INTRODUCED BROWSING MAMMALS IN NEW ZEALAND NATURAL FORESTS: ABOVEGROUND AND BELOWGROUND CONSEQUENCES

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Abstract. Forest dwelling browsing mammals, notably feral goats and deer, have been introduced to New Zealand over the past 220 years; prior to this such mammals were absent from New Zealand. The New Zealand forested landscape, therefore, presents an almost unique opportunity to determine the impacts of introduction of an entire functional group of alien animals to a habitat from which that group was previously absent. We sampled 30 long-term fenced exclosure plots in indigenous forests throughout New Zealand to evaluate community- and ecosystem-level impacts of introduced browsing mammals, emphasizing the decomposer subsystem.

Browsing mammals often significantly altered plant community composition, reducing palatable broad-leaved species and promoting other less palatable types. Vegetation density in the browse layer was also usually reduced. Although there were some small but statistically significant effects of browsing on some measures of soil quality across the 30 locations, there were no consistent effects on components of the soil microfood web (comprising microflora and nematodes, and spanning three consumer trophic levels); while there were clear multitrophic effects of browsing on this food web for several locations, comparable numbers of locations showed stimulation and inhibition of biomasses or populations of food web components. In contrast, all microarthropod and macrofaunal groups were consistently adversely affected by browsing, irrespective of trophic position. Across the 30 locations, the magnitude of response of the dominant soil biotic groups to browsing mammals (and hence their resistance to browsers) was not correlated with the magnitude of vegetation response to browsing but was often strongly related to a range of other variables, including macroclimatic, soil nutrient, and tree stand properties.

There were often strong significant effects of browsing mammals on species composition of the plant community, species composition of leaf litter in the litter layer, and composition of various litter-dwelling faunal groups. Across the 30 locations, the magnitude of browsing mammal effects on faunal community composition was often correlated with browser effects on litter layer species composition but never with browser effects on plant community composition. Browsing mammals usually reduced browse layer plant diversity and often also altered habitat diversity in the litter layer and diversity of various soil faunal groups. Across the 30 locations, the magnitude of browser effects on diversity of only one faunal group, humus-dwelling nematodes, was correlated with browser effects on plant diversity. However, browser effects on diversity of diplopods and gastropods were correlated with browser effects on habitat diversity of the litter layer. Reasons for the lack of unidirectional relationships across locations between effects of browsers on vegetation community attributes and on soil invertebrate community attributes are discussed.

Browsing mammals generally did not have strong effects on C mineralization but did significantly influence soil C and N storage on an areal basis for several locations. However the direction of these effects was idiosyncratic and presumably reflects different mechanisms by which browsers affect soil processes. While our study did not support hypotheses predicting consistent negative effects of browsing mammals on the decomposer subsystem through promotion of plant species with poorer litter quality, our results still show that the introduction of these mammals to New Zealand has caused far-ranging effects at both the community and ecosystem levels of resolution, with particularly adverse effects for indigenous plant communities and populations of most groups of litter-dwelling mesofauna and macrofauna.

Key words: alien organisms; browsing; decomposer food web; deer; goats; herbivory; macrofauna; mesofauna; microbial biomass; microfauna; New Zealand forests; plant litter.

Manuscript received 6 June 2000; revised 22 February 2001; accepted 23 February 2001; final version received 16 March 2001.
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INTRODUCTION

In terrestrial ecosystems, browsing by herbivores has important indirect effects on belowground properties and processes, in particular the mineralization of soil C and N (Holland et al. 1992, Molvar et al. 1993, Pastor et al. 1993, Frank and Groffman 1998). Several mechanisms have been proposed to explain how herbivory affects soil processes and the organisms that govern these processes (Bardgett et al. 1998b), but three emerge as being consistently important. First, animals return organic matter and nutrients to the soil in relatively labile forms as dung and urine, which may stimulate soil activity (Ruess and McNaughton 1987, Bardgett et al. 1998a, Mulder and Ruess 1998). Second, herbivory can affect soil biota by inducing physiological changes at the whole-plant level, either by altering the biomass and productivity of the browsing plant (Ruess et al. 1998; but see McNaughton et al. 1998), or by inducing the browsed plant to produce biomass, and subsequently litter, of altered quality and decomposability (Seastedt et al. 1988, Tuomi et al. 1988, Kielland et al. 1997, Kaitaniemi et al. 1998). Third, on a longer temporal scale, browsing mammals preferentially feed upon plant species with a higher resource quality (Coley et al. 1985, Grime et al. 1996), often resulting in their replacement in the plant community by species which are better defended but have poorer resource quality (Augustine and McNaughton 1998, Ritchie et al. 1998), ultimately causing retardation of soil processes (Pastor et al. 1988, 1993; but see De Mazancourt and Loreau 2000). The effects of herbivores on soil processes via the above mechanisms are increasingly recognized as important in influencing plant nutrition and plant growth, resulting in major feedbacks between the aboveground and belowground compartments of ecosystems (McNaughton et al. 1988, De Mazancourt et al. 1998, 1999, Mulder and Ruess 1998).

While research on how herbivores affect soil processes is increasing, remarkably little is known about how they influence the components of the soil food web which ultimately regulate these processes. However, there is evidence that the effects of herbivory on the microbial biomass can be positive (Ruess and Seagle 1994, Bardgett and Leemans 1995, Stark et al. 2000), negative (Pastor et al. 1988), or neutral (Wardle and Barker 1997) depending on the system being considered. There is some evidence from the few studies available that aboveground herbivory may also influence higher trophic levels of decomposer food webs, for example microbe-feeding nematodes (Yeates 1976, Seastedt et al. 1988, Merrill et al. 1994), microarthropods (Leetham and Milchunas 1985, Bardgett et al. 1993), litter-associated gastropods (Suominen 1999), and various soil-associated macrofauna (Suominen et al. 1999). Foliar herbivory can also alter the composition of specific groups of soil biota (Milchunas et al. 1998, Suominen 1999, Suominen et al. 1999) although Milchunas et al. (1998) concluded that these effects tended to be small especially when compared with the effects of herbivores on composition of aboveground biota such as plants and birds.

The influence of herbivory on the diversity (including taxonomic richness) of consumer groups comprising the decomposer food web remains largely unexplored. Herbivory often increases plant diversity (Zeevalking and Fresco 1977, Collins et al. 1998), probably by reducing competitive exclusion (Grace and Jutila 1999), although both positive and negative effects on diversity are possible depending on the mechanisms involved (Olff and Ritchie 1998, Proulx and Mazumder 1998). The effects of plant diversity on decomposer diversity are poorly understood, although reasons can be presented both for and against a relationship between decomposer diversity and plant diversity (Wardle et al. 1999, Hooper et al. 2000). Suomonen (1999) found gastropod diversity was consistently reduced by browsing while Leetham and Milchunas (1985) and Wall-Freckman and Huang (1998) found no effect of browsing on the diversity of microarthropods and nematodes, respectively.

Despite the dearth of information, the potential effects of browsers on populations of soil organisms and soil community structure may control ecosystem processes in the longer term (Milchunas et al. 1998). The composition of the decomposer food web can operate as a key regulator of mineralization processes (Ingham et al. 1986, Bengtsson et al. 1996), plant nutrient acquisition (Setälä and Huhta 1991), and ultimately plant growth (Alphei et al. 1996, Laakso and Setälä 1999). The indirect influence of browsing on soil communities is therefore likely to operate as a critical link in maintaining feedbacks between the soil subsystem and the plant–herbivore subsystem (e.g., McNaughton et al. 1988, Pastor et al. 1988, De Mazancourt et al. 1998, Mulder and Ruess 1998).

Several species of browsing mammals were liberated in New Zealand between the 1770s and 1920s, including Capra hircus L. (feral goats) and deer (most notably Cervus elaphus scoticus Lüömb [red deer]); prior to this, forest dwelling browsing mammals were absent from New Zealand. Since their introduction, browsing mammals have become widespread and abundant throughout most of the forested landscape of New Zealand. Several studies have shown, mainly through the use of fenced exclosures, that introduced browsing mammals commonly reduce vegetation density in the browse layer and alter vegetation composition by favoring unpalatable ferns and monocotyledonous species at the expense of faster-growing, palatable, broad-leaved species (Conway 1949, Williams 1955, Wallis and James 1972, Jane and Pracy 1974, Smale et al. 1995). New Zealand’s native mega-herbivores, moas (Aves: Dinornithiformes), became extinct through human hunting probably around or before AD 1400 (Hol-
daway and Jacomb 2000). While the ecological impact of these browsers remains unclear, their browsing habits were probably very different from those of deer and goats (Atkinson and Greenwood 1989, Caughey 1989) and the effects of moa browsing on vegetation are believed to have been considerably less severe than those of introduced browsing mammals (McGlone and Clarkson 1993).

There is increasing interest in understanding the ecological significance of alien organisms in new environments (Vitousek et al. 1997). The New Zealand forested landscape presents an almost unique opportunity to determine the impacts of introducing an entire functional group of alien organisms (forest-dwelling browsing mammals) to an environment from which that group was absent. In this context, we aimed to test the following four interrelated hypotheses so as to better understand the community- and ecosystem-level impacts of introduced browsing mammals in New Zealand, with emphasis on effects of browsers on the biotic components of the decomposer subsystem, through the use of long term animal exclosure plots:

**Hypothesis 1.**—Browsing greatly reduces vegetation density in the browse layer and shifts dominance to unpalatable plant species; this, in turn, adversely affects soil chemical properties and various constituents of the decomposer food web. This hypothesis is consistent with the findings of Pastor et al. (1988, 1993) for boreal forests, and builds upon earlier studies in New Zealand forests suggesting that browsing mammals induce dominance of certain plant functional types above others (Wallis and James 1972, Jane and Pracy 1974).

**Hypothesis 2.**—Browsing mammals alter plant community species composition, which, in turn, influences the species composition and quality of litter, and therefore the composition of the main taxa of soil organisms. This hypothesis predicts that the magnitude of effects of browsing mammals on soil communities will be determined by the magnitude of effects of browsers on plant community composition.

**Hypothesis 3.**—Browsing mammals may induce positive or negative changes in plant diversity, and these effects are matched by corresponding predictable shifts in the diversity of litter types entering the decomposer subsystem, and ultimately in the diversity of various components of the belowground biota.

**Hypothesis 4.**—Reductions in populations and biomasses of soil biota due to browsing will reduce belowground processes such as C mineralization, resulting in a greater storage of C and N on an areal basis in the litter and humus layers of browsed forests.

**Methods**

**System and sampling strategy**

Our study utilized a series of long-term, fenced, browsing mammal exclosures. From the 1950s to the 1980s the former New Zealand Forest Service (NZFS) established several hundred exclosures throughout New Zealand to assess the impacts of introduced deer and goats on vegetation in natural forests. With the dissolution of the NZFS in the late 1980s, maintenance of the vast majority of these exclosures was discontinued and many are no longer effective at excluding browsing mammals, although it is likely that over 100 still remain in adequate condition. These exclosures have the advantage of being scattered throughout most of New Zealand’s forest types and climatic regions, and are sufficiently distant from major tracks and routes to reduce the incidence of human interference; many can only be accessed by several hours walking or by helicopter or boat. They represent a unique resource for addressing questions about how the introduction of a whole functional group of alien animal species can alter ecosystem properties.

For the present study, we selected 30 exclosures, representing a wide geographic range and encompassing most of New Zealand’s major forest types (Fig. 1, Table 1; all sites subsequently referred to by the codes in the left hand column of Table 1). Only exclosures that were at least 13 yr old were considered. The main browsing mammal in most locations was *C. elaphus*, with several locations supporting *C. hircus*, and with the dominant browser in some areas being *Dama dama* L. (fallow deer), *Odocoileus virginianus* Zimmerman (white tailed deer), or *Macropus eugenii* Desmarest (Dama wallaby). These exclosures do not exclude introduced arboreal browsing mammals such as *Trichosurus vulpecula* Kerr (brushtail possum), or introduced rodents. Twenty nine of the exclosures were established by the NZFS, while one (S21) was set up by the University of Canterbury’s School of Forestry. Most exclosures were ~400 m² or 20 × 20 m (mean ± 1 SE = 431 ± 76 m²). Each exclosure was sampled once between 25 September 1997 and 26 May 1999. While we acknowledge that a one-time sampling cannot reflect temporal trends in our response variables, we restricted our sampling to the spring and autumn months to avoid any extremes of temperature and moisture that may have confounded the results.

The exclosures were not initially replicated, a problem that characterizes the vast majority of published exclosure studies (see Stohlgren et al. 1999), particularly those that involve older exclosures. However, because most of the exclosures in our study were relatively large and because the focus was on belowground properties effectively sampled over smaller spatial scales, we employed a stratified sampling regime (cf., Stark et al. 2000). For each location we set up four subplots (usually 4 × 4 m) per exclosure, with one subplot in each corner, and each subplot usually at least 1.5 m away from the fence; adjacent subplots were at least 8 m apart in the vast majority of cases. We also set up four 4 × 4-m subplots outside the exclosure, each paired with one of the inside-exclosure subplots.
and located at least 3 m outside the fence. The four pairs of subplots (each consisting of an inside-exclosure subplot and an outside-exclosure subplot) served as the unit of replication for each location.

For each subplot at each location we measured both browse-layer vegetation (0–2 m height layer) and ground-layer vegetation (0–10 cm height layer). Density of browse-layer vegetation was measured using a height frequency method (Scott 1965, Dickinson et al. 1992). A 2-m pole marked at 10-cm increments was positioned vertically, and for each plant species the presence of any vegetation intercepting a prescribed cylinder (adjacent to the pole and indicated by horizontal circular guide rings attached to the pole) of diameter 5 cm was recorded for each of the twenty 10-cm height classes. This pole was positioned twenty

Fig. 1. Distribution of the 30 locations that were sampled. Location codes are as for Table 1.
times within each subplot (in a 4 × 5 grid), resulting in a maximum possible score of 400 intercepts for each species in the browse layer. Ground layer vegetation was assessed in each subplot by using a point intercept method (Goodall 1952). A frame with five points 20 cm apart was projected downwards and all plant species intercepted by each point were recorded. This frame was positioned twenty times in each subplot, resulting in a maximum possible score of 100 intercepts for each species.

Humus and litter samples were collected from each subplot for chemical, microbial, and microfaunal analysis. Several square quadrats (usually 30 × 30 cm) were placed in each subplot and litter and humus were collected separately within these quadrats. In each subplot, sufficient quadrats were sampled to provide enough material for the required analyses and in most cases at least three quadrats per subplot were sampled.

All litter was combined within each subplot, as was all humus. A separate collection of litter from each subplot was made specifically for the extraction of soil mesofauna and macrofauna. Here, litter was collected from six circular areas of 34 cm diameter in each subplot; all litter was combined for each subplot.

**Litter and humus analyses**

Humus and litter sampled using the square quadrats was weighed and the gravimetric moisture content (80°C, 24 h) measured to determine the total mass of litter and humus present in each subplot on an areal

<table>
<thead>
<tr>
<th>Site code</th>
<th>Dominant tree species†</th>
<th>Mammals excluded‡</th>
<th>Altitude (m. a.s.l)</th>
<th>Annual rainfall (mm)</th>
<th>January mean temp. (°C)</th>
<th>July mean temp. (°C)</th>
<th>Year exposure established</th>
<th>Tree species richness</th>
<th>Tree basal area (m²/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>Aga. aus., Bei. tar.</td>
<td>Cap. hir.</td>
<td>250</td>
<td>1974</td>
<td>17.5</td>
<td>9.9</td>
<td>1984</td>
<td>8</td>
<td>114</td>
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<tr>
<td>S3</td>
<td>Kun. eri.</td>
<td>Dam. dam.</td>
<td>110</td>
<td>1377</td>
<td>17.9</td>
<td>9.6</td>
<td>1983</td>
<td>5</td>
<td>31</td>
</tr>
<tr>
<td>S4</td>
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<td>Cap. hir.</td>
<td>120</td>
<td>2218</td>
<td>18.3</td>
<td>8.8</td>
<td>1983</td>
<td>4</td>
<td>66</td>
</tr>
<tr>
<td>S5</td>
<td>Mel. ram., Cya. med., Kni. exc.</td>
<td>Cer. ela., Mac. cug.</td>
<td>310</td>
<td>1739</td>
<td>17.3</td>
<td>7.0</td>
<td>1984</td>
<td>3</td>
<td>35</td>
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<td>Cer. ela.</td>
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<td>1453</td>
<td>16.9</td>
<td>6.0</td>
<td>1961</td>
<td>8</td>
<td>49</td>
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<td>Cer. ela.</td>
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<td>1476</td>
<td>16.8</td>
<td>5.9</td>
<td>1961</td>
<td>3</td>
<td>28</td>
</tr>
<tr>
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<td>Cer. ela.</td>
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<td>2212</td>
<td>18.0</td>
<td>7.4</td>
<td>1968</td>
<td>8</td>
<td>49</td>
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<td>Cya. smi., Bei. taw.</td>
<td>Cap. hir.</td>
<td>490</td>
<td>2536</td>
<td>16.0</td>
<td>7.3</td>
<td>1983</td>
<td>6</td>
<td>45</td>
</tr>
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<td>Pod. hal., Gri. lit., Phy. alp.</td>
<td>Cer. ela.</td>
<td>995</td>
<td>2415</td>
<td>13.4</td>
<td>3.1</td>
<td>1985</td>
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<tr>
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<td>Pod. hal., Cor. ban., Bra. rot.</td>
<td>Cap. hir.</td>
<td>900</td>
<td>4742</td>
<td>12.5</td>
<td>4.7</td>
<td>1972</td>
<td>4</td>
<td>7</td>
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<td>Cer. ela.</td>
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<td>1327</td>
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<td>5.0</td>
<td>1982</td>
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<td>Cer. ela.</td>
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<td>1901</td>
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<td>5.2</td>
<td>1982</td>
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<td>Cer. ela.</td>
<td>800</td>
<td>1535</td>
<td>13.8</td>
<td>2.9</td>
<td>1963</td>
<td>5</td>
<td>55</td>
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<td>Cer. el.</td>
<td>560</td>
<td>1615</td>
<td>14.8</td>
<td>3.2</td>
<td>1963</td>
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<td>55</td>
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<tr>
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<td>Cer. ela.</td>
<td>710</td>
<td>1565</td>
<td>14.3</td>
<td>2.3</td>
<td>1963</td>
<td>6</td>
<td>32</td>
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<tr>
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<td>Cer. el.</td>
<td>1300</td>
<td>2594</td>
<td>10.4</td>
<td>–1.0</td>
<td>1970</td>
<td>1</td>
<td>149</td>
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<td>Wei. rac., Lib. bid., Pod. tot.</td>
<td>Cer. ela.</td>
<td>460</td>
<td>3932</td>
<td>14.5</td>
<td>3.8</td>
<td>1966</td>
<td>7</td>
<td>84</td>
</tr>
<tr>
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<td>Cer. el.</td>
<td>470</td>
<td>5896</td>
<td>14.2</td>
<td>3.6</td>
<td>1967</td>
<td>11</td>
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<td>2958</td>
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<td>1968</td>
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<tr>
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<td>0.6</td>
<td>1972</td>
<td>1</td>
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<tr>
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<td>Cer. el.</td>
<td>540</td>
<td>1141</td>
<td>12.7</td>
<td>2.7</td>
<td>1964</td>
<td>3</td>
<td>155</td>
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<tr>
<td>S24</td>
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<td>Cer. el.</td>
<td>640</td>
<td>1127</td>
<td>11.9</td>
<td>2.3</td>
<td>1976</td>
<td>1</td>
<td>72</td>
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<tr>
<td>S25</td>
<td>Met. umb., Wei. rac.</td>
<td>Odo. vir.</td>
<td>75</td>
<td>1331</td>
<td>12.4</td>
<td>5.4</td>
<td>1979</td>
<td>6</td>
<td>192</td>
</tr>
<tr>
<td>S26</td>
<td>Odo. rac., Odo. rac., Odo. rac.</td>
<td>Cer. ela.</td>
<td>55</td>
<td>1329</td>
<td>12.6</td>
<td>5.6</td>
<td>1979</td>
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<td>36</td>
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<tr>
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<td>Odo. rac., Odo. rac., Odo. rac.</td>
<td>Cer. ela.</td>
<td>75</td>
<td>1331</td>
<td>12.4</td>
<td>5.4</td>
<td>1979</td>
<td>7</td>
<td>81</td>
</tr>
</tbody>
</table>


§ Meters above sea level.

|| Number of tree species of >5 cm diameter at 1.3 m height, on a plot of 400 m².
basis. Each sample was then homogenized and a representative subsample used to determine C and N concentrations (using a Leco FP-2000 analyzer; Laboratories Equipment Corporation, St. Joseph, Michigan, USA) and pH. Storage of C and N on an areal basis in the litter and humus layers was determined from these figures.

For each litter sample, a representative subsample (~100 g wet mass) was hand sorted into leaf litter, twig litter and amorphous material. All leaf litter was then hand sorted into component species. Oven dry mass (80°C, 24 h) of all sorted material was then determined.

A subsample of each homogenized sample was selected for microbial measurements; all samples were stored at 4°C until the time of measurement. In the case of humus, this material was sieved to 4 mm while the litter layer material was cut into fragments of 1 cm whenever necessary. Microbial basal respiration of each subsample was determined as described by Wardle (1993). This involved adjusting 3 g (dry mass) humus or litter to 150% moisture content (dry mass basis), placing it in a 130-mL airtight incubation vessel, and incubating at 22°C. CO₂-C evolution between 1 h and 4 h of incubation was then determined by injecting 1-mL subsamples of headspace gas into an infrared gas analyzer. Substrate-induced respiration (SIR; a relative measure of active microbial biomass) was determined using the approach of Anderson and Domsch (1978), as modified by West and Sparling (1986) and Wardle (1993). This was performed as for basal respiration, but with an amendment of 10 mg glucose/g material at the beginning of the incubation.

Total microbial biomass C and N was determined for each humus sample, using the fumigation–extraction procedure described by Wardle and Ghani (1995), modified from Brookes et al. (1985) and Vance et al. (1987). This technique cannot be reliably applied to litter, so the litter samples were not analyzed using this approach. Briefly, duplicate subsamples (5 g dry mass) of each humus sample were fumigated with chloroform and a further two were left nonfumigated; these subsamples were extracted with 0.5 mol/L K₂SO₄ for 2 h on an end-over-end shaker. These samples were then centrifuged and filtered and stored at 4°C until analysis was complete. Total C in the fumigated and nonfumigated extracts was determined on a Shimadzu 500 TOC analyzer (Shimadzu Corporation, Kyoto, Japan; Ghani et al. 1999). These extracts were also analyzed for N using micro-Kjeldahl analysis. Microbial C and N were determined by using the differences in C and N between the fumigated and nonfumigated subsamples with transformation multipliers of 2.22 (Brookes et al. 1985, Wu et al. 1990). Water soluble C concentrations were also determined for each humus sample as described by Wardle and Ghani (1995) by extracting 10 g (dry mass; sieved to 4 mm) humus in 20 mL water for 30 min using an end-over-end shaker at 20°C. Amounts of total soluble C in these extracts were then determined as described above.

A preweighed subsample (usually ~100 g wet mass) of each homogenized humus and litter layer sample was used for microbial and enchytraeid determination by using a tray variant of the Baermann method (Southey 1986, Yeates et al. 1993b). Total nematodes, rotifers, copepods, tardigrades, and enchytraeids were counted under a stereomicroscope at 40× before being killed and fixed by addition of an equal volume of boiling 8% formaldehyde. Subsequently, a mean of 126 nematode specimens from each sample were identified to nominal genus or family level and placed into six functional groupings occupying three trophic levels, following Yeates et al. (1993a, b). These trophic groupings (with component functional groups in brackets) were: microbe feeders (bacterial feeders and fungal feeders), predators (top predators and “omnivores”), i.e., predators that feed at more than one trophic level), and herbivores (plant parasites and plant associates).

The leaf litter material collected from each subplot for mesofauna and macrofauna assessments was extracted in its entirety by placing it in a Tullgren (modified Berlese) funnel for a period of 6–14 d depending on the bulk and moisture content of the litter. Invertebrates were captured in ethylene glycol and stored in 70% ethanol prior to sorting and identification. Following Tullgren funnel extraction, the samples were sieved and all material passing through a 5-mm mesh was scanned using a binocular microscope for shells of gastropod species not extracted in the funnels. The groups of mesofauna enumerated included Collembola and Acari (the latter separated into Oribatida, Astigmata, Mesostigmata, and Prostigmata). Main groups of macrofauna counted included Coleoptera (identified to family), Staphylinidae (Coleoptera; identified to subfamily), Stratiomyidae (Diptera) larvae, Gastropoda (identified to species), Isopoda, Amphipoda, Diplopoda (identified to family), Chilopoda, Araenida, Pseudoscorpionidea, and Opiliones.

**Community-level assessments**

For each group of taxa that we assessed (including litter), we aimed to determine the effects of browsing on community composition. These groups (and the taxonomic resolution to which they were identified) included plants in the browse layer (species level), plants in the ground layer (species level), leaf litter in the litter layer (species level), litter layer habitat composition (separated into twigs, amorphous material, and leaf litter sorted into species), Nematoda in litter (family level), Nematoda in humus (family level), Gastropoda in litter (species level), Diplopoda in litter (family level), Staphylinidae in litter (subfamily level), and Coleoptera in litter (family level). To determine the degree of dissimilarity of community composition inside vs. outside for each exclosure (cf. Milchunas and Lauenroth 1993, Milchunas et al. 1998) for each of these ten
groups, we quantified the dissimilarity between each subplot inside the exclosure and the corresponding subplot outside the exclosure, using the community dissimilarity index of Whittaker (1952). This index increases with increasing dissimilarity of community composition, and ranges from 0 (community composition identical between the two subplots) to 1 (community composition mutually exclusive between the subplots).

To determine the effect of browsing on community diversity, the Shannon-Weiner diversity index was calculated for each subplot for each of these ten groups; the index based on the litter habitat composition of the litter layer was used as a measure of microhabitat diversity (i.e., litter habitat diversity). Taxonomic richness, i.e., number of taxa noted for each subplot, was also determined for each of the groups except for litter layer habitat composition.

**Statistical analyses**

Our study enabled us to assess the effects of browsing mammals on response variables at two contrasting scales: within each location and across all 30 locations. At the within-location scale, the effect of browsing mammals on each response variable was assessed by paired $t$ tests in which the four subplots inside each exclosure were compared with the corresponding four subplots outside it; data was transformed by log, square root, or ranking whenever necessary to satisfy assumptions for parametric analysis. For the community dissimilarity index data, it was not possible to test directly for statistical significance of exclosure effects because each datum includes information from both inside and outside the enclosure. Therefore, to test whether community composition of each of the ten groups of taxa mentioned earlier differed significantly between inside and outside the enclosure for each location, Principal Components Analysis (PCA) was used to derive principal components scores for each of the eight subplots at that location which summarized the overall community composition data for that group. Paired $t$ tests were then used to determine whether the principal component scores for the main two axes, determined for each subplot, differed significantly between inside the enclosure and outside it, and therefore whether the community composition of that group significantly differed inside vs. outside the enclosure (see Wardle et al. 1999).

At the across-location scale, paired $t$ tests were also used for testing effects of browsing on the various response variables that we measured, but with each of the 30 locations serving as a single unit of replication. In addition, correlation and multiple stepwise regression were used to evaluate the possible influence of a range of independent variables on the magnitude of effect of browsing mammals on the populations (or biomasses) of various groups of soil organisms (calculated as $[\text{population inside exclosure} - \text{population outside exclosure}]$; see Milchunas and Lauenroth 1993) across all 30 locations. These independent variables included plant browse layer biomass and community characteristics, and litter and humus chemical properties (and effects of browsers on each of these variables), as well as such factors as site macroclimate, forest stand properties, altitude, latitude, and age of exclosure. Macroclimatic variables were determined for each location using climate-surface models (Leathwick and Stephens 1998) and included mean annual rainfall; mean July, January, and annual air temperature; mean annual humidity; mean solar radiation; and mean annual potential evapotranspiration. Forest stand properties included tree species richness, diversity (Shannon-Weiner index), and basal area for all trees with diameter $\geq 5$ cm at 1.3 m height, measured on a 400 m$^2$ plot at each location. Correlation and multiple stepwise regression analysis were also used to determine whether community dissimilarity (between inside and outside exclosure) of each soil animal group (Nematoda, Staphylinidae, Coleoptera, Diplopoda, Gastropoda) across the 30 locations was more closely related to community dissimilarity of browse layer plants and/or litter across these locations, or was instead related to some of the independent variables mentioned above. Similar analyses were performed to determine whether effects of browsing on diversity of these animal groups across locations were related to browsing effects on plant, leaf litter, and litter layer habitat diversity; or whether other variables instead emerged as being of importance.

**Results**

**Plant responses**

Plant density in the browse layer (i.e., pole intercept frequency) was greater inside than outside the exclosures for 25 of the 30 locations, and these effects were significant at $P = 0.05$ for 13 locations (Fig. 2). Further, when the data for all 30 locations were pooled, plant density in the browse layer was significantly greater inside than outside the enclosures (Fig. 3). In contrast, for the 16 locations in which some ground layer vegetation was present, there were several instances in which density in the ground layer was greater outside than inside the enclosure, and these effects were significant at $P = 0.05$ for five locations (Fig. 2). There were no overall significant differences in the vegetation density of the ground layer between inside and outside exclosures when data were pooled for all locations (Fig. 3).

Browsing mammals affected the relative importance of different plant species in the browse layer, and there were clear differences in composition inside vs. outside for several exclosures (Fig. 4). At 12 locations, several larger leaved plant species were very abundant inside the enclosure and effectively absent outside it. Species that were frequently severely reduced by browsers in-
Fig. 2. Plant density and soil chemical properties inside and outside of 30 browsing mammal exclosure plots. I, inside exclosure; O, outside exclosure. For each panel, locations are arranged in order of decreasing effect of browsers on the density of plants in the browse layer (calculated as [density inside exclosure – density outside exclosure]/[density inside exclosure]).
cluded Genistoma rugosum J. R. Forst. & G. Forst., Astelia spp., Griselinia littoralis Raoul, and Coprosma spp. (especially C. grandifolia Hook. f.). However, there were instances in which some plant species were clearly promoted by browsing, and these tended to include smaller-leaved shrubs [i.e., Cyathodes juniperina J. R. Forst. and G. Forst., Leucopogon fasciculatus (G. Forst.) A. Rich], and some fern species [e.g., Blechnum spp., Polystichum vestitum (Forst. F.)]. Browsing mammals also induced large changes in the vegetation composition of the ground layer (Fig. 5); browsing significantly enhanced the cover of sedges (Uncinia spp.) at five sites and the grass Hymenophyllum Hook. f. and filmy ferns (Hymenophyllum spp.) at two sites.

Humus and litter chemical properties

In nearly all of the 30 locations there was no significant effect of browsing mammals on either N concentration or C to N ratio of the litter layer (data not presented), although when the data were averaged across all 30 locations, the C to N ratio was marginally significantly lower inside (50.0) than outside (53.6) the exclosures (t = 2.08, P = 0.043; Fig. 3). Seven locations showed significant effects of browsers on humus N concentration although the direction of this response varied among locations (Fig. 2); only four showed significant effects on humus C to N ratio (data not presented) and there were no significant effects when data were averaged across all 30 locations (Fig. 6). Ten and 11 locations showed significant effects of browsers on pH in the litter and humus layers, respectively, roughly equal numbers of locations showed stimulation and reduction of pH by browsers, and when the data were averaged across all 30 locations there were no significant differences inside vs. outside exclosures (Figs. 3 and 6). Over a quarter of the locations also showed significant effects of browsers on humus soluble organic C concentrations (Fig. 2), and, averaged across the 30 locations, concentrations were significantly greater inside (422 µg C/g humus) than outside (351 µg C/g humus) exclosures (t = 2.16, P = 0.040; Fig. 6).

For many of the 30 locations, browsing mammals significantly affected C and N storage on an areal basis in the humus and (to a lesser extent) litter layers (Fig. 7). Despite the strength of these effects in several cases, the direction of browser effects was highly idiosyncratic, with browsers significantly promoting sequestration of C and N in some cases and having the reverse effect in others. When averaged across all 30 locations there were no overall effects of browsing mammals on C or N storage in litter or humus, and the magnitude of the effect of browsers on C and N storage was not significantly correlated with the magnitude of effect of browsers on either vegetation density or vegetation composition (dissimilarity index data) across sites.

Components of the soil microfood web

Our measurements enabled us to assess the effects of browsing mammals on the soil microfood web, which includes the microflora and microfauna, and which spans at least three consumer trophic levels (Fig. 8). The soil microbial biomass responded significantly to browsers at several locations, whether measured by fumigation–extraction or SIR (Fig. 8). There were also several instances of significant effects of browsers on the C to N ratio of the microbial biomass (Fig. 8). Microbial basal respiration, indicative of C mineralization rate, was less strongly influenced by browsing mammals, with five and four locations showing significant responses in the litter and humus layers respectively (data not presented).

Analysis of the within-exclosure data across the 30 locations revealed that microbial biomass in the humus was most closely correlated with substrate N concentration (for both the SIR and fumigation–extraction data) while microbial biomass in the litter layer was most closely related to substrate pH (Table 2). Microbial biomass showed little consistent relationship with most climatic or forest stand properties across locations (Table 2 and data not presented). Further, all microbial parameters showed idiosyncratic responses to browsers, with both strong positive and negative effects being detected, and with no net effect of browsers on any microbial variable when the data from all 30 locations were averaged (Figs. 3 and 6). The magnitude of effects of browsing mammals on the microflora was not significantly related to the magnitude of effects of browsers on vegetation density or composition (quantified using dissimilarity indices), or age of exclosures, across locations. However, the response of microbial biomass (fumigation–extraction) to browsers was highly positively correlated with the effects of browsers on humus N concentration across the 30 sites (R² = 0.323, P = 0.003).

The effects of browsing mammals on the soil microfood web were clearly multitrophic in nature for several locations; populations of microbe-feeding and predaceous nematodes were significantly affected by browsers in both the humus and litter layers in nearly half the sites (Fig. 8). There were also frequent sig-

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* For each location in each panel, the shaded bar is the larger of the two. Location codes correspond to Table 1. The symbols +, *, **, and *** indicate that the inside and outside values differ at P = 0.10, 0.05, 0.01, and 0.001, respectively. NA = statistical test not performed because samples for all replicates needed to be combined to provide sufficient humus for analysis; ND = not determined.
**Fig. 3.** Box-and-whisker plots summarizing data for the response to browsing mammals of autotrophs and components of the decomposer food web in the litter layer for all 30 locations. The index $V$ (Wardle 1995), determined for each response variable for each location, becomes increasingly negative if the value is increasingly greater outside the exclosure relative to inside it, and increasingly positive if it becomes increasingly greater inside the exclosure than outside it; the index ranges from $-1$ to $+1$, with 0 indicating no difference. For each variable, the box encompasses the middle half of the data (values of $V$) between the first and third quartiles, the bisecting line is at the value of the median, and the horizontal line outside the box represents the typical range of data values. Asterisks indicate outlier values. *P* values are for paired *t* tests comparing the significance of the difference between the value of the variable inside the exclosure and that outside the exclosure across the 30 locations. For each variable, locations with values of or very close to 0 both inside and outside the exclosure are not included.

<table>
<thead>
<tr>
<th>Component Type</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autotrophs</td>
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</tr>
<tr>
<td>Browse layer</td>
<td></td>
</tr>
<tr>
<td>Ground layer</td>
<td></td>
</tr>
<tr>
<td>Resource Base</td>
<td></td>
</tr>
<tr>
<td>pH</td>
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<td>C to N ratio</td>
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</tr>
<tr>
<td>Microflora</td>
<td></td>
</tr>
<tr>
<td>Microbial biomass</td>
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</tr>
<tr>
<td>Microfauna</td>
<td></td>
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<td>Copepoda</td>
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</tr>
<tr>
<td>Nematoda (predaceous)</td>
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<td>Tardigrada</td>
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<tr>
<td>Mesofauna</td>
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<td>Prostigmata</td>
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<tr>
<td>Macrofauna</td>
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<td>Corculionidae</td>
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<td>Hydrophilidae</td>
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</tr>
<tr>
<td>Isopoda</td>
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</tr>
<tr>
<td>Diplopoda</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Staphylinidae (predaceous)</td>
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<tr>
<td>Araenida</td>
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<tr>
<td>Pseudoscorpionidea</td>
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<tr>
<td>Opiliones</td>
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</tr>
<tr>
<td>Chilopoda</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
significant effects of browsers on the ratio of bacterial feeding to fungal feeding nematodes, and therefore on the relative importance of the bacterial vs. fungal energy channels. Again the effects of browsing mammals on all nematode variables were idiosyncratic, with no overall significant effect of browsers on nematode populations across the 30 locations (Figs. 3 and 6). Similar patterns were also noted for other, less numerous, soil microfood web components, i.e., tardigrades, copepods, and rotifers (Figs. 3 and 6).
FIG. 5. Density of plant species in the ground layer inside and outside of the 16 browsing mammal exclosure plots in which a ground layer vegetation was present. All units are mean total numbers of intercepts per 100 points (see Methods: System and sampling strategy). Only plant species with a mean score of two intercepts either inside or outside the exclosure are included. I, inside exclosure; O, outside exclosure. For each location in each panel, the shaded bar is the larger of the two. Location codes correspond to Table 1. The symbols +, *, **, and *** indicate that the inside and outside values differ at $P = 0.10$, 0.05, 0.01, and 0.001, respectively. Species abbreviations are as for Table 1 and Fig. 4; additional ones are as follows: Ble. cha. = Blechnum chambersii; Ble. fil. = B. filiforme (Cunn.) Ettingsh; Ble. flu. = B. flaviatile (R. Br.) Salomon; Hym. dem. = Hymenophyllum demissum (Forst. f.) Swartz; Hym. dil. = H. dilatatum (Forst. f.) Swartz; Hym. mul. = H. multifidum (Forst. f.) Swartz; Hym. san. = H. sanguinolentum (Forst. f.) Swartz; Hym. sp. = Hymenophyllum sp.; Lyc. vol. = Lycopodium volubile Forst. f.; Met. rob. = Metrosideros robusta A. Cunn.; Mic. ave. = Microlaena avenacea (Raoul) Hook. f.; Phy. pus. = Phymatosorus pustulus (Forst. f.) Large, Braggins and Green; Unc. cla. = Uncinia clarata Kük; Unc. sp. = Uncinia sp.; Unc. unc. = U. uncinata (L. f.) Kük.

Analysis of the within-exclosure data across the 30 locations found that nematode populations often showed significant relationships with soil chemical properties (e.g., substrate pH, N concentration, and soil C on an areal basis), and in the case of microbe-feeding nematodes, total annual precipitation (Table 2). However, there was no relationship between the magnitude of effects of browsers on nematode populations and the magnitude of effects of browsers on vegetation density, vegetation composition, or age of exclosure across the 30 locations. However, multiple stepwise regression analysis revealed that a significant proportion of the total variation across the 30 locations for the effects of browsers on nematode abundance could be explained in terms of several other independent variables including substrate properties, tree stand characteristics and effects of browsers on organisms of lower trophic levels (Table 3). This was especially apparent for microbe-feeding nematodes in litter and predaceous nematodes in humus, for which 50% and 64% of the total variation could be explained, respectively.

Mesofaunal and macrofaunal responses

Browsing did not affect the abundance of enchytraeids within locations (data not presented), and across the 30 locations there was no significant overall effect of browsers on enchytraeid abundance (Fig. 3). However, the other groups of mesofauna (all microarthropods) showed consistent and very clear responses to browsers (Fig. 9), regardless of trophic position. Effects of browsers on abundances of microarthropods were negative for all but one of the 63 instances in which a significant effect at $P = 0.05$ was detected (Fig. 9). Across the 30 locations for the within-exclosure data, all mesofaunal groups except the Mesostigmatidae showed significant relationships with some substrate and macroclimatic variables (Table 2), but not with forest stand variables (data not presented). Further, when the results were averaged over all 30 locations the effects of browsers on microarthropod populations were highly significant for all groups (Fig. 3). The magnitude of effects of browsers on microarthropod populations did not reflect the magnitude of effects of...
browsers on vegetation density, vegetation composition, or age of exclosure across the 30 locations. However, multiple stepwise regression analysis showed that significant amounts of variation across the 30 sites in the effects of browsers on various microarthropod groups could be effectively explained by macroclimatic variables, density of browse layer vegetation inside the exclosure, and the effects of browsers on soil chemical properties including soil storage of C and N (Table 3).

Responses in abundance of macrofauna to browsing mammals were similar to those of mesofauna, and again there were consistent, and often very strong, reductions of all the dominant macrofaunal groups by browsers (Fig. 10); all but one of the 138 effects depicted in Fig. 10 which were significant at \( P < 0.05 \) involved reductions of abundance by browsers. For the within-exclosure data across the 30 locations, populations of five of the eight macrofaunal groups were significantly correlated with mean January temperature, and some also showed significant relationships with substrate quality variables (Table 2); there were, however, few relationships with forest stand variables across locations. When averaged across all 30 locations, populations of all 13 macrofaunal groups tested were significantly reduced by browsing mammals (Fig. 3), irrespective of trophic position. The magnitude of macrofaunal population response to browsers across the 30 locations was generally not significantly related to the effect of browsers on browse-layer vegetation density or composition, nor to age of exclosure. However, for eight of the most abundant macrofaunal groups a statistically significant proportion of the variation across the 30 locations with regard to their population response to browsing could be explained by combinations of variables reflecting soil chemical, litter compositional, forest stand, and macroclimatic properties. (Table 3). For the Gastropoda, Diplopoda, and Amphipoda, over 50% of the variation across locations in terms of response to browsers could be explained by combinations of variables such as litter properties, browser effects on areal storage of C and N, and location altitude (Table 3).

**Community dissimilarity**

The community dissimilarity analyses revealed that community structure differed significantly between inside and outside of the exclosure plots for several locations, and for five groups of organisms (plants in the browse layer, nematodes in humus, nematodes in litter, diploids, and gastropods) at least 60% of all sites showed significant differences between inside and outside the exclosure (Fig. 11). Across the 30 locations, there were no animal groups for which community dissimilarity was significantly related to plant community dissimilarity (Table 4). Further, dissimilarity measures for litter species composition were not significantly re-
lated to those for plants. However, dissimilarity indices for litter nematodes, gastropods, and diplopods were all significantly related to dissimilarity indices for species composition of litter across the 30 sites, and litter nematode dissimilarity was very strongly correlated with litter habitat dissimilarity (Table 4). Over 60% of variation across locations with regard to dissimilarity indices for litter could be explained by stepwise multiple regression relationships incorporating various site variables including tree diversity at the site (Table 5). Stepwise multiple regression relationships could also explain >40% of the total variation across sites for community dissimilarity for three of the faunal groups (litter nematodes, gastropods, and diplopods) in terms of combinations of independent variables such as litter dissimilarity indices, soil chemical properties, tree basal area, and macroclimatic properties (Table 5).

Community diversity

In most locations browsing mammals reduced plant diversity (Shannon-Weiner index) in the browse layer; diversity was greater inside the exclosure than outside for all but three locations and for half the locations the effects were significant at $P = 0.05$ (Fig. 12). However, this trend did not occur for the ground layer vegetation and in the majority of instances diversity in this layer was greater outside the exclosure. Averaged across all 30 locations, diversity indices were significantly reduced by browsers for vegetation in the browse layer but not in the ground layer (Table 5). Diversity indices calculated for litter species, litter habitat, nematodes, diplopods, and gastropods were also often affected by browsers but these effects were idiosyncratic with roughly equal numbers of cases of stimulation and reduction by browsing (Fig. 12); diversity indices were not significantly influenced by browsing mammals for these groups when averaged across all 30 locations (Table 6). However, diversity indices calculated for coleopteran families and staphylinid subfamilies were, when significantly influenced by browsers, usually greater outside the exclosure (Fig. 12). Averaged across all 30 locations, there was a significant increase in diversity of both these groups by browsers (Table 6). Plant species richness responses to browsers generally paralleled those for plant diversity indices, with a mean reduction by browsers of species richness across all locations of 38% in the browse layer (Table 6). Diplopod family richness was only significantly affected by browsers for two locations (data not presented) but when the data were averaged across locations there was a statistically significant, although small, reduction in richness (Table 6). Gastropod species richness was sig-
Fig. 8. Properties of litter and humus microfood web components (microflora and nematodes) inside and outside of 30 browsing mammal exclosure plots. FE = fumigation-extraction method; SIR = substrate induced respiration; mf = microbe feeders; bf = bacterial feeders; ff = fungal feeders. Other symbols and legend are as for Fig. 2, and locations are arranged in the same rank order for each panel as for Fig. 2.

significantly reduced by browsers in nine locations (and no significant positive effects of browsers were found; data not presented), and when the data were averaged across locations species richness was significantly reduced by a mean of 13% by browsing, corresponding to a loss of 2.4 species per location (Table 6). When the within-exclosure data for the 30 locations was considered, diversity indices of most groups were
Table 2. Pearson’s correlation coefficients between soil organism biomasses (microbial data) or populations (faunal data) and selected soil chemical and macroclimatic variables, for n = 30 locations.

<table>
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<tr>
<th>Size class</th>
<th>Organism group</th>
<th>Substrate pH</th>
<th>Substrate N concentration</th>
<th>Storage of C in litter (areal basis)</th>
<th>Mean annual rainfall</th>
<th>Mean annual temperature</th>
<th>Mean annual solar radiation</th>
</tr>
</thead>
<tbody>
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<td>Microflora</td>
<td>Microbial biomass (SIR: humus)</td>
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<tr>
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<td>Microflora</td>
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<td>0.438*</td>
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<tr>
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<td>Microbe-feeding Nematoda (humus)</td>
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<td>-0.428*</td>
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<tr>
<td>Mesofauna</td>
<td>Microbe-feeding Nematoda (litter)</td>
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<td>Predaceous Nematoda (humus)</td>
<td>-0.536**</td>
<td>0.279</td>
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<td>Predaceous Nematoda (litter)</td>
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<td>Mesofauna</td>
<td>Collembola</td>
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<td>-0.126</td>
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</tr>
<tr>
<td>Mesofauna</td>
<td>Orbatida</td>
<td>0.333†</td>
<td>-0.241</td>
<td>-0.313†</td>
<td>-0.137</td>
<td>0.470**</td>
<td>0.459**</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Mesostigmata</td>
<td>0.109</td>
<td>0.031</td>
<td>0.031</td>
<td>0.077</td>
<td>0.000</td>
<td>0.130</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Protostigmata</td>
<td>0.419*</td>
<td>0.308†</td>
<td>-0.151</td>
<td>-0.167</td>
<td>0.328†</td>
<td>0.420†</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Staphylinidae (predaceous)</td>
<td>0.197</td>
<td>0.236</td>
<td>-0.100</td>
<td>-0.262</td>
<td>0.242</td>
<td>0.228</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Isopoda</td>
<td>0.339†</td>
<td>0.134</td>
<td>-0.256</td>
<td>-0.122</td>
<td>0.546**</td>
<td>0.158</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Diplodopa</td>
<td>0.207</td>
<td>0.161</td>
<td>-0.309†</td>
<td>-0.104</td>
<td>0.527**</td>
<td>0.339†</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Amphipoda</td>
<td>0.392*</td>
<td>0.380†</td>
<td>-0.362*</td>
<td>0.187</td>
<td>0.400*</td>
<td>0.200</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Staphylinidae (predaceous)</td>
<td>0.197</td>
<td>0.236</td>
<td>-0.100</td>
<td>-0.262</td>
<td>0.242</td>
<td>0.228</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Gastropoda</td>
<td>0.327†</td>
<td>0.420*</td>
<td>-0.288</td>
<td>-0.154</td>
<td>0.408*</td>
<td>0.189</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Isopoda</td>
<td>0.339†</td>
<td>0.134</td>
<td>-0.256</td>
<td>-0.122</td>
<td>0.546**</td>
<td>0.158</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Amphipoda</td>
<td>0.207</td>
<td>0.161</td>
<td>-0.309†</td>
<td>-0.104</td>
<td>0.527**</td>
<td>0.339†</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Chilopoda</td>
<td>0.432*</td>
<td>0.134</td>
<td>-0.371*</td>
<td>0.054</td>
<td>0.282</td>
<td>0.161</td>
</tr>
</tbody>
</table>

Note: Only inside-exclosure data were included in analyses.
†, *, **, *** Correlation coefficient statistically significant to 0 at P = 0.10, 0.05, 0.01, and 0.001, respectively.
|| Log-transformed variable.

Table 3. Results of stepwise multiple regression analysis relating the magnitude of browsing effects on soil faunal populations to external environmental factors, for n = 30 locations.

<table>
<thead>
<tr>
<th>Size class</th>
<th>Reduction by browsing of:†</th>
<th>Independent variables in relationship‡</th>
<th>R²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microfauna</td>
<td>Microbe-feeding Nematoda (humus)</td>
<td>ln(ASIRH) (-)</td>
<td>0.236</td>
<td>0.006</td>
</tr>
<tr>
<td>Microfauna</td>
<td>Microbe-feeding Nematoda (litter)</td>
<td>TSH (-); DDOC (+); NOR (+)</td>
<td>0.504</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Predaceous Nematoda (humus)</td>
<td>NLI (-); TNSP (-); DMF (+)</td>
<td>0.641</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Predaceous Nematoda (litter)</td>
<td>DMIC (+); ln(RF) (-)</td>
<td>0.348</td>
<td>0.007</td>
<td></td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Collembola</td>
<td>DNAREA (+); JULT (+); PCOV (+)</td>
<td>0.463</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Orbatida</td>
<td>ACAREA (-); JULT (+); PCOV (+)</td>
<td>0.445</td>
<td>&lt;0.002</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Mesostigmata</td>
<td>DNAREA (+); APHH (-)</td>
<td>0.541</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mesofauna</td>
<td>Prostigmata</td>
<td>SOLRAD (-)</td>
<td>0.323</td>
<td>0.001</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Gastropoda</td>
<td>DNAREA (+); VALTIT (-); CNLI (-)</td>
<td>0.596</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Isopoda</td>
<td>STAREA (+); VALTIT (-)</td>
<td>0.458</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Amphipoda</td>
<td>PHH (+); LDIS (+); ln(ANL) (-)</td>
<td>0.522</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Staphylinidae (predaceous)</td>
<td>NH (+); PDIS (+)</td>
<td>0.262</td>
<td>0.017</td>
<td></td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Areanida</td>
<td>DNAREA (+); LDIS (+)</td>
<td>0.345</td>
<td>0.005</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Opiliones</td>
<td>PHLI (+); SOLRAD (+)</td>
<td>0.358</td>
<td>0.003</td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Chilopoda</td>
<td>STAREA (+); APOCV (-)</td>
<td>0.422</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Note: Only terms that explain a statistically significant proportion of the variation of the response variable at P = 0.05 are included in each relationship.
† Expressed as ([population inside exclosure] – [population outside exclosure])/[population inside exclosure).
‡ (+) or (-) after a variable indicates a positive or negative relationship between the independent variable and the response variable. Abbreviations as follows: ACAREA, ANL, APOCV, APHH, ASIRH = absolute value of proportional reduction by browsing, i.e., ([value inside exclosure] – [value outside exclosure])/[value inside exclosure] of humus C storage per unit area, N concentration of litter, density of browse layer vegetation, humus pH, and humus SIR, respectively; ALTIT = altitude (meters above sea level), CNLI = C-to-N ratio of litter inside exclosure; DDOC, DCAREA, DMF, DMIC, DNAREA = proportional reduction by browsing of humus soluble C, humus C storage on an areal basis, populations of microbe-feeding nematodes, humus microbial biomass (fumigation–extraction), and humus N storage on an areal basis; JUL = mean July temperature (°C); LDIS = dissimilarity index D for plant litter species composition (inside vs. outside exclosure); NLI = concentration of N (%) inside exclosure for litter and humus, respectively; NOR = northing (relative scale based on latitude of site); PDIS = dissimilarity index D for plant species composition of browse layer (inside vs. outside exclosure); PCOV = density of browse layer vegetation inside exclosure (intercepts per 200 points); PHH, PHLI = pH inside exclosure of humus and litter, respectively; RP = ratio of rainfall to potential evapotranspiration; SOLRAD = solar radiation (MJ m⁻² d⁻¹); STAREA = tree stem density (no./ha); TNSP = tree species richness per 400 m²; TSH = tree species diversity (Shannon–Weiner diversity index).
significantly related to few forest stand or substrate variables, but diversity of several groups was significantly correlated with mean January temperature (i.e., the Shannon-Weiner diversity values for litter species \( R^2 = 0.151, P = 0.042 \)), staphylinid beetles \( R^2 = 0.257, P = 0.005 \), humus nematodes \( R^2 = 0.144, P = 0.033 \), and litter nematodes \( R^2 = 0.244, P = 0.006 \), and species richness for gastropods \( R^2 = 0.257, P < 0.001 \)). Across the locations, the effects of browsers on diversity of humus nematodes, but not of any other faunal group, was significantly related to the response of browse layer vegetation diversity to browsers (Table 7). Meanwhile, the effect of browsers on gastropod diversity was significantly related to the effect of browsers on leaf species diversity in the litter layer, and browser effect on diplopod diversity was significantly related to browser effect on litter layer habitat diversity (Table 7). With one exception there were no significant correlations between the effects of browsers on any two groups of animal taxa (Table 7). Stepwise multiple regression revealed few relationships between browser effects on diversity of faunal groups and independent site variables across the 30 locations. However, the magnitude of browser effects on gastropod diversity across sites was significantly related to site humidity \( R^2 = 0.339, P < 0.001 \), and browser effects on coleopteran and staphylinid diversity were both significantly related to the effects of browsers on humus C storage on an areal basis \( R^2 = 0.279, P = 0.003 \) and \( R^2 = 0.191, P = 0.017 \), respectively). The magnitude of response of diplopod diversity to browsers was best predicted by a multiple regression relationship incorporating mean January temperature and the effect of browsers on habitat diversity in the litter layer \( R^2 = 0.550, P < 0.001 \).

**DISCUSSION**

**Plant and soil food web responses**

The response of the plant community to browsing was generally consistent with our first hypothesis; browsing usually reduced vegetation density and often severely reduced palatable, larger-leaved (notophyllous, sensu Raunkiaer [1934], Webb [1956]) species causing domination by unpalatable small-leaved (nanophyllous and leptophyllous, sensu Raunkiaer [1934]) species, ferns, and ground layer monocotyledonous plants. This is consistent with studies showing shifts in the relative abundance of different plant functional types following browsing in New Zealand forests (Wallis and James 1972, Jane and Pracy 1974) and elsewhere (Augustine and McNaughton 1998, Virtanen 1998). The increases in abundance of unpalatable species often observed outside the exclosures was presumably due to release from competition with palatable species, as well as improved light levels at the ground layer (Ritchie et al. 1998, Huisman et al. 1999, Suominen et al. 1999). Plant species with larger leaves and
Fig. 10. Populations of macrofaunal groups in litter inside and outside of 30 browsing mammal exclosure plots. Symbols and legend are as for Fig. 2, and locations are arranged in the same rank order for each panel as for Fig. 2.
specific leaf areas are often less well defended and have higher nutrient concentrations when compared with species that produce smaller, longer lived, leaves (see Grime 1979, Coley et al. 1985, Cornelissen et al. 1999), meaning that these larger leaved species are both more likely to be palatable to herbivores and produce litter of superior quality for decomposers (Cornelissen et al. 1999). The significantly lower litter layer C to N ratio and higher humus soluble C content inside exclosures across all 30 locations is consistent both with this trend and with our first hypothesis, and is presumably due to superior litter quality of those plant species dominating inside the exclosure (see Grime et al. 1996). This effect is, however, relatively small and may therefore be insufficient to exert detectable effects on the soil biota.

Our first hypothesis was not supported when the components of the belowground microfood web were considered; for each of the three consumer trophic levels (microbes, microbe-feeders, predators), as many locations showed reduction as showed stimulation by browsers (Fig. 8). This means that, while browsing mammals had mostly unidirectional effects above-ground, these were not necessarily matched below-ground. The idiosyncratic response of microbes and microflora to browsing mammals presumably reflects the range of mechanisms through which browsers can affect belowground biota and which sometimes have directly opposite consequences (Bardgett et al. 1998b); it is the relative balance of these mechanisms which determines the observed response of belowground organisms. For example, dung and urine return by browsers could positively affect the belowground biota (see Ruess and McNaughton 1987, Mulder and Ruess 1998), while plant compositional changes (as per our hypothesis) may have the reverse effect. It is also apparent that the effects of browsers on the soil microfood web are tritrophic; frequently the highest trophic level (i.e., the predatory nematodes which occupy the tertiary consumer trophic level) responded (either positively or negatively) to browsers when the lower ones did not, and vice versa. This is consistent with earlier experimental and theoretical work suggesting that different components of the soil microfood web are affected differentially by top-down vs. bottom-up forces following manipulation of the resource base (Wardle and Yeates 1993, De Ruiter et al. 1995, Mikola and Setälä 1998). Browsing mammals also changed the composition of individual trophic levels within the microfood web; frequently significant (although idiosyncratic) effects were noted both for the microbial C to N ratio and for the ratio of fungal feeding to bacterial feeding nematodes. This latter result indicates that browsers can induce important shifts between the bacterial-based and fungal-based energy channels in soil food webs (see Moore and Hunt 1988, Bardgett et al. 1998b).

All mesofaunal groups (except Enchytraeidae) and all macrofaunal groups were consistently reduced by browsing mammals. Although the direction of these results is consistent with our first hypothesis, this is unlikely to reflect changes in litter quality by browsers; the soil microfood web components, which are far more intimately associated with the resource than are most of these organisms, did not show a unidirectional response. Further, reduction of mesofaunal and macrofaunal groups occurred even for those locations in which browsers increased the quality of the resource base (e.g., sites S3, S5, and S9). The consistently adverse effects of browsing mammals on these organisms is therefore more likely to reflect the physical effects of browsers, for example disturbance caused by trampling and scuffing. The intensity of scuffing and treading (and resultant disturbance, compaction, and reduced substrate porosity) caused by hoof pressure from deer and goats can be considerable, and is likely much more severe than that caused by the extinct species of browsing moas (Duncan and Holdaway 1989). In this context, it is significant that, when data were pooled across all 30 locations (Fig. 3), browsers had no overall effect on any of those faunal groups that occupy the aqueous component of the litter layer and which are intimately associated with the leaf substrate, and had adverse overall effects on all free living faunal groups that are more exposed to external environmental factors. This is consistent with studies showing that larger, free-living, soil animals are less resistant than smaller ones to exogenous disturbances (Wardle 1995). At some sites, reduction of mesofaunal and macrofaunal groups may have also resulted from effects of browsers on plant properties allowing increased light incidence at the ground layer (Suominen et al. 1999) and unfavorable microclimatic changes (Kielland and Bryant 1998). However, this was clearly not the case in all instances, because some locations that demonstrated strong responses to browsers of several faunal groups (e.g., sites S1, S4, and S29) showed no detectable effect of browsing on vegetation density or composition.

Across the 30 locations, we failed to find significant relationships between the magnitude of effect of browsers on browse layer vegetation density or composition (dissimilarity index data), and the magnitude of effect of browsers on the abundance of any group of soil biota. This is inconsistent with our first hypothesis. Our multiple regression analyses (Table 3) suggest that the resistance of soil biota to browsers is instead determined by a suite of other factors. For many faunal groups, over half of the across-location variation for the effects of browsers on their densities could be explained by combinations of other site-based factors such as belowground nutrient status, macroclimate, forest stand properties, and the responses of lower trophic levels and nutrients to browsers. This is consistent with previous studies indicating that habitat characteristics (e.g., nutrient status of the system, C availability, macroclimate) can determine the resistance, and other components of stability, of populations and biomasses of...

Community dissimilarity

Browsing mammals strongly affected the dissimilarity of communities inside vs. outside exclosures for several locations and for all groups of organisms considered. However, there was no evidence that the community dissimilarity of any faunal group was significantly related to plant community dissimilarity across the 30 locations, in direct contrast to the predictions of our second hypothesis. Dissimilarity indices for three litter-dwelling animal groups were instead significantly correlated with dissimilarity indices for litter composition across the locations, suggesting that browsing mammals can alter community composition of some faunal groups through altering community composition of litter in the litter layer. This implies a level of specificity of resources for the component organisms of these three groups. All three faunal groups that showed this relationship are mainly either microbe-feeders or microbidetritivores. Different types of litter support different communities of microorganisms (Widden 1986, Carreiro and Koske 1992) and litter-dwelling fauna which feed on microbes (in particular fungi) show distinct feeding specificity (Visser and Whittaker 1977, Kliromonas et al. 1992). Further, as was the case for the belowground faunal population data, community dissimilarity inside vs. outside exclosures for these three groups was highly significantly related to combinations of various site variables (Table 5), indicating that site factors also govern resistance of belowground animals to browsing mammals at the community level.

The second hypothesis did not hold because, while browser effects on community structure of some belowground faunal groups were related to browser effects on the composition of their habitat in the litter layer across the 30 locations, the magnitude of browser effects on litter species composition clearly did not reflect the magnitude of browser effects on plant community composition. The effect of browsers on litter compositional dissimilarity inside vs. outside exclosures was instead strongly related to other, independent site variables (Table 5). Browsing mammals clearly induced changes in the community composition of dead leaves in the litter layer, and these effects must have ultimately resulted from changes in the composition of aboveground vegetation; the absence of a link between the two with regard to the magnitude of dissimilarity across locations can only be explained by the magnitude of browsing-induced effects either on aboveground production (and hence litterfall), or on litter quality and associated decomposition rates of resident litter, also differing across locations.

Community diversity

There were large shifts in plant diversity due to browsing mammals, consistent with our third hypothesis. These effects were usually negative, although a small subset of locations did show significant increases in plant diversity in the ground layer. Several earlier studies have detected enhanced plant diversity due to aboveground mammalian herbivory, particularly in grasslands (Zeevaarting and Fresco 1977, Collins et al. 1998) probably through a reduction in competitive exclusion (Grace and Jutila 1999), an increased incidence of inedible plant species (Milchunas et al. 1988), and disturbance effects (Olff and Ritchie 1998). However, in nutrient-poor ecosystems, diversity may reduce grazing because limited resources prevents vegetation regrowth after grazing (Proulx and Singh 1991, Proulx and Mazumder 1998). Our exclosure sites were probably quite nutrient poor in relation to those used for most other comparable studies (for our 30 locations, C-to-N ratios in the litter layer ranged from 30 to 108 and in the humus layer from 16 to 46), and may be within the range for which browsing would be expected to reduce diversity (Proulx and Mazumder 1998). Further, unlike other exclusion studies, New Zealand forests did not evolve in the presence of the browsing mammals being investigated, and the extinct megaherbivores (moas) would not have exerted effects of comparable intensity (McGlone and Clarkson 1993). Plant species of New Zealand’s forests may therefore not have evolved to thrive under high mammalian browsing pressure, such as is the case for other floras (Westoby 1989).

We found that the magnitude of effect of browsing mammals on diversity of only one animal group, humus-dwelling nematodes, was significantly correlated with the magnitude of effect of browsers on browse-layer vegetation diversity across the 30 locations. Reduction of browse-layer plant species richness was matched by reduced richness of gastropod species and diplopod families across all 30 sites, but the magnitude of reduction of richness of these animal groups was

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**FIG. 11.** Community dissimilarity indices for various groups of organisms (including litter), indicating degree of dissimilarity of community structure inside vs. outside browsing mammal exclosure plots. For each panel, locations are arranged in order of decreasing dissimilarity between inside and outside exclosure for plant species in the browse layer. Location codes correspond to Table 1. The symbols +, *, **, and *** indicate that community structure differs significantly between inside and outside the enclosure at $P = 0.10$, 0.05, 0.01, and 0.001, respectively, as determined by paired $t$ tests on principal axes derived by Principal Components Analysis (see Methods: Statistical analyses). ND = not determined; N = no ground layer vegetation present.
not correlated with the magnitude of reduction of plant species richness across locations. The level of reduction of gastropod species richness by browsers was comparable to that observed by Suominen (1999) for a series of browsing mammal exclosures in Scandinavia. Our finding that the magnitude of response of browsing gastropod and diplopod diversity was correlated with the magnitude of browser effects on leaf litter species diversity or litter layer habitat diversity across all exclosures is consistent with earlier studies showing microhabitat diversity to be influenced by microhabitat diversity (Anderson 1978, Sulkava and Huhta 1998). Even though browsing mammals reduced vegetation diversity in the browse layer across all 30 locations, diversity of both coleopteran subfamilies and staphylinid subfamilies was enhanced by browsers (Table 6). Given that taxonomic richness of these groups was not affected by browsers, this means that browsers consistently reduced the population sizes of some taxa in these groups more than others. In most instances, our third hypothesis was not supported because the magnitude of effects of browsers on vegetation diversity across the 30 locations did not correlate with the magnitude of browser effects on soil animal diversity. This is probably in part because effects of browsers on plant diversity did not cause corresponding predictable shifts in habitat diversity. These results are consistent with the findings of Wardle et al. (1999) that loss of plant species from a plant community can either cause increases or decreases in the diversity of soil organisms, depending on the plant species removed, and suggests that different plant species may have substantially different effects on overall belowground habitat diversity (Hooper et al. 2000).

### Soil processes

In contrast to our fourth hypothesis, browsing mammals did not consistently reduce C mineralization (litter

### Table 4. Pearson’s correlation coefficients between different groups of taxa (including plant litter) with regard to the community dissimilarity index D calculated for inside vs. outside exclosures, across n = 30 locations.

<table>
<thead>
<tr>
<th>Dissimilarity index (inside vs. outside exclosure) for:</th>
<th>Plants (browse layer)</th>
<th>Litter (leaf species)</th>
<th>Litter (habitats diversity)</th>
<th>Nematoda (humus)</th>
<th>Nematoda (litter)</th>
<th>Gastropoda</th>
<th>Diplopoda</th>
<th>Staphylinidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter (leaf species)</td>
<td>-0.270</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter (habitats diversity)</td>
<td>0.047</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nematoda (humus)</td>
<td>0.152</td>
<td>0.110</td>
<td>-0.021</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nematoda (litter)</td>
<td>0.223</td>
<td>0.398*</td>
<td>0.570***</td>
<td>0.116</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td>0.058</td>
<td>0.401*</td>
<td>0.236</td>
<td>0.160</td>
<td>0.148</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diplopoda</td>
<td>0.050</td>
<td>0.371*</td>
<td>0.148</td>
<td>0.077</td>
<td>0.094</td>
<td>0.442*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Staphylinidae</td>
<td>-0.093</td>
<td>0.161</td>
<td>0.183</td>
<td>0.344</td>
<td>0.157</td>
<td>0.601***</td>
<td>0.167</td>
<td>0.870***</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>0.037</td>
<td>0.162</td>
<td>0.290</td>
<td>0.224</td>
<td>0.148</td>
<td>0.460*</td>
<td>0.178</td>
<td>0.870***</td>
</tr>
</tbody>
</table>

**Note:** Dissimilarity indices were calculated using families for Nematoda, Diplopoda, and Coleoptera; subfamilies for Staphylinidae; and species for Gastropoda.

* ** ***Correlation coefficient is significantly different from 0 at P = 0.05, 0.01, and 0.001, respectively.

† Not determined on the basis of representing a spurious correlation.

### Table 5. Multiple regression relationships relating values of the dissimilarity index D (calculated for determining dissimilarities of community structures inside vs. outside exclosures) for various taxa (including plant litter) to external environmental variables, across n = 30 locations.

<table>
<thead>
<tr>
<th>Dependent variables</th>
<th>Independent variables in relationship†</th>
<th>R²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter (leaf species)</td>
<td>TSH (+); CNHI (−); PCOV (+)</td>
<td>0.650&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Litter (habitat)</td>
<td>TSH (+); ALTIT (−); BASAR (−)</td>
<td>0.621&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Humus Nematoda (families)</td>
<td>SIR (−)</td>
<td>0.2100.014</td>
<td></td>
</tr>
<tr>
<td>Litter Nematoda (families)</td>
<td>ln(RP) (−); ACNL (−); LDISH (+)</td>
<td>0.575&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Gastropoda (species)</td>
<td>ln(RAIN) (−); SOLRAD (−); LDIS (+)</td>
<td>0.531&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Diplopoda (families)</td>
<td>DCLAREA (+); BASAR (−)</td>
<td>0.4070.001</td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** Only terms that explain a statistically significant proportion of the variation of the response variable at P = 0.05 are included in each relationship. Coleopteran and Staphylinid relationships are not presented because no relationships were significant at P = 0.05.

† (+) or (−) after a variable indicates a positive or negative relationship between the independent variable and the response variable. Abbreviations are as for Table 3; additional ones include: ACNL = absolute value of proportional reduction by browsing of litter CN ratio; BASAR = tree basal area (m²/ha); CNHI = C-to-N ratio of humus inside exclosure; DCLAREA = proportional reduction by browsing of litter C storage on an areal basis; LDIS, LDISH = dissimilarity index (inside vs. outside exclosure) for litter leaf species community structure and litter habitat, respectively; RAIN = mean annual precipitation (mm); SIR = humus SIR inside exclosure.
**Fig. 12.** Diversity indices for various groups of organisms (including litter) inside and outside of 30 browsing mammal exclosure plots. Symbols and legend are as for Fig. 2, but, for each panel, locations are arranged in order of decreasing effect of browsers on the diversity of plants in the browse layer (calculated as \( \frac{\text{diversity inside exclosure} - \text{diversity outside exclosure}}{\text{diversity inside exclosure}} \)).
and humus respiration); indeed, relatively few locations showed significant effects and the overall effect of browsers across the 30 locations was not significant. Earlier studies have shown that browsing effects on C and N mineralization can be negative (e.g., Pastor et al. 1988, 1993; see also Ritchie et al. 1998), positive (e.g., McNaughton et al. 1988, Kielland et al. 1997), or neutral (e.g., Molvar et al. 1993, Burke et al. 1999), probably because of the varied ways in which browsers may affect soil organisms, especially those in the soil microfood web (Bardgett et al. 1998b and this study). In this light, we also found no consistent effect of browsing mammals on litter or humus C and N storage on an areal basis. Although there were strong statistically significant effects at several locations, these effects were idiosyncratic, again pointing to a range of mechanisms with opposing effects on net soil C and N sequestration. These mechanisms involve the effects of browsers on both soil biological properties and plant species composition. There is evidence that forest plant species can differ tremendously in their effects on belowground soil C and N storage (Binkley and Giardina 2000) and it is conceivable that different plant species which are eaten out by deer and goats across sites vary in their effects on storage of C and N.

### Conclusions

Our study failed to entirely support any of our four hypotheses, indicating that while the mechanisms proposed by Pastor et al. (1988, 1993) may have applied in some locations they clearly did not in others, and when the data was averaged across all 30 locations there was little support for these hypotheses at least with regard to belowground processes and mechanisms. Although browsing mammals had generally predictable effects aboveground, browser effects on the soil microfood web and soil processes were idiosyncratic, and the directions of effects were presumably governed by the balance of different mechanisms by which browsers can potentially influence the belowground system (see Bardgett et al. 1998b). The unidirectional response of the litter mesofauna and macrofauna to browsing, although consistent with our hypotheses, is more likely to reflect physical effects of browsers than browsing-induced shifts in resource quality.

### Table 6. Diversity of plants, litter, and soil biota inside and outside exclosure plots, averaged across all 30 locations.

<table>
<thead>
<tr>
<th>Biota</th>
<th>Shannon-Weiner diversity index</th>
<th>Richness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inside</td>
<td>Outside</td>
</tr>
<tr>
<td>Plant species (browse layer)</td>
<td>1.97</td>
<td>1.29</td>
</tr>
<tr>
<td>Plant species (ground layer)</td>
<td>0.89</td>
<td>0.88</td>
</tr>
<tr>
<td>Leaf litter species</td>
<td>1.89</td>
<td>1.80</td>
</tr>
<tr>
<td>Litter habitat diversity</td>
<td>1.29</td>
<td>1.19</td>
</tr>
<tr>
<td>Nematode families (humus)</td>
<td>2.16</td>
<td>2.14</td>
</tr>
<tr>
<td>Nematode families (litter)</td>
<td>2.12</td>
<td>2.05</td>
</tr>
<tr>
<td>Gastropod species (litter)</td>
<td>2.58</td>
<td>2.56</td>
</tr>
<tr>
<td>Diplopod families (litter)</td>
<td>1.32</td>
<td>1.33</td>
</tr>
<tr>
<td>Staphylinid subfamilies (litter)</td>
<td>2.26</td>
<td>2.47</td>
</tr>
<tr>
<td>Coleopteran families (litter)</td>
<td>2.35</td>
<td>2.58</td>
</tr>
</tbody>
</table>

**Notes:** The t values were determined using paired t tests with n = 30 locations (i.e., 29 df) except for the plant species (ground layer) in which only the 14 locations with a vegetated ground layer present were used. ND = not determined.

### Table 7. Pearson’s correlation coefficients between taxa (including plant litter) with regard to browsing effects on the Shannon-Weiner diversity index, across n = 30 locations.

<table>
<thead>
<tr>
<th>Effect of browsing on diversity index of:</th>
<th>Plants (browse layer)</th>
<th>Litter (leaf species)</th>
<th>Litter (habitat diversity)</th>
<th>Nematoda (humus)</th>
<th>Nematoda (litter)</th>
<th>Gastropoda</th>
<th>Diplopoda</th>
<th>Staphylinidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter (leaf species)</td>
<td>ND†</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Litter (habitat diversity)</td>
<td>0.245**</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Nematoda (humus)</td>
<td>0.466**</td>
<td>0.153</td>
<td>-0.255</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Nematoda (litter)</td>
<td>0.120</td>
<td>0.042</td>
<td>0.190</td>
<td>0.004</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>0.167</td>
<td>0.369*</td>
<td>0.250</td>
<td>0.185</td>
<td>-0.052</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Diplopoda</td>
<td>-0.061</td>
<td>-0.071</td>
<td>-0.574***</td>
<td>0.279</td>
<td>-0.120</td>
<td>0.087</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Staphylinidae</td>
<td>-0.127</td>
<td>0.028</td>
<td>-0.088</td>
<td>0.187</td>
<td>0.127</td>
<td>0.169</td>
<td>0.183</td>
<td>0.511**</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>0.050</td>
<td>-0.100</td>
<td>-0.033</td>
<td>0.079</td>
<td>0.205</td>
<td>-0.162</td>
<td>-0.129</td>
<td>0.511**</td>
</tr>
</tbody>
</table>

**Notes:** For each taxonomic group the data are expressed as ([diversity index inside exclosure] − [diversity index outside exclosure])/[diversity index inside exclosure]. Diversity indices were calculated using families for Nematoda, Diplopoda, and Coleoptera; subfamilies for Staphylinidae; and species for Gastropoda.

† Not determined on the basis of representing a spurious correlation.
Finally, our study enabled us to evaluate the effects of an introduced functional group of organisms on the structure and function of indigenous communities in which that group was previously absent. Only a handful of studies have considered how alien organisms affect key properties of indigenous communities and ecosystems (i.e., invasive plants, Vitousek and Walker 1989; invasive invertebrates, Beggs and Rees 1999, Carroll and Hoffmann 2000). As a result of its very recent colonization by humans, New Zealand presents an opportunity, unparalleled in most parts of the world, for investigating ecological consequences of introduced alien organisms. Our results demonstrate that the introduction of deer and goats to New Zealand forests has caused far-ranging but often unpredictable effects at both the community- and ecosystem-level of resolution, with particularly adverse effects for indigenous plant communities and populations of most groups of litter-dwelling mesofauna and macrofauna.

ACKNOWLEDGMENTS

We thank the following people for information enabling us to relocate exclosure plots, for accompanying us on some of our field trips, or for help in sampling and backpacking soil and litter from the field: Peter Abbott, Phil Alley, Nils Anthes, Bruce Burns, Larry Burrows, David Byers, Alison Evans, John Gow, Sean Husheer, Merilyn Merrett, Juha Mikola, Claire Newell, Marcy and Rory Rowe, Bianca Ryburn, Karl Schasching, Mark Smale, Cam Speedy, and John von Tunzelman. John Leathwick provided the macroclimate data for the thirty locations and Bianca Ryburn, Moira Dexter, and Kate Orwin provided laboratory assistance. Anouk Wanrooy prepared the illustrations and Peter Bellingham, Bruce Burns, and Claire Newell assisted with plant identifications. The New Zealand Department of Conservation is acknowledged for providing permits for us to sample most of these enclosures and for providing accommodation in several instances. The Rakura Maori Land Trust gave us permission to sample the Stewart Island exclosures. Rob Allen, Peter Bellingham, Claire de Mazancourt, Christa Mulder, Duane Peltzer, J. M. Caughley, and two anonymous reviewers provided helpful comments on earlier versions of this manuscript. This work was supported by the New Zealand Marsden Fund and the National Foundation for Research, Science, and Technology.

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