

Causes and consequences of ground disturbance by feral pigs (*Sus scrofa*) in a lowland New Zealand conifer–angiosperm forest

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Published online: 21 November 2014

Abstract: The ecological impacts of feral pigs (*Sus scrofa*) are of concern in many places around the world. One noticeable impact is soil disturbance, although the causes and consequences are often unclear. We measured the effect of ground disturbance by feral pigs on seedling recruitment and soil ecology over 25 months on a forested riparian terrace at Waitutu, south Fiordland, New Zealand, and assessed the diet of pigs from the area from stomach contents of animals shot by hunters. Foraging by feral pigs for below-ground food disturbed between 7.4% and 12.4% of the soil. Pigs were seven times more likely to redisturb a site than to disturb a new site. Below-ground food items constituted a third of pigs' diet and were dominated by stag beetle larvae. Sites disturbed by feral pigs had shorter seedlings compared with undisturbed sites, but this was due to pigs' choice of sites rather than a consequence of the disturbance. Net temporal changes in density and height of seedlings were similarly slow in both disturbed and undisturbed sites. The basal respiration of microbes in soils recently disturbed by pigs was significantly higher than that for undisturbed soils. There was a suggestion that disturbed soils had higher ratios of fungi to bacteria than undisturbed soils ($P = 0.06$). This may reflect either disturbance favouring fungi over bacteria or selection of sites with more fungi or more of their main prey, the fungivorous stag beetle *Dorcus helmsii*. Our results indicate that pigs disturb soil primarily to forage for food and that the consequences of disturbance for seedling regeneration and soil ecology are limited or neutral. The consequences of ground disturbance and predation for populations of animal prey, such as the stag beetles, require further investigation.

Keywords: diet; ecosystem engineers; Fiordland; forest dynamics; invasive species; seedlings; soil microbes; Waitutu

Introduction

Feral pigs (*Sus scrofa*) have a wide global distribution and occupy diverse habitats (Long 2003). In New Zealand feral pigs occur in many habitats over about 34% of the country (Fraser et al. 2000). The success of feral pigs is due, in part, to their high intrinsic rate of increase (Choquenot et al. 1996) and broad omnivorous diet (Ballari & Barrios-García 2014). The availability of dietary protein (from animals, plants and fungi) is thought to be a key factor limiting the abundance of feral pigs because piglets need a minimum amount of protein to grow and survive, while adult females need a minimum amount for successful reproduction (Giles 1980; McIlroy 2005). Pavlov (1980) suggested a protein diet of at least 15% was required by sows to avoid reabsorption of embryos. In some habitats pigs (and their wild boar ancestors) sometimes obtain this protein from above-ground sources such as mast (Tisdell 1982; Servanty et al. 2009). For example, mast fruiting of tawa (*Beilschmiedia tawa*) and hīnau (*Elaeocarpus dentatus*) was speculated to cause an increase in pig abundance and subsequent decline when the fruit was absent (Thomson & Challies 1988). Another New Zealand study found that the seeds of mataī (*Prumnopitys taxifolia*) were common (and still viable) in the faeces of feral pigs in Marlborough (O'Connor & Kelly 2012). Animal protein is also intermittently available

to New Zealand feral pigs, largely as carrion such as when possums are killed in fur harvesting or control operations and carcasses left in situ (Thomson & Challies 1988).

Pigs appear to disturb soil in search of below-ground foods when above-ground foods are most scarce (Ballari & Barrios-García 2014). Below-ground protein, mostly from invertebrates such as earthworms and beetle larvae, may provide a more consistently available source of protein in New Zealand ecosystems, although probably more energetically costly to obtain.

The below-ground foraging of feral pigs causes obvious disturbance of the soil. Indirect impacts may occur when the soil disturbance selectively favours some microbial, animal or plant taxa, or if the disturbance relocates soil nutrients or changes below-ground decomposition rates (Krull et al. 2013). While some effects might be positive if the disturbance creates sites suitable for seedling regeneration (Wardle 1984), it is generally assumed that the effects will be negative (Wardle 1984; McIlroy 2005). The negative effects might range from a direct impact on the species being eaten (Coleman et al. 2001; Hone 2002), to consequences for the species indirectly affected as the soil is turned over by pigs (Alexiou 1983; Hone 2002). Permanent ecosystem changes may occur if pigs act as ecosystem engineers by 'modulating the availability of resources to other species by causing physical state damages

in biotic or abiotic materials' (Jones et al. 1994).

Few studies, however, have demonstrated significant and consistent effects of ground disturbance by pigs, suggesting the biological consequences are more subtle than the visual impacts suggest. For example, in New Zealand Krull et al. (2013) found seedling density was not affected by pig disturbance although seedling species richness was lower in disturbed areas in forests of the Waitakere Ranges. They also found that nitrate concentration was higher in areas disturbed by pigs than in undisturbed areas. Whether this elevated nitrate was a consequence of pigs' activity or simply because pigs preferentially disturb sites with higher nitrates is unclear (see our discussion for a similar conundrum with respect to microbial activity). Similarly, in tropical rainforest in northern Queensland, Australia, seedling numbers increased inside exclosures and decreased outside them, but there was no evidence of an effect on surface litter biomass, below-ground plant biomass or earthworm biomass (Mitchell et al. 2007). In the absence of exclosures, Hone (2002) reported a negative relationship between plant species richness and the extent of soil disturbance by pigs in the Australian Capital Territory.

The objective of our study was to evaluate the causes and consequences of ground disturbance by feral pigs in a lowland New Zealand conifer–angiosperm forest. We addressed four questions: (1) What foods are feral pigs obtaining from below ground? (2) What is the extent and dynamics of ground disturbance by feral pigs? (3) What are the impacts of soil disturbance by feral pigs on seedling abundances, heights and composition of the common species? (4) What are the effects on below-ground microbial biomass and activity?

Methods

Study area

The study was conducted in mixed conifer–angiosperm forest growing on recent alluvial outwashes (< 25 000 years old; Mark et al. 1988; Ward 1988) along the Waitutu and Crombie catchments, Waitutu Forest, south-western South Island, New Zealand (46.4° S, 167.2° E). Annual rainfall is estimated at 1600–2400 mm (Mark et al. 1988) and the mean January (summer) and July (winter) temperatures are 12°C and 5°C, respectively (Ward 1988). The forest canopy¹ is dominated by two angiosperms – *Lophozonia menziesii* and *Weinmannia racemosa* – but three conifers (*Dacrydium cupressinum*, *Podocarpus hallii*, *Prumnopitys ferruginea*) and two other angiosperms (*Fuscospora cliffortioides* and *Metrosideros umbellata*) are also present (Mark et al. 1988; Coomes et al. 2005). The subcanopy is dominated by six angiosperm tree species (*Raukaua simplex*, *Carpodetus serratus*, *Fuchsia excorticata*, *Griselinia littoralis*, *Pseudowintera colorata* and *Schefflera digitata*), two tree-ferns (*Cyathea smithii* and *Dicksonia squarrosa*), and the liane *Ripogonum scandens*. There is a dense ground cover of ferns dominated by *Blechnum discolor*. The forest floor is deeply shaded (<2% light transmission; Coomes et al. 2005). For further details about the alluvial outwash soil and forest see Coomes et al. (2005) and Parfitt et al. (2005).

Feral pigs have been present throughout Waitutu Forest since at least 1925 and are most common in coastal and

alluvial habitats (Lovelock 1985). Other introduced mammals are present and while the herbivores may affect seedling recruitment and survival, none cause any mass disturbance of the soil that could be mistaken for the foraging from feral pigs. Red deer (*Cervus elaphus scoticus*) have been present in Waitutu Forest since c. 1920 (Holloway 1950) and were in moderate numbers during our study (Forsyth et al. 2005, 2011). Brushtail possums (*Trichosurus vulpecula*) colonised the area around 1970 (Lovelock 1985) but were at low densities during our study after intensive control in 1997 by the Department of Conservation (Wilson et al. 2006). Ship rats (*Rattus rattus*), mice (*Mus musculus*) and stoats (*Mustela erminea*) are also present (Wilson et al. 2006).

Diet

Stomach contents were collected from 14 feral pigs shot within the study area by recreational and contract hunters during 2000–2006. Each sample was washed through a 2-mm sieve, and 10 g of the larger fractions sorted and identified to species level where possible, oven-dried at 80°C for 3 days and then weighed (Chimera et al. 1995).

Extent and effects of ground disturbance

We measured the extent of soil disturbance by pigs. Seventy line-transects, each 10 m long, were established on the riparian terraces of the Crombie and Waitutu rivers. The start and end points of each transect were marked with a peg. The start locations and direction of each transect were randomly selected with any repeated start selections not used. The start-to-end distances of all soil disturbance caused by pigs was measured along each transect in March, June and November 2001, March and October 2002, and April 2003, i.e. six repeated measurements. This allowed us to estimate the percentage of the area disturbed on the riparian terraces (Hone 1988).

Circular 0.4-m² seedling plots were established at three (or occasionally four) fixed points at 1, 5 and 9 m from the start along each of the 70 transects and on an additional 41 transects established following the selection procedures described above. At first measurement, the soil state on each seedling plot could be undisturbed with no sign of pig impacts, or could have various ages of disturbance from recent with freshly overturned soil through to very old, with the latter being completely covered by leaf litter but the depression caused by the pigs' disturbance still visible. Patches of disturbance could also fully recover (i.e. once this latter state was indiscernible from undisturbed plots) or could be re-disturbed between assessments. The state of each seedling plot could therefore be undisturbed, disturbed, recovered or re-disturbed.

The number and height of all seedlings of each species on the seedling plots were measured six times between March 2001 and April 2003 as above. Seedlings and ferns 1–100 cm in height were sampled, although most (90%) were ≤ 10 cm. Few seedlings of dicotyledons attained heights of 10 cm, but the ferns often reached the upper height limit of 100 cm. We assessed net changes of seedlings at the plot level rather than individual seedling demography. This was because it was not practical to tag and follow the fate of individual seedlings, which were often very small, very numerous and typically ephemeral. Annual probabilities of plot disturbance, recovery and re-disturbance were estimated by converting measurement intervals to years and assuming that subsequent intervals for each plot were mutually independent. Estimates were based on maximum likelihood and assumed a binomial error structure.

¹ Plant names follow the New Zealand Plant Names database: <http://www.nzflora.landcareresearch.co.nz>.

We used linear mixed models to assess temporal changes in seedling density and mean seedling height for plots classified as disturbed from their first measurement and for plots that were never disturbed by feral pigs. Intercepts and slopes describing change were allowed to vary for disturbed/undisturbed plots (as a group) and for individual plots. The analysis was limited to 281 plots measured at least four times and excluded re-disturbed measurements in initially disturbed plots.

We compared the relative frequency of plant species and seedling mean height at first measurement on plots we classified as never subsequently disturbed by pigs against those that were subsequently disturbed. To test if pigs preferentially disturbed or avoided plots with certain seedling heights or species composition we compared the relative frequency of subsequently disturbed plots against expectations from a null model that assumed complete randomness. The null model was based on a randomisation procedure (Manly 1997). We first subsampled all initially undisturbed plots, we then took 5000 copies of this dataset and in each dataset we randomly 'disturbed' 14 plots (the same number of plots that were disturbed within the monitoring interval). We sampled without replacement so that each plot could be 'disturbed' only once. Next, for each set of 'disturbed' plots, we computed how frequently each species, or seedling height-class, was affected by 'disturbance'. Lastly, we compiled the frequencies for the 5000 sets of 'disturbed' plots and, for each species, or seedling height-class, computed the 0.025 and 0.975 quantiles of how frequently they were 'disturbed'. These represent upper and lower frequencies to be expected by random disturbance when the probability of falsely rejecting the null hypothesis is $\alpha = 0.05$. Beyond these boundaries the disturbed plots were statistically different from a random selection, suggesting some ecological mechanism may be involved.

In October 2002, we selected 10 sites with substantial fresh pig ground disturbance, and 10 adjacent sites with no apparent history of disturbance. Ten 1-kg subsamples of soil were taken from each of the paired sites, sampling down to a maximum depth of 30 cm and excluding the litter layer. The soil samples were stored at room temperature for up to 5 days while in the field until returned to the laboratory where they were held in a freezer for up to 6 months until analysed (see Wardle (1993) for details on the methodology). Thawed subsamples from each site were pooled and sieved through a 4-mm mesh for subsequent analyses.

Microbial biomass and activity were determined on the pooled and sieved soils. The moisture content of soil subsamples (15 g dry weight equivalent) was adjusted to 55% moisture either by air drying or rewetting with a fine mist of water, before subsamples were placed in a 130-ml airtight vessel (microcosm) and incubated at 22°C for 3 days to allow the soil conditions to stabilise. Microcosm tops were removed daily for 10 min to equilibrate the atmosphere and check the weights, and (if required) the soil moisture was readjusted to 55% on the day of the assay. Microbial biomass was determined by basal respiration; the evolution of carbon dioxide (CO₂) between 1 h and 4 h was measured by injecting 1-ml samples of headspace gas into an infrared gas analyser. Microbial activity was determined by substrate-induced respiration (SIR) (Anderson & Domsch 1978), which was measured in the same way as for basal respiration but the microcosms had been amended with 90 mg of glucose at the start of the SIR assay (Wardle 1993).

Two measures of microbial community composition were made. The first assessed the composition of microbial

phospholipid fatty acids in fungal and bacterial membranes (PLFAs) using the method described by Wardle et al. (2003). The abundance of the fatty acids extracted was expressed as relative nanomoles per gram of dry soil using the standard nomenclature of Tunlid et al. (1989). The ratio of fungal PLFA to bacterial PLFAs was used as an estimate of the relative importance of the fungal and bacterial energy channels. The second approach involved characterising active microbial communities on the basis of their ability to utilise different carbon and amino acid substrates and generate the substrate utilisation profile for each soil following Wardle et al. (2003). In brief, 28 individual microcosms were prepared with pre-assay soil mixture adjusted such that after amendment with different carbon/nitrogen substrates the moisture content would be 55%. One microcosm was the no-substrate control with moisture adjusted to 55% with sterile distilled water. The other 27 microcosms were individually amended with one of the following substrates: L-arginine, L-asparagine, L-cysteine, L-glutamic acid, DL-histidine, L-serine, DL-tyrosine, D-glucosamine, L-glutamine, N-methyl-D-glucamine, urocanic acid, D-glucose, DL-mannose, L-ascorbic acid, citric acid, Na-formate, D, gluconic acid, α -ketobutyric acid, α -ketoglutaric acid, DL-malic acid, malonic acid, oxalic acid, pantothenic acid, quinic acid, L-tartaric acid, uric acid, and tween-80. Substrate solutions were prepared at 0.3 M for amino acids, amines and aromatics, 1.5 M for carbohydrates, and 2.0 M for carboxylic acids. Substrates were added as 1 ml to each microcosm with 1 ml sterile distilled water added to 'wash' the substrate evenly into the soil. The amended samples were incubated and the headspace sampled (after 1 h and 4 h of incubation) for CO₂ concentration exactly as described for basal respiration. The respiration value for the sample not amended with substrate was then subtracted from the respiration values, so as to provide an absolute measure of respiratory response of the microbes to each of the added substrates.

The phospholipid fatty acid and substrate utilisation profile methods provide robust measures of soil microbial biomass as they are thought to encompass a greater proportion of the microbial community than that stimulated by the classical substrate-induced respiration method where only glucose is added. They quantify the function and community diversity of the microbial biomass but, as with most tools available for such analyses, both are stronger indicators of bacterial activity at the expense of fungal activity in the soil.

Results

Diet

Feral pigs from Waitutu were omnivorous, eating invertebrates, vertebrates (presumably by scavenging), fruit and seeds, plants and fungi (Table 1). Animal matter made up 36%, fruit and seeds 33%, ferns 16%, leaves, stems and roots of plants 13%, and fungi <2% of the pigs' diet. Below-ground dietary items were dominated by the adults and larvae of the stag beetle *Dorcus (Geodorcus) helmsii*; this species was 27% of the pigs' diet by dried weight and occurred in all but two of the pigs (Table 1). The seeds of miro (*Prumnopitys ferruginea*), the fruit and stems of supplejack (*Ripogonum scandens*), and the fronds and stipes of the fern *Cyathea smithii* were important foods by weight and were also found in most samples (Table 1).

Table 1. Main food items (means above 0.5 g dried weight) eaten by 14 feral pigs (*Sus scrofa*) from Waitutu Forest, Fiordland, New Zealand.

Food items	Dry weight (g)	% dry weight	Frequency (%)
<i>Dorcus helmsii</i>	26.5 ± 14.8	27.0	85.7
Earthworms	0.7 ± 0.9	0.7	28.6
Mammals	5.2 ± 8.3	5.3	7.1
Birds	2.7 ± 5.1	2.7	7.1
<i>Prumnopitys ferruginea</i> seeds	15.2 ± 14.1	15.4	57.1
<i>Ripogonum scandens</i> fruit	9.3 ± 13.2	9.5	71.4
<i>Elaeocarpus dentatus</i> fruit	7.9 ± 11.2	8.0	14.3
All fruit and seeds		33.0	
<i>Ripogonum scandens</i> stems	3.3 ± 4.5	3.4	21.4
<i>Griselinia littoralis</i>	2.0 ± 2.4	3.4	57.1
Roots	5.7 ± 7.9	5.8	21.4
<i>Cyathea</i> spp.	15.5 ± 10.5	15.8	71.4
Fungi	1.6 ± 2.8	1.6	35.7

Extent and effects of ground disturbance

At any one time, between $7.4 \pm 4.0\%$ (in March 2002) and $12.4 \pm 4.4\%$ (in March 2001) (95% confidence intervals) of the area showed evidence of disturbance by pigs as new sites were disturbed and previously disturbed sites recovered. There were no significant differences in the extent of disturbance among the sampling periods. A cumulative total of $17.6 \pm 0.5\%$ of the monitored area was disturbed by pigs during our 25-month study. Areas classified as freshly disturbed in March 2001 were usually still visible in March 2002, but most had returned to a recovered state by October 2002. On average there was a 39% probability that disturbed areas would recover in one year meaning that, on average, a disturbed area would take an average of 2.6 years to recover. The probability that an undisturbed area would be disturbed in a year was $P = 0.03$. The annual probability that a disturbed area would be re-disturbed was $P = 0.21$. That is, at some stage over the 25 months of the study pigs were much more likely to re-disturb places they had already disturbed than they were to disturb new sites.

At the first measurement, disturbed plots had fewer (Wilcoxon signed-rank test $W = 19724$, $P < 0.0001$) and shorter ($W = 19030$, $P < 0.0001$) seedlings than plots that were undisturbed (Fig. 1). Total seedling densities increased at similar rates in undisturbed ($1.09 \pm 1.90 \text{ year}^{-1}$) and initially disturbed plots ($1.38 \pm 1.75 \text{ year}^{-1}$) during the two years of monitoring (Fig. 2a, b). Mean seedling height changed little in undisturbed (slope = $0.11 \pm 5.58 \text{ cm year}^{-1}$) and disturbed (slope = $-0.46 \pm 4.10 \text{ cm year}^{-1}$) plots (Fig. 2c, d). For plots disturbed during the monitoring period, the direction and magnitude of change was variable, with only slightly more frequent decreases in seedling abundance and mean heights. In the period immediately after disturbance, seedling numbers declined in 9 of the 14 plots and mean seedling heights declined in 8 of these 14 plots.

Although the number of seedling plots disturbed within the monitoring period was small ($n = 14$), there was a trend that plots with short seedlings were more often disturbed by feral pigs than plots with tall seedlings (Fig. 3a). The frequency of species in plots disturbed during the monitoring period

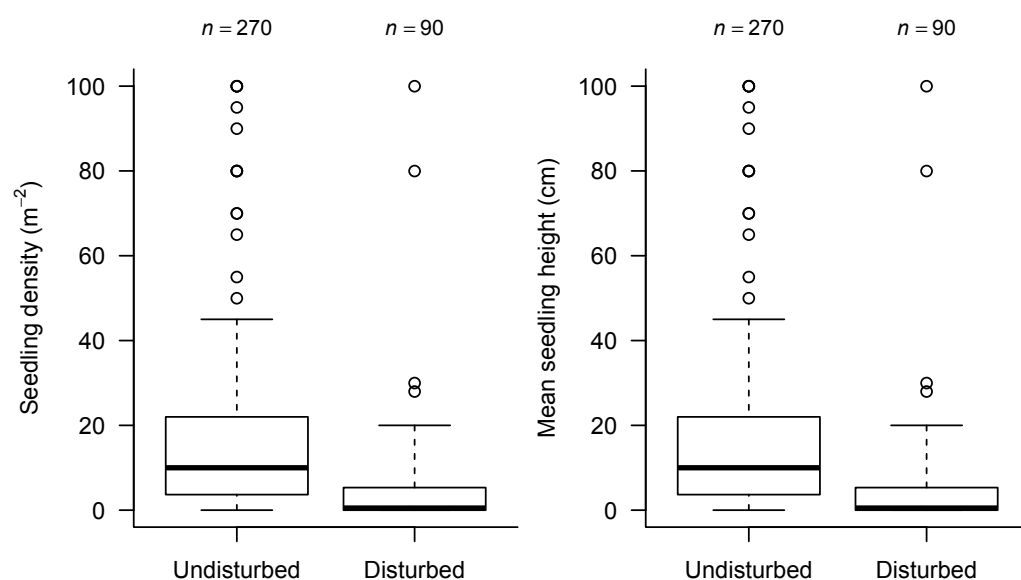


Figure 1. Density of seedlings and mean seedling height at first measurement (March 2001) for undisturbed and disturbed plots. Bold lines indicate medians, boxes' bottom and top indicate 25th and 75th percentiles, error bars indicate 10th and 90th percentiles, points are outliers.

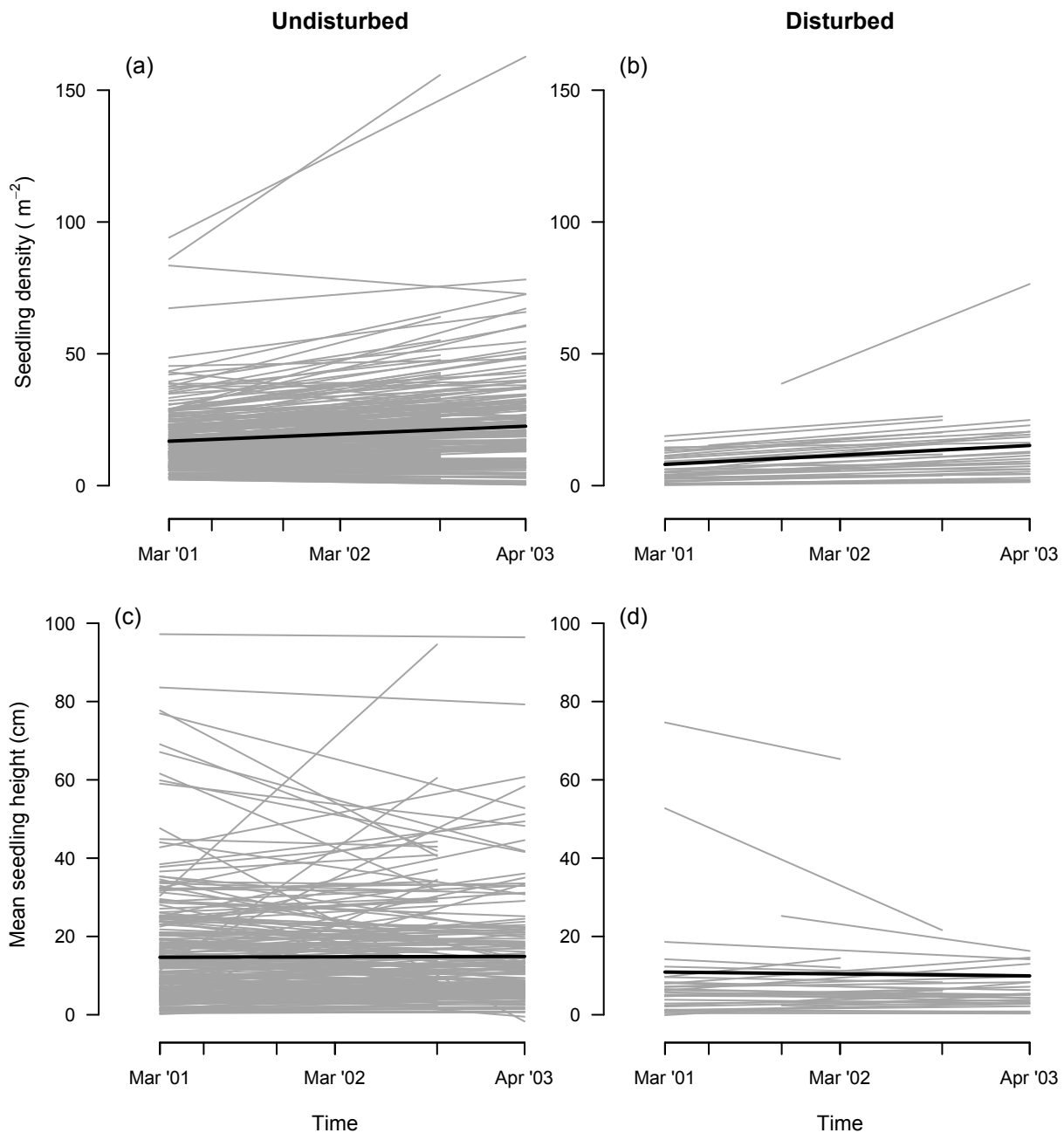


Figure 2. Temporal trends in seedling density and mean seedling height for individual plots (grey lines) and for groups (black lines) of never disturbed and initially disturbed plots between the initial measurements in March 2001 and the final measurement in April 2003.

mostly reflected their overall occurrence in undisturbed plots. However, a few species (*Coprosma rotundifolia*, *C. serrulata*, *Griselinia littoralis* and *Pseudowintera colorata*) were more often present in plots that were subsequently disturbed than was expected by chance (Fig. 3b).

Soil disturbance by pigs had minimal effect on the soil microbial community. Microbial basal respiration was significantly higher in soils disturbed by pigs than in undisturbed soils ($P = 0.05$). However, differences between all other measures of microbial biomass were non-significant (Table 2). There was a suggestion that disturbed soils had a higher ratio of fungi to bacteria than undisturbed soils ($P = 0.06$) although fungal biomass did not differ between the sites ($P = 0.16$).

Discussion

Feral pigs dig in the ground for food, mostly invertebrates. At Waitutu, pigs gained 27% of their diet from below-ground animals, a higher percentage than in two of the three other New Zealand pig populations studied (Table 3). Fungal biomass is difficult to measure directly in stomach samples (McIlwee & Johnson 1998), and so the low biomass figures reported in this and other studies may underestimate the importance of this dietary item. Most fungi that we could identify were above-ground fruiting bodies.

The total area disturbed by feral pigs on the Waitutu alluvial terraces (7.4%) was higher than that reported for two other areas in New Zealand. Krull (2012) measured annual

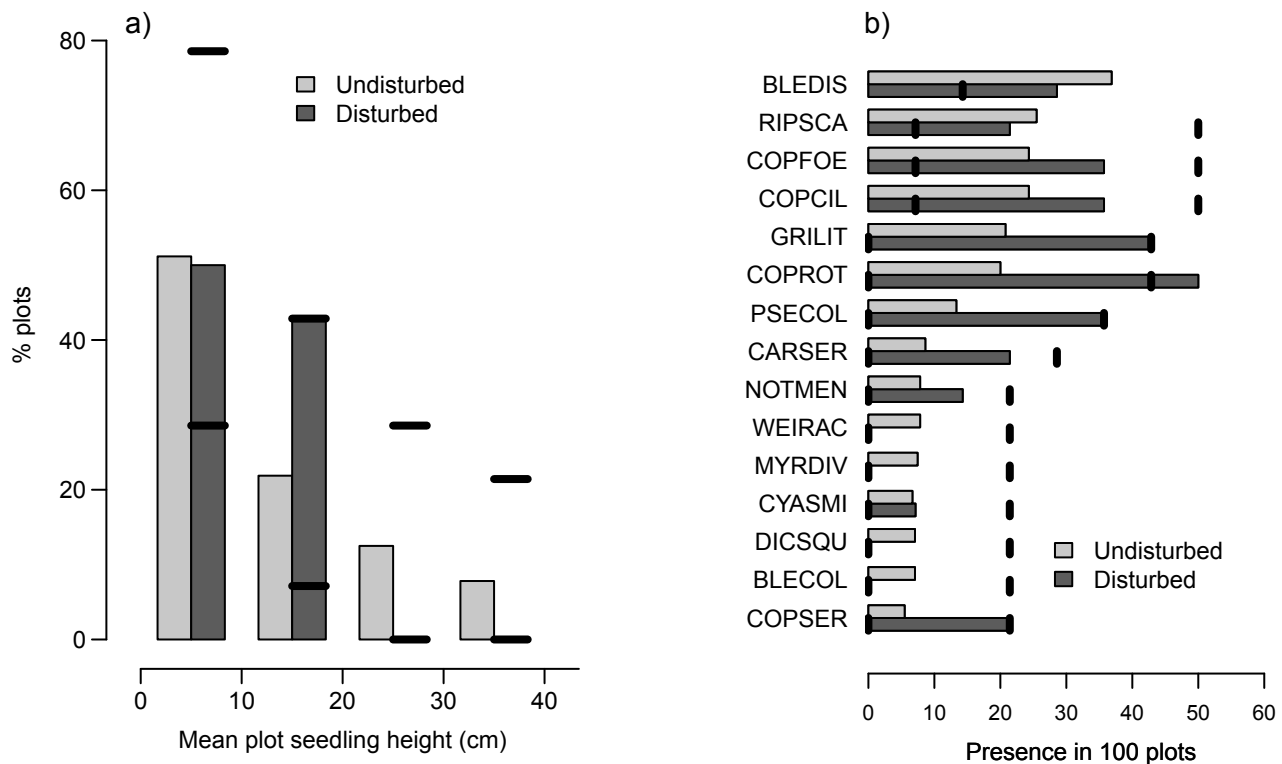


Figure 3. Frequency of mean seedling height (a) and species presence (b) at first measurement for plots that remained undisturbed by pigs ($n = 256$) or that were disturbed by pigs ($n = 14$) within the duration of the study. Bars are recorded frequencies. Bold segments represent 95% confidence intervals for a null model of randomly disturbed plots (computed as the 2.5 and 97.5 percentile of frequencies from 5000 randomised disturbances). Only common heights and species are shown (those recorded in at least 14 plots) to emphasise choice over detectability. Due to the low number of subsequently disturbed plots, the minimum non-zero frequency that could be detected within these was 7% (i.e. $1/14 \times 100$).

BLEDIS = *Blechnum discolor*, RIPSCA = *Ripogonum scandens*, COPFOE = *Coprosma foetidissima*, COPCIL = *Coprosma ciliata*, GRILIT = *Griselinia littoralis*, COPROT = *Coprosma rotundifolia*, PSECOL = *Pseudowintera colorata*, CARSER = *Carpodetus serrata*, NOTMEN = *Nothofagus menziesii*, WEIRAC = *Weinmannia racemosa*, MYRDIV = *Myrsine divaricata*, CYASMI = *Cyathea smithii*, DICSQU = *Dicksonia squarrosa*, BLECOL = *Blechnum colensoi*, COPSER = *Coprosma serrata*.

Table 2. Quantification of the standing and active microbial biomass and the functional and community structure of the soil microbial biomass in soils disturbed by pig foraging activity (disturbed) or soils that had not been recently disturbed by pig activity (undisturbed), using respiration and phospholipid determinants. PLFA = phospholipid fatty acid profiles, SIR = substrate induced respiration, SUP = substrate utilisation profile.

Variable	Units	Disturbed ($n = 10$)	Undisturbed ($n = 10$)	<i>P</i> -value
<i>Standing microbial biomass</i>				
Total PLFA	Relative nmol PLFA g^{-1} dry soil	204	210	0.83
Basal respiration	μg CO_2-C g^{-1} dry soil h^{-1}	0.5	0.2	0.05
Fungal biomass	Relative nmol PLFA g^{-1} dry soil	16	12	0.16
Bacterial biomass	Relative nmol PLFA g^{-1} dry soil	153	148	0.83
<i>Active microbial biomass</i>				
SIR	μg CO_2-C g^{-1} dry soil h^{-1}	3.5	2.4	0.30
Total SUP	μg CO_2-C g^{-1} dry soil h^{-1}	82.2	43.3	0.10
<i>Functional microbial descriptors</i>				
Microbial biomass	BR-to-SIR	0.2	0.1	0.19
Functional diversity index	Evenness %	61	59	0.36
Fungal-to-bacterial ratio	None	0.11	0.08	0.06

Table 3. Percentage (by dried weight) of the diet of New Zealand feral pigs from above- and below-ground sources in four New Zealand forests. Data sources: Waitutu (this study), Te Urewera (Thomson & Challies 1988), Auckland Island (Chimera et al. 1995), D'Urville Island (J. Parkes, unpubl. data).

Area	Waitutu	Te Urewera	Auckland I.	D'Urville I.
Number of pigs sampled	14	104	33	32
Above-ground plants	19.2	17.6	54.6	71.8
Above-ground fruit and fungi	34.6	36.7	3.7	24.1
Above-ground carrion	8.0	15.1	5.4	0.1
Below-ground plants	5.8	17.4	8.4	0.1
Below-ground animals	27.0	13.2	27.8	3.5

disturbance of between 1.4% and 3.7% over four years in the Waitakere Ranges, Auckland. Batema and Meddens (2006) reported 2.8% disturbance in an area of scrub and grassland in the Hawkeswood Range in North Canterbury. However, the area disturbed at Waitutu is similar to estimates from other places around the world, i.e. generally less than 10% (see Hone 1988, and references therein).

The density and height of seedlings was lower in areas disturbed by pigs than in areas not recently disturbed. However, when we considered plots disturbed during the study ($n = 14$) there was only marginally more reductions than there were increases in seedling density and heights, suggesting that differences between areas with and without signs of disturbance was not an immediate consequence of pigs' activities. Rather, it suggests that pigs more often disturb sites that already have fewer seedlings. Indeed, plots with shorter seedlings tended to be disturbed more often than expected by chance.

Although the composition of seedling species was similar on disturbed and undisturbed plots, four species were more common on sites disturbed by pigs. Three (*Coprosma rotundifolia*, *C. serrulata* and *Griselinia littoralis*) are palatable to deer, but one (*Pseudowintera colorata*) is highly unpalatable to deer (Forsyth et al. 2002, 2005) – and apparently to pigs. However, the explanation that pigs select these sites because they eat the seedlings and go on to dig up the soil is not supported by our diet data. A more likely explanation is that the unknown below-ground factors determining why pigs dig in the soil also favour these plant species.

Surprisingly, once a site had been disturbed there was, on average, little long-term consequences for seedling size and abundance. Net temporal changes in density and height of seedlings were minor and resembled the slow net basal changes in undisturbed sites. The long-term fate of the seedlings will, assuming the site is not re-disturbed by pigs, depend more on other herbivores such as red deer, possums and rodents and on the light environment – generally very low as a consequence of a dense fern tier on these riparian sites (Coomes et al. 2005). Deer do not usually browse plants less than c. 10 cm tall (Wilson et al. 2006; Bee et al. 2009). Therefore, they will have little direct effect on what germinates and establishes, but once the seedlings grow above about 10 cm then species palatability and accessibility to deer browsing determines seedling fate. Monitoring of seedling growth and mortality rates at Waitutu inside and outside deer fences showed lower growth and higher mortality of angiosperms compared with conifers when deer were present. Simulations of forest structure from these results predict deer browsing will eventually alter forest canopies at Waitutu (Forsyth et al. in press). Overall, our results suggest that ground disturbance by feral pigs does not have substantial impacts on most seedling dynamics at Waitutu, and hence that

their effects on forest dynamics will be minor relative to those of other invasive mammalian herbivores.

Somewhat surprisingly, the functional response of the soil microbial biomass to the activity of pigs disturbing the soil was generally neutral. While an increase in the soil microbial biomass (measured by basal respiration) associated with pig activity was marginally significant, all other indices of microbial activity showed no significant differences between disturbed and undisturbed sites. This suggests that the catabolic activity of the soil microbial community is largely mediated by the same pool of microbes in soils disturbed by pigs and in undisturbed soils. While fungal biomass and ratios of fungi to bacteria were slightly higher in disturbed soils than undisturbed soils, these differences were not significant. Further work would be required to explore these hints at differences. If they are real the effect is the opposite of what would be expected from soils disturbed by tillage. In the agricultural setting, tillage favours a shift towards increased bacterial metabolism relative to fungal metabolism (Wardle et al. 1999), suggesting that our understanding of below-ground dynamics in forest ecosystems cannot necessarily be extrapolated from the better studied managed soil systems.

It is not clear whether differences between disturbed and undisturbed sites are caused by the pigs' activities, or whether pigs select sites that already have a high fungal biomass. Our study design cannot distinguish between these alternatives. That is, pigs may be selecting sites to forage because they already have more food. Stag beetle larvae eat soil and extract nutrients from the bacteria and fungi present (Sherley et al. 1994). Pigs appear to scent below-ground food and often dig small exploratory areas (J. Parkes, pers. obs.). Presumably, if pigs find a preferred food item then they explore further and give up when satiated or when no further morsels are discovered (e.g. Brown 1988). A disturbed site at Waitutu had a much higher probability of being re-disturbed than an undisturbed site. This suggests some features of a site make it a favoured place for a pig to forage below ground. We suggest that pigs at Waitutu were foraging below-ground in patches that have more fungi and so also more stag beetle larvae. Exploring this hypothesis further would require an understanding of the spatial patterns of stag beetle larvae and their resources; and exploring the impacts on the invertebrate prey such as the stag beetles would require monitoring the changes in disturbed patches as they recover or are re-disturbed – neither of which would be a trivial exercise.

We were expecting the obvious physical soil disturbance caused by feral pigs to have overt and measurable consequences for native biota inferred by other studies (e.g. Cole & Litton 2014). However, we did not find this to be true at Waitutu. Seedlings of only a few species were affected by the soil

disturbance, and the differences in microbial activity between disturbed and undisturbed sites were few and more likely to reflect selection of such sites by pigs' prey and thus pigs' foraging than to be caused by the foraging itself.

The consequences of feral pig ground disturbance for prey populations are not known either for our site or more widely in New Zealand. Our diet study showed that the local stag beetle is potentially affected. *Dorcus helmsii* is the most widespread species of the genus (Holloway 2007), but other Lucanidae beetles are classified as nationally critical (three species) or nationally endangered (two species) (Leschen et al. 2012). More generally, it has been suggested, again from diet studies or evidence of predation, that feral pigs threaten some New Zealand invertebrate species, such as the carabid beetle *Megadromus speciosus* on Arapawa Island (Pawson & Armstrong 2007) and *Powelliphanta* snails (Walker 2003). Elsewhere, feral pigs removed between 62% and 93% of earthworms from areas studied in northern Australia (Pavlov & Edwards 1995). Whether such prima facie evidence of adverse impacts justifies controlling pig numbers and if so by how much requires more sophisticated studies to link changes in pig densities (from control or as they naturally fluctuate) to the dynamics of the prey species.

Acknowledgements

This research was funded by the former New Zealand Ministry of Science and Innovation Ecosystem Resilience Outcome-Based Investment (Contract C09X0502), investment of Landcare Research's retained earnings, and the New Zealand Department of Conservation. We are grateful for the assistance of Department of Conservation (Murihiku Area) staff in this project, and to Graham Metzger and other members of the Waitutu Incorporation for permission to work on iwi land. Johan Groeters (Wairaurahiri Jet) and the pilots at South West Helicopters assisted with transport and Peanut Osborne provided hospitality at Waitutu Lodge. We thank David Wardle for his advice on the soil analyses, Richard Heyward and Nigel Young for conducting most of the fieldwork, Morgan Coleman for analysing pig diets, and Bruce Warburton and Andrew Woolnough for comments on the manuscript. We also appreciate the thorough comments on the manuscript by Chris Lusk and two referees.

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Received 4 April 2014; accepted 3 September 2014