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The Impact of Feral Pigs on Rainforest Dynamics in North-Eastern Australia

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ABSTRACT: Feral pigs threaten biodiversity worldwide by altering ecosystem structure and function. The most noticeable effect of pigs on ecosystems is disturbed soil caused by their rooting foraging behaviour, which can impact upon invertebrate populations, nutrient cycles, and plant regeneration. In this study, we assessed the impact of feral pigs on rainforest dynamics in north-eastern Australia by comparing plots where fencing had been used to exclude pigs for 2 and 14 years with unfenced plots at continual risk to pig damage in both the wet and dry seasons. Rainforest dynamics were quantified using a range of earthworm, soil, litter, and plant characteristics, and we used mixed linear models to explain the response of these variables to both plot type and season. Our results show that feral pigs do not have a strong impact on rainforest dynamics. The only significant result was greater litter moisture in the fenced compared to unfenced long-term plots. In contrast, the majority of response variables exhibited significant seasonal differences. For the plot type and season interaction effect, the only significant result was litter biomass in the long-term plots. There was no significant difference between means for the fenced and unfenced plots within the wet and dry seasons; however, litter biomass was greater in the unfenced plots during the wet season and, conversely, greater in the fenced plots during the dry season. Overall, our results show that season has a greater impact on rainforest dynamics than feral pigs.

KEY WORDS: Australia, disturbance, exclosure, fence, feral pigs, pest management, rainforest, revegetation, *Sus scrofa*, swine

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INTRODUCTION

Invasive species are known to affect the structure and function of ecosystems and may threaten biological diversity through predation, competition, and habitat modification (Gabor and Hellgren 2000, McNeely and Schutyser 2003, Sutherst 2000). Feral pigs (*Sus scrofa*) occupy many different habitats worldwide and can cause extensive economic and environmental damage to these habitats (Gabor and Hellgren 2000, McNeely and Schutyser 2003). The most notable environmental impact of feral pigs is the soil disturbance that results from rooting foraging behaviour, which can impact upon soil structure, soil invertebrate populations, nutrient and water cycles, and plant species succession and regeneration (e.g., Choquenot et al. 1996, Mitchell et al. 2007, Nogueira-Filho et al. 2009, Siemann et al. 2009, Singer et al. 1984).

In the Wet Tropics World Heritage Area of northeast Queensland, Australia, the feral pig is regarded as the most important vertebrate pest, based on its current and potential impacts in the region and the difficulty of its control (Harrison and Congdon 2002). Although the biodiversity of rainforest fauna in this region is poor by international standards, it is rich by Australian standards (Crome 1990) and provides important habitat for the *in situ* conservation of many endemic, threatened and endangered flora and fauna (DEWHA 2008, WTMA 2006).

This study assessed the impact of feral pigs on lowland rainforest in north-eastern Australia by comparing plots where fencing had been used to exclude pigs for 2 and 14 years with unfenced plots at continual risk to pig damage in both the wet and dry seasons. We used mixed linear models to explain the response of earthworm, soil, litter, and plant characteristics to both plot type and season.

METHODS

Site Description

The study area was Cape Tribulation, located in the Wet Tropics of Queensland, Australia. The region is predominantly rainforest and was inscribed into the World Heritage List in 1988 for its outstanding natural values (DEWHA 2008, UNESCO World Heritage Centre 2009). The mean annual temperature is 26°C and the mean annual rainfall is 2,096 mm at Low Isles, the nearest weather station, approximately 35 km south of the study area (Bureau of Meteorology 2009). Rainfall is markedly seasonal with approximately 70% falling during the wet season from December to March (Bureau of Meteorology 2009).

Ten fenced and 5 unfenced plots were established in 3 lowland rainforest sites by the Queensland Parks and Wildlife Service in 1994 (R. Russell, pers. commun.). We surveyed 10 of these plots in 2008 to assess rainforest dynamics following the long-term (14-year) exclusion of feral pigs; the plots were originally classified as fenced damaged plots (n = 5), in areas where severe pig damage had already occurred, or unfenced plots (n = 5) at continual risk to pig damage. The remaining 5 plots were classified as fenced undamaged, in areas with little or no pig damage before fencing, and were not used in this study due to severe cyclone damage to 2 of the plots. We also established 2 fenced and 2 unfenced plots at each site (*n* = 12) in August 2007 to assess rainforest dynamics following the short-term (2-year) exclusion of feral pigs (Figure 1). There is no reliable estimate of pig density in the study area, but it is probably similar to reported densities of 3.3 pigs per km^2 in lowland rainforests of the dry tropics (Mitchell 2002).

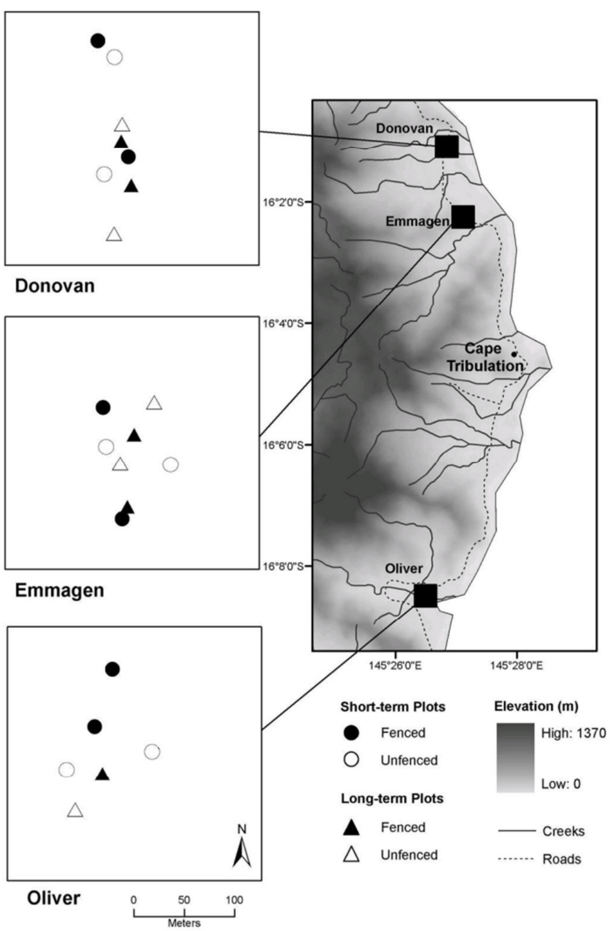

Figure 1. Three study sites located in Cape Tribulation on the northeast coast of Queensland, Australia.

Fence Design

Long-term fenced plots were built 10 × 10 m using ring-lock mesh (150 × 150 mm), and stood 90 cm above the ground. The fences were supported by steel posts at 3-m intervals and an additional steel post in each corner at a 45° angle. Plain wire was attached to the top and bottom strand of the ring-lock mesh and a secondary weld mesh fence was used at ground level, standing 40 cm high. The fences were secured at ground level with 60-cm metal pegs driven into the ground. The long-term unfenced plots were also 10 × 10 m and marked out with steel posts.

Short-term fenced plots were built 6 × 6 m using weld mesh steel (100 × 100 × 3.5 mm), and stood 90 to 100 cm above ground. The fences were buried 20 to 30 cm in the ground and were supported by steel posts at 2-m intervals where the weld mesh sheets were connected. A 5 × 5 m sampling area was marked inside the fenced plots with sand pegs. The short-term unfenced plots were 5 × 5 m and marked out with steel posts.

The fenced plots effectively excluded pigs for the duration of our study. The fence design still enabled access by smaller mammals and birds of flight, with bandicoot (*Isoodon macrourus*) diggings observed in some plots. It is possible that some large fauna were also excluded from the fenced plots, including cassowaries (*Casuarius casuarius johnsoni*), which are important for seedling dispersal and hence regeneration.

Sampling Design

The short-term plots were surveyed immediately following plot establishment, and the long-term plots were surveyed 14 years after the plots were established. The short-term plots were surveyed biannually for 2 years to determine if season had any influence on rainforest dynamics; surveys occurred in the dry (October 2007, 2008) and wet (May 2008, 2009) seasons. Similarly, the long-term plots were surveyed biannually in the wet (April 2008) and dry (November 2008) seasons, but for only 1 year.

The sampling area within each plot was divided into 1 × 1-m quadrats and the same sampling effort applied to fenced and unfenced, and short- and long-term plots. Within each plot, 3 quadrats were used to estimate earthworm biomass, 6 were used to assess soil and leaf litter attributes, and 6 were used for plant frequencies. Quadrats were systematically assigned to response variables prior to the first survey to minimise the effects of fencing on short-term plots and disruptive sampling methods.

Response Variables

Rainforest dynamics were quantified using a range of earthworm, soil, litter, and plant characteristics (Table 1). Earthworms were manually removed from the soil in the field rather than using a more rigorous method in the laboratory, due to a request from an indigenous traditional owner to limit the amount of soil we removed from the rainforest. Some small species and immature specimens may have been missed using this method; however, other studies using similar methods have recovered between 84 and 99% of earthworm biomass (Lee 1985). Soil chemical analyses were only conducted on soil collected 0 to 10 cm from the surface due to the expense of analyses if partitioned deeper into the soil horizon, and also because pig rooting in our plots did not occur >25 cm deep. Seedlings were separated into 2 categories, <10 cm and 11 to 100 cm high, as the former generally had higher frequencies and were more variable between seasons.

Soil Chemical Analysis

Soil samples were frozen during fieldwork to minimise reactions that may alter soil chemical fertility. On return to the lab, the samples were air-dried, sieved at 2 mm, and quadrat samples within the same plot (*n* = 6) were combined so there was only 1 sample per plot per survey.

Table 1. Explanatory and response variables used to assess rainforest dynamics.

Explanatory Variables	Description
Site	Three sites labelled Oliver, Emmagen and Donovan; site names relate to nearby creeks.
Plot type	Fenced or unfenced plot type.
Season	Wet or dry season.
Response Variables	**Description**
Worm biomass	Dry weight biomass (g/m^2) of earthworm cocoons and adults, including gut content. Specimens collected by hand from 30 × 20 × 10 cm samples.
Soil chemical analysis	See 'Soil Chemical Analysis' section below.
Soil moisture	Soil moisture content calculated as a mean percentage of dry soil weight from 2 samples.
Soil compaction	Dynamic drop cone penetrometer used to record the distance of penetration after each drop of the hammer to a minimum depth of 30 cm, and the mean of 5 replications calculated (MPa). Method modified from Nelson (2006).
Litter biomass	Dry weight biomass (g/m^2) of leaf litter, excluding woody stems, bark, and reproductive parts (e.g., fruits and flowers).
Litter moisture	Litter moisture content calculated as a percentage of dry litter weight.
Seedlings	Frequency of seedlings <10 cm and 11 to 100 cm high.
Saplings	Frequency of saplings, >100 cm high and diameter at breast height <10 cm.
Trees	Frequency of trees >100 cm high and diameter at breast height >10 cm.

Table 2. Untransformed mean and standard errors of response variables for short- and long-term plots in the fenced and unfenced treatments. Bold values indicate a significant difference between plot types ($P < 0.05$).

Response Variables	Short-term Plots ($F_{1, 10}$)				Long-term Plots ($F_{1, 8}$)			
	Fenced		Unfenced		Fenced		Unfenced	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Worm biomass (g/m^2)	7.2	0.8	5.2	0.7	8.9	2.6	5.0	1.5
Soil chemical analysis								
EC (dS/m)	0.062	0.006	0.061	0.006	0.080	0.006	0.060	0.006
pH_w	5.3	0.1	5.2	0.1	5.1	0.1	5.2	0.1
pH_{Ca}	4.2	0.1	4.1	0.1	4.1	0.1	4.1	0.1
NO_3-N (mg/kg)	4	1	3	1	1	<1	3	1
NH_4-N (mg/kg)	3.0	0.4	3.0	0.4	3.3	0.4	2.3	0.4
Bicarb-P (mg/kg)	8	1	7	1	9	1	7	1
Total-N (%)	0.14	0.01	0.13	0.01	0.14	0.02	0.11	0.01
Total-P (%)	0.013	0.001	0.012	0.001	0.013	0.002	0.010	0.002
Organic-C (%)	2.3	0.2	2.2	0.2	2.9	0.4	2.0	0.4
C:N ratio	17	1	17	1	20	1	17	2
Soil moisture (%)	24.2	2.1	22.1	2.9	28.5	5.1	23.8	6.2
Soil compaction (MPa)	2.1	0.2	2.3	0.2	1.6	0.2	1.7	0.3
Litter biomass (g)	320.2	24.2	281.8	25.1	313.9	44.0	334.0	55.9
Litter moisture (%)	57.5	6.1	50.1	5.7	**131.5**	**31.3**	**57.2**	**12.1***
Seedlings <10 cm (*n*)	6.6	0.8	5.7	0.6	31.5	10.7	13.5	3.7
Seedlings 11-100 cm (*n*)	1.4	0.3	1.6	0.4	15.4	3.9	3.6	1.5
Saplings (*n*)	0.4	0.1	0.3	0.1	0.2	0.1	0.6	0.2
Trees (*n*)	0.07	0.02	0.13	0.03	0.43	0.11	0.34	0.11

Electrical conductivity (EC) was measured using a 1:5 soil/water extract solution (Method 3A1), and the same suspension then used to measure pH in water (Method 4A1) and 0.01M $CaCl_2$ (Method 4B2) (Rayment and Higginson 1992). Bicarbonate extractable phosphorus was determined by manual colorimetric procedures of the Colwell method (Method 9B1); and mineral nitrogen was extracted with 2M KCl and nitrate (NO_3) and ammonium (NH_4) nitrogen measured using an automated colorimetric finish (Method 7C2) (Rayment and Higginson 1992). Total nitrogen was determined by automated colorimetric procedures using the Kjeldahl wet oxidation method (Method 7A2); and the same suspension then used to measure total phosphorus using an automated colorimetric procedure (Method 9G2) (Rayment and Higginson 1992, Taylor 2000). Soil organic carbon was determined by the Heanes wet oxidation method (Method 6B1), and the ratio of total organic carbon to total nitrogen calculated (Method 8A1) (Rayment and Higginson 1992).

Data Analysis

Quadrat means for each plot were analysed with a mixed linear model using the MIXED procedure in SAS (2004). Response variables were modelled by plot type and season with a random effects statement to account for replicate plot types within each site. A least-squares means statement was used for each fixed effect modelled using Tukey adjusted pairwise comparisons. The interaction fixed effect also used the slice option (by season) to determine if there was a significant difference between plot types within the wet and dry seasons. Short- and long-term plots were analysed separately, and any reference of plot type or season to 2 and 14 years is based on mean values over all surveyed periods.

RESULTS

The majority of response variables showed no significant difference between plot types following the short- and long-term exclusion of feral pigs (Table 2). The only significant result was greater mean litter moisture in the fenced compared to unfenced long-term plots.

In contrast, the majority of response variables exhibited significant seasonal differences (Table 3). Soil moisture, litter moisture and earthworm biomass were significantly greater in the wet than dry season for both the short- and long-term plots. Extractable phosphorus, ammonium, and carbon-nitrogen ratios were significantly greater in the wet season, but only for the long-term plots; and pH in water and calcium chloride, nitrate, and the frequency of seedlings <10 cm high were significantly greater in the wet season, but only for the short-term plots. In contrast, soil compaction was significantly greater in the dry than wet season for both the short- and long-term plots. Litter biomass, electrical conductivity, and total nitrogen were significantly greater in the dry season, but only for the short-term plots; and total phosphorus and organic carbon were significantly greater in the dry season for the short-term plots, but were significantly greater in the wet season for the long-term plots.

For the plot type and season interaction effect, the only significant result ($F_{1, 8} = 5.13$, $P = 0.05$) was litter biomass in the long-term plots. There was no significant difference between means for the fenced (235.1 ± 45.6 g/m^2) and unfenced plots (348.4 ± 102.6 g/m^2) in the wet season, and the fenced (392.6 ± 59.6 g/m^2) and unfenced plots (319.7 ± 58.4 g/m^2) in the dry season; however, litter biomass was greater in the unfenced plots during the wet season, and conversely, greater in the fenced plots during the dry season.

Table 3. Untransformed mean and standard errors of response variables for short- and long-term plots in the wet and dry seasons. Bold values indicate a significant difference between seasons (* P < 0.05, ** P < 0.01, *** P < 0.001).

Response Variables	Short-term Plots ($F_{3, 30}$)					Long-term Plots ($F_{1, 8}$)				
	Wet		Dry			Wet		Dry		
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
Worm biomass (g/m^2)	**7.3**	**0.7**	**5.1**	**0.7**	*	**10.1**	**2.7**	**3.8**	**0.9**	*
Soil chemical analysis										
EC (dS/m)	**0.049**	**0.005**	**0.074**	**0.006**	***	0.072	0.007	0.068	0.008	
pH_w	**5.4**	**0.1**	**5.2**	**0.1**	***	5.2	0.1	5.2	0.1	
pH_{Ca}	**4.1**	**0.1**	**4.1**	**0.1**	*	4.1	0.1	4.1	0.1	
NO_3-N (mg/kg)	**4**	**1**	**2**	**< 1**	**	3	1	2	< 1	
NH_4-N (mg/kg)	2.7	0.4	3.2	0.4		**3.2**	**0.5**	**2.4**	**0.4**	*
Bicarb-P (mg/kg)	7	1	8	1		**10**	**1**	**6**	**1**	**
Total-N (%)	**0.13**	**0.01**	**0.14**	**0.01**	**	0.13	0.02	0.13	0.01	
Total-P (%)	**0.012**	**0.001**	**0.013**	**0.001**	***	**0.012**	**0.002**	**0.011**	**0.002**	*
Organic-C (%)	**2.1**	**0.2**	**2.3**	**0.2**	**	**2.7**	**0.4**	**2.2**	**0.4**	*
C:N ratio	17	1	17	1		**20**	**1**	**17**	**1**	*
Soil moisture (%)	**27.6**	**2.8**	**18.7**	**1.9**	***	**38.5**	**5.4**	**13.8**	**1.5**	**
Soil compaction (MPa)	**1.9**	**0.2**	**2.6**	**0.2**	***	**1.2**	**0.1**	**2.2**	**0.3**	*
Litter biomass (g)	**234.5**	**15.4**	**367.6**	**25.0**	***	291.8	56.2	356.1	41.2	
Litter moisture (%)	**69.2**	**5.9**	**38.4**	**3.9**	***	**133.8**	**29.9**	**54.9**	**13.8**	**
Seedlings < 10 cm (*n*)	**7.6**	**0.7**	**4.8**	**0.6**	**	27.2	10.2	17.9	6.1	
Seedlings 11 to 100 cm (*n*)	1.6	0.3	1.4	0.3		9.3	3.4	9.7	3.7	
Saplings (*n*)	0.3	0.1	0.3	0.1		0.4	0.2	0.5	0.2	
Trees (*n*)	0.11	0.03	0.08	0.02		0.39	0.11	0.38	0.11	

DISCUSSION

Our results show that feral pigs do not have a strong impact on rainforest dynamics. The only significant result was greater litter moisture in the fenced plots after the exclusion of pigs for 14 years, and this was unexpected as litter biomass did not significantly differ between plot types. One plausible reason for the difference in litter moisture is that the long-term exclusion plots had greater understorey and canopy cover, reducing radiance on the forest floor and consequently decreasing evaporation. Similar to our study, Mitchell et al. (2007) also found no impact of feral pigs on litter biomass after 2 years exclusion; however, Singer et al. (1984) found significantly more leaf litter in fenced than unfenced plots after 3 years.

Earthworm biomass and the frequency of seedlings <10 cm high were not significantly different between plot types. This is consistent with Mitchell et al. (2007), who reported similar results for the same region. However, fenced plots generally had more earthworms and seedlings, particularly after 14 years pig exclusion. Ickes et al. (2001) reported that the frequency of seedlings was greater in fenced plots after the exclusion of pigs from tropical rainforest for 2 years and that seedling mortality did not differ between plot types. The different seedling frequency results between studies maybe due to environmental factors that can influence seedling germination and plant growth, such as soil moisture, irradiance, and nutrient availability (Adam 1992, Doust et al. 2006, Peverill et al. 1999). Nonetheless, Sweetapple and Nugent (2004) suggested that feral pigs had little impact on seedling regeneration, as rooted areas were generally large enough to include undug terrain on which seedlings could establish, even when soils were heavily disturbed.

Soil organic carbon was also not significantly different between plot types, and similar results have been reported by other studies (Groot Bruinderink and Hazebroek 1996, Singer et al. 1984). Although not significant, the long-term fenced plots had a higher mean for organic carbon and the carbon-nitrogen ratio than the unfenced plots, indicating that some carbon accumulation is occurring at a greater rate than its breakdown (Rayment and Higginson 1992). Siemann et al. (2009) reported significantly higher carbon-nitrogen ratios in fenced plots, but attributed the result more to reductions in soil nitrogen rather than changes in organic carbon. The higher soil nitrogen observed in unfenced plots is consistent with accelerated rates of nitrogen mineralization due to the more rapid integration of litter into the soil by feral pigs (Siemann et al. 2009). This supports Singer et al. (1984), who found increased inorganic nitrogen in soils intensively rooted by feral pigs than in areas where pigs had been excluded for 3 years. However, inorganic and total nitrogen were not significantly different between plot types in our study, and similar results have also been reported for inorganic nitrogen (Moody and Jones 2000), net nitrogen mineralization rates (Cushman et al. 2004), and total nitrogen (Groot Bruinderink and Hazebroek 1996).

In contrast to the impact of feral pigs, the majority of response variables exhibited significant seasonal differences. Greater soil and litter moisture in the wet season was expected, due to an increase in rainfall associated with this time of year. Nonetheless, there can be potential negative effects from either too little or too much rainfall. For example, rainfall influences earthworm activities, as they move deeper into the soil and remain inactive when soil moisture decreases, and they may move to the surface when soil floods and becomes anaerobic (Baker and Barrett 1994, Lee 1985). Our results support these seasonal behaviours, with significantly greater earthworm biomass found in the wet season.

Greater soil compaction in the dry season was also expected, as penetration resistance is known to increase with decreasing soil water content (Cass 1999, Spain et al. 1990, Vanags et al. 2004). However, compacted soils can then have negative effects on other dynamics, such as reducing levels of biological activity (Spain et al. 1990), restricting root growth and impeding seedling emergence (Bengough et al. 2001, Cass 1999). Russell-Smith and Setterfield (2006) found that the mortality of rainforest seedlings increased in the dry season due to declining soil moisture, and that seedling densities were greater at perennially moist than seasonally dry sites. In addition, above-average rainfall can be beneficial to seedling survival in areas with dry soil moisture, but detrimental in areas with seasonally inundated (wet) soil moisture due to drowning or soil saturation (Mitchell et al. 2007). Our study did not investigate seedling survival, but we found significantly less seedlings <10 cm high in the dry season short-term plots. Although the seasonal difference between seedling frequencies in the long-term plots was not significant, it also reflects the trend of fewer seedlings in the dry season, indicating that low soil moisture can be detrimental to seedling survival.

Soil organic carbon was significantly different between seasons, but the results were not consistent, with higher values in the short-term plots in the dry season but in the long-term plots in the wet season. Nonetheless, the carbon-nitrogen ratios indicate that the humus is generally well broken down, with the exception of some carbon accumulation occurring in the wet season long-term plots, as indicated by the higher carbon-nitrogen ratio mean (Rayment and Higginson 1992). Schuur et al. (2001) reported decreased litter decomposition rates and soil reduction-oxidation potentials with increased rainfall, and suggested that reduced soil oxygen availability in wetter soils may limit microbe activity and hence decrease decomposition rates, resulting in increased soil carbon storage. The positive correlation of soil organic carbon with rainfall (Baldock and Skjemstad 1999) supports our result of higher organic carbon in the wet season.

Strong and Mason (1999) reported that nitrate can leach deeper into the soil profile with heavy rainfall and may also decline with prolonged water-logging. However, in the short-term plots, we found that nitrate was significantly greater in the wet season and total nitrogen was significantly greater in the dry season. This is consistent with Kiese et al. (2008), who reported higher nitrification rates during the wet than dry season. However, soil nitrification rates generally peak around 60 to 65% water-filled pore space and can be reduced at higher proportions due to anaerobic conditions, such as saturated soil moisture (Kiese et al. 2008, 2005). Kiese et al.

(2008) proposed that they did not observe decreased nitrification rates in the wet season due to lower-than-average rainfall during their study, resulting in less than 65% water-filled pore space. Greater nitrate during the wet season in our study is most likely also due to lower soil moisture contents, as surveys occurred in the late-wet season, approximately 1 to 2 months after peak rainfall.

Rainforests are complex ecosystems, and generalisations regarding processes are difficult due to spatial and temporal heterogeneity in climate, soil, and topography (Doherty et al. 2000). Although the importance of characteristics are generally examined separately, in reality their influences are simultaneous and interactive (Barbour et al. 1999). Our results show that season has a greater impact on rainforest dynamics than feral pigs, in both the short- and long-term plots. However, this does not indicate whether feral pigs do or do not have an impact on individual earthworm and plant species. Soil moisture is particularly important and can affect seedling germination, plant growth, organic matter decomposition, nutrient concentrations, and earthworm activities.

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