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

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Abstract Feral pigs (*Sus scrofa*) are a widespread invasive species, and cause biotic disturbance. This study evaluated the impacts associated with ground disturbance by feral pigs in the North Island of New Zealand. Exclosure cages were erected over feral pig-disturbed ground and visually undisturbed ground (the latter as controls). Buried resin bags and litter bags were located in these plots to examine differences in soil nutrients and decomposition rates and seedling/sapling recruitment (abundance, species composition and richness) was monitored over 21 months. No difference was found in the litter decomposition between the disturbed and visually undisturbed plots. Significantly more nitrate (NO_3-N/NO_2-N) was found in the disturbed exclosures. Seedling density was not significantly affected by feral pig disturbance. However, seedling/sapling species richness was lower in disturbed areas. Species composition changes occurred at disturbed sites with species increasing and decreasing in density after feral pig disturbance. However, no pattern was observed between species that were negatively affected by feral pig disturbance.

This study shows that feral pig disturbance affects vegetation through direct removal, but also indirectly through increased nitrate, potentially leading to seedling and sapling species composition changes. Feral pigs are known to return to previously disturbed areas to re-disturb. These areas may remain in a re-disturbed state if not protected, and through continued disturbance and increased nitrate, ecosystem changes may occur, especially in characteristically nutrient poor environments.

Introduction

Invasive species may impact communities by reducing species diversity, changing environmental conditions and altering ecological processes (Chapin 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. Disturbance is often recognized as an important factor in determining ecosystem composition and structure (Tierney and Cushman 2006; Pickett and White 1985; Sousa 1984). Connell (1978) described the intermediate disturbance hypothesis in which species diversity can be maximized with an optimum level of disturbance. However, a change in disturbance regime could result in the loss of species diversity and also

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promote the spread of invasive non-native plant species (D'Antonio et al. 1999; Cushman et al. 2004). Some ecosystems have evolved with the presence of biotic disturbance agents (mainly native mammals) (Cushman et al. 2004; Singer et al. 1984; Sherrod and Seastedt 2001) that are integral to the structure and function of these ecosystems. However, 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 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 are native to Eurasia, but have become widely distributed across the world through introductions to Africa, North and South America, Australasia and many oceanic islands (Barrios-Garcia and Ballari 2012).

Feral pigs physically change their local environment through disturbance by rooting for food and damaging the surrounding vegetation and forest floor (Hone and Robards 1980; Engeman et al. 2005). The damage caused by feral pigs may be direct (Thomson and Challies 1988), although Tierney and Cushman (2006) have also found that feral pig disturbance has indirect effects on the plant assemblages in grassland ecosystems and Hone (2002) showed similar results in a sub-alpine ecosystem. Indirect effects of feral pig disturbance include changes in the composition and structure of the ecosystem through changes in species richness and diversity, facilitating non-native growth and conversely reducing the biomass of native species (Hone 2002; Tierney and Cushman 2006; Aplet et al. 1991; Cushman et al. 2004; Siemann et al. 2009). Feral pigs have also been shown to decrease carbon to nitrogen ratios in the soil in a number of studies, leading to further changes in the surrounding vegetation such as higher plant productivity, increased non-native plant assemblages, and increased microhabitat diversity (Singer et al. 1984; Siemann et al. 2009).

Previous studies have highlighted the impacts feral pigs have on tropical, grassland and temperate deciduous ecosystems (Bratton 1975; Barrios-Garcia and Ballari 2012; Cushman et al. 2004; Mitchell and Mayer 1997; Mitchell et al. 2007; Singer et al. 1984; Tierney and Cushman 2006). The majority of these studies have also been conducted in places with native mammalian biotic disturbance agents (in Australia and the US). However, in this study we examine 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 tillage) that feral pigs perform. The New Zealand feral pig (*S. scrofa*) is descended from domestic pigs released in New Zealand by the European settlers in the eighteenth century (King 2005). Since then they have become established and widespread, occupying approximately 93,000 km^2 or 35 % of the country (King 2005). Feral pig ground disturbance presents a novel biological process in New Zealand forests and feral pigs occupy a vacant niche, as no native species currently perform ground disturbance. Feral pigs are therefore predicted to have an impact on the ecosystem by changing ecological processes (Shea and Chesson 2002; Vitousek et al. 1996).

This study aims to determine the effects of feral pig disturbance on soil nutrient availability, litter cover, litter decomposition, seedling/sapling recruitment (including abundance, species richness and composition) and non-native plant establishment, by comparing feral pig disturbance sites with undisturbed controls. Based on previous studies in other ecosystems (Singer et al. 1984; Siemann et al. 2009) we predict that feral pigs will increase soil nutrients (particularly nitrate) and increase decomposition rates, which will have a lasting effect on successional processes, increase species richness and non-native establishment and change species composition.

Methods

Study site

The Waitakere Ranges in Auckland, New Zealand is a regional park of over 16,000 ha which extends from 36° to 37°S and from 174° to 174°E (0–474 m above sea level). In this area of podocarp/broadleaf dominated temperate rainforest feral pigs are present at a density of 8.23 feral pigs per km^2 (Krull 2012). No other mammalian ungulates are found there. All experimental sites were established in areas with similar soil moisture and light levels, in mature cutover forest where the dominant canopy species were *Dacrydium cupressinum*, *Agathis australis*, *Knightia excelsa*, *Hedycarya arborea* and *Kunzea ericoides* (Esler 1983).

Experimental design

To study the impacts of feral pig disturbance and its recovery, areas of feral pig freshly disturbed ground and visually undisturbed controls were fenced off at 12 sites to exclude feral pigs. Feral pig ground disturbance could affect vegetation in the surrounding area; therefore we erected visually undisturbed controls at distances of 1 and 10 m from disturbed exclosures. Feral pig disturbance was sought (primarily by following feral pig tracks) and a site was established when an area of feral pig disturbance (1.5–3 m in diameter) was encountered. At each site exclosures were erected in the center of a patch of fresh feral pig disturbance, which are now referred to as 'disturbed exclosures'. Fresh disturbance was classified as any disturbance that contained little or no plant litter and where unearthed soil was still visibly moist. Exclosures were also established 1 m from the edge of the feral pig disturbance and at 10 m from the edge of the feral pig disturbance at each site, which are now referred to as 'visually undisturbed exclosures'. Feral pig disturbance is generally visible on the forest floor for approximately 2 years in this forest type (Krull 2012). Therefore, we deduce that our 'visually undisturbed' plots had not been disturbed for at least two years. There were three exclosure plots (disturbed, 1, 10 m) at each site (n = 12). The sites were established in June 2009 and were monitored for

21 months or until the feral pig disturbance was no longer discernible to the naked eye. This study is not a manipulative experiment in terms of the addition or removal of feral pigs and their associated disturbance, and therefore it is a possibility that the differences between disturbed and visually undisturbed plots may have existed prior to exclosure establishment. A 'pre-treatment' measurement to account for such differences was not possible as it was not feasible to predict where a feral pig might disturb. Feral pigs may specifically select belowground foraging areas where food resources are high or where soil is easier to disturb, particularly in areas close to watercourses (Krull 2012). However, there is no evidence to suggest that feral pigs preferentially disturb in areas of increased nutrients, especially at the small scale examined in this study. Thus, we conclude that the visually undisturbed exclosures are sufficient controls to be compared with the corresponding disturbed exclosures. Exclosures were chosen to be 98 cm in diameter to fit a single seedling monitoring area. The exclosures were built using a 325 cm section of weld mesh (50 × 50 mm mesh hole size and 1.5 m in height) in a cylindrical shape. The cylinder was secured to the ground using garden stakes and steel weed mat pins.

Nutrient availability

Soil nutrient availability was measured using ion exchange resin (IER) bags (Binkley 1984; Binkley and Matson 1983). Nylon resin bags were made from pantyhose and filled with approximately 5 g of BDH resin Amberlite MB6113, labelled with a metal tag. One resin bag was buried at 10 cm depth in the soil in each exclosure. After 12 months the resin bags were unearthed, 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 2 M KCl per sample, shaken in an orbital shaker for 30 min (100 rpm), and the resulting liquid was used to determine the concentrations of NH_4-N, NO_3-N/NO_2-N and PO_4-P in a QuickChem 8000 flow injection analyzer using an ASX500 series auto sampler (Lachat Instruments, Colorado). This equilibration/extraction method does not recover all adsorbed NH_4-N, NO_3-N/NO_2-N and PO_4-P, but relative comparisons among sites are valid (Hart and Binkley 1984).

Litter cover and decomposition

Percentage litter cover was estimated visually over the entire plot to the nearest 5 %, every 3 months for 21 months. Litter decomposition was assessed using the litter bag technique (Crossley and Hoglund 1962; Coleman et al. 2004). Pigeon wood (*H. arborea*) leaves 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 randomly selected from the tree and oven dried (60 °C for 48 h) before placement of 5–8 g of litter into nylon mesh (5 mm) litterbags (10 × 20 cm). For each litterbag, the weight of oven dried leaf litter placed into the bag was recorded. Inside each exclosure plot, three litterbags were pinned to the ground. One litterbag from each exclosure was collected after 8, 16 and 32 weeks in the field. All soil was brushed from the litter bag and the leaf material was then oven dried at 60 °C for 48 h and reweighed. Dry weights of the reweighed leaf material (retrieved from the field) were subtracted from the initial dry weight. Relative loss was calculated by dividing mass lost by original weight, which was then converted to mass remaining using the calculation: $1 -$ relative loss. Ash-correction was not used in this analysis as we were comparing relative decomposition across treatments and did not require absolute decomposition values.

Seedling/sapling density, species richness, and species composition

To measure seedling/sapling 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). Native woody seedlings and saplings within this plot were identified to species and recorded as a count within each of the following height tiers; <15, 16–45, 46–75, 76–105 and 106–135 cm. Seedlings/saplings that forked visibly above or at ground level were considered the same plant. Non-native plant species were estimated as percentage cover at each exclosure and control plot at 21 months after feral pig disturbance.

Statistical analysis

All graphs and statistical tests were performed using the statistical programme R (version 2.8.1) and SAS (version 9.3). For all data we tested for differences in distance from disturbance (disturbed, 1 and 10 m). Resin bag data and environmental data could not be transformed to normality; therefore non-parametric Kruskal–Wallis tests were used for these analyses. Litter decomposition 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 ($W = 0.9893$, $p = 0.1092$); Levene's tests were also conducted to ensure homogeneity of variance within factors. Differences in decomposition were then tested using a 2-way ANOVA.

Litter cover, species richness and seedling/sapling density involved repeated measurements; therefore mixed model analyses using an unbalanced design and restricted maximum likelihood (REML) were required. It was appropriate to use a linear mixed model (LMM) for the percentage litter cover. However, both species richness and seedling/sapling density were measured as counts per unit area, and generalized linear mixed models (GLMM) were appropriate for these data. The effects tested within the models were distance (disturbed, 1, 10 m), time (between repeated measures) and the interaction between distance and time.

The LMM analysis was fitted to the raw litter cover data but examination of the resulting residual plots indicated that a transformation was required. A logit transformation was applied and the LMM was then fitted for a second time on the resulting data. The Tukey–Kramer method was then used to gain p values for multiple pairwise comparisons. The GLMM fitted to the species richness and seedling/sapling density data assumed the response variable follow a Poisson distribution, using the log link function. Therefore reported geometric means and confidence intervals estimated from the fitted GLMM Poisson model are on the natural log-scale. Due to the assumption of a Poisson distribution it is not appropriate to report the 'mean SE' on a continuous scale. Instead, upper and lower 95 % confidence limits for the mean are calculated.

The composition of seedling species was analyzed 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). We used the Analysis of Similarities (ANOSIM) routine, with 999 permutations, to analyze differences between the sites, time periods and distance from disturbance (disturbed, 1

and 10 m) treatments. 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 and Warwick (2005) use the definitions of: well separated $R > 0.75$, clearly different $R > 0.5$, and barely separable $R < 0.25$. In addition we used SIMPER analyses to examine which taxa contributed the most to the differences at disturbed, 1 m and 10 m exclosures (Clarke and Warwick 2005). A distance-based test for homogeneity of multivariate dispersions (PERMDISP) was also used to test for differences in the dispersion at different distances from disturbance.

Results

Nutrient availability

There was no effect of distance from feral pig disturbance on levels of ammonium (Kruskal–Wallis, $X^2 = 0.889$, $df = 2$, $p = 0.641$) or phosphate (Kruskal–Wallis, $X^2 = 0.708$, $df = 2$, $p = 0.702$) absorbed by IER bags. However, there was a significant difference between plant available nitrate (NO_3-N/NO_2-N) levels at the disturbed and 10 m exclosures (Kruskal–Wallis, $X^2 = 3.752$, $df = 1$, $p = 0.053$) but not between the disturbed and 1 m exclosures, meaning that there may be a decreasing gradient of plant available nitrogen at distances further from feral pig disturbance (Fig. 1).

Litter cover and decomposition

There was no significant difference in the interaction between distance and time for litter cover (Table 1).

However, there were significant differences in percentage litter cover between different distances from disturbance ($p = 0.005$) and between sampling times ($p = 0.025$). There was 35 % more litter cover in the 1 m exclosures when compared to the disturbed ($p < 0.0001$) and 48 % more in the 10 m exclosures when compared to the disturbed ($p < 0.0001$), but only 13 % more in the 10 m exclosures when compared to the 1 m ($p = 0.014$). The litter cover in the disturbed and 1 m exclosures followed a similar pattern throughout the study which was different to the pattern shown in the 10 m exclosures (Fig. 2). Tukey–Kramer comparisons showed there was a significant increase in litter cover between 6 and 15 months ($p = 0.0379$). Analysis of the litter decomposition data showed a significant difference between sites ($F = 2.684$, $df = 11$, $p = 0.021$). However, no significant difference was found in the litter decomposition at differing distances from feral pig disturbance ($F = 1.27$, $df = 2$, $p = 0.294$).

Seedling/sapling density, species richness and species composition

The GLMM for seedling and sapling density showed no significant interaction between the effects and no significant difference in distance from disturbance (Table 2). The GLMM for species richness showed no statistically significant interaction between distance and time. There was also no evidence of a time effect on species richness. However, there was a significant difference in species richness with distance from disturbance ($p = 0.051$) (Table 3). Geometric mean species richness was lowest in the disturbed exclosures, highest in the 1 m exclosures with an intermediate value in the 10 m exclosures (Fig. 3). No

Fig. 1 Mean milligrams of NO_3-N/NO_2-N per kilogram of ion exchange resin, in feral pig disturbed exclosures and visually undisturbed exclosures 1 m and 10 m from feral pig disturbance, including standard *error bars*
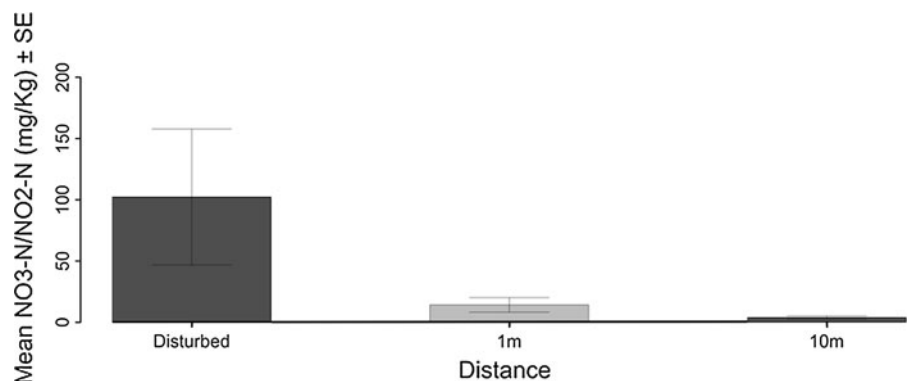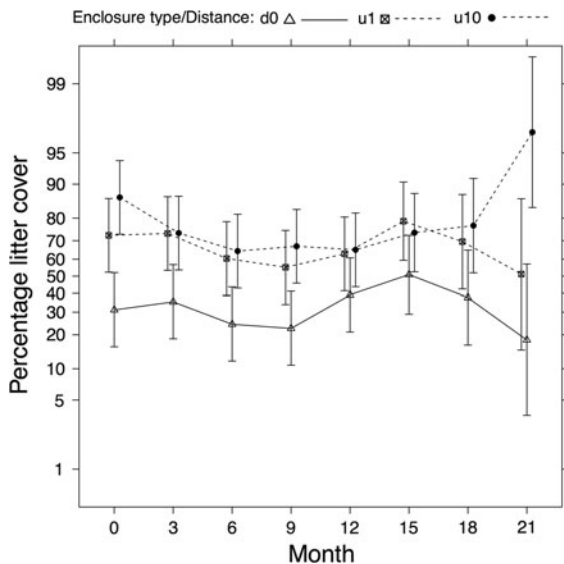
Table 1 Global hypothesis tests of fixed effects for litter cover, showing the numerator (Num) and denominator (Den) degrees of freedom (df), the F-statistic (F value) and p value

Effect	Num df	Den df	F value	p value
Distance	1	199	8.05	0.0050
Time	7	200	2.35	0.0252
Distance × Time	7	199	1.46	0.1841

Table 2 Global hypothesis tests of fixed effects for seedling density, showing the numerator (Num) and denominator (Den) degrees of freedom (df), the F-statistic (F Value) and the p value

Effect	Num df	Den df	F value	p value
Distance	1	198.6	0.05	0.8231
Time	7	200.7	1.77	0.0951
Distance × Time	7	198.6	0.83	0.5639

Table 3 Global hypothesis tests of fixed effects for species richness, showing the numerator (Num) and denominator (Den) degrees of freedom (df), the F-statistic (F value) and p value

Effect	Num df	Den df	F value	p value
Distance	1	200.0	3.85	0.0510
Time	7	201.2	1.34	0.2319
Distance × time	7	200.0	0.13	0.9961

Fig. 2 Mean percentage litter cover over time for feral pig disturbed exclosures (d0) and visually undisturbed exclosures 1 m (u1) and 10 m (u10) from feral pig disturbance, adjusted for differences between sites. The *error bars* indicate the lower and upper 95 % confidence intervals for the means

Fig. 3 Geometric means of seedling/sapling richness for feral pig disturbed exclosures (d0) and visually undisturbed exclosures 1 m (u1) and 10 m (u10) from feral pig disturbance, adjusted for differences between sites. The *error bars* indicate the lower and upper 95 % confidence intervals of the means

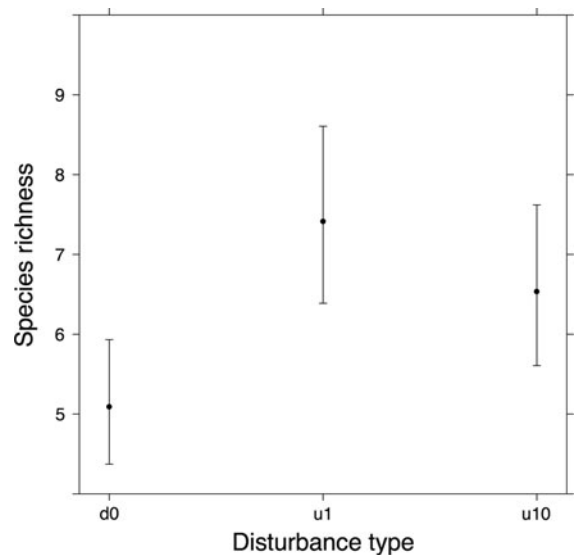non-native plants were recorded in the exclosures during the study period.

A one-way ANOSIM showed a separation in species composition among the sites ($R = 0.538$, $p = 0.001$). A 'non separable' pattern was revealed for time (sensu Clarke and Warwick 2005) ($R = -0.10$, $p = 1.0$) in a two-way ANOSIM including site and time. A two-way ANOSIM with site and disturbance showed a clear separation in the species composition related to distance from disturbance ($R = 0.535$, $p = 0.001$). A SIMPER analysis then determined which native species were contributing to the dissimilarities between the groups. The species found to contribute 90 % of the dissimilarity between the groups are displayed in Table 4. Only cotyledons and *Coprosma grandifolia* were found in higher abundance in the disturbed areas, whilst all other

species were at lower abundances in the disturbed plots when compared to 1 m and 10 m plots. There were several species that showed a gradient of increased abundance (some species more than doubled in abundance) with distance from disturbance, these included; *K. excelsa*, *K. ericoides*, *H. arborea*, *C. lucida*, *Ripogonum scandens* and *Leucopogon*

fasciculatus, which was not recorded in the disturbed plots. Another group of species were at highest abundances in the 1 m exclosures but decreased in the disturbed and 10 m exclosures, these included *Pseudopanax crassifolius*, *Rhopalostylis sapida*, *Geniostoma rupestre* and *Clematis* spp. Only *C. grandifolia* was at similar abundance in the disturbed and 1 m exclosures and decreased in abundance in the 10 m exclosures. Two of the large podocarp species, *A. australis* and *D. cupressinum* were at lowest abundance in the disturbed plots but were found at similar abundance in the 1 and 10 m plots. A similar pattern was also seen in *Myrsine australis*. This analysis highlighted the increase in cotyledons in the disturbed areas but also the decrease in abundance of a variety of species with differing growth traits (large trees through to small shrubs). A distance-based test for homogeneity of multivariate dispersions (PERM-DISP; $F_{231} = 9.24$, $p = 0.001$) showed a significant difference in the dispersions of the disturbed, 1 m and 10 m groups, which indicated a greater variation in the species composition at 1 m and 10 m sites.

Discussion

Feral pigs had no effect on ammonium or phosphate levels in the soil. However, feral pigs significantly changed the soil nitrate availability, as predicted. An order of magnitude more plant available nitrate was found in the disturbed plots and there was a decreasing gradient of nitrate with distance from feral pig disturbance. In experiments designed to simulate feral pig disturbance, Kotanen (1997) found nitrogen levels and decomposition differed between sites where soil excavation had taken place and where soil had been mounded up. In our study we noted that feral pig disturbance areas have an initial 'crater' where the feral 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 decreasing gradient of soil nitrate, which may be due to leaching of these nutrients from the disturbance site and 'apron' into the surrounding area. Frank and Evans (1997) suggest that defecation and urination may contribute to elevated levels of nitrogen in ungulate accessible areas through the addition of ammonia, although Siemann et al. (2009) suggest elevated levels are the result of accelerated

rates of nitrogen mineralization, through the rapid integration of the original litter layer with the soil. Another study found that feral pig disturbance accelerated the leaching of minerals from the leaf litter, which then accelerated decomposition and altered nutrient cycling (Singer et al. 1984). This study found no effect of feral pig disturbance on litter decomposition, which was contrary to our hypothesis and may suggest that the higher nitrate levels are not linked to increased nitrogen mineralization from accelerated decomposition. Due to the lack of a pre-disturbance comparison, we cannot rule out the possibility that feral pigs preferentially disturb in areas with higher soil nitrate, possibly related to increased belowground food resources. 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 feral pigs and altitude, and Hone (2002) found most ground disturbance by feral pigs was associated with drainage lines on level ground. Similarly, ground disturbance was positively correlated with terrace topography (flat areas of ground next to watercourses) in a New Zealand study (Krull 2012). Ground disturbance by feral 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). Topography is likely correlated with the presence of certain vegetation types, which may also influence disturbance preference by feral pigs, although Krull (2012) found no difference in canopy cover or soil moisture between disturbed and visually undisturbed plots suggesting that these variables were not involved in influencing spatial variation in feral pig disturbance. Plant productivity and ecosystem function are affected by nitrate levels (Bonkowski and Scheu 2004; Schowalter 2000), therefore an increase in soil nitrate associated with feral pig disturbance may have an effect on the nitrogen cycle, with flow on effects for plant growth. This may be especially detrimental in the New Zealand temperate forest ecosystem that has evolved in the absence of biotic disturbance agents such as feral pigs that turn over the soil to greater depths than large birds may have done in the past.

Table 4 Differences in average native species abundance with distance from feral pig disturbance; the higher abundance scores for each numbers are highlighted in bold

Species	Disturbed	1 m	10 m	Esler life model	Dispersal method	Shade tolerance
Cotyledon	**2.21**	1.93	1.22	Seedling	Various	Various
K. excelsa R. Br.	0.55	1.00	**1.14**	Large tree	Wind	Low
K. ericoides (A. Rich) Joy Thomps.	0.03	0.11	**0.60**	Large tree	Wind	Low
H. arborea J.R. Forst. & G. Forst.	0.58	0.81	**1.01**	Medium tree	Bird	Moderate
C. lucida J.R. Forst. & G. Forst.	0.03	0.13	**0.25**	Small tree	Bird	Low
L. fasciculatus (G. Forst.) A. Rich.	0.00	0.22	**0.31**	Tall shrub	Bird	Moderate
R. scandens J.R. Forst. & G. Forst.	0.17	0.57	**0.71**	Stem climber	Bird	Moderate
P. crassifolius (Sol. ex. A. Cunn.) K. Koch.	0.49	**0.70**	0.47	Large tree	Bird	Moderate
R. sapida H. Wendl. & Drude.	1.23	**1.84**	1.30	Palm	Bird	High
G. rupestre J.R. Forst. & G. Forst.	0.51	**0.61**	0.42	Tall shrub	Unspecialized	Moderate
Clematis spp.	0.12	**0.37**	0.20	Stem climber	Wind	Low
C. grandifolia Hook. F.	**0.80**	0.96	0.55	Small tree	Bird	Moderate
D. cupressinum Lamb.	0.07	**0.39**	0.35	Large tree	Bird	High
A. australis (D. Don.) Lindl.	0.12	**0.23**	0.20	Large tree	Water	Moderate
M. australis (A. Rich.) Allan.	0.18	**0.47**	0.39	Medium tree	Bird	Moderate

Esler life model shows the species growth traits; seed dispersal method and shade tolerance is also displayed for each species (from www.ecotraits.landcareresearch.co.nz)

Litter cover was drastically reduced after feral pig disturbance and did not reach 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 was not significantly different between disturbed and undisturbed areas, which may have been due to the higher levels of plant available nitrogen in the disturbed areas, increasing seedling recruitment. Other studies have found that feral pig disturbance 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, 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 feral 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 into the understory canopy, therefore slowing and impeding the regeneration process. Bratton (1975) found similar results in the Great Smoky Mountains National Park with prolonged feral pig disturbance causing a drastic reduction in the percentage of mature flowering individuals in the forest canopy. The results from

our study suggest that low levels of feral pig disturbance may increase seedling recruitment by providing increased nitrate and ideal seedbed conditions. However, repeated disturbance at a location could have serious effects on plant assemblages, eventually leading to a lack of understory vegetation.

Our study showed a difference in plant species composition in the disturbed plots when compared with the visually undisturbed. Only cotyledons and a species of small tree (*C. grandifolia*) were found in higher densities in the disturbed exclosures when compared with the visually undisturbed. The majority of other species contributing to the composition changes were found at reduced densities in the disturbed exclosures. The species that were negatively affected in the disturbed exclosures covered a range of growth traits, from shrubs through to large trees, palms and stem climbers. However, four species that make up the main canopy of the surrounding forest were substantially reduced in density in the disturbed areas, which indicates that high levels of feral pig ground disturbance could lead to a decline in these canopy species. One species (*L. fasciculatus*) was not found in any of the disturbed areas throughout the study, which could indicate a local loss of this understory species if feral pig disturbance was to continue. No pattern can

be seen within the group of species negatively affected by feral pig disturbance as this contains both wind dispersed and bird dispersed species, species from characteristically high and low fertility systems and both light demanding and shade tolerant species. Comparisons with Hawai'i are highly relevant as these islands share a similar evolutionary history with New Zealand. Hawai'ian studies have found that the removal of feral pigs (and other ungulates) increased the frequency (Weller et al. 2011; Loh and Tunison 1999) and density (Cole et al. 2012) of understory species, whilst another study found the density of tree seedlings was higher in long-term feral pig exclosures (Busby et al. 2010). There was no evidence of an increase in species from a particular canopy zone in our New Zealand study. Although, it is possible that the cotyledons benefitting from feral pig disturbance are arising from the seed bank. Enright and Cameron (1988) state that only disturbance which 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. Previous studies have shown changes in species composition after continuing feral pig disturbance over an extended time period (Bratton 1975; Aplet et al. 1991; Siemann et al. 2009). This study has shown similar changes in seedling and sapling species composition, and it is possible that repeated feral pig disturbance over a number of years could lead to canopy composition changes.

This study also shows a decline in species richness. In Australia, Hone and Martin (1998) found that plant species richness in grassland decreased as feral pig rooting increased. This was supported by another study which showed a negative relationship between plant species richness and the extent of feral pig rooting, with plant richness declining to zero with extensive feral 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 feral pig disturbance rates were high and species had little time to recover (Hone 2002;

Hone and Martin 1998) 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 feral pig rooting, however richness of exotic species recovered much more rapidly, and persisted in feral pig disturbed areas. Cushman et al. (2004) conducted a four year exclosure experiment in a coastal grassland community. They found that whilst disturbance by feral pigs increased the species richness of both native and non-native species, it also reduced the biomass of native and non-native species in different 'patches'. Cushman et al. (2004) concluded that the observed vegetation changes were due to space clearing via feral pigs, creating greater opportunities for colonization and reduced competition, and that feral pig disturbance therefore promoted the continued invasion of the habitat by non-native plants. Studies in Hawai'i have shown an increase in non-native plant cover after feral pig disturbance but believe this is not related to feral pig removal (Loh and Tunison 1999; Stone et al. 1992). Our study found no evidence for or against feral pig facilitation of weeds, as we found no non-native plant cover in either the feral pig disturbed or undisturbed areas. Cushman et al. (2004) and Tierney and Cushman (2006) conducted their studies in grassland communities over long periods with no feral pig exclusion from disturbed sites, whereas our 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 non-native plant source. Therefore, feral pig facilitation of non-native plant species at our sites within a temperate rainforest may have been less likely.

It is possible that repeated feral pig disturbance and continued addition of nitrate, could alter plant available nitrate so as to cause a change in the forest canopy composition, towards an assemblage of species that benefit from feral pig disturbance. This could be of particular importance in ecosystems with characteristically nutrient poor soil and plant assemblages consisting of species with evolved tolerance to these conditions. Bloomfield (1953) and Wyse et al. (2012) have shown that kauri (A. australis) considerably modify soil conditions in the forests where they comprise the canopy, and by increasing the acidity and

decreasing the plant-available nutrients in this soil, facilitate the formation of unique plant assemblages tolerant of depressed nutrients. Increased availability of nitrogen to this ecosystem through repeated disturbance by feral 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) and was one of the species negatively affected by feral pig disturbance. Therefore the impact of feral pigs and prolonged nutrient addition to this ecosystem could have more severe ecosystem wide effects than in grassland ecosystems and tropical ecosystems where the impacts of feral pigs have been previously studied.

This study shows that low levels of feral pig disturbance may not have drastic effects on soil, seedling and sapling communities. Significant increases in plant available nitrate may actually benefit short-term seedling recruitment. Seedling density was not significantly affected by feral pig disturbance. However, seedling and sapling species richness was decreased associated with feral pig disturbed areas and species composition changes did occur with a number of important canopy species negatively affected by feral pig disturbance. It is recognized that feral pigs re-disturb areas after certain periods of time and may do this often (Kotanen 1995). This could mean that feral pig rooted areas remain in a frequently re-disturbed state if not protected, which could result in much higher levels of nitrogen in the soil and may also result in a serious decline in the number of species and composition of mature plants. This could lead to ecosystem changes with repeated disturbance events in forests with characteristically nutrient poor soils. This suggests that feral pig control could be crucial in maintaining the ecosystem processes, plant communities and structure in feral pig disturbed areas by reducing feral pig numbers and thereby reducing disturbance frequency. Land managers should seriously consider the implications of feral pig disturbance on ecosystem processes and plant assemblages, and conduct appropriate feral pig control to manage feral pig numbers and reduce feral pig disturbance to acceptable rates.

The results of this study show that invasive species such as feral pigs can be damaging to native ecosystems by directly and indirectly altering environmental conditions and ecosystem processes. The New Zealand environment has evolved in the absence of biotic disturbance agents such as feral pigs, which provide a novel biological process in this ecosystem. Whilst our study has shown the effects of feral pig disturbance on seedling/sapling species richness, composition and soil nitrate availability, further study should be conducted on the long term effects of repeated disturbance events which may have a more serious effect on the ecosystem as a whole. 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 feral pig control.

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