COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Contrasting responses of soil nematode communities to native and non-native woody plant expansion

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Abstract

Woody plant expansion into grasslands is widespread, driven by both successions to dominance by native woody species or invasion by non-native woody species. These shifts from grass- to woody-dominated systems also have profound effects on both above- and belowground communities and ecosystem processes. Woody-plant expansion should also alter the functional composition of the soil biota, including that of nematodes, which are major drivers of soil food-web structure and belowground processes, but such belowground impacts are poorly understood. We determined whether succession by a widespread native (*Kunzea ericoides*) and invasion by a non-native woody species (*Pinus nigra*) into tussock grasslands affect the composition of nematode functional guilds and the structure of nematode-based food webs. Although increasing dominance by woody species in both systems altered the functional guild composition of the nematode community, we found contrasting responses of nematode functional guilds to the different dominant plant species. Specifically, nematode communities reflected conditions of resource enrichment with increasing *K. ericoides* tree cover, whereas communities became structurally simplified and dominated by stress-tolerant nematode families with increasing *P. nigra* tree cover. Because nematodes regulate both bacterial- and fungal-dominated food webs in soils, these shifts could in turn alter multiple ecosystem processes belowground such as nutrient cycling. Incorporating species' functional traits into the assessment of habitat-change impacts on communities can greatly improve our understanding of species responses to environmental changes and their consequences in ecosystems.

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Introduction

Increasing dominance of woody species, either through successional processes or biological invasion by trees and shrubs, is a widespread change in grassland systems. Woody expansion of native and non-native plants can be driven by multiple factors, such as fire suppression, restoration and invasions (Walker et al. 2009). Expansion of non-native woody species is considered one of the main drivers of global environmental change (Rundel et al. 2014), as the rate and impacts of these species on the new environment can exceed those of the expanding native species (e.g., invasion by pines across biogeographic regions, Davis et al. 2019). Nevertheless, native trees expanding due to land-use or climate change can also be major drivers of environmental change (Kochy and Wilson 2001). These changes in vegetation towards woody dominance of native and non-native

species can strongly alter aboveground biodiversity (Báez and Collins 2008; Pawson et al. 2010), soil chemistry (Chen et al. 2000; Liao et al. 2008) and even modify biodiversity of belowground food webs (Biederman and Boutton 2009; Dickie et al. 2011; Reid and Emery 2018).

Among soil invertebrates, nematodes are a major driver of soil processes such as organic matter decomposition and nutrient cycling (Neher 2001; Irshad et al. 2011) and can be particularly susceptible to woody expansion because they are strongly affected by plants both directly through resource (C) inputs (De Deyn et al. 2004; Porazinska et al. 2007) and indirectly through water availability and soil physical structure (Philippot et al. 2013). For example, the community composition of nematodes responds strongly to different tree stocking rates in agroforestry regimes (Yeates et al. 2000). Also, a decrease in taxonomic richness of the overall nematode community has been observed with increasing aboveground tree biomass of an invasive non-native pine species, although not under increasing biomass of a native woody species (Dickie et al. 2011). Even though soil biodiversity plays a major role in determining ecosystem function and processes (Wardle et al. 2000; Gagic et al. 2015), there is limited knowledge of whether woody succession or invasion disturbs or stabilizes belowground functional guilds and community structure.

Functional traits can be used to understand the responses of soil biota to woody expansion (Pey et al. 2014; Moretti et al. 2017), and particularly trait syndromes related to feeding group and species' life history strongly reflect functional and biotic responses to environmental changes. For instance, nematode species having similar life history strategies (life span, reproduction mode and habitat susceptibility) and feeding preferences can be grouped into functional guilds (Ferris et al. 2001), which in turn have similar responses to environmental changes. A nematode community that is dominated by K-strategists (i.e., persister species) indicates a habitat of long-durational stability, i.e., the habitat has had favourable conditions for relatively long periods, allowing development of more trophic links and a more complex structured food web (Bongers 1990; Ferris et al. 2001). In contrast, dominance of r-strategists (i.e., colonisers) indicates an ephemeral habitat, i.e., a habitat having sporadic periods of favourable conditions, where the resident nematodes are those adapted to stress conditions, forming a simpler more basal food web (Bongers 1990; Ferris et al. 2001).

These coordinated changes in nematode functional guilds can be summarised using well-established indices (Bongers 1990; Yeates 1994; Bongers and Bongers 1998; Bongers and Ferris 1999) that are useful for assessing community responses to global environmental factors (Cesarz et al. 2015). For example, information on nematode species abundances and their ability to colonise disturbed habitats (coloniser–persister classification equivalent to r–K

strategies classification) can be used to estimate an ecological measure of environmental disturbance (maturity index) (Bongers 1990). Moreover, this information combined with nematodes' feeding preferences can inform about resource or nutrient availability as well as the condition of the food web (Ferris et al. 2001). Therefore, nematodes can be useful for studying changes in functional structure and composition of belowground food webs.

We evaluated changes in soil nematode life strategies and functional guilds across woody expansion by a native (*Kunzea ericoides*) and an invasive non-native (*Pinus nigra*) tree species into tussock grasslands to determine how increasing dominance by different woody plant species influences nematode community structure and composition. In particular, we tested two hypotheses: (1) the proportion of nematode coloniser species increases with increasing tree cover, because nematode communities would be adapted to a grassland habitat with no woody vegetation. (2) These changes in the proportion of different life strategy groups will be reflected in a nematode community dominated by stress-tolerant guilds with a simplified community structure with increasing tree cover. To test these hypotheses, we used nematode data from Dickie et al. (2011) together with new information on species abundances of all taxa and information on nematode life strategies.

Materials and methods

Study region and sampling

We selected two study sites (ca. 21 km apart) in an abandoned grazing area of the Canterbury region of South Island, New Zealand. Both sites were previously dominated by the indigenous tree species *Fuscospora cliffortioides* (Hook.f.) Heenan & Smissen (formerly *Nothofagus solandri* var. *cliffortioides*) prior to anthropogenic burning. This produced relatively large areas of tussock grassland and shrubland, which currently comprise about a quarter of New Zealand's land area. The region has largely been used for low-impact pastoral farming following the introduction of domestic grazing mammals. Both sites are dominated by a mixture of native and non-native grasses and forbs (e.g., *Agrostis capillaris*, *Hieracium* spp., *Festuca novae-zelandiae*), sparse native shrubs (e.g., *Leptospermum scoparium*, *Discaris tomentosa*) and have similar soil texture (24% sand, 51% silt, 26% clay and 11% sand, 58% silt, 32% clay for the Avoca and Mt Barker sites, respectively).

These areas are characterised by very slow recovery of woody species and invasion by non-native species, following historical fire. Historically, fires initially removed the largely native forest cover starting from ca. 750 BP following Polynesian settlement, and then a second wave

of fires occurred from ca. 1840 driven by the expansion of pastoral farming by Europeans (Perry et al. 2014). In recent decades, these areas have been destocked or the land use has shifted from pastoral farming to conservation, and this has resulted in the expansion of woody species. After being left ungrazed, both sites are undergoing mono-dominant succession from grassland to woody vegetation: the Avoca site is undergoing succession to the dominant shrub *Kunzea ericoides* (with the largest trees measured at 54 years old and up to 8 m in height), whereas the Mt Barker site is undergoing invasion to the non-native tree species *Pinus nigra* (with the largest trees 22 years old and ca. 15 m height) (Coutts et al. 2012). *Kunzea ericoides* is a small-leafed, light-demanding, evergreen, ectomycorrhizal Myrtaceous tree that forms dense stands in early succession. *Pinus nigra* is a large coniferous evergreen tree, considered invasive in New Zealand. For more details of the study sites, see Dickie et al. (2011).

Within each site, we sampled 15 large plots (20×20 m, see also Hurst and Allen 2007; Dickie et al. 2011) in 2008 along the plant expansion gradient spanning from 0% tree cover (no trees) to over 90% tree cover ($n = 15$ at each site). To find plot centres in a stratified random fashion, we first ran five replicate transects crossing areas of high and low density of trees, placing potential plot centres at predetermined regular intervals. Preliminary density estimates were made and 15 plots were randomly selected from the larger pool of potential plot centre locations in order to span the tree-cover gradient, while ensuring that three plots were representative of each end of the gradient (i.e., 0% and > 90%). Within the centre 5×5 m area of each plot, we collected six 65-mm-diameter soil cores of the A-horizon (approx. 100 mm depth at both sites). Soil samples were pooled within plots for subsequent analyses. All samples were stored at 4 °C until processing. Bulk density was measured on soils collected using three-replicate, 62-mm-diameter, 30-mm-long steel cores within each of three forest and three grassland (no tree) plots at each site. Mean bulk density was used for all analyses because neither site showed a significant response of soil bulk density to woody expansion ($p > 0.05$ for both sites).

We extracted nematodes from a c. 100 g wet-weight subsample of A-horizon soil using the tray method (Whitehead and Hemming 1965). From each sample, we counted nematodes on one-quarter of a Doncaster counting dish and final abundances were calculated as four times this number. Nematode abundance was expressed as density of individuals m^{-2} within the soil A-horizon density determined volumetrically from the soil core dimensions and soil bulk density (as described in Dickie et al. 2011). The sample was then heat-fixed with an equal volume of boiling 8% formaldehyde, and approximately 100 individuals from each sample were slide-mounted for identification.

Nematodes identification, classification and community indices

We identified nematodes up to genus level and when further identification was possible, genera into morphospecies. After taxonomic identification, individual nematode taxa were assigned to one of five feeding categories according to their feeding preferences (plant feeders, bacterial feeders, fungal feeders, predators or omnivores) (Yeates et al. 1993) and allocated to life strategy (c–p) groups, according to the coloniser–persister classification (analogous to the *r–K* classification). Based on this classification, nematodes can be separated into five classes representing their life strategies, ranging from colonisers (c–p 1: short life cycles, high colonisation ability, high reproduction rate, tolerance to various types of disturbance) to persisters (c–p 5: long life cycles, low colonisation ability, few offspring, sensitivity to disturbance) (Bongers 1990). The combination of the different life strategy groups in a community determines the functional guild composition (Bongers and Bongers 1998).

To assess changes in the structure and function of the nematode communities, we used five indices: sigma maturity index (ΣMI), maturity index of free-living nematodes (MI), plant-parasitic index (PPI), enrichment index (EI) and structure index (SI). ΣMI reflects the proportion of the different c–p groups for the whole nematode community, and MI and PPI the proportion of different c–p groups for free-living and plant-parasitic nematodes, respectively. Higher values of these indices indicate the predominance of "persister" life history nematodes (Bongers 1990). EI and SI are calculated based on the proportion of different nematode functional guilds determined by species life strategies (c–p groups) and feeding preferences. In particular, EI indicates the resource status of the ecosystem, with high values indicating high soil enrichment and fertility (Ferris et al. 2001). On the other hand, SI reflects the level of complexity of the community, with high SI indicating high connectedness, i.e., more trophic links and redundancy (Ferris et al. 2001). The nematode community indices were calculated using the Nematode Indicator Joint Analysis programme (Sieriebriennikov et al. 2014). Equations for each index calculation can be found in the supplementary material.

Analyses

We analysed the two sites (native vs. non-native woody plant expansion) independently, as without multiple native and non-native species it would be impossible to determine whether species origin per se causes any differences between them. To evaluate the effects of woody plant expansion on the proportion of nematodes with different life strategies (c–p groups), we used generalised linear models with the proportion of each c–p group (i.e., the number of individuals

of each c–p group, 1–5, divided by the total number of individuals in the sample) as the response variable in a different model and tree per cent cover as the predictor variable in all models and reported both test statistics (t) and p values. For these models, we used quasibinomial error distribution because the equidispersion assumption of the binomial models was not achieved (Zuur et al. 2009). In addition, to assess changes in the structure and function of nematode communities with woody plant expansion, we used linear regressions, entering each nematode community index as a response variable (on different models) and tree per cent cover as the predictor variable in all models. Finally, to determine whether nematode community changes could be driven by overall nematode abundance changes, we tested whether total nematode abundance (response variable) changed with tree per cent cover (predictor variable) using a linear regression. All analyses were performed in the R environment (R Core Team 2017). We tested for the normality and homoscedasticity assumptions of all Gaussian models.

Results

We identified 47 nematode taxa across all sampling plots (Table S1), with an average of 14 ± 4 [mean $\pm$ SD] taxa per sampling plot. Overall nematode abundance did not change with *Kunzea ericoides* (native) or *Pinus nigra* (non-native) tree cover (Fig. 1, Table S2). Nematodes from all classes (c–p 1 to c–p 5) of the coloniser–persister classification (equivalent to the *r-K* strategies classification) were present in our study. Most taxa were classified according to their life strategy as c–p 2 ($n=19$) and c–p 4 ($n=14$) with very few taxa classified as c–p 1 ($n=2$) or c–p 5 groups ($n=5$); c–p 3 had intermediate number of taxa ($n=7$) (Table S1).

Increasing *K. ericoides* tree cover only led to a significant increase in the proportion of c–p 1 nematodes ($t=3.359$, $p=0.009$) (Fig. S1, Table S3), driven by an increase in the relative abundance of bacterial feeder Rhabditidae

nematodes (Fig. 2, S2). No significant changes were detected in c–p groups 2–5 with increasing *K. ericoides* tree cover (Fig. 3a, S1, Table S3), even though some groups such as plant feeders c–p 5 were completely absent when *K. ericoides* tree cover was highest (Fig. 2). Conversely, increasing *P. nigra* tree cover led to a significant increase in the proportion of c–p 2 nematodes ($t=2.844$, $p=0.014$) (Fig. S1, Table S3), both bacterial and plant feeders (Fig. 2). Also, a significant decrease in the proportion of c–p 3 and c–p 5 ($t=-3.012$, $p=0.012$; $t=-3.451$, $p=0.004$, respectively) (Fig. 3b, S1, Table S3), particularly within plant and bacterial feeders (Fig. 2), was observed when increasing *P. nigra* tree cover, whereas no significant changes were observed in the proportion of c–p 1 and c–p 4 nematodes (Fig. S1, S2, S5, Table S3). Plots without *P. nigra* tree cover presented only half the number of c–p 2 species than plots with $>90\%$ *P. nigra* tree cover (Fig. S1). In particular, the plant feeder *Tylenchus* sp. 1 became dominant with increasing *P. nigra* tree cover, whereas taxa such as *Cephalenchus*, *Monhystera* and *Ditylenchus* were completely absent when *P. nigra* exceeded 90% cover (Fig. S3). In addition, only one c–p 5 taxa, from the family Aporcelaimidae (omnivore, Fig. S6), was able to colonise plots with $>90\%$ *P. nigra* tree cover, whereas the plant feeder *Dorylaimellus*, which represented the second most abundant c–p 5 taxa in this site, was completely absent (Fig. S6).

When assessing changes in the overall nematode community structure and function, we found that the sigma maturity index (ΣMI), i.e., computed for the whole nematode community, and the plant-parasitic index (PPI) did not change with increasing *K. ericoides* tree cover ($t=-1.164$, $p=0.265$; $t=-1.138$, $p=0.276$, respectively) (Fig. 4a, e), even though the maturity index calculated based only on free-living nematodes decreased significantly ($t=-2.864$, $p=0.013$) (Fig. 4c, Table S2). On the contrary, ΣMI and PPI significantly decreased when *P. nigra* tree cover increased ($t=-2.352$, $p=0.035$; $t=-5.206$, $p<0.001$, respectively) (Fig. 4b, f, Table S2), due to changes in the proportion of

Fig. 1 Nematodes abundance (density of individuals m^{-2}) across *Kunzea ericoides* (**a**) and *Pinus nigra* (**b**) woody expansions (measured by tree per cent cover)
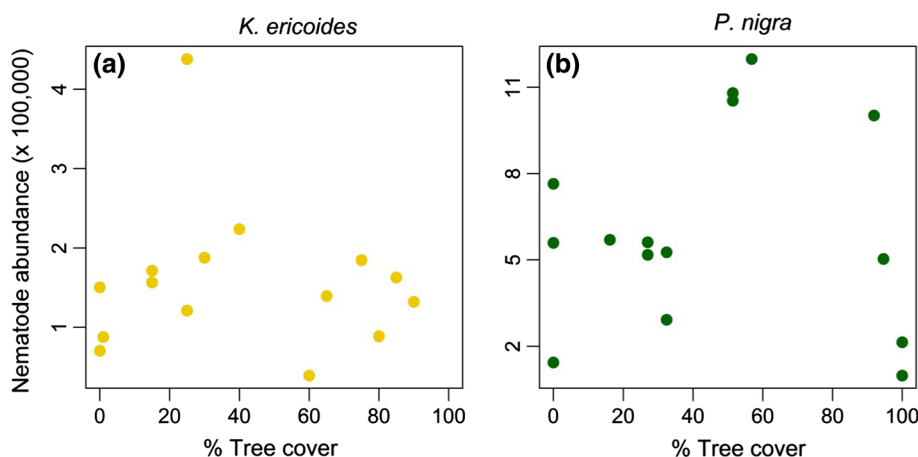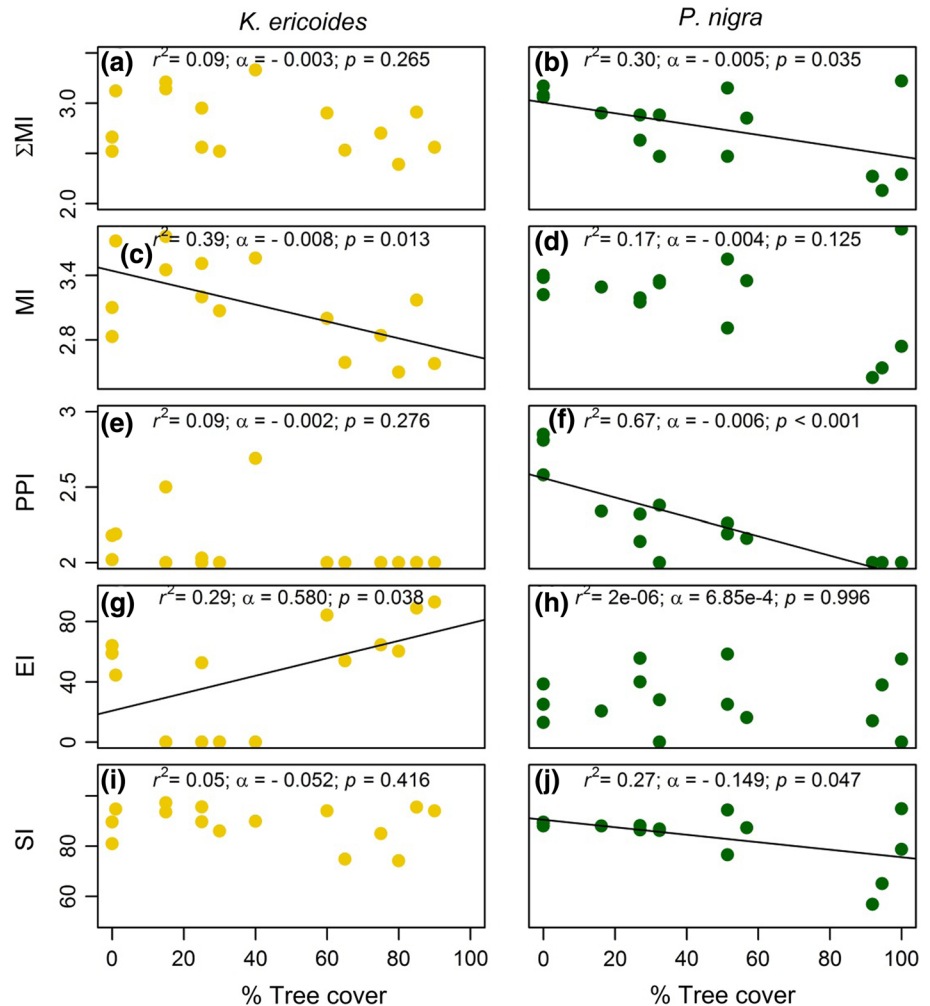
Fig. 2 Proportion of nematodes abundance (density of individuals m^{-2}) with different c–p strategies within each trophic group (plant feeders, bacterial feeders, fungal feeders, predators, omnivores) across *Kunzea ericoides* and *Pinus nigra* woody expansions. c–p Strategies of nematodes range from 1 (ruderal, disturbance-adapted species) to 5 (persistent); see "Materials and methods" for details
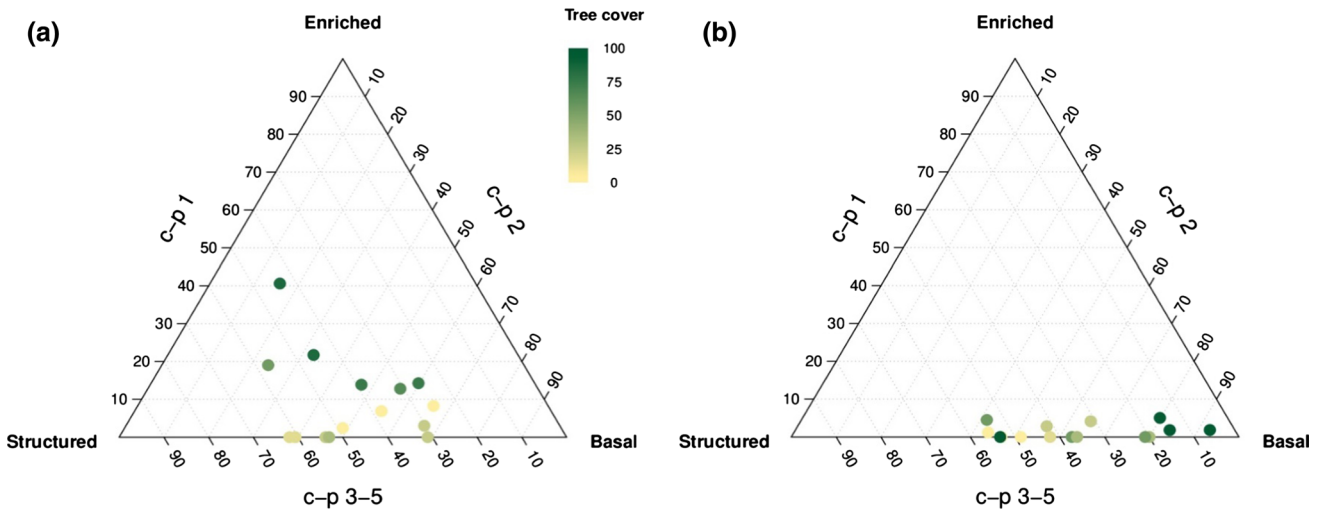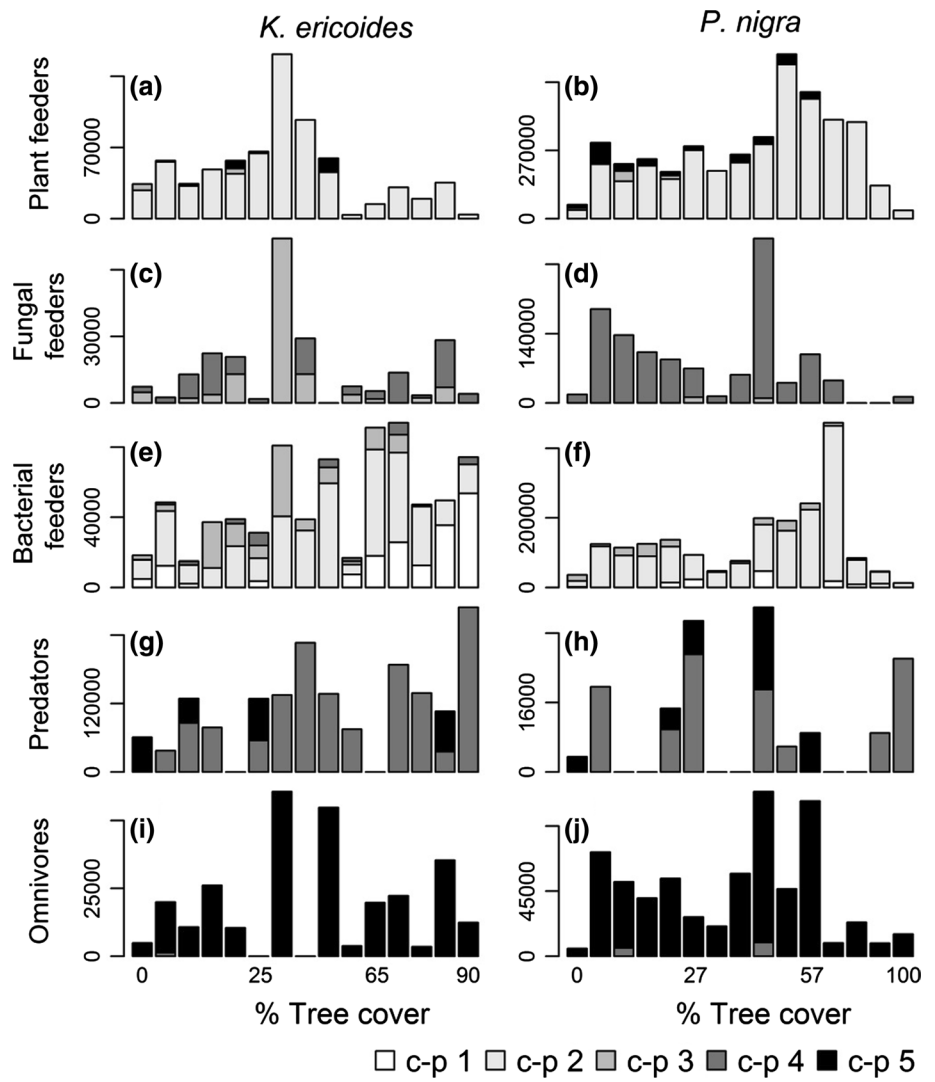
Fig. 3 Shifts in proportional distribution of nematode life strategy (c–p) groups across *Kunzea ericoides* (**a**) and *Pinus nigra* (**b**) woody expansions. c–p strategies of nematodes range from 1 (ruderal, disturbance-adapted species); see "Materials and methods" for details. Increasing tree cover led to nematode communities with **a** a higher proportion of c–p 1, and **b** higher and lower proportion of c–p 2 and c–p 3–5, respectively

c–p 2 and 3 (Fig. S1), whereas no significant changes were observed in MI ($t = -1.640$, $p = 0.125$) (Fig. 4d, Table S2). The enrichment index (EI) only increased significantly with *K. ericoides* tree cover ($t = 2.315$, $p = 0.038$; Fig. 4g) and remained unchanged with increasing *P. nigra* tree cover ($t = 0.005$, $p = 0.996$; Fig. 4h, Table S2). Finally, there were no significant changes in structure index (SI) values when increasing *K. ericoides* tree cover ($t = -0.839$, $p = 0.416$; Fig. 4i), but a significant decrease in SI was observed when increasing *P. nigra* tree cover ($t = -2.195$, $p = 0.047$; Fig. 4j, Table S2).

Discussion

The expansion of woody species into grasslands through succession or invasion can strongly alter aboveground ecosystem processes and biodiversity (Báez and Collins 2008; Pawson et al. 2010), but the effects of these changes on belowground systems remain poorly understood (Dickie et al. 2011; Coyle et al. 2017; Wardle and Peltzer 2017).

We show that an increase in woody species into tussock grassland alters the dominant life strategies and functional guild composition of soil nematode communities and that these effects differ between succession to a dominant native species (*K. ericoides*) and invasion by a non-native invasive species (*P. nigra*).

The proportion of coloniser (*r*-strategist) species in the nematode community increased with increasing tree cover of both woody species, supporting our first hypothesis. However, the coloniser life strategy groups that drove such changes differed between the two woody species. Increasing tree cover of the native *K. ericoides* led to an increase in the proportion of c–p 1 enrichment opportunist nematodes of the Rhabditidae family, which enter a metabolically reduced *dauerlarva* stage (which allows them to survive harsh conditions) and can respond rapidly to flushes of resource availability (i.e., nutrient enrichment pulses). Rhabditidae nematodes were the most abundant bacterial feeding nematodes in plots with > 85% *K. ericoides* tree cover, suggesting that the previously observed increase in bacterial energy channels in this woody succession gradient (Dickie et al. 2011)

was largely driven by nematodes of the Rhabditidae family. Conversely, increasing tree cover of the invasive *P. nigra* led to an increase in the proportion of c–p 2 nematodes. *Tylenchus* sp. 1 was the taxa with the highest relative abundance of the c–p 2 group in plots having > 90% *P. nigra* tree cover. Species of the Tylenchidae family are ectoparasites or root-hair feeders (Yeates et al. 1993) and have been previously found to be more generalist in their feeding preferences (Wilschut et al. 2018), which could favour them to adapt to changes in resource availability driven by increases in *P. nigra* abundance.

Differences in plant rhizosphere characteristics among species (Kourtev et al. 2003) can alter the composition and activity of microbial communities and hence indirectly drive changes in nematode communities (Saj et al. 2009). Here, changes in microbial communities appear to favour short life cycle free-living nematodes under increasing *K. ericoides* tree cover, causing a decrease in the maturity index of free-living nematodes (MI). Nevertheless, such changes were not sufficiently strong to drive changes at the whole community level (ΣMI). On the other hand, ΣMI decreased with increasing *P. nigra* tree cover, mostly due to a decrease in herbivorous nematodes with relatively slow growth and longer life cycles (decrease in PPI), indicating that herbivorous nematodes sensitive to environmental perturbations are more susceptible to increasing *P. nigra* tree cover.

Previous studies suggest that non-native plant species can benefit in their non-native range as natural enemies are unable to exploit them (Schaffner et al. 2011) due to their novel chemistry (Macel et al. 2014). This in turn could increase the herbivory pressure over natives, as natural enemy impacts would be concentrated on native species (Engelkes et al. 2008), further facilitating non-native species expansion. Although we cannot rule out that *P. nigra* is relatively unaffected by herbivorous nematodes, our results show far fewer herbivorous nematodes with long life cycles and slow reproduction under increasing *P. nigra* tree cover. Our results, along with previous studies looking at variation in chemical novelty caused by range-expanding plant species (Wilschut et al. 2017), suggest that responses of herbivorous nematodes can be plant species-specific (Morriën et al. 2012). Overall, these observations support a view that increasing abundance of different woody plant species into grasslands fundamentally shifts the dominant functional types of soil nematodes and therefore the multiple ecosystem processes driven by them (e.g., De Deyn 2017).

Similarly, nematode community structure responded differently to increasing dominance of different woody species. In particular, nematode communities in the *K. ericoides* succession did not show any signs of food-web simplification (i.e., ΣMI and SI did not change across the tree cover gradient). In fact, nematode communities under increasing *K. ericoides* cover became more enriched (EI increased), mainly

due to an increase in the proportion of short-lived c–p 1 taxa, which respond positively to any level of environmental quality enrichment. This suggests that litter of *K. ericoides* is more favourable to the nematode soil community than the highly acidic litter of *P. nigra* (Dickie et al. 2011), which has been found to negatively affect soil biota (Kappes et al. 2007). In addition, the decline in the sigma maturity index (ΣMI) with increasing *P. nigra* tree cover suggests that the community becomes dominated by nematode families that increase under disturbances or stress conditions. Hence, increasing *P. nigra* tree cover led to more basal communities, characteristic of disturbed habitats, and dominated by short-lived c–p 2 organisms (Ferris et al. 2001).

The decline in the structure index (SI) across the *P. nigra* expansion also indicates a simplification of the nematode community structure, with a lower complexity and redundancy, also observed under increasing age of invasive Fabaceae trees (Biederman and Boutton 2009). Nevertheless, structured and highly diverse nematode communities have been observed in *P. nigra*'s natural range (Armendariz et al. 1996), suggesting that changes in the structure and complexity of the nematode-based food web may respond differently to both woody plant species and location. Future studies assessing differences in nematode community structure across the native and invasive range of plant species could shed light on this matter. Also, a decrease in the complexity, and potentially stability, of nematode communities under *P. nigra* expansion highlights that the active management of invading non-native gymnosperm trees should ensure that soil nematode diversity (Dickie et al. 2011), nematode community structure and thus multiple belowground processes are not compromised.

Although we cannot directly compare the impacts of native vs. non-native woody species expansion into grasslands on nematode communities in this study, as differences could be the result of, e.g., distinct root traits among species rather than their origin, the overall structure of the soil nematode community responded differently to each woody species. In particular, under a native angiosperm (*K. ericoides*) succession, the nematode community reflected conditions of increasing enrichment, whereas under a non-native invasive gymnosperm (*P. nigra*) expansion, the nematode community became less mature, having a more basal and simplified food web. The effects of increasing canopy cover on the soil nematode community composition and structure were stronger under *P. nigra*, likely reflecting inputs of acidic litter which alters soil pH (Dickie et al. 2011) and can negatively affect soil biota (Kappes et al. 2007). Because *P. nigra* is outside of its natural range in the study area, it is possible that nematodes are less adapted to microhabitat and resource changes compared to native *K. ericoides*. Further studies assessing the response of nematode communities to other native and non-native woody species expansions are necessary to better

understand the influence of native vs. non-native species on belowground communities and the fundamental ecosystem processes driven by them.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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