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Changes in the community structure and diversity of soil invertebrates across the Franz Josef Glacier chronosequence

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Abstract

Following the creation of new land surfaces, there is an initial build-up phase of ecosystem development, but after a prolonged absence of major disturbance a retrogressive (decline) phase often follows due to reduced nutrient availability over time. Although many studies have considered how the soil community changes during the build-up phase, the response of this community to the retrogressive phase is poorly known. We measured litter and soil communities of microfauna and macrofauna along the Franz Josef Glacier chronosequence in New Zealand that spans ca. 120,000 years, and includes well-established build-up and retrogressive stages. We aimed to assess whether the abundances, community structure and diversity of these groups show the same pattern across the sequence as that for vegetation. With regard to microfaunal abundances, litter-dwelling microbe-feeding nematodes were most abundant in the first stage of the chronosequence, but several other groups of microfauna in both the soil and litter increased sharply during the first few stages and declined sharply during the last (retrogressive) stages. The ratios of bacterial- to fungal-feeding nematodes in both soil and litter were lowest for the final stages of the chronosequence, and (in the case of soil) for some of the early stages, pointing to domination by the fungal-based energy channel at those stages for which soil organic matter content or quality were lowest. This is consistent with the fungal-based energy channel being better adapted than the bacterial-based channel for resource-poor conditions. The main groups of macroinvertebrates typically had their lowest abundances at the very early and late stages of the chronosequence, although the relative abundances of different taxa differed during the intermediate stages. Taxonomic diversity of nematodes and macroinvertebrates in both litter and soil varied strongly with chronosequence stage but differed among taxa; diversity of only one group (macroinvertebrates in litter) declined significantly during retrogression. Diversity of nematodes and macroinvertebrates along the sequence did not closely match tree diversity or soil chemical properties, but community composition of these groups was often related to tree community composition and ratios of soil C to N, C to P and N to P. Different groups of soil invertebrates show contrasting responses to chronosequence stage, probably because they differ in their relative response to bottom-up and top-down controls. However, the abundance of most groups increased during the build-up phase and declined during retrogression. As such, the build-up and decline phases observed for plant communities and ecosystem processes across long-term chronosequences also apply to soil communities, pointing to the importance of resource availability as a major driver of soil biota during long-term ecosystem change.

Keywords: Chronosequence; Community composition; Diversity; Franz Josef; Macrofauna; Microfauna; Nematode; Retrogression; Succession

1. Introduction

Following the occurrence of major disturbances and creation of new geological surfaces, primary succession occurs, and this involves the build-up of plant biomass to a maximal biomass stage. This build-up phase has been extensively studied, and there is ample evidence during this phase of broadly predictable trends in both aboveground and belowground ecosystem processes (Walker and Chapin, 1987; Walker and del Moral, 2003), including large increases in soil carbon (C) through photosynthesis

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and soil nitrogen (N) through biological N fixation (Odum, 1969; Schlesinger, 1990; Walker and del Moral, 2003). However, there is increasing recognition that in the long-term absence of catastrophic disturbance, the maximal plant biomass phase is often followed by an ecosystem decline phase or period of 'ecosystem retrogression', during which a long-term reduction in plant biomass and ecosystem process rates occurs (Walker et al., 1983; Wardle et al., 1997, 2004b; Richardson et al., 2004; Vitousek, 2004, 2006). This decline phase has received far less attention than the build-up phase, and is therefore less well understood. However, it is becoming increasingly recognized that this decline is frequently associated by reduced availability over time of key soil nutrients, notably phosphorus (P) (Walker and Syers, 1976; Crews et al., 1995; Vitousek and Farrington, 1997; Wardle et al., 2004b).

There has been significant recent interest in evaluating the linkages between aboveground and belowground communities and the consequences of these linkages for ecosystem processes (van der Putten et al., 2001; Wardle et al., 2004a). Further, it has been recognized that long-term chronosequences offer opportunities for understanding how these linkages operate in the temporal dimension (Wardle, 2002; Bardgett et al., 2005). As such, several studies have investigated how communities of soil biota develop during the build-up phase of succession, and how these changes parallel the plant community. These include studies on communities of microorganisms (Tscheko et al., 2003), mycorrhizal fungi (Jumpponen et al., 2005), nematodes (Yeates, 1971; Wasilewska, 1994), microarthropods (Chauvat et al., 2003; Hodkinson et al., 2004) and earthworms (Scheu, 1992). However, how communities of soil biota respond to the decline or retrogressive stages of ecosystem development, and whether these changes parallel those observed for aboveground communities, has been seldom explored (Wardle et al., 2004b; Williamson et al., 2005). Despite the dearth of studies on soil community responses to retrogression, such information would greatly assist our understanding of whether and how aboveground and belowground communities are linked over very long temporal scales (e.g., over millenia), as well as the factors that drive these linkages.

In this study, we assess the changes that occur in soil invertebrate communities during the build-up and retrogressive phases of long-term ecosystem development, through the use of a well-characterized chronosequence. Specifically, we aimed to characterize changes in the main groups of soil microfauna and macrofauna (macroinvertebrates) along this sequence, and to determine the changes in the community structure and taxonomic diversity of the dominant microfaunal group (i.e., nematodes) and the macrofauna along the chronosequence. Our hypotheses were that (1) soil microfauna and macrofauna densities increase during the build-up phase of succession and decline during retrogression, because they track the changes in soil fertility and vegetation biomass that occurs during the build-up and decline phases; (2) soil faunal groups from different trophic levels will respond differently along the chronosequence because they are affected to varying degrees by bottom-up control (i.e., changes in nutrient availability and resource quality) relative to top-down and abiotic factors and (3) community structure and diversity of microfauna and macrofauna will change during the build-up and retrogression phases in a similar way to that for plants, because of the important role of plant communities in driving invertebrate communities.

2. Methods

2.1. Study site and sample collection

The study was conducted along the forested Franz Josef Glacier chronosequence in the South Island of New Zealand (43°25′S, 170°10′E). The annual rainfall of the area is 3800–6000 mm/year and the mean temperature is 15 °C in January and 7 °C in July. The parent material consists of chlorite schist, biotite schist and gneiss. This chronosequence has resulted from the retreat of the Franz Josef Glacier and spans ca. 120,000 years, making it one of the longest characterized chronosequences in existence (Stevens and Walker, 1970; Wardle et al., 2004b; Almond et al., 2001). In addition, the entire sequence has been unaffected by forest harvesting or anthropogenic disturbance. Earlier work on this chronosequence has demonstrated that across the chronosequence tree biomass increases sharply for the first few hundred years as soil fertility develops, and after 60,000 years shows a distinct decline (Wardle et al., 2004b). This decline is associated with the reduction of availability of P from the soil over time (Stevens and Walker, 1970), and an associated decline in the ratio of N to P in both foliage and plant litter (Richardson et al., 2004; Wardle et al., 2004b). During the decline phase, there is also a distinct reduction in the photosynthetic capacity of the dominant tree species (Whitehead et al., 2005), litter decomposition rates (Wardle et al., 2004b) and soil microbial biomass and activity (Wardle and Ghani, 1995). The nine stages across the chronosequence that we considered, in increasing age, are

- *Stage 1*. 60 years. Short forest dominated by several species, notably the nitrogen-fixing shrub *Coriaria arborea*, and *Melicytus ramiflorus* and *Schefflera digitata*.
- *Stage 2*. 150 years. Short forest dominated by *Myrsine divaricata*, *Griselinia littoralis* and *Olearia avicenniaefolia*.
- *Stage 3*. 250 years. Short forest dominated by *S. digitata*, the tree fern *Cyathea smithii*, *Weinmannia racemosa* and *Metrosideros umbellata*.
- *Stage 4*. 500 years. Forest dominated by *W. racemosa* and *M. umbellata*, with understory of *Pseudowintera colorata* and *M. divaricata* and the tree fern *C. smithii*.
- *Stage 5*. 1000 years. Forest dominated by *W. racemosa* and *M. umbellata*, with understory of *S. digitata*, *P. colorata* and the tree ferns *C. smithii* and *Dicksonia squarrosa*.

- *Stage 6*. 5000 years. Forest dominated by *M. umbellata* and *W. racemosa*, with understory of *S. digitata* and the tree ferns *C. smithii* and *D. squarrosa*.
- *Stage 7*. 12,000 years. Forest dominated by *W. racemosa*, *Dacrydium cupressinum* and *Prumnopitys ferruginea*, with understory of *Quintinia acutifolia* and the tree fern *D. squarrosa*.
- *Stage 8*. 60,000 years. Forest dominated by *W. racemosa*, *D. cupressinum* and *M. umbellata*, with understory of *Q. acutifolia* and the tree fern *D. squarrosa*.
- *Stage 9*. 120,000 years. Shrubby forest dominated by *Phyllocladus alpinus*, *Manoao colensoi*, *Leptospermum scoparium*, *Podocarpus hallii*, *Q. acutifolia* and shrubs (*Coprosma* spp.).

Field measurements and sampling were performed in January 2005. For each of the nine stages, we identified four replicate plots; each plot was circular with a 10 m radius. For each plot, the diameters of all trees were recorded at a height of 1.3 m (i.e., stems with diameter >3 cm). These data were used to calculate the basal area of each tree species, total tree species richness, and the Shannon–Weiner diversity index for each plot. Tree basal area was used here as a surrogate for standing tree biomass because no species-specific allometries between size and biomass are available (Wardle et al., 2004b). Trees are the dominant life form of vegetation for all stages of this chronosequence and comprise the vast majority of the standing plant biomass.

For each plot, we collected the entire litter layer above the soil surface within each of two 30×30 cm quadrats, and combined them into a single sample for that plot. In addition, for each plot we collected all the soil present in each of two 15×15 cm quadrats (located within the 30×30 cm quadrats used for litter collection) to 5 cm depth and combined them into a single sample.

2.2. Soil and litter sample analyses

A subsample (representing two-thirds of the total sample volume) of each soil and litter sample was carefully hand sorted for all macrofauna present (i.e., all fauna $\geqslant 1$ mm). The major groups included the Amphipoda (Talitridae), Annelida (Megascolecidae), Araenida, Chilopoda, Coleoptera, Diplopoda, Diptera (larvae) and Isopoda (Oniscoidea). All macrofauna were identified to family level.

A second subsample (100 mL) of each soil and litter sample was used for quantification of enchytraeids and microfauna, i.e., nematodes, copepods, rotifers, ostracods and tardigrades, using a variant of the tray extraction method of Yeates (1978). Microfauna were counted live at $40\times$ magnification before fixing the suspension by the addition of an equal volume of boiling 8% formaldehyde. Subsequently an average of 122 nematodes per sample was identified to nominal genus, and placed into six functional groups, following Yeates et al. (1993). These groups are bacterial-feeders, fungal-feeders, top predators, omnivores (i.e., predators that feed at more than one trophic level), plant-feeders and plant associates. Microbe-feeders were determined as the sum of bacterial- and fungal-feeders. The nematode channel ratio, NCR = bacterial-feeders/(bacterial-feeders + fungal-feeders) (Yeates, 2003) was used as a ratio of bacterial- to fungal-feeding nematodes.

A third subsample of each soil and litter sample was used for quantifying gravimetric soil moisture content, to allow all microfaunal and macrofaunal data to be expressed on a per unit dry weight basis of litter or soil. Part of each soil subsample was also used for determination of total C concentration through the Leco furnace method with infrared detection, total N concentration using micro-Kjeldahl analysis, and total P concentration as described by Jackson (1958).

2.3. Data analysis

Taxonomic richness was determined for trees in each plot (at the species level), nematodes in each soil and litter sample (at the genus level) and macroinvertebrates in each soil and litter sample (at the family level). The Shannon–Weiner diversity index was also used as a relative measure of species diversity for the tree data, generic diversity for the nematode data, and family diversity for the macroinvertebrate data. Principal components analysis (PCA) was used to provide variables summarizing the overall community composition for trees, nematodes in litter, nematodes in soil, macroinvertebrates in litter and macroinvertebrates in soil. All ordinations were performed on data expressed as proportions of totals.

For all response variables with the exception of all macroinvertebrate abundance data (but including the diversity indices and ordination score data), one-way analysis of variance (ANOVA) was used to test for the overall effect of chronosequence stage; differences among means were then evaluated using Tukey's honestly significant difference (HSD). Data were transformed if needed to satisfy the assumptions of ANOVA. For the macroinvertebrate abundance data, for which assumptions of normality could not be satisfied even after transformation, the non-parametric Kruskall–Wallis test was instead used to assess overall effects of chronosequence stage; here differences among means were then evaluated using the Mann–Whitney *U*-statistic.

Correlation analyses were used to test for community-level associations across the 36 plots between trees, nematodes and macroinvertebrates, using measures of taxonomic richness, the Shannon–Weiner diversity index, and primary ordination (PCA) scores for these groups. Correlation analysis was also used to test for relationships between these community-level variables for nematodes and macroinvertebrates, and tree basal area, concentrations of soil C, N and P, and ratios between soil C, N and P.

3. Results

3.1. Tree and soil data

Tree basal area was significantly influenced by chronosequence stage; it increased sharply from stages 1 to 4, and decreased sharply at the end of the chronosequence (Table 1). Soil C concentration showed a similar pattern of initial increase and subsequent decrease (Table 1). There were significant increases in the ratios of C to N, C to P and N to P (Table 1) over time.

3.2. Invertebrate abundances

Densities in the litter layer of all nematode-feeding groups except plant-feeding and plant-associated nematodes showed significant responses to chronosequence stage (Table 2). Microbe-feeding nematode densities were greatest at the first stage of the chronosequence, and did not differ significantly among the other eight (Fig. 1). Densities of bacterial- and fungal-feeders showed similar declines over time (data not presented), while the nematode channel ratio (ratio of 'bacterial-feeding' to 'bacterial-feeding + fungal-feeding' nematodes) declined significantly between stages 7 and 9. Omnivorous and predatory nematodes in litter responded significantly to chronosequence stage (although only weakly in the case of predatory nematodes), and were maximal at intermediate chronosequence stages (Fig. 1 and data not presented). For the other microfaunal groups in the litter layer, only copepods and ostracods responded significantly to chronosequence stage. Copepods were maximal at intermediate stages of the chronosequence (Fig. 1), while ostracods were only marginally significantly influenced by chronosequence stage and showed no distinct patterns (data not presented).

Densities in the soil layer of microbe-feeding, bacterial-feeding, omnivorous and plant-associated nematodes responded significantly to chronosequence stage (Table 2). All groups showed maximal abundance at intermediate chronosequence stages (Fig. 1 and data not presented). Further, the nematode channel ratio was maximal at the intermediate stage and at stage 1 of the chronosequence (Fig. 1). Of the other microfaunal groups in the soil layer, only copepods responded significantly to chronosequence stage (Table 2) and were maximal at intermediate stages (Fig. 1).

For the 10 most abundant groups of macroinvertebrates (shown in Table 3; these collectively comprised 73% of the total number of individuals counted), four groups responded significantly to chronosequence stage in the litter layer and a different four groups responded significantly in the soil layer (Table 3). The four responsive groups in

Table 2
F- and *P*-values derived from one-way ANOVA testing for effects of chronosequence stage on densities of soil nematode and other microinvertebrate groups in litter and soil layers

Microinvertebrates	Litter layer		Soil layer	
	F-value	*P*-value	*F*-value	*P*-value
Total nematodes	**5.25**	**<0.001**	**5.81**	**<0.001**
Microbial-feeding nematodes	**11.97**	**<0.001**	**4.99**	**<0.001**
Bacterial-feeding nematodes	**11.47**	**<0.001**	**7.77**	**<0.001**
Fungal-feeding nematodes	**6.92**	**<0.001**	1.68	0.147
Nematode channel ratio[a]	**3.65**	**0.005**	**6.20**	**<0.001**
Predatory nematodes	**2.77**	**0.022**	1.66	0.154
Omnivorous nematodes	**4.28**	**0.002**	**4.65**	**0.001**
Plant-feeding nematodes	0.87	0.550	1.91	0.099
Plant-associated nematodes	2.00	0.085	**6.42**	**<0.001**
Enchytraeids	1.47	0.214	1.06	0.416
Rotifers	1.06	0.419	1.25	0.308
Tardigrades	1.11	0.387	1.67	0.153
Copepods	**4.10**	**0.003**	**18.17**	**<0.001**
Ostracods	**2.78**	**0.022**	0.87	0.553

Degrees of freedom for all analyses are 8,27.
[a]Ratio of 'bacterial-feeding' to 'bacterial-feeding + fungal-feeding' nematodes.

Table 1
Tree basal area and soil chemical properties across the nine stages of the Franz Josef Glacier chronosequence

Stage	Tree basal area (m^2/ha)	Soil C (%)	Soil C to N ratio	Soil C to P ratio	Soil N to P ratio
1	9.5 f	14.7 bc	15.3 c	138.1 d	8.91 c
2	29.0 ef	13.1 bc	18.9 bc	174.2 cd	9.22 c
3	123.3 abc	13.3 bc	18.7 bc	186.2 cd	9.88 c
4	159.2 a	25.4 abc	22.0 abc	369.1 bcd	16.53 bc
5	63.6 def	14.9 bc	19.1 bc	182.7 cd	9.31 c
6	151.9 ab	38.6 a	26.0 ab	498.0 abc	17.85 abc
7	90.9 bcd	29.5 ab	29.6 a	677.4 ab	22.84 ab
8	76.1 cde	21.4 abc	29.7 a	567.1 ab	19.26 abc
9	13.6 f	10.7 c	26.1 ab	743.3 a	29.67 a
F-value*	**21.32**	**5.77**	**8.57**	**11.51**	**8.23**
P-value*	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**

**F*- and *P*-values derived from one-way ANOVA; degrees of freedom = 8,27. Within each column numbers followed by the same letter are not significantly different at $P = 0.05$ (Tukey's HSD test).

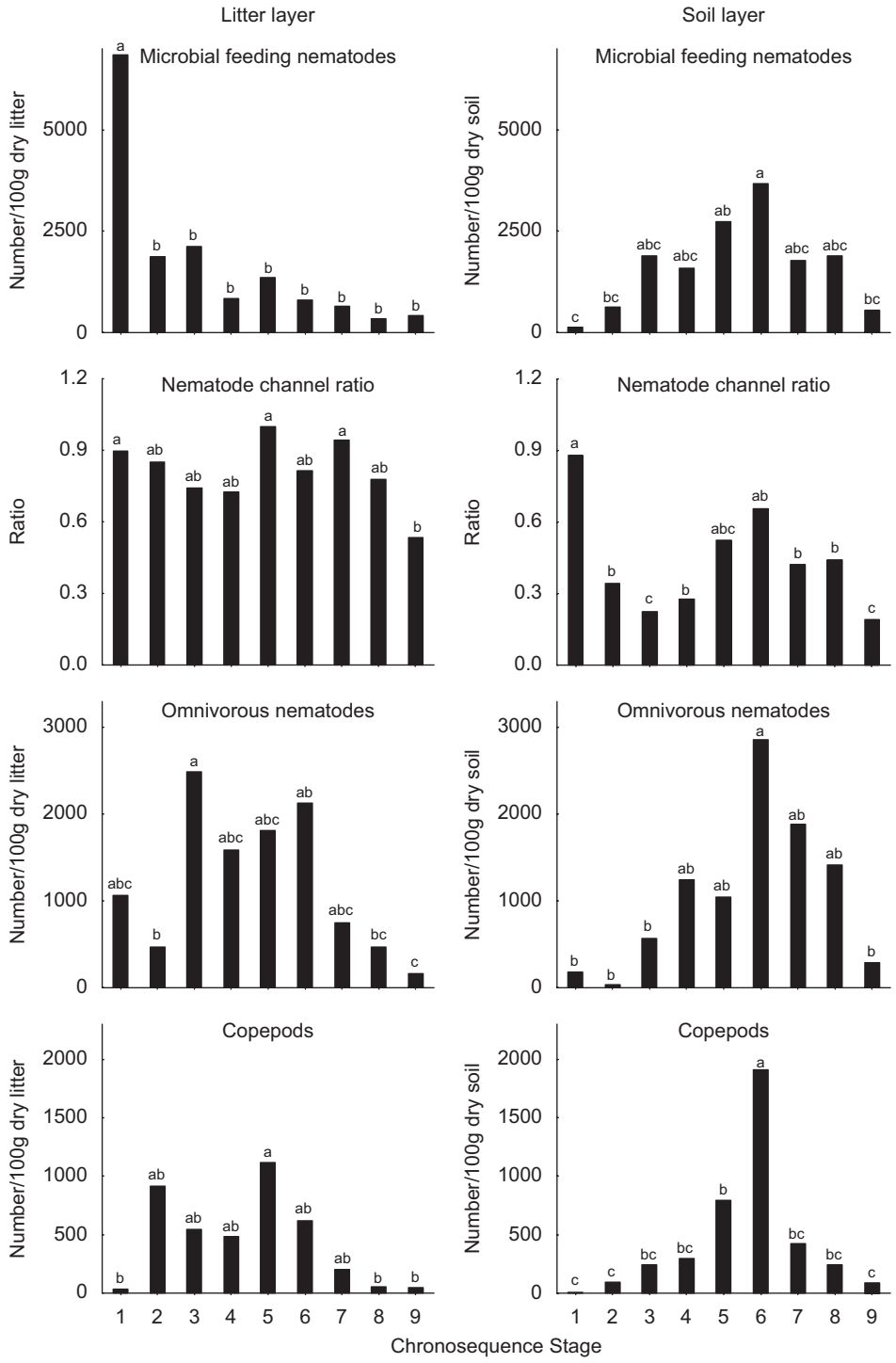

Fig. 1. Abundances of selected microinvertebrate groups in soil and litter for nine stages across the Franz Josef chronosequence (1, youngest stage; 9, oldest stage). Within each panel, bars topped with the same letters are not significantly different at $P = 0.05$ (Tukey's HSD test). The 'nematode channel ratio' is the ratio of 'bacterial-feeding nematodes' to 'bacterial-feeding + fungal-feeding nematodes'. ANOVA results for the effect of chronosequence stage on these groups are shown in Table 2.

the litter layer were all detritivores, i.e., Megascolecidae, Talitridae, Diplopoda and Tipulidae. Megascolecidae showed the highest density in stage 2, Talitridae and Tipulidae were most abundant in stage 5, and Diplopoda was most abundant in stages 2, 3 and 5 (Fig. 2 and data not presented). The lowest values for these groups all occurred at stage 9. For the mineral soil layer, the four groups that showed significant responses were the detritivorous Oniscoidea, predatory Chilopoda, and herbivorous Dascillidae and Curculionidae larvae (Table 3). Of these groups,

Table 3
H- and *P*-values derived from Kruskall–Wallis tests, for effects of chronosequence stage on major groups of soil macroinvertebrates in litter and soil

Microinvertebrates	Litter layer		Soil layer	
	H-value	*P*-value	*H*-value	*P*-value
Megascolecidae	**24.56**	**0.002**	8.68	0.370
Talitridae	**18.66**	**0.017**	11.00	0.202
Oniscoidea	10.52	0.231	**21.00**	**0.007**
Aranei	10.37	0.240	15.17	0.056
Diplopoda	**24.27**	**0.002**	8.89	0.352
Chilopoda	8.91	0.350	**18.62**	**0.017**
Tipulidae larvae	**17.98**	**0.021**	7.06	0.530
Carabidae (adults + larvae)	14.20	0.077	5.90	0.659
Dascillidae larvae	7.21	0.514	**21.60**	**0.006**
Curculionidae larvae	9.85	0.276	**22.34**	**0.004**

Degrees of freedom are 8,36.

Dascillidae were maximal at stage 4 and the other three groups were maximal at stage 8 (Fig. 2 and data not presented).

3.3. Community-level responses

Taxonomic richness was significantly responsive to chronosequence stage for all studied groups: trees, litter and soil nematodes, and litter and soil macroinvertebrates (Fig. 3). Tree species richness increased for the first three stages, and later declined slightly, but not significantly (Fig. 3). Litter and soil nematodes had the greatest number of genera in stage 1; this number significantly declined at stage 2 and thereafter showed no significant trends (Fig. 3). Litter and soil macroinvertebrates showed an increase in the number of families from stages 1 to 3, and thereafter fluctuated (but in a similar way to each other), while for stage 9 family richness showed a sharp decline for the litter layer only (Fig. 3). Community diversity, assessed using the Shannon–Weiner index, was also significantly responsive to chronosequence stage for all groups (Fig. 3). Tree community diversity showed the highest diversity at stage 9 and the lowest at stage 4 (Fig. 3). Litter and soil nematode communities showed the highest diversity at stage 1; the lowest diversity occurred at stages 4 and 5 for the litter layer and stage 2 for the soil layer (Fig. 3). Litter and soil macroinvertebrate communities showed an increase in diversity from stages 1 to 3. However, in the litter layer, macroinvertebrate diversity showed a decrease at stage 9, while in the soil layer there was a higher diversity at stages 8 and 9 than at stage 4 (Fig. 3).

For the ordination analyses, the principal ordination axis (PCI) for the tree community data, and the nematode and macroinvertebrate community data in both the litter and soil layers, was significantly affected by chronosequence stage. The second ordination axis (PCII) for the tree and nematode communities (but not for the macroinvertebrate communities) was also significantly affected by chronosequence stage (Fig. 4). For the tree data, PCI separated out stage 2 from the other stages, while PCII separated stages 7 and 9 from some of the intermediate stages (Fig. 4). For nematodes in the litter layer, PCI separated stage 1 and to a lesser extent stage 2 from most of the other stages, while PCII separated stage 9 from the other stages (Fig. 4). With regard to nematodes in the soil layer, PCI greatly separated stage 1 from stage 8 (with the other stages occupying intermediate stages). For macroinvertebrates in the litter layer, the greatest separation was between stages 8 and 9, while in the soil layer stages 8 and 9 were significantly separated from most of the earlier stages (Fig. 4).

Correlation analysis showed that for the taxonomic richness data, there were no significant relationships across the 36 plots between any pair of groups except between macroinvertebrates in litter and macroinvertebrates in the soil layer (Table 4). Further, there were no significant relationships between the community diversity (Shannon–Weiner index) of any pair of groups, except between trees and macroinvertebrates in the soil layer (Table 4). With regard to the scores for the primary ordination axes (PCI), nematodes in soil showed significant relationships with all other groups, and macroinvertebrates in soil showed significant relationships with all other groups except nematodes in litter (Table 4).

Across the 36 plots, generic richness of nematodes was significantly correlated with the soil C to P and N to P ratios, and family richness of litter macroinvertebrates was correlated with tree basal area (Table 5). Community diversity (Shannon–Weiner diversity index) of litter nematodes was significantly correlated with C to N, C to P and N to P ratios, while diversity of nematodes in soil and macroinvertebrates in soil were significantly correlated with tree basal area (Table 5). For the primary ordination scores (PCI), all faunal groups were significantly correlated with the soil C to N ratio, and all groups except macroinvertebrates in soil were significantly correlated with the C to P and N to P ratios. Further, PCI for macroinvertebrates in both soil and litter were significantly correlated with tree basal area (Table 5).

4. Discussion

4.1. Tree and soil data

Our measurements of tree basal area (a surrogate for tree biomass) and soil chemical properties across the Franz Josef chronosequence confirm that there are distinct build-up and decline phases across this sequence (Stevens and Walker, 1970; Wardle et al., 2004b). The decline phase is known to be associated with diminishing quality of resources for plants, and in particular the relative availability of P, as the chronosequence proceeds (Stevens and Walker, 1970; Richardson et al., 2004). This increasing limitation by P and decline in plant community biomass is consistent with findings of other studies on

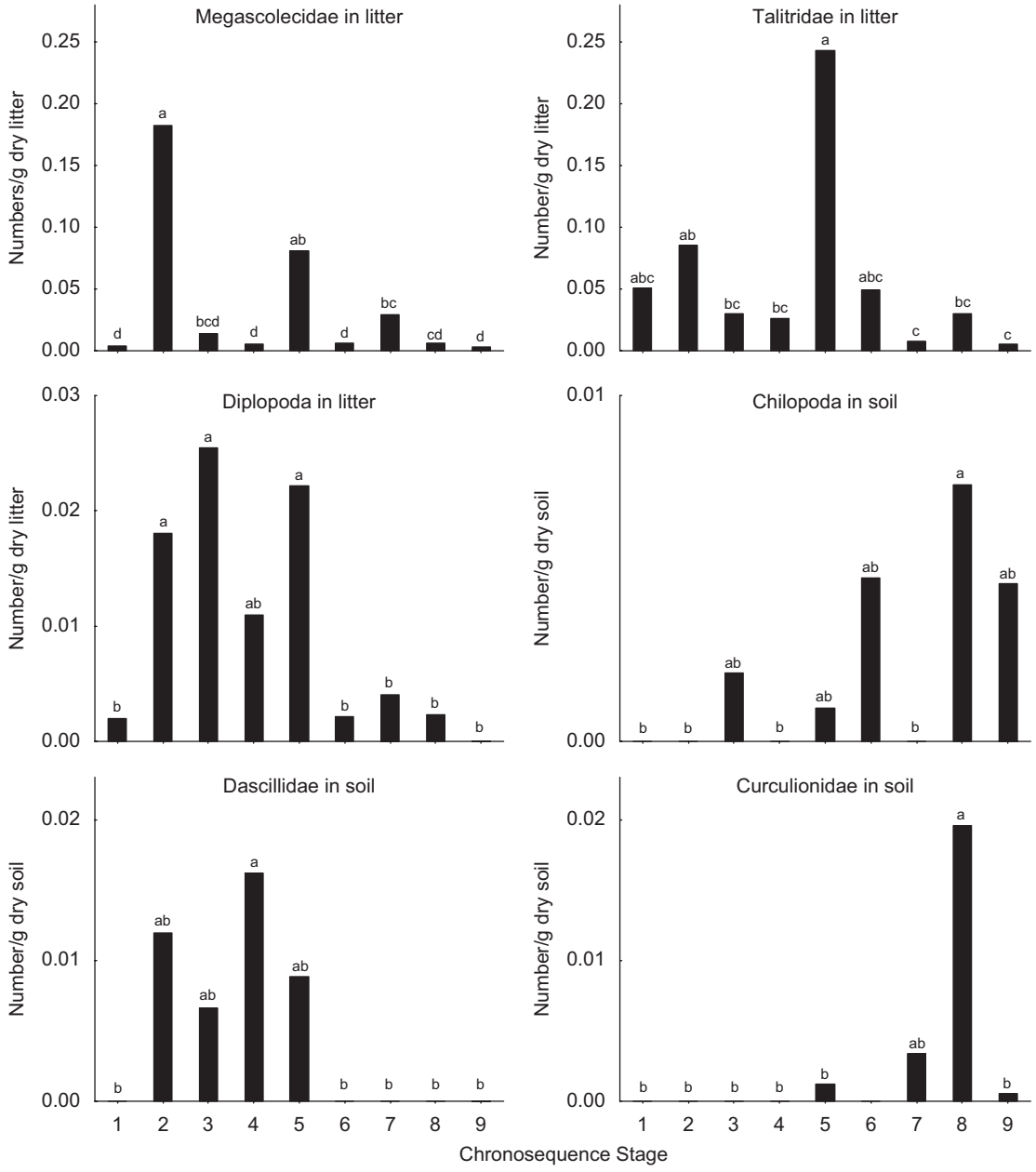

Fig. 2. Abundances of selected macroinvertebrate groups in soil and litter for nine stages along the Franz Josef chronosequence. Within each panel, bars topped with the same letters are not significantly different at $P = 0.05$ (Mann–Whitney U-statistic). Results from Kruskall–Wallis tests for the effect of chronosequence stage on these groups are shown in Table 3.

long-term chronosequences that include retrogressive stages (Vitousek, 2004; Wardle et al., 2004b; Coomes et al., 2005).

4.2. Invertebrate abundances

In the litter layer, we found densities of microbe-feeding nematodes to decline over time, with three- to 10-fold more nematodes in the first stage than in all the subsequent stages. These high initial numbers may reflect the high quality of plant litter that is associated with early successional plant species (Grime, 1979; Walker and Chapin, 1987; see also foliar N and P values for this system in Richardson et al., 2004). The decline in microbe-feeders during the first few stages could also be associated with increasing densities of their predators (both 'top predators', and 'omnivores' or predators that feed on more than one trophic level) during these stages. This is consistent with other studies pointing to strong top-down control of microbe-feeding nematodes by predation (Mikola and Setälä, 1998), and increasing densities of predatory nematodes during the build-up phase of succession (Wardle et al., 1995). The fact that several groups of litter microinvertebrates (i.e., predatory and omnivorous nematodes; copepods) declined during the later stages of the chronosequence is likely due to the poor quality of litter

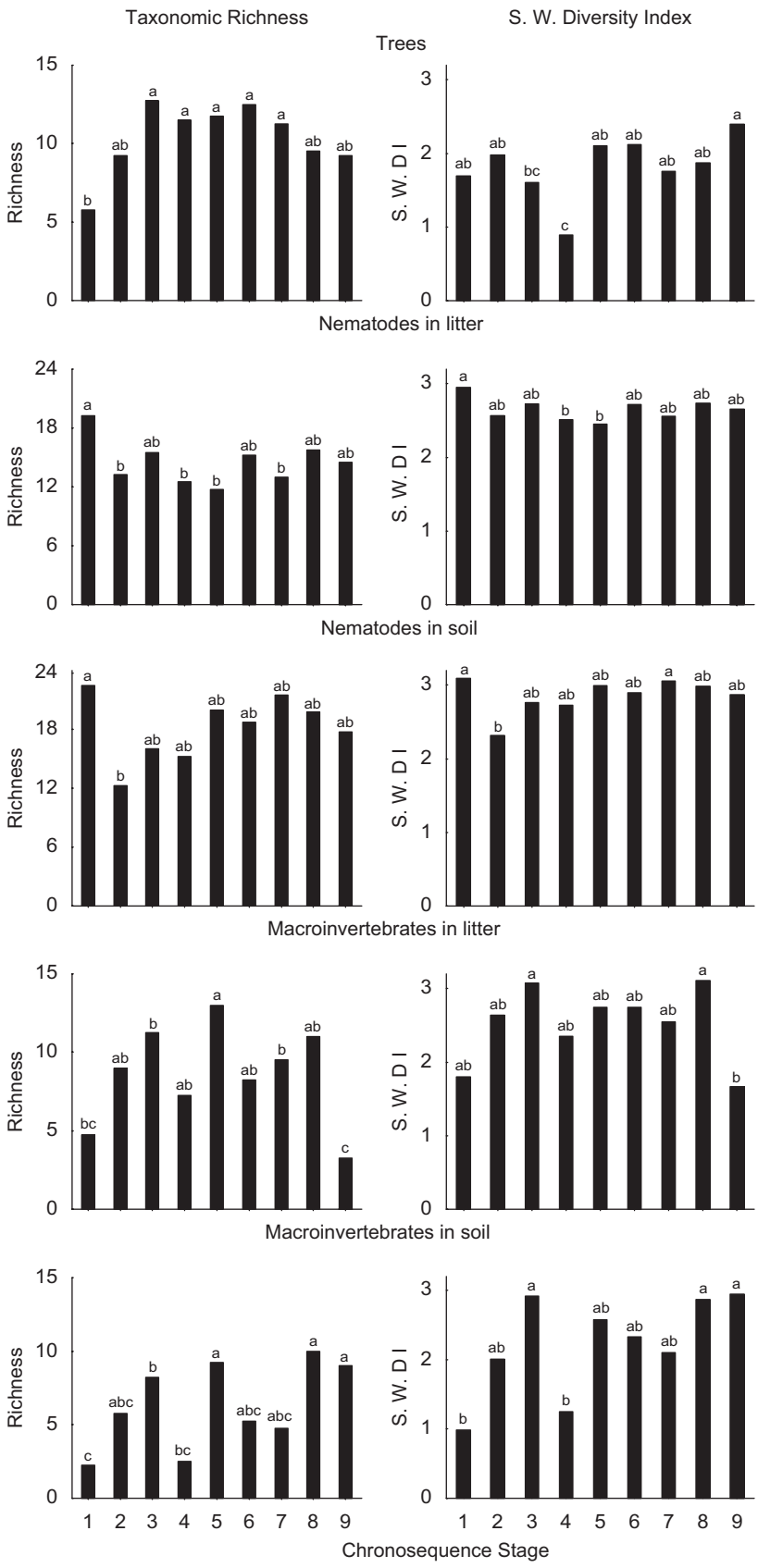

Fig. 3. Taxonomic richness and diversity (Shannon–Weiner diversity index) for trees, and for nematodes and macroinvertebrates in both the litter and soil layers, for nine stages along the Franz Josef chronosequence. Measures of richness and diversity for tree data are at the species level, for the nematode data are at the generic level, and for macroinvertebrate data are at the family level. *F*- and *P*-values are derived from one-way ANOVA testing for effects of chronosequence stage on community richness and diversity (degrees of freedom for all analyses are 8,27). Within each panel, bars topped with the same letters are not significantly different at $P = 0.05$ (Tukey's test).

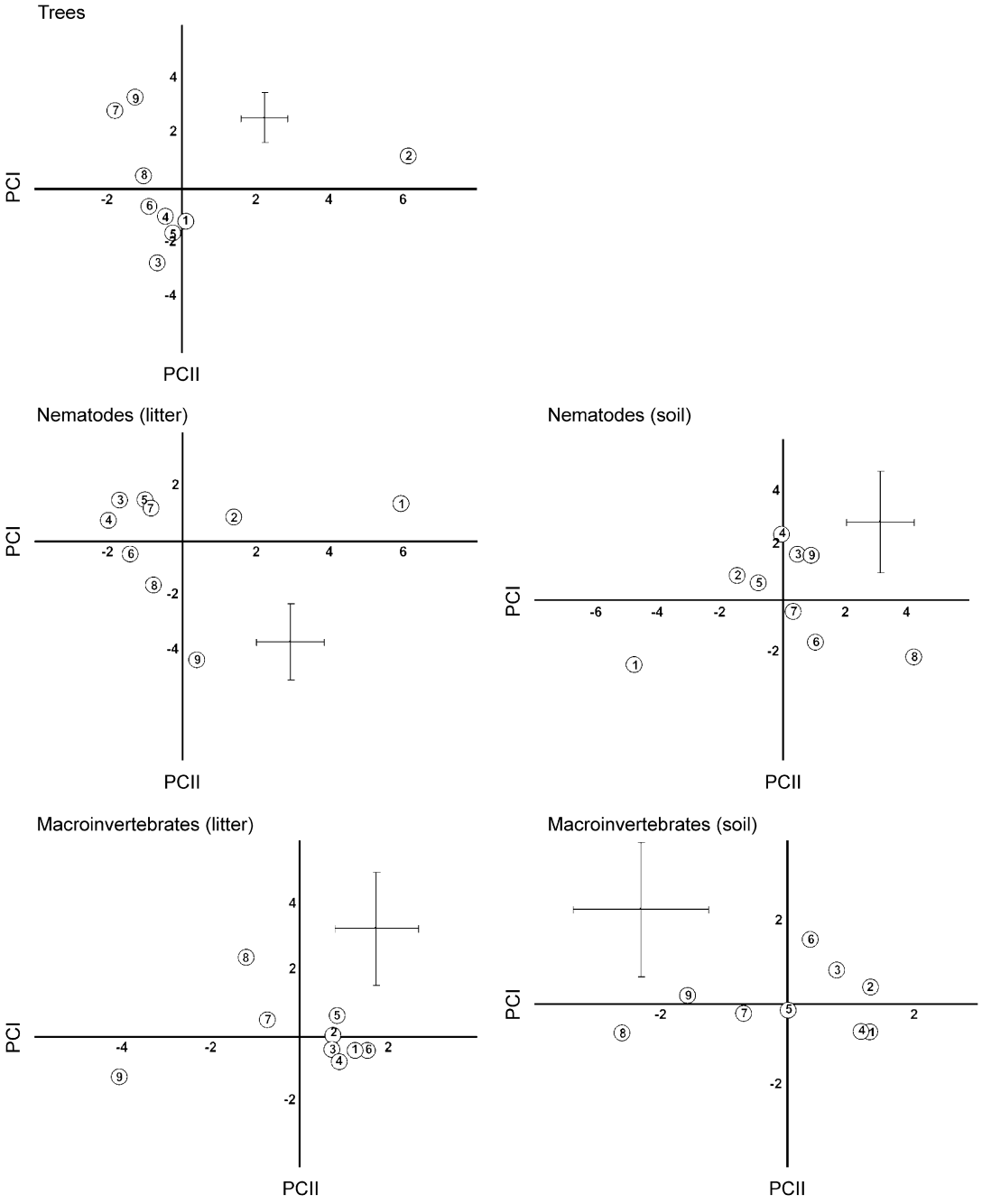

Fig. 4. Ordination biplots summarizing community structure, using scores for the two primary ordination axes derived using principal components analysis (PCI and PCII) for the tree, nematode and macrofaunal community data. Numbers inside circles represent stage of chronosequence (mean of four plots; see Section 2 for description of stages). *F*- and *P*-values are derived from one-way ANOVA testing for effects of chronosequence stage on the values of scores of the primary ordination axes (PCI and PCII) derived from principal components analysis, for tree, nematode and macroinvertebrate communities. Horizontal and vertical bars are Tukey's honestly significant differences at $P = 0.05$ for PCI and PCII, respectively. The proportion of total variation explained by PCI and PCII is 16.5% and 11.3% for trees, 15.0% and 9.0% for litter nematodes, 11.8% and 8.3% for soil nematodes, 15.8% and 10.1% for litter macroinvertebrates, and 10.3% and 9.9% for soil macroinvertebrates.

produced by dominant tree species during retrogression (Vitousek, 2004; Wardle et al., 2004b). The non-responsiveness of plant-feeding and plant-associated nematodes to chronosequence stage in the litter is because the density of these groups in this layer was very low throughout, presumably due to the dearth of food resources (live roots) in this layer.

In the mineral soil layer, all microfaunal groups that responded significantly to chronosequence stage increased up to stage 6, then sharply declined. This is consistent with earlier work showing the basal trophic level of the soil food web (i.e., the microbial biomass) to be greatest at intermediate stages of this chronosequence (Wardle and Ghani, 1995), and points to multitrophic responses of the

Table 4
Pearson's correlation coefficients between tree community variables (richness, diversity and ordination scores) and soil invertebrate community variables (richness, diversity and ordination scores) across the Franz Josef Glacier chronosequence, for $n = 36$ plots

Community response variable		Nematodes in soil	Nematodes in litter	Macroinverts[a] in soil	Macroinverts in litter
Taxonomic richness	Trees	−0.071	−0.320	0.169	0.254
	Macroinverts in litter	−0.056	−0.219	**0.330***	
	Macroinverts in soil	0.091	−0.069		
	Nematodes in litter	0.296			
Shannon–Weiner diversity index	Trees	0.131	−0.042	**0.371***	0.031
	Macroinverts in litter	−0.103	−0.163	0.236	
	Macroinverts in soil	0.208	0.010		
	Nematodes in litter	0.298			
Principal component axis 1	Trees	**0.364***	0.310	**0.413***	0.266
	Macroinverts in litter	**0.398***	0.086	**0.599*****	
	Macroinverts in soil	**0.596*****	0.230		
	Nematodes in litter	**0.679*****			

Asterisks (*, ** and ***) indicate that correlation coefficient differs significantly from zero at $P = 0.05$, 0.01 and 0.001, respectively.
[a]Macroinvertebrates.

Table 5
Pearson's correlation coefficients between soil invertebrate community variables, and tree basal area and soil nutrient measurements

Community response variable	Taxonomic group	Tree basal area	Soil C to N ratio	Soil C to P ratio	Soil N to P ratio
Taxonomic richness	Nematodes in soil	0.304	0.130	−0.144	−0.250
	Nematodes in litter	−0.148	0.282	**0.328***	**0.322***
	Macroinverts[a] in soil	−0.147	0.219	0.252	0.254
	Macroinverts in litter	**0.344***	0.106	−0.159	−0.268
Shannon–Weiner diversity index	Nematodes in soil	**0.375***	0.278	−0.023	−0.147
	Nematodes in litter	−0.078	**0.364***	**0.325***	**0.348***
	Macroinverts in soil	−0.016	0.315	0.326*	0.311
	Macroinverts in litter	**0.375***	0.253	−0.061	−0.188
Principal component axis 1	Nematodes in soil	0.315	**0.389***	**0.568*****	**0.599*****
	Nematodes in litter	0.063	**0.675*****	**0.578*****	**0.487****
	Macroinverts in soil	**0.692*****	**0.419***	0.312	0.248
	Macroinverts in litter	**0.341***	**0.659*****	**0.557*****	**0.472****

Asterisks (*, ** and ***) indicate that correlation coefficient differs significantly from zero at $P = 0.05$, 0.01 and 0.001, respectively.
[a]Macroinvertebrates.

soil food web to the build-up and decline phases. This response matches the response of tree biomass to chronosequence stage, suggesting that forests with a high plant biomass also support high densities of microinvertebrates. The decline observed after stage 6 is also reflective of diminishing quality of resources (i.e., organic matter content, and increasing ratios of C to N, C to P and N to P) in the soil. In any case, consistent with our first hypothesis, our results confirm that the pattern of vegetation build-up and decline observed across long-term chronosequences also applies to the soil microinvertebrate community.

The soil microfood web consists of distinct fungal- and bacterial-based energy channels (Coleman et al., 1983; Moore and Hunt, 1988). Our results show that the nematode channel ratio (i.e., the ratio of 'bacterial-feeding' to 'bacterial-feeding + fungal-feeding' nematodes) declines during the final chronosequence stage in the litter layer and the final three stages in the soil layer, pointing to increased importance of the fungal-based channel during retrogression. The fungal-based channel is far more conservative than the bacterial-based channel at retaining nutrients and preventing nutrient leakage (Coleman et al., 1983; Wardle, 2002), and is therefore expected to dominate in nutrient limited systems such as the retrogressive stages of the chronosequence. This result is consistent with other studies pointing to increased dominance of fungi relative to bacteria during retrogression (Wardle et al., 2004b), as well as the study of Williamson et al. (2005) that found increased domination by the fungal-based energy channel during retrogression along a chronosequence of terraces of marine origin. For the soil layer, the high value for the nematode channel ratio at stage 1 was due to very low densities of fungal-feeders present, while the low ratio values for stages 2–4 could be reflective of low soil organic

matter content and therefore reduced resource availability for the soil biota.

The macroinvertebrate groups that were responsive to chronosequence stage were most likely influenced by shifts in resources across the sequence. For the macroinvertebrates inhabiting the litter layer the principle resource is the litter itself, while for those inhabiting the soil the main resources would be tree roots and organic matter (Sadaka and Ponge, 2003). Consequently, in the litter layer, all four groups that responded significantly to chronosequence stage were litter-feeders, while two of the three most responsive groups in the soil itself were root-feeders. Soil macrofauna are mainly regulated by bottom-up control (Scheu and Schaefer, 1998; Sanders and Gordon, 2003), and across the chronosequence macroinvertebrate groups usually had their lowest densities in stages 1 and 9 where tree biomass and therefore quantity of resources produced by the trees is lowest. However, soil macrofauna abundance is also affected by other resource characteristics such as resource quality and physical structure of the litter (Salamon et al., 2006). Different groups of macrofauna can respond quite differently to these factors (Wardle et al., 2006), and this may explain the differences in relative abundance between macrofaunal groups across the intermediate stages (stages 2–8) of the sequence. These differences between groups are in concordance with our second hypothesis, by showing that the importance of bottom-up control in influencing soil invertebrate densities differs among contrasting groups. This is consistent with literature pointing to different groups of soil invertebrates varying in their relative responsiveness to top-down forces, bottom-up forces, and predation (Wardle et al., 1995; Mikola and Setälä 1998). However, low densities at the final stage of the chronosequence were observed for most macroinvertebrate groups, meaning that they showed a similar pattern of decline during retrogressive stages as observed for the vegetation and the main microfaunal groups, consistent with our first hypothesis.

4.3. Community-level responses

Community taxonomic richness and diversity (Shannon–Weiner index) responded significantly to chronosequence stage for all groups of organisms considered. However, there was little concordance between different groups of taxa with regard to the response of their diversity to chronosequence stage. Tree species richness increased initially then remained unchanged; nematode generic richness in both litter and soil decreased initially then increased again (though not significantly); and macroinvertebrate family richness peaked at intermediate stages for litter and some intermediate and late stages for soil. Broadly similar patterns were found for the Shannon–Weiner index, except for tree diversity which was least at stage 4 because of domination of basal area by large individuals of the tree *M. umbellata*. Inconsistent with our third hypothesis, there was little relationship across the 36 plots between diversity of trees, nematodes and macroinvertebrates (Table 4), indicating that soil biotic diversity is at best only weakly coupled with plant diversity. This is consistent with earlier studies pointing to diversity of soil biota being influenced more by plant community composition than by plant diversity (Porazinska et al., 2003; De Deyn et al., 2004). However, richness and diversity of nematodes was significantly related to measures of soil fertility, and diversity of soil nematodes and litter macroinvertebrates was positively related to tree basal area (Table 5). These findings concur with previous studies pointing to resource availability as an important determinant of the diversity of soil organisms (Hooper et al., 2000; Wardle, 2006). Our results also show that both above- and below-ground diversity does not change markedly during retrogression, except for litter macroinvertebrates.

Community composition of trees, nematodes and macroinvertebrates were all strongly affected by chronosequence stage, and the earliest and latest stages were often separated from intermediate stages by the ordination analyses. Further, the community composition data for the different groups were often strongly correlated with each other (Table 4), and consistent with our third hypothesis, both soil nematode and soil macroinvertebrate communities were significantly related to tree communities. This points to important linkages between plant and soil communities across the chronosequence. This could arise either because of plant community composition driving soil community composition (Hooper et al., 2000; Wardle, 2006) or because both plant and soil community structure were similarly influenced by variation in soil fertility across the sequence. It has previously been shown that tree community composition varies strongly with ratios of C to N, C to P and N to P in the soil across the sequence (Richardson et al., 2004; Wardle et al., 2004b), and the present study shows that this is also largely true for the soil invertebrate community (Table 5). Further, our results highlight that plant and soil invertebrate communities can show distinct compositional associations with each other even when plant and soil diversity *per se* do not (Wardle, 2006).

5. Conclusions

Our results provide evidence that soil invertebrate communities can show similar patterns to those of plant communities in the long-term absence of catastrophic disturbance. Abundances of all soil faunal groups except microbe-feeding nematodes in litter showed an increase during initial chronosequence stages and a decline later on. Different groups of soil fauna peaked at different stages, presumably because taxa differ in their responses to bottom-up and top-down controls across the sequence (Wardle et al., 2006). However, there is consistent evidence of reduced abundances of soil biota during the retrogressive stages. Further, although the diversity of soil organisms does not change greatly during retrogression

(except for litter macroinvertebrates), community composition of these organisms does. As such, nutrient limitation during retrogression emerges as a major driver of invertebrate communities, and this points to resource availability serving as a major driver of a range of invertebrate taxa during long-term ecosystem change.

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