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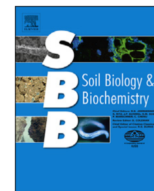

Responses of communities of soil organisms and plants to soil aging at two contrasting long-term chronosequences

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ABSTRACT

Soil fertility and vegetation are major drivers of soil communities. Soil community responses to vegetation development and associated changes in soil fertility have been mostly reported for chronosequences that span time scales from decades to centuries. Here we evaluated soil communities for two contrasting chronosequences, the Franz Josef chronosequence in southern New Zealand caused by glacial retreat and spanning 120,000 years, and the Cooloola chronosequence in eastern Australia caused by aeolian movement of sand that spans 700,000 years. Both chronosequences feature later-phase retrogressive stages characterized by reduced nutrient availability and plant stature. We hypothesized that soil communities would mirror the patterns of vegetation across these long-term chronosequences with organism biomasses, abundances and diversity increasing throughout early stages of the succession and declining at retrogression stages. The hypothesis was not consistently supported. Bacterial and fungal biomass increased across the youngest chronosequence stages but remained unchanged across the later stages, while fungal-to-bacterial ratios increased throughout. Microbial biomass was related to soil nitrogen concentrations across both chronosequences. Invertebrate abundance and richness increased during the early stages of ecosystem development in both chronosequences, but different groups peaked at different stages at each chronosequence, and not all invertebrate groups declined during the retrogressive stages. Invertebrate groups had no consistent correlations with biotic or abiotic ecosystem properties across either chronosequence. Our study demonstrates that soil organisms track changes in plant biomass and richness and soil fertility during the initial stages of both chronosequences, but with increasing age of the chronosequences, these relationships weaken and other factors drive the soil community. Possible explanations for the different patterns in soil communities at the two chronosequences include that they differ strongly in soil organic matter, nutrient concentrations and abundances of soil organisms (all of which are much higher at Franz Josef than Cooloola), overlaid with different macroclimate and geology, so that different factors are likely to restrict the presence of particular organisms across both chronosequences. As such, while soil fertility and vegetation are widely recognized as important drivers of the soil community, the manner in which these factors directly and indirectly shape the soil community can vary greatly across organism groups, among chronosequences, and over the time scales that ecosystems develop.

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1. Introduction

Explaining spatiotemporal patterns of the abundance and diversity of soil organisms across communities remains a major challenge in ecology (Decaëns, 2010). Soil fertility and vegetation composition are two of the main drivers of soil communities (Bardgett, 2002; Wardle, 2005; Nielsen et al., 2010). As ecosystems

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develop after disturbances, large shifts in the floristic and functional composition of the vegetation and concomitant changes in soil fertility should be matched by corresponding changes in the soil community. However, responses of soil communities during ecosystem development, such as observed across chronosequences, differ because of factors such as the vegetation present, abiotic properties, and the type and intensity of disturbance that initiated the chronosequence (Hågvar and Abrahamsen, 1984; Chauvat et al., 2011; Perez et al., 2013). Further, chronosequence-based studies often compare soils that differ in age by a few centuries or less, and often involve secondary successions resulting from human activities (e.g. Perez et al., 2013). Long-term chronosequences, spanning thousands of years, have been investigated to a much lesser extent, but have proven valuable for studying how the interactions between above- and belowground ecosystem properties develop over long time-scales (Peltzer et al., 2010; Walker et al., 2010; Laliberté et al., 2012).

During early primary succession, the availability of nitrogen (N) is often limiting, but N levels rapidly increase due to biological N_2 fixation, while levels of phosphorus (P) become increasingly accessible because of microbial activity and weathering of the basal substrate (Walker et al., 1981; Clein and Schimel, 1995). Early-successional plant communities are typically composed of fast-growing species with high quality litter that promotes rapid nutrient turnover through decomposition. As primary succession proceeds and organic matter accumulates in the soil, nutrients become less available and there is a tighter and slower cycling of nutrients through the ecosystem. In the absence of major soil disturbances for millennia or longer, ecosystems can develop to a state of ‘ecosystem retrogression’ characterized by strong nutrient limitation, very slow decomposition rates, and reduced vegetation stature, biomass and productivity (Walker et al., 1987; Wardle et al., 2004; Peltzer et al., 2010). Recent work along long-term chronosequences indicates that microbial communities are closely aligned with pedogenesis and vegetative change during retrogression (Jangid et al., 2013; Clemmensen et al., 2015; Krüger et al., 2015; Martínez-García et al., 2015). However, studies of soil communities integrated alongside information on vegetation that encompass both long-term ecosystem development and retrogression are scarce (e.g. Williamson et al., 2005; Doblas-Miranda et al., 2008), and very little is known about the responses across soil food web levels.

In this study, we quantified the soil community (microbes, nematodes, mites and springtails), plant community and soil abiotic conditions across each of two contrasting, long-term chronosequences. Each chronosequence contains distinct build-up and retrogressive phases that are characterized by strong shifts in vegetation composition, plant biomass and soil nutrient availability: a 700,000-year-old chronosequence in Queensland, Australia that has formed during sand dune development (Thompson, 1981; Walker et al., 1981), and a 120,000-year-old chronosequence in southern New Zealand that has developed following glacial retreat (Walker and Syers, 1976; Richardson et al., 2004). Across each chronosequence, we characterized the communities of vascular plants, soil microbes, nematodes and microarthropods.

We hypothesized that: 1) soil microbial biomass and invertebrate abundance follows vegetation biomass and patterns in nutrient availability (soil fertility), in that abundance and biomass will increase with initial vegetation succession but decrease as vegetation biomass and nutrient availability declines during retrogression. 2) Invertebrate taxonomic richness will follow changes in plant species richness along both chronosequences, in line with experimental studies which indicate that higher plant richness can promote richness of soil invertebrates (Wardle et al., 1999; Spehn et al., 2000; Eisenhauer et al., 2011; Sabais et al., 2011). 3) Declines in soil fertility during retrogression will affect the composition of soil microbes and various trophic groups of the soil fauna. Specifically, as ecosystem development and retrogression proceed, there should be an increase in the fungal to bacterial ratio because fungi are better suited to nutrient-limited conditions than are most bacteria (Bowen and Harper, 1990; Griffiths et al., 1999; Kramer and Gleixner, 2006), and this should in turn lead to changes in the relative abundance of bacterial- and fungal-feeding invertebrates. By addressing these three hypotheses in combination along two contrasting chronosequences, we aim to better understand how the driving roles of vegetation development and concomitant shifts in soil fertility impact on the structure of soil communities.

2. Materials and methods

2.1. Site descriptions

The Cooloola chronosequence (Coaldrake, 1960; Thompson, 1981; Walker et al., 1981) is situated in the Great Sandy National Park on the east coast of Australia, 200 km north of Brisbane (26°S, 153°E; 30–160 m above sea level; Table S1). The mean January and July temperatures are 24 °C and 16 °C respectively, and the total annual precipitation is 1474 mm. This chronosequence involves sand dunes of different ages that develop through aeolian movement of sand; it spans 700,000 years and includes 9 sites (Thompson, 1981; Wardle et al., 2004). It begins as an unvegetated mobile sand dune. Vegetation biomass accumulates with site age and biomass declines at retrogression sites as a result of P limitation (Walker et al., 1981; Wardle et al., 2004, 2008; Chen et al., 2015). Vegetation at the younger sites is dominated by *Monotoca* sp. Fraser Island P. Baxter 777 (e.g., Leiper et al., 2008) (Ericaceae), *Banksia integrifolia* (Proteaceae) and *Callitris columellaris* (Cupressaceae), while the peak biomass sites are dominated by *Corymbia intermedia*, *Angophora woodsiana*, and *Eucalyptus pilularis* (all Myrtaceae) and the older retrogressive sites are dominated by *Banksia aemula* (Proteaceae) and *Leptospermum trinervium* (Myrtaceae) (Walker et al., 1981).

The Franz Josef chronosequence (Walker and Syers, 1976) is in the South Westland region of New Zealand (43°S, 170°E; 155–285 m above sea level; Table S1). The mean January and July temperatures are 15 °C and 7 °C, respectively, and the total annual precipitation ranges from 3800 to 6000 mm. This chronosequence involves surfaces of different ages caused by the retreat of the Franz Josef Glacier; it spans 120,000 years and includes 9 sites. The first site consists of newly exposed gravel. Vegetation peak biomass occurs at around 5000 years and the retrogression decline sets in after 70,000 years. Vegetation at the youngest site is dominated by the nitrogen-fixer *Coriaria arborea* (Coriariaceae) with *Aristotelia serrata* (Elaeocarpaceae), *Melicytus ramiflorus* (Violaceae) and *Schefflera digitata* (Araliaceae). Sites with peak biomass are dominated by *Dacrydium cupressinum* (Podocarpaceae), *Metrosideros umbellata* (Myrtaceae), and *Weinmannia racemosa* (Cunoniaceae), while the retrogressive sites are dominated by *Lepidothamnus intermedius*, *Manoao colensoi* and *Phyllocladus alpinus* (all Podocarpaceae).

At each of the 9 sites for both chronosequences, a permanent 20 m × 20 m quadrat was established for plant community measurements (except for the 5th of the 9 stages at Franz Josef; Table S1). We measured the diameter at breast height (dbh at 1.3 m) of all trees ≥ 3 cm diameter in the quadrat, and converted tree diameter to biomass using species-specific allometric equations (e.g. Westman and Rogers, 1977; Birk and Turner, 1992; Montagu et al., 2005; Basuki et al., 2009; Holdaway et al., 2014). Equations for closely related species were used if they were unavailable for

particular species. In each quadrat, all vascular plant species present, including understory species not used for dbh measurements, were counted to quantify species richness. For the trees, diversity using Shannon entropy H' (Jost, 2006) was calculated for each quadrat by using the estimates of biomass for each species. Vegetation data from permanent quadrats along both chronosequences are archived in New Zealand's National Vegetation Survey databank (www.nvs.landcareresearch.co.nz).

Within the centre of each 20 m × 20 m quadrat, six 1 m × 1 m plots were marked out in two rows of 3 plots at 5 m distance for quantifying soil communities. We emphasize that as soil communities are structured at much smaller spatial scales than forest vegetation, much smaller plots are needed to assess the soil communities. However, the mean measures of soil communities in multiple small plots within a larger plot can be directly compared with vegetation measures from the larger plot (Williamson et al., 2005; Doblas-Miranda et al., 2008). The Cooloola chronosequence was sampled between the first week of October and the first week of December 2011, which is at the end of the dry season. The Franz Josef chronosequence (which does not have a dry season) was sampled during the second week of December 2011 and the second week of January 2012. Vegetation surveys were performed during November 2011 and January 2013 at Cooloola and Franz Josef, respectively. Within each plot, we collected 20 intact soil samples (1.7 cm diameter and 5 cm depth). Soil samples from within each plot were bulked, creating one composite sample per plot which was used for measurements of soil chemistry and the microbial and nematode communities (see below); these composite samples served as units of replication within each chronosequence site, in line with earlier work along these and other chronosequences (Wardle et al., 2004; Doblas-Miranda et al., 2008; Wardle et al., 2009). Soil samples were stored at 4 °C until they were processed, always within 3 days of sample collection.

To quantify the micro-arthropod community (i.e., springtails and mites), we collected 12 soil cores (each 10 cm diameter and 5 cm deep) from each quadrat which were arranged as a grid of 12 m by 8 m with 4 m between cores; these cores were kept intact and served as units of replication within chronosequence sites. The higher sampling density relative to that used for microbes and nematodes was chosen to accommodate the high spatial heterogeneity of soil micro-arthropods (Gao et al., 2014). Due to extraction limitations, 27 samples were collected per week along the Cooloola chronosequence (making sure that 3 samples were collected at each site during the weekly samplings); this was continued for 4 weeks until all 12 samples for each site had been collected. The nine chronosequence sites along the Franz Josef chronosequence were sampled twice; the first 6 samples per site were collected during the second week of December 2011 and the second 6 samples were collected during the second week of January 2012. There were no statistically significant differences in micro-arthropod abundance between sampling dates (data not presented).

2.2. Soil abiotic properties and microbial community composition

A homogenized subsample of each soil sample was sieved (5 mm mesh) for analysis of soil abiotic properties and microbial community composition. Each subsample was analysed for water content (by oven-drying at 105 °C for 48 h), pH (Mettler Toledo MP 220 pH meter), organic C and total N (Dumas dry combustion using a Leco TruMac) and P (Kjeldahl), NH_4^+ and NO_3^- (colorimetric quantification of KCl extracts on a QuikChem 8500 flow injection analyser) and available P (bicarbonate-extractable or Olsen P) following Blakemore et al. (1987).

The soil microbial community was quantified through PLFA analyses. Fresh homogenized soil samples were freeze-dried at the country of origin shortly after collection and sent to the Swedish University of Agricultural Sciences in Umeå for extraction and analyses. Extracted fatty acids were expressed as relative nmoles per g of dry soil using standard nomenclature. The PLFAs i15:0, α15:0, i16:0, 16:1ω9, 16:1ω7t, 16:1ω7c, i17:0, α17:0, cy17:0, 18:1ω7 and cy19:0 were used to calculate bacterial biomass, while the PLFAs 16:1ω5, 18:2ω6 and 18:1ω9 were used to calculate fungal biomass. Mono-unsaturated and cyclic fatty acids (16:1ω9, 16:1ω7t, 18:1ω7) were grouped as gram-negative bacteria (gram-), while branched PLFAs (i15:0, α15:0, i16:0, 16:1ω7c, i17:0, α17:0, cy17:0 and cy19:0) were grouped as gram-positive bacteria (gram+). The PLFA 16:1ω5 was used to quantify the abundance of arbuscular mycorrhizal fungi (AMF). Fungal to bacterial ratios (F:B) were calculated from the sum of fungal-associated PLFAs divided by the sum of bacteria-associated PLFAs (Frostegård and Bååth, 1996).

2.3. Nematodes

A 100–200 g (wet weight), homogenized, unsieved subsample of each soil sample was used to characterize the nematode community. Nematodes were extracted using a sugar flotation method (modified from Jenkins, 1964). Nematodes were heat-killed, and fixed using 35% formaldehyde diluted to 4%. Subsequently, approximately 150 nematodes per sample were identified to family level, and placed into six feeding groups following Yeates et al. (1993), i.e. bacterial feeders, fungal feeders, root-associated, plant-associated, omnivores and predators. For each soil sample nematode densities were expressed per unit soil weight. For each sample we also used these data to determine the number (i.e., richness) of nematode families and the ratio of fungal-feeding nematodes to bacterial-feeding nematodes.

2.4. Micro-arthropods

The Franz Josef samples were placed in a modified Tullgren extractor (van Straalen and Rijninks, 1982) for 3 weeks and animals were stored in 70% ethanol. The sandy Cooloola soil samples were not suitable for use in a Tullgren extractor (the optimal means of extraction for most soils, including those from Franz Josef); instead the soil was carefully crumbled by hand and placed in a funnel with a mesh at the bottom, below which there was a collection tube with 70% ethanol. The soils were left undisturbed for a week to allow the micro-arthropods to migrate down into the funnel (Hopkin, 2007). While it was necessary to use different extraction procedures for Franz Josef and Cooloola, we maintain that this difference would not introduce biases when comparing stages within each of the two chronosequences. Springtails were identified to genus or species level where possible following Greenslade and Ireson (1986) and Greenslade (1991) for Cooloola, and Salmon (1940) for Franz Josef. Mites were classified into Oribatida, Astigmata-Prostigmata (A-P) and Mesostigmata following Weigmann (2006) and Krantz and Walter (2009), and where possible further identified to families, for both chronosequences. Springtails were grouped in three classes that indicate the typical stratification across the soil continuum: 1) eu-edaphic species that tend to live deeper in the soil, 2) hemi-edaphic species that live primarily among the upper litter layers, and 3) epi-edaphic species that tend to live on top of the soil (Gisin, 1943). This classification was used as it incorporates a large suite of species traits that can help explain springtail abundance patterns in response to environmental factors (Krab et al., 2010; Bokhorst et al., 2012). Richness values were based on the number of species or genera for springtails and the number of families or higher order taxa for mites. A complete list of all invertebrate species, families and groups encountered is available as online supplementary file S1.

2.5. Statistical analyses

For each of the two chronosequences, differences between chronosequence sites in soil characteristics, microbial biomass, soil invertebrates (abundance and richness) and F:B ratios were tested with one-way Analyses of Variance (ANOVA) and Tukey's honest significant difference (HSD) post hoc tests to identify differences among sites. The six bulked samples per site (for the abiotic, microbial and nematode data) or 12 cores per site (micro-arthropod data) served as the units of replication. To reduce each community-level data set to fewer variables, we applied Non-Metric Multidimensional Scaling (NMDS) with Bray-Curtis distances using proportional abundance data for each of the following groups: plant species, springtail species, mite families/orders, nematode families and microbial PLFAs. Objects ordinated closer to one another are more similar than those further apart. Low stress values (<0.1) indicate a good representation of the applied dimension reduction, while stress values above 0.20 should be interpreted with caution. One-way ANOVAs on the NMDS scores as described above were then used to identify significant differences among chronosequence sites for each group of soil organisms. For all ANOVAs, homogeneity of variance was tested with a Levene's test of equality and log-transformation was applied when necessary.

To identify potential drivers of the observed plant, microbial and invertebrate variables for each chronosequence, we used correlation analyses to relate these variables to soil abiotic factors, as well as (where appropriate) to plant and microbial variables. For these analyses we used each chronosequence stage as an independent data point (N = 9) because of lack of independence of plots within stages and because for plant variables we had one measurement per stage. In addition, we fitted regression lines (linear, polynomial or logarithmic) through the mean values of the 9 chronosequence sites to identify the responses of soil characteristics and plant, microbial and invertebrate data to chronosequence site (i.e., log-transformed time in years since the chronosequence started) for both chronosequences. All statistical analyses were carried out using SPSS 22.0 (IBM SPSS Statistics for Windows, version 22.0, Armonk, NY, USA).

3. Results

3.1. Abiotic soil properties

There were often large changes across both chronosequences in several soil abiotic properties (Table 1). Soil water content was lowest at the youngest site but otherwise showed no consistent pattern at Cooloola, whereas it peaked at intermediate sites at Franz Josef. Soil pH declined with site age along both chronosequences, i.e., from 6.6 to 4.9 for Cooloola and from 5.8 to 4.6 at Franz Josef. Soil organic C (%) increased with site age for both chronosequences but only declined at the 120,000 yr Franz Josef site. Soil nutrient concentrations were much greater throughout at Franz Josef than at Cooloola (e.g., mean total P was 548 ppm at Franz Josef vs. 26 ppm at Cooloola). Total soil N initially increased and was greatest at intermediate site ages for both chronosequences. There was no clear pattern in extractable NO_3^-, except for a very large peak at the 70 yr site at Franz Josef. Extractable NH_4^+ was greatest across the youngest (<500 yr) sites of both chronosequences. Total soil P decreased for both chronosequences over time, i.e., from 36 ppm to 7 ppm at Cooloola and from 990 ppm to 89 ppm at Franz Josef. Meanwhile, Olsen P was greatest at intermediate sites and lowest at the oldest site for both chronosequences. Correlation coefficients between the abiotic variables across chronosequence sites are presented in Table S2.

3.2. Plant community composition

At Cooloola, plant biomass initially increased and then declined at the final three sites (Fig. 1a). The 120,000 yr site at Cooloola had particularly high biomass compared with the other sites as a result of high wood density *Eucalyptus pilularis* individuals up to 2 m dbh. Plant species richness initially increased rapidly but did not show strong trends for the older sites (Fig. 2a). There were large compositional shifts across the chronosequence (Fig. 3a and S1); the plant community showed a clear separation along the first and second NMDS axes (hereafter NMDS1 and NMDS2) with the youngest sites (75–120,000 yr) associated with *Acacia disparrima*, *Allocasuarina littoralis*, *Banksia integrifolia* and *Monotoca* sp. and the

Table 1
Abiotic soil characteristics of the Cooloola and Franz Josef chronosequence. All values are means of 6 replicates with SE between brackets. For each variable, values with different letters indicate significant (Tukey HSD $P < 0.05$) differences between sites. Curve estimations (relationships) are based on the mean values of each chronosequence site (n = 9). NS = not significant, - = negative relation, + = positive relation, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Site age (yr)	Water content (%)	pH	Organic C (%)	N (%)	NO_3^- (mg/kg)	NH_4^+ (mg/kg)	Total P (Kjeldahl) (mg/kg)	P (Olson) (mg/kg)
Cooloola								
1	0.5 (0.3) a	6.6 (0.1) a	0.1 (0.0) a	0.01 (0.00) a	0.00 (0.00) a	0.05 (0.03) b	36.3 (3.0) bc	0.9 (0.3) ab
75	1.7 (0.4) bc	6.1 (0.1) b	1.8 (0.4) bc	0.07 (0.01) cd	0.01 (0.00) a	0.03 (0.01) ab	45.7 (3.8) c	1.8 (0.1) c
750	3.9 (0.3) bc	6.0 (0.0) b	3.1 (0.3) bc	0.09 (0.01) d	0.01 (0.00) a	0.01 (0.03) ab	46.9 (3.9) c	0.9 (0.1) ab
3000	0.3 (0.0) a	5.8 (0.1) b	1.3 (0.3) ab	0.04 (0.00) abc	0.01 (0.00) a	0.00 (0.01) ab	30.1 (3.6) b	0.6 (0.1) a
7750	3.9 (0.4) bc	5.4 (0.1) c	1.1 (0.3) ab	0.03 (0.00) ab	0.00 (0.00) a	0.00 (0.01) ab	13.9 (1.8) a	0.7 (0.0) ab
120,000	1.7 (0.6) b	4.9 (0.1) d	3.1 (0.5) c	0.07 (0.01) cd	0.00 (0.00) a	0.00 (0.00) ab	38.3 (4.3) b	1.3 (0.1) b
265,000	3.3 (0.5) bc	5.1 (0.0) cd	1.9 (0.3) bc	0.04 (0.00) abc	0.00 (0.00) a	0.00 (0.00) a	7.8 (1.5) a	0.7 (0.1) a
500,000	3.8 (0.3) bc	5.0 (0.1) d	1.8 (0.1) bc	0.04 (0.00) abc	0.03 (0.01) a	0.00 (0.01) ab	7.6 (0.9) a	0.5 (0.1) a
700,000	3.3 (0.5) c	4.9 (0.0) d	3.1 (0.3) bc	0.04 (0.00) bc	0.00 (0.00) a	0.00 (0.00) ab	7.0 (0.4) a	0.5 (0.0) a
Relationship	NS	+cubic***	+logarithmic*	NS	NS	NS	+cubic*	NS
Franz Josef								
5	53.4 (4.6) a	5.8 (0.0)de	3.6 (0.3) a	0.15 (0.03) a	0.93 (0.54) a	9.14 (3.88) c	990.0 (35.3) d	6.4 (0.7) ab
70	138.0 (15.3)ab	5.9 (0.0) e	10.9 (3.3) abc	0.74 (0.13) c	73.1 (17.6) b	4.47 (1.01) abc	950.0 (66.9) d	13.5 (3.3) abc
130	164.7 (39.3)ab	5.7 (0.1) d	10.8 (3.3) abc	0.53 (0.11) abc	0.15 (0.07) a	8.49 (1.63) bc	876.3 (106.5) cd	17.7 (3.8) bc
500	310.4 (46.1) b	4.8 (0.0) c	14.8 (3.3) bc	0.68 (0.11) bc	0.07 (0.03) a	3.57 (0.64) ab	633.6 (107.3) bc	19.3 (3.7) c
1000	137.3 (17.5)ab	4.6 (0.0) a	10.7 (1.3) abc	0.46 (0.05) abc	0.09 (0.04) a	1.38 (0.31) a	305.3 (37.4) a	7.3 (0.9) ab
5000	180.3 (33.9)ab	5.0 (0.1)ab	17.4 (4.4) bc	0.61 (0.12) bc	0.13 (0.10) a	1.30 (0.38) a	361.4 (44.3) ab	15.5 (4.3) abc
12,000	161.8 (35.8) b	4.6 (0.1) a	19.0 (4.1) c	0.57 (0.10) bc	0.10 (0.06) a	0.94 (0.31) a	375.8 (31.6) a	10.5 (3.3) abc
70,000	139.8 (13.7)ab	4.4 (0.0) a	14.3 (3.4) abc	0.50 (0.07) abc	0.05 (0.00) a	1.43 (0.37) a	349.4 (33.5) a	11.3 (1.4) abc
120,000	85.7 (7.3) ab	4.6 (0.0) b	6.6 (0.7) ab	0.27 (0.02) ab	0.06 (0.01) a	0.35 (0.05) a	88.5 (7.5) a	4.5 (0.6) a
Relationship	-quadratic*	-linear**	-cubic*	NS	NS	-logarithmic*	- linear***	NS

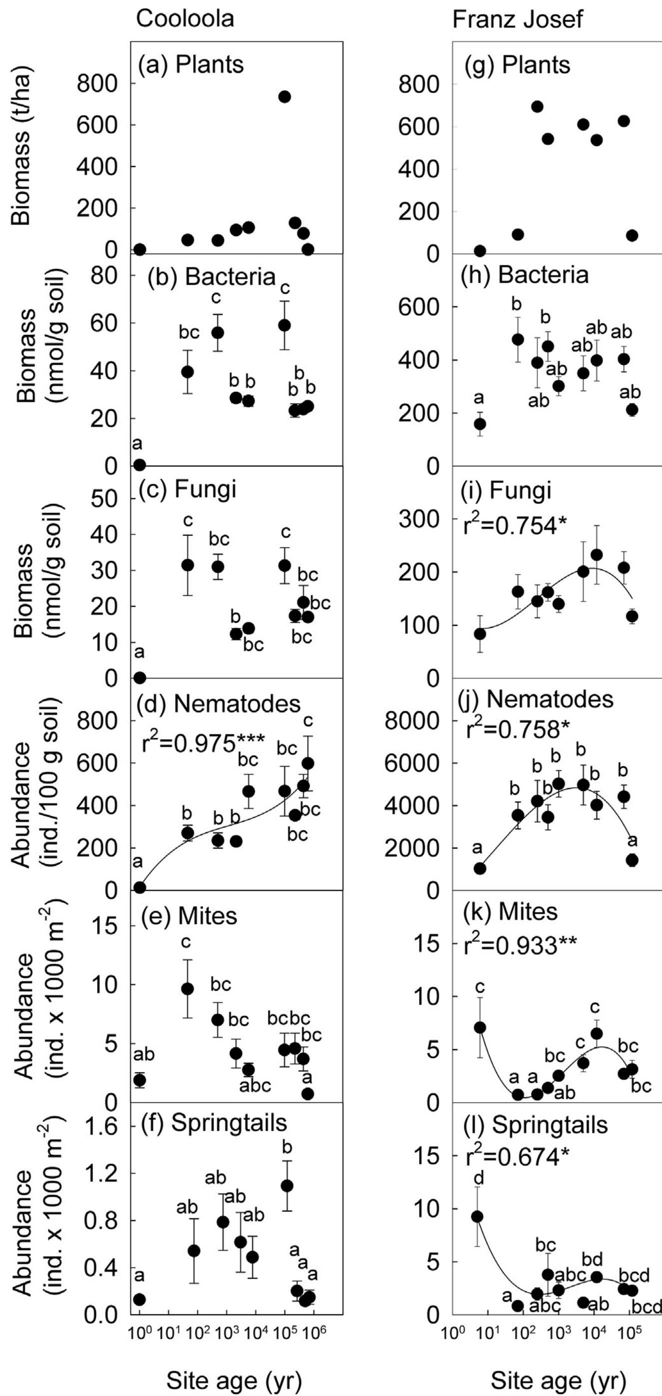

Fig. 1. Biomass of plants, bacteria and fungi and the abundance of nematodes, mites and springtails in relation to site age (years) across the Cooloola and Franz Josef chronosequences. Data points are means of n = 6 for the bacteria, fungi and nematodes and n = 12 for the mites and springtails. Error bars are SE which are sometimes smaller than the data points. Significant differences between sites are indicated by different letters based on Tukey's HSD ($P < 0.05$) following ANOVA (Table S3). Values of r^2 are based on fitted polynomial regressions with each chronosequence site representing an independent data point, and are presented only when significant at $P = 0.05$. * < 0.05, ** < 0.01, *** < 0.001.

oldest sites (265,000–700,000 yr) associated with *Banksia aemula* and *Angophora costata*.

At Franz Josef, plant biomass was lowest at the first two and final sites, and much greater at all other sites (Fig. 1g). Plant species richness doubled from the 70 yr site to the 1000 yr site and declined

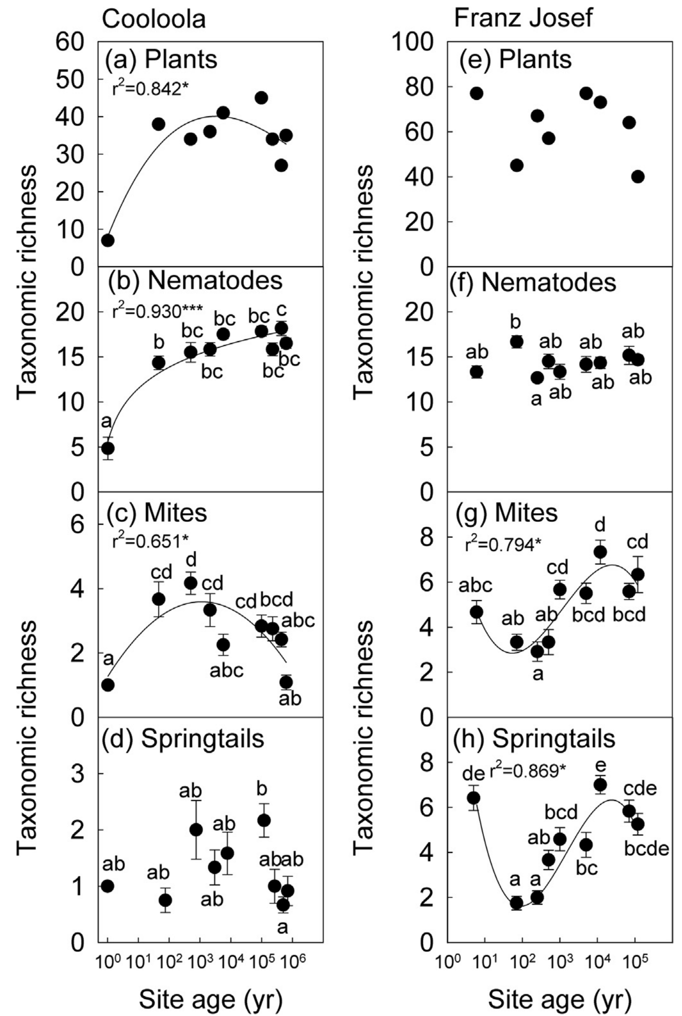

Fig. 2. Taxonomic richness of plants, nematodes, mites and springtails in relation to site age (years) across the Cooloola and Franz Josef chronosequences. Data points are means of n = 6 for nematodes and n = 12 for springtails and mites with SE as error bars. Significant differences between sites are indicated by different letters based on Tukey's HSD ($P < 0.05$) following ANOVA (Table S3). Values of r^2 are based on fitted polynomial regressions with each chronosequence site representing an independent data point, and are presented only when significant at $P = 0.05$. * < 0.05, ** < 0.01, *** < 0.001.

at the oldest site (Fig. 2e). There were large changes in composition across the chronosequence which were separated by NMDS1 (Fig. 3b and S1). The youngest stages (5–70 yr) which had the lowest scores were associated with *Coprosma lucida*, *Aristotelia serrata* and the N_2-fixing shrub *Coriaria arborea*, while the oldest stage (120,000 yr) which had the highest scores were associated with *Phyllocladus alpinus*, *Leptospermum scoparium* and *Podocarpus cunninghamii*. Plant NMDS1 scores were negatively correlated with soil P and pH for both chronosequences (Table S2).

3.3. Microbial biomass and community composition

For both chronosequences, biomass of bacteria, and fungi, and of gram+ and gram− bacteria and AMF, were lowest at the youngest site (Fig. 1b,c,h,i; Fig, S3), but otherwise there were few obvious or consistent patterns. At Cooloola, the microbial community of the youngest site (1 yr) differed greatly from all other sites along NMDS1, while intermediate sites (3000–120,000 yr) differed from the other sites along NMDS2 due to high proportions of most gram-

bacteria at these sites (Fig. 3c). At Franz Josef, the microbial community of the younger sites (5–500 yr) differed from the older sites (1000–120,000 yr) along NMDS1 as the latter had a higher proportion of fungal PLFA and lower proportions of gram-bacteria (Fig. 3d). Bacterial and fungal biomass were positively correlated with soil organic C and N for both chronosequences (Table 2) while at Cooloola plant species richness was also positively correlated with all microbial groups (Table S2). Further, soil water content and soil available P were correlated with bacterial biomass at Franz Josef (Table 2). Microbial NMDS1 scores were positively correlated with plant species richness at Cooloola, while at Franz Josef NMDS1 was negatively correlated with soil P; for both sequences NMDS1 was negatively correlated with pH (Table S2).

3.4. Nematode abundance and community composition

At Cooloola, abundances of total nematodes and of most nematode feeding groups, as well as taxonomic richness, generally increased with site age and did not decline at the retrogressive sites (Fig. 1d and Fig. 2b; Fig. S3a–f). According to the NMDS, the 75 and 750 yr sites had the lowest NMDS2 scores while the oldest sites (265,000–700000 yr) had the highest (Fig. 3e). At Franz Josef, nematode total abundance and abundances of most of the nematode feeding groups peaked at 70–70,000 yr (Fig. 1j; S3g–l), but there was no clear pattern in nematode taxonomic richness (Fig. 2f). The nematode community composition of the youngest (5–500 yr) sites differed from the remainder through having lower NMDS1 scores, and the youngest site also had the lowest NMDS2 scores (Fig. 3f).

At Cooloola, the abundance of total nematodes and of all nematode groups were negatively related to soil pH; total nematode abundance was also positively related to plant species richness, soil organic carbon and F:B (Table 2, Table S2). Nematode taxonomic richness was positively correlated with plant species richness, soil organic C, AMF, F:B and negatively with soil pH (Table S2). At Franz Josef, nematode abundance was correlated with a range of variables including tree biomass, soil organic C, soil N, water content, bacteria, gram + bacteria and fungi (Table 2). However, taxonomic richness was unrelated to any environmental variables (Table S2). For Cooloola, NMDS1 for nematodes was positively correlated with

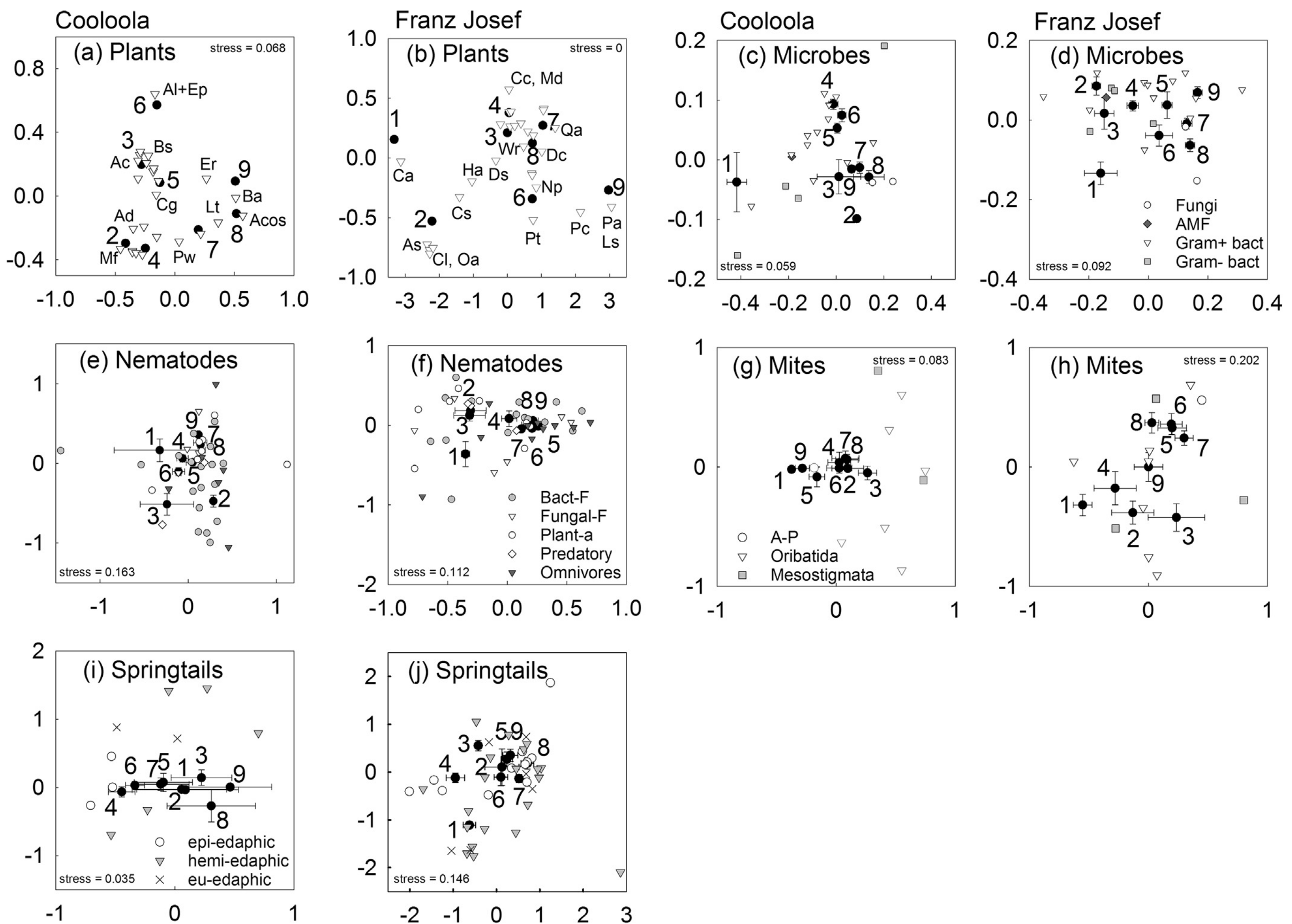

Fig. 3. Plots of Non-metric Multidimensional Scaling of the plant, microbial (PLFA), nematode, mite and springtail communities along the Cooloola and Franz Josef chronosequence. Data points are means of n = 6 for the nematodes and microbes and n = 12 for the mites and springtails. There were no replicate plots for the plant community data. Error bars are SE but in some cases are smaller than data points. The numbers (1–9) represent the chronosequence sites with increasing age (see Table S1). Smaller data points indicate constituent taxa used in the ordination. Abbreviations for the plant species (a and b): Ac = *Acacia complanata*, Acos = *Angophora costata*, Ad = *Acacia disparrima*; Al = *Allocasuarina littoralis*; Ac = *Angophora costata*; Bs = *Banksia serrata*; Ba = *Banksia aemula*; Cc = *Coprosma ciliata*; Ep = *Eucalyptus pilularis*; Er = *Eucalyptus racemosa*; Lt = *Leptospermum trinervium*; Pw = *Phebalium woombye* and f): As = *Aristotelia serrata*; Ca = *Coriaria arborea*; Cl = *Coprosma lucida*; Cs = *Carpodetus serratus*; Dc = *Dacrydium cupressinum*; Ds = *Dicksonia squarrosa*; Ha = *Hedycarya arborea*; Mf = *Monotoca* sp. Fraser Island; Md = *Myrsine divaricate*; Np = *Neomyrtus pedunculata*; Oa = *Olearia arborescens* and *O. avicenniifolia*; Wr = *Weinmannia racemosa*; Ls = *Leptospermum scoparium*, Pa = *Phyllocladus alpinus*, Pc = *Podocarpus cunninghamii*; Pl = *Podocarpus laetus;* Pt = *Podocarpus totara*; Qa = *Quintinia acutifolia*. (g–h) A–P: Astigmata-Prostigmata.

Table 2
Correlation coefficients (r-values) of soil bacterial and fungal biomass and invertebrate total abundances with site variables along the 9 sites of the Cooloola and Franz Josef chronosequences. NMDS1 and NMDS2 represent the first and second scaling axes of Non-Metric Multidimensional Scaling (NMDS) analyses. Gram+ = Gram positive bacteria, Gram- = Gram negative bacteria, AMF = Arbuscular mycorrhizal fungi, F:B = Fungal to Bacterial ratio. M-NMDS1 and M-NMDS2 = Microbial NMDS1 and NMDS2. Bold values indicate that r is significantly different to 0 at $P = 0.05$.

	Cooloola					Franz Josef				
Site variables	Bacteria	Fungi	Nematodes	Mites	Springtails	Bacteria	Fungi	Nematodes	Mites	Springtails
Site age	0.241	0.285	**0.833**	−0.266	−0.043	0.076	0.528	0.264	0.200	−0.254
Tree biomass	0.591	0.432	0.282	0.203	**0.734**	0.549	**0.687**	**0.824**	−0.174	−0.183
Plant species richness	**0.754**	**0.686**	**0.855**	0.289	0.550	−0.168	0.230	0.165	0.534	0.402
Tree diversity	0.602	0.324	0.355	0.481	**0.740**	0.598	0.204	0.591	**−0.727**	−0.369
Plant NMDS1	−0.568	−0.374	**0.743**	**−0.697**	**−0.656**	0.026	0.384	0.244	0.092	−0.234
Plant NMDS2	0.208	−0.141	0.419	−0.377	0.488	0.026	0.065	0.020	0.198	**0.737**
Organic carbon	**0.833**	**0.847**	**0.755**	0.242	0.527	**0.718**	**0.950**	**0.805**	−0.030	−0.375
Nitrogen	**0.938**	**0.928**	0.430	0.614	**0.669**	**0.956**	**0.682**	**0.787**	−0.590	**−0.656**
Total P (Kjeldahl)	0.368	0.290	−0.476	0.589	0.488	0.115	−0.422	−0.221	−0.405	0.108
P (Olson)	0.415	0.532	−0.139	0.604	0.361	**0.740**	0.406	0.569	−0.573	−0.295
pH	−0.262	−0.299	**−0.819**	0.286	−0.026	−0.021	−0.463	−0.311	−0.356	−0.060
Water content	0.285	0.415	**0.661**	−0.112	−0.088	**0.807**	**0.654**	**0.769**	−0.432	−0.394
Bacteria			0.550	0.570	**0.828**			**0.755**	−0.630	−0.547
Gram+			0.562	0.584	**0.774**			**0.817**	−0.446	−0.464
Gram-			0.542	0.614	**0.742**			0.584	**−0.822**	−0.586
Fungi			0.611	0.613	0.551			**0.747**	0.038	−0.386
AMF			**0.684**	0.449	**0.684**			0.517	**−0.825**	**−0.657**
F:B			**0.730**	0.207	−0.277			−0.135	**0.826**	0.201
M-NMDS1			**0.942**	0.260	0.056			0.166	0.487	−0.007
M-NMDS2			0.243	−0.155	0.504			0.299	**−0.760**	**−0.668**

the microbial F:B, while at Franz Josef it was negatively correlated with soil P and pH (Table S2).

3.5. Mite abundance and community composition

At Cooloola, the total abundances of mites and of most mite groups, and taxonomic richness were greatest at intermediate sites (Fig. 1e and Fig. 2c, S4a–c). The mite community for the 750 yr site had the highest scores for NMDS1 while the 1 yr, 7750 yr and 700,000 yr sites had the lowest; this was due to due to the low proportional abundance of Oribatida and Mesostigmata at those sites with low NMDS1 scores (Fig. 3g). At Franz Josef, total and oribatid mite abundances and mite taxonomic richness were least at the 70 yr and 130 yr sites; Astigmatid-Prostigmatid and Mesostigmatid abundances peaked at some of the older sites (Fig. 1k and Fig. 2g, S4d–f). The mite communities of the 5 yr site had the lowest NMDS1 scores while several intermediate sites had the highest scores, due the lower relative proportion of most mite taxa at the 5yr site (Fig. 3h). The youngest sites (5–130 yr) had lower NMDS2 scores than did the other sites due to lower proportions of Astigmata-Prostigmata (Fig. 3h).

For Cooloola, total mite abundance was not correlated with any environmental variable (Table 2), while Oribatida, Mesostigmata and taxonomic richness were positively correlated with most microbial groups and with soil N (Table S2). At Franz Josef, total mite abundance was positively related to the microbial F:B ratio and negatively to tree diversity, gram-bacteria and AMF (Table 2). Further, abundance of all mite groups and taxonomic richness was related to the microbial F:B ratio, and Oribatida was also negatively related to tree diversity, gram-bacteria and AMF (Table S2). At Cooloola, mite NMDS1 scores were positively correlated with soil N and all soil microbial groups, while at Franz Josef mite NMDS1 scores were positively related to plant NMDS1 scores (Table S2).

3.6. Springtail abundance and community composition

At Cooloola, the abundance of total, epi-edaphic and hemi-edaphic springtails, and springtail taxonomic richness peaked at intermediate sites (75–120,000 yr; Fig. 1f and Fig. 2d, S5a–c). The NMDS analyses revealed no differences in springtail community structure overall between the Cooloola chronosequence sites (Fig. 3i, Table S3). At Franz Josef, total springtail abundance and abundance of hemi-edaphic and eu-edaphic springtails was highest at the youngest (5 yr) site, but there were no consistent trends beyond that, while springtail taxonomic richness was least at the 70 yr and 130 yr sites (Fig. 1l and Fig. 2h, S5d-f). For the springtail community composition, the 500 yr site differed from all other sites except for the 5 and 250 yr sites along NMDS1 (Fig. 3j). For NMDS2, the 5 yr site had lower scores than did all the other sites which reflected the high proportion of various *Onychiurus* and *Ceratophysella* species (Supplementary invertebrate data S1).

For Cooloola, springtail abundance was positively correlated with tree biomass, tree diversity, soil N, gram- and gram+ and total bacteria and AMF (Table 2). At Franz Josef, springtail abundance showed negative correlations with soil N and AMF (Table 2). At Cooloola taxonomic richness was correlated with tree diversity and gram+ and total bacteria, while at Franz Josef it was negatively correlated with tree diversity, gram-bacteria and AMF but positively with F:B (Table S2). Hemi-edaphic springtail abundance was positively correlated with tree diversity at Cooloola and negatively with tree diversity, biomass and soil water content at Franz Josef, while abundance of eu-edaphic and epi-edaphic springtails were each correlated with several variables for both sequences (Table S2). For springtails NMDS1 was not related to any variables at Cooloola, but positively related to microbial NMDS1 and negatively to total P at Franz Josef (Table S2).

3.7. Fungal to bacterial energy channel ratios

At Cooloola, the F:B ratio was lowest at the youngest (1 yr) and highest at the oldest (700,000 yr) sites (Fig. 4a), and was not significantly correlated with any of the measured variables (Table S2). At Franz Josef, the F:B ratio was lowest at the 70–500 yr sites (Fig. 4b) and was negatively correlated with soil P.

At Cooloola, the ratio of fungal-feeding to bacterial-feeding nematodes increased from the 750 yr site onwards (Fig. 4c). This ratio was negatively correlated with both soil pH and total P (Table S2). At Franz Josef, the ratio of fungal-feeding to bacterial-

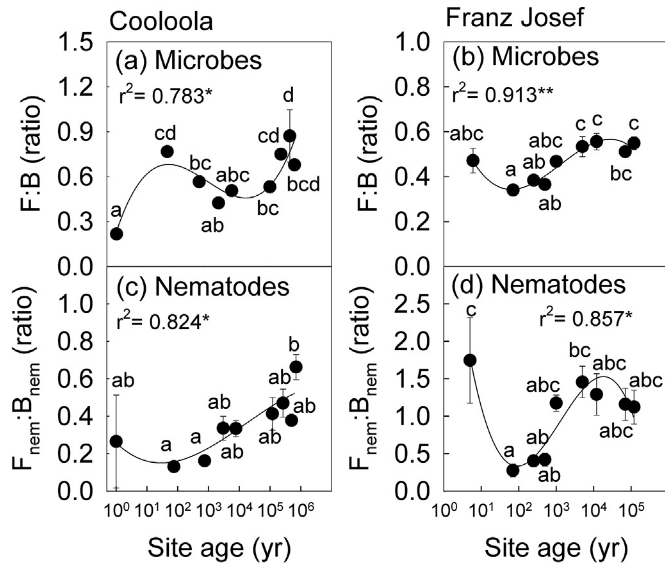

Fig. 4. Fungal to bacterial PLFA ratio and the ratio of fungal-feeding to bacterial-feeding nematodes in relation to site age (years) across the Cooloola and Franz Josef chronosequences. Data points are mean of n = 6 with SE as error bars which are sometimes smaller than data points. Significant differences between sites are indicated by different letters based on Tukey's HSD ($P < 0.05$) following ANOVA (Table S3). Values of r^2 are based on fitted polynomial regressions, with each chronosequence site representing an independent data point. * < 0.05, ** < 0.01, *** < 0.001.

feeding nematodes was lowest in the 70–500 yr sites (Fig. 4d). This ratio was negatively correlated with tree diversity, total bacteria, gram-bacteria and AMF and positively correlated with the F:B ratio (Table S2).

4. Discussion

Both chronosequences showed clear increases in available nutrients, plant biomass and richness, and abundance or biomass of some soil organism groups at the start of the soil chronosequences and declines of these at the oldest, retrogressive sites, in line with what has often been shown for long-term chronosequences, and in line with our first hypothesis (Wardle et al., 2004, 2008; Peltzer et al., 2010). This is consistent with ecosystem nutrient capital building up during the first few centuries of primary succession, and the availability of these nutrients then declining over millennial time scales (Walker and Syers, 1976; Peltzer et al., 2010). The fact that aboveground and some belowground properties show some similar patterns of responses at both chronosequences despite large differences in macroclimate, geology, levels of organic matter, soil moisture, and total and available forms of soil N and P, mean that changes in soil fertility during both ecosystem build-up and retrogression may consistently be powerful ecological drivers in highly contrasting settings (Wardle et al., 2004).

We also found partial support for our first hypothesis that soil communities would mirror the patterns of vegetation, as the abundance of bacteria, fungi and some invertebrate groups initially increased in parallel with plant biomass, especially from the first to second chronosequence sites (Fig. 1). However, beyond these early sites, there were instances in which the abundance, biomass and richness of several groups of soil organisms did not change consistently or did not follow the changes in vegetation or nutrient availability. Further, there were often contrasting responses of the same groups to site age between Cooloola and Franz Josef, and several groups were not correlated to the same plant and soil variables for the two chronosequences, indicating that different drivers were at play (Table S2). The fact that some groups of soil organisms showed contrasting differences to the same drivers in the two chronosequences is likely to be due in part to the fact that the soils in Franz Josef contain considerably higher levels of organic matter, available soil nutrients and densities of soil biota than do soils of comparable stages in Cooloola. While our data do not allow us to identify a precise mechanistic explanation as to why specific groups of organisms sometimes show contrasting responses to these gradients, these differences are associated with the fact that these groups are primarily correlated with different variables across the two chronosequences and are therefore limited by different factors. Despite this, the decline in soil biota with retrogression occurred commonly for both chronosequences, pointing to some broadly comparable responses to long term soil aging in two highly contrasting settings.

While biomass of microbial groups was correlated with soil C and N content across both chronosequences, these did not always decline during retrogression in the manner that we hypothesized. This could be because the biomass of these groups was more strongly affected by the presence of specific plant taxa that dominate at specific sites (Latz et al., 2015), or because there were compositional shifts within these groups towards taxa that are better adapted to the low soil fertility of retrogressive sites but with no net change in biomass occurring (Lambers et al., 2008; Fierer et al., 2010; Martínez-García et al., 2015). Of the invertebrates, nematode abundance initially increased and then decreased with increasing site age for the Franz Josef chronosequence, which is in line with some earlier findings on retrogressive chronosequences (Doblas-Miranda et al., 2008) as well as with our first hypothesis. In contrast, nematode abundance increased with increasing age across all (including the retrogressive) sites for the Cooloola chronosequence. However, this pattern was primarily driven by plant-feeding nematodes (Fig. S3), which may have benefited from shifts in plant community composition (Fig. 3a and S1) towards dominance by Proteaceae species (e.g., *Banksia aemula*) that produce cluster roots with a high surface area (Lamont, 2003). Proteaceae species which produce cluster roots are well known to be susceptible to root knot nematodes (Cho, 1977).

Springtails and mites showed a hump-shaped response to chronosequence site age at Cooloola which involved a distinct decline in abundance during retrogression. For Franz Josef there was also a decline relative to some earlier sites, but this was not statistically significant. High abundance of soil microarthropods at early successional stages after glacial retreat is not uncommon (Janetschek, 1949; Kaufmann, 2001; Matthews and Vater, 2015) and probably reflects a higher abundance of pioneer species (r-strategists) of microorganisms and algae (Sigler and Zeyer, 2002; Turicchia et al., 2005; Schutte et al., 2009; Martínez-García et al., 2015) that may be less protected against grazing and serve as a readily available food source for microarthropods. As such, our results are in line with studies showing that mites and springtails often rapidly reach a high abundance very early during succession as plants and microbes colonize (Zaitsev et al., 2006; Bokhorst et al., 2014). At Cooloola, a sharp decline in mite abundance then followed that was likely due to the rapid development of nutrient-limiting conditions and thus the reduced amount and quality of food resources (Awmack and Leather, 2002; Bokhorst et al., 2015; Bokhorst and Convey, 2016). At Franz Josef, although mite abundance showed a less clear association with soil age, it also showed a close linkage to the soil F:B ratios across the chronosequence (Table 2), in line with the most dominant mite group (Oribatida) being comprised mainly of fungal-feeders (Maraun et al., 1998b). Further, total springtail abundance at Franz Josef was negatively correlated with soil N and AMF abundance. This pattern is driven primarily by the density of the soil-dwelling (eu-edaphic)

springtails which was negatively correlated with soil N across the nine sites (Table S2), and appears to be due to the very high springtail abundance at the 5 yr site and overall lower abundance at older sites at Franz Josef.

Nematode and mite richness increased with plant species richness along the early Cooloola sites, thereby providing some support for our second hypothesis, but these patterns were not found at Franz Josef. However, when we excluded the 5 yr site (glacier forefront), there was a clear increase in springtail and mite richness at Franz Josef from the 70 yr site onwards. There was also a significant decline in richness in mites and, to a lesser extent, springtails at the oldest (retrogressive) site at Cooloola (but not at Franz Josef), which occurred despite no strong corresponding decline in plant richness. The initial increases of invertebrate richness with plant species richness is in line with results from experimental studies (De Deyn et al., 2004; Sabais et al., 2011). However, the lack of consistent concordance between invertebrate richness and plant richness along the older sites of the chronosequence indicates that other factors such as the direct effects of low soil nutrient availability, or plant species identity (and thus functional traits of the dominant plant species), may have played a more important role (Wardle et al., 1999; Viketoft et al., 2009; Bokhorst et al., 2014). We know that the functional traits of dominant species and soil microbial communities are often closely linked (de Vries et al., 2012), and recent work along the Franz Josef chronosequence showed that arbuscular mycorrhizal fungal niche differentiation was more strongly driven by host plant identity than by soil fertility (Martínez-García et al., 2015). Therefore, although the richness of some invertebrate groups initially follows plant richness patterns, other factors, such as plant identity, resource quantity and quality, biotic interactions within the soil food web or abiotic constraints are likely to become more important as drivers of invertebrate richness during later stages of ecosystem development (Hooper et al., 2000; Wardle, 2006).

As expected, fungal to bacterial ratios generally increased with soil age, providing support for our third hypothesis. This pattern was also generally reflected in the ratio of fungal-feeding to bacterial-feeding nematodes, especially when the youngest site was excluded, indicating an overall trend for the fungal-based energy channel to become relatively more important with increasing soil age. Specifically, as nutrients become limiting for plant growth at the older (retrogressive) chronosequence sites, the functional composition of the vegetation changes with concomitant declines in litter quality, which leads to accumulation of recalcitrant compounds in the soil organic layer favouring fungi over bacteria (van der Heijden et al., 1998; Wardle et al., 2004; Chapman et al., 2006). However, not all fungal groups showed the same response to soil age. For example, AMF declined at the older (>1000 yr) Franz Josef sites (Fig. S2), indicating that although there were overall increases in fungal biomass, changes within the fungal community are important (Martínez-García et al., 2015). Identifying such changes in more detail would require additional approaches, such as molecular sequencing techniques, to characterize the relative contributions of different components of the fungal community (e.g., Clemmensen et al., 2015).

At Cooloola, mite and springtail abundances responded in fairly similar ways as did fungal biomass to soil age. Given that most of these micro-arthropod groups rely on fungi as a food source, this suggests the possibility of bottom-up regulation across the chronosequence. In contrast, at Franz Josef, micro-arthropods and fungal biomass did not show closely coordinated responses to soil age, suggesting that factors other than the mass of fungi present was regulating micro-arthropod densities. Such factors could include variation in abiotic variables or the types of fungi present. Springtails and mites showed some negative relationships with the biomass of AMF at Franz Josef; AMF are known to inhibit the growth and reproduction of springtails (Klironomos et al., 1999) and could therefore have reduced their abundances. The composition of the fungal community may have an important role in regulating micro-arthropod densities that is not captured in measures of total fungal biomass or the relative importance of fungal-based versus bacterial-based energy channels, especially given the preference of many micro-arthropods for certain fungal species (Kaneko et al., 1995; Maraun et al., 1998a, 1998b; Koukol et al., 2009). Therefore, to better predict and understand soil invertebrate patterns along long-term ecosystem development, we need to recognize not just the role of changes in the microbial community, but also the specific feeding preferences of the various components of the soil invertebrate community that are still very poorly understood (Schneider et al., 2004).

4.1. Conclusions

This study was initiated to better understand the drivers of soil communities during ecosystem development and retrogression in two contrasting long-term soil chronosequences, i.e., one in Australia that was formed during sand dune development, and one in New Zealand that developed following glacial retreat. For both chronosequences we showed that at the initial stages major microbial and invertebrate groups usually follow changes in plant biomass, richness and soil fertility, but that these patterns frequently do not hold at later stages of ecosystem development and retrogression, and that different organism groups have contrasting responses to the same gradient. This indicates that during long-term ecosystem development there are stages or points in time beyond which components of the soil community are driven primarily by factors other than the direct effects of plant biomass, species richness and soil fertility; these could include soil food web interactions, local-scale disturbances that are independent of chronosequence stage, or changes in plant trait spectra and functional types (Bardgett et al., 2005). Further, the link between the plant and the soil communities over time may be most apparent at finer levels of taxonomic resolution (species or genus) (e.g., Martínez-García et al., 2015). To further disentangle the factors that drive soil community changes across large environmental gradients we need more information about the specific feeding preferences of higher trophic levels (beyond very broad groupings such as bacterial or fungal feeders, or predators) (Kardol et al., 2016). While soil fertility and vegetation composition are important drivers of the soil community, our study highlights that the manner in which these factors directly and indirectly influence the soil community can vary greatly across organism groups and among chronosequences over the time scales that ecosystem development occurs.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.12.014.

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