



Fungal diversity, woody debris, and wood decomposition in managed and unmanaged Patagonian *Nothofagus pumilio* forests

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Abstract

Fungal diversity, woody debris, and wood decomposition were assessed in *Nothofagus pumilio* forests with and without forest management (controls) in Argentina, and were related with the forest structure and microclimate. We established a wood decomposition assay to determine mass loss of branches and twigs in two decay classes (1, incipient and 2, intermediate decay stage), and used generalized linear mixed-effects models to evaluate whether fungal diversity and mass loss differed between treatments (managed forests and controls). We found no differences in richness nor in abundance between treatments, and their community composition was similar. However, *Botryobasidium vagum*, *Phanerochaete velutina*, and *Sistotrema brinkmanii* were more abundant in managed forests, and *Amyloathelia aspera* was more abundant in controls. Branches in the intermediate decay stage showed greater mass loss in managed forests than in controls, but mass loss of the other debris types did not differ between treatments. The volume of coarse woody debris was greater in managed forests than in controls, and had a positive effect on fungal richness. Our results indicate that *N. pumilio* forest management did not generate evident changes in fungal diversity, or in wood decomposition after 20 years of the forest management. However, the higher mass loss of branches in the intermediate decay stage observed in managed forests suggests that there were some factors operating in those forests in the past which may have accelerated decomposition. This highlights the need for studies evaluating changes in canopy cover, microclimate, and fungal community, including potential key species, in the short term and the long term after forest management.

Keywords Ecosystem process · Forest ecology · Lenga · Patagonia · Wood-inhabiting fungi

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Introduction

Biodiversity influences ecosystem functioning (Loreau et al. 2001), but how ecosystem functioning and biodiversity are related is still poorly understood. Decomposition is a key process in ecosystem functioning because it causes the recycling of carbon and nutrients from dead organic matter (Swift 1977). Thus, understanding how biodiversity and decomposition are related is extremely important to forest conservation and sustainable management.

In forest ecosystems, the decomposition of wood is an essential and complex process regulated by different factors: environmental conditions, decomposer organisms, and wood traits. Their relative importance may change over time, during the different stages of this process (Weedon et al. 2009). For example, van der Wal et al. (2015) reported that moisture content is a relevant factor at the beginning of decomposition but then, as wood decomposition proceeds, the composition of the fungal community becomes more relevant for this

process. Regarding wood traits, there is a general consensus that macronutrients, in particular nitrogen and phosphorus, are key factors in woody material decomposition because decomposer organisms do not have to invest energy towards nitrogen and phosphorus acquisition and can use it only for lingocellulase synthesis (Sinsabaugh et al. 1993; Weedon et al. 2009).

Wood-inhabiting fungi are the main decomposer organisms in temperate forests (Rayner and Boddy 1988); hence, they play a key role in nutrient cycling and soil formation (Lonsdale et al. 2008) and, consequently, in forest maintenance. The diversity of wood decomposer fungi is affected by microclimate and by the amount, types, and decay stage of the woody debris present in the forest (Parisi et al. 2018; Olou et al. 2019). Previous studies have reported that fungal diversity peaks in the most highly decayed substrates (Rajala et al. 2012; Tomao et al. 2020). Besides, a positive effect of increased stand structure heterogeneity on abundance and diversity of wood-inhabiting fungi has been reported by Persiani et al. (2016). Regarding microclimate, which is highly related to canopy cover, there is inconsistency on how it affects fungal diversity. Some studies reported that wood-inhabiting fungal diversity is negatively correlated with canopy openness and that fungal community composition changes in response to changes in canopy cover (Bässler et al. 2010; Horák et al. 2016). But another study reported no effect of canopy openness on fungal diversity (Bässler et al. 2016). The relationship between canopy cover and fungal diversity seems to be influenced by other factors too. For example, Brazee et al. (2014) did not find an effect of canopy openness on fungal abundance and diversity alone, but found a positive effect when testing the effect of canopy openness in combination with the addition of coarse woody debris in the forest on fungal diversity.

Anthropogenic disturbances, particularly intense forest management, can affect microclimatic conditions (Aussenac 2000) and modifies the amount, availability, and variety of woody debris on the forest floor (Abrego and Salcedo 2013). In particular, in *Nothofagus pumilio* forests, the volume of coarse woody debris in managed forests can be more than double than in unmanaged forests, because local forest companies only harvest adequate wood for sawn wood (Klein et al. 2008). Forest management may affect decomposer biodiversity because of its effects on forest microclimate and woody debris and also because it changes the structure, tree cover, and plant community composition of the forest (Chen et al. 1999; Edmonds et al. 2000; Tomao et al. 2020). In their meta-analysis based on 120 comparisons of species richness between unmanaged and managed forests throughout Europe, Paillet et al. (2010) reported that different taxonomic groups displayed contrasting responses to forest management; particularly for fungi, they found that species richness was higher in unmanaged than in managed forests.

Accordingly, other authors reported that fungal community diversity is influenced by forest management (Dvořák et al. 2017; Tomao et al. 2020 and references therein), but the direction of this influence depends on different factors such as canopy openness, percentage of tree retention, remaining dead wood and stumps, and complexity of forest structure after management. Intensive forestry with high canopy openness (> 50%), high basal area extraction, and high dead wood extraction decreases fungal diversity. Nevertheless, a forestry management where canopy cover remains high ($\geq 50\%$), or with low basal area extracted (< 30%), or where dead wood is left in the forest floor, has fungal diversity shows low or no impact on fungal diversity. Moreover, forest managements that retain woody debris in the forests increase structural complexity and microhabitat availability may result in the improvement of fungal diversity. Besides the direction of forest management influence on fungal communities, it is worth noticing that, if forest changes caused by forest management affect the fungal community, they might also impact on the decomposition process.

The diversity and structure of the fungal community are known to affect decomposition (Hättenschwiler et al. 2011), but no clear relationships between decomposition rates and decomposer diversity in natural conditions have been demonstrated so far (Parisi et al. 2018). It is a standard view of ecology that increased microbial diversity will result in enhanced nutrient cycling because of functional niche complementarity (additive effect) or a greater intensity of resource exploitation (synergistic activities) (van der Wal et al. 2013). This view is supported by previous studies that showed a positive relationship between wood-inhabiting fungal richness and wood mass loss (Rajala et al. 2012; van der Wal et al. 2015; Tarvainen et al. 2020). However, in vitro and field-based manipulative studies have shown that the diversity-decomposition relationship was saturated at rather low species levels (up to 10 species) (Setälä and McLean 2004; Dang et al. 2005; Gessner et al. 2010) and that the idiosyncratic relationship (where one species has a greater influence on ecosystem processes than others) is most frequently observed in communities with more than 10 species (Nielsen et al. 2011). In other words, intermediate levels of fungal diversity accelerate decomposition in soil (Setälä and McLean 2004) and wood (Toljander et al. 2006), but higher levels of fungal diversity are associated with slow decomposition (Dang et al. 2005; Deacon et al. 2006; Toljander et al. 2006; Fukami et al. 2010; Gessner et al. 2010; Nielsen et al. 2011).

Nothofagus pumilio (lenga) forests, the main native forest resource in Patagonia, have historically been managed (Martínez Pastur et al. 2003; Bava and Rechene 2004). Previous studies in shelterwood systems in these forests have reported lower humidity and greater radiation and wind speed in managed than in unmanaged forests (Caldentey et al. 1999;

Promis et al. 2010). Effects of management on biodiversity have been widely studied for different taxa (plants, bryophytes, insects, and birds) in Tierra del Fuego (Deferrari et al. 2001; Spagarino et al. 2001; Lencinas et al. 2008, 2009, 2011, 2014; Peri et al. 2016) and for plants in Chubut (Silva et al. 2016). The results of these studies show that the effects of forest management on biodiversity differ according to the management system, time elapsed since forest intervention, and the taxonomic group considered. Also, litter and wood decomposition in these forests has been documented in several studies (Frangi et al. 1997; Decker and Boerner 2006; Ibarra et al. 2011; Mansilla 2012; Moretto and Martínez Pastur 2014; Gallo 2017; Gallo et al. 2019) that determined mass loss of different kinds of forest debris. Diversity of aphylloroid fungi growing on *N. pumilio* trees and fallen wood has also been reported (Greslebin 2002; Greslebin and Rajchenberg 2003; Rajchenberg 2006; Gorjón et al. 2012). However, no studies have assessed whether aphylloroid fungal diversity changes with forest management and whether wood decomposition changes with forest management and/or with changes in fungal diversity.

Given the importance of understanding the relationship between the Funga and wood decomposition in Patagonian Andes forests under management, we addressed some relevant knowledge gaps. Our objective was to determine whether there were changes in the aphylloroid fungal community and in wood decomposition in managed *N. pumilio* forests, in comparison with the surrounding unmanaged forests. Specifically, we assessed whether fungal diversity and mass loss of fine woody debris differed between managed and unmanaged forests. Moreover, we evaluated the contribution of some key factors, such as the amount and physicochemical traits of woody debris and some environmental variables, to the fungal diversity and mass loss values observed in managed and unmanaged forest.

Materials and methods

Study area

The study was conducted in pure *N. pumilio* stands in three sites in Chubut province, Argentina. The sites were located in a north–south gradient along *N. pumilio* distribution. Site 1 was the northernmost site (S 42°46' W 71°28'), site 2 was at an intermediate gradient (S 43°49' W 71°28'), and site 3 was southwards (S 44°50' W 71°43') (Online Resources, Fig. 1). In each site, two stands corresponding to two treatments were selected: one in a managed forest (hereafter, MF) and the other in an unmanaged (unlogged) forest, i.e. control (hereafter, C). The MF stands had been logged 16–18 years before this study, with low to medium intensity (Online Resources, Table 1). Unmanaged neighbor stands (less than

1000 m apart from MF) were selected as control stands to represent the previous situation of managed forests. No previous management was recorded for these areas, but some individual tree extraction could have occurred. In each stand, a study plot of ¼ hectare was defined. A full characterization of each plot based on the measurement of different variables is shown in Online Resources, Table 2.

Structural and climatic stand characterization

On each plot, all trees (diameter > 10 cm) were counted and the diameter at breast height (DBH) was measured. The basal area was determined as the sum of all cross-sections of the stems at 1.3-m height of the trees within the plot. Inside the plot, 15 circular subplots of 0.8-m radius were regularly established (Online Resources, Fig. 2). Tree cover (measured as the percentage of canopy cover from a skyward-oriented photograph of canopy taken from the forest floor) and the number and height of saplings (trees with diameter < 10 cm) were measured in each subplot.

In addition, temperature and relative humidity were recorded on each plot with a data logger (EL-USB-2 Lascar, UK) every 3 h during the study period (from May 2012 to April 2015) to characterize the microclimatic conditions of the stands. Precipitation was inferred from the interpolated climate surfaces developed by Hijmans et al. (2005), with records from the 1950–2000 period. This surface has a 30 arc min spatial resolution (0.86 km²).

The geographical location and altitude of each plot were recorded with a Garmin global positioning system unit and the aspect was evaluated in the center of the plot with a compass.

Fungal sampling

Fungal sampling was conducted in the fall and the spring of 2012 and 2013 (4 samplings). To avoid sampling bias due to climatic conditions that affect fruiting body production, the MF and C plots of each site were surveyed at the same time, and all sites were surveyed within 10–15 days. Ten circular subplots of 4-m radius (50 m²) were randomly established within each study plot in each sampling; hence, subplots were different in each sampling (Online Resources, Fig. 2). The total surface sampled in the 4 samplings was 2000 m². In the subplots, all woody debris > 1-cm diameter and living trees were inspected for the presence of aphylloroid fungi (Corticaceae and Polyporaceae *s.l.*). All basidiomata were recorded or collected when it was not possible to identify them in the field. Basidiomata growing on woody debris < 1 cm in diameter were sampled in a sub-subplot of 1.3-m radius located in the center of the 4-m radius subplot. The collected basidiomata were taken to the lab, air-dried, and kept for further identification. To determine abundance,

only the basidiomata recorded on different woody debris were considered different “individuals.”

Measurements of fungal diversity

To evaluate the effectiveness of our sampling, accumulation curves of the observed species richness and of several different estimators (Chao 1, Chao 2, ACE, ICE, and bootstrap) were calculated per each subplot unit for each dataset (MF and C). Accumulation curves were calculated using ESTIMATES V. 9.1.0 (Colwell 2013) using 1000 random iterations of the survey periods without replacement.

Alpha diversity was evaluated on each plot using abundance and richness of the 40 subplots; diversity was determined with the Shannon–Wiener (H') index.

The variation in species composition among sites (beta diversity) was evaluated by analyzing the similarity between MF and C fungal communities, using the Bray–Curtis dissimilarity index (Bray and Curtis 1957):

$$BC_{ij} = 1 - ((2C_{ij}) / (S_i + S_j))$$

where C_{ij} is the sum of the lesser values only for those species in common between both sites, and S_i and S_j are the total number of specimens counted at both sites. Index value = 0 indicates identical species assemblage, while index value = 1 indicates totally different species assemblage. This index was chosen because it includes not only the presence but also the abundance of species. A cluster analysis was conducted based on the Bray–Curtis index and using Ward distance as a clustering method.

Measurements of number and volume of coarse and fine woody debris

The number and the volume of coarse (CWD: ≥ 10 cm in diameter) and fine (FWD: from 1 to < 10 cm in diameter) woody debris were measured. Measurements of CWD were performed in the entire plot (2500 m²), while those of FWD were performed in the same 15 subplots of 0.8-m radius used for saplings and canopy cover measurement. In both cases, the largest and smallest diameter and length of all woody debris found on the forest floor were measured. Height and diameter of all stumps were also measured, but only in MF plots because no stumps were found in C plots. Each woody debris was assigned to one of three decay stages: incipient, intermediate, or advanced. Decay stages were defined according to the natural process observed in the forests, and were assigned to each woody debris mainly according to its wood hardness and shape, and the presence of bark. The incipient decay stage represented the beginning of the decomposition process and included woody debris with almost intact bark and sound wood with high resistance to

knife penetration (up to 0.5 cm); this decay stage conserved the shape and wood hardness. The intermediate decay stage included altered wood, mostly decorticated and with visible changes in color and other physical characteristics; the shape was conserved or slightly altered, and wood hardness was altered but still partially conserved (knife penetrates more than 0.5 cm but cannot cross the woody debris). The advanced decay stage included much decayed wood, with evident changes in their physical properties; shape and wood hardness were totally altered, knife penetrated deeply in the woody debris, and wood could be disaggregated by hand.

Woody debris volume was determined as $\text{Volume} = 1/3 * \pi * h (R^2 + r^2 * r)$, where h is the height, R is the largest radius, and r is the smallest radius. Stump volume was determined as $\text{Volume} = \pi * (r)^2 * h$.

Decomposition assay

To determine whether mass loss of branches and twigs differed between MF and C, a decomposition assay with FWD in two diameter categories: B = branches (> 1 cm in diameter) and T = twigs (< 1 cm in diameter), and in two decay classes: 1 (incipient decay stage) and 2 (intermediate decay stage) was installed on each study plot (Online Resources, Fig. 2). Two decay classes (hereafter, DC) were defined within the decay stages previously mentioned: DC1 corresponded to the most intact woody debris in the incipient decay stage, and DC2 corresponded to those woody debris in the intermediate decay stage that were decorticated with a reduced resistance to knife penetration (> 0.5 cm up to 1 cm), but maintaining its shape. We defined this narrower DC1 and DC2 classes within the incipient and intermediate decay stages previously defined in order to diminish results variance caused by the variability of the woody debris at the beginning of the assay. Woody debris in the advanced decay stage was not included because they easily disaggregate leading to unreliable results due to material loss. The materials for the assay were obtained from the same stand where the assay was installed: FWD in DC1 was obtained from recently fallen crowns, and FWD in DC2 was collected from the forest floor. Hereafter, the four types of woody debris will be named as 1B (branches in DC1), 1T (twigs in DC1), 2B (branches in DC2), and 2T (twigs in DC2).

Branch portions of 25 cm in length were cut and processed as follows: 5-cm portions (hereafter, subsamples) were taken for physicochemical analyses, and the remaining 20-cm portions (hereafter, samples) were used to determine mass loss in the field assay. Twigs from the same stand and the same DC were cut into 10-cm-long portions and mixed to obtain a composite sample. The composite sample of each stand and each DC was then divided into 10-g portions (samples); five of them were separated for chemical analyses and the rest were used to determine mass loss in the field assay.

The decomposition field assay was conducted using the in situ litterbag method. Litterbags were made of fiberglass mesh (2 mm). Branch litterbags contained 4 branches from the same DC and twig litterbags contained 10 g of the composite sample from the same DC.

To determine mass loss over time, in March 2012, 10 branch litterbags from each DC and 10 twig litterbags from each DC were placed on the forest floor of each study plot. Two branch litterbags and 2 twig litterbags (1 for each DC) were randomly placed on the forest floor in 10 subplots, regularly arranged within the plot. The material was harvested after 3 and 2 years for branches and twigs, respectively. The retrieved material was wrapped in plastic bags and transported from the forests to the laboratory, where it was cleaned and oven-dried at 60 °C until constant weight. Mass loss was determined as a percentage of the original dry mass. Then, the mass loss of the 4 branches from each litterbag was averaged.

Measurements of branch and twig chemical traits

Branches were ground with a drill, and twigs were ground in a laboratory mill. Carbon content was determined by dry combustion at 430 °C. Nitrogen (N) content was measured using the standard semi-micro Kjeldahl procedure (Bremner and Mulvaney 1983) and phosphorus (P) content by spectrophotometry with ICP-OES Shimadzu simultaneous high resolution (model 9000). Cell wall components (hemicellulose, cellulose, lignin) and extractive contents were determined by successive extractions with neutral detergent (extractives) and acid detergent (hemicellulose), hydrolysis with 72% H₂SO₄ (cellulose) and ignition at 500 °C (lignin) (van Soest 1963). Carbon, cell wall components, and extractive contents were assessed in 12 branch subsamples and 5 twig samples from each plot. Nitrogen content was assessed in 6 branch subsamples and 5 twig samples from each plot. Phosphorus was assessed in 3 branch subsamples and 3 twig samples from each plot.

Density of woody debris

Density of branches at the beginning of the decomposition assay was assessed in 12 subsamples in each DC from each plot and determined as $\delta = \text{dry mass/saturated volume}$, according to Gayoso (2013).

Data analyses

Fungal richness, abundance, and Shannon diversity index were analyzed using generalized linear mixed-effects models (GLMM) (Zuur et al. 2009). Collinearity was checked between predictors, and variables with magnitudes greater than the pre-selected threshold were removed ($r = \pm 0.5$).

The models included the predictor management (two classes: MF and C) and the following covariates: canopy cover, mean temperature, mean humidity, CWD volume, and FWD volume as fixed effects; the random effect of the factor site (with three levels, sites 1, 2, and 3) was included as a random intercept to model between site variations. An automatic backward stepwise approach was applied for model selection using the command “drop1”, and the best-fitting model did not include any of the covariates. However, because the model that included CWD volume as covariate showed that this variable seems to be associated with fungal variables, generalized linear models (GLM) that included CWD volume as a fixed effect were also performed for fungal richness, abundance, and diversity to explore this possible association. The fungal richness response variable was modeled assuming a Poisson distribution of errors and log link function, while fungal abundance was modeled with a Gamma family distribution and log link function. A Gaussian family distribution and log link function were used for Shannon diversity. Residual plots were examined for model validation following the protocol described by Zuur et al. (2009): (i) residuals versus fitted values, (ii) residuals versus each explanatory variable included and not included in the model, using the packages *lattice* (Sarkar 2008) and *ggplot2* (Wickham 2016).

To analyze beta diversity, the dissimilarity matrix (constructed with the Bray–Curtis index) was submitted to cluster analysis, with clusters built using the Ward linkage method because it minimizes the total error sum of squares in the dendrogram (Legendre and Legendre 1998).

Woody debris mass loss was also analyzed using GLMM. Collinearity was checked between predictors, and environmental, fungal, and woody debris variables with magnitudes greater than the pre-selected threshold were removed ($r = \pm 0.5$). Different models that included the predictor treatment (two classes: MF and C), the woody debris type (four classes: 1B, 1 T, 2B, 2 T), their interaction, and the covariates mean humidity, mean temperature, canopy cover, fungal abundance, and percentage of hemicellulose were tested as fixed effects. To take into account the spatial structure of the data, the random effect of subplots nested within the factor site was included. Random intercepts that model between-site and between-subplot variation within the site were employed. The command “drop1” was used for model selection, and the best-fitting model did not include any of the covariates. The response variable was modeled assuming a Gamma distribution of errors and log link function. Residual plots were examined as described above.

Although the contribution of the structural and microclimatic variables, as well as of the woody debris physicochemical traits, to the different models was checked and discarded, paired *t* tests were also performed to analyze whether there were differences in structural and microclimatic variables

and in woody debris physicochemical traits between managed and unmanaged forests. In addition, to assess the variation ranges of mean values and standard errors, descriptive summary measures of the structure and environmental characteristics of each treatment were obtained.

Modeling was performed in R software, version 3.6.2 (R Core Team 2016) via the RStudio software, version 1.2.5033 (RStudio Team 2016), using “glm” and “glmer” functions from lme4 package. The function “drop1” from the same package was used for model selection, and the function “lsmeans” from lsmeans package was used to perform the contrasts. Cluster analysis was conducted in InfoStat software (Di Rienzo et al. 2013). To create the artworks, Infostat software and Corel DRAW X7 were used.

Results

Funga

A total of 2777 specimens of aphylloroid fungi corresponding to 49 species were recorded in MF plots, and a total of 2291 specimens of aphylloroid fungi corresponding to 43 species were recorded in C plots.

The species accumulation curve of observed richness (Fig. 1) did not reach asymptote in any of the two treatments, but the slope of the curve was not steep, especially in MF. In the MF treatment, by the end of the randomized accumulation curves, only Chao 1 and Chao 2 estimators reached an asymptote; other estimators were still increasing (Fig. 1A). The estimations of species richness for the MF treatment were 54 and 55 for abundance-based indexes (Chao 1 and ACE respectively), 56 and 59 for incidence-based indexes (ICE and Chao 2 respectively), and 54 for bootstrap. In the C treatment, Chao 1 and Chao 2 estimators had negative

slopes at the end of the accumulation curve; meanwhile, the curves of the other estimators were still increasing (Fig. 1B). The estimations of species richness for the C treatment were 51 and 56 for abundance-based indexes (ACE and Chao 1 respectively), 53 and 54 for incidence-based indexes (Chao 2 and ICE respectively), and 48 for bootstrap. According with these estimators, representativeness ranged from 83 to 92% in the MF treatment and 77 to 90% in the C treatment. Species accumulation curves in each study plot are shown in Online Resources, Fig. 3.

The mean fungal richness of MF plots was 35.67 (± 1.67) and of C plots was 30.67 (± 3.71). The mean fungal abundance of MF plots was 926 (± 41.3) and of C plots was 764 (± 40.3). The mean fungal diversity (H') was 2.09 (± 0.12) in MF plots and 1.94 (± 0.10) in C plots. According to the best-fitting models, which only included treatment (managed vs. control forests) as a fixed effect, fungal richness, abundance, and diversity were similar in both treatments (p value = 0.305, 0.111, and 0.869 respectively). The volume of CWD had a significantly positive effect on fungal richness, but not on fungal abundance or diversity (Table 1).

The species assemblage was also similar between treatments. Cluster analysis using the Bray–Curtis dissimilarity index showed that MF and C stands of each site were more similar between them than between stands of the same treatment from different sites. This indicates that geographical location has a greater influence than treatments on fungal diversity (Fig. 2). Site 1 showed the maximum dissimilarity between treatments (0.20), while sites 2 and 3 showed very low dissimilarity (0.14 and 0.11 respectively).

MF and C indicate managed forest and control, respectively. Each stand is labeled with the treatment and site number.

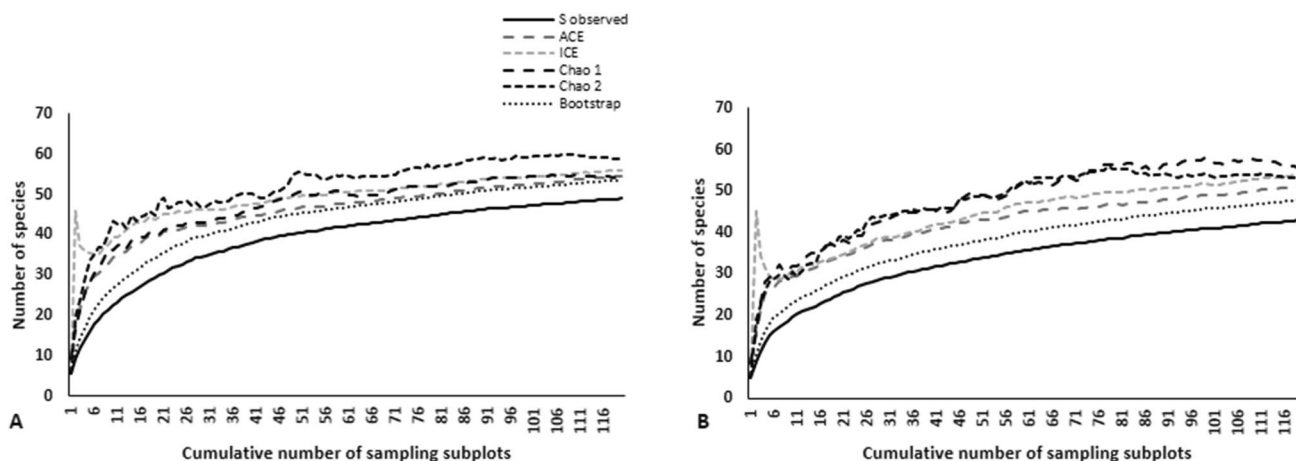


Fig. 1 Species accumulation curves in managed forest (A) and control (B)

Woody debris, structural, and microclimatic variables.

Coarse woody debris volume was significantly greater in MF than in C, but no differences were found in fine woody debris volume. Structural and climatic variables, as well as sapling density and average height of the highest saplings,

showed similar mean values in MF and C, except for the basal area of the forest, which was significantly greater in C than in MF (Table 2).

Structural and environmental variables showed more dissimilar values between sites than between treatments (Online Resources, Table 2).

Table 1 Generalized linear models for the effect of volume of CWD on fungal richness, abundance, and diversity

Model	Explanatory variables	$\beta \pm SE$	z value	p value
Fungal_richness	Intercept	1.517 ± 0.085	17.751	< 2e-16
	CWD_volume	0.001 ± 0.0002	2.908	0.0036
t value				
Fungal_abundance	Intercept	18.642 ± 5.508	3.385	0.0009
	CWD_volume	0.0245 ± 0.016	1.512	0.1321
Fungal_diversity	Intercept	1.100 ± 0.134	8.236	2.82e-14
	CWD_volume	0.0001 ± 0.0004	0.255	0.7990

Explanatory variables, parameter estimates (β) ± standard error, z, t, and p values are shown
 Bold values indicate significant differences ($p < 0.05$)

Fig. 2 Hierarchical dendrogram of the cluster analysis showing dissimilarity (Bray–Curtis index) between fungal assemblages of the 6 stands

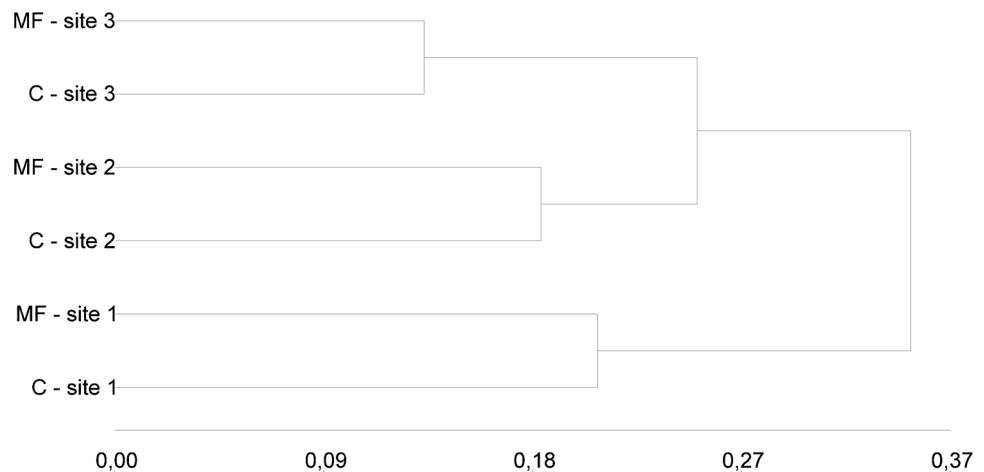


Table 2 Structural and microclimatic variables, and woody debris volume from different treatments (MF managed forest; C, control)

Variable	MF	C	t value	p value
Mean temperature (°C)	5.7 (0.28)	5.5 (0.10)	0.96	0.4380
Maximum temperature (°C)	29.3 (0.93)	27.3 (0.73)	1.31	0.3206
Minimum temperature (°C)	− 13.5 (1.40)	− 12.8 (1.86)	− 0.92	0.4557
Mean humidity (%)	72.8 (1.53)	73.0 (2.77)	− 0.12	0.9162
Minimum humidity (%)	12.0 (1.44)	12.5 (1.04)	− 0.33	0.7745
Canopy cover (%)	55.3 (6.01)	69.3 (0.67)	− 2.59	0.1225
Basal area (m ² ha ^{−1})	25.5 (4.8)	55.9 (9.67)	− 5.99	0.0268
Average height of the highest sapling (cm)	133.2 (45.52)	30.67 (13.86)	2.65	0.1181
Sapling density (saplings ha ^{−1})	35,166.67 (17,253.82)	44,000.00 (19,495.73)	− 1.22	0.3472
CWD volume (m ³ ha ^{−1})	418.3 (69.8)	239.8 (61.9)	5.33	0.0335
FWD volume (m ³ ha ^{−1})	27.8 (6.6)	21.03 (5.0)	− 0.54	0.6445

Mean values of each variable and standard error (in brackets), t parameter value, and p values are shown
 Bold values indicate significant differences ($p < 0.05$)

Decomposition assay

The best-fitting model to assess changes in decomposition across treatments included treatment, woody debris type, and their interaction as predictor variables. This model showed that there was a significant effect of the interaction between treatment and woody debris type on mass loss (p value = 0.0145). According to this model, significantly greater values of mass loss for branches in DC2 were found in MF compared with C (Fig. 3; Table 3). In the other woody debris types, no significant differences were found between MF and C (Table 3).

Density of branches at the beginning of the decomposition assay did not significantly differ between treatments (paired t tests: $t = -0.08$, $p = 0.943$ and $t = 1.8$, $p = 0.214$ for DC1 and DC2 respectively). However, branches in DC2 tended to be less dense in MF than in C, while branches in DC1 were almost equally dense in both treatments (Online Resources, Fig. 4). Values of components and nutrients of branches and twigs from MF and C were similar (Online Resources, Table 3).

Discussion

Based on previous findings that wood-inhabiting fungi are sensitive to forest structure and, thus, that forest management alters the fungal community (Juutilainen et al. 2014; Persiani et al. 2016; Tomao et al. 2020), we expected to find differences in fungal diversity, and possibly also in woody debris mass loss, between *Nothofagus pumilio* forests that had been subjected to forest management and those that had not. Contrary to our expectations, we found no significant differences in aphylloroid abundance or diversity between managed and control forests. In addition, none of the structural and/or microclimatic variables of the forest significantly contributed to the modeling of fungal diversity in relation to forest management. The only observed association was that

Table 3 Contrasts for the generalized linear mixed model for the effect of treatment, woody debris type, and their interaction

Contrast	MF	C	$\beta \pm SE$	p value
MF_1B—C_1B	35.0 \pm 1.9	32.2 \pm 3.3	0.008 \pm 0.004	0.5687
MF_1T—C_1T	25.8 \pm 2.1	20.9 \pm 0.9	0.013 \pm 0.005	0.1695
MF_2B—C_2B	36.3 \pm 2.4	23.4 \pm 2.7	0.019 \pm 0.005	0.0012
MF_2T—C_2T	24.4 \pm 2.3	23.5 \pm 3.3	0.006 \pm 0.005	0.9193

Mean mass loss in each treatment (MF, managed forest; C, control) for each woody debris type (B, branch; T, twig; 1, DC1; 2, DC2) and standard error, parameter estimates (β) and standard error (in bracket), and p value are shown

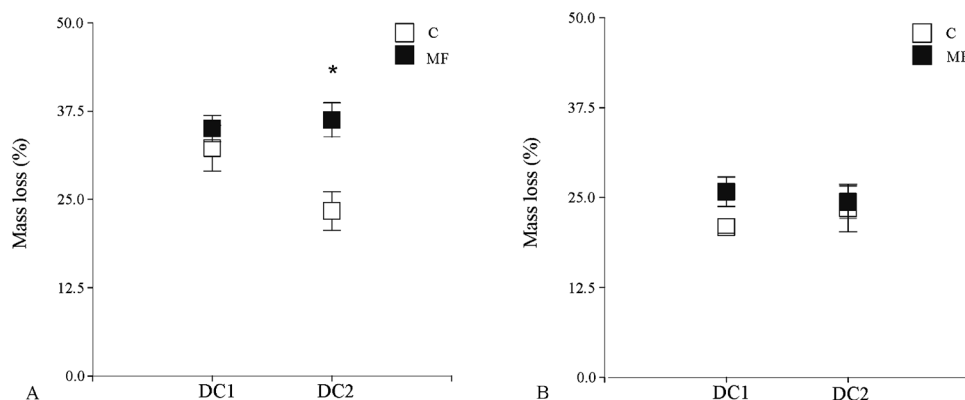
Bold values indicate significant differences ($p < 0.05$)

aphylloroid fungal richness increased with the increase of CWD volume.

It is understandable that the structural and microclimatic variables in this study did not contribute to the modeling of the response variables because they did not show significant differences between MF and C, except for the basal area that, as could be expected, was significantly greater in unmanaged forests. The variables that we initially predicted to be associated with changes in fungal diversity (i.e., canopy cover and average humidity) showed similar mean values in MF and C. This result might indicate that approximately 20 years after the intervention, the crown expansion of the remaining trees filled the gaps, at least partially and, together with the growth of saplings, generated similar conditions of vegetation cover at the forest floor level. Thus, microclimatic variables, which are highly affected by tree cover, were similar in MF and C.

Dead wood, the other variable reported affecting wood-inhabiting fungal species diversity, was more abundant in managed forests since logging of *N. pumilio* stands leaves a great amount of residues, because only sawn wood is extracted and rotten logs and crowns are left on the forest floor (Klein et al. 2008). This could have contributed to the slightly higher richness and abundance of aphylloroid species in MF, as shown by the association between species

Fig. 3 Mass loss of branches and twigs in different decay classes. **A** branches; **B** twigs. DC1, incipient decay class; DC2, intermediate decay class; MF, managed forests; C, control. Mass loss is presented as a percentage of initial mass. Mean values (\pm standard error). *indicates significant differences ($p < 0.05$)



richness and CWD, similar to what has been observed in temperate and tropical forests (Tomao et al. 2020).

Surprisingly, mass loss showed significant differences between MF and C, although in only one of the woody debris types evaluated: branches in the intermediate decay stages. Branches and twigs with sound wood and intact bark, as well as twigs in the intermediate decay stages, showed similar mass losses. The lack of significant differences in decomposition in most of the woody debris types analyzed is a reasonable result because the key factors of this process (fungal diversity and environmental variables), which were expected to be affected by forest management, showed no significant differences between treatments. The other key factor that regulates wood decomposition, wood chemical traits, did not contribute to mass loss modeling and showed similar mean values between treatments (Online Resources, Table 3).

The question that remains to be answered is why mass loss of branches in DC2 was greater in MF than in C. A possible explanation could be that it was greater due to the interaction of forest management with some physical characteristics of DC2, but in that case the same response could be expected for mass loss of twigs, which did not differ between treatments. We did not find any substantial differences in physicochemical traits of woody debris between MF and C, although at the beginning of the decomposition assay, the wood density of woody debris in DC2 showed a pattern of lower values in MF stands than in C stands (Online Resources, Fig. 4). This led to the formulation of another hypothesis to explain why we only observed differences in branches in DC2: the greater mass loss of this woody debris type in managed forest may have been the result of factors occurring in the past and no longer taking place at the present. Branches in DC2 have been on the forest floor for many years, as opposed to branches in DC1 which belonged to recently fallen trees; hence, the slightly lower density of branches in DC2 in MF forest could be related to factors that accelerated decomposition or produced faster degradation of some component in the first years after intervention but are no longer operating. The reason mass loss of twigs in DC2 did not differ between treatments could be that, because of their very small diameter, the twigs reaching the forest floor at the same time as branches in DC2 should have been almost totally decomposed by the beginning of the study (Gallo et al. 2019); thus, the twigs in DC2 used in the experiment must have reached the forest floor later than the branches in DC2.

Alternatively, the greater mass loss of branches in DC2 in managed forest could have been due to the interaction of forest management with some key group of decomposer organisms. Previous studies have shown that the type of interactions between fungal species determines the relationship between fungal diversity and decomposition rate

(van der Wal et al. 2013) and that changes in community composition, are more important than richness for carbon dynamics (Nielsen et al. 2011). In our study, we did not find substantial changes in community composition, and the most abundant species were almost the same in MF and C (Online Resources, Table 4). However, as woody debris in the intermediate decay stage were the substrate of most of the recorded basidiomata (51% in MF and 48% in C) (Online Resources, Table 5), it is possible that small changes in species abundance associated with this decay stage could have led to the observed mass loss changes. As mentioned by Nielsen et al. (2011), some species have a greater influence than others on ecosystem processes. The Friedman non-parametric analysis of variance (Online Resource, Table 6) showed significant differences between MF and C in the abundance of basidiomata of only four species: *Amyloathelia aspera* (more abundant in C than in MF), and *Botryobasidium vagum*, *Phanerochaete velutina*, and *Sistotrema brinkmanii* (more abundant in MF than in C). Among these species, *P. velutina* is the most important wood decomposer. This white-rot fungus has high efficiency to produce extracellular enzymes capable of completely degrading lignocellulose (Lee et al. 2014), and it was most frequently recorded (almost 60% of basidiomata) on woody debris in the intermediate decay stage (Online Resources, Table 5). It should be noted that we assessed aphylloroid fungal diversity through the presence of basidiomata, which need specific conditions to develop. This implies an underestimation of fungal diversity. However, as fungal sampling was done at the same time in all sites, the variability in fruiting body formation due to climatic conditions was minimized; hence, the data from MF and C plots are comparable.

The greatest effects of *N. pumilio* forest management (shelterwood method) on biodiversity are usually observed in the first years after cutting and these effects diminish substantially when the forest canopy closes during the initial growth phase of the forest, returning to values similar to the one of the unlogged forest when the mature phase is reached (Deferrari et al. 2001; Martínez Pastur et al. 2002; Pérez Flores et al. 2019). Our study sites were in the initial growth phase and, possibly, the relatively low harvest intensity contributed to rapid tree cover recovery. Also, a positive effect of forest management on aphylloroid fungi is plausible because traditional silvicultural practices in *N. pumilio* forests create great amounts of woody debris immediately after logging (Klein et al. 2008) that enhance diversity of wood-inhabiting fungi (Tomao et al. 2020). This highlights the need to perform studies to understand how fungal diversity responds to the different phases the forest goes through after logging.

On the other hand, Lencinas et al. 2017 showed that harvesting impacts on plants and beetles were not uniform in *N. pumilio* forests along a regional gradient in Tierra del Fuego,

and that the differences seem to be related with the composition of original assemblages of species of each site and the influx of species from surrounding environments. Thus, the wide geographical range of our study sites, even though contributed to *N. pumilio* forest representativeness, could have diminished the possibility of detecting differences between treatments due to the variations along the geographical gradient. This is in accordance with Tarvainen et al. (2020) who found an effect of geographic factors, especially climate, on decomposition and fungal community composition along a gradient of forestry induced disturbance but could not detect any effect of forestry.

Finally, regarding forest management in a landscape context, traditional forest use in Chubut province consisted in the selective cut of the better timber trees, which generally did not exceed 10% of forest trees (López Bernal et al. 2012). The application of forest management systems, which ranged from a group selection system up to a variation of shelterwood-cut systems, started in Chubut province after 1980 (López Bernal et al. 2012). However, as in other forests of Patagonia, these theoretical forest management methods were not fully applied and only the first cuts were implemented, without the final shelterwood removal and any intermediate treatments (Gea-Izquierdo et al. 2004). Moreover, as harvesting has been focused in the most accessible and highest site quality forests (Gea-Izquierdo et al. 2004), they were usually applied to small and scattered areas, resulting in discontinued managed patches in a matrix of no or slightly logged forests. This was the case of the MF areas of this study, which had been subject of the first cut of a shelterwood-cut system applied to a total area of < 10 ha, where the surrounding forest remained unlogged or with scattered extraction of selected individuals. This situation contributes to mitigate the effects of harvest on fungal diversity because even if some species were negatively affected by harvest, the surrounding unlogged forest constituted a source of inoculum from which the original biodiversity of logged areas could have been restored through recolonization.

Conclusions

This study is the first to conjointly analyze the diversity of wood-inhabiting fungi and wood decomposition in managed vs. unmanaged forests. It is also the first study on fungal diversity in relation to wood decomposition in South American temperate forests. It describes wood decomposition and their main control variables in managed vs. unmanaged forest stands. Our aim was to find a pattern that could be associated with forest management. We found a greater mass loss of branches in the intermediate decay stage in managed stands, but we did not find differences in any of the assumed key variables. In particular, fungal diversity and fungal community

composition were similar between managed and unmanaged forests, although some fungal species were more abundant in one of the two treatments. The scope of this study does not allow us to explain the difference in decomposition between MF and C, but we hypothesize that it could be related to effects of forest management that occurred in the past but that no longer take place. Further experiments are needed to disentangle the complex interactions between environmental and woody debris characteristics driving the differences in mass loss in DC2. These studies should focus on forests that were managed at different times in the past so that the changes in decomposition and its control factors can be analyzed after disturbance. Such studies should analyze variation over time in canopy cover, microclimate and fungal community, including potential key species as *Phanerochaete velutina*.

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Data Availability Most of the data generated and/or analyzed during this study are included in this published article and in its additional information files. If the datasets needed are not there, they are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

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