

IMPACT OF HISTORICAL CHANGES IN LAND USE ON THE SOIL FAUNA*

Summary: Replacing native forests and grasslands with plantations, pastures and crops has resulted in both contraction of ranges and exploitation of modified habitats by native species, and both general and restricted dispersal of introduced species of soil fauna. Contraction is shown by native earthworms, land snails, ring nematodes and various arthropods, while the areas with changed land use suggest certain native insects are more numerous than 150 years ago. Damage to pastures by grass grub and porina show clearly how native species can exploit modified habitats. Introduced Lumbricidae make a positive contribution to soil processes in pastures throughout New Zealand. The distribution of cyst nematodes reflects the distribution and intensity of cultivation of the hosts with which they arrived. Changes in soil structure, such as with the elimination or introduction of earthworms, can have marked effects on other soil animals. The faunal changes found are consistent with changes in land use; habitat protection for floristic and scenic reasons will help preserve both known and unknown elements of the soil fauna.

Keywords: earthworms; insects; nematodes; distribution; range expansion; range contraction; habitat modification; land use.

Introduction

This paper reviews what is known about historic changes in the soil fauna. Unfortunately, there is no adequate baseline. Taxa as large as the 85mm tusked weta (as yet undescribed) are still being discovered (Meads, 1990). Some Maori place names refer to soil animals (e.g., Kaitoke - earthworms, Kihikihi - cicadas) and others indicate good crops which must have reflected good soil processes (e.g. Mamaranui - large cultivations, Te Ahuahu - mound for kumaras; Miller, 1971), so there are some traditional records of the soil biota.

There have been relatively few studies on the effect of land management or vegetation change on the New Zealand soil fauna excluding those related to plant pathogens (Egunjobi, 1971; Luxton, 1967; McColl, 1974; Stout and Dutch, 1967; Yeates *et al.*, 1976; Yeates, 1988).

The soil fauna here is taken to include animals in the L, F and H horizons as well as those of the mineral soil (reptiles and birds are not included in this review). All these animals feed either directly on plants or in the decomposer cycle (the grazing and detritus food webs of Petersen and Luxton, 1982) so are all dependent on plants as primary producers.

Thus, as vegetation is changed so is the optimum distribution of the soil fauna.

The most extensive changes in land use brought about by Europeans have been the removal of forests and tussock grasslands and substitution of crops, pastures (particularly ryegrass - *Lolium perenne* L. / white clover - *Trifolium repens* L.) and plantations (particularly *Pinus radiata* D. Don). The soil fauna shows the effect of these changes through (i) contraction of ranges of native species, (ii) exploitation of modified habitats by native species, and (iii) general and restricted dispersal of introduced species.

Contraction of ranges of native species

The reduction in ranges of larger soil animals readily comes to notice. However, apart from the examples given, many species are undoubtedly decreasing and their original distribution will never be known directly.

Earthworms

According to Easton (1987) the natural distribution of native perichaetine earthworms can be associated with the distribution of forests about 1840, with dry corridors acting as ecological barriers between forests. Lee (1959, 1961) has described how the range of native earthworms was decreased by habitat

*Paper presented to the joint New Zealand Ecological Society and New Zealand Society of Soil Science symposium on "Historical change in New Zealand ecosystems", Heretaunga, August 1989.

modification through forest removal. When native forest was cleared, burned, and pasture established, the soil and its biota were exposed more directly to extremes of climate as well as to stock-treading, to introduced plant species, and to a changed organic regime. These influences led to the disappearance of the native megascolecid earthworm fauna, of which only 8-12 of the approximately 170 species seem to have occurred naturally in a given area. The loss of native earthworms with deforestation presumably affected soil structure and nutrient cycling, although their contribution to forest soil processes is unknown. The reduced range of native earthworms means that there is little direct competition with introduced earthworms which exploit modified habitats (see below).

Land snails

Powelliphanta (O'Connor) snails usually live in the deep, moist, non-acidic leaf mould that accumulates under some types of forest and scrub (Meads, Walker and Elliott, 1984). They have a reduced range as a result of forest clearance. Introduced feral pigs (*Sus scrofa* L) not only eat land snails but also eat potential snail food and destroy snail habitat. In modified habitats, dehydration is a major cause of reduction in snail populations. All three introduced species of rats (*Rattus exulans* (Peale), *R. rattus* (L), *R. norvegicus* (Berkehout)) eat *Powelliphanta*, and particularly in lowland forest remnants threaten their survival (Meads *et al.*, 1984). Predation by introduced blackbirds (*Turdus merula* L) and song thrushes (*T. philomelos* Hartert) also impacts on *Powelliphanta* populations.

Current land snail species diversity on the Manukau peninsula appears to have been influenced by a number of actors (Table 1). The 57 species found in Jones Bush by Solem, Climo and Roscoe (1981) are not regarded as the potential maximum diversity (82 species naturally occur on the peninsula). Solem *et al.* (1981) suggested that *Omphalorissa*

purchasi (Pfeiffer) (Hydrocenidae) and *Laoma leimonias* (Gray) (Runctidae) could be placed in Crispes Bush to restore a natural component to the fauna.

Cromwell chafer

This flightless, plant-feeding scarab beetle (*Prodontria lewisi* Broun) is now confined to less than 100 hectares near Cromwell, although if it has always been restricted to its existing soil types (Cromwell sand and Molyneux very shallow loamy sand), its original distribution appears to have been only some 325 hectares (Watt, 1979; Anon., 1984). While the combination of habitat modification and predation by the introduced little owl (*Athene noctua* (Scopoli)) appears to limit *P. lewisi*, this scarab also illustrates the very narrow habitat range of some species.

Giant and tusked wetas (Stenopelmatidae)

These forest-dwelling animals with a two year life-cycle are generally vegetarian. Conversion of forest and scrubland to agricultural use has greatly reduced their available habitat (Buller, 1867). While their size (up to 71g) prevents giant wetas (*Deinacrida* White) jumping, their defences are a tough exoskeleton and heavily spined rear legs. On the other hand, tusked wetas ("*Hemiandrus*" Ander) jump well but do not have spiny rear legs. Predation by rats has significantly reduced the range of these wetas. The tusked weta of Middle Island in the Mercury Group, the largest (85mm long) of New Zealand's ground burrowing wetas, has survived in milk tree (*Streblus banksii* (Cheeseman) C. Webb) forest as a result of the absence of mammalian predators (Meads, 1990). However, with the succession of vegetation and the action of burrowing seabirds, this species is threatened by habitat change (M.J. Meads, *pers. comm.*).

Ring nematodes

These superficially annulated nematodes are frequent in samples from Chatham Island, Campbell Island, and the Auckland Islands. They occur regularly in mainland samples from both undisturbed native forests and tussock grasslands although there are sites at which they are replaced by related, more drought tolerant genera. Of 38 mainland forest sites studied, ring nematodes have been found at 22 (58%). However, they are uncommon in improved pastures, having been found at only 3 of 127 (2.3%) sites sampled (Yeates, *unpubl.*). In native forests, species of *Criconemoides* Taylor are more abundant in the organic horizons than the mineral soil, and at a single site there may be vertical separation of species on a size basis (Fig. 1), with a larger species in the F horizon than in the more compact H horizon. After conversion to pasture *Criconemoides* is generally

Table 1: Number of native land snail species found in six forest remnants on Manukau Peninsula (adapted from Solem *et al.*, 1981).

Locality	Species	Forest status
Jones Bush	57	Good. Representative lowland bush
Crispes Bush	48	Regenerating. Now fenced
Harveys Bush	44	Trampled by stock
Awhitu Gully	32	Milled for kauri; limited stock access
Limestone Downs	32	Burnt in part; too degraded to reach high diversity
Track Gully	24	Pumping station; too small to reach high diversity

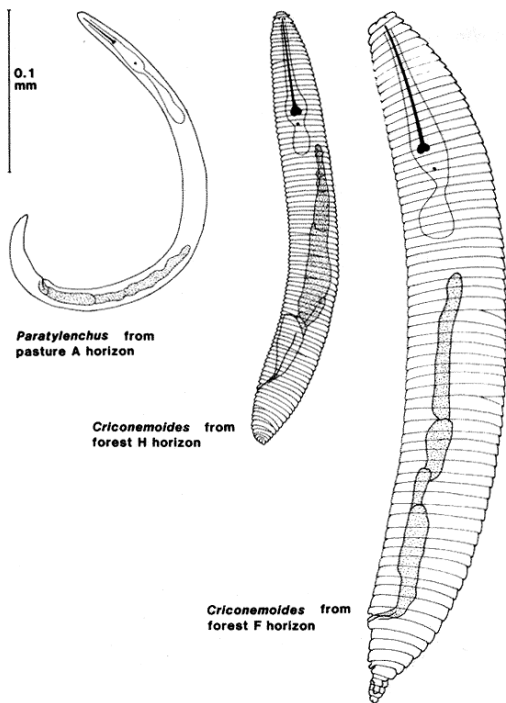


Figure 1: General body form and relative size of three criconematid nematodes (Nematoda: Tylenchida: Criconematidae) found in the central North Island. The two 'Criconemoides' (ring nematodes) are frequent in the native forest of Manganahuehu Scenic Reserve while the improved pasture on the opposite side of the road contains abundant Paratylenchus (pin nematode) but no Criconemoides (Yeates, unpubl.).

absent, but the related, smaller *Paratylenchus* Micoletzky (Fig. 1) is often abundant. Forest clearance has led to a reduction in the range of ring nematodes.

Soil and litter fauna

One of the characteristics of the indigenous soil and litter fauna is the low diversity of ants (Hymenoptera: Formicidae), apparently a reflection of cooler

temperatures (Moeed and Meads, 1986). In their absence, there has been a radiation of small invertebrates including Coleoptera, Hemiptera, Thysanoptera and Mollusca. The insects found in six Westland forest types by McColl (1974), show the diversity of the litter and soil fauna and how it is markedly reduced with the imposition of a *Pinus radiata* stand (Table 2). An average of 12 taxa of Curculionidae were found in native forests, but none were detected in the *P. radiata* plantation.

Exploitation of modified habitats by native species

In many cases exploitation of modified habitats is indicated only by association of some native species with introduced plants whose localised abundance provides at least local opportunities not available 150 years ago.

Native bees

The Colletidae and Halictidae are solitary soil-nesting bees and while soil textural preferences range from high clay content to shifting sand, most known nests occur in sites disturbed by man (Scott, 1984). They visit and collect nectar and pollen not only from native plants (especially Myrtaceae, Fabaceae, Asteraceae) but also from introduced plants including lucerne (*Medicago sativa* L), sweet clover (*Melilotus alba* Medikus), yarrow (*Achillea millefolium* L), kiwifruit (*Actinidia deliciosa* (A. Chev) Liang et A. R. Ferg.), carrots (*Daucus carota* L), brassicas (*Brassica* L), *Prunus* L and *Pyrus* L (Scott, 1984). Given the area under such introduced crops and the exploitation of disturbed sites for nests, these bees have probably increased in numbers in the past 150 years. Donovan (1980) reported some native bee species outnumber honey (*Apis mellifera* L) and bumble bees on many native and introduced plants, indicating that they are enjoying considerable competitive success.

Crickets

Small, black field crickets of the genus *Pteronemobius* Jacobson (Gryllidae) are found throughout most of

Table 2: Taxa of Lepidoptera and Coleoptera found in L. F. H and A horizons of six Westland forest types (adapted from McColl, 1974).

Forest type	Landform	Lepidoptera	Coleoptera: Curculionidae	Other Coleoptera	Total Coleoptera
Podocarp/beech	terrace	16	14	48	62
Podocarp/beech	slope	20	17	52	69
Podocarp/beech	steep land	13	12	31	43
<i>Nothofagus menziesii</i> (Hook. f)	terrace	14	8	39	47
Podocarp/hardwood	terrace	3	9	21	30
<i>Pinus radiata</i>	terrace	2	0	16	16

lowland New Zealand and show a distinct preference for short to medium height grasses which are unmown or lightly grazed. According to McIntyre (1978) their small size enables them to move easily beneath the thin layer of litter which typically covers grassland soils. Grazing of tussock grasslands may have reduced population densities of *Pteronemobius*, but they have been able to increase their range by exploiting lightly grazed pasture areas previously under forest.

Grasshoppers

Two species of native shorthorned grasshoppers (Acrididae) occur in the North Island and 13 in the South Island rangelands; many species have restricted distribution in the tussock grasslands. While such alpine grasshoppers commonly consume no more than 1-2% of annual primary production, in some areas up to 59% of the annual foliage production by some plant species can be grazed and such grazing may lead to local death of plant populations (White, 1978). Due to modifications to the tussock grasslands over the past 120 years, vegetation conditions are probably more favourable to grasshoppers than previously and grasshopper damage of the habitat may be greater than previously (Scott, 1984).

Huhu

Prionoplus reticularis White (Coleoptera: Cerambycidae) qualifies as a member of the soil fauna because its larvae inhabit dead logs, of both native and exotic trees, which comprise part of the organic horizons. It was recognised by the Maori as a food source. Rapid colonisation of wind-thrown logs (particularly *Pinus radiata*) by this large species give it economic importance in exotic forestry operations, and its exploitation of this modified habitat means it is assured of a widespread distribution.

Compressed weevil

Ireninus compressus (Broun) (Curculionidae) is an endemic species, with adults up to 6mm long, found throughout New Zealand. Adults may cause damage to introduced blackcurrants (*Ribes nigrum* L), carrots and brassicas (Scott, 1984). The larvae take about 9 months to mature and live underground, feeding on roots. May (1966) reported larvae occur beneath pastures from Canterbury to North Auckland. Thus, the species remains widespread and abundant, having successfully exploited modified habitats.

Ichneumonids

Two species (*Pterocormus promissorius* (Erichson) and *Lissopimpla excelsa* (Costa)) are endemic to Australasia and parasitise the cosmopolitan armyworm (*Mythimna separata* (Walker)). *P. promissorius* parasitises the

pupation cells in the topsoil after digging, whereas *L. excelsa* uses a long external ovipositor to infect buried hosts (Scott, 1984). As European management has led to population eruptions of armyworms these ichneumonids have benefitted - however, a strain of the braconid wasp *Apanteles ruficrus* (Haliday) introduced in 1971/72 as a biological control agent for armyworm (Hill and Atkins, 1983) may have offset any such advantages for the ichneumonids.

Grass grub

Costelytra zealandica (White) is a native insect which occurs throughout New Zealand and is still found in indigenous tussock grasslands; at Cass, Merton (1980) found up to 100 larvae m⁻². Adult beetles do little damage to pasture although they will feed on leaves of many brassicas, trees and shrubs (including kiwifruit); larval densities in pasture soil may exceed 1000 m⁻² (East and Pottinger, 1975) and damage to the roots of introduced, permanent pasture can be devastating. Ryegrass and white clover are highly susceptible to attack, but lucerne, lotus (*Lotus* L), phalaris (*Phalaris aquatica* L), tall fescue (*Festuca arundinacea* Schreb.) and cocksfoot (*Dactylis glomerata* L) are resistant to or tolerant of larval attack (Scott, 1984). Withdrawal of DDT and other organochlorine insecticides in the late 1960s led to major damage problems in pastoral agriculture.

Perhaps a decade after pesticides were withdrawn grass grub populations collapsed due to some degree of re-establishment of natural control by pathogens such as protozoa (*Nosema* Niigeli, *Mattesia* Naville), milky disease (*Bacillus* Cohn) and amber disease (*Serratia* Bizio). East and Wigley (1985) described such biological factors underlying the collapse of grass grub populations in the central North Island. Other diseases include nematodes and tachinids. Grass grub populations can also be influenced by manipulating sward height and stock trampling, to influence egg survival and larval mortality (East and Pottinger, 1983).

When integrating pathogens into pest management it is important to remember the third dimension of natural systems. This was emphasised by the results of Dale (1966) who found greater nematode parasitism of grass grub larvae around the roosts of starlings (*Sturnus vulgaris* L) and magpies (*Gymnorhina tibicen* (Latham)) than in open spaces. Indigenous birds feeding on localised populations of grass grub were not as gregarious as introduced starlings and magpies. 150 years ago transmission of parasites between grass grub larvae was presumably dependent upon contact between grass grubs or with their faeces. The nest-boxes for starlings which appeared on farms in the 1970s may have aided transmission of pathogens - if avian predation did not inhibit pathogen spread by decreasing host density.

The presence of shrubs in grasslands may be important for *Proscissio cana* Hutton (Diptera: Tachinidae) to have significant effect on grass grub numbers (Merton, 1980). Australian work (Davidson, 1981) has also drawn attention to the entomological benefits of trees in rangelands, and in New Zealand the enforced patchiness of such trees could increase visual diversity and have positive ecological effects on land use.

Porina

Species of *Wiseana* Viette are another native insect problem in improved pastures, with the caterpillars emerging from tunnels up to 45cm deep to feed on foliage of many introduced plant species. Management which increases humidity near the soil surface favours larval survival. As with grass grub, biological agents (viruses and nematodes; Longworth, 1982) have potential for controlling these native species which are successfully exploiting the modified environment.

Plant feeding nematodes

Establishment of extensive pastures has provided opportunities which have been exploited by nematodes of the genus *Paratylenchus* (Fig. 1). Although present in low numbers in forests, *Paratylenchus* populations in pasture often exceed 400 000 m⁻² (Yeates, 1981a). Further work is required to document increases in the abundance of other plant-feeding nematodes following the conversion of forests to pasture lands.

Parasites of the soil fauna

Just as soil animals are integral parts of soil processes those animals are part of another matrix which includes factors such as parasites controlling their populations. When an animal species becomes extinct so, too, do its obligate parasites. The population eruptions of grass grub and porina after the removal of organochlorine insecticides were in part due to the loss of the natural infection by parasites, and it may take a decade for surviving parasite populations to develop to levels at which they again have a dampening effect on population oscillations, although the treeless structure imposed on the landscape by the present land use may limit their effectiveness. There are undescribed collections of nematodes parasitic in native earthworms and land snails (Yeates, *unpubl.*). There are Diptera which have larval stages parasitic in earthworms (*Pollenia* Robineau-Desvoidy; see Dear, 1985). Our knowledge of the biology and taxonomy of such parasites is meagre.

General and restricted dispersal of introduced species

Few soil animals have been deliberately introduced, but available data shows that the introduced species present have achieved differing degrees of distribution.

Cyst nematodes

Clover cyst nematode (*Heterodera trifolii* Goffart), which is of Mediterranean origin, is now widespread in our improved pastures, being found in 116 of 127 pasture sites sampled (Yeates, *unpubl.*). Although its cysts are not particularly resistant to desiccation the species has become as widespread as its principal host, white clover. In contrast, *Heterodera fici* Kir'yanova, whose chief host is the fig (*Ficus carica* L.), is known from only one tree in Nelson and it probably arrived there from Europe with that tree. Potato cyst nematodes (*Globodera rostochiensis* (Wollenweber) and *G. pallida* (Stone) are a pest on potatoes (*Solanum tuberosum* L.) and have been detected in some important potato growing areas (Pukekohe, Opiki, Marshlands, Outram) and in many home gardens; in most cases populations have reached damaging levels only after many years of limited crop rotation; its abundance is limited by the availability of suitably cropped fields. These two species appear to have reached New Zealand from South America via Europe where they have been an economic problem for over 100 years. Cereal cyst nematode (*Heterodera avenae* Wollenweber) is known from South Canterbury, and as with potato cyst nematode, it reaches large, damaging populations only when suitable hosts are grown repeatedly.

Bumble bees

Bumble bees (*Bombus* Latr.) are beneficial insects which nest about 10cm below the soil surface. They were introduced to improve pollination of clovers, and despite human attempts to disperse them two of the four species have restricted distributions. Their distribution appears to be partly restricted by a relative dearth of suitable nest sites (Donovan and Wier, 1978).

Earthworms

While there has been dramatic reduction in the range of the native Megascolecidae due to European changes in land use, introduced species of Lumbricidae have benefitted. *Aporrectodea caliginosa* (Savigny) is the most widespread of the peregrine species (i.e., species transported by man or whose dispersal has been facilitated by man) of earthworms in New Zealand (Lee, 1987). Improvements of soil structure, soil hydraulic characteristics and

productivity following accidental or deliberate introduction are so dramatic and cost-effective (Stockdill, 1982) that there has been a campaign to extend the distribution of a range of potentially beneficial earthworm species in pastures (Springett, 1987). The pasture management regime adopted affects not only such beneficial earthworms but also detrimental species such as grass grub and porina (Brock, 1986).

Work in New Zealand was the first to demonstrate that the effects of lumbricid activity on soil affected soil nematode populations, in addition to the 'agronomic' characters already mentioned (Table 3). In general, introduction of lumbricids to New Zealand pastures leads to a 50% reduction in nematode abundance and a swing in their trophic habits from bacterial feeding to fungal feeding (Yeates, 1981b). In Wehenga silt loam there was a remarkable shift in the size composition of the mononchid nematode guild (Table 4); within this group the decrease in numerical abundance is offset by a shift in favour of larger genera so the biomass is unchanged. Earthworm activity also affects collembolan populations. Marinissen and Bok (1988) found that in the presence of earthworms, collembola occurred deeper in the soil (this may have protected them from adverse climatic conditions) and were larger than in the absence of earthworms.

While lumbricids flourish under pastoral conditions, when land use again changes to agroforestry their populations may effectively disappear (Table 5). However, I know of no such work in which changes in earthworms have been followed in a direct indigenous / exotic forest conversion.

Table 3: *Effects of Lumbricidae on soil properties and soil faunal populations in Wehenga silt loam under pasture (0-10cm soil depth; from Stockdill, 1982 and Yeates, 1981b).*

Property/population	Worms absent	Worms present
Field capacity (% dry weight)	42.0	51.7
Wilting point (% dry weight)	15.6	16.2
Available moisture (mm area ⁻¹)	18.3	31.0
Organic carbon (%)	3.54	4.46
Infiltration (mm h ⁻¹)	14.0	26.4
Herbage Dry Matter (kg ha ⁻¹)		
Sept-May 65-66	9 400	12 100
Sept-May 66-67	7 800	8 490
Plant and soil nematodes (m ⁻²)	10 425 000	5 297 000
Comprising "fungal feeders"	1 549 000	1 115 000
"bacterial feeders"	5 203 000	461 000
"plant feeders"	2 926 000	2 070 000
"predators"	244 000	89 000
other feeding types	503 000	1 562 000

Table 4: *Effect of presence or absence of worms on mononchid nematodes in Wehenga silt loam (after Yeates, 1987).*

	Worms absent	Worms present
Abundance (m ⁻²)		
<i>Clarkus</i>	157900	42700
<i>Cobvonchus</i>	83600	5000
<i>Iotonchus</i>	2400	41300
Total	244000	89000
Biomass (mg m ⁻²)		
<i>Clarkus</i>	179	56
<i>Cobbonchus</i>	85	7.4
<i>Iotonchus</i>	23	222
Total	287	285.4
Length of females (μm)		
<i>Clarkus</i> (n=131)	1269	
<i>Cobbonchus</i> (n=29)	1604	
<i>Iotonchus</i> (n=8)	3586	

Table 5: *Effect of agroforestry with Pinus radiata plantations at 3 densities on lumbricids (from Yeates, 1988).*

<i>Pinus radiata</i> density (no. ha ⁻¹)	lumbricid density (no. m ⁻²) after 2 year	alter 13 year	Pasture production at 12y (kg dry matter ha ⁻¹)
0	547	378	9922
50	435	283	8515
100	304	150	5891
200	389	0	1265
400	287	1	c300

Conclusion

In the past 150 years, changes in land use have greatly influenced the distribution and abundance of the soil fauna. While many native species have suffered, others such as grass grub and porina have been able to exploit the modified environment. Some introduced species such as bumble bees and earthworms have been deliberately dispersed for economic benefit while introduced plant pathogenic nematodes show ranges reflecting both climate and our management of their host plants. Changes in soil structure associated with earthworm activity can have dramatic effects on the ecology of other soil animals.

While the known changes are not unexpected it is hoped that preservation of unknown elements of the native soil fauna and its parasite fauna will be adequately achieved by habitat protection for more obvious floristic and scenic reasons.

Acknowledgements

I am grateful to M.J. Meads of DSIR Land Resources for access to his unpublished work on wetas and for reviewing the manuscript. Dr J.M.

Marshall of DSIR Plant Protection confirmed the information on cyst nematode distribution. Comments by a referee (T. Jackson, MAF Technology) led to a significant improvement in the paper.

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