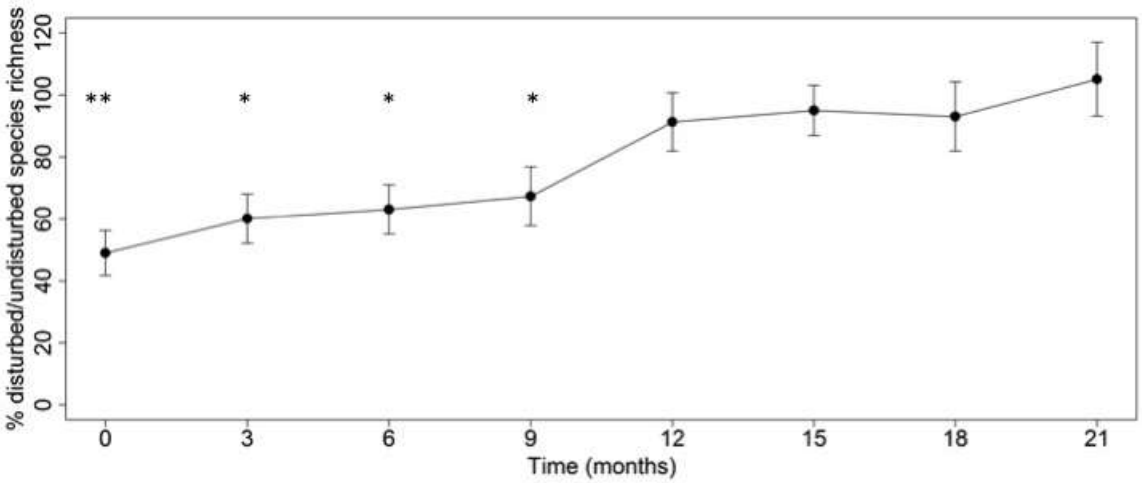

Figure 2.7 Species richness in the disturbed plots compared to the undisturbed (100%) over time following ground disturbance by pigs. * $P < 0.05$, ** $P < 0.001$.

2.3.5 Species composition

Due to the differences in canopy among some of the sites, the species composition analysis was performed using sites that shared a similar podocarp broadleaf canopy (n = 10). The majority of these sites had recovered at 18 months, therefore this analysis was carried out on the data up to and including 15 months. A one way ANOSIM showed a separation in species composition among the sites (R = 0.651, P = 0.001). A two way ANOSIM including site and time and showed a 'barely separable' pattern for time (*sensu* Clarke & Warwick 2005) (R = -0.04, P = 0.97). However, a two way ANOSIM with site and disturbance, showed a clear separation in the species composition among disturbed and undisturbed plots (R = 0.632, P = 0.001). A visual representation of the separation between disturbed and undisturbed plots is provided by an NMDS (Fig. 2.8).

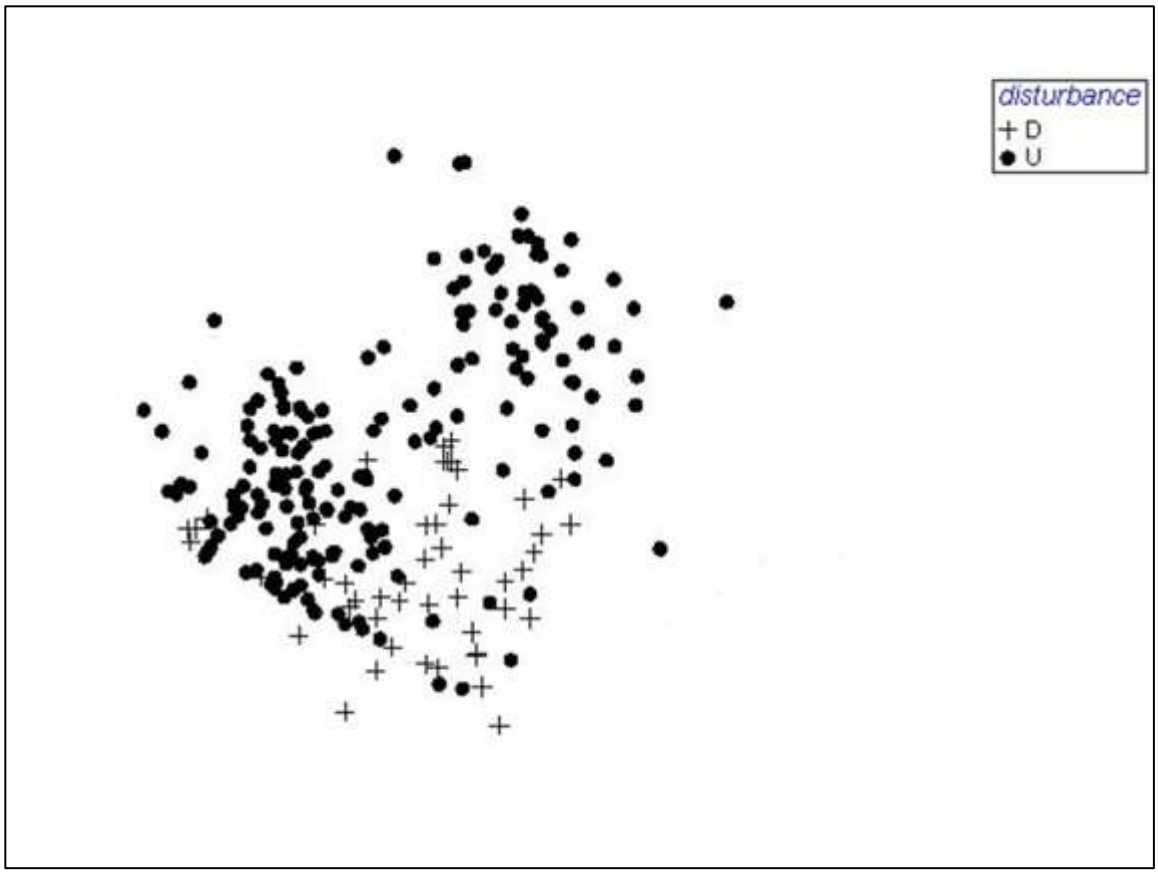

Figure 2.8 Plant seedling species assemblages in the disturbed (D) and undisturbed (U) plots in podocarp broadleaf forest. Calculated using Bray-Curtis dissimilarities with square-root transformed species abundance data. Stress value: 0.15.

A SIMPER analysis was then conducted, to determine which species were contributing to the dissimilarities between the groups. The species found to contribute 90% of the dissimilarity between the groups are shown in Table 2.2. Two groups of species are identified in Table 2.2: those species that recovered to greater densities in the disturbed plots than in the undisturbed at 15 months, and species that failed to recover in the disturbed plots. Rangiora (*Brachyglottis repanda*) returned to the disturbed areas most quickly post disturbance, and at 0 months was already at densities five times that seen in undisturbed plots. Unidentifiable cotyledons returned to disturbed plots almost immediately, and 3 months post disturbance the densities were eight times higher in the disturbed plots than in undisturbed plots. Hangehange *(Geniostoma rupestre)*, kanono (*Coprosma grandifolia*), akeake (*Dodonaea viscosa*), pigeon wood (*Hedycarya arborea*), kauri (*Agathis australis*), nikau (*Rhopalostylis sapida),* mahoe (*Melicytus ramiflorus*), lancewood (*Pseudopanax crassifolius*), kahikatea (*Dacrydium dacrydioides*) and mapou (*Myrsine australis*) were all quick to recover to undisturbed densities (within 3 months after disturbance) and at 15 months were all recorded in the disturbed plots at densities double (or more) those in the

undisturbed plots. Karamu (*Coprosma lucida*) took 15 months to recover to three times the undisturbed density. Supplejack (*Ripogonum scandens*) and rewarewa (*Knightia excelsa*) returned to the disturbed plots immediately but did not recover to undisturbed densities within the 15 months of this study. Rimu (*Dacrydium cupressinum*) and houhere (*Hoheria populnea*) took 3 months to return to disturbed plots and increased to greater densities than were observed in the undisturbed plots at 9 and 3 months (respectively), but subsequently declined in numbers and were not recorded in the disturbed plots at 12 or 15 months. Kanuka (*Kunzea ericoides*) returned to the pig disturbed plots at 15 months and only reached 30% of the density seen in the undisturbed plots. Mingimingi (*Leucopogon fasciculata*) did not return to disturbed plots.

A distance-based test for homogeneity of multivariate dispersions (PERMDISP; F_{244} = 11.52, P = 0.003) showed a significant difference in the dispersions of the disturbed and undisturbed groups, which combined with the nMDS (Fig. 2.7) indicates a greater variation in the species composition at undisturbed sites.

Table 2.2 Ratio of disturbed / undisturbed species density per m^2 shown over time. Grey highlighted species indicate species that recovered to greater densities than the undisturbed plots, while non-highlighted species indicate those species that did not recover to undisturbed densities.

	Time since ground disturbance by pigs (months)					
Species	**0**	**3**	**6**	**9**	**12**	**15**
Cotyledon	0.44	8.70	24.19	22.86	22.67	33.23
Geniostoma rupestre	0.47	1.82	1.55	1.30	4.00	15.38
Melicytus ramiflorus	0.00	1.52	0.00	1.78	1.78	6.40
Dodonaea viscosa	0.15	2.43	2.53	3.69	7.74	5.82
Coprosma grandifolia	0.41	2.62	3.81	4.31	3.48	5.16
Brachyglottis repanda	5.33	3.56	16.00	3.90	4.67	4.57
Pseudopanax crassifolius	0.38	1.98	1.42	2.51	3.39	4.40
Rhopalostylis sapida	0.65	2.77	2.39	2.34	3.63	3.35
Coprosma lucida	0.00	0.00	0.00	0.00	0.00	3.00
Agathis australis	0.29	1.23	1.45	4.00	2.67	2.00
Hedycarya arborea	0.26	1.12	1.30	1.63	1.89	2.67
Dacrycarpus dacrydioides	0.36	3.32	4.67	4.34	7.23	2.29
Myrsine australis	0.00	1.88	1.52	0.84	2.18	2.13
Ripogonum scandens	0.07	0.25	1.04	0.59	0.39	0.70
Knightia excelsa	0.06	0.66	0.56	0.00	0.84	0.59
Kunzea ericoides	0.00	0.00	0.00	0.00	0.00	0.26
Dacrydium cupressinum	0.00	0.27	0.30	1.12	0.00	0.00
Hoheria populnea	0.00	16.00	4.32	0.00	0.00	0.00
Leucopogon fasciculata	0.00	0.00	0.00	0.00	0.00	0.00

2.4 Discussion

As predicted, feral pigs significantly changed the soil nutrient availability. Plant available nitrate was higher in the disturbed plots by an order of magnitude. The area affected by pig ground disturbance was found to extend at least 1 m away from the actual disturbance area, in nutrient changes and decomposition effects. In experiments designed to simulate ground disturbance by pigs, Kotanen (1997) found nitrogen levels and decomposition differed between sites where soil excavation had taken place and where soil had been mounded up. This study noted that ground disturbance areas have an initial 'crater' where the pig has excavated the soil, immediately surrounded by an 'apron' (*sensu* (Merret et al. 2000) where this excavated soil has been moved to. This may explain the impacts of disturbance on soil nutrients and decomposition extending past the crater itself. Kotanen also found that nitrogen levels decreased with distance from the disturbed area, which may be due to leaching of these nutrients from the disturbance site into the surrounding area. Frank and Evans (1997) suggest that in the USA, native ungulate defecation and urination may contribute to elevated levels of nitrogen in pig accessible areas through the addition of ammonia, although Siemann et al. (2009) suggest elevated levels are the result of accelerated rates of nitrogen mineralization via the rapid integration of the original litter layer with the soil. Another study found that ground disturbance by pigs accelerated the leaching of minerals from the leaf litter, which then accelerated decomposition and altered the nutrient cycling (Singer et al. 1984). The decomposition process involves three stages. The first involves the leaching of chemicals from the plant leaf litter and colonization by fungi. The second stage involves further breakdown of the plant matter and debris via invertebrate consumption and deposition of finer particles (invertebrate faeces). This facilitates the third stage which involves further microbial decomposition and the incorporation of the debris into the humus layer of the soil (Schowalter 2000, Gullan and Cranston 2005). The rates and processes of this decomposition play a crucial role in the nitrogen and carbon cycle which in turn affects plant productivity and ecosystem function (Schowalter 2000, Bonkowski and Scheu 2004). Pigs may alter all of the stages of the decomposition process through their disturbance and the results from this study show an effect on the nitrogen cycle, which may have flow-on effects for plant growth. This may be especially detrimental in New Zealand temperate forest ecosystems that have evolved in the absence of biotic disturbance agents such as pigs, that turn over the soil to greater depths than large birds may have done in the past.

Litter cover and seedling abundance were drastically reduced after pig ground disturbance. Litter cover did not return to undisturbed levels in the time period of this study. However this could have been slowed somewhat by the exclosure cage, which would have impeded horizontal litter movement by the wind. Seedling density recovery for small seedlings (less than 15 cm in height)

in pig disturbed areas occurred in a relatively short time period (at 3 months) which may have been aided by the higher levels of plant available nitrate in the disturbed areas. Other studies have found that ground disturbance by pigs may create optimum seedbed conditions and remove competitors to enhance the recruitment of certain species to the disturbed site (Aplet et al. 1991, Siemann et al. 2009). However, it took much longer for larger seedlings (16–75 cm) to recover to undisturbed densities (18 months or more). This could have implications for forest structure. If an area is inhabited by a high density of feral pigs, it is unlikely that the area would be left to recover for more than 18 months (especially as pigs are known to return to the same site to forage and disturb the same area of ground more than once (Kotanen 1995)). Repeated disturbance could prevent seedling recruitment, therefore slowing and/or impeding the regeneration process. Bratton (1975) found similar results in the Great Smoky Mountains National Park with prolonged ground disturbance by pigs causing a drastic reduction in the percentage of mature flowering trees in the forest canopy. The results from the current study suggest that repeated disturbance at a location could have serious effects on plant assemblages, eventually leading to a lack of replacement of canopy trees.

This study showed a difference in plant species composition in the disturbed plots when compared with the undisturbed. Two groups of species were identified, those that increased to densities that were higher than the densities seen in the undisturbed plots and a second group that did not recover in the disturbed plots. This indicates that there are some species that may benefit from ground disturbance by pigs and dominate seedling recruitment in disturbed areas, at the cost of other species that are detrimentally affected by pig ground disturbance. One species (mingimingi) did not return to the disturbed plots throughout the study, which could indicate a local loss of this species if ground disturbance by pigs was to continue. No obvious pattern can be seen in the two groups of species; both groups contain wind dispersed and bird dispersed species, species from characteristically high and low fertility systems, and both light demanding and shade tolerant species. Although, it is possible that the species benefitting from ground disturbance by pigs are arising from the seed bank. Enright and Cameron (1988) state that only disturbance that clears litter cover and provides more light will stimulate seeds from the seed bank, and that a standard canopy gap from a tree fall often increases litter cover leading to existing seedlings comprising the recovery in these areas (the re-sprouting of damaged seedlings and increased growth of undamaged individuals). This suggests that the initial removal of litter cover by feral pigs and the slow recovery of vegetation cover may have contributed to the change in species composition at the disturbed sites. While previous studies have shown changes in species composition after continuing ground disturbance by pigs over an extended time period (Bratton 1975, Aplet et al. 1991, Siemann et al. 2009), this study has highlighted that compositional changes can take place after a single disturbance event.

This study also shows a short-term decline in species richness after ground disturbance by pigs. In Australia, Hone (2002) found that plant species richness in grassland decreased as pig rooting increased. This was supported by another study which showed a negative relationship between plant species richness and the extent of pig rooting, with plant richness declining to zero with extensive pig rooting (Hone 2002). Species richness data was variable in many studies, possibly explained by the intermediate disturbance hypothesis (Connell 1978). The Australian studies were conducted where pig ground disturbance rates were high and species had little time to recover (Hone and Martin 1998, Hone 2002), whereas other studies found an increase in species richness associated with intermediate levels of disturbance. Tierney and Cushman (2006) found a temporal difference in their data; species richness of native plants increased steadily through time following pig rooting, however, richness of exotic species recovered much more rapidly and persisted in pig-disturbed areas. Cushman et al. (2004) conducted a 4-year exclosure experiment in a coastal grassland community. They found that whilst disturbance by pigs increased the species richness of both native and exotic species, it also reduced the biomass of native and exotic species in different 'patches'. Cushman et al. (2004) concluded that the observed vegetation changes were due to space clearing via pigs, creating greater opportunities for colonization and reduced competition, and that ground disturbance by pigs therefore promoted the continued invasion of the habitat by exotic plants. The current study found no evidence of this, and found no significant difference in the weed cover between pig disturbed and undisturbed areas. Cushman et al (2004) and Tierney and Cushman (2006) conducted their studies in grassland communities over long periods with no pig exclusion from disturbed sites, whereas this study was conducted over 21 months following a single disturbance event, sites were inside established forest patches with closed canopies, lower light regimes and no nearby weed source. Therefore, pig facilitation of weeds at disturbance sites within temperate rainforests may be less likely.

It is possible that repeated ground disturbance and continued addition of nitrate could alter soil nutrients so drastically as to cause a major change in the forest canopy composition, shifting it toward an assemblage of species that benefit from pig ground disturbance. This could be of particular importance in ecosystems with characteristically nutrient poor soil and plant assemblages consisting of species evolved to tolerate these conditions. Bloomfield (1953) and Wyse et al. (2011) have shown that kauri (*Agathis australis*) considerably modify soil conditions in the forests where they are the dominant canopy tree, and, by increasing acidity and decreasing plant-available nutrients in this soil, facilitate the formation of unique plant assemblages tolerant of depressed nutrients. Increased availability of nitrate to this ecosystem through repeated disturbance by pigs could result in drastic changes in the nutrient regime in this forest type and

also trigger a change in plant assemblages. Kauri is an important canopy tree in the upper half of the North Island of New Zealand, and is a dominant canopy tree in the Waitakere Ranges, where this study was conducted, therefore the impact of feral pigs and prolonged nutrient addition to this ecosystem could have more severe and ecosystem-wide effects than in grassland and tropical ecosystems where the impacts of feral pigs have been previously studied.

This study shows that soil and seedling communities affected by pig ground disturbance can recover relatively quickly if protected from re-disturbance. Significant increases in decomposition and plant available nitrate may actually benefit short-term seedling recruitment. Seedling density was shown to recover within 18 months after ground disturbance by pigs, however the key to the recovery of these areas was the 18-month time period from the initial disturbance. It is recognized that pigs re-disturb areas after certain periods of time and may do this often (Kotanen 1995). Consequently, pig rooted areas may remain in a disturbed state if not protected, which could result in much higher levels of nitrate in the soil and a serious decline in the number of species and density of mature plants. Species composition was affected in the pig-disturbed areas with an increase of species that may benefit from ground disturbance by pigs. This could lead to ecosystem changes within forests with characteristically nutrient poor soils where there are repeated disturbance events occurring. Therefore, the control of pigs could be crucial in maintaining ecosystem processes, plant communities and structure in pig-disturbed areas. Land managers should seriously consider the implications of repeated disturbances on ecosystem processes and plant assemblages, and conduct appropriate pig control to manage pig numbers and reduce ground disturbance to acceptable rates.

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Chapter 3 – Absence of evidence is not evidence of absence: feral pigs as vectors of soil borne pathogens

Abstract

Invasive soil borne pathogens are a major threat to forest ecosystems worldwide. The newly discovered soil pathogen, *Phytophthora* 'taxon Agathis' (PTA) is a serious threat to endemic kauri (*Agathis australis*: Araucariaceae) in New Zealand. This study examined the potential for feral pigs to act as vectors of PTA. The research investigated whether snouts and trotters of feral pigs carry soil contaminated with PTA, and using these results determined the probability that feral pigs act as a vector. The soil on trotters and snouts from 457 pigs was screened for PTA, using various baiting techniques and molecular testing. The study detected 26 species of plant pathogens in the soil on pig trotters and snouts, including a different *Phytophthora* species (*P. cinnamomi*). However, no PTA was isolated from the samples. A positive control experiment showed a test sensitivity of 0-3% for the baiting methods and the data obtained were used in a Bayesian probability modelling approach. This showed a posterior probability of 35-90% (dependent on test sensitivity scores and design prevalence) that pigs do vector PTA, and estimated that a sample size of over 1000 trotters would be needed to prove a negative result. This research concluded that feral pigs cannot be ruled out as a vector of soil-based plant pathogens and that there is still a high probability that feral pigs do vector PTA, despite the negative results. This research also highlights the need to develop a more sensitive test for PTA in soils due to unreliable detection rates using the current method.

3.1 Introduction

Invasive species are a prominent threat to forest health worldwide through competition, predation, hybridization and disease transmission (Falk-Petersen et al. 2006, Hansen 2008). While invasive vertebrates and pest plants are a serious threat, many forests of the world are also being affected by microscopic soil-borne invaders (Hansen 2008). Microbes are generally understudied in invasion biology especially in natural ecosystems, perhaps due to their complex and cryptic life cycles. However, alien pathogens may impact communities and ecosystems by reducing species diversity, altering environmental conditions and modifying ecological processes (Chapin III et al. 2000, Gurevitch and Padilla 2004). Lodge (1993) has highlighted the importance of studying community interactions that determine invasion success, instead of studying communities or colonist species in isolation. This is of particular importance with soil borne pathogens, because assisted movement of soil borne disease is required for rapid spread over large distances, natural spread being slower and localized. Therefore, for effective management of invasive soil borne diseases, pathways of spread must be investigated.

Lockwood et al. (2007) split the invasion process into four stages, the first stage involves the transport of the invader to a new location, the second stage then involves invader establishment, and the third stage population increase and spread. These stages of invasion can be affected by a vector (Ruiz and Carlton 2003) which is defined as the conveyance that moves a non-native propagule to its novel location (Lockwood et al. 2007). Vectors may influence the number of individuals transferred to a new area and the number of transfer events initiated (related to propagule pressure) (Colautti et al. 2006). Faster transport may also improve the survivorship of the invader (Ruiz and Carlton 2003). The vector may also increase chances of establishment through targeted vectoring to an optimum environment (increasing niche opportunity) (Shea and Chesson 2002, Ruiz and Carlton 2003). Therefore understanding vector pathways is crucially important to adequate response and management of soil borne pathogen spread.

New Zealand's endemic kauri tree, *Agathis australis*, is the only member of its genus in New Zealand. Kauri is known to host two species of soil borne *Phytophthora* pathogens that cause ill health, *P. cinnamomi* (known to be invasive), and *Phytophthora* 'taxon Agathis' (PTA) (thought to be invasive) (Beever et al. 2009). *P. cinnamomi* is found widely in natural kauri stands and has been linked with some tree deaths, especially in poorly drained sites (Podger and Newhook 1971). PTA is now of greater concern to kauri health and has been spreading rapidly throughout the natural kauri range, causing canopy thinning, defoliation, large bleeding lesions on the lower trunk and eventual tree death (Beever et al. 2009). Based on the first report of this disease (Gadgil 1974) and subsequent recent work (Beever et al. 2009), distinctive symptoms exclusively

on kauri, rapid spread, and its similarity to *Phytophthora katsurae* (native to Taiwan), Beever et al. (2009) theorize that PTA was introduced to New Zealand.

The genus *Phytophthora* translates from Greek to mean 'plant destroyer'. Members of the genus *Phytophthora* are amongst the most serious threats to agriculture and cause devastating diseases in hundreds of plant hosts (Judelson and Blanco 2005). *Phytophthora* species have been studied extensively in agricultural systems, although little has been published on the effects and pathways of spread of these pathogens in natural forest habitats. *Phytophthora* species are eukaryotic, microscopic 'fungus like', soil borne organisms. They are taxonomically classified as oomycetes and owe much of their pathogenic success to the combination of asexual and sexual production of spores (Judelson and Blanco 2005). *Phytophthora* species persist in the soil and infected plant tissue, predominantly as dormant resting spores (oospores and clamydospores) but reproduce through the production of motile, biflagellate, infective zoospores (Wilcox 1992).

Phytophthora can be dispersed either in soil via water movement on the soil surface, or via the movement of soil by vectors, such as humans and other animals (Ristaino and Gumpertz 2000). Keast and Walsh (1979) found that *Phytophthora cinnamomi* could be successfully transported through the gastrointestinal tracts of termites (*Nasutitermes exitiosus*) and birds (*Pachycephala pectoralis* and *P. rufiventris*) in Australia. Similarly, Li et al. (2010) found that *P. cinnamomi* could survive gut passage in pigs and viable spores were excreted up to 7 days post ingestion. Kliejunas and Ko (1976) confirmed other vectors of *P. cinnamomi* when they isolated the pathogen from human boots, vehicle tires and also from the trotters of feral pigs (*Sus scrofa*). However, PTA is a newly discovered species and no previous work has been conducted on the potential vectors of this pathogen. Feral pigs have a known association with soil due to disturbance caused when foraging for plant parts, invertebrates and fungi below ground. This close association with soil and the relatively high abundance of feral pigs in the North Island of New Zealand (King 2005) makes them a suspect in the investigation and subsequent management of PTA vectors. Evidence of vectoring is required to justify the expensive and often controversial culling of feral pigs in northern New Zealand forests in order to manage the disease.

The aim of this research was to evaluate whether pigs vector PTA. More specifically, I investigated whether snouts and trotters of feral pigs carry soil infected with PTA by obtaining the trotters and snouts from culled pigs and screening for PTA in the associated soil. We then analysed these data in a Bayesian modelling framework to determine the probability that pigs vector PTA.

3.2 Methods

3.2.1 Pathogen detection in soil associated with pigs

The Auckland Council contracted hunters for pig culling operations in the Waitakere Ranges Regional Park, Auckland, New Zealand (extending from 36.53 to 37.03°S and from 174.27 to 174.34°E). In this area of podocarp/broadleaf dominated temperate rainforest pigs are present in substantial, but un-quantified numbers. No other mammalian ungulates are present. The culls started in October 2008 and occurred approximately every 3 months. Nine culling operations were sampled in total with the last cull sampled in August 2011. Where the pig kill was accessible, hunters collected one trotter chosen at random, and the snout of the culled pig. Each was stored separately in a labelled bag. The snout and trotter were then refrigerated (4˚C) for a maximum of 7 days until the soil sampling could take place.

Two different methods were used to extract the soil from the trotters; swabbing (based on Dance et al.'s (1975) methods of isolating *Phytophthora* species) and washing (aimed at optimising soil recovery from the trotters). Overall, 457 individual pigs were sampled, with 364 snouts sampled (snout presses), 189 trotter samples swabbed (swabbed trotters), and 268 trotter samples washed (washed trotters).

The snout samples were directly pressed onto an agar plate containing clarified V8 P_5ARPH agar (a selective media for *Phytophthora*, containing antibiotics and antifungals to select against bacteria and true fungi). The agar plates were incubated in the dark at 18–20°C and checked every two days for 10 days. Sub-cultures were taken of any *Phytophthora*-like growths, which were put onto a general PDA media to induce production of aerial mycelia. After incubation of these plates for 10 days, *Phytophthora*-like cultures were then DNA sequenced. DNA was extracted from the samples by scraping mycelia from the agar plates using a pipette tip. The pipette tip was then put into an eppendorf tube containing 420 µl of tissue extract buffer and 4.2 µl protease K enzyme from the Corbette robot DNA purification kit. After a 30 second vortex, the tubes were incubated at 56ºC for one hour, and centrifuged at 16 000 rpm for 3 minutes. 220 µl of the supernatant was removed and loaded onto X-tractor Gene robot (Qiagen) for DNA extraction).The robot was run according to manufacturer's instructions (Qiagen). The ITS gene was targeted for amplification using ITS6 (Cooke and Duncan 1997) and ITS4 (White et al. 1990). Successful amplifications were then confirmed by running the PCR products on a 1.5% agarose gel stained with ethidium bromide at 150 V for 30 minutes. A sequencing PCR reaction was then completed and the completed reaction was then cleaned using Applied Biosystem's Big Dye Xterminator purification kit and loaded onto an ABI Genetic Analyser 3031XL, sequencing

machine (Applied Biosystems). Sequencing results were compared against GenBank using BLAST search for identification.

For the swabbed trotters, soil was swabbed from them using sterile cotton buds. The soil was swabbed into a sterile petri dish; any hair on the trotter matted with soil was also shaved into the dish using a scalpel blade. The petri dishes were then sealed to keep in any moisture and were stored at 10°C until baiting was ready to commence. To isolate *Phytophthora* from a soil sample the soil has to be flooded with water and 'baited' with plant tissue to induce the production of infective motile zoospores. Baiting involved a variation of the needle baiting technique used by Dance et al. (1975) which was developed as the national standard operating procedure by three separate Crown Research Institutes in New Zealand during the National Kauri Dieback Biosecurity Response (Beever et al. 2010). Collected and stored soil (from the swabbing method) was macerated within the petri dishes to eliminate clumps, and then air-dried for 2 days. These samples were then spray-moistened with reverse osmosis (RO) water, until the soil surface was shiny. They were left for an hour and then re-sprayed to target any clods of soil. They were left for a further 4 days at room temperature to stimulate any *Phytophthora* oospores. After 4 days, the soil was transferred to a 600 ml container, flooded with RO water and immediately baited using lupine radicles (*Lupinus* spp.) and Himalayan cedar (*Cedrus deodara*) needles which were floated on the water's surface. The baited samples were incubated for 2 days at 20°C. After incubation, the bait tissues were removed and rinsed in sterile RO water. They were then transferred to a 70% ethanol solution for 30 seconds and rinsed in sterile RO water for a second time. The bait tissues were blotted dry with a paper towel and placed onto clarified V8 P_5ARPH agar plates. All plates were incubated at 18°C for 10 days. After 10 days of incubation any growths that looked similar to *Phytophthora* mycelia were then subsampled to clarified V8 P_5ARPH to obtain a pure culture and then onto PDA media. These were incubated again at 18°C for 10 days and then DNA sequenced (using the methods previously described) to obtain a species level identification. Fungal by-catch on plates was identified by light microscopy where possible.

For the washed trotters, each trotter was placed in a separate plastic container with approximately 270 ml of RO water. The trotter was then washed of all soil, until the hair was as clean as possible. The water in each container was then baited immediately using the above methods.

3.2.2 Sensitivity testing

To assess the ability of the techniques used to detect PTA, a positive control experiment was undertaken, testing all the techniques used. PTA (sourced from the Landcare Research ICMP culture collection) was grown on PDA (potato dextrose agar) media at 20ºC. From the growing

edge of cultures, 6.5 mm-diameter plugs of agar were placed into clarified V8 juice broth and incubated at 20ºC for 56 days. PTA was harvested from the V8 (vegetable) juice broth and macerated in a Waring Blender for 20 seconds. Viable oospore numbers were estimated by staining with a 0.1% solution of tetrazolium chloride. The oospore solution was then assessed using a haemocytometer to estimate viable oospore numbers. The solution used for the positive control was calculated to have approximately two hundred and fifty thousand viable oospores per ml. This concentration is thought to be 100 times higher than naturally present in soil (Bellgard. Pers. Comm.). Sterilised soil was sieved to remove any large clumps. Then 66 600 ml containers were filled with 100 g of the sieved sterilised soil with 10 ml of the oospore suspension and 20 ml of sterile RO water and thoroughly mixed. A separate container was used for each pig sample; 66 trotters and 40 snouts were used, which had been sterilised using 95% ethanol. Each sample was pushed into soil spiked with PTA to simulate a pig stepping in, or rooting in, infected soil. The samples were then refrigerated for 7 days. The snout samples were then pressed onto clarified V8 PARPH plates. Thirty-three trotter samples were washed and baited; the remaining 33 samples were swabbed following the methods above.

3.2.3 Analysis of pig vectoring probabilities

To calculate the probability of feral pigs carrying PTA, a Bayesian probability model was constructed using the test sensitivity data and expert prior probabilities. The analysis calculates the probability of PTA being present given a negative test.

This research aimed to establish the probability that pigs carry PTA given that all the tests are negative ($[PTA^+|Tests^-]$). Using Bayes theorem the following equation is obtained:

$$[PTA^+|Tests^-] = (1 - SeGroup) \times [PTA^+] / ((1-SeGroup) \times [PTA^+] + (1 - [PTA^+]))$$

$[PTA^+]$ denotes the *prior* probability that pigs carry PTA, (what was perceived before the study was conducted). This was set at 90% based on pigs known association with soil through their natural foraging behaviour, anecdotal evidence of extensive ground disturbance by pigs under infected kauri trees in the Waitakere Ranges and Kliejunas and Ko (1976) and Li (2010) who found that pigs vector *P. cinnamomi* in Hawaii and Australia.

SeGroup is the sample group sensitivity which is calculated using:

$$SeGroup = 1 - (1 - SeTest \times P^*)^n$$

SeTest is the test sensitivity data from the positive control tests and *n* is the number of pig samples tested. P* is the design prevalence, the minimum prevalence detected. For this value, expert opinions were elicited following Kuhnert et al.'s (2010) guidelines where possible. Twenty

six experts were asked to contribute their opinion, of which twenty two replied. They were asked; 'in their opinion what was the probability that any snout or trotter collected in the Waitakere Ranges would carry PTA'. The experts were split into groups according to occupations and research interest with means created for each group. These groups included mycologists (*n* = 4), pig hunters (*n* = 3), land managers (*n* = 13) and ecologists (*n* = 3).

The variability of the results was explored using the differing *SeTest* values from the test sensitivity experiments and also the range of means for design prevalence from the different groups of experts.

3.3 Results

3.3.1 Pathogen detection in soil associated with pigs

A number of oomycete and fungal species were isolated from the soil carried on pig trotters and snouts (Table 3.1). Many of these species were 'by-catch' as the methods used were optimized to isolate *Phytophthora* species from soil samples and to select against true fungi (through the use of specific antifungals in the media). Therefore the percentages of trotters carrying these pathogens are not presented as it would provide a false representation of the prevalence of these pathogens. Whilst a related species of *Phytophthora (P. cinnamomi*) was found and 25 other plant pathogens, PTA was not isolated from the soil collected from the trotters or snouts.

Table 3.1 Microbial species isolated from soil associated with trotters and snouts of feral pigs.

Species	**Reported plant pathogen**	**Trotter /or snout**	**Isolation method**
Acremonium spp.	Y	T and S	S and W
Actinomucor spp.	N	T	W
Alternaria alternata	Y	T	S and W
Aureobasidium pullulans	N	T and S	S and W
Bacterium spp.	Y/N	T	S
Botryotinia fuckeliana	Y	T	W

Chaetomium spp.	Y	S	P
Cladosporium cladosporiodes	N	T and S	S and W
Cylindrocarpon destructans	Y	T	S
Cylindrocarpon spp.	Y	T	W
Fusarium lateritium	Y	T	W
Fusarium oxysporum	Y	T	W
Fusarium solani	Y	T	W
Gibberella spp.	Y	T	W
Gliocladium roseum	N	T	S
Mortierella alpina	N	T	W
Mortierella elongata	N	T	W
Mortierella gamsii	N	T and S	P and W
Mortierella minutissima	N	T	W
Motieriella spp.	N	T and S	P and W
Mucor spp.1	N	T and S	S and W
Mucor spp.2	N	T and S	S and W
Paecilomyces spp.	N	T	W
Penicillium spp.1	Y/N	T and S	P
Penicillium spp.2	Y/N	T and S	S and W
Phialophora spp.	Y	T	S

Phytophthora cinnamomi	Y	T	W
Pythium diclinum	Y	T	W
Pythium helicandrum	Y	T	W
Pythium heterothallicum	Y	T	W
Pythium spp.	Y	T	W
Pythium torulosum	Y	S	P
Pythium tracheiphilum	Y	T	W
Pythium vexans	Y	T	W
Rhizopus oryzae	Y	T and S	S and W
Rhodotorula spp.	N	T	S
Sclerotinia spp.	Y	T	W
Trichoderma hamatum	N	T	S
Trichoderma spp.	N	T and S	S and W
Verticillium spp.	Y	T	S
Yeast spp. 1	N	T and S	S and W
Yeast spp. 2	N	T and S	S and W
Yeast spp. 3	N	T and S	S and W

Species isolated from a trotter (T) or snout (S)

Method of soil isolation: washing (W), swabbing (S) or pressing (P)

Status as a plant pathogen: Y=yes, N=no, Y/N=yes or no dependent on differing species

3.3.2 Sensitivity testing

PTA was detected from 3% of the trotters (*n* = 33) that were pushed into soil spiked with known concentrations of PTA oospores and then washed and baited. No PTA was detected from the swabbed trotters (*n* = 33) pushed into PTA-positive soil or when snouts were pressed into the PTA-positive soil (*n* = 40) and then pressed directly onto agar.

3.3.3 Analysis of pig vectoring probabilities

The expert opinion means were variable between occupational groups (Table 3.2). The expert opinion of pigs as vectors from the 'managers' was the highest and the 'ecologists' the lowest. The overall mean of all 22 expert opinions was 0.26, which may be used as a reasonable estimate of design prevalence.

Table 3.2 Mean and standard error of expert prior opinions for each occupational group

Occupational group	**Mean**	**Standard Error**	**(*n*)**
Overall mean	0.26	0.0597	22
Ecologists	0.05	0.0282	3
Hunters	0.20	0.20	3
Managers	0.35	0.079	13
Mycologists	0.23	0.160	4

The posterior value of the Bayesian model varies greatly depending on the sample size of pigs tested, the test sensitivity and also design prevalence (expert opinion) values (Fig. 3.1 and 3.2). Using a test sensitivity value of 0 for the swabbed trotters and pressed snouts yields a constant posterior probability of 0.90 for any number of pigs tested (this is based on the original prior probability of 0.90) therefore these tests were not displayed in Fig 3.1. With a test sensitivity of 0.03 (268 washed trotters) there is between 0.35 and a 0.86 posterior probability that pigs carry PTA depending on the expert prior opinion used.

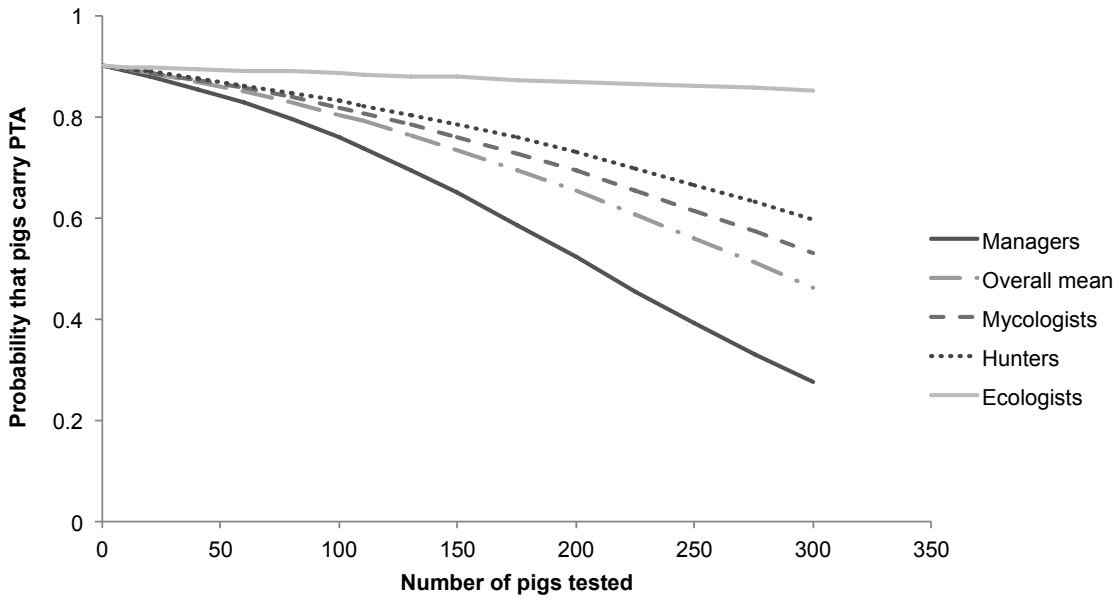

Figure 3.1 Bayesian analysis based on a *SeTest* value of 0.03 for different design prevalence values based on expert group opinion. Overall prior probability was set at 0.90.

With a design prevalence based on the overall mean of the expert opinions there is a 53% probability that feral pigs vector PTA using the washed trotters, and a 90% probability for the swabbed trotters and pressed snouts. Extrapolations of the data used in Fig. 3.1 show that a sample size of over 1000 pigs would have been needed to reduce the probability of pigs carrying PTA to zero. These data show that the greater the test sensitivity values the lower the probability of pigs as vectors of PTA (more confidence that there is no type II error) (Fig 3.1). Larger sample sizes also lower the probability of pigs as vectors of PTA as a larger proportion of the pig population has been sampled (Fig 3.2). Larger design prevalence (expert opinion) values also lower the probability of pigs vectoring PTA as this value contributes to group sensitivity value (*SeGroup*) value (Fig. 3.1 and 3.2).

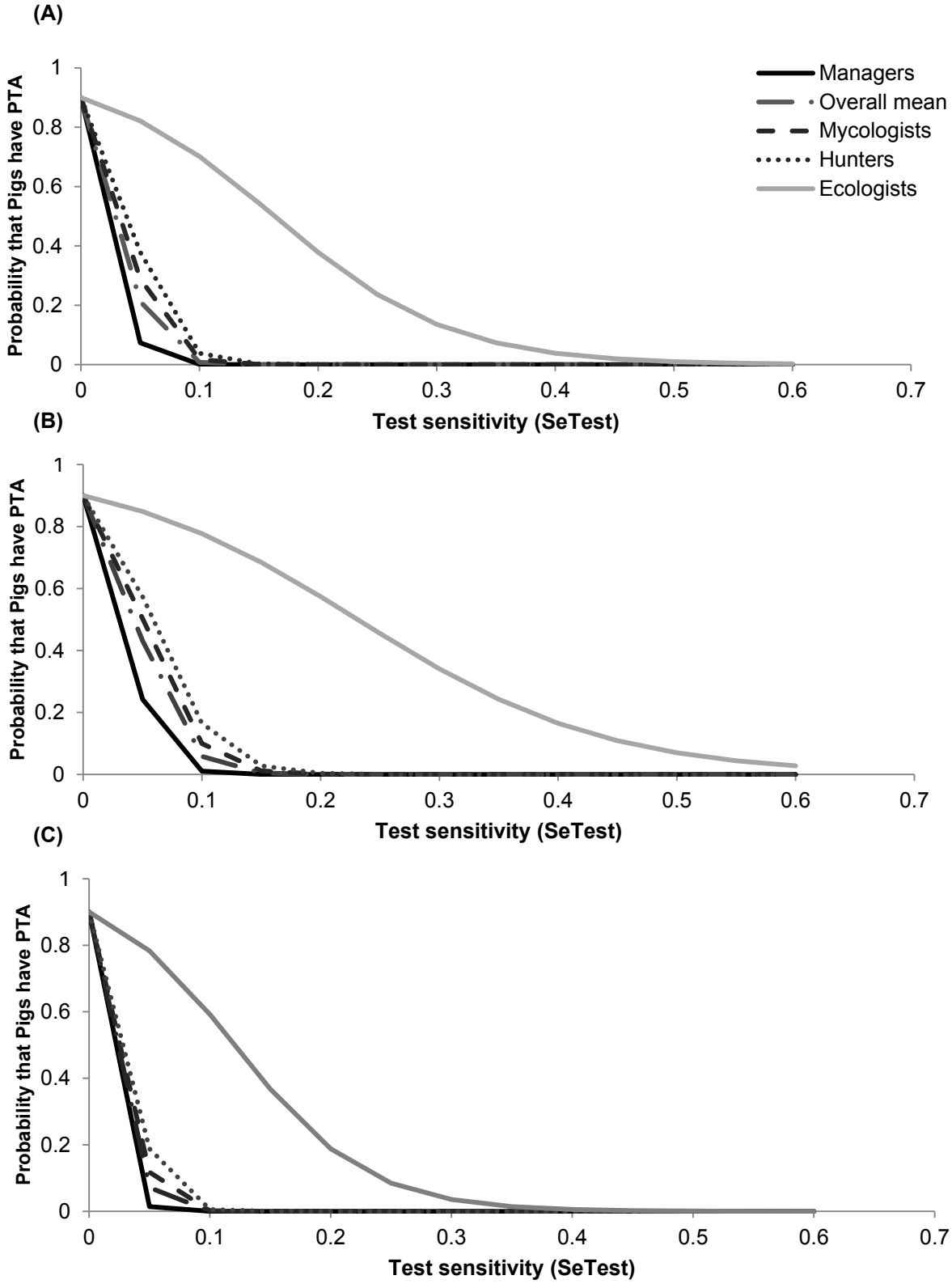

Figure 3.2 Bayesian analysis based on a sample size of (A) 268 washed trotters (B) 189 swabbed trotters, (C) 364 pressed snouts with differing design prevalence values based on expert prior opinion.

3.4 Discussion

This research has shown that feral pigs are a potential vector of a large number of soil borne plant pathogens. Twenty six species of known plant pathogens were found on the trotters and snouts of feral pigs, some of which are particularly aggressive (e.g. *Sclerotinia, Fusarium,* and *Botrytis*). Several plant pathogenic oomycete species including, *Pythium heterothallicum* and *P. vexans,* were identified and further demonstrated proof-of-concept that soil borne spores of disease agents can be routinely vectored by feral pigs in forests. For example, *Pythium vexans* has been previously associated with plant decline and diseases in forest ecosystems in Australia, China, Hawaii and North Carolina (Kliejunas and Ko 1975, Vawdrey et al. 2005, Zeng et al. 2005, Ivors et al. 2008). The method used in this study was not optimized for collecting genera other than *Phytophthora*, and many more fungi may have been found using other methods of isolation. Many species of invertebrates are known vectors of plant pathogens (Evans 1973, El-Hamalawi and Menge 1996, Louis et al. 1996, Nault 1997), but few studies have investigated vertebrates as vectors. Feral pigs should be of particular interest due to their foraging habits and transport of soil. Therefore more targeted research into the extent of the role feral pigs play in vectoring would benefit the understanding of vector pathways of other plant diseases.

Whilst no PTA was found in the soil associated with the pigs sampled, *Phytophthora cinnamomi* was isolated from the soil collected from a pig trotter which confirms the results of Kliejunas and Ko (1976) and Li (2010). *P. cinnamomi* is found widely in natural kauri stands and has been linked with tree mortality, especially in poorly drained sites (Podger and Newhook 1971). *P. cinnamomi* has also been linked with seedling mortality in nursery beds (Newhook and Podger 1972) and has been found in both regenerating and mature kauri (Beever et al. 2009). However, Beever et al. (2009) also conclude that *P. cinnamomi* plays a minor role in the health of adult kauri, and that at some sites abnormal conditions may lead to disease.

Opinions from a variety of experts were elicited to gain a representation of the varying opinions on pigs as vectors of PTA. Expert opinions elicited in the Bayesian modelling process varied widely and managers made considerably higher estimates than ecologists. The ecologist, mycologist and hunter groups also had higher variance in their estimates than the managers. The hunter and manager groups may have been influenced more by the politics of the pig hunting (and the hunters' desire to continue hunting), whereas the ecologist and mycologist groups may have focused more on the complexities of the question asked.

The Bayesian modelling shows the importance of developing a sensitive test to isolate PTA. A test sensitivity of 0.2 would have increased the ability to reject pigs as a vector of PTA. However

given the current test sensitivity, a sample size of over 1000 pigs would be needed to prove a negative result. The results from modelling the current values for test sensitivity and design prevalence estimate that there is a 35–90% probability that pigs may be a vector of PTA despite no evidence of an association with the disease. The test used in the isolation of PTA is the national standard operating procedure (SOP) developed by three Crown Research Institutes in New Zealand during the National Kauri Dieback Biosecurity Response and is based on widely accepted methods of isolating *Phytophthora* species (Dance et al. 1975, Beever et al. 2010). A test sensitivity of between 0 and 3% renders the SOP unreliable when applied to small soil samples from culled pigs. On that basis this study has serious implications for the biosecurity response for this organism that involve pig management. A recent report has calculated and compared PTA detection probabilities between the three Crown Research institutes currently using the standard baiting SOP. These probabilities ranged between 0.22–0.56 when testing 200 grams of soil from around kauri trees known to be infected with PTA (Beauchamp 2011). At best, PTA can only be detected in the soil directly below infected trees, one out of every two times it is tested. As soil samples from the pigs were between 0.5–5 grams, a decline in test sensitivity was expected, although not to the extent shown here. There is also a possibility that the low detectability of PTA within soil samples may be attributed to logistical impediments, such as; transportation of the samples, their storage and also a delay in processing time between collection and baiting.

Studies have shown unequivocally that PTA is present in the soil around kauri trees, and that this disease is killing kauri (Beever et al. 2009, Beever et al. 2010, Dick and Bellgard 2010, Bellgard et al. 2011). The association of pigs with soil is clear through their natural behaviour of rooting (below ground foraging). Observational evidence has also recorded feral pigs rooting beneath infected kauri; Hill and Davies (Unpublished) note 98 occurrences of pig rooting below known PTA-infected trees. This research also discovered that soil naturally adheres to pig's trotters and snouts with approximately 0.5–5 grams of soil collected from each sample. I therefore conclude that, although this study failed to detect PTA, there is still a possibility that PTA was present in the soil samples from the pig snouts and trotters, and that the test methods used failed to detect it. Other studies have also failed to detect PTA from likely sources including a survey of *Phytophthora* species within streams in catchments with infected kauri stands (Randall 2011) and also a survey of soil carried on human boots that had walked around infected trees (Pau'uvale 2011). No detection probabilities were calculated for these studies, although the results highlighted here could suggest that there is a chance that these studies may also have failed to detect the presence of PTA that was present. On that basis it cannot currently be ruled out that PTA may be carried in soil on human boots, pig trotters and in stream water. PTA has spread quickly throughout the North Island of New Zealand since the first record on the mainland

(previously only found on Great Barrier Island) was noted in 2007 (Beever et al. 2009). If indeed pigs, humans and water are not the vectors of PTA, then what could be the mechanism for spread of this organism over large distances (further than neighbouring trees)? It is important to develop improved methods for isolating PTA with higher test sensitivities. Managing the spread of this disease is critical to preserving the kauri forests of the North Island, and to do this the vectors of this disease must be established. *Phytophthora* species are notoriously difficult to isolate from soil (Tsao 1990, Davidson and Tay 2005), although Davidson and Tay (2005) isolated *P. cinnamomi* from 100% of their positive controls, in comparison to 0–3% in this study. It may be that PTA zoospores are not adequately attracted to the lupin and cedar needles being used for bait, or that there is a structural difference with PTA spores (as yet unknown) causing the difficulty with isolation. Therefore I conclude that optimization of the baiting technique needs to be conducted and serological or DNA test methods should also be pursued as an alternative to baiting when isolating PTA.

Feral pigs may also enhance the susceptibility of kauri trees to the PTA disease indirectly through disturbance. Diseases are recognized to attack weakened systems; Schoeneweiss (1975) states that any disturbance may predispose plants to disease. Therefore regardless of whether pigs are vectors of PTA, they may facilitate the establishment of this disease through the disturbance they cause around kauri root zones. Kauri ill health is known to occur when their root zones are compromised, even without PTA (Sando 1936). Ground disturbance by pigs around these root zones could also lead to the destruction of the pūkahukahu (mound of decaying litter surrounding the base of the tree) and destroy any beneficial mycorrizhal associations. Pig introduction of foreign bacteria and other plant pathogens could also compromise kauri health, making PTA infection more likely.

Feral pigs cannot be discounted as a vector of PTA. Although this study failed to isolate PTA from the soil associated with pigs, the sensitivity of the test used made this an unreliable method. Bayesian modelling showed a 35–90% chance that pigs may vector PTA. Future research should focus on developing an appropriate test to isolate PTA from soil, with reliable test sensitivities, before vectors of PTA are investigated. Therefore, continued culling to reduce pig densities is recommended due to: the seriousness of the PTA disease and its implications on the health and survivorship of kauri forests, the close association of feral pigs with soil, their potential to spread this disease, the unknown effects disturbance around kauri root zones has on the risk of PTA infection, and the numerous plant pathogens associated with soil carried by pigs. Furthermore, pig management might be targeted in areas free of PTA infection to halt disease spread and protect disease-free areas of forest.

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Chapter 4 − The effects of feral pig control on pig density and ground disturbance.

Abstract

To assess the success of an invasive species management program, the efficiency and effectiveness of the program must be quantified. This is often measured as the number of animals removed in a control operation and the efficiency with which this is achieved. However, management programs should also measure success as a reduction in negative impacts, which should be the ultimate goal of management. This study describes a three-year pig-culling program in the Waitakere Ranges Regional Park, Auckland, New Zealand, and determines its effects on pig density and the extent of pig ground disturbance (impact). The pig-culling program was initiated in August 2008 and ran for 3 years; all pig kills and hunter hours were recorded. Over this period, pig ground disturbance was monitored over twenty-three 200m transects located throughout the Ranges and change in percentage disturbance along each transect calculated through time. Cumulative kills through time were modelled using simple regression. The relationship between ground disturbance and time was also modelled using regression. These models were used to estimate the number of days required to reduce ground disturbance to zero and the projected cumulative kills to achieve this. This projected kill was interpreted as a reasonable estimate of the pre culling pig population, and used as an estimate of ecological carrying capacity (*K*). A logistic population model was used to project changes in pig density over the course of the study and change in ground disturbance by pigs evaluated against this. Percentage ground disturbance data shows that certain areas of the Waitakere Ranges were highly disturbed by feral pigs. These areas were more likely to be terraces (flat topography next to watercourses) than other topographic features. The mean estimate of pig density (at *K*) was 8.23 ± 0.70 pigs/km^2 for the Waitakere Ranges, which was comparable to equivalent environments in other studies. The population trajectory across the culling program showed an initial reduction in the pig population and ground disturbance, which then levelled off. This is consistent with later removals of pigs balancing the rate of population recovery. This study shows the effectiveness of a pig-culling program in reducing ground disturbance over a short period of time, especially in areas where ground disturbance was particularly high and the associated impacts may have been severe. However, both pig density and the reduction in pig ground disturbance have levelled off and an increase in hunter effort in the Waitakere Ranges is probably needed to further reduce these management outcomes.

4.1 Introduction

The type of management used to reduce the impact of an invasive species may differ at each stage of the invasion process (Grice 2009). Eradication is generally only feasible prior to the naturalization phase, or for small isolated populations (Grice 2009). Therefore, once naturalization has taken place and range expansion has occurred, sustained control may be the only option available to land managers (Grice 2009). Grice (2000) defines a strategic approach to managing invasive species as the temporal and spatial distribution of effort that achieves a specified reduction in impacts at the least cost. Therefore, any management program must be both effective and efficient. To be effective, a management program will reduce a population to a target level, or limit its impacts to an acceptable degree. To be efficient, a management program will achieve this with the least amount of cost (in time and resources).

Feral pigs are a widespread invasive species in many countries (Singer et al. 1984, Coblentz and Baber 1987, Hone 1988, Katahira et al. 1993, Pinet and Brun 2004, Engeman et al. 2007, Parkes et al. 2010) including New Zealand (Wodzicki 1950, Thomson and Challies 1988, King 2005). Feral pigs were released by colonists on mainland New Zealand in the 1700s (Clarke and Dzieciolowski 1991) and are now regarded as a valuable hunting resource and a cultural food for Māori (Nugent et al. 1996). This makes assessing the benefits of pig control in reducing the negative impacts of pigs of key importance to local councils and land managers in combatting the negative perception of pig control in New Zealand.

Assessment of the efficiency and effectiveness of many management programs is evaluated as the number of invasive animals removed and the time or cost taken to achieve this. However, another (and arguably more important) factor in the assessment of management effectiveness, relates to the success of reducing the impact of the invasive species (Clayton & Cowan 2010). When controlling invasive species there is often an assumption that there is a positive relationship between the number of pests and the damage that they cause (Hone 2007). Although, the impact of an invasive species can be related to population density in a number of ways (Yokomizo et al. 2009). Yokomizo et al. (2009) propose three nonlinear forms that a density-impact curve may take (Fig. 4.1). Curve I is a low impact threshold curve, where the impact remains high until the population is reduced to low densities. In contrast, curve IV is a high impact threshold curve, where the impact remains low until populations approach high densities. In curve II, impact increases rapidly at intermediate population densities, and curve III demonstrates a proportional relationship between density and impact (Yokomizo et al. 2009). Many management programs explicitly assume that any reduction in invasive species density will achieve a reduction in invasive species impacts without measuring or even observing this

outcome (Reddiex et al. 2006, Yokomizo et al. 2009, Clayton and Cowan 2010). However, depending on the density-impact relationship, impacts may not be reduced by any given reduction in pest density, or may vary depending on whether initial pest density is high, low or intermediate (e.g. curve II Fig. 4.1).

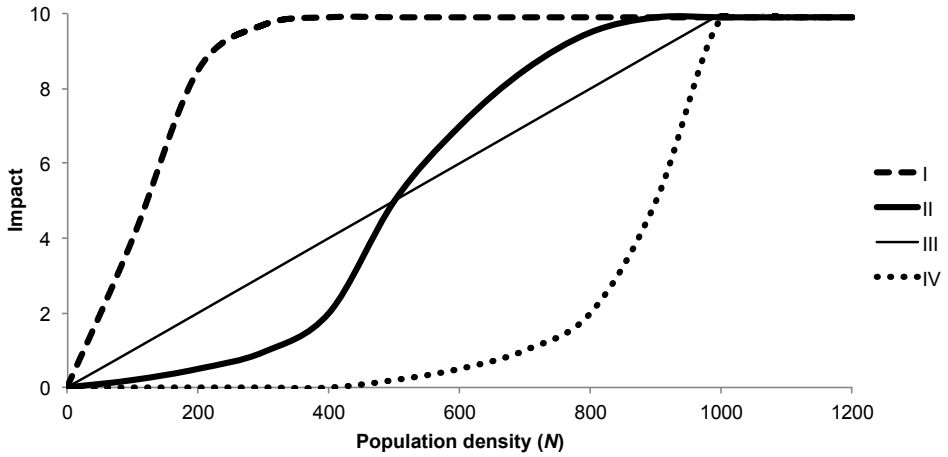


Figure 4.1 Density-impact curves (Yokomizo et al. 2009), demonstrating four different relationships between population density and impact.

Understanding the form of the relationship between invasive species density and impact is therefore of key importance in developing or evaluating pest control strategies. The benefit of invasive pig control, in terms of impact reduction, has been quantified by Choquenot et al. (1997) by relating a decrease in pig density with an increase in the percentage of pregnant ewes successfully rearing lambs in Australia. Feral pigs have also been shown to have a wide range of impacts on native environments in New Zealand through ground disturbance, which causes a reduction in understory plant species abundance and diversity, changes in species composition and disruption of ecosystem processes (Chapter 2). Therefore a common aim of the management of feral pigs in conservation settings is to reduce the extent of pig ground disturbance and thereby minimise impacts on the ecosystem (http:/www.biosecurityperformance.af.govt.nz/, accessed 12 February 2012).

Hone (1996, 2007) reviewed a number of studies relating feral pig ground disturbance and pig abundance, with support for a linear relationships in the majority of studies, although some studies found ground disturbance by pigs was curvilinearly related to ground disturbance. The extent of disturbance is related to invasive species abundance, food/resource availability and landscape features (Hone 2007). This suggests that the relationship between pig ground

disturbance and pig abundance may vary with habitat and above ground food availability. Modelling by Hone (1988) predicted that ground disturbance by feral pigs is negatively related to vegetation (above-ground food) abundance and therefore the extent of disturbance may be curvilinearly related to feral pig density, suggesting that some threshold pig density will coincide with reduced above ground food availability and a consequent increase in below ground foraging leading to ground disturbance. An empirical study by Hone (2002) found that the relationship between ground disturbance and frequency of pig dung (an index of feral pig abundance) was curvilinear and concave (similar to curve I Fig. 4.1) with a rapid increase in disturbance at low pig abundance. This could be related to depletion of above ground food availability, driving feral pigs to forage below ground at a low pig abundance threshold. This also implies that a small reduction in the pig population would not yield a substantial decrease in cumulative ground disturbance. However, in areas where above ground food is more freely available, the threshold pig abundance driving below ground foraging behaviour could be higher, shifting the threshold for ground disturbance to higher pig densities (i.e. more similar to curve IV Fig. 4.1). Under these circumstances, the relationship would imply that small reductions in pig density could result in large reductions in ground disturbance by pigs. However, if pig abundance is proportionally related to ground disturbance, and above ground food availability is supplemented by the same per capita rate of below ground foraging at all pig population levels, a decrease in pig abundance will yield a proportional decrease in ground disturbance (Hone 2007).This underpins the importance of assessing the relationship between pig abundance and ground disturbance, and that the assumption that impacts will be reduced by any reduction in pig density is not necessarily correct.

This study describes a large-scale pig-culling program undertaken in the Waitakere Ranges Regional Park over the course of three years, and analyses its effects on pig density and the extent of ground disturbance (impact) caused by pigs. The implications for the effectiveness of the program are discussed.

4.2 Methods

4.2.1 Study site

The Waitakere Ranges in Auckland, New Zealand, is a regional park managed by Auckland Council. It is over 16 000 ha, extending from 36.53 to 37.03°S and from 174.27 to 174.34°E, ranging in altitude between 0–474m above sea level. In this area of podocarp/broadleaf dominated temperate rainforest (Wardle 1991), pigs are present in substantial, but previously un-

quantified numbers. Pig hunting is illegal in the Waitakere Ranges and therefore any pig mortality due to un-official hunting should be low.

As the Auckland Council was conducting culling throughout the Waitakere Ranges, there was no opportunity for a replicated 'non culling' control site for this study. Therefore, we assume that in the absence of culling, the feral pig population in the Waitakere Ranges would settle at an approximately stable carrying capacity and any dynamics that the population displayed after culling was initiated was in response to the culling program. This is an appropriate assumption as the climate in this area is reasonably stable and food resources are available year-round (Thomson and Challies 1988). Therefore these factors are unlikely to destabilise the feral pig carrying capacity.

4.2.2 Pig culls

The Waitakere Ranges were split into three hunting blocks of approximately equal size (block 1= 6258 ha, block 2=5504 ha, block 3=5591 ha). Teams of professional hunters were selected by application and assigned a hunting block. The first cull was initiated in August 2008 and there was approximately 6 months between the next two culls after which culling operations were completed every season (3 months). The last cull included in this study culminated in August 2011, with a total of 9 culling operations over the course of the study. Each hunting team returned to the same hunting block for each cull. Although, a different hunting team was used in hunting block 2 for the fourth cull due to the unavailability of the original hunters.

Hunting was carried out on foot by hunters with teams of dogs; kills were preferably made with a knife although in cases where dogs were in danger, firearms were used. Hunter hours, number of kills per day, and kill locations were recorded.

Cumulative kill was calculated for each hunting block over the entire study period, the relationship between cumulative kill and time (days) was modelled using both a linear regression and polynomial regression. This relationship was expected to be curvilinear, because the relationship between pig density and kill rate was expected to take the form of a functional response, as observed in predator-prey theory (Hone 1994). Other studies have demonstrated this relationship for a range of culling methods applied to a number of pest species including pigs (Choquenot 1988, Ridpath and Waithman 1988, Hone 1994, Maas 1997, Choquenot et al. 1999). The functional response hypothesises that as prey (pigs) are progressively removed from a system, they become harder to find and catch, and predator (hunter) search time consequently increases leading to a reduction in kill rate. If the relationship between kill rate and pig density took the form of a functional response, cumulative kill over time should level off once pig densities equivalent to reduced kill rate are achieved (Choquenot et al. 1999).

4.2.3 Ground disturbance

Transects were established to monitor pig ground disturbance prior to culling operations in 2008. The Waitakere Ranges were split into 2.8 km^2 blocks and a transect was established in the centre of each block. Twenty three 200-m transects were established throughout the Ranges. These transects were monitored four times over the course of this study. The first monitoring round took place in November 2008, the second in September 2009, the third in December 2010 and the last in August 2011. Monitoring these transects involved walking the length of the transect line and measuring the extent and age of any pig ground disturbance encountered up to 1m on either side of the line. No other mammalian ungulates are found in the Waitakere Ranges, so disturbance patches are clearly linked to feral pigs. Disturbance age was assessed using established photo standards to classify into fresh, medium and old disturbance. The soil in fresh disturbance was characterised as bare (free of leaf litter) and still damp, medium aged disturbance was differentiated by the presence of substantial amounts of leaf litter, and old disturbance by the presence of litter and small seedlings. Every 10 m along the transect a number of environmental variables were also recorded: canopy type; physiography; and drainage. Drainage was assessed as good medium or poor using using Hurst and Allen (2007). A site is described as having good drainage when runoff is fast and little accumulation of water occurs after rain; moderate drainage when runoff is slow and water accumulation in hollows occurs for several days after rain; and poor drainage where water stands for extended periods. Canopy type was classified using the dominant canopy species in the area (podocarp-broadleaf, broadleaf-regenerating and mature broadleaf) (Wardle 1991) and physiography classed as ridge (including spurs), incline, gully or terrace (Hurst and Allen 2007).

To examine the ground disturbance data at a coarse scale, the proportion of ground disturbance (new, medium or old) along each transect was calculated for each monitoring period. For a finer scale analysis, transects were split into 5 cm lengths and the age of the disturbance in each length (if any) was noted for each monitoring period. Ground disturbance over time was then modelled, using linear and polynomial regressions between ground disturbance and time (days), as this relationship was also expected to be non-linear (Hone 1988).

To test for correlations between the environmental variables and the extent of ground disturbance, the transect data from the first monitoring period (before the onset of culling) in the most highly disturbed transects (n = 7) were used. These transects were selected as they contain most of the useful data on ground disturbance. An arcsine transformation was performed on the

proportion of ground disturbance along each transect, which was then used in correlated with each environmental variable.

4.2.4 Projecting changes in pig density over the culling program

Pre-culling density estimates were obtained for each hunting block, and for the Waitakere Ranges as a whole, using projections based on the regression models fitted to changes in ground disturbance and cumulative pig kills over the course of the culling program. The model describing change in ground disturbance for each hunting block over time was used to estimate days to zero ground disturbance. These estimates were then applied to the regression models describing cumulative kill for each hunting block over time in order to estimate the theoretical kill that would need to be achieved to reduce ground disturbance to zero. Assuming that ground disturbance would decline to zero only when all pigs were eliminated from a hunting block, these estimates provide a plausible measure of the size of populations inhabiting each hunting block prior to the commencement of culling, and a reasonable basis for estimating pre-culling density. The implications of this assumption are explored in the discussion.

Changes in pig density over the course of the culling program for each hunting block were projected from a simple logistic population model. The model accounted for the removals made within each block, assuming that pre-culling density estimates were a good estimate of pig density at carrying capacity (K) and assuming the intrinsic rate of increase for pig populations in the Waitakere Ranges was 0.8 (Choquenot et al. 1996). Using these calculations the trajectory of the projected pig population increase and decrease in each hunting block was modelled over the course of the pig culling operation. The mean total ground disturbance was calculated from all transects present within each block and compared with reductions in pig density.

4.3 Results

4.3.1 Pig culls

Polynomial regressions were fitted to the relationship between time and cumulative kill for each block to test for curvilinearity in the relationship. No polynomial coefficients were statistically significant; therefore linear regressions were fitted to describe the relationship (Table 4.1).

Table 4.1 Summary of linear regressions of cumulative kill through time for each hunting block.

	Intercept	Slope	R^2	*F*-value	*df*	*P*-value
Block 1	37.92	0.307	0.988	582.71	7	<0.001
Block 2	57.18	0.227	0.977	295.72	7	<0.001
Block 3	30.42	0.233	0.982	381.21	7	<0.001

4.3.2 Ground disturbance

Ground disturbance in 2008 was concentrated on a small proportion of transects (Fig. 4.2) (mean total ground disturbance 3.7% ± 1.4). After the onset of culling (2009), ground disturbance still tended to be concentrated on the same transects, although it increased on some of the previously less disturbed or undisturbed transects (Fig. 4.2) (3.7% ± 1.2). By 2010 ground disturbance was reduced over most of the transects, including the heavily disturbed areas (1.5% ± 0.5), and in 2011 there were slightly higher levels of ground disturbance in some heavily disturbed areas (e.g. transects B and C) but ground disturbance levels stayed reasonably similar to the previous monitoring period (1.4% ± 0.5).

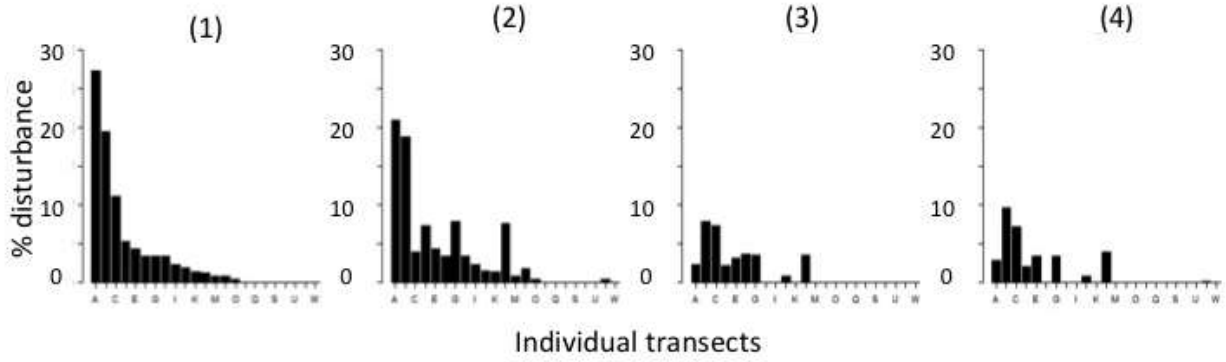


Figure 4.2 Percentage ground disturbance along individual transects (ordered from most disturbed to least disturbed in 2008, the order was then repeated for each year) in monitoring round (1) 2008, (2) 2009, (3), 2010, and (4) 2011.

Polynomial regressions were fitted to the relationship between time and overall ground disturbance for each block to test for curvilinearity. There was no statistical support for any of the polynomial coefficients, therefore linear regressions were fitted to this relationship (Table 4.2).

Table 4.2 Summary of linear regressions on pig ground disturbance through time for each hunting block.

	Intercept	**Slope**	**R^2**	***F*-value**	***df***	***P*-value**
Block 1	0.062	4.90×10^{-5}	0.805	2.72	2	0.103
Block 2	0.033	-1.70×10^{-5}	0.807	8.37	2	0.102
Block 3	0.018	-8.84×10^{-6}	0.209	0.53	2	0.543

The prevalence of pig ground disturbance on the seven most disturbed transects at the commencement of the study (see (1) in Fig. 4.2) was correlated with some topographical variables. There was a strong positive correlation between pig ground disturbance and terrace topography (flat areas next to watercourses). There were also negative correlations between ground disturbance by pigs and ridges and gullies although these relationships were non-significant at the 5% level (*P* values = 0.12 and 0.14 respectively). There was also a strong correlation between ground disturbance by pigs and litter cover (Table 4.3).

Table 4.3 Correlation coefficients between the proportion of ground disturbed and environmental variables for the seven most disturbed transects at the commencement of the study (df = 5).

Variable	**Correlation coefficient**
Ridge	-0.64
Gully	-0.61
Incline	-0.31
Terrace	0.79*
Good drainage	-0.23
Medium drainage	0.19
Poor drainage	-0.21
Podocarp broadleaf canopy	0.25
Mature broadleaf canopy	0.22
Regenerating broadleaf canopy	-0.42
Litter cover	0.85*

*$P<0.05$

4.3.3 Projecting changes in pig density over the culling program

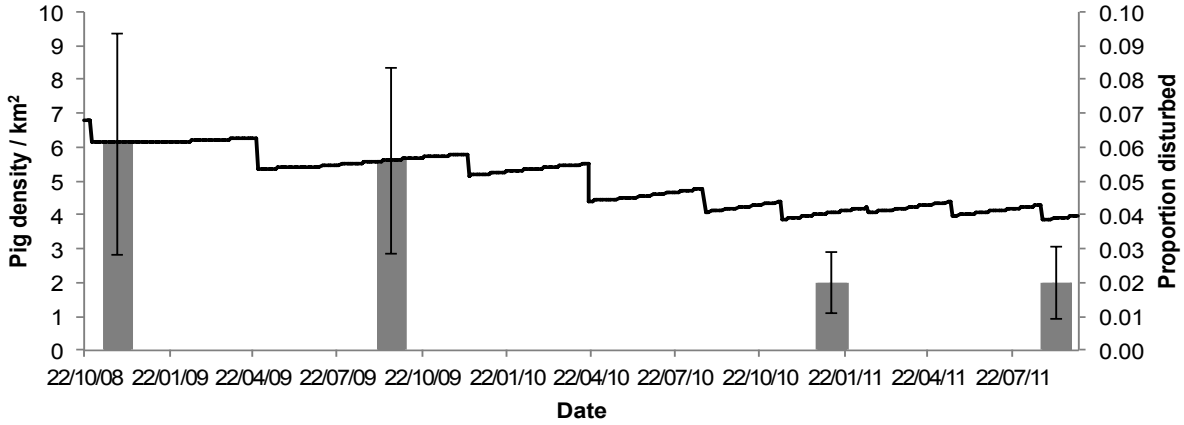
Pre culling population estimates obtained by projecting the number of days until zero ground disturbance in each block, indicated a total feral pig population size in the Waitakere Ranges of 1427 animals (sum of all blocks) (Table 4.4). This equates to a mean population density of 8.23 ± 0.70 pigs/km^2. Pre culling population density estimates for individual hunting blocks were assumed to be unbiased estimates of *K*, and used as a basis for projecting changes in pig density for each block over the course of the culling program (Fig. 4.3). Projected changes in population density indicate that for all hunting blocks an initial reduction in pig density was followed by a levelling off. This suggests that following initial reductions, hunting teams were extracting a sustainable yield of pigs rather than achieving any further reduction in underlying population density.

Changes in mean proportion of ground disturbance by pigs follow a similar pattern of initial reduction followed by a levelling off. Mean pig ground disturbance stayed the same in the last two monitoring periods for all blocks (Fig. 4.3).

Table 4.4 Summary of the days required to reduce pig ground disturbance to zero and the corresponding predicted pre-culling pig population and pre and post-culling density estimates

	Days	**Pigs**	**Initial pig density (pigs/km^2)**	**Post culling pig density (pigs/km^2)**
Block 1	1265	426.3	6.8	3.9
Block 2	1927	494.6	8.9	6.7
Block 3	2036	505.8	9	6.9
Mean ± SE	1742.7 ± 241.2	475.6 ± 24.9	8.23 ± 0.70	5.8 ± 0.97

(1)



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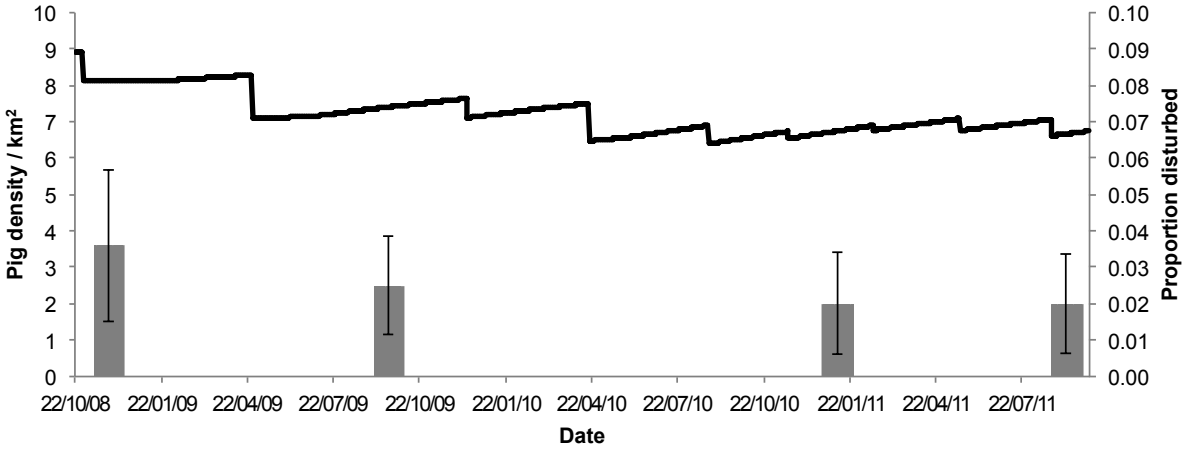

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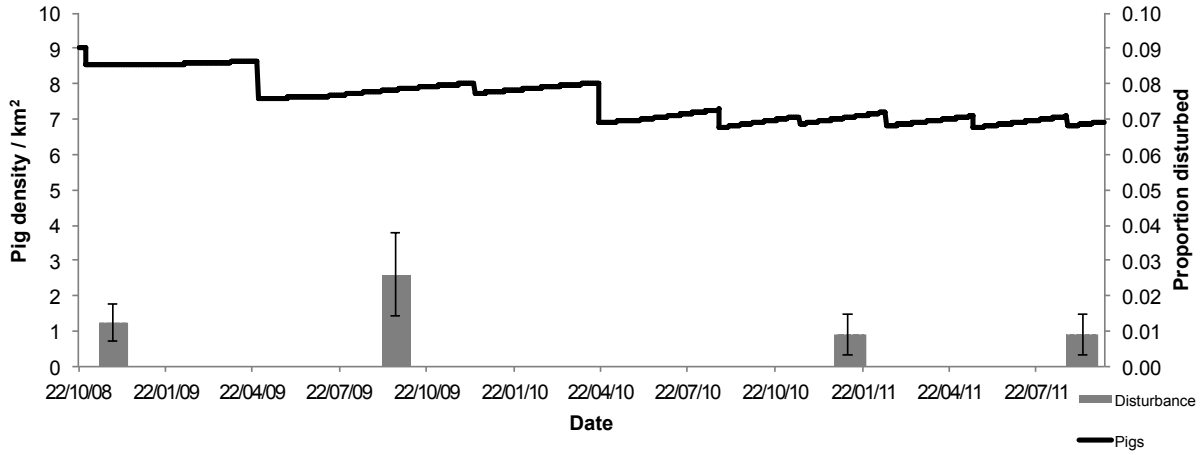


Figure 4.3 Change in modelled pig population densities and observed mean pig ground disturbance (±SE) for each hunting block (1, 2 and 3), throughout the pig-culling operation.

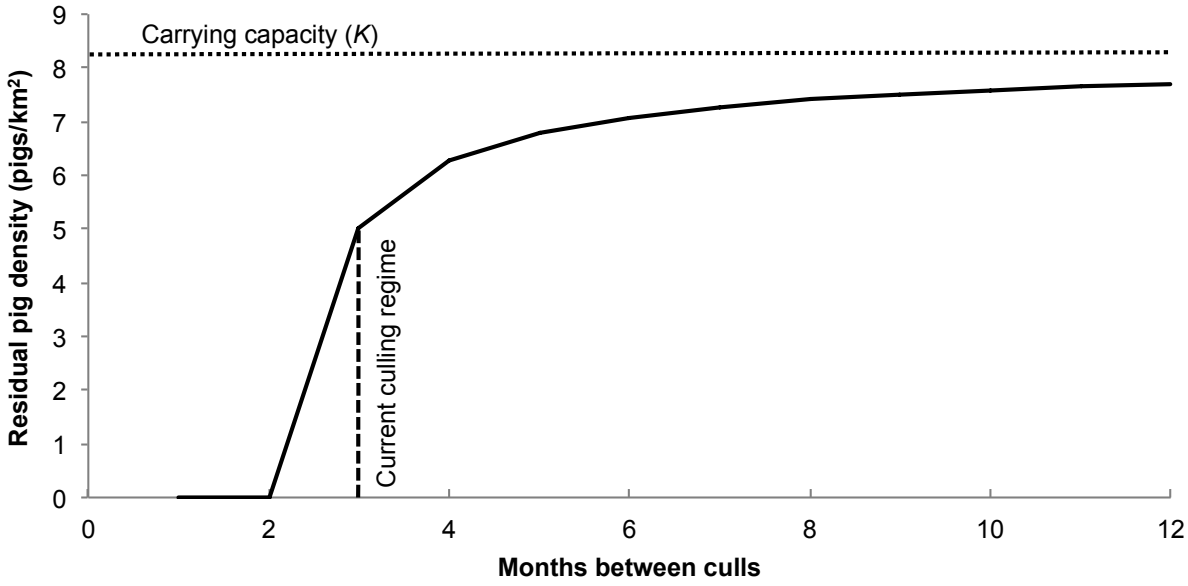
4.4 Discussion

4.4.1 The effect of the culling program on pig density

The assessment of the effectiveness of the culling operation in the Waitakere Ranges suggests that it did not reduce the feral pig population substantially, instead holding it at densities yielding high recruitment, which effectively saturated hunting effort. This conclusion is consistent with the linear increase in cumulative kills observed over time for all hunting blocks, hunting teams being apparently unable to reduce pig density to levels where hunting efficiency declined. Choquenot et al. (1999) found that for helicopter shooting in Australian floodplains, hours per kill increased exponentially at low pig densities, implying that hunting efficiency reduced rapidly below some threshold density. This would result in an asymptotic decline in cumulative kills over time once reduction below this threshold density was achieved.

To explore why the culling program had limited effectiveness on the population, the generalized population model described above was used to predict the average residual pig densities following 10 years of culling, where culling was undertaken every 1–12 months. The generalised model used the average estimate of *K* from across hunting blocks (8.23 pigs/km^2), and a culling effectiveness of 0.37 kills/km^2, which was the mean density of kills in the last four culls undertaken. The last four culls were used to derive average culling effectiveness because these were undertaken quarterly and over a shorter timeframe than earlier culls. The relationship between culling interval and residual pig density is shown in Fig. 4.4 (A). All culling regimes reduced pig density below *K*. However, substantial reductions in pig density were not achieved until the interval between culling sessions reduced below 6 months (twice a year), accelerating to effective extinction for intervals of 1–2 months (12 and 6 times a year, respectively). The existing regime for the Waitakere Ranges (3 month interval, 4 culls each year) produced a residual pig density of 5.1 pigs/km^2, comparable to the average estimated post culling population density of 5.8 pigs/km^2. Fig. 4.4(B) shows population productivity (*rN*) predicted by the generalised model used to estimate residual pig densities as a function of underlying pig density. This figure predicts that at a residual pig density of 5.1 pigs/km^2, the Waitakere Ranges population would yield 1.54 pigs/km^2 through recruitment. The current culling regime for this population comprises 4 culling sessions, averaging 0.37 kills/km^2 effectiveness, or an annual removal of 1.48 pigs/km^2. This supports the contention that the current culling effort is saturated by recruitment and will not achieve further reductions in the density of the underlying pig populations without an increase in frequency or effectiveness.

(A)



(B)

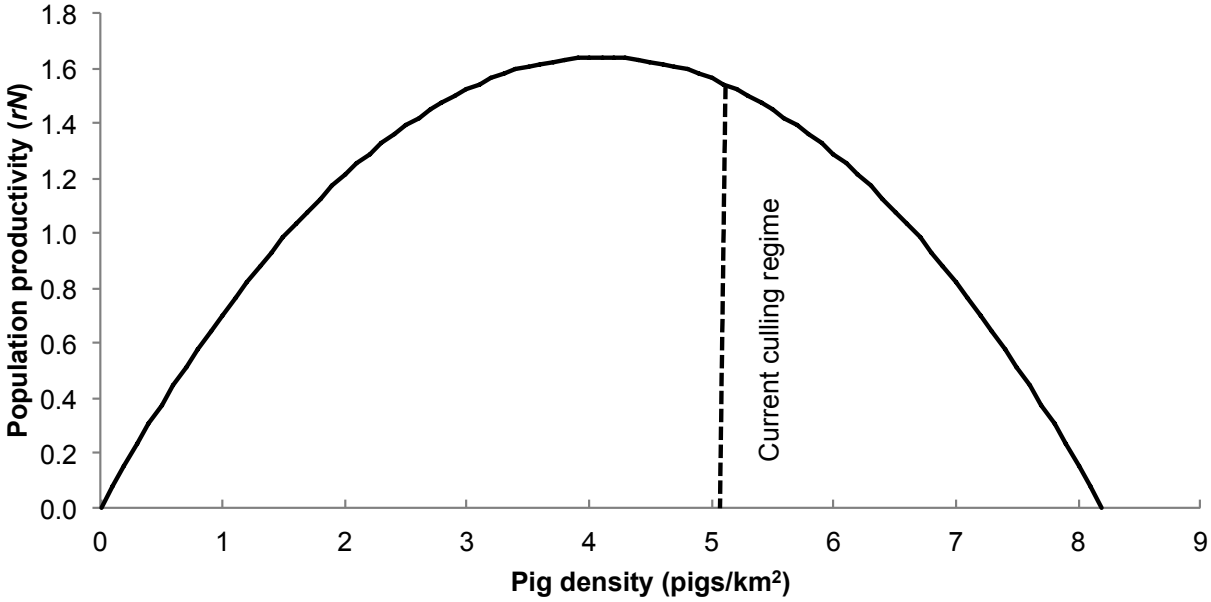


Figure 4.4 (A) Changes in residual pig density (pigs/km^2) when culled at different time intervals for 10 years, (B) population productivity at differing pig densities. The current culling regime is holding pig density at 5.01 pigs/km^2, which is below 8.23 pigs/km^2 (*K*)

4.4.2 The effect of the culling program on ground disturbance

A review of studies by Hone (2007) found evidence for both linear and curvilinear relationships between ground disturbance and pig abundance. A prediction that ground disturbance would be curvilinearly related to pig abundance, with disturbance being proportionally higher at high pig density due to increased competition for above ground food resources would imply that the extent of ground disturbance over the course of this culling program should have declined at a progressively slower rate as the pig population was reduced below *K*. However, polynomial regression analysis did not support a curvilinear decline in ground disturbance over time for this culling program, and linear models were fitted instead. This may be related to the use of overall ground disturbance (relating to the total proportion of disturbed ground), instead of new ground disturbance (relating to newly disturbed ground that occurred during a defined time period). Using the total proportion of ground disturbed may mean that the residual ground disturbance from earlier time periods (and therefore earlier pig population levels) are masking the relationship.

Continuing to monitor ground disturbance as the culling program continues or hunting effort increased should be undertaken to obtain more accurate estimates of pre cull pig density. Although for management purposes, the current pig density figures give an approximation of pig numbers in the Waitakere Ranges and a measure of the difference in pig density between the hunting blocks. The estimates also provide valuable information about the effort required to reduce pig numbers further and to continue to reduce levels of ground disturbance. The average pig density estimates calculated in this study (8.23 pigs/km^2) are similar to those from studies conducted in comparable environments. Singer (1981) calculated pig density at 7.6–9.2 pigs/km^2 in North Carolina, a study in California estimated a density of 5–8 pigs/km^2 (Barrett 1978), and a density of 10 pigs/km^2 was calculated for Australian marshes (Saunders and Bryant 1988) and 6.13 pigs/km^2 in Australian floodplains (Hone 1990). These estimates are lower than 21–34 pigs/km^2 observed on Santa Catalina Island (Baber and Coblentz 1986), and higher than those calculated for other habitats such as; 1 pig /km^2 in a woodland environment in South-East Australia (Hone 1988), and a density of 0.8 pig /km^2 in Hawaii (Katahira et al. 1993). However, feral pigs in a New Zealand forest have been reported to gain their highest proportion of food from above ground sources and at least one third of their diet from fallen fruit (Thomson and Challies 1988) which indicates that this habitat could plausibly support a density of 8.23 pigs/km^2 at carrying capacity.

It is clear from the coarse analysis of the disturbance transects that hunting achieved an initial reduction in pig ground disturbance. Ground disturbance was substantially reduced within the first year of the culling program in the Waitakere Ranges, and this was most prominent in some heavily disturbed transects that had previously been the most highly disturbed by feral pigs.

Before the start of the culling program, pigs were disturbing ~30% of the most disturbed transects. Some of these locations were maintained in a state of frequent disturbance (with the highest levels of re-disturbance in the Waitakere Ranges). These locations were of particular concern due to the impacts feral pig ground disturbance could be having on biodiversity and ecosystem processes. Ground disturbance has been shown to reduce plant species abundance and diversity with a disruption to understory structure (Chapter 2). A change in plant species composition was also observed, and it is likely that high levels of continued feral pig re-disturbance could cause major changes in the canopy tree species assemblage (Chapter 2). Therefore it is of great importance that the high levels of ground disturbance in these areas have been reduced through the implementation of a pig-culling program.

Pig ground disturbance in the Waitakere Ranges was patchy and certain areas were frequently re-disturbed. This indicated that there might be some non-random factor or factors that influenced the spatial pattern in ground disturbance by pigs. In Australia, Mitchell et al. (2007) reported most feral pig ground disturbance occurred in swamp and creek habitats, Hone (1988) recorded a positive correlation between ground disturbance by pigs and altitude, and Hone (2002) found most ground disturbance by pigs was associated with drainage lines on level ground. This study found similar results and ground disturbance was positively correlated with terrace topography (flat areas of ground next to watercourses). Ground disturbance by pigs is likely controlled by their ability to disturb the ground which is related to the penetration resistance of the soil (Hone 1988, Choquenot and Parkes 2005), and productivity of the soil ecosystem. Wet soils are generally less compacted (have lower penetration resistance) than drier soils, and have higher productivity (Wardle 2002). Terraces next to watercourses were mostly damp areas, which may have aided the pigs' ability to disturb the soil, or attracted pigs to them. Topography is likely also correlated with the presence of certain vegetation types, which may influence disturbance. The canopy type classification used in this study when assessing vegetation may have been too broad to appropriately assess any correlations with disturbance; however, observations from terraced areas noted a dominance of kahikatea (*Dacrycarpus dacrydioides*), nikau (*Rhopalostylis sapida*) and *Coprosma* species. Correlating the incidence of ground disturbance by pigs with certain topographic variables could have implications for management. For example, land managers could target ground disturbance monitoring at terrace sites but avoid steep inclines and ridges.

This study has demonstrated the relationship between pig density and impact (ground disturbance). It provides estimates of the density of feral pigs in the Waitakere Ranges, which are critical for answering management questions, and has also shown the initial effectiveness of a pig-culling program to reduce feral pig ground disturbance, after which, pig numbers and ground

disturbance have been maintained but no further reductions have been achieved. This highlights the need for a reassessment of the hunting effort used in the culling program in the Waitakere Ranges if a continued reduction in the feral pig population (and ground disturbance) is desired. The management aim to reduce feral pig ground disturbance has been achieved to some degree, however further reductions could be made if effectiveness could be improved by increasing effort or employing different control methods. An assessment of the cost-benefit ratio of increasing hunting effort in the Waitakere Ranges is required to make further management decisions on the benefit of reducing ground disturbance to lower levels.

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Chapter 5 – Modelling changes in pig populations and ground disturbance

Abstract

Reducing the impact of invasive species on native biodiversity is the most common goal in invasive species management. However, monitoring management outcomes is crucial in determining if this goal has been achieved. High rates of feral pig ground disturbance are linked with increased biodiversity impacts. Therefore, to achieve positive biodiversity outcomes feral pig management should focus on reducing ground disturbance rather than feral pig abundance. This study parameterises a model created by Choquenot and Parkes (2005) with data from a feral pig management program conducted in the Waitakere Ranges. The model links pig ground disturbance rates to pig density and is used to simulate different management scenarios and predict their effect on reducing ground disturbance. The model is used to provide management recommendations for pig control in the Waitakere Ranges by identifying the management scenarios that would be most effective and efficient in reducing pig ground disturbance. Two versions of the model were constructed for comparison, a fixed frequency culling model and a monitor-based culling model. The fixed frequency culling model triggered culls after a fixed time period (3, 6, 9 or 12 months) whereas the monitor-based culling model conducted monitoring after a fixed time period (3 months) but only initiated culling if the proportion of ground disturbance was greater than a specified trigger value (0.05, 0.10, 0.15, 0.20). The fixed frequency culling model showed an equilibrium point between ground disturbance and ground recovery at a pig density of 7.25 pigs/km^2, ground disturbance increasing when pig density was above this level. Triggering control based on time periods longer than 3 months allowed recovery of pig densities above the equilibrium level and therefore proportions of ground disturbance increased. Ground disturbance was consistently reduced when triggering control based on proportion ground disturbed (monitor-based control model). Although, the costs of these scenarios were higher than fixed frequency culling, because of the additional cost of measuring ground disturbance. The models predict that reductions in ground disturbance can be achieved through reasonably modest reductions in pig density. However, monitoring ground disturbance (outcome monitoring) is crucial to ensure the success of control programs in achieving management goals. Despite higher costs, a monitor-based culling regime is recommended for the continued management of feral pigs in the Waitakere Ranges as it would guarantee a reduction in ground disturbance, which is the overall management goal.

5.1 Introduction

An increasing amount of invasive species management is conducted with the goal of reducing impacts on native biodiversity (Reddiex et al. 2006, Clayton and Cowan 2010). However, evaluating the results of management interventions and whether or not their goal has been reached requires monitoring (Choquenot et al. 1996). Monitoring can be approached by assessing changes in pest populations as the of end-result of control ('operational monitoring') or through some estimate of the effectiveness of the control for protecting biodiversity ('outcome monitoring') (Choquenot et al. 1996). As the ultimate goal of many control programs is focused on positive biodiversity outcomes, then the monitoring strategy employed should be similarly focused, advocating the inclusion of outcome monitoring. Recent studies have highlighted the lack of outcome monitoring in a large proportion of control programs in Australia and New Zealand (Reddiex et al. 2006, Clayton and Cowan 2010), despite the importance of monitoring in evaluating a control program's effectiveness. A review of feral pig control in Australia revealed that the main objectives for pig control were habitat conservation followed by threatened species protection (Reddiex et al. 2006). However, in 75% of the pig control programs surveyed by Reddiex et al. (2006) no operational or outcome monitoring was conducted.

The negative impacts of feral pigs on biodiversity and ecosystem functioning can be related to feral pig ground disturbance. In Australia, ground disturbance has been shown to impact biodiversity by changing vegetation communities (Mitchell and Mayer 1997, Hone 1999, Mitchell et al. 2007). Similar impacts have been observed in India and the United States (Bratton 1975, Singer et al. 1981, Sekhar 1998, Engeman et al. 2007) and in this study, ground disturbance altered both below ground ecosystem processes and above ground vegetation structure and communities (Chapter 2). Regular and extensive feral pig ground disturbance could cause major changes to the interactions between above and below ground communities, and lead to a change in forest composition and structure (Bratton 1975, Chapter 2). More frequent ground disturbance may lead to a higher chance of feral pigs vectoring soil borne pathogens and an increase in the incidence of plant disease (Chapter 3). Therefore if eradication of feral pigs is not possible, the maintenance of these ecosystems in their present form will rely on sustained feral pig control and monitoring.

This necessitates a shift to management programs that focus on reducing feral pig ground disturbance, rather than feral pig numbers *per se*. Many pig control regimes rely only on assessments of 'indices of relative abundance' before and after control programs to determine pig densities, or have implemented 'set and forget' management where pig culls are initiated after a certain time period. These regimes often assume ground disturbance (or other impacts) have been reduced without explicitly monitoring this (Choquenot et al. 1996, Reddiex et al. 2006). It has been proposed that future management strategies

may focus on setting feral pig ground disturbance thresholds to trigger control, thereby maintaining ground disturbance at an acceptable level (Choquenot and Parkes 2001). Ideally any management strategy would also focus on benefit maximisation or cost minimisation (Choquenot and Parkes 2001) by achieving the greatest reduction in biodiversity impacts for available resources or some specified level of impact reduction at the lowest cost. Models allow these considerations to be evaluated and the most effective management strategy to be determined.

Choquenot and Parkes (2005) developed a model that relates pig ground disturbance levels with pig abundance. This study parameterises the Choquenot and Parkes (2005) model using data from a feral pig management program in a temperate rainforest in the Waitakere Ranges, Auckland, New Zealand. The study explores the relationship between pig abundance and disturbance in the Waitakere Ranges and identifies the most cost effective and beneficial control strategies for reducing ground disturbance. Some management recommendations are drawn from these results.

5.2 Methods

5.2.1 Pig abundance and ground disturbance

This study used a deterministic model of feral pig ground disturbance developed by Choquenot and Parkes (2005), which has not been previously parameterised from empirical data. The model is formulated as two linked differential equations:

$$dU/dt = U + n[R - m\,(R / R + U)]$$
$$dR/dt = R + m(U / R + U) - n[R - m\,(R / R + U)]$$

Where any area of susceptible ground is disturbed (R) or undisturbed (U). Ground changes from undisturbed to disturbed at a rate of m and recovers (or reverts back to an undisturbed state) at a rate of n. To simulate variation in ground disturbance for a semi-arid rangelands ecosystem, Choquenot and Parkes (2005) set the rate of ground disturbance (m) by relating this to available pasture biomass, assuming food availability would influence ground disturbance by pigs.

Because food availability was not measured directly in this study, the effect food might have on rates of ground disturbance (m) was tested by evaluating the relationship between ground disturbance and pig population density (N), expressed as a proportion of estimated carrying capacity (K):

$$m = m_{max}\,(N/K)^{\Phi}$$

Where m_{max} is the maximum rate of ground disturbance and Φ is a parameter determining whether ground disturbance was proportionally or curvilinearly related to *N*/*K*.

The rates of disturbance and recovery for this model were obtained using the data described for each of the three hunting blocks in Chapter 3. Ground disturbance monitoring transects were split into 5cm blocks and the age of the disturbance in each block (if any) was noted for each monitoring period (n = 4). These data were compared between monitoring periods and the change from one disturbance state to another was recorded. The daily rate of new disturbance (*m*) was calculated as the proportion of the transect that had changed from a less recently disturbed to more recently disturbed state (e.g. undisturbed to disturbed, or old disturbance to fresh disturbance) divided by the number of days between the beginning of each monitoring session. The daily rate of ground recovery (*n*) was calculated as the proportion of the transect that changed from a more recently disturbed to less recently disturbed state (e.g. disturbed to undisturbed, or fresh disturbance to old disturbance). Mean disturbance and recovery rates were calculated for the three hunting blocks between each of the three monitoring sessions, yielding nine estimates for *m* and *n*, respectively. Pig density related to each ground disturbance and recovery estimate was calculated from the population projections for each hunting block generated in Chapter 4 (Fig. 4.2), expressed as a proportion of *K* for each hunting block (Table 4.4).

To explore the effect pig management may have on the abundance of pigs and the extent of ground disturbance in the Waitakere Ranges, simulation models were constructed based on data and relationships described in this thesis. The structure of the models is shown diagrammatically in Figure 5.1.

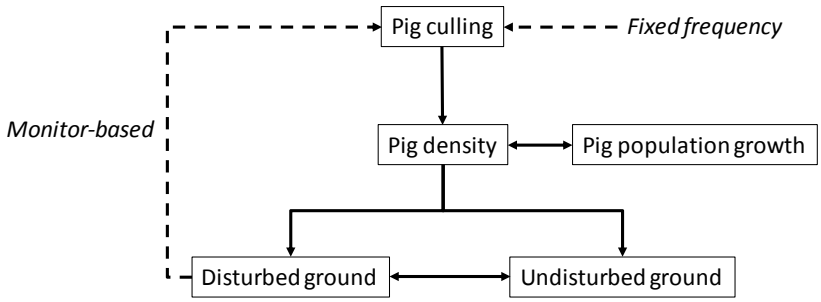

Figure 5.1 Diagram showing the structure of the simulation models developed to explore links between pig management, pig density and changes in the level of ground disturbance caused by pigs in the Waitakere Ranges.

Pig density (*N*) varied with population growth rate and the effects of culling. Quarterly population growth rate varied according to the logistic population model described in Chapter 4, using the average of

estimates for K across the three hunting blocks (K = 8.23 pigs/km^2). Daily rate of ground disturbance (m) varied with N/K, according to the model described above. Daily rate of ground disturbance recovery (n) was set at the mean level observed across all hunting blocks. Daily variation in m and n were applied to project changes in the proportion of ground disturbed using the differential equations developed by Choquenot and Parkes (2005). As shown in Chapter 4, ground disturbance was not uniform over the entire Waitakere Ranges and not all areas have the potential to be disturbed. Therefore disturbance was modelled over 41% of the Waitakere Ranges (calculated from the proportion of the combined length of transects where disturbance was observed) and used an initial value of R (0.06) which was the measured proportion of ground disturbed at the first monitoring session, averaged across all transects where disturbance was observed.

Two versions of the model were developed for comparison: fixed frequency culling, where culls were triggered at set time intervals, and monitor-based culling, where ground disturbance monitoring occurred at constant time intervals, with culling triggered at a threshold level of ground disturbance. The fixed frequency culling model triggered culling at 3, 6, 9 or 12 month intervals (i.e. 1–4 culls/annum). The monitor-based culling model conducted ground disturbance monitoring quarterly, initiating culling if the proportion of ground disturbance was greater than specified trigger values of 0.05, 0.10, 0.15, 0.20 (i.e. 5–20% on average of the monitored transects). Each cull removed 0.37 pigs/km^2, which was the mean density of kills in the last four culls undertaken in this study. The last four culls were used to derive mean culling effectiveness, because these were undertaken quarterly and over a shorter timeframe than earlier culls (Chapter 4). The average cost of a culling program and undertaking ground disturbance monitoring were calculated from records kept of these activities by Auckland Council staff. Culling and monitoring costs averaged $24,000 and $6,900 per operation, respectively. All simulation models ran for 30 years, with the pig population starting at K, and culling initiated in year 1.

5.3 Results

A polynomial regression test was used to evaluate the form of the relationship between m (expressed as an annual rate) and N/K for data combined across all three hunting blocks. The polynomial term was positive (c = 0.745), significant at a reduced α-level (t = 2.00, p = 0.10), and its inclusion in the regression dramatically improved the model fit (Adjusted R^2 = 0.53 for the polynomial regression, compared with 0.29 for the linear regression), providing strong support that the increase in m accelerates at higher values of N/K. The model described above was fitted to the relationship using a non-linear least squares approach (R-development Core Team, 2009), and is shown in Fig 5.2 (parameter estimates: m_{max} = 0.069 ± 0.055, Φ = 8.47 ± 5.44).

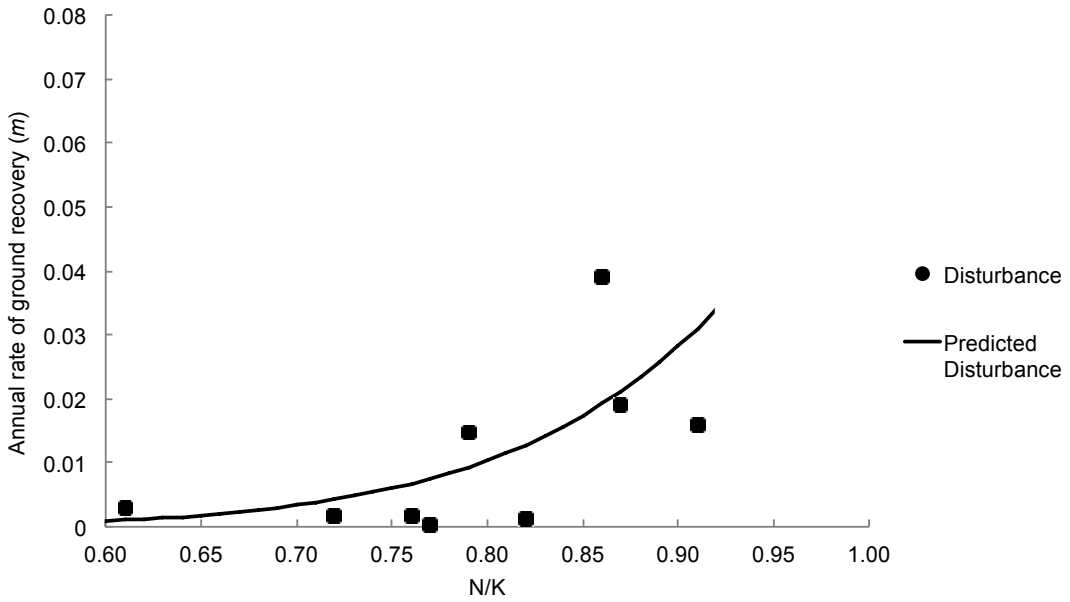

Figure 5.2 Observed and predicted rates of new ground disturbance (*m*) related to pig density (expressed as a proportion of carrying capacity: *N/K*).

A regression of *n* (again expressed as an annual rate) on *N/K* indicated no relationship between the rate of ground disturbance recovery and pig abundance (R^2 = 0.13, F = 0.11, p = 0.76). The mean rate of ground disturbance recovery was 0.024/annum (SE = 0.005).

Simulation modelling shows a 3 month fixed frequency culling regime reduces pig density over a number of years to a level where offtake from culling simply removes the growth of the underlying pig population (i.e. its sustainable yield), and no further reductions in pig density are achieved (Fig. 5.3). Despite the limited effect this regime has on pig density, the rate of new ground disturbance declines steeply, resulting in a steady continuing decline in the proportion of pig disturbed area. However, if the interval between fixed frequency culls is increased to 6, 9 or 12 months, the trajectory of ground disturbance is reversed indicating an ongoing increase in the proportion of ground disturbed (Table 5.1). The reason for this result can be identified by re-examining the model linking the rate of ground disturbance (*m*) to pig density as a proportion of *K* (Fig. 5.1). This model indicates that the rate *m* will be in equilibrium with the rate of ground disturbance recovery (*n*), at a pig density of 7.25 pigs/km^2. Therefore, the simulation model predicts that at pig densities above this level, the proportion of ground disturbed will increase and conversely ground disturbance will decrease at pig densities below this level. Setting an interval for fixed frequency culling greater than 3 months leads to pig densities that average greater than 7.25 pigs/km^2, leading to ongoing increases in the proportion of ground disturbed.

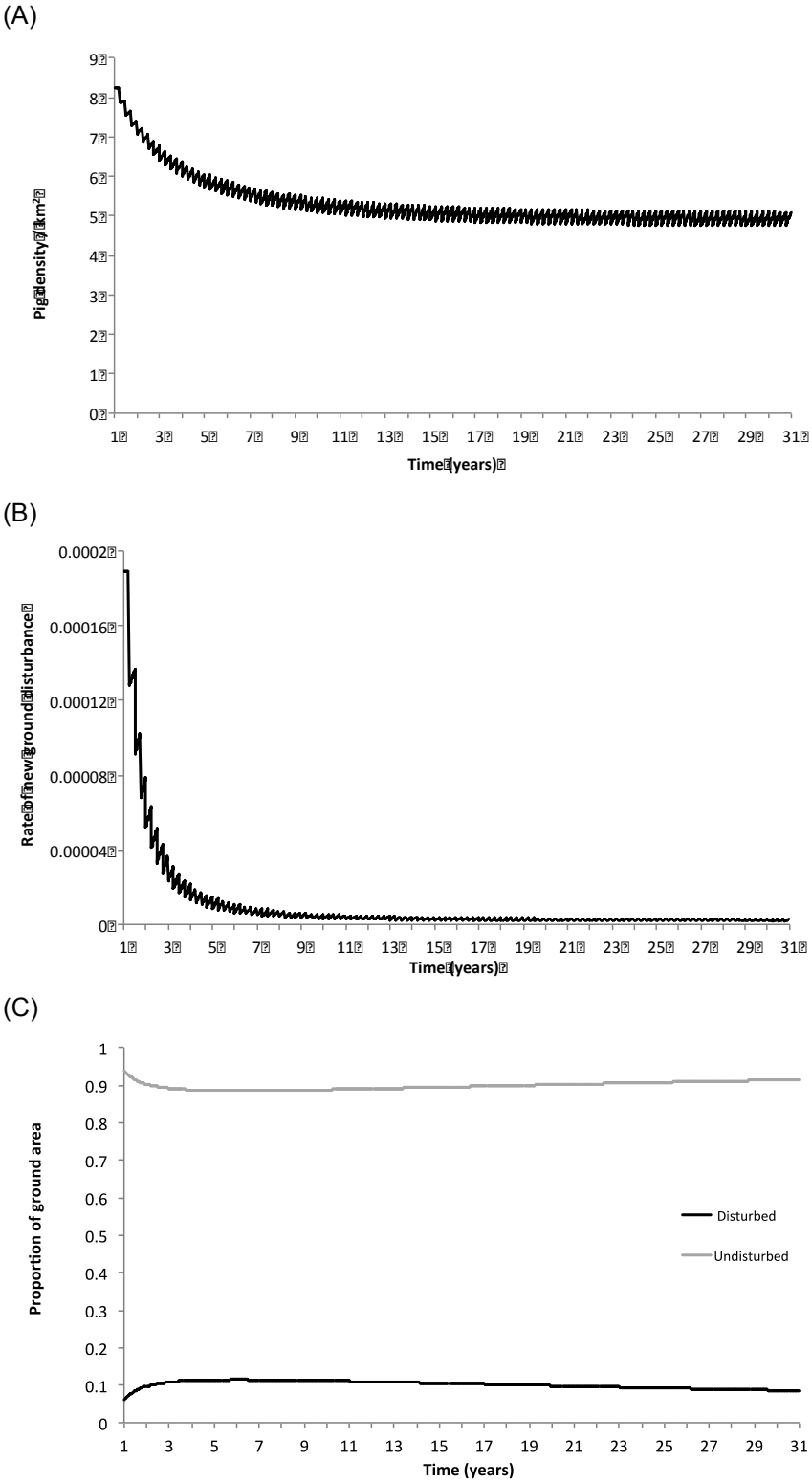

Figure 5.3 Fixed frequency culling (3 month interval between culls) showing changes over the course of 30 years in: (A) pig density, (B) rate of new ground disturbance and (C) proportions of disturbed and undisturbed ground.

Table 5.1 Results of the simulation model iterations for fixed frequency culling (triggered by months between culls) and monitor-based culling (triggered by proportion ground disturbed, when monitoring every 3 months), showing the change in pig ground disturbance over time and the yearly effort required to achieve this result.

Model	**Trigger**	**Mean pig density ***	**Mean annual rate of ground disturbance***	**Trajectory of ground disturbance**	**Proportion ground disturbed after 30 years**	**Culls/year**	**Annual cost (NZD)**
	3	5.0	0.008	Decreasing	0.08	4.0	95 200
Fixed	6	7.1	0.020	Increasing	0.35	2.0	48 000
frequency	9	7.5	0.040	Increasing	0.47	1.3	32 000
	12	7.7	0.040	Increasing	0.53	1.0	24 000
	0.05	6.0	0.008	Equilibrium	0.08	4.0	122 800
Monitor-	0.10	6.1	0.012	Equilibrium	0.10	3.9	120 400
based	0.15	6.4	0.019	Equilibrium	0.15	3.5	111 600
	0.20	6.7	0.026	Equilibrium	0.20	3.1	102 800

**After 10 years*

The simulations of monitor-based culling produced different outcomes than fixed frequency culling (Table 5.1). At the lowest ground disturbance trigger for culling (0.05 of transects disturbed), this strategy was identical to simply culling every three months. This is because 30 years was insufficient time for the proportion of ground disturbed to decline below the threshold level of 0.05 and as a consequence, control was triggered every time ground disturbance was assessed. However, as the ground disturbance trigger for culling was increased, the frequency of culling declined, leading to higher pig densities and proportions of ground disturbed that exactly mirror the trigger used to initiate culling. Under these circumstances, pig densities often exceeded 7.25 pigs/km^2, and the rate of ground disturbance exceeded the rate of ground recovery. This situation could only persist until the cumulative effect of high pig density on the proportion of ground disturbed meant that the culling trigger was exceeded, at which point culling would resume, reducing pig densities below 7.25 pigs/km^2 until ground disturbance fell below the nominal threshold level. In essence, this approach to culling establishes a strong feedback cycle between pig density and ground disturbance, with culling providing the negative feedback mechanism. It is important to note that while results for longer intervals between monitoring sessions are not presented here, their dynamics are essentially the same as for monitor-based culling at a 3 month interval. The critical difference is that the period required for the system to approach an equillibrium between pig density and the proportion of ground disturbed increases exponentially as longer periods between ground disturbance monitoring are considered.

Monitor-based culling was also more costly than fixed frequency culling, although it maintained the desired level of ground disturbance (Table 5.1).

5.4 Discussion

Rates of ground disturbance by pigs increase at high pig population densities, inferring that high population densities, and subsequent high intraspecific competition, reduce freely available above ground food resources, and drive more frequent below ground foraging. This relationship indicates that most ground disturbance occurs close to carrying capacity, which was predicted by Choquenot and Parkes (2005) (who used pasture availability as a surrogate for food limitation). This study used pig density as a proportion of carrying capacity to modify the rates of *m*, which is a cruder method of accounting for changes in pig ground disturbance as it relies on the assumption that carrying capacity is stable. However, this method used quantitative data, which was not available to Choquenot and Parkes (2005). Dietary studies suggest that feral pigs in New Zealand forests gain the largest proportion of their food from freely available above ground vegetation sources, including one third of their diet sourced from the fruit of tree species that are common in the Waitakere Ranges (Thomson and Challies 1988). Thomson and Challies (1988) state that feral pigs in the Urewera Ranges (podocarp-tawa forest) have access to fruit for 6–9 months of the year, year-round access to animal protein and vegetation rich in carbohydrates. They observed fluctuations in the pig population, which probably related to decreased fruit fall. Therefore it is possible that the carrying capacity of feral pigs in the Waitakere Ranges also fluctuates with fruit availability (which may vary with season, and weather events), although fluctuations are likely to be small due to the presence of year-round protein and alternative carbohydrate sources.

As ground disturbance rates increase steeply at pig population densities approaching *K*, it follows that the greatest reductions in the rate of new ground disturbance should occur when pig control reduces the population to levels below carrying capacity and the rate of new ground disturbance declines at progressively lower pig densities. The 7.25 pigs/km^2 equilibrium point (above which ground disturbance rates increase substantially) supports this assumption, implying that maintaining pigs below this equilibrium density will ensure ongoing reductions in ground disturbance. This suggests that substantial reductions in pig ground disturbance can be acheived without necessarily making huge reductions in pig density, reducing pigs from the 8.23 pigs/km^2 carrying capacity to below 7.25 pigs/km^2 is a required reduction of ~ 1 pig/km^2 to impose reductions in ground disturbance rates. Furthermore, the simulation model iteration that made the largest reduction in pig ground disturbance, reduced pig density to 6 pigs/km^2, which is an achievable reduction in pig density (achieved in hunting block 1, Chapter 4). The fixed frequency culling simulation demonstrated that to maintain the pig population below the equilibrium pig density, control must be implemented every 3 months. Intervals of greater than 3 months between culling operations allowed recovery of the pig population and resulted in the

maintenance of the pig densities above the equilibrium level (and consequently increased ground disturbance).

Choquenot and Parkes (2005) estimated m_{max} as a daily per capita rate (5.57 m^2/pig/day), assuming pigs at a density of 1.8 pigs/km^2 would produce an equilibrium level of ground disturbance of 10% when they had access to virtually no above ground food. In this study the maximum daily rate of ground disturbance was estimated to be 0.00019 at N/K = 1. Taking the average K across hunting blocks (8.23 pigs/km^2) as a good estimate, this corresponds to a maximum daily per capita rate of ground disturbance of 23 m^2/pig/day, much higher than that estimated by Choquenot and Parkes (2005). The maximum observed daily rate of ground disturbance was 0.00013 which corresponds to a daily per capita rate of 16 m^2/pig/day. In either case, the empirically derived estimates obtained in this study imply a much greater propensity for pigs to forage below ground under conditions of food shortage than the values assumed by Choquenot and Parkes (2005). Conversely, daily rates of ground recovery measured in this study (average 0.00007) were lower than those estimated by Choquenot and Parkes (2005) (0.0009). However, their estimate was based on a measure of overall disturbance recovery calculated from Hone (1987). The measure of ground recovery used in this study was more accurately a reflection of cumulative effects of recovery and ongoing ground disturbance, although from a heavily controlled pig population. A daily rate of ground disturbance recovery of 0.00007 implies it would take 42 years for all disturbed ground to fully recover, if no further ground disturbance occurred. To assess whether this prediction was consistent with the recovery of disturbed ground along large-scale transects, maximum change in the average level of older disturbance along transects was calculated for each hunting block divided by the days between monitoring sessions. This provided an equivalent measure of n to that estimated by Choquenot and Parkes (2005); being a cumulative measure of disturbance recovery and ongoing new disturbance. Average change in older ground disturbance across hunting blocks was 0.00004, equivalent to 66 years for full ground recovery. This lower rate of recovery is consistent with the rate used in the models, given it includes ongoing disturbance by the pig population. This suggests a dramatically slower rate of disturbance recovery for the Waitakere Ranges than that assumed by Choquenot and Parkes (2005).

Fixed frequency culling was cheaper than monitor-based culling, as conducting both monitoring and culls is more expensive than culls alone. Although, all monitor-based scenarios achieved the desired reduction in ground disturbance. Comparing the simulation models, the outcomes from the 3 month fixed frequency culling and 0.05 monitor-based culling were similar, although, the 3 month fixed frequency cull scenario was the most cost effective in achieving the same reduction in ground disturbance. Therefore in recommending the most cost effective and beneficial control

regime for feral pig control in the Waitakere Ranges, initiating pig culling every 3 months on a 'set and forget basis' seems the best scenario. However, the success of this scenario depends on maintaining a kill density of 0.37 pigs/km^2 per cull, any decline in kill density could lead to a recovery in pig populations above the equilibrium pig density and result in a continuing increase in pig ground disturbance levels. The likelihood of maintaining the required kill density for the next thirty years (as specified by the model) is low, and the lack of monitoring in this scenario could lead to increasing disturbance levels despite maintaining a 3 month culling regime. This could result in an overall failure of pig culling to achieve the desired management outcome (reduction in ground disturbance) and a waste of effort (both hours and cost). This suggests that monitor-based culling, whilst the more expensive option, holds more guarantees of reducing overall ground disturbance. The monitor-based culling model is also based on a maintained removal of 0.37 pigs/km^2 per cull although, in real time, if kill density were to drop and disturbance rates to increase, culls would be initiated more frequently and reductions in ground disturbance would continue to be maintained. This control method is adaptive management and would inform managers of the outcomes of monitoring and allow adjustments to the culling program throughout its use. Therefore, initiating culling at a set disturbance threshold would be the recommended culling regime to consistently achieve management goals, although land managers may choose a threshold disturbance level according to the biodiversity outcomes they wish to achieve.

Feral pig management should focus on achieving reductions in ground disturbance to reduce biodiversity impacts. The Choquenot and Parkes model (2005) was parameterized with data from the Waitakere Ranges and demonstrated the use of this model in aiding management decisions to control feral pigs. This study has shown that reductions in ground disturbance can be achieved through minimal reductions in pig populations. However, monitoring ground disturbance (outcome monitoring) is crucial to ensure the success of control programs in achieving management goals. A monitor-based culling regime is recommended for the continued management of feral pigs in the Waitakere Ranges as it would guarantee a reduction in ground disturbance by pigs, which is the overall management goal.

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Chapter 6 – General discussion

6.1 Research summary

The aims of this research were to: 1) investigate the impacts of feral pigs on vegetation, ecosystem processes and plant pathogen transmission in a temperate rainforest; 2) determine the relationship between feral pig density and disturbance; and 3) evaluate threshold levels for pig management through the use of a model simulating differing pig control regimes. Feral pigs in New Zealand are perceived as both a valuable hunting resource by some sectors of the community, but also as a pest by managers of natural environments. However, other than dietary studies (Thomson and Challies 1988), the negative impacts of feral pigs had not been previously quantified. Determining the role of feral pigs in vectoring *Phytophthora* Taxon *Agathis* (PTA) was important due to the recently reported severity of disease in kauri (*Agathis australis*) (Chapter 3). This thesis has demonstrated that feral pigs increase litter decomposition rates and soil nutrients in disturbed areas, they also cause an initial decline in seedling density and species richness and may cause long term changes in species composition (Chapter 2). Furthermore, feral pigs vector a large number of plant pathogens and ground disturbance could increase the chance of pathogen spread. No PTA was found in the soil associated with feral pigs, although this is likely due to the small soil samples obtained and the low detectability (Chapter 3). Therefore feral pigs may still be implicated in the spread of this disease due to their close association with infected soil (through observations of disturbance under infected trees), their ability to transport soil containing other plant pathogens on their trotters and snouts, including the closely related *P. cinnamomi* (Chapter 3).

Feral pig density was curvilinearly related to new ground disturbance, with disturbance proportionally higher at high pig densities, which is likely related to intraspecific competition for above ground food resources driving below ground foraging (Chapter 5). Ground disturbance was also spatially patchy and positively correlated with topography (specifically terraces) (Chapter 4). Model simulations showed that a reduction in ground disturbance by pigs can be made without making a large reduction to the pig population in the Waitakere Ranges (Chapter 4 and 5), and that threshold levels for ground disturbance could be a useful management tool, maintaining ground disturbance at a defined level. This method was more costly than fixed frequency culling, although monitor-based culling guarantees a reduction in ground disturbance (and therefore a

reduction in negative impacts, including plant pathogen spread), which cannot be guaranteed with fixed frequency culling (Chapter 5). Therefore, impact mitigation should be achieved through establishing a disturbance threshold.

The results of this research have direct relevance to the Waitakere Ranges, but are also relevant to temperate forests in other parts of New Zealand. I will discuss the implications of this in the following discussion.

6.1 Impacts and extent of ground disturbance

This research has shown that feral pigs impact native podocarp broadleaf forest through increased decomposition rates and nutrients in disturbed soils, reducing plant species diversity, changing species composition and disturbing vegetation understory structure (Chapter 2). Feral pigs also act as a vector for a large number of soil borne plant pathogens and cannot be excluded as a possible vector of *Phytophthora* Taxon *Agathis* (PTA) (Chapter 3).

Feral pig ground disturbance is unlike any other biotic disturbance in New Zealand, current or historical. Historically, the avifauna (which included large birds such as moa and rails) may have caused scarification to the soil (Bond et al. 2004), although this was likely to be a light scratching in the litter layer and top soil layer and dissimilar to the turning over of the soil that feral pigs perform. Burrowing seabirds were also present in the prehistoric forests of New Zealand, and in addition to creating burrows, may have added nutrients to these ecosystems (Mulder and Keall 2001, Roberts et al. 2007). Although a permanent burrow dug by a seabird is again dissimilar in action to the turning of soil by feral pigs. Introduced deer (Cervidae) (also widespread in New Zealand) are known to cause some scraping of the ground but this disturbance is also shallow and does not mimic feral pig ground disturbance. Therefore ground disturbance by pigs is a novel type of disturbance in New Zealand ecosystems that has pronounced effects on the native environment (Chapter 2 and 3).

Despite the novelty of the type of disturbance caused by feral pigs, the consequences for native vegetation is similar to that of other introduced ungulates and possums (*Trichosurus vulpecula*). Introduced deer and goats (*Capra hircus*) inhibit the regeneration of many plant species by browsing, changing vegetation species composition and structure (Chimera et al. 1995, Nugent et al. 2001, Forsyth et al. 2003). Possums can also change forest structure and species composition, although Nugent et al. (2001) suggests that possum would have less influence on the long-term direction and extent of forest change than ungulates. A recent international review of non-indigenous ungulates as threats to biodiversity (Spear and Chown 2009) recommended

the eradication of feral pigs on islands and to consider removal from continental areas where possible, as they considered that the threats posed by feral pigs were more wide reaching than those of other ungulates. They noted that whilst non-indigenous ungulates were widely believed to threaten biodiversity through the consumption of vegetation, and hybridization with native ungulate species, feral pigs also threatened animal species through predation and competition, have negative impacts on soil function and cause trophic cascades (Spear and Chown 2009).
Possums, deer and goats are widely controlled in New Zealand (Parkes and Murphy 2003). The large scale possum control conducted in New Zealand is largely driven by the Animal Health Board due to possums being the main wildlife vector of bovine tuberculosis (Parkes and Murphy 2003). Feral goats and deer are controlled due to their negative impacts on vegetation through browsing (Parkes and Murphy 2003). However, feral pigs have also been identified as reservoirs for bovine tuberculosis (Nugent et al. 1996, Nugent et al. 2003), and as stated previously have similar impacts to ungulates and possums on native vegetation. It is surprising then that of the 16 regional and unitary authorities (RUAs), all control possums, six (37%) control goats and deer whilst only four (25%) control pigs (http:/www.biosecurityperformance.maf.govt.nz/, accessed 12 February 2012). It appears this is due to the minimal research on the impacts of feral pigs to date and the negative perception towards pig control held by some sectors of the community. The evidence provided in this thesis may enable managers to place pig control as a higher management priority.

Feral pigs are the only ungulates to inhabit the Waitakere Ranges, and therefore competition for above ground resources should be comparatively lower than in areas where other ungulates are present (Chapter 5). In addition to the lack of other ungulates in the Waitakere Ranges, possums are controlled to low levels (<1 Residual Trap Catch Index (RTCI) J. Craw, pers. comm.). Possums have been described as the greatest consumer of fruit and flowers in New Zealand mixed forest (Innes et al. 1995), and may drastically reduce the availability of fallen fruit. A feral pig dietary study in the Urewera Ranges (where possums and deer are controlled) determined that one third of feral pig diet was native fruit and 17% of their diet was obtained via grazing (Thomson and Challies 1988). Any interspecific competition (e.g. from possums) for these food sources could drive feral pigs to forage for food below ground more frequently. Therefore it is reasonable to assume that the extent of feral pig ground disturbance may increase in forests where other ungulate species and possums are present. Additive impacts on biodiversity may therefore also occur in forest where other ungulate species and possums are present. Deer and goats are noted to preferentially browse palatable species, leaving the forest understory dominated by unpalatable species (Nugent et al. 2001). High rates of feral pig ground disturbance could further reduce the understory species diversity, as only particular unpalatable species may survive in pig-disturbed ground. Therefore the impacts observed in Chapter 2 and the extent of

disturbance observed in Chapter 4 in the Waitakere Ranges could be conservative estimates compared to other forest blocks where possums and other ungulates have removed most of the above ground food resources. There may also be higher impacts associated with areas that have been repeatedly disturbed by pigs (which was not included in my research). Therefore my research may show the minimum impacts that could occur due to ground disturbance by pigs.

Parker et al. (1999) proposed an equation to evaluate the impact of an invasive species, calculated as the range of a species multiplied by its abundance and its per capita impact on biodiversity. Nugent et al. (1996) estimated that there were approximately 1.2 feral pigs/km^2 in New Zealand, based on an extrapolation of the estimate of pigs harvested nationally. Using Fraser et al.'s (2000) feral pig range estimation (Range = 93 000 km^2, calculated using ungulate population reports from Department of Conservation (DOC) and regional councils) Nugent et al. (1996) therefore estimated 110 000 feral pigs were present in New Zealand. Using the average density calculated in this study for the Waitakere Ranges (8.3 pig/km^2), a much higher estimate of 762 600 feral pigs in New Zealand is calculated. Although this estimate is substantially higher, it is more reliable than Nugent et al.'s (1996) estimate as it is based on empirical data. McIlroy (1989) estimated a density of 12–43 pigs/km^2 for an area dominated by pasture and bracken in Mt Harte near Murchison. McIlroy (1989) also estimated with the density of a nearby frequently hunted population at 3–8 pigs/km^2, and the difference between the two populations was attributed to the lower hunting frequency and higher food availability at the higher density site. However, despite the expectation of higher pig densities in areas with freely available food (especially pasture dominated sites), the methods used by McIlroy (1989) to estimate population density were not adequately described and are likely to be an overestimation. Whilst the densities calculated in this thesis may be an underestimation of the true density (due to the modelling methods; Chapter 5), I believe the upper end of McIlroy's (1989) estimation (43 pigs/km^2) is highly unlikely in New Zealand forests, especially in forests where other ungulates are present and interspecific competition for food is high (constraining the pig population). The extent of disturbance demonstrated in this study should also be regarded as a low estimation. As stated previously, habitats with increased intra and interspecific competition would result in higher rates of disturbance. Habitats where above ground food is constrained or only seasonally available would also incur higher levels of ground disturbance. Annually disturbed areas extrapolated for the entire country from Fraser et al.'s (2000) range estimation presents a scale over which biodiversity and ecosystem impacts of feral pigs are observed. Fraser et al.'s (2000) range estimation was conducted in 2000 and was based on DOC and regional council reports of pig populations and is the best range estimation available, although it may also be an underestimation due to pig range expansion over the last 11 years, and the presence of unreported populations in 2000. The extent of ground disturbance throughout New Zealand was

calculated using a range of 93 000km^2 (suggested by Fraser et al. 2000), multiplied by the average disturbance rate observed in the Waitakere Ranges (before the onset of culling), which equalled 0.07 per annum (Chapter 5). This leads to an approximate area estimate of 6 510 km^2 disturbed by pigs annually in New Zealand (approximately 2.5% of the country). There is no doubt that this value is an underestimation, as the amount of disturbance would increase in habitats with less above ground food availability (although pig densities may also decrease), and the range estimation it is based on is also likely an underestimation. Therefore it may be postulated that in some areas of New Zealand where feral pigs are more numerous, and intraspecific and interspecific competition is high, the ground disturbance rates and total proportion of disturbed ground could be markedly higher than that found in the Waitakere Ranges.

6.3 Management recommendations for the Waitakere Ranges

Based on the model simulations in Chapter 5, a monitor-based culling regime is recommended for the Waitakere Ranges. Fixed frequency culling was determined to be the less expensive option, but this regime does not account for any reductions in culling effectiveness, which would result in an increase feral pig ground disturbance. Therefore implementing a monitor-based culling regime (which controls pigs based on disturbance monitoring) will ensure the maintenance of ground disturbance at an acceptable threshold level, thereby reducing the impacts on biodiversity. An Environment Court challenge from the 'Tokoroa Pig Hunting Club' resulted in the recent removal of feral pigs and deer from Waikato Regional Council's (Environment Waikato) Regional Pest Management Strategy (RPMS) where they were previously listed as a biosecurity pest (E.W 2007). The pig hunting club argued that Environment Waikato had failed to undertake outcome monitoring to demonstrate the negative effects of feral pigs and deer. Therefore, although the monitor-based culling regime is more costly than fixed frequency culling, it will provide data on outcomes for biodiversity and enable informed management decisions, reducing the risk of legal challenges.

The results of Chapter 4 indicate that increasing the kill effectiveness could theoretically drive the pig population in the Waitakere Ranges to extinction (Chapter 4) and provide a more cost effective solution. Whilst it may be possible to achieve this increase with additional hunting teams or increased culling frequency, this would dramatically increase the cost of pig control. Increasing kill effectiveness through the use of a toxin(s) would be less costly than making incremental increases in hunting effectiveness. Many pig control programs in Australia have successfully used a variety of pig toxins to achieve population reductions (Hone and Pedersen 1980, Choquenot et

al. 1996, Cowled et al. 2006) and toxins are consistently reported to be the cheapest form of control per hectare (Choquenot et al. 1996). There are currently no toxins approved for use on feral pigs in New Zealand, although sodium monofluoroacetate (1080), warfarin and other toxins are being explored (S. Hix, Pers. Comm.). There are problems with the use of toxins associated with non-specificity, but also animal welfare implications. Strong public adversity to toxin use requires any decision to control pigs with toxin be thoroughly researched.

Fencing areas to exclude feral pigs may be an option to protect areas of special significance (e.g. areas currently free of PTA disease). Fences are expensive and require a high level of maintenance to reduce breaches. Choquenot et al. 1996 argue that they are also ineffective as control tools so should only be considered to reduce the impacts of feral pigs on high value areas. However, Day and MacGibbon (Day and MacGibbon 2007) report the development of the Xcluder™ fence, which successfully excluded all invasive species tested (including feral pigs).

6.4 Future research

Whilst this research has shown the effects of a single disturbance event on seedling recruitment and composition, soil nutrient availability and litter decomposition (Chapter 2), further research should be conducted on the long term effects of repeated disturbance events which may have a cumulative and therefore serious effect on the ecosystem as a whole. The impacts described in this thesis may be applicable to similar forest types around New Zealand, although the impacts of pigs may vary in substantially different habitats such as wetlands. Studies conducted in grassland ecosystems in California have demonstrated a rapid increase in exotic plant species regeneration after ground disturbance by pigs (Cushman et al. 2004, Tierney and Cushman 2006), and therefore it is reasonable to expect similar impacts to be occurring in dryland ecosystems in New Zealand. Alpine ecosystems may be more severely impacted by feral pig ground disturbance than lowland forests due to slower rates of ground recovery.

The research conducted in this thesis did not determine whether the nitrate increase in pig disturbed areas was linked to increased nitrogen mineralisation (though increased decomposition processes) or added to the soil in the process of ground disturbance (by pig defecation and urination). Further study conducted in this area may also focus on the per capita impact of pigs (including per capita nutrient addition), which could then provide more insight into the Parker et al. (1999) impact equation (stated above).

Chapter 4 highlighted the correlation between ground disturbance by pigs and specific topographical features (flat areas next to water courses). Research into optimising ground

disturbance monitoring and control (specifically toxins) by targeting these areas, and reducing management in areas where pigs are less likely to frequent and disturb, would increase the cost effectiveness of pig management. Developing spatially explicit models for applying pig management in specific areas would also maximize cost-benefit ratios.

Chapter 3 described the ability of feral pigs to transport plant pathogens. Feral pigs were shown to carry soil on their trotters and snouts, and although other plant pathogens (including P. *cinnamomi*) were found, PTA was not detected, which was likely due to the low detectability. Future research should focus on developing an appropriate test to isolate PTA from small soil samples, with reliable test sensitivities, before any vectors of PTA are investigated in the future. If a reliable test for PTA can be developed, feral pig vectoring of PTA should be investigated by obtaining soil from the entire body of the pig, rather than just the trotters and snouts. Research should also be conducted into whether PTA can survive passage through a pig's digestive tract and be spread via pig faeces. A study investigating the survival of *Phytophthora cinnamomi* through feral pig digestive tracts in Australia (Li et al. 2010), found that viable spores were excreted up to 7 days post ingestion. Therefore, passage through pigs must be considered a possible means of long distance dispersal for a congeneric of *P. cinnamomi*, PTA.

Feral pig management in New Zealand could benefit from further research into the development of a pig toxin or toxins. The efficient use and effectiveness of such toxins should also be investigated. Control could then be implemented in large tracts of land (targeted in high risk areas), which may be particularly beneficial in remote areas that are PTA free.

6.5 Recommendations for New Zealand

Many invasive species in New Zealand are managed as pests because of their perceived impacts or threats posed to native biodiversity (King 2005, Clayton and Cowan 2010). A recent review of the control programs conducted by local government regional and unitary authorities in New Zealand (RUAs), found that the most frequent primary justification for pest control was biodiversity protection (Clayton and Cowan 2010). Most of these control programs listed 'increased dominance of native species and improved forest integrity' as a desired outcome. However, over half of the RUAs surveyed by Clayton and Cowan (2010) conducted no outcome monitoring, in fact only a small fraction (~7%) of the total funding for pest control was spent on monitoring results and outcomes (Clayton and Cowan 2010). Clayton and Cowan (2010) state that collectively RUAs are the second largest managers of animal and plant pests in New Zealand and spend ~40% of the New Zealand government-funded animal and plant pest management budget (in excess of $100 million per year). The lack of outcome monitoring performed by RUAs

brings into question their ability to justify their pest management programs and expenditures, and highlights the need for robust assessments of outcomes for future management programs.

Feral pigs are currently listed on seven of the sixteen existing Regional and Unitary Authorities' (RUAs) Regional Pest management Strategies (RPMSs) in New Zealand (Table 6.1) (http:/www.biosecurityperformance.maf.govt.nz/, accessed 12 February 2012). Of the RUAs listing feral pigs on their RPMS, five state that the goal is to minimise impacts and/or protect biodiversity and only four are conducting sustained management of feral pig populations within their region (Table 6.1).

Table 6.1 Regional and Unitary Authorities (RUAs) that list feral pigs on their Regional Pest Management Strategy (RPMS), the type of management program undertaken and the objectives of the program.

RUA	Management Program	Goal
Auckland	Pest	a) Minimise impacts in areas of High Conservation Value (HVC); and b) Promote community awareness of the impacts of feral pigs c) Prevent the spread of feral pigs into areas currently free of the species.
Hawkes Bay	Site Led	Assist land occupiers undertake control at sites of regional significance
Taranaki	Surveillance	Promote public understanding and facilitate voluntary control
Greater Wellington	Site Led	Achieve improvement in the ecological health and diversity of Key Native Ecosystems using a range of suitable indicators
Canterbury	Biodiversity Pest	Reduce populations and maintain at levels sufficient to protect biodiversity values in targeted areas
Southland	Suppression and exclusion	a) To prevent pigs establishing on islands where they do not presently exist, or where Feral pig eradication has taken place b) To minimise impacts of Feral pigs within HVC area c) To raise community awareness of the cultural, biodiversity and economic impacts of Feral pigs.
Chatham Islands	Containment	Minimise the impact of feral pigs on the biodiversity by maintaining low densities in HVC areas

As a result of the impacts revealed in this research and the estimated extent of feral pig ground disturbance throughout the country, I recommend that feral pigs be incorporated on all RUA's RPMSs to be managed in areas of high conservation value. This should be of particular importance in Northland, Bay of Plenty and Waikato where *Agathis australis* (kauri) and feral pigs overlap in distribution, and the potential for PTA vectoring is high. This study found no PTA in the soil associated with feral pigs and therefore pig control cannot be recommended on this basis alone. However, the likelihood of feral pigs as vectors of this disease remains high (Chapter 3). As stated previously, the potential for impacts may be more severe in forests where other ungulates and possums are present, therefore all conservation areas should be considered for feral pig control.

Further thought should also be given to management strategies for feral pigs that incorporate impact data into the considerations for the timing, frequency and intensity of pig control (Chapter 5). Conducting feral pig control with no disturbance monitoring in place is not cost effective, as disturbance levels can rise whilst control is taking place (Chapter 5) and the management goal (reduction in disturbance impacts) may not be achieved. Most RUAs incorporated 'reducing impacts' in their goal for feral pig control (Table 6.1), but conducted no outcome monitoring and assumed that any level of pig control would accomplish reductions in impacts (Clayton and Cowan 2010). This assumption is clearly not supported and insufficient control could lead to increases in ground disturbance. Chapter 5 demonstrates that changing the frequency of control can have major implications on ground disturbance reductions, and conducting culling at a fixed frequency larger than 3 months apart would not decrease levels of pig ground disturbance. Therefore any management program should include outcome monitoring (ground disturbance transects are recommended as a monitoring method) and reassess the control regime accordingly in an adaptive management process. The model used in Chapter 5 could be applied to other culling regimes around the country and highlights that ground disturbance can be reduced by pig control regimes for $5.50–$7.10 per hectare for a single operation. Furthermore, pig management should be targeted in high value conservation areas (including areas free of PTA infection) and the effectiveness confirmed in areas free of PTA infection to halt disease spread and protect disease-free areas of forest. Fencing areas to protect disease-free trees of significance could also be considered. Although reducing pigs to low densities would reduce the incidence of disturbance and consequently the chances of disease vectoring.

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