

## Mite density, not diversity, declines with biomass removal in Patagonian woodlands

Margarita M. Fernández<sup>a,b,c,\*</sup>, Cecilia Casas<sup>d,e</sup>, José C. Bedano<sup>f</sup>, David M. Eissenstat<sup>c</sup>, Margot W. Kaye<sup>c</sup>, Ivana M. García<sup>a,b</sup>, Marcelo E. Kun<sup>g</sup>, Lucas A. Garibaldi<sup>a,b</sup>

<sup>a</sup> Universidad Nacional de Río Negro, Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural, Río Negro, Argentina

<sup>b</sup> Consejo Nacional de Investigaciones Científicas y Técnicas, Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural, Río Negro, Argentina

<sup>c</sup> Dept. of Ecosystem Sciences and Management, The Pennsylvania State University, Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, PA 16802, USA

<sup>d</sup> IFEVA, Universidad de Buenos Aires, CONICET, Facultad de Agronomía, Av. San Martín 4453 (C1417DSE), Buenos Aires, Argentina

<sup>e</sup> Universidad de Buenos Aires, Facultad de Agronomía, Departamento de Recursos Naturales y Ambiente, Cátedra de Edafología, Av. San Martín 4453 (C1417DSE), Buenos Aires, Argentina

<sup>f</sup> Depto. de Geología / Depto. Ciencias Naturales e ICBA (UNRC-CONICET), FCFEYQY, Universidad Nacional de Río Cuarto, Córdoba, Argentina

<sup>g</sup> Laboratorio de Zoología, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Quintral 1250, Bariloche, Río Negro, Argentina

### ARTICLE INFO

#### Keywords:

Acari  
Oribatida  
Density  
 $\alpha$ -Diversity  
Biomass removal  
Woodlands

### ABSTRACT

Belowground biodiversity loss from anthropogenic causes is far less addressed and quantified than aboveground biodiversity loss. Soil fauna supports soil productivity and biogeochemical cycles, and their decline needs further research. We tested the effects of a woodland harvest gradient (0, 30, 50, and 70% biomass removal) on litterfall, mesofauna density, and Oribatida diversity in three sites of northwestern Patagonia (Argentina). Sites contrasted in plant community structure and productivity. Acari from litter and soil were compared. Annual litter production showed a 58% decline at the highest harvest intensity level, which was constant across sites. Litter structural  $\alpha$ -diversity decreased with the highest intensity harvest only at the high productivity site. The density of soil-inhabiting Acari did not change with increasing harvest intensity, while the density of Acari inhabiting the litter decreased by 65% at the highest harvest intensity. Within Acari, Oribatida inhabiting the litter had the most significant density decline with increasing harvest intensity. Oribatida richness and  $\alpha$ -diversity only differed among sites, suggesting resistance to increasing biomass removal despite shifts in litter production and litter structural diversity. Prostigmata did not respond to increasing biomass removal either in soil or litter. Our study is the first to assess Acari response to an aboveground biomass removal gradient in southern woodlands. Applying high biomass removal to low productivity sites can compromise micro detritivore density and thus, impair its functional role. Site productivity should be considered in management plans entailing conservation of soil fauna in southern woodlands.

### 1. Introduction

An improved understanding of the relationship between changes in plant communities and belowground biota dynamics post-disturbance is a challenge for sustainable forestry (Powers et al., 1999; Doran and Zeiss, 2000; Schoenholtz et al., 2000). Efforts to assess the effects of anthropogenic disturbances on aboveground diversity are abundant, but few studies examine belowground diversity (Wall et al., 2015; Cameron et al., 2019; Geisen et al., 2019). Belowground diversity is an essential

component of ecosystem function. For example, soil fauna community structure and composition strongly influence soil quality, which is the capacity of a soil to maintain or enhance water quality, air quality, and human health (Karlen et al., 1997; Bach et al., 2020). Moreover, managing plant structural diversity, horizontal complexity, and resource provision can be more relevant for predicting soil biota response to disturbance (Schuldt et al., 2019; Tomao et al., 2020). Using quantitative disturbance experiments can identify biological thresholds for belowground invertebrates. Still, to the best of our knowledge, these

\* Corresponding author at: Dept. of Ecosystem Sciences and Management, Pennsylvania State University, Forest Resources Building, University Park, State College, PA 16802, USA.

E-mail address: [mmf5814@psu.edu](mailto:mmf5814@psu.edu) (M.M. Fernández).

<https://doi.org/10.1016/j.apsoil.2021.104242>

Received 23 April 2021; Received in revised form 22 September 2021; Accepted 24 September 2021

Available online 1 October 2021

0929-1393/© 2021 Elsevier B.V. All rights reserved.

studies are scarce in forests and non-existing in woodlands outside the northern hemisphere.

Awareness of soil fauna's relevance for ecosystem functionality has increased significantly (Wall et al., 2008; Grandy et al., 2016; Soong and Nielsen, 2016; Bach et al., 2020). For instance, mesofauna are microarthropods whose body length is between 0.1 and 2 mm. They have a critical role in nutrient cycling and soil health (Lavelle et al., 2006). Oribatida is one of the main mesofauna taxa present in the soil and litter of woodlands and forests (Petersen and Luxton, 1982). They contribute to organic soil formation, nutrient mineralization, and litter decomposition in temperate areas (García-Palacios et al., 2013; Maaß et al., 2015). Detritus and leaf litter are essential for mesofauna for various reasons: they buffer microclimate fluctuations, provide habitat heterogeneity and sustain food sources (Luxton, 1972; Anderson, 1978; Johnston and Crossley, 1996; González-Polo et al., 2013). To improve sustainable ecosystem management, we must understand the relationship between mesofauna dynamics, aboveground biomass, and litter management.

Mesofauna dynamics after forest cuts have been studied in the northern hemisphere with contradictory results. For example, after 2.5 years of treatments, Acari density decline was greatest in cut corridors and areas with clear-cuts (Lindo and Visser, 2003; Battigelli et al., 2004); while over the same time period, Oribatida mite density was similar in cut and uncut plots even with high biomass removal (Rousseau et al., 2018a). In relation to recovery times, some studies found that microarthropods density recovered to uncut levels faster (Bird et al., 2004; Chauvat et al., 2009), while others found that neither Acari density nor diversity recovered even after 8–10 years from clear-cuts (Blair and Crossley, 1988; Lindo and Visser, 2004; Malmström et al., 2009; Rousseau et al., 2018b). Some studies related density declines with loss of microbial biomass and fine root biomass for detritivore groups (Lindo and Visser, 2003), while other studies highlight the role of coarse- and fine-detritus for conserving Acari density despite high biomass removal (Rousseau et al., 2018a). In contrast, predators (i.e., Mesostigmata) showed no response (Bird et al., 2004) or increased their density after harvest (Bird et al., 2004; Battigelli et al., 2004). Collectively, these results suggest that microarthropods show irregular recovery rates after disturbance (Vanbergen et al., 2007). However, the relationships among microarthropod dynamics, disturbance gradients, and aboveground plant productivity (Bengtsson et al., 1998) remains unexplored and may offer new insights on potential trajectories.

Contemporary forestry practices often negatively impact soil fauna. Clear-cut harvest and alternatives (i.e., partial cut, gap felling, stump harvest with blading, full-tree extraction) are detrimental to soil structure and soil organic matter, negatively affecting mesofauna density (Siira-Pietikäinen et al., 2001; Lindo and Visser, 2004; Malmström et al., 2009; Rousseau et al., 2018a, 2018b). Moreover, blading, stump, and forest floor removal changes plant diversity, soil cover, and detritus provision (Marshall, 2000; Battigelli et al., 2004; Lilles et al., 2018). Overall, these practices are associated with high levels of disturbance (e.g., logging, site preparation, >70% biomass removal) and often lead to a decrease in the  $\alpha$ -diversity of mesofauna (Thomas et al., 1999; Lindo and Visser, 2004; Jandl et al., 2007; Rousseau et al., 2018a). It is unclear what happens to mesofauna when the disturbance is caused by increments of one harvesting tactic, such as biomass removal in strips. Studying the response of mesofauna to a disturbance gradient should improve our understanding of the quantitative relationship between harvest intensity, resource provision for mesofauna (litterfall), and their tolerance threshold to aboveground harvesting in woodlands.

The impacts of biomass removal on leaf litter supply affect mesofauna in litter directly compared to those in the soil (Donegan et al., 2001; Hättenschwiler et al., 2005; Nielsen et al., 2010; Mori et al., 2015). Litter and debris increase mesofauna diversity because they create microhabitat heterogeneity in organic layers (Déchéne and Buddle, 2010; González-Polo et al., 2013). Opening the canopy with clear-cut harvest practices increases exposure to drought and heat,

which may negatively affect mesofauna density in the forest floor (Siira-Pietikäinen et al., 2001; Lindo and Visser, 2004). Yet, plant productivity could play a significant role in regulating the response of organisms in partially harvested sites. Litter production often increases with canopy openings; therefore, the diversity of mesofauna in medium and high productivity sites with low and intermediate disturbance intensity could increase (Huston, 2014). In Patagonia, strip-harvest biomass removal could compromise sustainable firewood provision and conservation of mesofauna in woodlands (Goldenberg et al., 2020). Still, there is no quantification of litter provision changes and the associated response of mesofauna along a biomass removal gradient in southern woodlands.

In Patagonia, woodlands support the region's highest biodiversity, providing residents with environmental and economic goods (Speziale and Ezcurra, 2011). Yet, because woodlands have low timber productivity, they are usually overexploited for firewood, replaced by exotic tree timber production, or degraded with crop and cattle production (Rusch et al., 2017). Local forestry policies require woodlands to be managed with sustainable plans ensuring multiple ecosystem services provision (sensu Law 26.331, 2007). Systematic strip harvesting is a promising option for firewood production, species enrichment, and many other ecosystem services in Patagonian woodlands (i.e., pollination, biodiversity) (Goldenberg et al., 2018; Coulin et al., 2019; Grossfeld et al., 2019; Agüero et al., 2020; Carrón et al., 2020; Chillo et al., 2020; Nacif et al., 2020). Soil mesofauna dynamics have been studied after fire disturbance (Rizzuto, 2018), but biomass removal impacts remain unexplored. In this work, we use mesofauna to understand the potential effects of biomass removal on belowground fauna.

Greater litter production after partial biomass removal could increase mesofauna density, microsite heterogeneity, and microhabitat availability contributing to oribatid diversity (Anderson, 1978). Since harvest can decrease plant competition and stimulate plant growth by increasing abiotic resources (i.e., water, light, nutrients), we believe that litter production and resource provision for mesofauna may increase at low disturbance (30% biomass removal). This outcome could vary according to site productivity in different landscape positions. Site productivity regulates plant growth after disturbance through differential nutrient and water availability. But also, site productivity may regulate understory plant diversity dynamics, which finally determines detritivores and predatory mesofauna taxa density (i.e., Oribatida, Mesostigmata) (Karg, 1993; Scherber et al., 2010; Chillo et al., 2020).

We present results from an aboveground biomass removal gradient in three contrasting woodlands in northwestern Patagonia (Argentina). We aimed to (1) explore the effects of increased biomass removal on Acari communities in litter and soil and (2) assess how litter production and its structural composition could be linked to mesofauna responses in sites with contrasting productivity. We hypothesize that: 1) litter production will respond positively to low harvest intensity because limited tree removal often stimulates primary productivity. High-intensity biomass removal lowers plant density enough to decrease litter production; 2) mesofauna density declines more in litter than soil with biomass removal because litter is directly exposed to changing abiotic conditions from canopy openings; 3) similar to litter production, in high productivity sites, mesofauna density will respond positively to low harvest intensity due to higher substrate availability. Mesofauna density will decline at medium and high-intensity biomass removal due to extreme forest-floor exposure, and 4) Oribatida richness and  $\alpha$ -diversity will respond positively to increasing harvest intensity in sites with higher plant productivity. In low productivity sites, increasing harvest intensity will decrease Oribatida richness and  $\alpha$ -diversity.

## 2. Materials and methods

### 2.1. Study site

This study was carried out near “El Foyel” (S 41° 38' 47", W 71° 29' 55") and “Los Repollos” (S 41° 46' 32", W 71° 28' 18"), Río Negro, in

northwestern Patagonia. The study region is a temperate forest/steppe ecotone with broadleaf woodlands dominated by *Nothofagus antarctica* ((G. Forst.) Oerst.). Climate is temperate-cold, with mean annual temperature ranging from 8 °C to 10 °C and rainfall concentrated during the winter (Gallopín, 1978; Reque et al., 2007, Table 1).

We selected three study sites that encompass the environmental and landscape heterogeneity of woodlands in NW Patagonia. In this region, the position on the landscape regulates nutrient availability, soil depth, and plant community structure (Table 1, Chauchard et al., 2015; Carrón et al., 2020). All these factors determine site quality and, therefore, plant productivity. We used mean annual increment (MAI,  $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ ) and basal area increment (BAI:  $\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$ ) as indicators of woody biomass productivity for the sites (Table 1, Goldenberg et al., 2020). The “High productivity” site is a mixed species woodland with a dominant tree height of about 4 m, located on a south-facing hillside in Foyel. Woody species found at this site are: *N. antarctica*, *Diostea juncea* ((Gillies & Hook.) Miers), *Schinus patagonicus* (Phil.) I.M. Johnst. ex Cabrera, *Lomatia hirsuta* (Lam.) Diels, and *Embothrium coccineum* (J.R. Forst. & G. Forst) (Fig. 1A). The “Mid-productivity” site is a mid-tall (3 m) mixed woodland located on a north-facing hillside in “El Foyel” (Fig. 1A). Dominant woody species are *N. antarctica*, *S. patagonicus*, *L. hirsuta*, *Fabiana imbricata* (Ruiz & Pav.), and *E. coccineum*. The “Low productivity” site is a monospecific woodland dominated by *N. antarctica* and located on a valley floor nearby the locality of “Los Repollos.” At the “Low productivity” site, all trees are no taller than 2.5 m in height (Fig. 1A). Sites are structurally different, with higher productivity and higher plant taxonomic and functional diversity in the high productivity site (Coulin et al., 2019; Chillo et al., 2020).

## 2.2. Experimental design

We quantified biomass removal using harvest intensity (HI) defined as the percent of basal area removed. Variation in HI was achieved by longitudinal harvesting strips of vegetation (strip-cutting) in plots of 1417.5  $\text{m}^2$  (31.5 × 45 m; Fig. 1B). All plots were harvested in strips of increasing width (1.5; 2.5 and 3.5 m), resulting in approximately 30%, 50%, and 70% of basal area removal, respectively (Fig. 1C). Within each strip, the vegetation was cut at ground level; woody debris was left as mulch, and coarse wood (> 4 cm diameter) was piled at the head of each strip (Fig. 1B). In the 0% HI plots (i.e., control) vegetation was left uncut. The experiment had four levels of harvest intensity of 0%, 30%, 50%, and 70%, with two replicates of each harvest treatment at each site (three sites, total = 24 plots).

**Table 1**

Sites characterization. \*MAI: Mean annual increment. \*G: Basal area. \*dg: Quadratic mean diameter. \*H: dominant height. \*T min: minimum annual average temperature. \*T max: maximum annual average temperature. \*P: mean annual precipitation. \*Soil temperature: mean temperature (March 2017). \*VWC: mean volumetric water content (March 2017). \*Solar rad: Mean annual solar radiation. Dasonomic data taken from Goldenberg et al. (2020).

Site	High productivity	Mid productivity	Low productivity
Slope orientation	South hillside	North hillside	–
Geographic position	Low hillside	Low hillside	Bottom valley
Soil depth (cm)	125	55	90
Soil taxonomy	Hapludands	Hapludands	Udivitrands
MAI ( $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$ )	3.6 ± 0.3	1.8 ± 0.3	0.4 ± 0.3
G ( $\text{m}^2 \text{ha}^{-1}$ )	46.7	34.8	23.52
T min (°C)	3	2	1.5
T max (°C)	15	14	15
P (mm)	1100	1100	1100
Solar rad ( $\text{W m}^{-2}$ )	155	165	170
Soil T (°C)	9.8	11.9	5.8
VWC (%)	75	54	89
Wind speed ( $\text{km h}^{-1}$ )	1.1	7.2	6.2

## 2.3. Annual litter production and litter structural diversity

The annual litter production was calculated as the sum of monthly litter production expressed as dry weight ( $\text{Mg ha}^{-1} \text{year}^{-1}$ ). Litter production was estimated using 0.25  $\text{m}^2$  square litter collectors ( $n = 20$  per plot) installed in a 5 × 4 m grid from the plot center. The collectors were constructed using 1-mm mesh, and four galvanized wire legs at 20 cm from the ground, which allowed for airflow and prevented damage from excessive moisture and microorganisms (Swift et al., 1979). Monthly litterfall collection was conducted from March 2017 to March 2018, except during the winter months (May to August). Once collected, samples were preserved in paper bags and transported to the laboratory, where they were oven-dried at 65 °C for 48 h and dry weight measured. Litter was classified into structural components: leaves, branches ≥ 2 cm in diameter, branches < 2 cm in diameter, reproductive material (flowers, seeds), and bark. With each element's proportion, a Shannon-Wiener Index for litter structural components was calculated for each plot (De Paz et al., 2013). We report mean (± standard error) for both litter variables.

## 2.4. Acari density

All three sites were sampled twice, in the autumns of one and three years after harvest (2015 and 2017). Samples from litter and soil were obtained from 5 random points per plot using a PVC corer (5 cm diameter, 10 cm depth). Mesofauna was extracted with Berlese-Tullgren funnels and preserved in 70% ethanol solution until sorting into taxa using a stereomicroscope. Acari were counted and sorted into suborders Oribatida, Prostigmata and Order Mesostigmata (Krantz and Walter, 2009). We calculated taxa density by pooling the five subsamples per plot (individuals  $\text{m}^{-2}$ ).

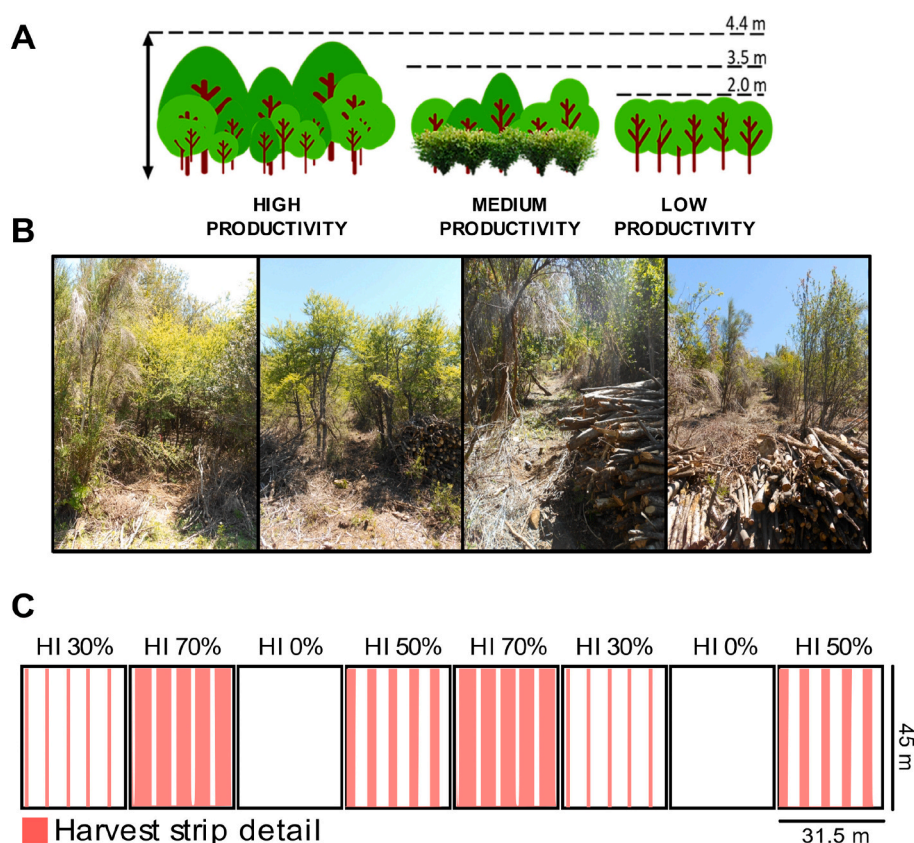
## 2.5. Oribatida morphospecies

For taxonomic analysis, oribatid mites sampled in 2017 were used. All adult individuals were cleared in 80% lactic acid solution, mounted in Hoyer's medium, and identified using a contrast phase microscope Leica DM1000 (800 × magnification). All individuals were identified to the morphospecies level (when possible) using keys by Balogh and Balogh (1992) and named following the nomenclature by Subías (2004, 15<sup>th</sup> update 2020). We used litter samples for taxonomic analysis. We then calculated species richness and  $\alpha$ -diversity (Shannon-Wiener Index) and used these indices to characterize oribatid mites' community structure and composition (Magurran, 2004).

## 2.6. Statistical analysis

All statistical analyses were done in R software (v.3.5.0, R Core Team, 2018). We used mixed-effects models to assess biomass removal influence on annual litter production, litter structural  $\alpha$ -diversity, mesofauna taxa density, oribatid mite richness, and  $\alpha$ -diversity. Mixed-effects models consider the hierarchical structure of the data combining fixed and random effects (Zuur et al., 2009; Seoane, 2014). We used multimodel inference as the inferential statistical framework (Burnham et al., 2011). We selected the minimum adequate model by the lowest AIC value (corrected form of the Akaike Information Criteria) using the dredge function (*MuMIn* package, Burnham et al., 2011). We calculated the relative importance (R.I.) of each predictor variable with the importance function (*MuMIn* package, Burnham et al., 2011). This function sums the ‘Akaike weights’ over all the models that include the predictor variable.

We assessed the influence of biomass removal on annual litter production and litter structural  $\alpha$ -diversity using the *lme4* package (Bates et al., 2015). The global mixed-effects model (GM) for annual litter production and litter structural  $\alpha$ -diversity considered the fixed effect of biomass removal (HI: 0, 30, 50, 70%), biomass removal squared (for



**Fig. 1.** Experimental design and detail of the treatment assignment per-block (site). A: Detail of the width on harvest strips by treatment in the high productivity site. HI is harvest intensity. Harvest strips are detailed in pink. B: Front view of harvest strip width in plots with different harvest intensity assignments on the high productivity site. From left to right: 0, 30, 50 and 70% HI. \*Photograph credits: Marcos Nacif. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

possible nonlinear responses), site (Low Productivity, Mid-Productivity, High Productivity), and their two-way interactions. In both models, we evaluated the random effect of plots. We assumed a normal distribution for both response variables and tested normality assumptions using graphical (i.e., residuals vs. fitted plots, residuals vs. predictors, Q-Q plot) and analytical methods (i.e., Shapiro-Wilk test). We corrected the heteroscedasticity with `varIdent` or `varExp` functions when needed (Zuur et al., 2009).

We analyzed the effects of increased biomass removal on Acari (total and each Suborder separately) density using a mixed-effects model per strata (i.e., soil, litter) (`glmmTMB` package, Brooks et al., 2017). The GM for density considered the fixed effect of biomass removal (HI: 0, 30, 50, 70%), biomass removal squared (for possible nonlinear responses), site (Low Productivity, Mid-Productivity, High Productivity), and their interactions for each strata (i.e., soil, litter). In the same models, we also evaluated the random effect of plots. We considered the date as relevant to detect lag effects from biomass removal on mesofauna taxa. Negative binomial error distribution and log link function were used according to the residual distribution of the density data.

We initially calculated Oribatida species richness and  $\alpha$ -diversity (exponential Shannon-Wiener Index) with different `vegan` package' functions (Oksanen et al., 2018). Oribatida richness was transformed as  $\log(\text{richness} + 1)$  to meet normality and homoscedasticity assumptions. We tested model assumptions using graphical (i.e., residuals vs. fitted plots, residuals vs. predictors, Q-Q plot) and analytical methods (i.e., Shapiro-Wilk test), correcting the heteroscedasticity with `varIdent` or `varExp` functions when needed (Zuur et al., 2009). We assessed biomass removal influence on the oribatid mite' richness and  $\alpha$ -diversity using the `lme4` package (Bates et al., 2015). The GM for richness and  $\alpha$ -diversity considered the fixed effect of harvest intensity (HI: 0, 30, 50, 70%), harvest intensity squared (for possible nonlinear responses), site, and their two-way interactions. In both models, we evaluated the random effect of plots.

We performed a non-metric multidimensional scaling analysis (NMDS) using the `metaMDS` function for visualizing the Oribatida community structure between sites and harvest intensity treatments (`vegan` package, Oksanen et al., 2018). NMDS was based on Bray Curtis dissimilarity, and both site and species scores were estimated using 999 free permutations. We assessed the differences in composition between sites and harvest intensity treatments using the `adonis` function (`vegan` package, Oksanen et al., 2018).

### 3. Results

#### 3.1. Response of annual litter production to harvest intensity gradient

Annual litter production responded negatively and nonlinearly to, with increasing harvest intensity across sites (Tables 2 and 3). Annual average litter production in the uncut plots varied from 1.38 ( $\pm$ ) 0.08 Mg ha<sup>-1</sup> year<sup>-1</sup> in the low productivity site to 1.42 ( $\pm$ ) 0.41 Mg ha<sup>-1</sup>

**Table 2**

Relative importance of each predictor from the global model for litter production (litter P), structural diversity (litter D), Oribatida richness and diversity. Relative importance values are calculated from the sum of the "Akaike weights" overall models, including the predictor variable. Bold relative importance values are variables or variable interactions included in the averaged minimum adequate model. Rows show: HI: harvesting intensity. HI<sup>2</sup>: harvesting intensity (nonlinear effect). Richness: Oribatida richness.  $\alpha$ -Diversity: Oribatida diversity (Shannon-Wiener Index).

Parameters	Litter P	Litter D	Richness	$\alpha$ -Diversity
HI	<b>0.91</b>	0.18	<0.05	<0.05
Site	0.14	<b>1.00</b>	<0.05	<0.05
HI: Site	<0.05	0.10	<0.05	<0.05
HI <sup>2</sup>	<b>0.91</b>	<b>0.89</b>	<0.05	<0.05
HI <sup>2</sup> : Site	<0.05	<b>0.85</b>	<0.05	<0.05

**Table 3**

Estimated fixed-effect coefficients of the minimum adequate model. Rows show: Date: 2015, 2017. Sites: High P, Mid P, Low P. HI: harvesting intensity. Columns show: Litter P: Annual litter production. Litter D: Litter  $\alpha$ -Diversity (Shannon-Wiener Index). Richness: Oribatida richness.  $\alpha$ -Diversity: Oribatida diversity (Shannon-Wiener Index).

Coefficients	Acari (Litter)	Oribatida (Litter)	Litter P	Litter D	Richness	$\alpha$ -Diversity
(Intercept)	7.79	8.84	1.34	0.91	n.s	n.s
Date	0.23	0.72	–	–	n.s	n.s
HI	0.79	–0.02	–0.0025	0.00025	n.s	n.s
HI <sup>2</sup>	n.s	n.s	–0.000072	–0.00002	n.s	n.s
Mid P	0.56	0.12	–	0.13	n.s	n.s
Low P	0.52	0.35	–	0.11	n.s	n.s
HI: High P	1.79	0.71	–	–	n.s	n.s
HI: Low P	–1.72	–4.18	–	–	n.s	n.s
HI <sup>2</sup> : High P	n.s	n.s	–	–0.00004	n.s	n.s
HI <sup>2</sup> : Low P	n.s	n.s	–	0.00003	n.s	n.s

Non significant parameters denoted as n.s.

year<sup>-1</sup> in the high productivity site (0% HI, Table 4). Litter production decreased by 58% at the 70% HI level compared to the uncut plots (0% HI, Fig. 2A).

Litter structural diversity had a nonlinear relationship with harvest intensity that differed among sites (Tables 2 and 3). The “High productivity” site showed a 54% decrease in litter structural  $\alpha$ -diversity at the highest intensity harvest compared to the uncut plot, mainly driven by a lower proportion of woody components (Fig. 2B; Fig. S1). The other sites showed stability of litter components across biomass removal treatments.

### 3.2. Acari density

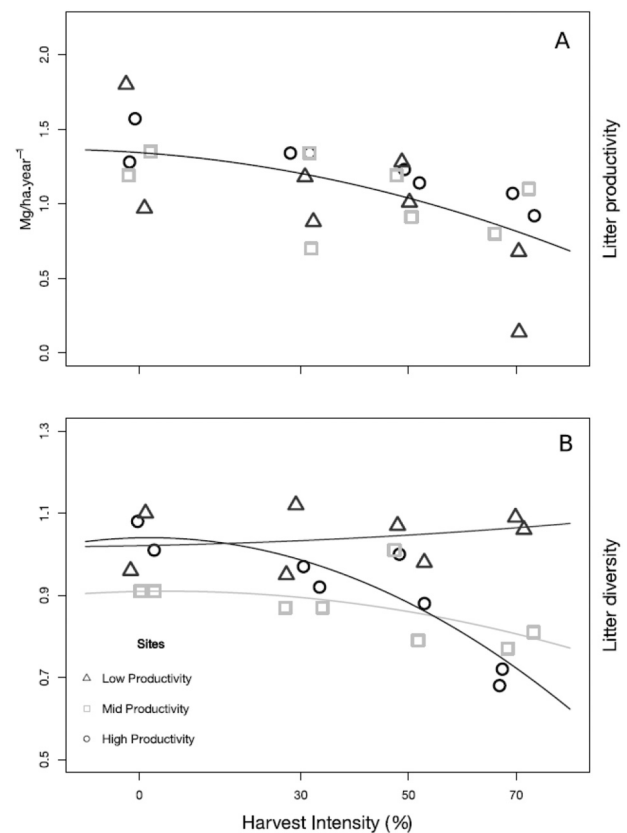
We collected a total of 3935 Acari combining one- and three-year post-harvest sampling. Pooling litter and soil, the density of Acari was approximately 32,504 (individuals m<sup>-2</sup>) at the uncut plots (Table S2). One year after harvest, Acari included 52.9% Oribatida, 29.3% Prostigmata, and 17.7% Mesostigmata. Three years after the harvest, Acari included 61% Oribatida, 21.3% Prostigmata, and 19.8% Mesostigmata.

In the litter, Acari density response to biomass removal was linear but variable among sites. Important predictors for Acari density in the litter were: the number of years after harvest (date) and the interaction between site and harvest intensity (Tables 3 and 5). In the “Low productivity” site, there was a negative relationship between density and harvest intensity that persisted three years after harvest (Fig. 3). At this

**Table 4**

Mean annual litter production (Litter P in Mg ha<sup>-1</sup> year<sup>-1</sup>), mean litter structural  $\alpha$ -diversity (Litter D), and oribatid diversity (H', both Shannon-Wiener index) ( $\pm$  standard error) per site and harvest treatment. Rows show: Litter P: Annual litter production (Mg ha<sup>-1</sup> year<sup>-1</sup>). Litter D: Litter structural  $\alpha$ -diversity (Shannon-Wiener index). H': oribatid  $\alpha$ -diversity (Shannon-Wiener Index).

Site		Harvest intensity (%)			
		0	30	50	70
Litter P	Mid Productivity	1.26 ( $\pm$ )	1.02 ( $\pm$ )	1.05 ( $\pm$ )	0.95 ( $\pm$ )
	High Productivity	0.1	0.3	0.1	0.1
	Low Productivity	1.42 ( $\pm$ )	1.34 ( $\pm$ )	1.18 ( $\pm$ )	0.99 ( $\pm$ )
	Productivity	0.1	0.0	0.1	0.1
Litter D	Mid Productivity	1.38 ( $\pm$ )	1.03 ( $\pm$ )	1.15 ( $\pm$ )	0.41 ( $\pm$ )
	High Productivity	0.4	0.1	0.1	0.3
	Low Productivity	0.91 ( $\pm$ )	0.87 ( $\pm$ )	0.89 ( $\pm$ )	0.79 ( $\pm$ )
	Productivity	0.0	0.0	0.1	0.0
H'	Mid Productivity	1.05 ( $\pm$ )	0.95 ( $\pm$ )	0.94 ( $\pm$ )	0.69 ( $\pm$ )
	High Productivity	0.05	0.0	0.1	0.0
	Low Productivity	1.03 ( $\pm$ )	1.03 ( $\pm$ )	1.03 ( $\pm$ )	1.08 ( $\pm$ )
	Productivity	0.1	0.1	0.1	0.0
Litter P	Mid Productivity	1.01 ( $\pm$ )	1.35 ( $\pm$ )	1.61 ( $\pm$ )	0.9 ( $\pm$ )
	High Productivity	1.0	0.7	0.3	0.9
	Low Productivity	1.3 ( $\pm$ )	1.9 ( $\pm$ )	1.12 ( $\pm$ )	0.6 ( $\pm$ )
	Productivity	0.03	0.1	0.2	0.6
Litter D	Mid Productivity	0.36 ( $\pm$ )	0.29 ( $\pm$ )	1.17 ( $\pm$ )	1.51 ( $\pm$ )
	Productivity	0.01	0.3	0.4	0.3



**Fig. 2.** Response of annual litter production (Mg ha<sup>-1</sup> year<sup>-1</sup>, A) and litter structural  $\alpha$ -diversity (B) to harvest intensity. Each point is the estimated litter production and structural diversity per plot ( $n = 5$  sub replicates). Lines are the predicted values from mixed-effects models. Sites: High productivity in circles, Mid productivity in squares, Low productivity in triangles.

site, we observed a 65% decline in Acari density in the litter, with the lower density overall after three years of biomass removal by harvest (Fig. 3, Table S1). In contrast, the relationship between the density of Acari and increasing biomass removal by harvest was positive on the mid- and high-productivity sites. Finally, there was no relationship between density and the predictors for soil inhabiting Acari (Table 5).

The density of Oribatida exhibited a linear relationship with harvest intensity in the litter, with shifting patterns depending on the sites (Fig. 3). The density of Oribatida in the “Low productivity” site presented a negative linear relationship with increasing biomass removal. In contrast, it had a weak positive relationship in the other sites (Tables 3 and 5). After one year, Mesostigmata in litter responded positively to increasing biomass removal in a pattern that varied among sites

**Table 5**

Relative importance of each predictor for Acari density in litter and soil. Relative importance values are calculated from the sum of the “Akaike weights” overall models, including the predictor variable. Relative importance values in bold are variables or variable interactions included in the averaged minimum adequate model. \*HI: harvesting intensity. HI<sup>2</sup>: harvesting intensity (nonlinear effect).

Coefficients	Litter			
	Acari	Oribatida	Mesostigmata	Prostigmata
Date	<b>1.00</b>	<b>0.99</b>	<b>0.99</b>	<b>0.95</b>
HI	<b>0.95</b>	<b>0.90</b>	<b>0.97</b>	0.55
Site	<b>0.91</b>	<b>0.70</b>	<b>0.77</b>	0.34
HI: Site	<b>0.76</b>	0.65	< 0.05	0.25
HI <sup>2</sup>	0.23	0.26	0.20	0.16
Date: HI	0.22	0.20	0.96	0.11
Date: Site	0.08	0.12	0.72	0.11
Date: HI <sup>2</sup>	< 0.05	< 0.05	< 0.05	< 0.05
HI <sup>2</sup> : Site	< 0.05	< 0.05	< 0.05	< 0.05
Date: HI: Site	< 0.05	< 0.05	< 0.05	< 0.05
Date: HI <sup>2</sup> : Site	< 0.05	< 0.05	< 0.05	< 0.05

Coefficients	Soil			
	Acari	Oribatida	Mesostigmata	Prostigmata
Date	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>	<b>0.93</b>
HI	0.40	0.28	0.28	0.43
Site	0.12	0.08	0.23	0.08
HI: Site	< 0.05	< 0.05	< 0.05	< 0.05
HI <sup>2</sup>	0.41	0.52	0.96	0.26
Date: HI	0.08	0.09	< 0.05	0.09
Date: Site	< 0.05	< 0.05	< 0.05	0.05
Date: HI <sup>2</sup>	0.22	0.36	0.95	< 0.05
HI <sup>2</sup> : Site	< 0.05	< 0.05	< 0.05	< 0.05
Date: HI: Site	< 0.05	< 0.05	< 0.05	< 0.05
Date: HI <sup>2</sup> : Site	< 0.05	< 0.05	< 0.05	< 0.05

(Fig. S2). Mesostigmata response was different between years in the soil but was constant across sites (Table 5). After three years from harvest, Mesostigmata showed a nonlinear negative relationship with increasing biomass removal. Prostigmata was not affected by increasing biomass

removal in soil or litter (Table 5).

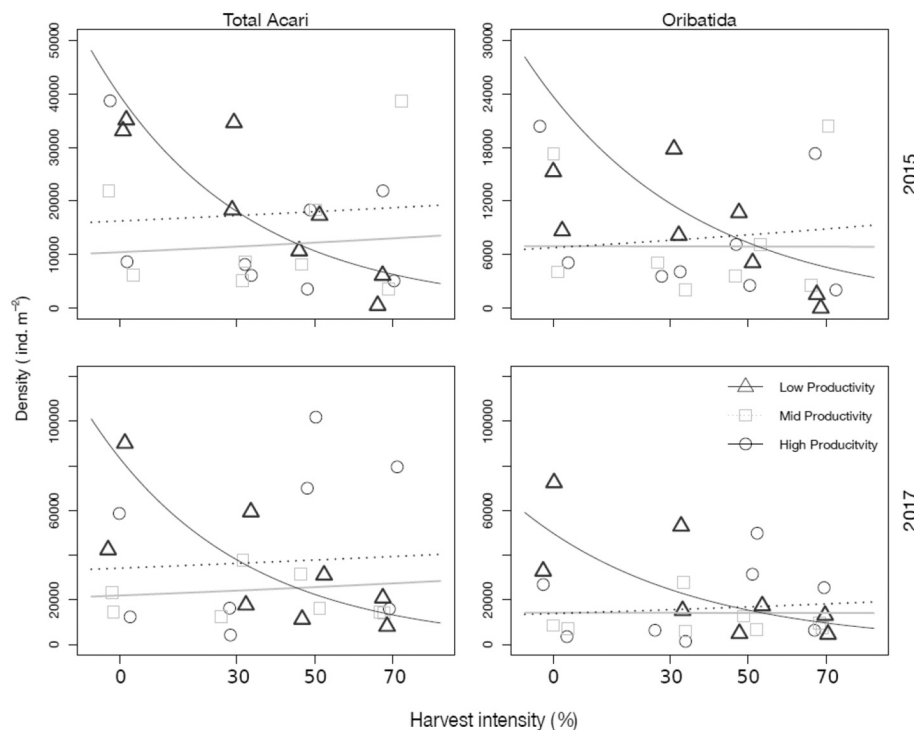
### 3.3. Oribatida richness, $\alpha$ -diversity, and community composition

We collected 1344 individuals from 24 morphospecies of oribatid mites and 17 different Oribatida families (Table S1). Of those individuals, 574 were adults that were used for taxonomic identification. The most common oribatid mite species ( $\geq 5\%$ ) 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) and *Lanceoppia kovacs* (Balogh & Csiszár, 1963) were among the most abundant morphospecies in the high productivity site. *Camisia* sp. was the most abundant Oribatida in the mid-productivity site. *P. australis* and *Oribatula* sp. comprised over 85% of the individuals found in the “Low productivity” site.

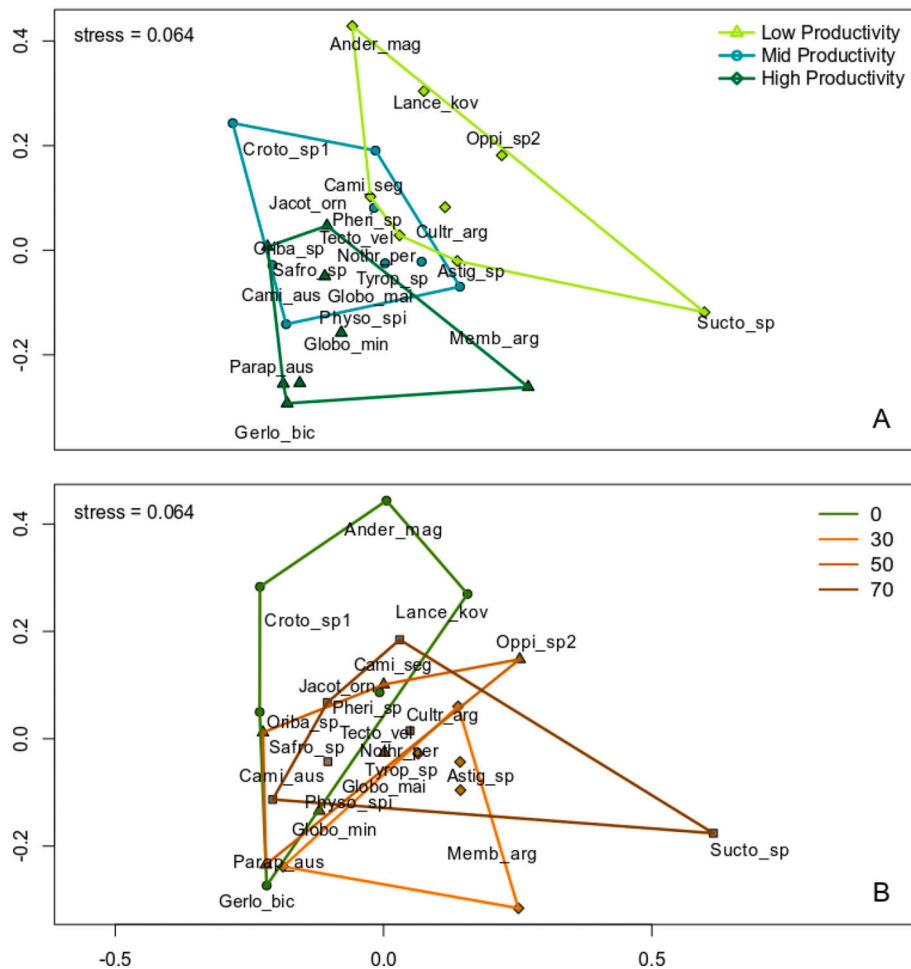
Oribatida richness and  $\alpha$ -diversity were not affected by increasing biomass removal, site, or their interaction (Table 2). Overall, the richness of oribatid mites was highest at the “Low productivity” site (21 species) and lowest at the Mid-productivity site (16 species). The assumption of homogeneity of multivariate dispersion was met for both ordinations (Fig. 4A,  $p = 0.34$ ; Fig. 4B,  $p = 0.70$ ). There was a gradient of dissimilarity in composition from the more productive site, the intermediate productivity site, and the less productive site. The “High productivity” site was significantly different in composition from the “Low productivity” site (Fig. 4A, adonis test:  $p = 0.015^*$ ). Important drivers of species compositional differences between sites were: *P. australis*, *Camisia* sp., and *Suctobelbella* sp. (Adonis test,  $p = 0.05^*$ ). The lack of differences in the oribatid mite community composition between the different harvest intensity treatments suggests that oribatid mites were resistant to increasing biomass removal (Fig. 4B, adonis test:  $p > 0.05$ ).

## 4. Discussion

We designed a systematic strip-harvest gradient to assess how controlled biomass removal impacts resource provision (litterfall) and



**Fig. 3.** Response of total Acari and oribatid mites density to harvest intensity in the litter. Each point is the pooled density per plot ( $n = 5$  sub replicates), and lines are the predicted values from mixed-effect models. Sites: High productivity in circles, Mid productivity in squares, Low productivity in triangles.



**Fig. 4.** Non-metric multidimensional scaling plot showing species composition per site (A) and per harvest intensity treatment (B) using Bray-Curtis dissimilarity as parameters. Significant differences in Oribatid community composition were detected between sites (adonis test:  $p = 0.015^{**}$ ). Codes for scientific names for Oribatida are detailed in Table S1.

microarthropods communities of three contrasting temperate woodlands in northwest Patagonia. A coarse taxonomic resolution was sufficient to detect changes in this community of micro invertebrates. Our results suggest that a combination of altered microhabitat and resource provision can condition Acari densities after high-intensity harvest. However, despite substantial variation in aboveground productivity across sites, Oribatida diversity exhibited similar resistance to biomass removal. Thus, site-specific responses of Acari taxa and plant community productivity should be considered when planning harvest systems with conservation goals.

Contrary to our expectation, we observed a negative impact of harvest intensity on litter provision with only site-specific changes on litter structural diversity, thus, rejecting our first hypothesis. The magnitude of litter production decline observed with biomass removal was similar to what Bahamonde et al. (2015) found between *N. antarctica* untreated and harvested forests (50% basal area removal). Lindo and Visser (2003) also quantified a similar decrease in litterfall when comparing uncut forests and partial cuts in mixed boreal forests 2.5 years after harvest. According to the Connector-Habitat Hypothesis, litter layer thickness and diversity of structural components build high microscale heterogeneity, promoting high Oribatida diversity (Aoki, 1977; Anderson, 1978; Wehner et al., 2016; Korboulesky et al., 2016). In this sense, the strong decline in litter structural diversity in sites with 70% biomass removal could be of concern because of the significant loss of woody structures. Interestingly, while we did not find a similar pattern between litter structural diversity decline or litter production decline with Oribatida

diversity.

Biomass removal impacted litter Acari more than soil Acari, confirming our second hypothesis. This differential vulnerability to biotic homogenization was reported by other authors (Siira-Pietikäinen and Haimi, 2009; Mori et al., 2015; Rousseau et al., 2019). In the “Low productivity” site, Acari-inhabiting litter experienced a 65% decline in density, in contrast to the stable response of Acari at mid- and high-productivity sites. Moreover, this decline in density matched annual litter production along the biomass-removal gradient at “Low productivity” sites which partially confirmed our third hypothesis. We expected that low biomass removal (30%) would increase overall plant growth and litterfall provision in mid- and high-productivity sites, but there was not an observable compensatory plant growth that counter-backed the elimination of vegetation in the short term (Lindo and Visser, 2004). In this sense, only detritivore taxa (i.e., Oribatida) were negatively affected by medium and high-intensity biomass removal, highlighting the relevance of litterfall as a resource for oribatids inhabiting litter.

Differential responses of Acari taxa to increasing biomass removal across sites could be due to shifts in understory microhabitats and litter provision. At high productivity sites for instance, mesostigmatid density in litter increased with increasing biomass removal (Fig. S2). This increase could be related to greater prey availability (e.g., Collembola) (Karg, 1993; Battigelli et al., 2004; Berch et al., 2007; Fernández et al., unpubl. data) or increased habitat quality from greater understory vegetation (Marshall, 2000; Chillo et al., 2020). Mesostigmatid density is usually positively related to understory plant richness and functional

diversity (Scherber et al., 2010; Chillo et al., 2020), which increased significantly in the mid- and high-productivity sites following disturbance. In contrast, detritivore taxa density (e.g., Oribatida) exhibited steep declines with high-intensity biomass removal (70%) (Déchéne and Buddle, 2009; Farská et al., 2014), while other Suborders remained similar to uncut woodland (Lindo and Visser, 2004). These contrasting responses among different mesofauna taxa reflect the complex interactions that can occur along biomass removal gradients of varying site productivity.

Contrary to our fourth hypothesis, we found that Oribatida richness,  $\alpha$ -diversity, and composition did not change with increasing biomass removal. The degree of soil disturbance may be key to understanding contrasting results in the literature. Our diversity results are in line with hand-felling in boreal forests (Bird et al., 2004), which also minimally affected the soil. In contrast, many studies that disturbed the soil using high-intensity harvest methods showed considerable decline in mesofauna density and diversity (Bird and Chatarpaul, 1986; Lindo and Visser, 2004; Déchéne and Buddle, 2009; Malmström et al., 2009; Rousseau et al., 2018a, 2018b). In these areas, harvesting practices causing soil compaction (Battigelli et al. 2004; Berch et al., 2007), in combination with blading, litter compositional changes, loss of woody debris, or removal of the organic material from the forest floor (Battigelli et al., 2004; Mori et al., 2015; Farská et al., 2014; Rousseau et al., 2018a, 2018b; Trentini et al., 2018) could be related to such drastic and long-term changes. In relation to this, we suspect that minimum disturbance to the soil from our strip-harvesting operations was a key factor (Chillo et al., 2020). Preserving both coarse and fine debris on the forest floor after biomass removal could have had a positive impact for oribatids resistance to disturbance (Johnston and Crossley, 1996; González-Polo et al., 2013; Rousseau et al., 2018a). Finally, compositional differences at our sites were observed only between Oribatida communities from the “High productivity” and the “Low productivity” sites. Even if both sites are dominated by *N. antarctica*, the “Low productivity site” has a monospecific canopy, which constitutes a relevant factor for the structuring of Oribatida community (Korboulewsky et al., 2016).

Our study provides new information for designing sustainable harvesting cycles in southern woodlands, extending benefits from firewood harvest to multiple ecosystem services relying on soil biota. Our focus on biomass removal highlights the sustainability of strip-harvest as a management option suitable for woodlands with contrasting productivity. Specifically, low- and mid-intensity strip harvest show potential to balance both firewood productivity and mesofauna conservation in mid- and high-productivity woodlands (Bengtsson et al., 1998; Goldenberg et al., 2020). Yet, careful consideration should be paid to high-intensity strip harvest because its negative effects on Oribatida populations can compromise decomposition and nutrient cycling at “Low productivity” sites (Srivastava et al., 2009; García-Palacios et al., 2013).

## 5. Conclusions

Our experimental approach allowed us to assess the trade-off between firewood biomass harvest and soil fauna conservation. There is potential to sustain mid-intensity harvests in sites with high and medium productivity without compromising microarthropods in the short term. Site productivity played a relevant role on regulating Acari response to increasing biomass removal. The strong density declines for detritivore Acari in “Low productivity” woodlands matched the overall trend for litter production, which highlights the role of litter provision for habitat and food conservation. Our study suggests that strip-harvest up to 70% of basal area can conserve Acari community structure regardless of site productivity. A coarse taxonomic resolution was sufficient to visualize impacts in these woodlands, which usually is a bottleneck to build ecological indicators including microarthropods. Management plans including firewood extraction in southern woodlands should incorporate site productivity considerations in management decisions for conserving soil fauna and long-term soil productivity.

## Declaration of competing interest

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.

## Acknowledgments

We are grateful to Dr. Susana Rizzuto and Julia Bazzani for their guidance on taxonomical identification. We also thank Waldo Rizzo, Silvina Hubry, Juan Agüero, Carolina Michel, Agustín Assaneo, Analía Mattiacci, Fiorella Laco-Mazzone, Dulce Gómez Carella, Marcos Nacif, Thilo Minich, Taylor Zehren, and Jacob Ray for their help with field-work and laboratory tasks. Financial support for this work was provided by Agencia Nacional de Promoción Científica y Tecnológica in Argentina (ANPCyT, grants PICT 2013-1073 and PICT 2016-0305, PI B 635 UNRN). Support for DME was partially provided by the USDA National Institute of Food and Agriculture and Hatch Appropriations under Project #PEN04744 (Accession #1023222). We also thank the Fulbright Program and Pennsylvania State University for the doctoral fellowship of Engr. M. Fernández.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2021.104242>.

## References

- Agüero, J.I., Pérez-Méndez, N., Torretta, J.P., Garibaldi, L.A., 2020. Impact of invasive bees on plant-pollinator interactions and reproductive success of plant species in mixed Nothofagus Antarctica forests. *Neotrop. Entomol.* 49 (4), 557–567. <https://doi.org/10.1007/s13744-020-00787-6>.
- Anderson, J.M., 1978. Inter- and intra-habitat relationships between woodland cryptostigmata species diversity and the diversity of soil and litter microhabitats. *Oecologia* 32 (3), 341–348.
- Aoki, J., 1977. Relation between fauna of soil mites (Oribatei) and human impacts in four main natural forest regions in Kanagawa Prefecture, Central Japan. *Bull. Inst. Environ. Sci. Technol.* 3, 121–133.
- Bach, E.M., Ramirez, K.S., Fraser, T.D., Wall, D.H., 2020. Soil biodiversity integrates solutions for a sustainable future. *Sustainability* 12 (7), 2662. <https://doi.org/10.3390/su12072662>.
- Bahamonde, H.A., Peri, P.L., Pastur, G.M., Monelos, L., 2015. Litterfall and nutrients return in Nothofagus Antarctica forests growing in a site quality gradient with different management uses in southern Patagonia. *Eur. J. For. Res.* 134 (1), 113–124. <https://doi.org/10.1007/s10342-014-0837-z>.
- Balogh, J., Balogh, P., 1992. *The Oribatid Mites' Genera of the World*. Hungarian Natural History Museum, Budapest.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Bojesen, Haubo, Christensen, R., 2015. *lme4: Linear Mixed-effects Models Using Eigen and S4*. R Package Version 1.1–7. 2014.
- Battigelli, J.P., Spence, J.R., Langor, D.W., Berch, S.M., 2004. Short-term impact of forest soil compaction and organic matter removal on soil mesofauna density and oribatid mite diversity. *Can. J. For. Res.* 34 (5), 1136–1149. <https://doi.org/10.1139/x03-267>.
- Bengtsson, J., Lundkvist, H., Saetre, P., Sohlenius, B., Solbreck, B., 1998. Effects of organic matter removal on the soil food web: forestry practices meet ecological theory. *Appl. Soil Ecol.* 9 (1–3), 137–143. [https://doi.org/10.1016/S0929-1393\(98\)00067-5](https://doi.org/10.1016/S0929-1393(98)00067-5).
- Berch, S.M., Battigelli, J.P., Hope, G.D., 2007. Responses of soil mesofauna communities and oribatid mite species to site preparation treatments in high elevation cutblocks in southern British Columbia. *Pedobiologia* 51 (1), 23–32. <https://doi.org/10.1016/j.pedobi.2006.12.001>.
- Bird, G.A., Chatarpaul, L., 1986. Effect of whole-tree and conventional forest harvest on soil microarthropods. *Can. J. Zool.* 64 (9), 1986–1993. <https://doi.org/10.1139/z86-299>.
- Bird, S.B., Coulson, R.N., Fisher, R.F., 2004. Changes in soil and litter arthropod abundance following tree harvesting and site preparation in a loblolly pine (*Pinus taeda* L.) plantation. *For. Ecol. Manag.* 202 (1–3), 195–208. <https://doi.org/10.1016/j.foreco.2004.07.023>.
- Blair, J.M., Crossley Jr., D.A., 1988. Litter decomposition, nitrogen dynamics and litter microarthropods in a southern Appalachian hardwood forest 8 years following clearcutting. *J. App. Ecol.* 683–698. <https://doi.org/10.2307/2403854>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9 (2), 378–400. <https://doi.org/10.3929/ethz-b-000240890>.



- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65 (1), 23–35. <https://doi.org/10.1007/s00265-010-1029-6>.
- Cameron, E.K., Martins, I.S., Lavelle, P., Mathieu, J., Tedersoo, L., Bahram, M., Eisenhauer, N., 2019. Global mismatches in aboveground and belowground biodiversity. *Conserv. Biol.* 33 (5), 1187–1192. <https://doi.org/10.1111/cobi.13311>.
- Carrón, A.I., Garibaldi, L.A., Márquez, S., Fontenla, S., 2020. The soil fungal community of native woodland in Andean Patagonian forest: a case study considering experimental forest management and seasonal effects. *For. Ecol. Manag.* 461, 117955 <https://doi.org/10.1016/j.foreco.2020.117955>.
- Chauchard, L., Frugoni, M., Novack, C., 2015. Manual de Buenas Prácticas para el Manejo de las Plantaciones Forestales en la Región de la Patagonia Andina. Buenos Aires.
- Chauvat, M., Zaitsev, A.S., Gabriel, E., Wolters, V., 2009. How do soil fauna and soil microbiota respond to beech forest growth? *Curr. Zool.* 55 (4), 272–278. <https://doi.org/10.1093/czoolo/55.4.272>.
- Chillo, V., Goldenberg, M., Pérez-Méndez, N., Garibaldi, L.A., 2020. Diversity, functionality, and resilience under increasing harvesting intensities in woodlands of northern Patagonia. *For. Ecol. Manag.* 474, 118–349. <https://doi.org/10.1016/j.foreco.2020.118349>.
- Coulin, C., Aizen, M.A., Garibaldi, L.A., 2019. Contrasting responses of plants and pollinators to woodland disturbance. *Austral. Ecol.* 44 (6), 1040–1051. <https://doi.org/10.1111/aec.12771>.
- De Paz, M., Gobbi, M.E., Raffaele, E., 2013. Mantillo de las especies leñosas de matorrales del NO de la Patagonia: abundancia, composición, estructura y heterogeneidad. *Bol. Soc. Argent. Bot.* 48 (3–4), 525–541. <https://doi.org/10.31055/1851.2372.v48.n3-4.7607>.
- Déchène, A.D., Buddle, C.M., 2009. Effects of experimental forest harvesting on oribatid mite biodiversity. *For. Ecol. Manag.* 258 (7), 1331–1341. <https://doi.org/10.1016/j.foreco.2009.06.033>.
- Déchène, A.D., Buddle, C.M., 2010. Decomposing logs increase oribatid mite assemblage diversity in mixed wood boreal forest. *Biodivers. Conserv.* 19 (1), 237–256. <https://doi.org/10.1007/s10531-009-9719-y>.
- Donegan, K.K., Watrud, L.S., Seidler, R.J., Maggard, S.P., Shiroyama, T., Porteous, L.A., DiGiovanni, G., 2001. Soil and litter organisms in Pacific northwest forests under different management practices. *Appl. Soil Ecol.* 18 (2), 159–175. [https://doi.org/10.1016/S0929-1393\(01\)00155-X](https://doi.org/10.1016/S0929-1393(01)00155-X).
- Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. *Appl. Soil Ecol.* 15 (1), 3–11. [https://doi.org/10.1016/S0929-1393\(00\)00067-6](https://doi.org/10.1016/S0929-1393(00)00067-6).
- Farská, J., Prejzková, K., Rusek, J., 2014. Management intensity affects traits of soil microarthropod community in montane spruce forest. *Appl. Soil Ecol.* 75, 71–79. <https://doi.org/10.1016/j.apsoil.2013.11.003>.
- Gallopín, G., 1978. Estudio Ecológico Integrado de la Cuenca del Río Manso Superior (Río Negro, Argentina). I. Descripción General de la Cuenca. In: *Anales de Parques Nacionales: órgano oficial del Servicio Nacional de Parques Nacionales (Vol. 14, No. 1)*.
- 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. *Ecol. Lett.* 16 (8), 1045–1053. <https://doi.org/10.1111/ele.12137>.
- Geisen, S., Wall, D.H., van der Putten, W.H., 2019. Challenges and opportunities for soil biodiversity in the anthropocene. *Curr. Biol.* 29 (19), R1036–R1044. <https://doi.org/10.1016/j.cub.2019.08.007>.
- Goldenberg, M.G., Gowda, J.H., Casas, C., Garibaldi, L.A., 2018. Efecto de la tasa de descuento sobre la priorización de alternativas de manejo del matorral Norpatagónico argentino. *Bosque (Valdivia)* 39 (2), 217–226. <https://doi.org/10.4067/S0717-92002018000200217>.
- Goldenberg, M.G., Oddi, F.J., Amoroso, M.M., Garibaldi, L.A., 2020. Effects of harvesting intensity and site conditions on biomass production of northern Patagonia shrublands. *Eur. J. For. Res.* 139, 881–891. <https://doi.org/10.1007/s10342-020-01292-6>.
- González-Polo, M., Fernández-Souto, A., Austin, A.T., 2013. Coarse woody debris stimulates soil enzymatic activity and litter decomposition in an old-growth temperate forest of Patagonia, Argentina. *Ecosystems* 16 (6), 1025–1038. <https://doi.org/10.1007/s10021-013-9665-0>.
- Grandy, A.S., Wieder, W.R., Wickings, K., Kyker-Snowman, E., 2016. Beyond microbes: are fauna the next frontier in soil biogeochemical models? *Soil. Biol. Biochem.* 102, 40–44. <https://doi.org/10.1016/j.soilbio.2016.08.008>.
- Grossfeld, J., Chauchard, L., Gowda, J.H., 2019. Debates: ¿Podemos manejar sustentablemente el bosque nativo de Patagonia Norte? *Ecol. Austral.* 29 (1), 156–163. <https://doi.org/10.25260/EA.19.29.1.0.775>.
- Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Syst.* 36, 191–218. <https://doi.org/10.1146/annurev.ecolsys.36.112904.151932>.
- Huston, M.A., 2014. Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology* 95 (9), 2382–2396. <https://doi.org/10.1890/13-1397.1>.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration. *Geoderma* 137 (3), 253–268. <https://doi.org/10.1016/j.geoderma.2006.09.003>.
- Johnston, J.M., Crossley, J.D.A., 1996. The significance of coarse woody debris for the diversity of soil mites. In: *Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity*. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, pp. 82–87.
- Karg, W., 1993. In: *Fischer, Jena (Ed.), Predatory Mites*, p. 523.
- Karlen, D.L., Mausbach, M.J., Doran, J.W., Cline, R.G., Harris, R.F., Schuman, G.E., 1997. Soil quality: a concept, definition, and framework for evaluation (a guest editorial). *Soil Sci. Soc. Am. J.* 61 (1), 4–10. <https://doi.org/10.2136/sssaj1997.03615995006100010001x>.
- Korboulewsky, N., Perez, G., Chauvat, M., 2016. How tree diversity affects soil fauna diversity: a review. *Soil Biol. Biochem.* 94, 94–106. <https://doi.org/10.1016/j.soilbio.2015.11.024>.
- Krantz, G.W., Walter, D.E., 2009. *A Manual of Acarology*, 3rd. Texas Tech University Press, Lubbock, TX.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Rossi, J.P., 2006. Soil invertebrates and ecosystem services. *Eur. J. Soil Biol.* 42, S3–S15. <https://doi.org/10.1016/j.ejsobi.2006.10.002>.
- Law 26.331, 2007. *Ley Nacional de Presupuestos Mínimos de Protección Ambiental de los Bosques Nativos*, 31310, Boletín Oficial, December 26th, 2007, 2.
- Lilles, E., Dhar, A., Coates, K.D., Haeussler, S., 2018. Retention level affects dynamics of understory plant community recovery in northern temperate hemlock-cedar forests. *For. Ecol. Manag.* 421, 3–15. <https://doi.org/10.1016/j.foreco.2017.12.033>.
- Lindo, Z., Visser, S., 2003. Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. *Can. J. For. Res.* 33 (9), 1610–1620. <https://doi.org/10.1139/x03-080>.
- Lindo, Z., Visser, S., 2004. Forest floor microarthropod abundance and oribatid mite (Acari: Oribatida) composition following partial and clear-cut harvesting in the mixed wood boreal forest. *Can. J. For. Res.* 34 (5), 998–1006. <https://doi.org/10.1139/x03-284>.
- Luxton, M., 1972. *Studies on the Oribatid Mites of a Danish Beech Wood Soil*. I. Nutritional Biology.
- Maaß, S., Caruso, T., Rillig, M.C., 2015. Functional role of microarthropods in soil aggregation. *Pedobiologia* 58 (2–3), 59–63. <https://doi.org/10.1016/j.pedobi.2015.03.001>.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwells.
- Malmström, A., Persson, T., Ahlström, K., Gongalsky, K.B., Bengtsson, J., 2009. Dynamics of soil meso- and macrofauna during a 5-year period after clear-cut burning in a boreal forest. *Appl. Soil Ecol.* 43 (1), 61–74. <https://doi.org/10.1016/j.apsoil.2009.06.002>.
- Marshall, V.G., 2000. Impacts of forest harvesting on biological processes in northern forest soils. *For. Ecol. Manag.* 133 (1–2), 43–60. [https://doi.org/10.1016/S0378-1127\(99\)00297-2](https://doi.org/10.1016/S0378-1127(99)00297-2).
- Mori, A.S., Ota, A.T., Fujii, S., Seino, T., Kabeya, D., Okamoto, T., Hasegawa, M., 2015. Biotic homogenization and differentiation of soil faunal communities in the production forest landscape: taxonomic and functional perspectives. *Oecologia* 177 (2), 533–544. <https://doi.org/10.1007/s00442-014-3111-7>.
- 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. *For. Ecol. Manag.* 458, 117738 <https://doi.org/10.1016/j.foreco.2019.117738>.
- Nielsen, U.N., Osler, G.H., Campbell, C.D., Burslem, D.F., van der Wal, R., 2010. The influence of vegetation type, soil properties and precipitation on the composition of soil mite and microbial communities at the landscape scale. *J. Biogeogr.* 37 (7), 1317–1328. <https://doi.org/10.1111/j.1365-2699.2010.02281.x>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Wagner, H., 2018. *Package 'Vegan'—Community Ecology Package*. 2019.
- Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* 288–388. <https://doi.org/10.2307/3544689>.
- Powers, R.F., Tiarks, A.E., Boyle, J.R., 1999. Assessing soil quality: practicable standards for sustainable forest productivity in the United States. In: *The Contribution of Soil Science to the Development of and Implementation of Criteria and Indicators of Sustainable Forest Management*, 53, pp. 53–80. <https://doi.org/10.2136/sssaspecpub53.c3>.
- R Core Team, 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reque, J.A., Sarasola, M., Gyenge, J., Fernández, M.E., 2007. Caracterización silvícola de nirañtales del Norte de la Patagonia Para la gestión forestal sostenible. *Bosque (Valdivia)* 28 (1), 33–45. <https://doi.org/10.4067/S0717-92002007000100006>.
- Rizzuto, S., 2018. *Ácaros de suelo en un bosque de Nothofagus pumilio afectado por el fuego, en la provincia de Chubut*. Faculty of Natural Sciences, National University of Austral Patagonia, Esquel, Argentina.
- Rousseau, L., Venier, L., Fleming, R., Hazlett, P., Morris, D., Handa, I.T., 2018a. Long-term effects of biomass removal on soil mesofaunal communities in northeastern Ontario (Canada) jack pine (*Pinus banksiana*) stands. *For. Ecol. Manag.* 421, 72–83. <https://doi.org/10.1016/j.foreco.2018.02.017>.
- Rousseau, L., Venier, L., Hazlett, P., Fleming, R., Morris, D., Handa, I.T., 2018b. Forest floor mesofauna communities respond to a gradient of biomass removal and soil disturbance in a boreal jack pine (*Pinus banksiana*) stand of northeastern Ontario (Canada). *For. Ecol. Manag.* 407, 155–165. <https://doi.org/10.1016/j.foreco.2017.08.054>.
- Rousseau, L., Venier, L., Aubin, I., Gendreau-Berthiaume, B., Moretti, M., Salmon, S., Handa, I.T., 2019. Woody biomass removal in harvested boreal forest leads to a partial functional homogenization of soil mesofaunal communities relative to unharvested forest. *Soil Biol. Biochem.* 133, 129–136. <https://doi.org/10.1016/j.soilbio.2019.02.021>.
- Rusch, V.E., López, D.R., Cavallero, L., Rusch, G.M., Garibaldi, L.A., Grosfeld, J., Peri, P., 2017. Modelo de estados y transiciones de los nirañtales del NO de la Patagonia

- como herramienta Para el uso silvopastoril sustentable. *Ecol. Austral* 27 (2), 266–278. <https://doi.org/10.25260/EA.17.27.2.0.240>.
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Beßler, H., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468 (7323), 553–556. <https://doi.org/10.1038/nature09492>.
- Schoenholtz, S.H., Van Miegroet, H., Burger, J.A., 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. *For. Ecol. Manag.* 138 (1–3), 335–356. [https://doi.org/10.1016/S0378-1127\(00\)00423-0](https://doi.org/10.1016/S0378-1127(00)00423-0).
- Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Härdtle, W., 2019. Multiple plant diversity components drive consumer communities across ecosystems. *Nat. Commun.* 10 (1), 1–11. <https://doi.org/10.1038/s41467-019-09448-8>.
- Seoane, J., 2014. ¿Modelos mixtos (lineales)? una introducción para el usuario temeroso. *Etología* (24), 15–37.
- Siira-Pietikäinen, A., Haimi, J., 2009. Changes in soil fauna 10 years after forest harvestings: comparison between clear felling and green-tree retention methods. *For. Ecol. Manag.* 258 (3), 332–338. <https://doi.org/10.1016/j.foreco.2009.04.024>.
- Siira-Pietikäinen, A., Pietikäinen, J., Fritze, H., Haimi, J., 2001. Short-term responses of soil decomposer communities to forest management: clear-felling versus alternative forest harvesting methods. *Can. J. For. Res.* 31 (1), 88–99. <https://doi.org/10.1139/x00-148>.
- Soong, J.L., Nielsen, U.N., 2016. The role of microarthropods in emerging models of soil organic matter. *Soil Biol. Biochem.* 102, 37–39. <https://doi.org/10.1016/j.soilbio.2016.06.020>.
- Speziale, K.L., Ezcurra, C., 2011. Patterns of alien plant invasions in northwestern Patagonia, Argentina. *J. Arid Environ.* 75 (10), 890–897. <https://doi.org/10.1016/j.jaridenv.2011.04.014>.
- Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M., Wright, J.P., 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* 90 (4), 1073–1083. <https://doi.org/10.1890/08-0439.1>.
- Subías, L.S., 2004. Listado sistemático, sinonímico y biogeográfico de los acaros Oribátidos (Acariformes: Oribatid) del mundo (excepto fósiles). – Graellsia, 60 (número extraordinario): 3–305, actualizado en enero de 2020. <https://doi.org/10.3989/graellsia.2004.v60.iExtra.218>.
- Swift, M.J., Heal, O.W., Anderson, J.M., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*, 5. Univ of California Press.
- Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., Austin, K.A., 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecol. Appl.* 9 (3), 864–879. [https://doi.org/10.1890/1051-0761\(1999\)009\[0864:PDIMFUfritu2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0864:PDIMFUfritu2.0.CO;2).
- Tomao, A., Bonet, J.A., Castaño, C., de Miguel, S., 2020. How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. *For. Ecol. Manag.* 457, 117678. <https://doi.org/10.1016/j.foreco.2019.117678>.
- Trentini, C.P., Villagra, M., Pámies, D.G., Laborde, V.B., Bedano, J.C., Campanello, P.I., 2018. Effect of nitrogen addition and litter removal on understory vegetation, soil mesofauna, and litter decomposition in loblolly pine plantations in subtropical Argentina. *For. Ecol. Manag.* 429, 133–142. <https://doi.org/10.1016/j.foreco.2018.07.012>.
- Vanbergen, A.J., Watt, A.D., Mitchell, R., Truscott, A.M., Palmer, S.C., Ivits, E., Sousa, J.P., 2007. Scale-specific correlations between habitat heterogeneity and soil fauna diversity along a landscape structure gradient. *Oecologia* 153 (3), 713–725. <https://doi.org/10.1007/s00442-007-0766-3>.
- Wall, D.H., Bradford, M.A., St. John, M.G., Trofymow, J.A., Behan-Pelletier, Valerie, Bignell, D.E., Wolters, V., 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate dependent. *Glob. Chang. Biol.* 14 (11), 2661–2677. <https://doi.org/10.1111/j.1365-2486.2008.01672.x>.
- Wall, D., Nielsen, U., Six, J., 2015. Soil biodiversity and human health. *Nature* 528, 69–76. <https://doi.org/10.1038/nature15744>.
- Wehner, K., Norton, R.A., Blüthgen, N., Heethoff, M., 2016. Specialization of oribatid mites to forest microhabitats—the enigmatic role of litter. *Ecosphere* 7 (3), e01336. <https://doi.org/10.1002/ecs2.1336>.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed-effects Models and Extensions in Ecology With R*. Springer Science & Business Media.