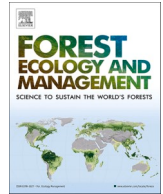




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## Intermediate harvesting intensities enhance native tree performance of contrasting species while conserving herbivore diversity in a Patagonian woodland

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## ABSTRACT

Sustainable forest management should optimise the balance between tree productivity and biodiversity conservation. One strategy to achieve both is the use of native plantations in biomass extraction systems. However, it is unknown how different native tree species and their herbivores respond to a gradient of biomass extraction. In a Patagonian woodland, we planted six native tree species of high wood value and contrasting physiological traits, in plots with increasing harvesting intensities (HI: 0, 30, 50 or 70% of basal area removal), and measured herbivory rates, herbivore guild diversity, and sapling survival and growth. To understand whether herbivore diversity in non-planted wild species was affected by harvesting intensity, we performed the same herbivore measures in six wild woodland plant species. Herbivory rates and herbivore guild diversity showed similar responses to HI, being highest on saplings growing at 30% (*N. dombeyi*, *N. antarctica*, *N. pumilio* and *N. alpina*) or 30% and 50% (*N. obliqua*) HI. Deciduous tree species were consumed at a higher rate and held more diverse guilds, whereas evergreen species were consumed at a lower rate or barely damaged. Differences among species seem to be mostly driven by leaf habit and nitrogen content. In turn, higher HI increased the heterogeneity of arthropod guild composition, being *N. alpina* and *N. pumilio* the species with most variation in guild composition across HI. Contrariwise, regarding the non-planted wild woodland species, there was no effect of HI on herbivory rates or guild diversity. Finally, planted tree species survived and grew more at 30% and 50% HI despite supporting higher leaf damage, except for *N. antarctica* which showed a similar survival rate across all HI. Species with highest performance were *A. chilensis* and *N. obliqua*; but differences regarding plant performance among species were not explained by their physiological traits. Approximately one-third to mid harvesting intensities in this Patagonian woodland were optimal for enhancing native tree plantation performance and sustaining herbivore guild diversity. Additionally, harvesting intensities did not affect guild diversity on woodland plants. Hence, both lines of evidence suggest an enhancement of both native-wood production and biodiversity conservation. Our study constitutes one step forward in the development of novel sustainable woodland management practices, applicable to other regions worldwide.

### 1. Introduction

Forests and trees cover about one-third of the world's land base and provide many different kinds of goods and services, where biodiversity conservation and wood supply remain at the top of the list (Horák et al., 2019). These ecosystems are heavily used as livelihoods and more than a quarter of the Earth's population depend on them (Landsberg and

Waring, 2014). However, practices to obtain forest and woodland goods usually imply massive clear-cuts and deforestation with the loss of typical vegetation and biodiversity. Nonetheless, more sustainable management practices could be applied in woodlands, such as combining tree harvesting of the original stand (i.e. firewood, posts) with native high value timber tree plantations.

Within a woodland management context, arthropod herbivory

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commonly has two opposite dimensions. Arthropods are potential pests but they also contribute to the woodland biodiversity (Maguire et al., 2015). Herbivory is one of the most important ecological interactions in the woodlands and arthropods are especially relevant among herbivores since they are the most diverse taxa and consume between 5 and 18% of the leaf mass (Turcotte et al., 2014). Some taxa can become pests, affecting plant performance due to leaf consumption or disease dispersion (Guyot et al., 2016). However, arthropods have the potential of also playing a positive role as pollinators in adult stages, as birds' food items and participating in the soil nutrient cycle (i.e. excrements, dead bodies) (Maguire et al., 2015). In a plantation combined with biomass extraction systems, herbivory needs to be monitored to assess whether planted trees performance is being affected and which harvesting intensity sustains more biodiversity within the remaining vegetation and the planted trees. Additionally, in a mixed plantation, different plant species might be differently preferred by herbivores because of their foliar traits (i.e. nitrogen content, toughness, C/N balance, etc.), their provenance (degree of association between local herbivores to trees from different areas of the region), their distribution, since plant species with wider distributions might be attacked at a higher rate by herbivores than more geographically restricted species (Paul et al., 2012; Forister et al., 2014; Kozlov et al., 2015a, 2015b), as well as due to the degree of specialization of the herbivores community (Novotny et al., 2010). Moreover, the effects of management intensity on the herbivory of planted trees might be affected by abiotic conditions, plant neighbours, or connectivity changes, which in turn might vary combined with unique features of the tree species (Paul et al., 2012; Underwood et al., 2014; Schuman & Baldwin, 2016). Yet, for Patagonian woodlands, as it happens in most forested ecosystems, it remains unknown how different tree species and their associated herbivores respond to a gradient of woodland extraction, and whether an optimum harvesting level exists that maximises both, plant performance and herbivore guild diversity.

In the case of low value timber ecosystems such as woodlands, a plausible practice in achieving sustainable woodland management would be to combine systematic harvesting with tree plantations. An ideal low-cost management procedure is to implement systematic biomass harvesting lines to commercialise smaller sized products (e.g. firewood, posts) instead of applying large clear-cut techniques. As a result, patches remaining within the original woodland have proved to enhance productivity, woodland health, resilience and biodiversity conservation, besides providing an initial economic income that helps cover the investment of planting trees (Gadow, 2006; Nacif, Kitzberger & Garibaldi, 2020; Goldenberg et al., 2020). Among plantation options, native tree plantations are a recommended option since they improve ecosystem and social value, conserve biodiversity and mitigate the risks associated to exotic species plantations such as fire propagation, potential invasion of plants, pathogens and/or other associated organisms (Cusack & Montagnini, 2004). In turn, plantations within a managed woodland, especially the ones composed by native tree species, improve features such as potential wood production, long term tree component and conservation of associated biodiversity (Bava, Loguercio & Salvador, 2015; Pretzsch, Forrester & Bauhus, 2017). Albeit, it remains a challenge to assess which native tree species could be ideal for such combined management practices; and what level of harvesting intensity would lead the highest tree productivity and sustained biodiversity.

In a plantation, the success of the initial stage following transplants (often saplings) is key to ensure good productivity. In this critical stage, survival and initial growth will be highly species-specific and context-dependent (Gadow, 2006). On the one hand, several intrinsic traits can shape species performance, such as shade and thermal range tolerance, growth rates, and biotic interactions depending on their mechanical and chemical traits (Pretzsch, Forrester & Bauhus, 2017). On the other hand, abiotic environmental conditions (here represented by harvesting intensities) would also interact with tree species leading to variable initial success of the plantation. For instance, planted trees could survive and grow more in large openings (i.e. increased harvested

areas) as radiation, mean temperature and available water increase (Piotto et al., 2003; Pafundi, Urretavizcaya & Defossé, 2014; Gönc et al., 2015). However, these large openings would also lead to more days of frost in winter, more hydric stress in summer and potentially more herbivory (Piper, Altmann & Lusk 2018). In this context, facilitation from wild trees and bushes to the planted saplings could be critical in some landscapes (Pretzsch, Forrester & Bauhus, 2017). Thus, plant response against a management stress gradient could be non-linear (Malkinson & Tielbörger, 2010; Nacif, Kitzberger & Garibaldi, 2020), meaning that plant performance does not simply increase or decrease with increasing harvesting intensities. Thus, even shade-intolerant species might be affected by high radiation levels, and plants that need shade protection cannot develop to their fullest (Bauhus et al., 2010; Liu et al., 2018). The different success rate among the planted species is relevant to inform managers about which species perform best under different scenarios (in terms of productivity) and sustain higher associated biodiversity for conservation purposes.

Historically, in Northwestern Patagonia, some types of woodlands have been heavily used for firewood extraction, cattle breeding and exotic tree plantation (Rusch et al., 2017). In the last decades, a renewed interest has emerged to sustainably manage these ecosystems (Grosfeld, Chauchard & Gowda, 2019), but appropriate levels of management intensity have been poorly assessed. These mixed woodlands are one of the most diverse ecosystems in the region (Speziale & Ezcurra, 2011) which also serve as a successional transition towards tall *Nothofagus* and/or *Austrocedrus chilensis* dominated forests (Veblen et al. 2006). Yet, they have rarely been used as natural nurseries for native tree plantations. Potential candidates for this management are trees of the *Nothofagus* genus and *A. chilensis*, prevalent canopy woody species of the temperate Patagonian forest which have traditionally been used for their high quality wood (Donoso & Promis, 2015). Moreover, these species are particularly interesting as they widely differ in their foliar traits, geographic distribution and dissimilarity from the local wild plants. Besides, the outcome of this study would directly contribute to enhance the management practices to improve production and conservation in several Patagonian land tracts.

The objective of our study is to assess how harvesting intensities and their associated environmental changes, influence arthropod herbivory rates and herbivore diversity, as well as sapling survival and growth, in six contrasting native high-quality wood species (i.e. *Austrocedrus chilensis* and five *Nothofagus* species) within a mixed woodland. In addition, we want to assess how harvesting intensities influence arthropod herbivory rates and herbivore diversity in six native wild woodland species. Specifically, our research questions addressed whether (1) there is an optimal harvesting intensity that can achieve both herbivore diversity conservation and high tree performance, (2) some plant species have better performance in this context while supporting diverse herbivore guilds and, (3) the herbivore diversity in non-planted wild plants is affected by harvesting intensities.

## 2. Materials and methods

### 2.1. Study site and harvesting experiments

This study was carried out during 2013 and 2014 on an experimental site, encompassing high-density multi-species woodlands, near El Foyel (Río Negro Province, Argentina, 41°38'48.44"S, 71°29'59.06"W), located at an altitude of 790 m.a.s.l. Woody broad-leaved species that conform the woodland are *Nothofagus antarctica* (Nothofagaceae), *Diostea juncea* (Rhamnaceae), *Schinus patagonicus* (Anacardiaceae), *Lomatia hirsuta* (Proteaceae), and *Embothrium coccineum* (Proteaceae) among others (Reque, 2007). The mean basal area is 46.7 m<sup>2</sup> ha<sup>-1</sup>, the mean basal diameter of trees is 6.1 cm and the mean dominant height is 4.4 m. The weather is cold-temperate with a seasonal precipitation during autumn and winter, reaching approximately 1100 mm annually. Mean annual temperatures range from 8 °C to 10 °C, with a maximum of 17 °C

and a minimum of 2.5 °C, annual relative humidity is around 75%, and the annual dew point is 3.9 °C. Frosts are present about 80 days per year, mainly during June-August. The soil, belonging to the group of Hapludands, is dark, slightly sandy with abundant roots (5.75 pH, 8.18 %C, and 0.49 %N).

Within this woodland, in May 2013, we applied four increasing levels of harvesting intensities in four plots (31.5 m × 45.0 m), meaning that we had one harvesting intensity level per plot (Nacif et al., 2020). The plots were aligned (east–west) and separated approximately 30 m from each other. We quantified harvesting intensities as the percentage of removed basal area (0%, 30%, 50% and 70%). Harvesting was done following six strips of different widths according to the harvesting intensities, across plots. In this way, in the plot with 30% harvesting intensity, the six strips had a width of 1.5 m (leaving a space of 3.0 m of intact vegetation in between strips). In the plot with 50% harvesting intensity the six strips were 2.5 m wide (remaining vegetation 2.0 m wide), and finally in the plot with 70% harvesting intensity the six strips were 3.5 m width (remaining vegetation 1.0 m wide). In the control plot, vegetation was left uncut (0% removal). Within the strips, all trees and bushes were cut with chainsaws and clearing saws at ground level, leaving them the possibility to regrow as these are mostly sprouting species. Young trees of *Austrocedrus chilensis* (D.Don) Florin et. Boutelje (ciprés de la cordillera), *Nothofagus alpina* (Poepp et Endl.) Oerst. (raulí), *N. antarctica* (G.Forst.) Oerst. (ñire), *N. dombeyi* (Mirb) Oerst. (coihue), *N. obliqua* (Mirb) Oerst. (roble pellín) and *N. pumilio* (Poepp et Endl.) Krasser. (lenga) were planted for sustainable production within the strips where harvesting was done, and their establishment success and growth was monitored for two growing seasons.

Among native Patagonian woody species, trees of *Nothofagus* genus and *A. chilensis* are prevalent canopy species with a high quality wood;




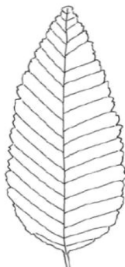


and thus, they are ideal candidates for plantations (Donoso & Promis, 2015). Even more, these species are particularly interesting as they widely differ in their foliar traits and geographic distribution (see Table 1; Appendix 1). *A. chilensis*, *N. antarctica*, *N. dombeyi*, and *N. pumilio* grow naturally in the latitude of the experimental site, and only *N. pumilio* naturally grows at approximately 200 m higher than the average experimental plots' altitude (Veblen et al. 1996). Even though, *N. alpina* and *N. obliqua* naturally grow at lower latitude, our experimental site included their potential planting area and genetic zone (Barbero et al., 2011; Azpilicueta et al., 2016).

In each of the six strips per plot, 30 saplings of every species were planted; for a total of 720 planted trees. Saplings were 3–4 years old and 0.3–0.9 m in height, which was an optimal plant age across species to improve their establishment after plantation, as younger stages are associated with higher mortality rates (Azpilicueta et al., 2010, Donoso Zegers, 2013). The saplings were bought from different nurseries, belonging to three different geographic sources in Río Negro and Neuquén Provinces for each species, but then we grew and acclimatized them under similar conditions for three weeks before transplanting. To account for any possible differences among origins, ten specimens per species from each source were used. Saplings were planted 1.5 m apart along each line, giving a plantation density of 1269 plants per hectare; these densities are expected to be compatible with the development of wild forest species (Azpilicueta et al., 2010). The planting process was achieved within four days.

In order to characterize the environmental conditions, at each harvesting intensity level, we measured: air temperature, relative air humidity (Ibutton DS 1923, U.S.), photosynthetic active radiation (PAR, using a Cavadevices Ceptometer, Arg.), soil moisture (Lutron PMS-714) and leaf area index (LAI) taken by hemispherical pictures across the

**Table 1**

Comparison between *A. chilensis* (Cupressaceae) and five species of *Nothofagus* (Nothofagaceae), for different features. OR: Own results. \*<sup>1</sup>Arthropod herbivory, leaf damage frequency. \*<sup>2</sup>Arthropod guild diversity (H). \*<sup>3</sup>Plant relative height growth rate (proportion). \*<sup>4</sup>Plant survival. \*<sup>5</sup>Light compensation point. \*<sup>6</sup>Water potential at 50% loss of stem hydraulic conductivity (P50). ARG: Argentina, CL: Chile.

							
Herbivory (proportion)* <sup>1</sup>	0,39	0,40	0,42	0,39	0,20	0	OR
Diversity (H) * <sup>2</sup>	0,62	0,71	0,54	0,58	0,35	0	OR
RGR(proportion) * <sup>3</sup>	0,13	0,19	0,073	0,043	0,10	0,29	OR
Survival (%) * <sup>4</sup>	58	78	54	42	35	80	OR
Leaf area (cm <sup>2</sup> )	4,6	8,5	5,6	27,0	3,6	0,05	Demaio et al., 2017
N (%)	2,28	2,55	2,36	2,30	1,38	0,84	Diehl et al., 2008
C/N (Proportion)	75	55	90	60	70	95	Diehl et al., 2003
SLA (m <sup>2</sup> g)	0,014	0,018	0,015	0,022	0,0097	0,0068	Diehl et al., 2003
LMA (g m <sup>-2</sup> )	70	57	66	46	103	148	Diehl et al., 2008
LCP (μmol quanta m <sup>-2</sup> s <sup>-1</sup> )* <sup>5</sup>	48,0 <sup>2</sup>	15,5 <sup>1</sup>	25,0 <sup>2</sup>	8,5 <sup>1</sup>	16,5 <sup>1</sup>	10,0 <sup>3</sup>	<sup>1</sup> Read & Hill, 1985; <sup>2</sup> Peri et al., 2009; <sup>3</sup> Gyenge et al., 2007
Xylem pressure (MPa)* <sup>6</sup>	-4,2 <sup>1</sup>	-3,2 <sup>1</sup>	-3,8 <sup>1</sup>	-2,7 <sup>2</sup>	-3,8 <sup>1</sup>	-4,2 <sup>3</sup>	<sup>1</sup> Bucci et al., 2012; <sup>2</sup> Dettman et al., 2013; <sup>3</sup> Sergent et al., 2020
Wood density (g cm <sup>-3</sup> )	680 <sup>1</sup>	590 <sup>1</sup>	590 <sup>2</sup>	520 <sup>1</sup>	650 <sup>1</sup>	495 <sup>2</sup>	<sup>1</sup> Dettman et al., 2013; <sup>2</sup> Tortorelli, 2009
Vegetation type	Broad-leaved deciduous	Broad-leaved deciduous	Broad-leaved Deciduous	Broad-leaved deciduous	Broad-leaved evergreen	Conifer evergreen (Scale-like leaf)	Gut, 2008
Latitudinal distribution (S)	ARG 36°30'-56°	ARG 36°50'-40°15'	ARG 35°35'-55°	ARG 39°24'-40°10'	ARG 38°30'-44°	ARG 37°7'-43°44'	Veblen et al., 1996
	CL 36°30'-56°	CL 33° - 41°30'	CL 35°35'-55°	CL 35° - 41°30'	CL 34°40'-48°	CL 32°39'-38°	

harvesting intensities (Nikon Coolpix 900 equipped with a hemispherical lens of 180°, the pictures were analyzed with the HemiView program). Air temperature and relative air humidity were measured throughout the second vegetative growing season, daily and every 30 min, with Dataloggers situated in the middle of one harvested strip at 0.75 m from the topsoil. Soil moisture and PAR were measured in December and February, three times in three strips per plot.

In order to measure arthropod herbivory, we randomly selected six saplings per species per strip (two saplings from each origin, 144 plants in total). In each individual, one small branch intentionally marked, at intermediate plant heights was sampled and arthropod herbivory was recorded in 18 leaves per branch, and then the values were averaged to obtain one value per tree. We measured arthropod herbivory for two growing seasons on four dates during spring (October and December) and summer (February and March), recording the same trees and branches every year and date, starting on October 2013. Arthropod herbivory was quantified by computing the frequency of leaf damage (number of damaged leaves/total), and the leaf area damaged quantified by visual estimation (the sum of leaf area damaged excluded galls and borers in this damage category), following the methodologies proposed by Garibaldi, Kitzberger & Chaneton, 2011. Herbivory measurements in the field were achieved within two or three days on every measure date. We classified arthropod herbivores and leaf damage into nine different guilds such as leaf chewers, bud feeders, hole feeders, skeletonizers, sticky feeders, surface abrasion feeders (grouped as exophagous feeders), and miners, sap-sucking and wrinkling feeders, and galls (grouped as endophagous feeders); protocols and classification were based on McQuillan (1993), Novotny et al. (2010) and Garibaldi, Kitzberger & Chaneton (2011). Guild diversity was analyzed with the Shannon-Wiener index, and the correlation with other indices, such as the Shannon evenness index and number of guilds for richness was explored (Magurran 2004). Finally, in order to characterize arthropod herbivory rates in the wild plants species within the woodland, we applied the aforementioned protocol for six common native tree/shrub species across the plots: *Nothofagus antarctica*, *Schinus patagonicus*, *Lomatia hirsuta*, *Embothrium coccineum*, *Maytenus chubutensis* (Celastraceae) and *Ribes cucullatum* (Grossulariaceae) (Appendices 1 and 2), by randomly selecting six individuals of similar size as the planted saplings per plot.

Planted tree performance was assessed by their survival rate and relative height difference within a growing season for two consecutive years. Relative height growth was defined as the difference between the maximum height of the apical meristem in April and the maximum height of the apical meristem in October divided by the maximum height of the apical meristem in October; used as a proxy of plant growth rate (West, 2014). For plant performance, we measured all the available planted trees (initially 120 plants for every native tree species).

## 2.2. Statistical analysis

We analyzed the effects of harvesting intensity on arthropod herbivory guild diversity, total leaf damage frequency and relative plant height growth rate, using linear mixed-effects models in R (R Core Team 2020), with the *lmer* function (lme4 package, Bates 2011). For sapling survival, we used generalised linear mixed-effects models, using the *glmer* function, of the lme4 package (binomial distribution, Bates 2011). These models take into account the hierarchical structure of the data at different levels or classes combining fixed and random effects (Zuur et al., 2009). The models considered the fixed effects of harvesting intensities (quantitative variable), squared harvesting intensities (to consider non-linear responses to harvesting), species (categorical variable), and year (categorical variable), as well as their interactions. In the same model, the random effects of plant origin and plot were evaluated. *A. chilensis* has not been included in the mixed-effects models, because herbivore consumption was almost 0 in every harvesting intensity category. As for the inferential statistical framework, multi-model

inference was used (Burnham et al., 2011). The minimum adequate model by the lowest AICc value (corrected form of the Akaike Information Criteria) using the function *dredge* (package MuMin, Burnham et al., 2011) was selected. We calculated the relative importance value for each predictor variable with the *importance* function in the package MuMin, which sums the 'Akaike weights' over all the models that include the predictor variable. We explored the correlation between herbivory rates, diversity indices and sapling performance variables using Spearman correlations, as well as the correlation of such variables with different plant leaf traits available in the literature. Finally, we used NMDS (Non metric multidimensional scaling) to explore guild composition and differences within species and harvesting intensities (using the function *metaMDS*, package Vegan, Oksanen et al., 2019). NMDS is an indirect gradient analysis approach which produces an ordination based on a distance or dissimilarity matrix. This tool was used to collapse information from multiple dimensions to be visualized and interpreted using rank orders (e.g, harvesting intensities, plant species and herbivore guilds).

## 3. Results

The mixed-effects models showed that for the planted species, harvesting intensity, species and year were important predictors for all response variables (see relative importance in Table 2, and estimated coefficients of the model in Appendix 3). We found double interactions between all the variables for all the models for planted species, and triple interactions for plant growth models (see relative importance in Table 2, and estimated coefficients of the model in Appendix 3). As regards to environmental conditions of plots, air summer temperature, PAR and annual frost increased with the increasing harvesting intensities, whereas relative air humidity and LAI decreased, and soil moisture was not affected (Appendix 4).

Herbivory rates and diversity patterns represented in our study equivalent parameters of biodiversity, as they behaved similarly within planted species in response to harvesting intensity. Yet, both parameters differ among the six planted species (Fig. 1), showing that native trees sustain variable arthropod biota and respond differently to harvesting intensity. Comparing herbivory rates among species beyond harvesting intensities, the evergreen species were consumed at a lower rate (*N. dombeyi*) or barely damaged (*A. chilensis*), whereas the deciduous ones, *N. pumilio*, *N. antarctica*, *N. obliqua*, and *N. alpina* were consumed at a higher rate. Also *N. pumilio*, *N. antarctica*, and *N. obliqua* harboured more diversity. In addition, for *N. dombeyi*, *N. antarctica*, *N. pumilio* and *N. alpina*, damage frequency mostly decreased with increasing harvesting intensities, whereas the damage frequency in *N. obliqua* was highest at intermediate harvesting intensities. Regarding richness of herbivory guilds, planted juvenile trees sustained up to 9 foliar herbivore guilds, varying between 3 and 9 among species and treatments (Appendix 5); additionally, guild richness decreased across harvesting intensities, with values of 7.8 at 0%, 7.8 at 30%, 5.8 at 50%, and 5.4 at 70% (Appendix 5). Leaf damage frequency and guild diversity were higher during the second year, except for *N. alpina* (Fig. 1). Leaf damage frequency and damaged leaf area were highly positively correlated, as were guild diversity, evenness and richness (Appendix 6).

NMDS analysis showed that higher harvesting intensities provide a more heterogeneous scenario for arthropod guild composition than lower ones. Additionally, the planted species and herbivore guilds showed specific responses and sensitivity to harvesting intensity. Among tree species, *N. alpina* and *N. pumilio* showed more variation in their herbivore composition guilds across harvesting intensities compared with *N. obliqua*, *N. antarctica* and *N. dombeyi*. As regards arthropod guilds, leaf chewers, skeletonizers and galls contributed the most to the difference among the planted tree species and harvesting intensities than any other guilds (Appendix 7).

In the case of the six native wild woodland species, the mixed-effects models showed that species and year were important predictors of

**Table 2**

Relative importance of each predictor variable. Relative importance values are calculated from the sum of the “Akaike weights” over all models which include the predictor variable. Bold relative importance values are variables or variable interaction included in the minimum adequate model (Harvesting<sup>2</sup> = squared Harvesting in order to consider non-linear responses to Harvesting Intensities).

	Planted species				Wild woodland species	
	Total herbivory	Guild diversity	Plant survival	Plant growth	Total herbivory	Guild diversity
Harvesting	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	0.25	0.48
Harvesting <sup>2</sup>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	0.25	0.49
Year	<b>0.99</b>	<b>0.98</b>	<b>1</b>	<b>1</b>	<b>0.97</b>	<b>0.62</b>
Species	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>
Year × Harvesting <sup>2</sup>	<b>0.68</b>	<b>0.80</b>	<b>1</b>	<b>1</b>	0.06	0.12
Year × Species	<b>0.93</b>	<b>0.95</b>	<b>1</b>	<b>1</b>	0.03	0.32
Species × Harvesting	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	0.12	0.31
Year × Species × Harvesting <sup>2</sup>	<0.01	0.26	0.21	<b>0.99</b>	<0.01	<0.01

damage frequency and guild diversity, but not harvesting intensity (Table 2, Fig. 2 and Appendix 3). In other words, for the non-planted wild species, leaf damage frequency and arthropod guild diversity were equally sustained irrespective of harvesting intensity (i.e. remaining woodland width bands). As shown before, the deciduous or semi-deciduous species were consumed at a higher rate than evergreen ones; and during the second year, damage frequency and guild diversity were higher than in the first year. Finally, they sustained up to 6 foliar herbivore guilds, varying between 1 and 6 among species and treatments, surprisingly sustaining fewer guilds than the planted trees (Appendix 8).

Finally, most planted species survived at highest rates at intermediate harvesting intensities (30% and 50%); in the case of *A. chilensis* and *N. dombeyi* their survival was also highest without any harvesting, and *N. antarctica* survived at a similar rate across all harvesting intensities (Fig. 3). The overall highest survival rates were recorded for *A. chilensis*, *N. pumilio* and *N. obliqua*. Similarly, all the saplings grew more at intermediate harvesting intensities, especially during the second year; except for *N. antarctica* for which higher harvesting intensities had more positive effects. This pattern was less obvious during the first year, as initially saplings grew dissimilarly and showed more linear responses to harvesting intensities.

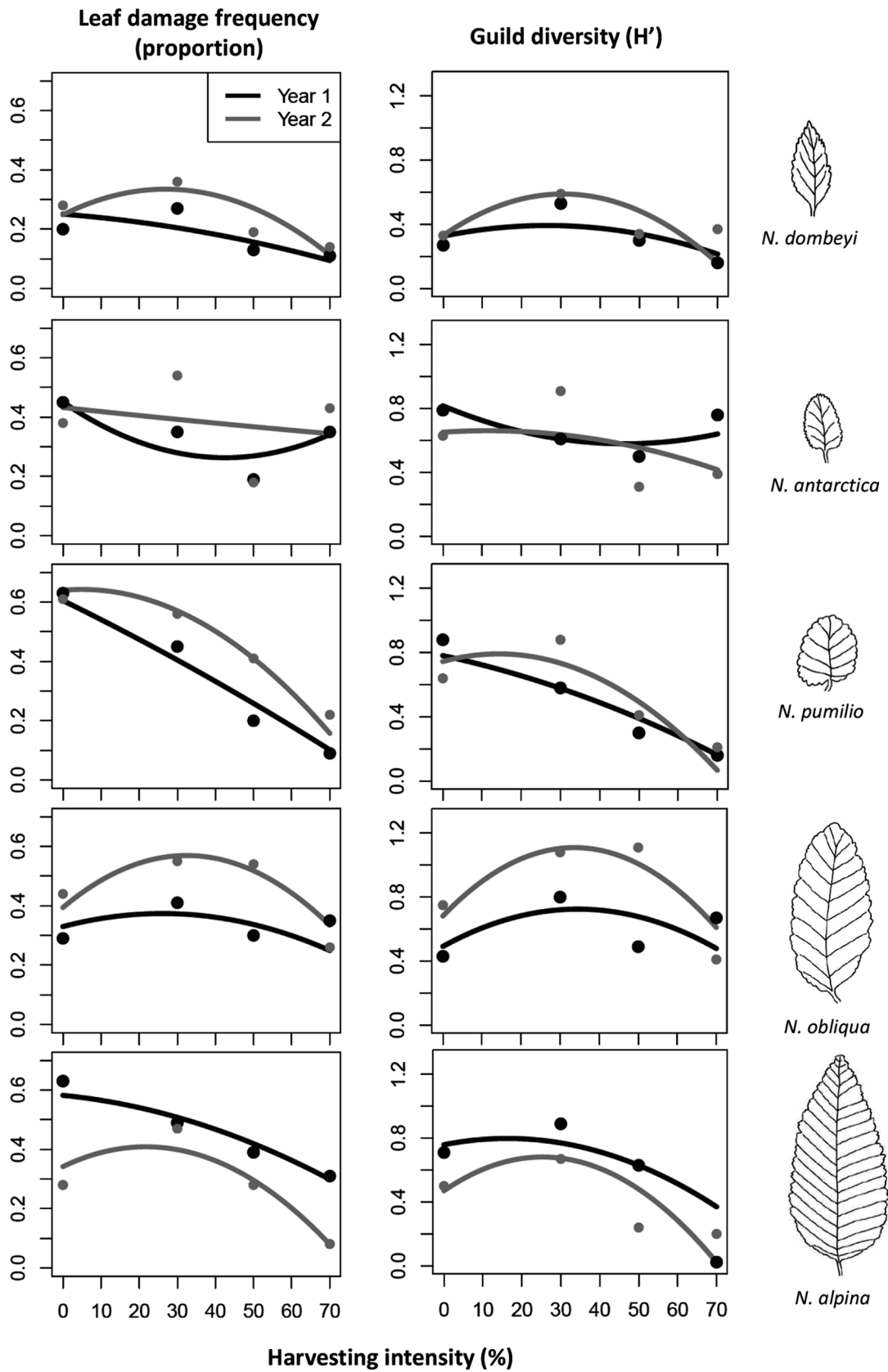
#### 4. Discussion

Achieving sustainable forest and woodland management practices remains a challenge across many ecosystems; yet, successful examples of combined practices that simultaneously enhance primary productivity and biodiversity conservation are rising (Chaudhary et al., 2016; Martínez Pastur et al., 2018; Grosfeld, Chauchard & Gowda, 2019). Here we demonstrated that intermediate harvesting intensities for biomass extraction in Northern Patagonian woodlands was positive for achieving both high herbivory rates and guild diversity on planted native trees, and greatest tree performance, despite higher leaf damage rates. At the same time, such management did not alter the herbivore guild diversity sustained by the wild woodland species, measured as foliar arthropod herbivores. Furthermore, intermediate harvesting intensities even provide economic returns to local owners in the short-term through extracted firewood and posts (Goldenberg et al., 2020).

Intermediate harvesting intensities might be quite different among forested landscapes, within Patagonian woodlands and across other temperate ecosystems, as stand structure, tree density and/or leaf area index vary from site to site. Thus, in our site, intermediate harvesting intensities (i.e.; 30–50%) corresponded to a suite of abiotic and biotic parameters that might be easier to contrast across other forested ecosystems. Specifically, in terms of environmental conditions we showed that low and mid harvesting intensities corresponded to 1.08 to 0.50 mol m<sup>-2</sup> yr<sup>-1</sup> leaf area index, between 83 and 89 frost days per year, and 323.36 to 535.86 nm of photosynthetic active radiation. On the other hand, for vegetation structure Goldenberg et al. (2020) measured that 30% and 50% harvesting intensities in a high productivity site

represented between 27.6 m<sup>2</sup> ha<sup>-1</sup> to 23.9 m<sup>2</sup> ha<sup>-1</sup> basal area, which corresponded approximately 3581 to 1591 plants ha<sup>-1</sup> remnant plant density and are 86.8 to 159.1 (m<sup>3</sup> ha<sup>-1</sup>) of firewood. Finally, on the same sites, Chillo et al. (2020) found that functional plant diversity was 0.08 to 0.17 Rao’s Q index, and taxonomic plant diversity was 3 to 10 Chao q1 index, for intermediate harvesting intensities. More importantly, beyond mean values, functional plant diversity was not threatened by intermediate harvesting intensities. The aforementioned mean values resulted in the best site conditions for planted species and associated herbivores.

Herbivory rates and diversity patterns behaved similarly within and across the planted native tree species, being both highest at lower and intermediate harvesting intensities. This pattern is not surprising as disturbance theory has often shown that highest local species diversity occurs at intermediate disturbance frequencies and/or intensities (intermediate disturbance hypothesis, Schowalter, 2012; Muiruri et al., 2019). Several mechanisms could explain this pattern. On the one hand, resource density and plant appearance positively affects arthropod abundance (Endara & Coley, 2011; Castagneyrol et al., 2013), and according to our results, both parameters were enhanced as the survival rate and growth of the planted trees were highest at intermediate harvesting intensities. On the other hand, increased temperature in forest gaps had been associated to higher herbivory and herbivore diversity in our southern temperate forests due to temperature limitations associated with shade (Piper, Altman & Lusk, 2018), likely explaining the spike of biodiversity here seen at intermediate harvesting intensities. Yet, as harvesting intensities increased, the exposure to harsher environmental conditions, could have negatively affected arthropod herbivory directly, as reported in other studies. For instance, even though higher harvesting intensities raise average annual temperatures benefiting arthropods, they also increase the annual thermal range and the number of days with frost, producing detrimental effects on arthropod abundance (Savilaakso et al., 2009; Paillet et al., 2010; Lencinas et al., 2014; Soler et al., 2016). Additionally, environmental conditions can indirectly affect arthropods through plant leaf traits, leading to altered leaf palatability due to, for example, excessive radiation (Mazía et al., 2012; Hambäck et al., 2014). Finally, lower harvesting intensities (lower than 30%) could imply more connectivity among plants, and more biomass for arthropod protection, oviposition, and development (Maguire et al., 2015), contributing to higher niche diversity and/or more available resources for larger populations. Interestingly, diversity was positively correlated with herbivory rates for almost all species, suggesting that the same or similar mechanisms could be at play for both variables. Overall trends were stronger over the second growing season following transplant, probably due to a combination of cumulative effects and higher temperatures in the second year (SMN, 2020). Hence, the general trend observed across most planted tree species of greatest diversity and frequency of interaction (i.e. herbivory rates) at 30% harvesting intensity, or even 50% for *N. obliqua*, highlights the essential role that native tree plantations within a native woodland have for conservation, since they harbour and maintain



**Fig. 1.** Response of leaf damage frequency (proportion) and guild diversity to harvesting intensity for the five *Nothofagus* species. Each point is the average value of a plot, and curves are the predicted values from mixed-effects models.

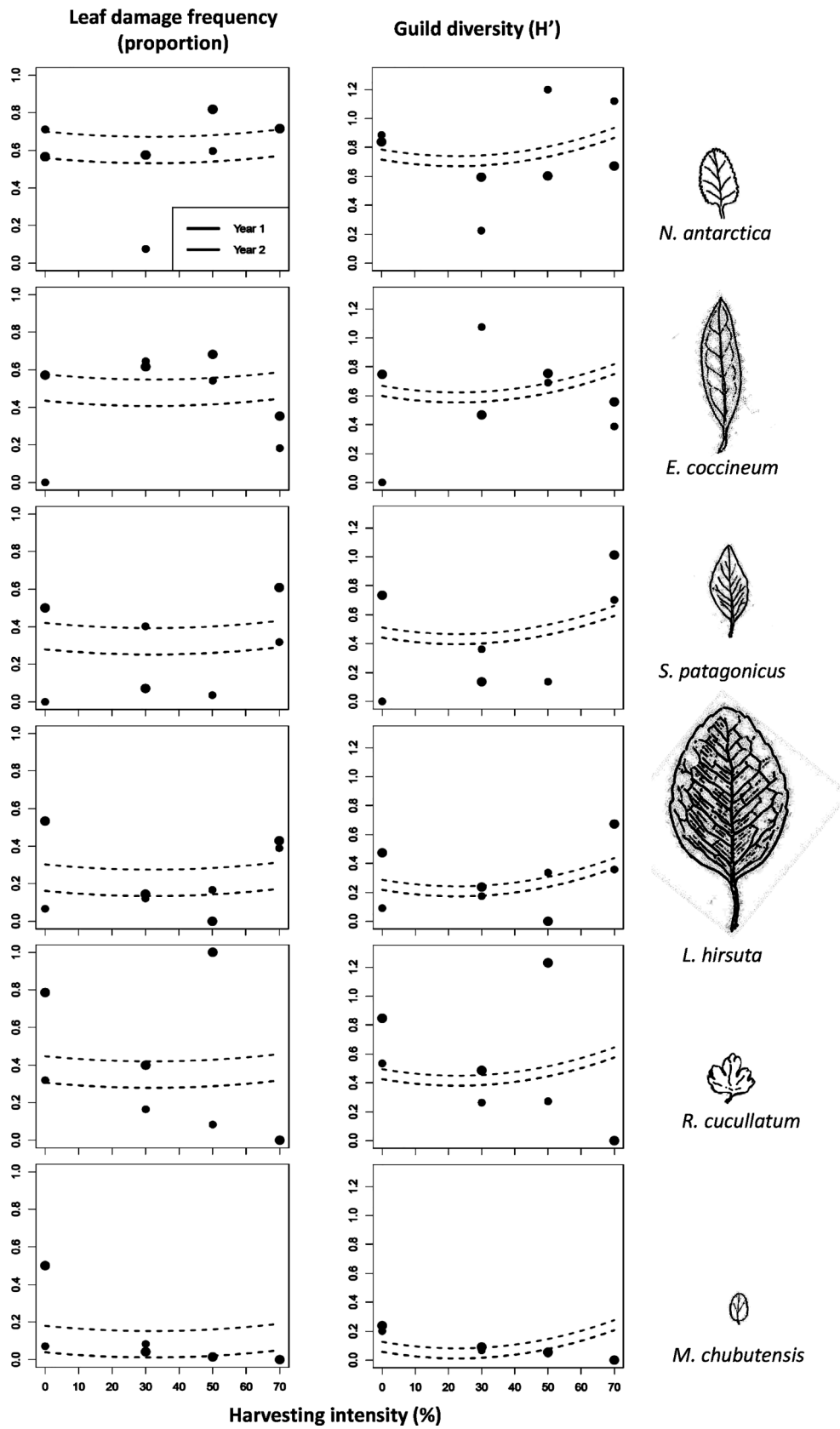


Fig. 2. Response of leaf damage frequency (proportion) and guild diversity to harvesting intensity for the six wild woodland species. Each point is the average value of a plot, and curves are the predicted values from mixed-effects models.

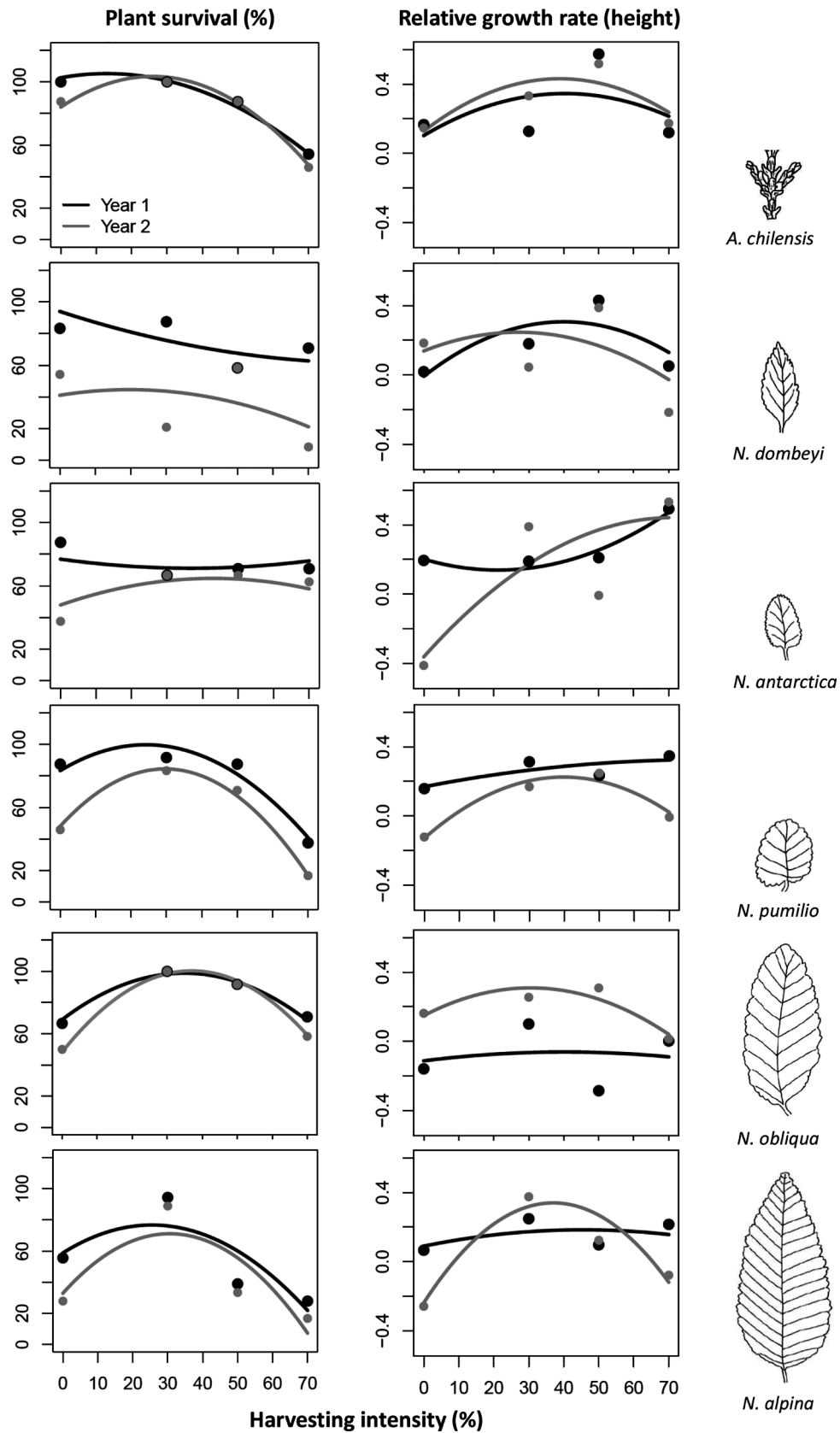


Fig. 3. Response of plant survival and growth to harvesting intensity for the six planted species. Each point is the overall survival or average growth value of a plot, and curves are the predicted values from mixed-effects models.



arthropod diversity.

Moreover, variability at the interspecific level was quite remarkable. Evergreen tree species were consumed at a lower rate (*N. dombeyi*) or barely damaged (*A. chilensis*), whereas deciduous ones were consumed at a higher rate. In addition, *N. pumilio*, *N. antarctica*, and *N. alpina* were consumed at a higher rate at lower harvesting intensities (0% and 30%) whereas *N. obliqua* was consumed at a higher rate at intermediate ones (30% and 50%). These differences in consumption rates among species were according to theory, since our deciduous species differ from evergreen ones not only in their foliar habit but also in their classification within the leaf economy spectrum (Poorter & Bongers, 2006, Wright et al., 2004). In this study, evergreen species resulted in resource conservative species, being their leaves less palatable to herbivores due to low nutrient content and high proportion of support tissue (Chabot & Hicks, 1982). Similar findings were reported by Piper et al. (2019), where *N. betuloides* (similar evergreen species) was less consumed than *N. pumilio*. In turn, deciduous species in this study are identified as a resource acquisitive species, since they have higher specific leaf area and higher nitrogen concentrations than evergreen species, as Diehl et al., (2008) measured. Thus, herbivory rates among species beyond foliar habit were probably mediated by interspecific variability in leaf nitrogen content (Whitfield et al., 2012), with high leaf N content species supporting more diverse guilds and higher consumption rates than low N content tree species (see Table 1 and Appendix 9). Furthermore, leaf traits seem to be more relevant than current species geographic distribution, as *N. obliqua* was highly consumed and sustained the most herbivore diversity despite being planted outside its distribution range. Yet, *N. antarctica* and *N. pumilio* were also consumed at high rates, probably due to their wide geographic distributions across the Patagonian region (Donoso, 2013) thereby increasing the chances of their antagonists presence. In contrast, even though previous studies have suggested that among several *Nothofagus* species, *N. dombeyi* is often consumed at a high rate (Donoso, 2013), we did not observe such trend. One possibility is that those results were reported on the cumulative damage on leaves of previous years, while in this work damage was only measured on new leaves. Additionally, *A. chilensis* did not register any significant damage, beyond rare mechanical ones and some fungi-like attacks, but no typical aphid consumption was observed as cited in Montalva et al., (2010). Furthermore, *N. obliqua* and *N. alpina* whose current distributions do not include the plantation area became a suitable habitat for local arthropod diversity.

Arthropod guild composition substantially changed among planted tree species and as a function of harvesting intensity treatments, with higher harvesting intensities leading to more heterogeneous communities among species, as NMDS analysis showed. Meaning that planted tree species at 0% and 30% harvesting intensities sustained more similar foliar arthropod communities (i.e., guild composition), than those same species at 50% and 70% harvesting intensities. Moreover, at higher harvesting intensities, most tree species showed large variation in guild composition, mostly driven by missing guilds. Additionally, tree species varied in their response to harvesting treatments. For instance, *N. alpina* and *N. pumilio* showed more variation in their guild composition among harvesting intensities than *N. obliqua*, *N. antarctica* and *N. dombeyi*. This means that, beyond interspecific differences in herbivory and diversity rates, some species were more susceptible to management techniques, sustaining often fewer foliar arthropod species and guilds. In turn, the arthropod guilds with higher consumption rates and contribution to these changes across harvesting intensities and plant species are contrasting, including exophagous (such as chewers with  $0.13 \pm 0.016$  damage frequency and skeletonizers with  $0.093 \pm 0.013$  damage frequency) as well as endophagous (like gall formers, with  $0.025 \pm 0.0095$  damage frequency). For the endophagous ones, this variation might be explained by their high specificity and low mobility (Novotny et al., 2010; Mazía et al., 2012), being more affected by micro-environmental changes within leaf tissues (Garibaldi, Kitzberger & Chaneton, 2011) than free-feeders. Yet, as less specific and more mobile guilds behaved

similarly (chewers and skeletonizers), other factors such as connectivity and foliar traits might be playing a key role. Finally, in terms of guild composition, the choice of which tree species to plant becomes relevant since some native trees above 50% harvesting intensities are more susceptible to guild loss, such is the case of *N. alpina* and *N. pumilio* while *N. obliqua*, *N. antarctica* and *N. dombeyi* appear to be less affected.

Contrariwise to the planted trees, for the six wild woodland species, there was no effect of harvesting intensity on the arthropod herbivory rates or guild diversity, even though there were different damage levels among them. This means that the remaining strips of woodland, up to the width evaluated here (i.e.  $1 \text{ m} \times 45 \text{ m}$  to  $3 \text{ m} \times 45 \text{ m}$ ), can still sustain similar diversity and ecological interactions despite the removal of large woodland biomass. This result might be explained by the role played by abiotic conditions and biotic interactions. Opposite to planted trees, which were in the middle of the harvested strips, non-planted wild species were surrounded by established vegetation, of conspecific and interspecific neighbours, within the remaining woodland strips; also connected to the remnant woodlands around the plots. In this way, the herbivores in non-planted wild species might be less affected by the environmental differences associated to harvested strips than herbivores in planted species. As seen for the planted species, consumption rate and guild diversity were greater during the second year, probably due to climatic differences between years since the second sampling season was warmer than the first one, and/or due to a re-composition effect after the disturbance caused by the harvesting intensities. Differences in herbivore damage among the wild species, although less significant than seen for the planted species, were probably also related to foliar habit and traits. Indeed, species consumed at the highest rate or those that sustained the greatest diversity of guilds were deciduous and have either high nitrogen and less tough leaves (*N. antarctica*, *R. cucullatum*) or were wintergreen but highly abundant in the woodland (*E. coccineum*) (see Appendix 2). In general, the wild species had similar herbivory rates and diversity as the planted tree species, but supported fewer guilds. This difference might be driven by the disparity in resource concentration between scenarios, as the wild plants sampled were surrounded by many more potential hosts than those in the plantation lines (Hambäck et al., 2014; Underwood, Inouye & Hambäck, 2014), and/or the planted native tree species provided higher quality leaves than the wild ones except for *A. chilensis* (Diehl et al., 2008). Nonetheless, the above mentioned settings can be comparable, as similar patterns arose between the unique species present in both, *N. antarctica*. Particularly, both wild and planted *N. antarctica* saplings had higher consumption rates and guild diversity compared with all the other species in both scenarios. In summary, our results suggest that as long as there are remnant patches within a continuous woodland, the measured ecological interactions, arthropod herbivory and guild diversity, might not directly depend on the percentage of biomass extraction.

While sustaining high arthropod herbivory could be detrimental for plant performance, here we observed that plant survival and growth rates were not correlated with herbivory measures. Probably, high herbivory along with high performance could be in part explained by the high herbivory tolerance reported for some deciduous *Nothofagus* species (Piper & Fajardo, 2014). Instead, in our system, plant performance seems to be affected directly by the environmental factors that the different harvesting intensities provide. Specifically, an increase in temperature of 2 °C and three to five more times of PAR light, probably drove the highest rates of survival of most planted species at intermediate harvesting intensities (30% and 50%); but see the case of *A. chilensis* and *N. dombeyi* where their survival was also highest without any harvesting, and *N. antarctica* that survived at a similar rate across all harvesting intensities. *Nothofagus* trees are shade intolerant and their regeneration dynamics is associated with forest and woodland disturbances and light gaps (Veblen et al., 1996; Donoso, 2013), but interventions with large biomass extraction (70% harvesting intensity) might intensify some factors that are also harmful to plant survival such as annual frost, high radiation levels and hydric stress (Ramírez et al.,

1997; Reyes-Díaz et al., 2005; Donoso, 2013; Charrier et al., 2015). Indeed, a few studies of *Nothofagus* seedling regeneration and plantation experiments mention greater success with low plant cover (Heinemann & Kitzberger, 2006; Lencinas et al., 2007; Martínez Pastur et al., 2011; Soto et al., 2015). In turn, *N. antarctica* survived similarly across all harvesting intensities, which is not surprising given that it is a species resistant to extreme environmental conditions, such as cold temperatures and high light exposure (Steinke et al., 2008). On the other hand, even though *N. dombeyi* is referred to as a species that needs high radiation levels (Donoso, 2013), in our study it had the lowest survival rate at maximum harvesting intensities during the second year, suggesting that it might be negatively affected by low humidity. The same pattern was observed in *N. alpina*. Furthermore, and contrary to the literature, *N. alpina*, did not result in the most shade resistant species (Donoso, 2013). Finally, *A. chilensis* survived more than the other species when there was no harvesting, due to its shade tolerance and early protection against high radiation levels (Urretavizcaya & Defossé, 2019). In sum, if a higher survival rate of the species is needed, *N. obliqua*, *N. pumilio* and *A. chilensis* are the ideal species while *N. antarctica* is the best species if the plantation site presents high variation in terms of canopy cover. Nonetheless, in general and across species, survival rates could be optimised through the application of intermediate management intensities, which would minimise the need of replanting.

In addition to plant survival rates, the success of a tree plantation is achieved when plant growth rates are sustained over time following transplant. Once again, microclimatic conditions of intermediate harvesting intensities improved the growth of all the species during the second year, except for *N. antarctica*; a pattern that was not obvious during the first year, as initially, plants grew dissimilarly. As the levels of light and temperature rose with the increasing harvesting intensities up to 50%, overall plant growth improved for all the planted tree species. Similar results were found regarding growth in *N. pumilio* (Martínez Pastur et al., 2011) and *N. obliqua* (Varela et al., 2012; Torres et al., 2018). However, plant growth patterns across harvesting intensities was not linear, as 70% harvesting intensities offered adverse growth conditions (Anderegg et al., 2015). In some cases, even negative growth rates were observed in the resprouting species *N. alpina*, *N. obliqua*, and *N. antarctica*, classified this way in Grosfeld, Chauchard & Gowda (2019).

Overall, intermediate harvesting intensities were an optimal management strategy, providing biomass such as firewood and posts, having positive effects on resprouts and woodland regeneration (Chaudhary et al., 2016; Goldenberg et al., 2020), and as showed here, providing open areas where native trees can successfully be planted. Even more, this management allowed the highest survival and growth rate of transplanted saplings of most high quality native woody species, while sustaining the highest foliar herbivore diversity. Thus, even in dry years where trees need more protection against desiccation, applying intermediate harvesting intensities would be a successful practice. Specifically, when biomass volume extraction (i.e. harvesting intensity) can be managed, *N. obliqua* and *A. chilensis* are the recommended species due to their best survival and growth rates. Moreover, at higher or variable harvesting intensities, *N. antarctica* showed better performance, thus being an ideal species for planting and restoring unfavourable sites, such as aforementioned extreme environmental conditions. Interestingly, *N. alpina* and *N. obliqua* showed positive results in terms of survival rate and arthropod interactions, despite being planted south of their natural distribution, highlighting that these species would be better for ecological interactions and biodiversity conservation than common planted exotic species that often decrease diversity (Nuñez & Paritsis, 2018). As regards survival and growth, in our data, differences among planted species were not explained by their physiological traits provided by the literature (Table 1 y Appendix 9). However, as Poorter & Bongers (2006) mentioned, several leaf traits are good predictors for plant performance under different scenarios. Therefore, further studies and assays would help determine whether differences among planted species

across harvesting intensities are explained by their physiological traits.

## 5. Conclusions

Harvesting techniques (i.e. for firewood and post extraction) combined with native tree plantation arise as an optimal management practice in the woodlands of Northwestern Patagonia, specifically when applied at low to intermediate harvesting intensities. Mid harvesting intensity provided a good scenario not only for planted native tree survival and growth, but also for maintaining rich herbivore communities in the planted trees, and on the remnant vegetation since harvesting intensity did not affect woodland wild species herbivores. This suggests that these combined management strategies are an ideal opportunity for sustainable management to maintain or increase biodiversity in the woodland ecosystem. Additionally, for all planted species, arthropod herbivory rates and guild diversity indices were highly correlated, either one being a good biodiversity indicator. Furthermore, leaf damage and guild diversity rates were not correlated with plant performance, highlighting the successful coexistence between the reported damage rates and the native tree plantation. More importantly, beyond the morphological and physiological differences among the planted tree species, harvesting intensities become a more determinant management practice for survival rates and plant growth than species identity.

Combined management practices, such as the ones proposed in our study, are still a challenge in many regions of the world, including Patagonia, regarding plantation cycle (temporal and economic aspects), woodland systematic harvesting, and cultural use of native trees. Yet, their multiple benefits are promising. For example, native tree plantations are needed worldwide as a long-term management strategy to prevent and deal with the impacts of biological invasions (i.e. invasive timber species, Simberloff et al., 2013). We encourage the application of our experimental approach to other systems, especially in forest and woodland landscapes where planted saplings need protection during their critical stages across dry seasons. Here, native tree plantations or trees genetically related to local ones, provided a suitable option for local herbivores, promoting a richer landscape without impairing plantation performance. Hence, our outcome calls for more empirical studies testing the generality of these trends across other temperate and tropical forested ecosystems.

## Authors contributions

LG and MN conceived the idea and designed the study. MN collected the data. MN, CQ and LG analyzed and interpreted the data and led the writing of the manuscript with substantial input from all co-authors. All authors gave final approval for publication.

## CRedit authorship contribution statement

**Marcos E. Nacif:** Conceptualization, Methodology, Formal analysis, Data curation, Investigation, Writing - original draft, Writing - review & editing. **Carolina Quintero:** Writing - original draft, Writing - review & editing. **Lucas A. Garibadi:** Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Funding acquisition.

## 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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118719>.

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