Nutrient addition hinders microarthropod-driven leaf litter decomposition in Patagonian woodlands

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Abstract

Global change threatens ecosystem functions, including those driven by soil fauna. In temperate forests, soil nutrients, litter quality, and microarthropods are essential players during litter decomposition. However, the impact of nutrient enrichment on the functional role of soil fauna remains poorly understood. We used a full factorial experiment to test the effects of nitrogen (N), phosphorus (P), and potassium (K) addition on litter decomposition through changes in soil conditions and litter quality. We incubated senesced leaves from fertilized and unfertilized control plots in litter bags with two different mesh sizes that included (2 mm) or excluded (45 µm) microarthropods. We assessed the interactive effects of nutrient addition and litter quality on microarthropod-driven decomposition using linear mixed-effects models. Nutrient addition was a stronger predictor than litter quality for organic matter remaining in litter bags over time. While N addition strongly influenced litter quality, it did not affect microarthropod activity in decomposition. P addition suppressed decomposition when microarthropods were present but enhanced it when microarthropods were absent. K strongly influenced litter quality and regulated the effects of phosphorus on decomposition. Microarthropods may promote decomposition under conditions of limited nutrient availability in both litter and soil, potentially enhancing microbial activity. The responses of fungi and microbes to nutrient enrichment may explain the relatively modest effect of microarthropods on decomposition. Our study shows that nutrient enrichment in temperate forests may limit microarthropod participation in decomposition by possibly altering microsite conditions or affecting the availability of alternative food resources, thereby influencing carbon fluxes.

Keywords: nutrient enrichment; decomposition; temperate woodlands; microarthropods

1. Introduction

Ecosystem functions are threatened by global change, including those mediated by soil organisms. One important global change process is nutrient enrichment, caused by excessive nutrient addition in ecosystems. The consequences of nutrient enrichment in ecosystems vary. For example, nutrient enrichment has widespread negative effects on aboveground and belowground biodiversity in forests (Isbell et al., 2013; Seabloom et al., 2021; Sullivan & Sullivan, 2018). These impacts should be addressed because biodiversity sustains ecosystem services and ecosystem resilience (Cardinale et al., 2012). Overall, soil organisms facilitate decomposition, soil formation, nutrient cycling, pest control, and stability of aboveground biodiversity, among other functions (Crowther et al., 2015; Delgado-Baquerizo et al., 2020). The unclear outcomes of nutrient enrichment for soil organisms are of concern when considering future scenarios of nutrient pollution and deposition (Galloway et al., 2008; Lilleskov et al., 2019; Phillips et al., 2019). With growing evidence that soil fauna (e.g., microarthropods) are of great importance for decomposition in temperate regions (García-Palacios et al., 2016), further regional descriptions of their performance under global change scenarios (e.g., nutrient enrichment) need immediate attention (Beaumelle et al., 2021; Eisenhauer et al., 2019).

Nutrient enrichment can drive changes in plant internal nutrient cycling and trophic cascades with potential consequences for litter decomposition. For example, increased nutrient availability can cause plants to change the characteristics of litter that are important to decomposers (i.e., cellulose, hemicellulose, lignin, C/N ratio) and their soil microhabitat (Gergócs & Hufnagel, 2016; Perez et al., 2013). Some studies suggest that changes in litter quality, usually characterized by C/N ratios, directly impact litter decay trajectories, and organic matter formation (Cotrufo et al., 2013). One possible pathway can be related to the disruption of the long-term affinity of soil biota with litter, with potential impacts on carbon flux and storage in organic matter (Elser et al., 2007; Harpole et al., 2011). While affinity between litter and microbiota is widely addressed in the literature (Freschet et al., 2012; Li et al., 2021; Palozzi & Lindo, 2018; Perez et al., 2013), for other soil organisms (e.g., soil fauna), these interactions remain obscure. Previous studies suggested that N enrichment could decrease soil respiration (Janssens et al., 2010) but also stimulate decomposition in the early stages of the process while reducing decomposition in later stages (Gill et al., 2021). The contribution of microarthropods may be important in the last stages of decomposition, as previous studies show that the presence of oribatid mites increases with recalcitrant material and after 24 months of litter decomposition in different ecosystems (Eissfeller et al., 2013; Fujii & Takeda, 2017; Heneghan et al., 1998; Marian et al., 2018). Whether response patterns observed in microbes apply to microarthropods is unclear and, so far, context-dependent. Understanding the interplay of nutrient addition with litter quality on higher trophic levels (i.e., microarthropods) is highly relevant for temperate ecosystems.

The microenvironment where decomposition occurs is strongly affected by nutrient enrichment. If changes in the soil microenvironment occur, its interaction with initial litter quality might impact the contribution of microarthropods to litter decay differentially (Freschet et al., 2012). For microarthropods this could explain why, in some cases, their activity during decomposition is not related exclusively to litter quality (Zieger et al., 2015). While in some systems, microarthropods prefer decomposing low-quality litter (Frouz et al., 2015; Irmler, 2000; Peguero et al., 2021), in other systems, microarthropods contribute more to decomposition of high-quality litter (Carrillo et al., 2011; Fujii et al., 2018). Another possible and partial explanation can be related to mismatches between nutrient availability and the physiological demands of microarthropods conditioning their performance during litter decomposition (Beaumelle et al., 2021; Frouz, 2018). However, temporal dynamics and changes in multiple nutrient availability effects on litter decomposition by different groups of soil organisms are still under investigation (Pichon et al., 2020; Smith & Bradford, 2003). A lack of understanding of soil multitrophic responses to nutrient enrichment could carry severe consequences for ecosystem productivity and belowground processes related to litter decomposition, like carbon efflux and nutrient leaching (Delgado-Baquerizo et al., 2020; Guerra et al., 2020; Maaroufi & De Long, 2020).

Few experimental studies address N interaction with P and K imbalances, even when it is crucial for understanding C cycling and other ecosystem processes in a global change context (Peñuelas et al., 2013; Sardans & Peñuelas, 2015). Areas of low nutrient deposition around the world have been proposed as ideal scenarios to test hypotheses related to nutrient enrichment (Vivanco, 2008). In temperate woodlands N is a limiting nutrient for vegetation growth, but P can also be limited at some sites in NW Patagonia (Diehl et al., 2008; Vivanco & Austin, 2008). Most South American ecosystems have not been exposed to high nutrient deposition levels like their northern counterparts. However, they are expected to experience greater nutrient deposition levels in the next three decades (Galloway et al., 2008).

Regions like northwestern Patagonia can help test hypotheses related to nutrient enrichment and ecosystem functioning. In NW Patagonia, mixed-species woodlands dominated by *Nothofagus antarctica* ((G. Forst.) Oerst.) constitute the most diverse plant community in the region and occupy 110,000 hectares (Reque et al., 2007). An increased interest in sustainable management in Argentinian woodlands demands scientific and management efforts to understand ecosystem functioning in response to anthropic disturbance (*sensu* Law 26.331, 2007). We aimed to determine which combinations of macronutrient addition (N, P, K) affected litter quality and if there were cascading effects on microarthropod-driven decomposition from nutrient changes in the senesced leaves. When nutrient availability increases through nutrient addition, plant nutrient limitations are alleviated, increasing litter quality (Fisk et al., 2014; Gonzales & Yanai, 2019; Vitousek et al., 2010). Since there is evidence of a strong relationship between N and P content in soil and tissues of deciduous species in Patagonian woodlands, we expected to see high correlations between nutrient content in soil and litter after fertilization (Diehl et al., 2003). We anticipated a significant increase in soil and foliar nitrogen (N) with N and K additions (Sardans & Peñuelas, 2015). However, for P and K addition, we expected more moderate effects in the soil pools. This is due to a) the mineral composition of the soil, which renders P less available (allophanic clays), and b) the rapid cycling of K in the litter may enhance microarthropod-driven decomposition by reducing the carbon to nitrogen (C/N) ratio. In some cases, higher N, P, and K concentrations in the litter might increase microarthropod-driven decomposition by decreasing the C/N ratio (Fujii et al., 2018; Peng et al., 2019). We predicted that: 1) additions of N and P would increase decomposition rates by enhancing litter nutrient concentrations and litter quality,2) microarthropod access to a litter of low C/N (higher quality) increase decomposition rates, and 3) microarthropods would contribute more to later decomposition stages than earlier ones due to their ability to access recalcitrant resources in the litter.

2. Materials and Methods

2.1 Study site

The study site is located in El Foyel (41° 38′ 47″ S, 71° 29′ 55″ W), Río Negro, northwestern Patagonia (Argentina, Figure 1A,1B). The site hosts broadleaf woodlands dominated by *N. antarctica,* accompanied by other woody species such as *Lomatia hirsuta* (Lam.) Diels ex J.F. Macbr., *Schinus patagonicus* (Phil.) I. M. Johnst. ex-Cabrera and *Diostea juncea* (Gillies ex Hook.) Miers (Kitzberger & Veblen, 1999). Woodlands are post-fire secondary succession, and in the absence of fire, their structural composition resembles transition states to forests dominated by *Austrocedrus chilensis* (D.Don) Pic.Serm. & Bizzarri. The climate in the area is temperate with warm dry summers (Csb, Köppen climate classification) characteristic of mediterranean-like ecosystems (Kottek et al., 2006). Mean annual temperature ranging from 8 °C to 10 °C, 920 mm mean annual rainfall concentrated during the winter, with an average of 120 frost days and 65% annual relative humidity (Gyenge et al., 2009; Reque et al., 2007). These woodlands grow at an altitude between 790 and 880 meters asl, on allophanic soils derived from volcanic ash of sandy to loamy texture (Andisols, Bockheim et al., 2014; Nacif et al., 2020). In most temperate areas N is considered more limiting than P for plant growth, but at our sites, the plant community can be co-limited by N and P (Diehl et al., 2008). This is because in volcanic soils P can be retained by precipitation or anion sorption in amorphous soil colloids (Parfitt et al., 2005).

2.2 Microarthropod community

The microarthropod community in our study site shows a community structure typical of temperate areas and comparable to previous studies in the region (Kun et al., 2010; Manzo et al., 2021; Rizzuto, 2018). In the study area, Fernández et al., (2022) found that the average microarthropod taxa densities were 20,000-35,000 individuals m^{-2} of Acari and 10,000 individuals m^{2} of Collembola, with an 80% Acari, 20% Collembola proportion. Moreover, Fernández et al., (2022) found that Acari community composition was approximately 80% detritivore/fungivorous (Oribatida and Prostigmata) and 20% predatory (Mesostigmata) at the study sites. The most abundant oribatid mite species (≥ 5%) across sites were: *Oribatula* sp., *Paraphauloppia australis* (Hammer, 1962), *Cultroribula argentinensis* (Balogh & Csiszár, 1963), and *Membranoppia (Pravoppia) argentinensis* (Balogh & Csiszár, 1963). *Tectochepeus velatus* (Michael, 1880),*Lanceoppia kovacsi* (Balogh & Csiszár, 1963), and *Camisia* sp. The complete list of Oribatid species for this study site is detailed in Kun et al., (2010) and Fernández et al., (2022).

2.3 Fertilization experiment

To evaluate the impact of the progressive addition of different macronutrients on the functional role of microarthropods in litter decomposition, we used a four-hectare fertilization experiment "*in situ*". During

October and November, and before the growing seasons of 2016, 2017, and 2018, we applied eight fertilization treatments resulting from a factorial combination of nitrogen (N), phosphorus (P), and potassium (K). Each of the eight treatments (unfertilized control, N, P, K, NP, NK, PK, NPK) was replicated in four blocks, resulting in 32 experimental plots of 31.5 m by 45 m (Figure 1C). The fertilization rates simulate an enrichment scenario with an additional 30% annual N mineralization (Vivanco & Austin, 2011) and high fertilization rates for P and K (*personal communication* 2016, Cremona, V., Kowaljow et al., 2010). While the rates used for all nutrients in our study do not happen naturally, the goal was to simulate an extreme nutrient enrichment scenario. We fertilized by hand at the beginning of each growing season (spring) at a nutrient rate of 100 kg ha^{-1} N (time-release urea) (Lindberg & Persson, 2004; Vivanco, 2008), 75 kg ha^{-1} P (triple-superphosphate), and 56 kg ha^{-1} of K (potassium sulfate) (Kim, 2008).

2.4 Soil sampling

In March 2018, after two seasons of fertilizer application, soil sampling was done to test soil pools of N, P, and K, pH, electrical conductivity, and organic matter. Soil samples were collected using a 3.5 cm diameter soil auger to a 20-cm depth along three longitudinal transects from all plots. Each transect comprised 3-4 sampling points with at least 5 m between two randomized points, making a total of ten sampling points per plot. Points sampled in each transect were randomized. Each soil sample was separated into 0-10 cm and 10-20 cm horizons for chemical analysis. Once collected, soil samples were homogenized by horizon before transporting to the laboratory. Each plot had a composite sample per horizon. Air-dried soil, sieved through a 2-mm mesh, was analyzed for extractable P (Bray and Olsen-P) and available K. Organic C and total N were analyzed in samples ground to pass a 0.5 mm mesh. Available K was extracted in 1 M ammonium acetate solution by flame emission spectrometry (IRAM 29577), total N by semi-micro Kjeldahl, and organic C by Walkley-Black wet digestion. All soil properties determinations are detailed in Table S1.

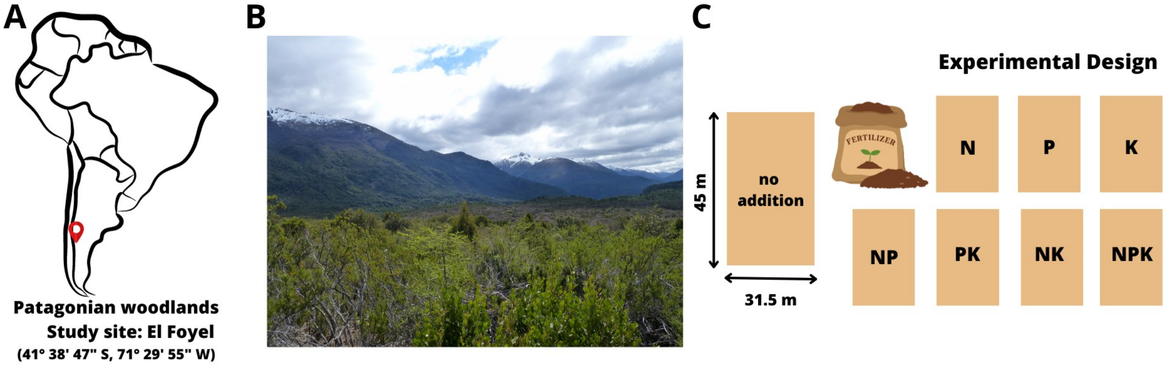

Fig.1. Study site and experimental design. A) Geographical location of study sites. B) Image of woodlands in NW Patagonia. C) The fertilization experiment comprised eight treatments (including unfertilized control) consisting of the addition of N, P, and K and their factorial combinations. All treatments were replicated in 4 blocks and resulting in 32 experimental units. Three fertilization seasons happened between 2016 and 2018.

2.5 Foliar nutrient concentration

We sampled leaves from *Nothofagus antarctica* trees (*n*=5) in each plot to determine foliar nutrient concentration during summer (December 2017) and autumn (March 2018). The foliar sampling and nutrient analysis followed protocols by Diehl et al., (2003). We used green leaf nutrient concentrations of N and P as a proxy for vegetation nutrient limitation in December 2017 (Güsewell, 2004; Reed et al., 2011). In April 2018, this sampling was repeated, but we used senescent leaves to characterize nutrient concentration (i.e., C, N, P, and K) and litter quality. After collection, the leaves were oven-dried 48 hours at 60° C, and a subsample for each plot was used to characterize the foliar nutrient concentration of N, P, K, and C. All foliar determinations are summarized in Table 1. We used the C/N ratio as a proxy for litter quality, where: high C/N ratios indicate low litter quality and low C/N ratios indicate higher litter quality.

Table 1. Nutrient concentration in *N. antarctica* senesced leaves among fertilization treatments (columns). N: nitrogen. P: phosphorus. K: potassium. C/N: carbon to nitrogen ratio. N/P: nitrogen to phosphorus ratio.

Treatment	N/P *mean ± SE*	C/N *mean ± SE*	N (%) *mean ± SE*	P (%) *mean ± SE*	K (%) *mean ± SE*
Control	8.86 ± 0.6	72.85 ± 3.7	0.68 ± 0.03	0.08 ± 0	0.2 ± 0.01
N	8.99 ± 2.2	56.23 ± 3.3	0.76 ± 0.1	0.11 ± 0.04	0.26 ± 0.1
P	6.38 ± 1.6	67.31 ± 13.5	0.75 ± 0.2	0.14 ± 0.1	0.2 ± 0.1
K	6.73 ± 1.8	63.5 ± 4.4	0.78 ± 0.05	0.14 ± 0.02	0.31 ± 0.04
NP	7.41 ± 1.0	52.23 ± 11.2	0.95 ± 0.2	0.13 ± 0.04	0.26 ± 0.1
NK	7.58 ± 1.2	55.24 ± 8.1	0.88 ± 0.1	0.12 ± 0.04	0.29 ± 0.1
PK	7.24 ± 0.6	53.31 ± 9.1	0.92 ± 0.2	0.13 ± 0.03	0.33 ± 0.1
NPK	4.79 ± 0.6	62.71 ± 6.4	0.79 ± 0.1	0.17 ± 0.01	0.34 ± 0.1

2.6 Decomposition experiment

We used a litter bag experiment to track organic matter remaining at different dates over three years, and in relation to nutrient addition, litter quality and microarthropods inclusion/exclusion. All decomposition treatments (combination of litter type and mesh size) were replicated at two microsites per plot (Fig. 2A). In total, 1120 litter bags were incubated in fertilized plots: 2 microsites x 4 mesh/litter type combinations x 5 retrieval dates x 28 plots (Fig. 2B). The control plots had two treatments corresponding to coarse and fine mesh litter bags filled with control litter, totalizing 80 litter bags: 2 microsites x 2 mesh/litter type combinations x 5 retrieval dates x 4 plots. In a plot with a certain fertilization treatment, we incubated litter bags with litter from the plot itself and litter bags filled with control litter (no fertilization).

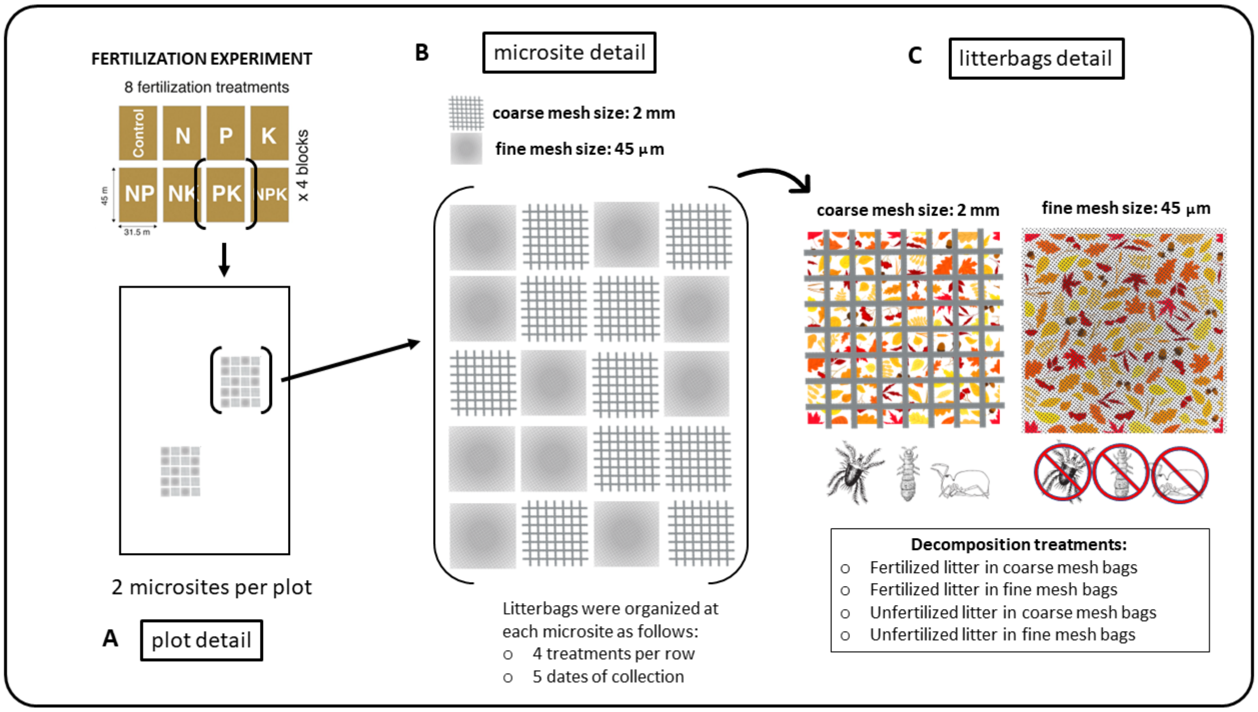

Figure 2. Design of decomposition experiment with two litter types (from fertilized and unfertilized control plots) with two different mesh sizes placed at two microsites per plot. A: Detail of location of microsites per plot. B: Microsite detail showing the organization of litter bags according to the number of collection dates and treatments. C: Litter bag construction details.

For instance, a plot fertilized with N+P would have 20 litter bags filled with litter from N+P fertilized trees and 20 litter bags filled with litter from trees in control plots. Litter bags were 15 x 15 cm filled with 1.5 grams of *N. antarctica* senesced leaves for all treatments. To isolate the effect of microarthropods we used litter bags built with two different mesh sizes: 2 mm (coarse mesh for macrofauna exclusion and microarthropods inclusion) and 45 µm (fine mesh-for microarthropods exclusion) (Fig. 2C). We filled the litter bags using leaves of *N. antarctica* since it is the dominant canopy species at the sites. Senescent litter was collected from the canopy of five dominant *N. antarctica* individuals at each plot in March 2018. To separate the effect of litter quality from the effect of nutrient addition on decomposition, we used litter from control plots (no fertilization) and fertilized plots. Litter bags were incubated at the surface of the forest floor, and they were collected at 41, 110, 195, 365, and 1022 days after installment (April 2018). After collection, litter bags were taken to the laboratory where they were oven-dried (60° C for 48 hours). Once dried, foreign material (i.e., rocks, seeds, roots, soil) was removed from each litter bag, and ash-free dry weight was determined.

2.7 Statistical Analysis

All data analysis was conducted in R 3.6.1 (R Core Team, 2019). As a baseline analysis, we adjusted several decomposition models to the litter bag data using the *litterfitter* package (Cornwell & Weedon, 2014). We found that a negative exponential model was inadequate for our litter decay data (Fig. S1), and we used organic matter remaining as our response variable instead of calculating common decay rates (Vivanco & Austin, 2011).

We tested the impact of fertilizer on soil and foliar nutrient concentration using linear mixed-effects models (LMM's). Models included the multiple nutrient interaction as fixed effects and the experimental block as a random effect. We used the Dunnett's test as a post-hoc contrast to compare mean values for all foliar variables after fertilization with the mean value in the control plots. Finally, we calculated the correlation of soil and foliar nutrient concentration for control and fertilized litter using the function *ggcor* from the package *ggplot2* (v3.3.5; Wickham, 2016).

To test the effect of fertilizer on organic matter remnant of litter decomposing with and without microarthropod access, we also GLMMs, where multiple nutrient interactions (NPK) interacted with mesh size as fixed factors (hypotheses 1 and 4). We built models for both litter from fertilized and control plots separately since we did not incubate litter from fertilized plots at control plots. The experimental block was considered a random effect for avoiding pseudo-replications (Zuur, 2009). We used the *glmmTMB* package (Brooks, 2017) to perform all the above-mentioned GLMM's and the *emmeans* R package to apply the post-hoc analyses (Lenth, 2021). We tested the goodness of fit for each model using the *DHARMa* package (Hartig, 2021). The "DHARMa" package uses a simulation-based approach to create readily interpretable scaled (quantile) residuals for fitted linear mixed models. We corrected the heteroscedasticity with constant variance function structure (varIdent) when needed (Zuur, 2009).

3. Results

3.1. Litter quality and microsite conditions

After two seasons of fertilization, adding multiple nutrients significantly modified the soil nutrient pools and senesced leaves of *N. antarctica.* Soil total N was marginally higher but, P, and K increased by 180%, and 75%, respectively, at the surface (0-10 cm) and subsurface (10-20 cm) horizons compared to the control (Table S1). N+P addition significantly increased N in senesced leaves (p=0.03), while N+P+K addition increased P and K concentrations (p=0.02) (Tables 2 and 3). Litter C/N decreased significantly with N and P addition, indicating improved litter quality (Fig. 3A). Control conditions (no fertilizer added to the plot) had the highest C/N ratio and lowest N and P concentrations in senesced leaves (Fig. 3B-C). Notably, treatments with addition of N (p=0.03), NP (p=0.02), NK (p=0.02), and PK (p=0.007) exhibited the highest increase in litter quality compared to the control (Tables 2 and 3, Fig. 3A).

Also, we observed that after fertilization K concentration in soils was positively correlated with K and P concentration in senesced leaves but only modestly for N (Fig.S2, K soil-K foliar *rho*=0.5, K soil-P foliar *rho*=0.65, K soil-N foliar *rho*=0.28).

Table 2. Mean differences in foliar nutrient concentration (%) and C/N ratio of senesced leaves of *N. antarctica* were compared among fertilization treatments and control plots. Bold values indicate statistically significant differences in mean comparisons using Dunnett's test (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$). N: nitrogen. P: phosphorus. K: potassium. C/N: carbon to nitrogen ratio.

Contrast	N foliar (%)	P foliar (%)	K foliar (%)	C/N foliar

N-Control	0.08	0.03	0.07	**-16.62****
P-Control	0.06	0.06	0.003	-5.53
K-Control	0.1	0.05	0.11	-9.35
NP-Control	**0.27***	0.06	0.07	**-20.61****
NK-Control	0.2	0.05	0.1	**-17.61***
PK- Control	0.24	0.03	**0.13***	**-19.54****
NPK-Control	0.11	**0.09***	**0.14***	-10.13

Table 3. Estimated fixed-effects coefficients for linear mixed-effects models assessing nutrients in senesced leaves of *N. antarctica* among fertilization treatments. Bold values represent indicate statistically significant effects after the Dunnett's test (*** *Pr (>Chisq)* <0.001; ** < 0.01; * < 0.05).

N: nitrogen. P: phosphorus. K: potassium. C/N: carbon to nitrogen ratio.

Fertilizer	**N foliar (%)**	**P foliar (%)**	**K foliar (%)**	**C/N foliar**
Control	0.7 (0.07)	0.07 (0.02)	0.19 (0.04)	72.9 (4.9)
N	0.07 (0.09)	0.03 (0.03)	0.07 (0.04)	**-16.6 (6.1)***
P	0.06 (0.09)	0.06 (0.03)	0.003 (0.05)	-5.5 (6.1)
K	0.1 (0.09)	0.06 (0.03)	**0.11 (0.05)***	-9.3 (6.1)
NP	**0.13 (0.1)***	-0.04 (0.04)	-0.001 (0.05)	**3.6 (5.9)***
NK	0.02 (0.1)	-0.04 (0.04)	-0.08 (0.06)	**8.3 (8.5)****
PK	0.07 (0.12)	-0.07 (0.04)	0.02 (0.06)	-4.6 (8.5)
NPK	-0.35 (0.18)	**0.08 (0.02)***	0.02 (0.09)	14.1 (12.4)

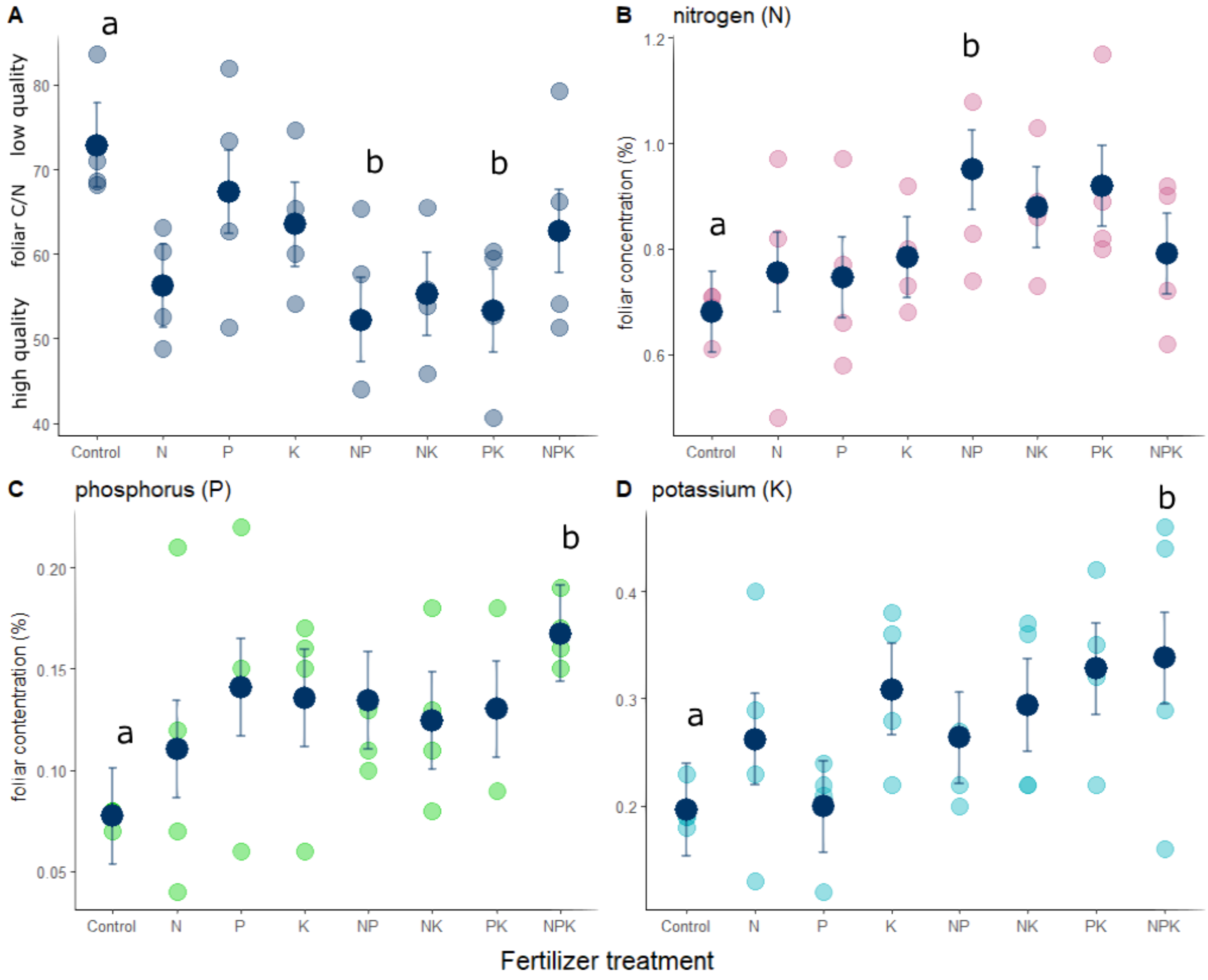

Figure 3. Nutrient concentration in senesced leaves of *N. antarctica* among treatments. A) C/N ratio, B) foliar nutrient concentration of nitrogen (N), C) foliar nutrient concentration of phosphorus (P), D) foliar nutrient concentration of potassium (K). Dark blue points and bars represent mean and standard error (± 1 SE, *n*=4) estimated from GLMM's. Raw data are presented as colored circles. Each color represents a different nutrient.

3.2. Microarthropod vs. nutrient addition impacts on litter decomposition

Fertilization had a greater impact than litter quality on organic matter remaining in litter bags, especially after one year (Fig. 4, Table 4 and Table S2). Nitrogen addition did not enhance decomposition significantly (Table 4, N: mesh, *p*> 0.05), but surprisingly, phosphorus (P) addition had a negative effect with K in litter decaying in coarse and fine mesh bags (Table 4, K:mesh, P:mesh, *p* < 0.05).

Overall, microarthropods had a minimal role in litter decay after one and three years of decomposition (Fig. 4, Table 4 and S2). Litter quality did not significantly affect organic matter remaining for both litter types across fertilization treatments (Table S2, Quality: *p*>0.05). Coarse and fine mesh litter bags showed an average litter matter loss of 50% after a year (Fig. 4A-B) and between 60 and 65% after 3 years. However, microarthropods' contribution to organic matter loss (coarse mesh bags) was not significantly different from microbiota contribution (fine mesh bags) at any time (Fig. S1, Table 4, Mesh: *p*=0.2).

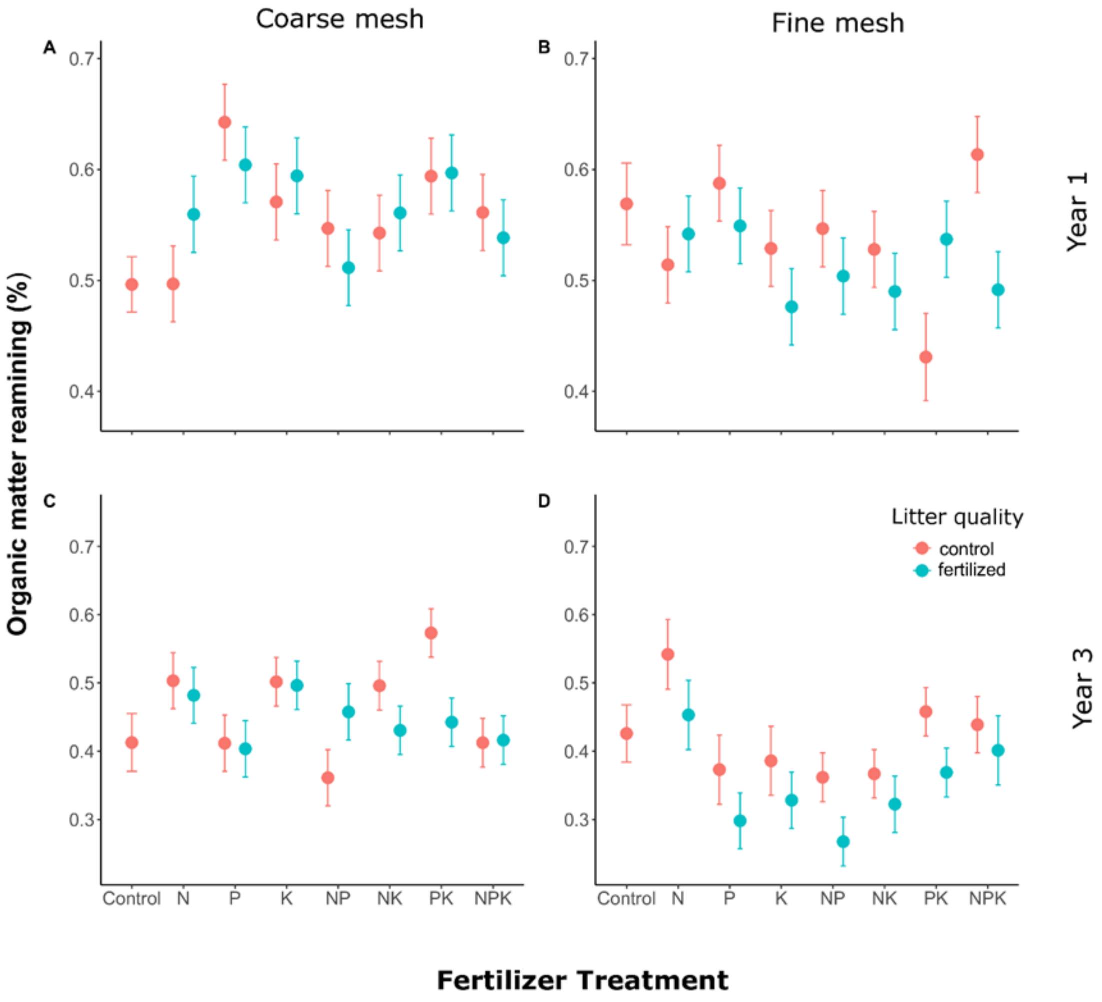

Figure 4. Average organic matter remaining in litter bags decomposing *N. antarctica* litter (unfertilized control litter in pink, fertilized litter in blue) in a multiple nutrient enrichment experiment. The microarthropods' effect on decomposition was measured by comparing organic matter remaining in coarse mesh (2 mm mesh size) and fine mesh (45 µm mesh size) litter bags. The upper panels (A and B) correspond to values for organic matter remaining after a year of decomposition in remaining after a year of decomposition at the field. The lower panel (C and D) corresponds to values for the remaining organic matter after three years of decomposition at the field. The left panel (A and C) corresponds to litter bags with microarthropod access (coarse mesh), and the right panel (B and D) corresponds to litter bags without microarthropod access (fine mesh). Filled points and standard error bars (± 1 SE, *n*=4) are the averaged mean organic matter and errors calculated using mixed-effects models (Table 4 and S2). A) Coarse mesh year 1. B) Fine mesh year 1. C) Coarse mesh Year 3. D) Fine mesh Year 3.

Table 4. Estimated fixed-effects coefficients for linear mixed-effects models assessing changes in organic matter remaining for control (unfertilized) litter under the factorial nutrient addition experiment. Intercepts were allowed to vary by block (random effect). In this table, the unfertilized control factor includes decomposing control litter in coarse mesh litter bags in control plots. For the litter quality comparison, refer to Table S2. Bold values represent statistically significant effects from the LRT test (*** *Pr (>Chisq)* <0.001; ** < 0.01; * < 0.05). OMR: organic matter remaining. N: nitrogen. P: phosphorus. K: potassium.

Treatment	**OMR (1 yr)**	**OMR (2.8 yr)**
Control	0.5 (0.02)	0.41 (0.04)
N	0.04 (0.03)	0.06 (0.05)
P	**0.15 (0.03)*****	0.004 (0.05)
K	0.08 (0.03)*	0.01 (0.05)
Mesh	0.07 (0.04)	-0.12 (0.05)

NP	-**0.14 (0.05)****	-0.07 (0.07)
NK	-0.07 (0.05)	-0.07 (0.06)
PK	**-0.13 (0.05)****	0.06 (0.07)
N: mesh	-0.08 (0.05)	-0.01 (0.07)
P: mesh	**-0.13 (0.05)***	-0.06 (0.07)
K: mesh	**-0.12(0.05)***	-**0.16 (0.07)***
NPK	**0.15 (0.06)***	0.007 (0.08)
NP: mesh	**0.14 (0.07)***	0.09 (0.08)
NK: mesh	0.13 (0.07)	0.04 (0.08)
PK: mesh	0.04 (0.07)	0.10 (0.08)

4. Discussion

Manipulating soil nutrient availability with fertilization identified pathways in which nutrient enrichment might affect microarthropod involvement in litter decay over three years. While litter quality is relevant for microarthropods (García-Palacios et al., 2013; Gergócs & Hufnagel, 2016; Ilieva-Makulec et al., 2006; Milcu & Manning, 2011; Smith & Bradford, 2003; Yang & Chen, 2009), we did not find any direct relationship between changes in litter quality due to fertilization and microarthropod activity in litter decomposition. A substantial proportion of the variation in organic matter remaining in coarse-mesh litter bags was related to the microsite soil conditions where litter was decomposing and whether it was fertilized previously or not. Our results challenge the expectation of a positive role of microarthropods in litter decomposition with increased nutrient availability. Instead, the role of microarthropods in decomposing recalcitrant litter in unfertilized control areas seemed of higher relevance for Patagonian woodlands. Long-term relationships between plant litter and decomposers are simultaneously built on litter traits and on the characteristics of the forest floor-soil matrix where litter decomposes (Freschet et al., 2012; Peguero et al., 2019; Pichon et al., 2020; Veen et al., 2018). Our results suggest that, in the short term, interactive responses at different trophic levels might explain context-dependent patterns observed in litter decay experiments, such as affinity to high or low litter quality. Below, we expand on the litter quality and fertilization pathways and its implications for microarthropod-driven decomposition in these temperate woodlands.

4.1. Litter quality interactions with litter bag mesh size

After two seasons of fertilization, senesced leaves displayed significant changes in nutrient concentration. Litter quality increased by approximately 30% (equivalent to a -20 C/N unit shift) with N+P and P+K additions compared to the control. This shift correlates with a higher contribution of soil fauna to the litter decay process in some forests (Yang & Chen, 2009). However, initial nutrient concentrations in litter also play a crucial role (Aerts, 1997; Rosenfield et al., 2020). With N+P and N+K additions, we observed initial litter N and P concentrations approximately 40-70% higher than control plots. For instance, N concentration in N+P litter increased by about 40% compared to control litter. These results suggest a positive role of K in nutrient acquisition for *N. antarctica* in Mediterranean woodlands. Adding K, along with N and P, led to higher N and P concentrations in senesced tissues. K concentration was highest in the litter with K and N+P+K addition and lowest in control plots. While a complete analysis of the K litter pool requires considering K loss through throughfall, it is still noteworthy to observe its impact on litter quality and its modification when combined with N+P, possibly through changes in resorption rates (Vergutz et al., 2012).

Despite the known interaction between litter quality and nutrient availability (García-Palacios et al., 2016), we observed no significant differences in litter decay related to litter quality. Patagonian woodlands are typically nitrogen-limited, leading us to anticipate a positive effect of nitrogen (N) addition on litter quality and decomposition rates (Vivanco & Austin, 2011). While the former held true, adding nitrogen did not increase decomposition in coarse-meshed bags. Surprisingly, phosphorus (P) played a more substantial role in determining organic matter remaining in litter bags than N, with a negative non-additive effect of P+K in coarse and fine mesh bags. The observed pattern suggests that P may suppress litter decay and raise the possibility of microarthropods exerting a top-down influence on microbial biomass. Other studies in temperate forests have found a positive correlation between fungal biomass and P addition (Nielsen, Wall, et al., 2015; Treseder & Allen, 2002; Wall et al., 2015), suggesting that N and P could be limiting for microbiota contributing to litter decomposition but not for microarthropods in these Mediterranean woodlands (Pompermaier et al., 2022). Despite no increase in litter decay after nutrient addition and in the presence of microarthropods, their contribution may still stimulate parallel processes during decomposition that are not directly related to organic matter decay and these have not been determined in this study.

4.2. Microsite conditions override the role of litter quality

Microarthropod-driven decomposition appears context-dependent, often tied to ecosystem nutrient limitations. For instance, with lower nitrogen (N) and phosphorus (P) availability, microarthropods play a more prominent role in litter decomposition and nutrient leaching (Peguero et al., 2021). These situations underscore microarthropod function as facilitators of microbial decomposition under nutrient-scarce conditions (Pompermaier et al., 2022). Interestingly, increasing soil P availability negatively impacted microarthropod densities while stimulating root production and associated mycorrhizal fungi (Nielsen, Wall, et al., 2015). We noted that P concentrations in litter and soil significantly increased in plots with P+K addition compared to the control by up to two-fold. In plots with P addition alone, we observed fewer microarthropod predators (Mesostigmata) and prey (Collembola) (Fernández, 2023). This result could be linked to a) a short-term suppression of litter decay in coarse mesh bags and b) enhanced decomposition of high-quality litter in fine mesh bags due to predation release. Our findings align partly with Hu et al., (2021), who found that higher P concentrations in litter impeded microarthropod-mediated organic matter loss, increasing decomposition only when P was limiting in the ecosystem. These observations may elucidate the higher organic matter remaining in coarse mesh litter bags with P addition and the reverse effect in fine mesh bags with P and P+K additions. Alternatively, microarthropods might not be constrained by P in this study system. A potential decline in mycorrhization after P addition could lead to microbial overgrazing by microarthropods, explaining the negative impacts on organic matter loss under P fertilization in coarse mesh bags (Fujii et al., 2018; Hu et al., 2021; Petersen & Luxton, 1982). The interactive effects of microarthropods and nutrient availability suggest that microsite conditions override the role of litter quality in litter decay in these Patagonian woodlands.

4.3. Nutrient addition on microarthropod activity.

Unique combinations of nutrient additions allowed us to explore microarthropod contribution to litter decomposition in various nutrient enrichment scenarios. Indeed, simultaneous N, P, and K addition was not tested previously in temperate woodlands despite the relevance of synergistic effects of multiple nutrient enrichment and widespread nutrient co-limitation across ecosystems (Allgeier et al., 2011; Elser et al., 2007). In a management and global change context, future nutrient deposition might happen as wet scavenging, aerosols and/or dry deposition in the southern hemisphere (Bobbink et al., 2010; Galloway et al., 2008). In such scenarios, soil fauna-driven decomposition under nutrient enrichment is a relevant but unexplored topic in Patagonian woodlands.

Decomposition data in our study showed a different pattern to similar decomposition studies in other temperate areas (Carrillo et al., 2011; Fujii et al., 2018; Handa et al., 2014; Milcu & Manning, 2011). This is because, in our study, microarthropods only contributed to decreasing organic matter remaining when they were accessing recalcitrant litter in control conditions. We did not measure the influence of higher trophic groups on microarthropod density and their contribution to litter decomposition; but it could be a factor to consider. If nutrient addition modifies the densities of predators (i.e., macroarthropods, Melguizo-Ruiz et al., (2020)), or any other higher trophic organisms (i.e., millipedes, earthworms, Yin et al., (2022)) that regulate habitat or resources for microarthropods then their contribution to decomposition can be compromised. Indeed, field manipulation of larger predators (i.e., macrofauna) caused litter decomposition by microarthropod to decrease by 40% (Melguizo-Ruiz et al., 2020). Moreover, our observations contradict previous research presenting microarthropods as a positive driver for litter decomposition (García-Palacios et al., 2013; Wall et al., 2008) but are in line with the minimum role of microarthropods in the early stages of litter decay (Eissfeller et al., 2013; Fujii & Takeda, 2017; Irmler, 2000). Overall, we found no explicit or straightforward impact of nutrient addition on microarthropod activity. Instead, the interactive effect of fertilizers in the microenvironment where litter was decomposing affected the contributions of microarthropods to litter decay.

4.4. Comparison to related studies

Litter decomposition is a complex process, to which microarthropods contribute in several ways to the delivery of different products. Some examples are their top-down effects on microbial biomass (Pompermaier et al., 2022) and their significant role in nutrient leaching (Frouz, 2018). If most microarthropods in these woodlands are secondary decomposers or scavengers, their role could be conditioned to the dynamics of fungi or microbes in response to nutrient addition, overshadowing direct effects of litter quality as if they were primary decomposers (Eissfeller et al., 2013; Pollierer et al., 2009). Indeed, 80% of oribatids described at this study site are fungivorous and/or detritivores (Fernández, 2023). Then, after nutrient addition, microarthropods could either negatively impact litter decay during decomposition or show no direct effect on organic matter loss, while potentially increasing microbial respiration and nutrient leaching over time (Fujii et al., 2018; Li et al., 2021).

In some ecosystems, nutrient scarcity reinforces microarthropods’ role in litter decomposition because their activity facilitates litter comminution and disposal of fecal pellets that are more likely to be colonized by microbes (Peguero et al., 2019). If the local microarthropod community has an affinity to recalcitrant litter, that might explain why we observed lower organic matter remaining in control conditions in coarse mesh bags in the first year. Still, this effect disappeared over time with repeated additions across all treatments. Then, an increase in nutrient availability in senesced tissues and the microenvironment with nutrient addition could disrupt this “facilitator” role of microarthropods (Nielsen, Prior, et al., 2015). A similar response was observed in an old-growth forest of *Nothofagus* sp. and during a similar timespan (Vivanco & Austin, 2011). Nitrogen addition disrupted long-term interactions between local litter and microbial decomposers, increasing decomposition significantly. The underlying mechanisms were related to increased soil respiration and changes in microbial efficiency to use the N in excess. While N addition alone was not relevant in disrupting decomposition in coarse or fine mesh litter bags in this study at any time, similar microbial mechanisms could be attributed to P addition in fine mesh bags. Then, even though we cannot confirm patterns from this experimental setup, we suggest that greater nutrient availability in the soil directly or indirectly impaired the role of microarthropods in the decomposition of “lower quality” litter (i.e., control) (Eissfeller et al., 2013; Hu et al., 2021; Zhou et al., 2020).

Microarthropods may facilitate decomposition when nutrient availability is low, both in litter and soil, possibly enhancing microbial decomposition and nutrient leaching in such conditions. The manipulation of microbial biomass and litter mixtures under the influence of interactive macronutrients could elucidate the factors responsible for microarthropod functional responses. Understanding the functional roles of key soil fauna groups is essential for constructing robust biogeochemical models.

5. Conclusions

Litter quality was strongly and positively influenced by the addition of N, N+P and P+K. However, these changes did not have a bottom-up effect on litter decomposition. Changes in decomposition trajectories were significantly correlated with microsite nutrient conditions, i.e. litter decomposed differently between control and fertilized conditions. Although microarthropod activity in litter decomposition can thrive under nutrient deficiencies, it did not differ significantly from microbial decomposition at any time in this study. The inhibitory effect of nitrogen (N) addition on microbial activity did not have the same influence on microarthropods in this study. Notably, only the interaction between phosphorus (P) and potassium (K) suppressed microarthropod participation in litter decomposition. Nitrogen addition strongly influenced litter quality, but did not directly affect microarthropod activity in decomposition. Phosphorus, on the other hand, had a stronger effect on microarthropod-driven decomposition, possibly through mechanisms related to litter quality and microbial pathways. Future studies should focus on the mechanistic pathways of microarthropod responses to physicochemical perturbations and their interactions with microbial communities. Our study assessed the relationships between the functional role of microarthropods as a whole group in litter decomposition and nutrient enrichment, a previously unexplored aspect in Patagonian woodlands. While soil fauna has been suggested as important decomposers in temperate regions, their role may only become apparent in the context of nutrient limitation or without the influence of global change driven nutrient enrichment.

Authors contributions

MM Fernández, N Pérez-Méndez and LA. Garibaldi designed the study. MM Fernández conducted the field and laboratory work. MW Kaye and DM. Eissenstat contributed to the data analysis and interpretation. MM Fernández led manuscript writing, and all other authors contributed to revisions and editing.

Data Availability Statement: Penn State University repository.

Conflict of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Aerts, R. (1997). Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship. *Oikos*, *79*(3), 439. https://doi.org/10.2307/3546886

Allgeier, J. E., Rosemond, A. D., & Layman, C. A. (2011). The frequency and magnitude of non-additive responses to multiple nutrient enrichment. *Journal of Applied Ecology*, *48*(1), 96–101. https://doi.org/10.1111/j.1365-2664.2010.01894.x

Beaumelle, L., Thouvenot, L., Hines, J., Jochum, M., Eisenhauer, N., & Phillips, H. R. P. (2021). Soil fauna diversity and chemical stressors: a review of knowledge gaps and roadmap for future research. *Ecography*, *44*(6), 845–859. https://doi.org/10.1111/ecog.05627

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., & De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*, *20*(1), 30–59. https://doi.org/10.1890/08-1140.1

Bockheim, J. G., Gennadiyev, A. N., Hartemink, A. E., & Brevik, E. C. (2014). Soil-forming factors and Soil Taxonomy. *Geoderma*, *226–227*, 231–237. https://doi.org/10.1016/j.geoderma.2014.02.016

Brooks, M. E. K. K. van B. K. J. M. A. B. C. W. N. A. S. H. J. M. M. B. B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Carrillo, Y., Ball, B. A., Bradford, M. A., Jordan, C. F., & Molina, M. (2011). Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil. *Soil Biology and Biochemistry*, *43*(7), 1440–1449. https://doi.org/10.1016/j.soilbio.2011.03.011

Cornwell, W. K., & Weedon, J. T. (2014). Decomposition trajectories of diverse litter types: a model selection analysis. *Methods in Ecology and Evolution*, *5*(2), 173–182. https://doi.org/10.1111/2041-210X.12138

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*(4), 988–995. https://doi.org/10.1111/gcb.12113

Crowther, T. W., Thomas, S. M., Maynard, D. S., Baldrian, P., Covey, K., Frey, S. D., van Diepen, L. T. A., & Bradford, M. A. (2015). Biotic interactions mediate soil microbial feedbacks to climate change.

Proceedings of the National Academy of Sciences, *112*(22), 7033–7038. https://doi.org/10.1073/pnas.1502956112

Delgado-Baquerizo, M., Reich, P. B., Trivedi, C., Eldridge, D. J., Abades, S., Alfaro, F. D., Bastida, F., Berhe, A. A., Cutler, N. A., Gallardo, A., García-Velázquez, L., Hart, S. C., Hayes, P. E., He, J.-Z., Hseu, Z.-Y., Hu, H.-W., Kirchmair, M., Neuhauser, S., Pérez, C. A., … Singh, B. K. (2020). Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution*, *4*(2), 210–220. https://doi.org/10.1038/s41559-019-1084-y

Diehl, P., Mazzarino, M. J., & Fontenla, S. (2008). Plant limiting nutrients in Andean-Patagonian woody species: Effects of interannual rainfall variation, soil fertility and mycorrhizal infection. *Forest Ecology and Management*, *255*(7), 2973–2980. https://doi.org/10.1016/j.foreco.2008.02.003

Diehl, P., Mazzarino, M. J., Funes, F., Fontenla, S., Gobbi, M., & Ferrari, J. (2003). Nutrient conservation strategies in native Andean-Patagonian forests. *Journal of Vegetation Science*, *14*(1), 63–70. https://doi.org/10.1111/j.1654-1103.2003.tb02128.x

Eisenhauer, N., Bonn, A., & A. Guerra, C. (2019). Recognizing the quiet extinction of invertebrates. *Nature Communications*, *10*(1), 50. https://doi.org/10.1038/s41467-018-07916-1

Eissfeller, V., Langenbruch, C., Jacob, A., Maraun, M., & Scheu, S. (2013). Tree identity surpasses tree diversity in affecting the community structure of oribatid mites (Oribatida) of deciduous temperate forests. *Soil Biology and Biochemistry*, *63*, 154–162. https://doi.org/10.1016/j.soilbio.2013.03.024

Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, *10*(12), 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x

Fernández, M. M. (2023). *Impacts of anthropic disturbance on microarthropods: implications for sustainable management in Patagonian woodlands*. The Pennsylvania State University.

Fernández, M. M., Casas, C., Bedano, J. C., Eissenstat, D. M., Kaye, M. W., García, I. M., Kun, M. E., & Garibaldi, L. A. (2022). Mite density, not diversity, declines with biomass removal in Patagonian woodlands. *Applied Soil Ecology*, *169*, 104242. https://doi.org/10.1016/j.apsoil.2021.104242

Fisk, M. C., Ratliff, T. J., Goswami, S., & Yanai, R. D. (2014). Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests. *Biogeochemistry*, *118*(1–3), 195–204. https://doi.org/10.1007/s10533-013-9918-1

Freschet, G. T., Aerts, R., & Cornelissen, J. H. C. (2012). Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *Journal of Ecology*, *100*(3), 619–630. https://doi.org/10.1111/j.1365-2745.2011.01943.x

Frouz, J. (2018). Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. *Geoderma*, *332*, 161–172. https://doi.org/10.1016/j.geoderma.2017.08.039

Frouz, J., Roubíčková, A., Heděnec, P., & Tajovský, K. (2015). Do soil fauna really hasten litter decomposition? A meta-analysis of enclosure studies. *European Journal of Soil Biology*, *68*, 18–24. https://doi.org/10.1016/j.ejsobi.2015.03.002

Fujii, S., Cornelissen, J. H. C., Berg, M. P., & Mori, A. S. (2018). Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient. *Functional Ecology*, *32*(3), 840–852. https://doi.org/10.1111/1365-2435.13027

Fujii, S., & Takeda, H. (2017). Succession of soil microarthropod communities during the aboveground and belowground litter decomposition processes. *Soil Biology and Biochemistry*, *110*, 95–102. https://doi.org/10.1016/j.soilbio.2017.03.003

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., Martinelli, L. A., Seitzinger, S. P., & Sutton, M. A. (2008). Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science*, *320*(5878), 889–892. https://doi.org/10.1126/science.1136674

García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, *16*(8), 1045–1053. https://doi.org/10.1111/ele.12137

García-Palacios, P., McKie, B. G., Handa, I. T., Frainer, A., & Hättenschwiler, S. (2016). The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology*, *30*(5), 819–829. https://doi.org/10.1111/1365-2435.12589

Gergócs, V., & Hufnagel, L. (2016). The effect of microarthropods on litter decomposition depends on litter quality. *European Journal of Soil Biology*, *75*, 24–30. https://doi.org/10.1016/j.ejsobi.2016.04.008

Gill, A. L., Schilling, J., & Hobbie, S. E. (2021). Experimental nitrogen fertilisation globally accelerates, then slows decomposition of leaf litter. *Ecology Letters*, *24*(4), 802–811. https://doi.org/10.1111/ele.13700

Gonzales, K., & Yanai, R. (2019). Nitrogen–phosphorous interactions in young northern hardwoods indicate P limitation: foliar concentrations and resorption in a factorial N by P addition experiment. *Oecologia*, *189*(3), 829–840. https://doi.org/10.1007/s00442-019-04350-y

Guerra, C. A., Heintz-Buschart, A., Sikorski, J., Chatzinotas, A., Guerrero-Ramírez, N., Cesarz, S., Beaumelle, L., Rillig, M. C., Maestre, F. T., Delgado-Baquerizo, M., Buscot, F., Overmann, J., Patoine, G., Phillips, H. R. P., Winter, M., Wubet, T., Küsel, K., Bardgett, R. D., Cameron, E. K., … Eisenhauer, N. (2020). Blind spots in global soil biodiversity and ecosystem function research. *Nature Communications*, *11*(1), 3870. https://doi.org/10.1038/s41467-020-17688-2

Güsewell, S. (2004). N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, *164*(2), 243–266. https://doi.org/10.1111/j.1469-8137.2004.01192.x

Gyenge, J., Fernández, M. E., & Schlichter, T. (2009). Effects on site water balance of conversion from native mixed forest to Douglas-fir plantation in N.W. Patagonia. *New Forests*, *38*(1), 67–80. https://doi.org/10.1007/s11056-009-9132-0

Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M. O., Jabiol, J., Makkonen, M., McKie, B. G., Malmqvist, B., Peeters, E. T. H. M., Scheu, S., Schmid, B., van

Ruijven, J., Vos, V. C. A., & Hättenschwiler, S. (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, *509*(7499), 218–221. https://doi.org/10.1038/nature13247

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E. S., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B., & Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters*, *14*(9), 852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x

Hartig, F. , & H. M. F. (2021). *Package "DHARMa". R package*.

Heneghan, L., Coleman, D. C., Zou, X., Crossley, D. A., & Haines, B. L. (1998). Soil microarthropod community structure and litter decomposition dynamics: A study of tropical and temperate sites. *Applied Soil Ecology*, *9*(1–3), 33–38. https://doi.org/10.1016/S0929-1393(98)00050-X

Hu, D., Wang, M., Zheng, Y., Lv, M., Zhu, G., Zhong, Q., & Cheng, D. (2021). Leaf litter phosphorus regulates the soil meso- and micro-faunal contribution to home-field advantage effects on litter decomposition along elevation gradients. *CATENA*, *207*, 105673. https://doi.org/10.1016/j.catena.2021.105673

Ilieva-Makulec, K., Olejniczak, I., & Szanser, M. (2006). Response of soil micro- and mesofauna to diversity and quality of plant litter. *European Journal of Soil Biology*, *42*, S244–S249. https://doi.org/10.1016/j.ejsobi.2006.07.030

Irmler, U. (2000). Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two deciduous forests. *Pedobiologia*, *44*(2), 105–118. https://doi.org/10.1078/S0031-4056(04)70032-3

Isbell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences*, *110*(29), 11911–11916. https://doi.org/10.1073/pnas.1310880110

Janssens, I. A., Dieleman, W., Luyssaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A. J., Grace, J., Matteucci, G., Papale, D., Piao, S. L., Schulze, E.-D., Tang, J., & Law, B. E. (2010). Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, *3*(5), 315–322. https://doi.org/10.1038/ngeo844

Kim, C. (2008). Soil carbon storage, litterfall and CO2 efflux in fertilized and unfertilized larch (Larix leptolepis) plantations. *Ecological Research*, *23*(4), 757–763. https://doi.org/10.1007/s11284-007-0436-2

Kitzberger, T., & Veblen, T. T. (1999). Fire-induced changes in northern Patagonian landscapes. *Landscape Ecology*, *14*(1), 1–15. https://doi.org/10.1023/A:1008069712826

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*, 259–263.

Kowaljow, E., Mazzarino, M. J., Satti, P., & Jiménez-Rodríguez, C. (2010). Organic and inorganic fertilizer effects on a degraded Patagonian rangeland. *Plant and Soil*, *332*(1–2), 135–145. https://doi.org/10.1007/s11104-009-0279-4

Kun, M. E., Martínez, P. A., & Gonzalez, A. (2010). Oribatid mites (Acari: Oribatida) from Austrocedrus chilensis and Nothofagus forests of Northwestern Patagonia (Argentina). *Zootaxa*, *2548*(1), 22. https://doi.org/10.11646/zootaxa.2548.1.2

Lenth, R. V. (2021). *emmeans: Estimated Marginal means, aka Least-Squares Means, r package version 1.6.1*.

Law 26.331.2007. Ley Nacional de Presupuestos Mínimos de Protección Ambiental de los Bosques Nativos, 31310, Boletín Oficial, December 26th, 2007, 2.

Li, X., Dong, W., Song, Y., Zhan, W., & Zheng, Y. (2021a). Soil mesofauna participating in driving home-field advantage differ between litter mass loss and nutrient release. *Applied Soil Ecology*, *163*, 103909. https://doi.org/10.1016/j.apsoil.2021.103909

Li, X., Dong, W., Song, Y., Zhan, W., & Zheng, Y. (2021b). Soil mesofauna participating in driving home-field advantage differ between litter mass loss and nutrient release. *Applied Soil Ecology*, *163*, 103909. https://doi.org/10.1016/j.apsoil.2021.103909

Lilleskov, E. A., Kuyper, T. W., Bidartondo, M. I., & Hobbie, E. A. (2019). Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: A review. *Environmental Pollution*, *246*, 148–162. https://doi.org/10.1016/j.envpol.2018.11.074

Lindberg, N., & Persson, T. (2004). Effects of long-term nutrient fertilisation and irrigation on the microarthropod community in a boreal Norway spruce stand. *Forest Ecology and Management*, *188*(1–3), 125–135. https://doi.org/10.1016/j.foreco.2003.07.012

Maaroufi, N. I., & De Long, J. R. (2020). Global Change Impacts on Forest Soils: Linkage Between Soil Biota and Carbon-Nitrogen-Phosphorus Stoichiometry. *Frontiers in Forests and Global Change*, *3*. https://doi.org/10.3389/ffgc.2020.00016

Manzo, R. M., Dadamia, M. M., & Rizzuto, S. (2021). New records of oribatid mites (Acari: Oribatida) from a Patagonian forest affected by wildfire in Argentina. *Revista Mexicana de Biodiversidad*, *92*(0), 923468. https://doi.org/10.22201/ib.20078706e.2021.92.3468

Marian, F., Sandmann, D., Krashevska, V., Maraun, M., & Scheu, S. (2018). Altitude and decomposition stage rather than litter origin structure soil microarthropod communities in tropical montane rainforests. *Soil Biology and Biochemistry*, *125*, 263–274. https://doi.org/10.1016/j.soilbio.2018.07.017

Melguizo-Ruiz, N., Jiménez-Navarro, G., De Mas, E., Pato, J., Scheu, S., Austin, A. T., Wise, D. H., & Moya-Laraño, J. (2020). Field exclusion of large soil predators impacts lower trophic levels and decreases leaf-litter decomposition in dry forests. *Journal of Animal Ecology*, *89*(2), 334–346. https://doi.org/10.1111/1365-2656.13101

Milcu, A., & Manning, P. (2011). All size classes of soil fauna and litter quality control the acceleration of litter decay in its home environment. *Oikos*, *120*(9), 1366–1370. https://doi.org/10.1111/j.1600-0706.2010.19418.x

Nacif, M. E., Kitzberger, T., & Garibaldi, L. A. (2020). Positive outcomes between herbivore diversity and tree survival: Responses to management intensity in a Patagonian forest. *Forest Ecology and Management*, *458*, 117738. https://doi.org/10.1016/j.foreco.2019.117738

Nielsen, U. N., Prior, S., Delroy, B., Walker, J. K. M., Ellsworth, D. S., & Powell, J. R. (2015). Response of belowground communities to short-term phosphorus addition in a phosphorus-limited woodland. *Plant and Soil*, *391*(1–2), 321–331. https://doi.org/10.1007/s11104-015-2432-6

Nielsen, U. N., Wall, D. H., & Six, J. (2015). Soil Biodiversity and the Environment. *Annual Review of Environment and Resources*, *40*(1), 63–90. https://doi.org/10.1146/annurev-environ-102014-021257

Palozzi, J. E., & Lindo, Z. (2018). Are leaf litter and microbes team players? Interpreting home-field advantage decomposition dynamics. *Soil Biology and Biochemistry*, *124*, 189–198. https://doi.org/10.1016/j.soilbio.2018.06.018

Parfitt, R. L., Ross, D. J., Coomes, D. A., Richardson, S. J., Smale, M. C., & Dahlgren, R. A. (2005). N and P in New Zealand Soil Chronosequences and Relationships with Foliar N and P. *Biogeochemistry*, *75*(2), 305–328. https://doi.org/10.1007/s10533-004-7790-8

Peguero, G., Folch, E., Liu, L., Ogaya, R., & Peñuelas, J. (2021). Divergent effects of drought and nitrogen deposition on microbial and arthropod soil communities in a Mediterranean forest. *European Journal of Soil Biology*, *103*, 103275. https://doi.org/10.1016/j.ejsobi.2020.103275

Peguero, G., Sardans, J., Asensio, D., Fernández-Martínez, M., Gargallo-Garriga, A., Grau, O., Llusià, J., Margalef, O., Márquez, L., Ogaya, R., Urbina, I., Courtois, E. A., Stahl, C., Van Langenhove, L., Verryckt, L. T., Richter, A., Janssens, I. A., & Peñuelas, J. (2019). Nutrient scarcity strengthens soil fauna control over leaf litter decomposition in tropical rainforests. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1910), 20191300. https://doi.org/10.1098/rspb.2019.1300

Peng, Y., Yang, W., Yue, K., Tan, B., & Wu, F. (2019). Impacts of soil fauna on nitrogen and phosphorus release during litter decomposition were differently controlled by plant species and ecosystem type. *Journal of Forestry Research*, *30*(3), 921–930. https://doi.org/10.1007/s11676-018-0664-z

Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., van der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M., & Janssens, I. A. (2013). Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature Communications*, *4*(1), 2934. https://doi.org/10.1038/ncomms3934

Perez, G., Aubert, M., Decaëns, T., Trap, J., & Chauvat, M. (2013). Home-Field Advantage: A matter of interaction between litter biochemistry and decomposer biota. *Soil Biology and Biochemistry*, *67*, 245–254. https://doi.org/10.1016/j.soilbio.2013.09.004

Petersen, H., & Luxton, M. (1982). A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. *Oikos*, *39*(3), 288. https://doi.org/10.2307/3544689

Phillips, H., Beaumelle, L., Tyndall, K., Burton, V., Cameron, E., Eisenhauer, N., & Ferlian, O. (2019). The effects of global change on soil faunal communities: a meta-analytic approach. *Research Ideas and Outcomes*, *5*. https://doi.org/10.3897/rio.5.e36427

Pichon, N. A., Cappelli, S. L., Soliveres, S., Hölzel, N., Klaus, V. H., Kleinebecker, T., & Allan, E. (2020). Decomposition disentangled: A test of the multiple mechanisms by which nitrogen enrichment alters litter decomposition. *Functional Ecology*, *34*(7), 1485–1496. https://doi.org/10.1111/1365-2435.13560

Pollierer, M. M., Langel, R., Scheu, S., & Maraun, M. (2009). Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios (15N/14N and 13C/12C). *Soil Biology and Biochemistry*, *41*(6), 1221–1226. https://doi.org/10.1016/j.soilbio.2009.03.002

Pompermaier, V. T., Campani, A. R., Dourado, E., Coletta, L. Della, Bustamante, M. M. da C., & Nardoto, G. B. (2022). Soil mesofauna drives litter decomposition under combined nitrogen and phosphorus additions in a Brazilian woodland savanna. *Austral Ecology*, *47*(1), 26–34. https://doi.org/10.1111/aec.13082

Reed, S. C., Vitousek, P. M., & Cleveland, C. C. (2011). Are patterns in nutrient limitation belowground consistent with those aboveground: results from a 4 million year chronosequence. *Biogeochemistry*, *106*(3), 323–336. https://doi.org/10.1007/s10533-010-9522-6

Reque, J. A., Sarasola, M., Gyenge, J., & Fernández, M. E. (2007). Caracterización silvícola de ñirantales del norte de la Patagonia para la gestión forestal sostenible. *Bosque (Valdivia)*, *28*(1). https://doi.org/10.4067/S0717-92002007000100006

Rizzuto, S. (2018). *Acaros de suelo en un bosque de Nothofagus pumilio afectado por el fuego, en la Provincia de Chubut*.

Rosenfield, M. V., Keller, J. K., Clausen, C., Cyphers, K., & Funk, J. L. (2020). Leaf traits can be used to predict rates of litter decomposition. *Oikos*, *129*(10), 1589–1596. https://doi.org/10.1111/oik.06470

Sardans, J., & Peñuelas, J. (2015). Potassium: a neglected nutrient in global change. *Global Ecology and Biogeography*, *24*(3), 261–275. https://doi.org/10.1111/geb.12259

Seabloom, E. W., Adler, P. B., Alberti, J., Biederman, L., Buckley, Y. M., Cadotte, M. W., Collins, S. L., Dee, L., Fay, P. A., Firn, J., Hagenah, N., Harpole, W. S., Hautier, Y., Hector, A., Hobbie, S. E., Isbell, F., Knops, J. M. H., Komatsu, K. J., Laungani, R., … Borer, E. T. (2021). Increasing effects of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time. *Ecology*, *102*(2). https://doi.org/10.1002/ecy.3218

Smith, V. C., & Bradford, M. A. (2003). Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. *Applied Soil Ecology*, *24*(2), 197–203. https://doi.org/10.1016/S0929-1393(03)00094-5

Sullivan, T. P., & Sullivan, D. S. (2018). Influence of nitrogen fertilization on abundance and diversity of plants and animals in temperate and boreal forests. *Environmental Reviews*, *26*(1), 26–42. https://doi.org/10.1139/er-2017-0026

Treseder, K. K., & Allen, M. F. (2002). Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. *New Phytologist*, *155*(3), 507–515. https://doi.org/10.1046/j.1469-8137.2002.00470.x

Veen, G. F. (Ciska), Keiser, A. D., van der Putten, W. H., & Wardle, D. A. (2018). Variation in home-field advantage and ability in leaf litter decomposition across successional gradients. *Functional Ecology*, *32*(6), 1563–1574. https://doi.org/10.1111/1365-2435.13107

Vergutz, L., Manzoni, S., Porporato, A., Novais, R. F., & Jackson, R. B. (2012). Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs*, *82*(2), 205–220. https://doi.org/10.1890/11-0416.1

Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. A. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. In *Ecological Applications* (Vol. 20, Issue 1).

Vivanco, L. (2008). *Efectos de la identidad y diversidad de especies de plantas sobre el reciclado de carbono y nutrientes en bosques templados en Patagonia, Argentina.* . Universidad Nacional de Buenos Aires.

Vivanco, L., & Austin, A. T. (2008). Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *Journal of Ecology*, *96*(4), 727–736. https://doi.org/10.1111/j.1365-2745.2008.01393.x

Vivanco, L., & Austin, A. T. (2011). Nitrogen addition stimulates forest litter decomposition and disrupts species interactions in Patagonia, Argentina. *Global Change Biology*, *17*(5), 1963–1974. https://doi.org/10.1111/j.1365-2486.2010.02344.x

Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan-Pelletier, V., Bignell, D. E., Dangerfield, J. M., Parton, W. J., Rusek, J., Voigt, W., Wolters, V., Gardel, H. Z., Ayuke, F. O., Bashford, R., Beljakova, O. I., Bohlen, P. J., Brauman, A., Flemming, S., Henschel, J. R., … Zou, X. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, *14*(11), 2661–2677. https://doi.org/10.1111/j.1365-2486.2008.01672.x

Wall, D. H., Nielsen, U. N., & Six, J. (2015). Soil biodiversity and human health. *Nature*, *528*(7580), 69–76. https://doi.org/10.1038/nature15744

Wickham, H. , C. W. , & W. M. H. (2016). *Package 'ggplot2'. Create elegant data visualisations using the grammar of graphics.* .

Yang, X., & Chen, J. (2009). Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. *Soil Biology and Biochemistry*, *41*(5), 910–918. https://doi.org/10.1016/j.soilbio.2008.12.028

Yin, R., Liu, Q., Tian, S., Potapov, A., Zhu, B., Yang, K., Li, Z., Zhuang, L., Tan, B., Zhang, L., Xu, Z., Kardol, P., Schädler, M., & Eisenhauer, N. (2022). Nitrogen deposition stimulates decomposition via changes in the structure and function of litter food webs. *Soil Biology and Biochemistry*, *166*, 108522. https://doi.org/10.1016/j.soilbio.2021.108522

Zhou, S., Butenschoen, O., Barantal, S., Handa, I. T., Makkonen, M., Vos, V., Aerts, R., Berg, M. P., McKie, B., Van Ruijven, J., Hättenschwiler, S., & Scheu, S. (2020). Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna. *Journal of Ecology*, *108*(6), 2283–2297. https://doi.org/10.1111/1365-2745.13452

Zieger, S. L., Eissfeller, V., Maraun, M., & Scheu, S. (2015). Incorporation of carbon and nitrogen from leaf litter differing in structural compounds into soil microarthropods of a deciduous forest. *Pedobiologia*, *58*(5–6), 219–227. https://doi.org/10.1016/j.pedobi.2015.10.001

Zuur, A. F. , I. E. N. , W. N. J. , S. A. A. , & S. G. M. (2009). *Mixed effects models and extensions in ecology with R : Vol. Vol. 574*. Springer.

Supplementary material. Table S1. Soil nutrient concentration (0-20 cm depth) among fertilization treatments (columns). N: nitrogen. P: phosphorus. K: potassium. E.C: Electrical conductivity in micro siemens (µS).

Soil	Control	N	P	K	NP	NK	PK	NPK
Surface (0-10 cm)								
N (%)	0.38 ± 0.09	0.37 ± 0.1	0.33 ± 0.1	0.32 ± 0.09	0.39 ± 0.11	0.38 ± 0.08	0.38 ± 0.02	0.35 ± 0.09
P Bray (mg kg^{-1})	0.55 ± 0.09	1.27 ± 0.59	1.54 ± 0.45	0.41 ± 0.2	1.67 ± 0.48	1.14 ± 0.34	1.62 ± 0.77	1.93 ± 0.9
P Olsen (mg kg^{-1})	19.11 ± 3.19	18.84 ± 3.15	32.17 ± 11.5	17.87 ± 3.99	34.9 ± 1.81	22.61 ± 8.26	25.39 ± 8.17	27.58 ± 8.2
K (meq L^{-1})	0.34 ± 0.05	0.34 ± 0.05	0.33 ± 0.08	0.63 ± 0.11	0.29 ± 0.07	0.48 ± 0.1	0.67 ± 0.11	0.57 ± 0.12
C (%)	8.28 ± 0.9	7.95 ± 0.72	7.65 ± 1.06	8.05 ± 0.91	8 ± 0.7	7.93 ± 0.8	8.1 ± 0.6	8.1 ± 0.82
pH	5.75 ± 0.1	5.52 ± 0.1	5.74 ± 0.1	5.79 ± 0.1	5.38 ± 0.2	5.63 ± 0.2	5.83 ± 0.02	5.83 ± 0.1
E.C (µS)	63.5 ± 19.4	100.16 ± 18.1	63.87 ± 18.1	79.93 ± 17.4	66.73 ± 6.2	83.77 ± 11.1	75.67 ± 8.9	103.46 ± 18.3
Subsurface (10-20 cm)								
N (%)	0.3 ± 0.08	0.25 ± 0.05	0.23 ± 0.05	0.21 ± 0.05	0.29 ± 0.07	0.3 ± 0.06	0.29 ± 0.04	0.26 ± 0.04
P Bray (mg kg^{-1})	1.1 ± 0.39	1.56 ± 0.67	1.13 ± 0.73	1.42 ± 0.62	0.7 ± 0.61	1.91 ± 1.47	1.04 ± 0.35	0.56 ± 0.45
P Olsen (mg kg^{-1})	12.15 ± 5.07	11.39 ± 3.31	17.4 ± 4.31	14.04 ± 2.46	15.46 ± 2.09	11.1 ± 2.29	15.7 ± 2.55	8.33 ± 0.94
K (meq L^{-1})	0.16 ± 0.04	0.22 ± 0.05	0.23 ± 0.05	0.32 ± 0.06	0.15 ± 0.05	0.26 ± 0.08	0.37 ± 0.07	0.33 ± 0.07
C (%)	8.75 ± 0.45	8.93 ± 0.36	7.93 ± 0.53	8.35 ± 0.45	8.87 ± 0.35	8.63 ± 0.4	9.55 ± 0.3	8.13 ± 0.41
pH	5.65 ± 0.2	5.49 ± 0.2	5.93 ± 0.1	5.79 ± 0.1	5.60 ± 0.2	5.59 ± 0.1	5.83 ± 0.06	5.84 ± 0.1
E.C (µS)	40.55 ± 7.7	71.2 ± 13.3	34.55 ± 4.7	49.58 ± 5.4	50.78 ± 8.3	58.59 ± 4.3	54.7 ± 2.5	81.61 ± 19.2

Table S2. Estimated coefficients and SE (brackets) for linear mixed-effects models assessing changes in organic matter remaining for fertilized litter and control litter decomposing in plots with nutrient addition. Intercepts were allowed to vary by block (random effect). In this table, the Intercept includes decomposing control litter in coarse mesh litter bags in plots with K addition. Bold values represent statistically significant effects from Likelihood Ratio Tests (LRT) (*** *Pr(>Chisq)* <0.001; ** < 0.01; * < 0.05). OMR: organic matter remaining. N: nitrogen. P: phosphorus. K: potassium.

Coefficients	**OMR Year 1**	**OMR Year 3**	**Coefficients**	**OMR Year 1**	**OMR Year 3**
Intercept	0.53 (0.03)	0.39 (0.05)	**Quality:P**	0.01 (0.07)	-0.02 (0.1)
Quality	-0.05 (0.04)	-0.06 (0.06)	**Quality:PK**	**0.16* (0.07)**	**-0.003**
mesh	0.04 (0.05)	0.12 (0.06)	**mesh:N**	-0.06 (0.07)	-0.15 (0.1)
N	-0.01 (0.05)	0.16 (0.06)	**mesh:NK**	-0.03 (0.07)	0.01 (0.08)
NK	0.00 (0.05)	-0.02 (0.07)	**mesh:NP**	-0.04 (0.07)	-0.12 (0.08)
NP	0.02 (0.05)	-0.02 (0.06)	**mesh:NPK**	-0.09 (0.07)	-0.14 (0.08)
NPK	0.08 (0.05)	0.05 (0.06)	**mesh:P**	0.01 (0.07)	-0.08 (0.09)
P	0.06 (0.05)	-0.01 (0.07)	**mesh:PK**	0.12 (0.07)	0.00 (0.08)
PK	-0.10 (0.05)	0.07 (0.06)	**Quality:mesh:N**	-0.04 (0.1)	0.01 (0.12)
Quality:mesh	0.08 (0.07)	0.05 (0.08)	**Quality:mesh:NK**	-0.02 (0.1)	-0.07 (0.11)
Quality:N	0.08 (0.07)	-0.03 (0.1)	**Quality:mesh:NP**	-0.07 (0.1)	0.14 (0.11)
Quality:NK	0.01 (0.07)	0.01 (0.1)	**Quality:mesh:NPK**	0.02 (0.1)	-0.01 (0.11)
Quality:NP	0.01(0.07)	-0.04 (0.1)	**Quality:mesh:P**	-0.08 (0.1)	0.01 (0.11)
Quality:NPK	-0.07 (0.07)	0.02 (0.1)	**Quality:mesh:PK**	**-0.18* (0.1)**	-0.09 (0.1)

Figure S1. Litter decay patterns for control litter decomposing in control plots. Grey points and full line correspond to fine mesh litter bags and the black points and line correspond to the coarse mesh litter bags. A Weibull model was the best for the litter bag data. Points and error bars (± 1 SE, *n*=4) are mean and standard error estimated with the *litterfitter* package (Cornwell and Weedon, 2014).

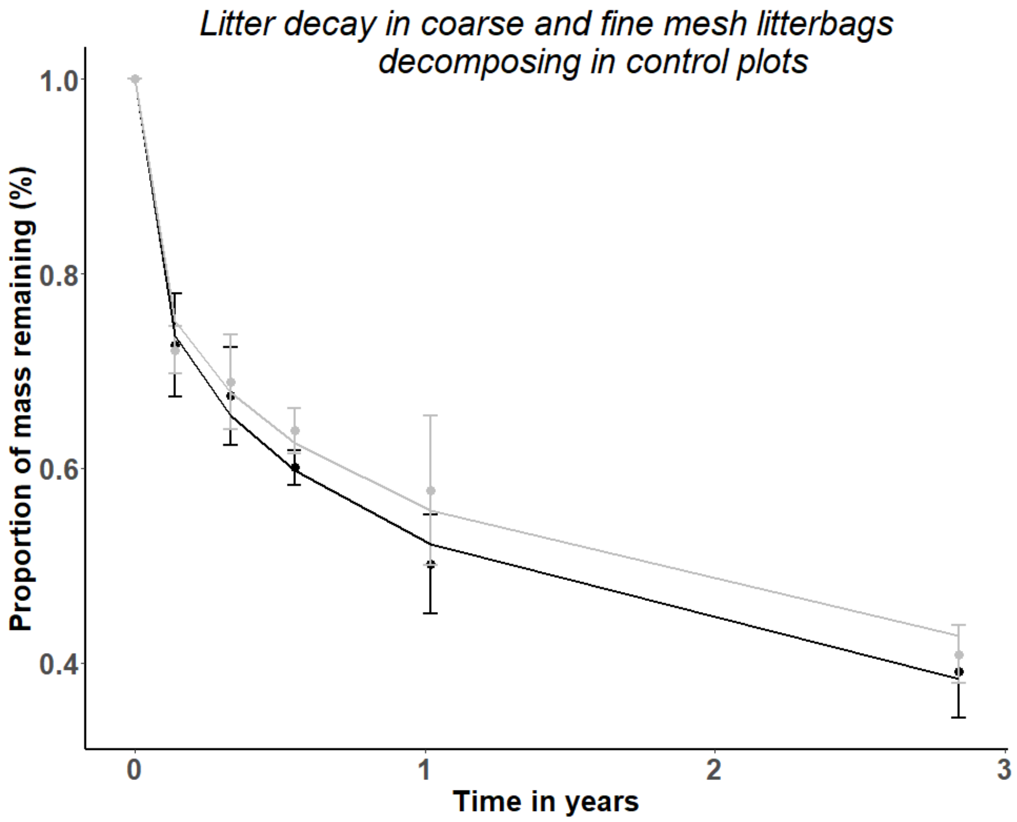

Figure S2. Correlogram showing correlations (Spearman'sSpearman's correlations) among foliar and soil nutrients. Positive correlations are displayed in green and negative correlations in pink. The circle size and intensity of the color are proportional to the correlation coefficients. N: nitrogen. P: phosphorus. K: potassium.