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Anthropogenic Impacts Allowed for the Invasion of Understory Species, Affecting the Sustainability of Management Practices in Southern Patagonia

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Abstract: Forest management aims to preserve integrity and ecosystem resilience. Conservation and species invasion patterns must be determined in managed landscapes. The objectives of this study were to identify proxies that allowed plant species invasion (natives and exotics) and define thresholds of human impacts to improve management. We also wanted to identify indicator species for different impacts and environments. A total of 165 plots were measured in *Nothofagus antarctica* forests and associated open lands (dry and wet grasslands) in Tierra del Fuego (Argentina). We found differences in the studied variables across the landscape and among different uses and impacts. Human impacts influence land types, emphasizing the importance of managing intensities. Indicator plant species allowed for the identification of potential ecological thresholds related to human impacts and the establishment of species linked to ecological and economic degradation, e.g., *Bolax gummifera* and *Azorella trifurcata* (cushion plants) were associated with high grazing pressure in grasslands and fires in forested areas, while *Rumex acetosella* and *Achillea millefolium* (erect herbs), typically associated with forested areas, were related to high harvesting pressures and fire impacts. These findings contribute to our understanding of the long-term effects of some human impacts (e.g., harvesting and ranching) and allow us to define variables of monitoring and indicator species for each impact type.

Keywords: forest resilience; invasive species; land use; silvopastoral systems; harvesting; ranching; fires

1. Introduction

Forest landscape patterns reflect the combined influence of relatively constant factors (e.g., climate and topography), species distributions (e.g., grasses, herbs, and trees), and its ecological inter-relationships [1–3]. Additionally, forest landscapes reflect the effects of natural and human disturbances [4,5]. Despite the fact that most forest ecosystems are able to recover from major perturbations within decades to half-centuries [6], some legacies of

forest disturbances can persist and alter the original plant understory [7], modifying the forest stand structure [8] and susceptibility to subsequent disturbances [9]. Furthermore, this susceptibility is closely related to the magnitude of these impacts [10].

Opportunistic invasive plants take advantage of the adverse effects of disturbances and the lack of resilience of impacted forests, which negatively affects native vegetation communities [11,12]. These invasive plants can cause significant ecological and economic harm in natural and managed forests [13], e.g., by altering ecological functions, including primary productivity, nutrient cycling, carbon sequestration, and tree regeneration [13,14]. The relationship between invasion success and resource availability is well documented [12,15]. The likelihood of establishment by invasive species is higher in disturbed areas with more resources (e.g., nutrient-rich sites) and depends on the biotic interactions among native and exotic plants [16,17]. Many associated patterns and plant strategies of invasion have been described, including environmental and landscape factors, such as soil, climate, land use, or anthropogenic disturbances [12,16,18].

One major challenge of forest management and conservation lies in defining the threshold of resilience of natural ecosystems [10], e.g., where hybrid or de novo ecosystems can be created due to the lack of recovery capacity of the managed or impacted stands. Human land uses increase landscape fragmentation, and, as a consequence, susceptibility to biological invasions [14,19,20]. In order to assess the impact of invasive species and to conserve biodiversity in human-dominated landscapes, we need to consider the role of the landscape context, and how it modulates the natural species assemblages [21].

Over the past century in Patagonia, human activities have become the main driver of change for native forests [10], where the main economic activities (e.g., extensive grazing and harvesting) alter the natural vegetation cover at the landscape level [22]. Furthermore, human disturbances (e.g., clear-cuts and fires) significantly change the forest structure, soil properties, ecological processes, and vegetation composition [8,23]. In fact, forest degradation is the main consequence of these extreme impacts with a total change in the provision of different ecosystem services, and it reduces their resilience capacity [24]. Vegetation changes are frequently associated with the dominance of non-native plant species over native plant species [25]; however, the increase in native species associated with open environments (e.g., grasslands) could also be a consequence of changing environmental conditions in natural forested landscapes [8].

Since European colonization (1850–1950), the Patagonian forests in Argentina have suffered different human impacts related to the improvement of provisioning ecosystem services, which led to changes in understory species to increase the growth and palatability of forage for livestock [8,10]. One of the most affected forest landscapes was the *Nothofagus antarctica* (commonly named ñire) forests in ecotone areas due to their relevant characteristics for grazing and timber, which is used for rural construction purposes [26]. In this context, one of the most extreme impacts was generated through intentional fires to decrease or remove the forest cover to maximize forage for livestock. More recently, silvopastoral systems (SPSs) were proposed as more sustainable alternatives (e.g., thinning) to obtain poles for fences and lumber and to open the forest canopy to stimulate the understory growth while maintaining shelter for cattle during winter [8,26]. However, grazing is the impact that prevails in all landscapes (open lands and forest lands), generating positive and negative trade-offs with the other described impacts [10].

The data collected through monitoring, especially over long periods, become indispensable for evaluating the consequences of ecosystem changes and supporting subsequent decision-making processes [27]. Monitoring provides key insights into ecology, environmental change, natural resource management, and biodiversity conservation [28,29], and specifically, long-term studies on forest ecosystems have been widely used to monitor changes in forest structure, composition, and services [27,30]. Over time, the need for measurable, simple, financially feasible, and reliable indicators for biodiversity has increased, but their development has resulted in an inhomogeneous landscape of quantitative and qualitative biodiversity indicators [31,32]. These indicators can be positively or negatively

impacted by harvesting or management actions [10,33]. Understanding the link between biodiversity indicators and management measures has been the focus of many comparative, descriptive, and experimental research studies in previous decades, but the relationship to management measures is still elusive [34]. Although the establishment and spread of invasive species is affected by a combination of biotic, abiotic, and landscape factors [14,35], studies that integrate multiple types of environmental data in predicting invasive species distributions are scarce [14,36,37].

The bio-indication of abiotic site conditions from environmental relationships of plant species has a long tradition [38,39]. Vascular plants were used for environmental indicators due to their ecological behaviors relating to the main environmental factors modified by natural and human-related impacts, including Patagonia in Argentina [22,40]. Data describing environmental indicators can be spatially and temporally referenced to understand changes to the environment over space and time, and they are thus important tools for decision making [41]. Invasive species that take advantage of disturbances or reduced resilience in impacted forests pose significant ecological and economic challenges. Their presence has adverse effects on critical ecosystem functions, including primary productivity, nutrient cycling, and tree regeneration [13,14,37]. The indicator plant species in SPSs in Patagonia were chosen according to its correlation to (i) losses in forage productivity due to the introduction of exotic species (e.g., quantity and quality of forage palatability) and (ii) losses of environmental quality (e.g., soil erosion) that allowed for the establishment of undesirable plant species [42]. Exotic species have invaded these austral forests since European colonization, and they became one of the main drivers of change, modifying the species assemblage of native forests. For example, *Rumex acetosella* has become one of the most frequent introduced species in disturbed environments since 1580 in the Magellan Strait [43,44], while *Achillea millefolium* was first reported in 1906 in Argentina and was identified as a weed that invades native grasslands [45]. *Hieracium pilosella* was more recently found during the 1990s [46], especially after disturbances (e.g., fires and overgrazing) [47–49], and was pointed as the biggest threat for profitable livestock farming [50,51]. Further, some studies reported the increase in native plant species associated with open habitats in impacted forests due to degradation processes [51], e.g., the encroachment of unpalatable plants in forested areas for cushion shrubs, such as *Azorella caespitosa*, *A. trifurcata*, and *Bolax gummifera*, which decline the productivity of grasses associated with over-grazing, clear-cuttings, or intense human-related fires [40,52].

Most studies try to understand the invasive ecology of the species [46–49,51], while other studies analyze the vegetation cover changes related to specific impacts [22,26,40,42,45,50,52]. However, to understand how specific species change in managed forest landscapes, it is necessary to analyze plant species while considering all of the environmental impacts and other associated impacts. The objectives of this study are to define the landscape and environmental characteristics that allowed for the invasion of exotic understory species and define the thresholds of the anthropogenic impacts to propose sustainable management practices. We want to answer the following questions: (i) Do the environmental characteristics of well-conserved natural ecosystems (topography, soil, and forest structure) reduce vascular plant invasion? (ii) Do changes in human-related impacts (livestock, harvesting, and fires) on environmental characteristics facilitate vascular plant invasion? (iii) Are there detectable thresholds for the changes generated by management practices (harvesting and livestock)? And (iv) are there indicator species for the different kinds of impacts (livestock, harvesting, and fires) and environments (open lands and forest lands)?

2. Materials and Methods

2.1. Study Area

Sampling was conducted at El Roble ranch, located in the central area of Tierra del Fuego (Argentina) at 54°01' to 54°02' SL and 67°41' to 67°43' WL (Figure 1A,B). We selected a forested landscape with a long history of impacts and human uses, which covers 432 ha of *Nothofagus antarctica* forests and associated open lands (dry and wet grasslands).

This forested landscape was mainly used for cattle grazing during the past century, and different management practices were implemented within this area: (i) thinning to promote SPS, increasing pastures under tree cover, and obtaining firewood and poles for fence construction, (ii) clear-cuts and pastures for livestock, and (iii) fires to remove trees and woody debris and accommodate pastures for livestock [8,10,52]. A total of 165 plots were measured using a systematic grid of 150×150 m across forest lands and open lands (Figure 1C). This design generates a limitation for our study, e.g., data independence in the landscape [53]. Additionally, an imbalance among the treatments exists due to the impacts not all being equally represented in the field, e.g., cattle density was higher in open lands than in closed forests.

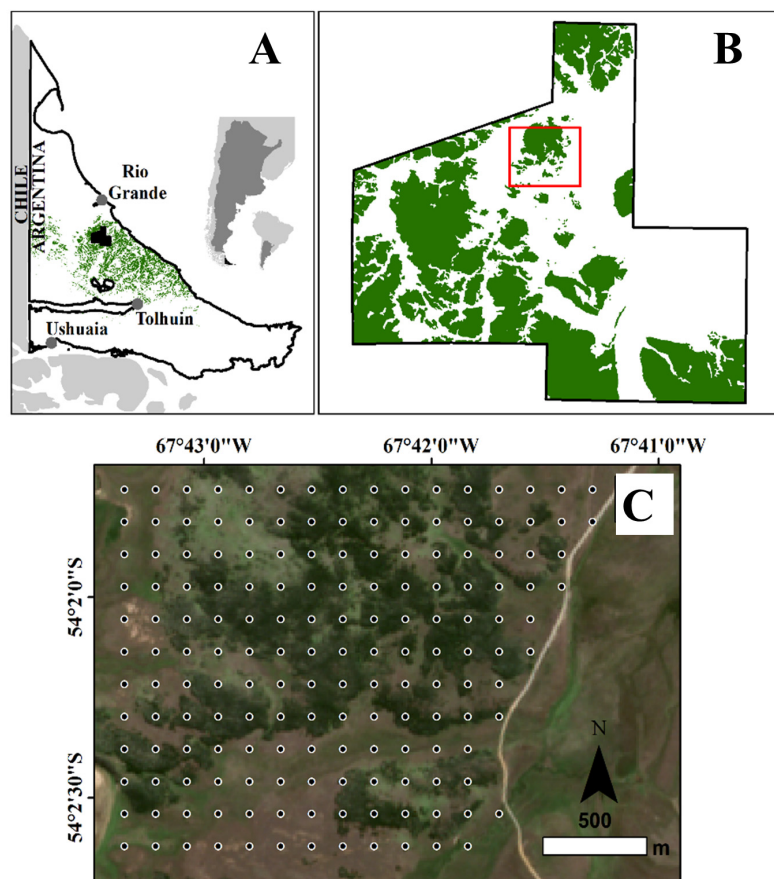


Figure 1. Location of the study area: (A) El Roble ranch (black) showing Tierra del Fuego province (line black), Argentina (dark grey), and *Nothofagus antarctica* forests (green); (B) location of the study site (line red) inside El Roble ranch; and (C) sample points ($n = 165$).

2.2. Sampling Design, Data Taking, and Calculations

Each plot was sampled using a 25 m transect from east to west of the center geographic point defined by the grid. We characterized each plot by their forest structures, environmental variables, animal uses, and understory plants. Forest structure was measured with one plot in the center of the transect using the point sampling method (BAF = 4) [54], obtaining the basal area (BA, $m^2 ha^{-1}$) with a Criterion RD-1000 (Laser Technology, Centennial, CO, USA), and the dominant height (DH, m) was denoted as the two tallest trees per plot, which were measured using a TruPulse 200 (Laser Technology, Centennial, CO, USA). BA was also relativized while considering the maximum value of the total sampling (BA_{max}, %) to define one tree occupancy index (0% to 100%). These data were complemented with hemispherical photographs, which were taken at the center of transects at 1.5 m above ground level with an 8 mm fisheye lens (Sigma, Kanagawa, Japan) mounted on a 35 mm full-frame digital camera (Nikon, Tokio, Japan), along with a tripod leveling head to ensure

a horizontal lens position was maintained. Each photograph was orientated with the upper edge towards the magnetic north, avoiding direct sunshine under evenly overcast skies or cloudless days. Gap Light Analyzer software v 2.0 [55] was used to define cover (overstorey crown and debris) (CC, %), as a percentage of open sky, and total direct radiation (DR, $W m^{-2}$) transmitted through the canopy and debris. The user-supplied input variables' details were presented by Martínez Pastur et al. [56]. Slope (SLO, %) was also measured using an inclinometer in the center of the transects. To characterize the soil layer, we collected two samples along each transect using a field borer (0–30 cm) of known volume after removing the litter. Samples were weighed before and after air-drying in laboratory conditions (24 °C) until constant weight was reached, obtaining soil moisture (SM, %) and soil bulk density (SBD, $gr cm^{-3}$) after coarse root debris, and stones >2 mm were removed by sieving. For chemical analyses, we pooled the individual soil samples into one combined sample per transect. Soil samples were finely ground to below 2 mm using a tungsten carbide mill, and we determined (i) the soil acidity (pH) in a suspension (air-dried samples and deionized water) of a soil/water ratio of 1:2.5 [57], (ii) the soil organic matter (SOM, %) and soil organic carbon (SOC, %) based on a dry combustion analysis (muffle furnace) and modeling [58], (iii) soil nitrogen (SN, %) with a semi-micro Kjeldahl method [59], and (iv) the soil extractable phosphorus (SP, ppm) using the Bray and Kurtz method [60].

We also recorded animal feces from native (*Lama guanicoe*, guanaco) and domestic animals (sheep, cows, and horses) along each transect (25 × 4 m, 100 m²). We used the number of feces as a proxy of animal use (animals ha⁻¹) according to the following: (i) we assumed that the feces were maintained in the forest floor for a period no longer than a calendar year (decomposition rates were low during summer due to low temperatures and high during winter due to mechanical effect of snow accumulation); (ii) average values of defecation per day were defined as 6.0 times per day for guanacos and 12.3 times per day for cows and horses; (iii) the requirements of dry matter forage (palatable plants) varied according to the animals (650 kg DM yr⁻¹ for guanacos and 3250 kg DM yr⁻¹ for cows and horses); and finally, (iv) we used sheep equivalent (SE, animal ha⁻¹) based on the animal species size to standardize the current livestock density [58].

To characterize the understory, we used the point-intercept method [61] with 50 intercept points (every 0.5 m) along each transect. At each point, we recorded bare ground, debris, and vascular and bryophyte species and calculated cover based on number of hits on each species along the transect, e.g., bare ground cover (BG, %), debris cover (>2.5 cm diameter) (DC, %), bryophyte cover (mosses and liverworts) (BC, %), and vascular plant cover, including tree regeneration less than 1.30 m height (RC, %), monocot plant cover of native species (MONO, %), monocot plant cover of exotic species (MONO-E, %), dicot plant cover of native species (DICO, %), and dicot plant cover of exotic species (DICO-E, %). We also surveyed the occurrence of degradation as indicator plant species at each sample point of each transect, including *Azorella caespitosa* (AZCA), *A. trifurcata* (AZTR), and *Bolax gummifera* (BOGU), which are mostly associated with open lands, and *Achillea millefolium* (ACMI), *Hieracium pilosella* (HIPI), and *Rumex acetosella* (RUAC), which are more related to forest lands. The first ones have been identified as early seral species that settle after disturbances, and the second ones have been identified as species that reduce the quality of the understory quality for grazing purposes [8,51,58]. These data allowed us to determine the plant species cover or species group cover (dicots, monocots, native, and exotic) following Moore [62] and Correa [63].

For further analyses, the sampled plots were integrated into a geographical information system (GIS), and Sentinel 2 images (resolution 10 m pixel) were used to manually classify environment types, grazing impacts, and harvesting and fire impacts as follows: (i) Environment types were defined as open lands (OLs) and forest lands (FLs). Open lands included dry grasslands (G) dominated by *Festuca gracillima* and *Empetrum rubrum* and wet grasslands (W) dominated by *Juncus scheuchzerioides*, *Carex curta*, *C. macrosolen*, and *Caltha sagittata* [8,51]. Forest lands were classified as closed forests (CF, >60% CC), open forests (OF, <60% CC), and edge forests (EF, 25 m strip of ecotone forests between

open lands and forest lands) (Figures 2 and 3A). (ii) Grazing impacts were defined as low grazing (LG) and high grazing pressure (HG). Grazing impact (0% to 100%) was calculated as the total animal use (native and domestic) relativized with the maximum value of sheep equivalents (SE, $n\ ha^{-1}$) recorded during sampling. Low grazing was considered when values were $<20\%$, while high grazing was considered when values were $>20\%$ (Figure 3B). Finally, we considered (iii) the harvesting and fire impacts on the forest lands, which were classified as unharvested areas (UH; natural forests without management or fire evidences), low harvested stands (LH; evidence of previous harvesting and $CC > 60\%$), high harvested stands (HH; evidence of previous harvesting and $CC < 60\%$), and stands with fire impacts (F), despite the intensity and kind of damage, detected during field sampling (Figures 2 and 3C).

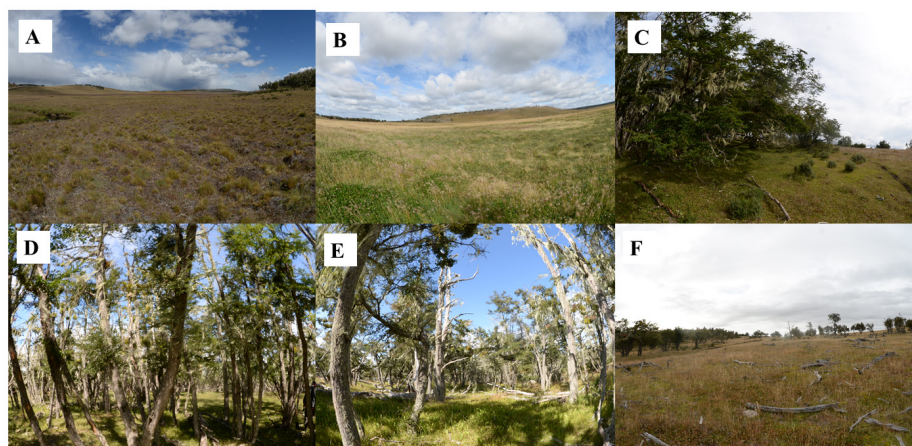


Figure 2. Examples of sampled environments. Open lands, including (A) dry grasslands and (B) wet grasslands, and forest lands, including (C) edge forests, (D) closed forests, (E) harvested forests, and (F) forests affected by fires.

2.3. Statistical Analyses

One-way ANOVAs were used to compare environment types (OL-G, OL-W, FL-CL, FL-EF, and FL-OF), grazing (OL-LG, OL-HG, FL-LG, and FL-HG), and harvesting or fire impacts (FL-UH, FL-LH, FL-HH, and FL-F) using Fisher's test and Tukey's test at $p < 0.05$. Parametric test using skewness was conducted before the analyses for each group of variables. These analyses were conducted using Statgraphics Centurion XVI software (Statistical Graphics Corp., The Plains, VA, USA). These treatments and levels were used to analyze (i) forest structure (CC, DR, DH, and BMax), (ii) topography and soil properties (SLO, SBD, SM, pH, SOC, SOM, SN, and SP), (iii) understory plant cover (BG, DC, RC, BC, MONO, MONO-E, DICO, and DICO-E), and (iv) indicator species cover (AZCA, BOGU, AZTR, HIPI, ACMI, and RUAC). Principal Component Analysis (PCA) was performed to evaluate patterns of plot distribution of environment types, impacts, and indicator species. In the first analyses, we evaluated the plots based on environment types (OLs and FLs) and impacts (grazing, harvesting, and fires) as responses to the complete pool of variables (four variables of forest structure, eight variables of topography and soil properties, and eight variables of understory cover, for a total of twenty variables). In the second group of analyses, PCA was employed to explore patterns in the cover of six degradation indicator plant species with environment types and impacts. We selected correlation coefficients among columns to obtain the final cross-product matrices. We also performed a Multi-Response Permutation Procedure (MRPP) to analyze statistical differences among groups of plots for each comparison. These analyses were conducted using PC-ORD 5.0 [64]. ANOVA, PCA, and MRPP were performed using the complete pool of plots and variables ($n = 165$) when analyzing environment types and grazing impacts, but we only used FL plots ($n = 111$) when harvesting, and fire impacts were considered. For the PCA of degradation indicator plant species, only plots with covers of 10% or higher

for at least one species were employed ($n = 66$ for environment types and impacts, and $n = 49$ for harvesting and fire impacts). Finally, we analyzed the relationship (average \pm standard error) between crown cover (CC) and animal density (SE, livestock, and guanacos) by considering (i) environment types (OL-G, OL-W, FL-CF, FL-EF, and FL-OF), (ii) grazing impacts (OL-LG, OL-HG, FL-LG, and FL-HG), (iii) harvesting and fire impacts in forest lands (FL-UH, FL-LH, FL-HH, and FL-F), and (iv) degradation indicator plant species cover (AZCA, BOGU, AZTR, HIPI, ACMI, and RUAC) compared with the average cover for all of the measured plots (TOTAL).

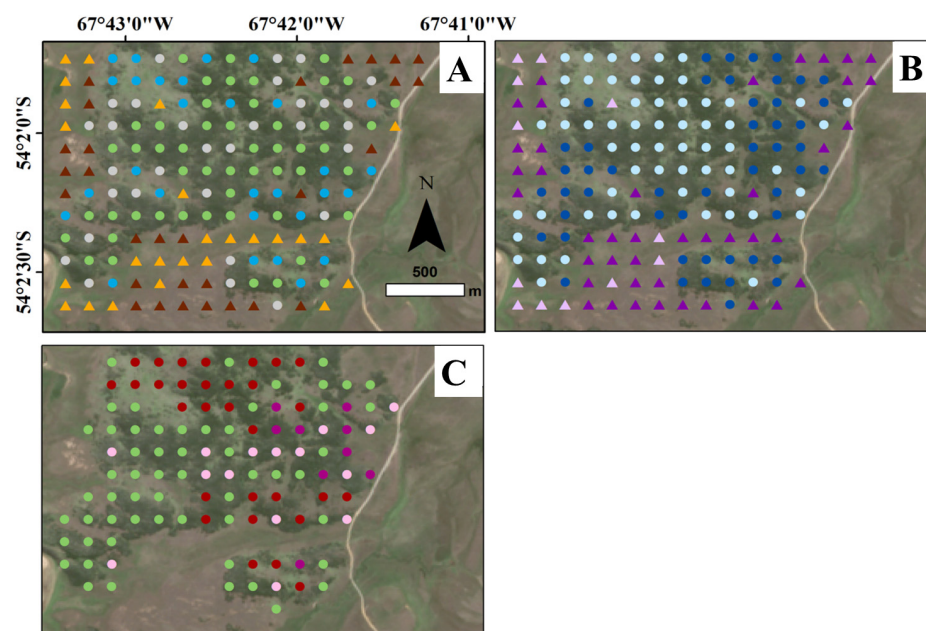


Figure 3. Sample points ($n = 165$) classified in open lands (OLs—triangles) and forest lands (FLs—circles) according to (A) environment types classified as dry grasslands (brown), wet grasslands (orange), closed forests (green), edge forests (grey), and open forests (blue); (B) grazing impacts classified as open lands with low grazing pressure (light purple), open lands with high grazing pressure (purple), forest lands with low grazing pressure (light blue), and forest lands with high grazing pressure (blue); and (C) harvesting and fire impacts in forest lands classified as unharvested areas (green), low harvested stands (light purple), high harvested stands (purple), and fire impacts (brown red).

3. Results

3.1. Landscape Characterization

The sample points were classified according to the different environment types and human-related impacts (Figure 3A), where 54 plots were classified as OLs (33%) and 111 were classified as FLs (67%), and occurring in an intermingled landscape with grasslands and not in continuous forest patches. The open lands included 29 plots of dry grasslands (54%) and 25 plots of wet (46%) grasslands. The forest lands included 51 plots of closed forests (46%), 31 plots of edge forests (28%), and 29 plots of open forests (26%). The grazing impacts greatly varied across the landscape, where a higher anthropogenic pressure was related to the open lands and the forest stands located close to these environments (Figure 3B). Our sampling detected more plots with higher grazed grasslands (78%), than lower grazed grasslands (22%) and more plots with lower (55%) than higher grazed forests (45%). Finally, considering the harvesting and fire impacts in FLs (Figure 3C), we found more unharvested stands (51%) located far away from roads than low (14%) or heavy (8%) harvested stands. Fires (27%) included more plots than harvesting and occurred during different periods and events despite their distances from roads.

3.2. Changes in the Environmental Characteristics

The forest structure, topography, and soil properties showed significant differences among environments and impact types (Tables 1 and 2). The forest structure showed differences among the OL and FL levels, where the forest stands presented higher crown cover and lower total direct radiation values (Table 1A). Additionally, closed forests showed higher values of forest structure (CC = 71.4%, DH = 8.5 m, BAm_{ax} = 51.1%), while edge and open forests did not present significant differences between them. Most of the topography and soil properties only showed differences between the wet grasslands and other treatments (dry grasslands and forests) (Table 2A). The wet grasslands presented the lowest values in slope (SLO = 2.1°) and soil bulk density (SBD = 0.37 gr cm³), with greater values in the soil moisture (SM = 107.3%), soil organic carbon (SOC = 22.3%), soil organic matter (SOM = 55.5%), and soil nitrogen contents (SN = 1.3%). However, the forest lands presented the highest values in pH and soil phosphorus (closed > edge > open forests).

Table 1. One-way ANOVAs of forest structure considering open lands (OLs) and forest lands (FLs) analyzing (A) different environment types considering dry grasslands (OL-G), wet grasslands (OL-W), closed forests (FL-CF), edge forests (FL-EF), and open forests (FL-OF); (B) grazing impacts considering open lands with low grazing pressure (OL-LG), open lands with high grazing pressure (OL-HG), forest lands with low grazing pressure (FL-LH), and forest lands with high grazing pressure (FL-HG); and (C) harvesting and fire impacts in forest lands considering unharvested areas (FL-UH), low harvested stands (FL-LH), high harvested stands (FL-HH), and stands with fire impacts (FL-F) as main factors, along with crown cover (CC, %), total direct radiation at ground level (TR, W m²), dominant height (DH, m), and basal area index (BAm_{ax}, %). Number of plots are indicated for each category (n).

	n	CC	TR	DH	BAm _{ax}
(A) Environment types					
OL-G	29	8.84 a	6.75 c	-	-
OL-W	25	10.37 a	6.75 c	-	-
FL-CF	51	71.40 d	2.61 a	8.50 b	51.10 b
FL-EF	31	39.63 c	5.02 b	7.23 a	17.62 a
FL-OF	29	22.31 b	6.15 c	7.51 a	8.06 a
<i>F</i>		219.29	111.68	10.41	59.00
(<i>p</i>)		(<0.001)	(<0.001)	(<0.001)	(<0.001)
(B) Grazing impacts					
OL-LG	12	10.60 a	6.75 b	-	-
OL-HG	42	9.25 a	6.75 b	-	-
FL-LG	61	51.05 b	4.04 a	7.90	34.02
FL-HG	50	48.09 b	4.42 a	7.86	26.21
<i>F</i>		46.20	29.45	0.02	2.35
(<i>p</i>)		(<0.001)	(<0.001)	(0.900)	(0.128)
(C) Harvesting and fire impacts					
FL-UH	57	50.79 a	4.11 b	7.87 ab	30.58 a
FL-LH	15	77.34 b	2.16 a	8.80 b	60.82 b
FL-HH	9	35.53 a	5.24 b	7.43 ab	13.33 a
FL-F	30	38.12 a	5.09 b	7.58 a	20.36 a
<i>F</i>		12.20	10.02	2.95	11.66
(<i>p</i>)		(<0.001)	(<0.001)	(0.040)	(<0.001)

F = Fisher's test; (*p*) = significance level. Values followed by different letters were significantly different with Tukey's test at *p* < 0.05.

Table 2. One-way ANOVAs of topography and soil properties considering open lands (OL) and forest lands (FLs) analyzing (A) different environment types considering dry grasslands (OL-G), wet grasslands (OL-W), closed forests (FL-CF), edge forests (FL-EF), and open forests (FL-OF); (B) grazing impacts considering open lands with low grazing pressure (OL-LG), open lands with high grazing pressure (OL-HG), forest lands with low grazing pressure (FL-LH), and forest lands with high grazing pressure (FL-HG); and (C) harvesting and fire impacts in forest lands considering unharvested areas (FL-UH), low harvested stands (FL-LH), high harvested stands (FL-HH), and stands with fire impacts (FL-F) as main factors, along with slope (SLO, °), soil bulk density (SBD, gr cm³), soil moisture (SM, %), soil acidity (pH), soil organic carbon (SOC, %), soil organic matter (SOM, %), soil nitrogen (SN, %), and soil phosphorus (SP, ppm). Number of plots are indicated for each category (n).

	n	SLO	SBD	SM	pH	SOC	SOM	SN	SP
(A) Environment types									
OL-G	29	4.17 b	0.75 b	31.19 a	4.54 a	7.68 a	19.13 a	0.46 a	12.43 a
OL-W	25	2.06 a	0.37 a	107.31 b	4.79 ab	22.31 b	55.47 b	1.26 b	16.25 ab
FL-CF	51	4.35 b	0.76 b	25.16 a	5.03 b	7.44 a	18.53 a	0.41 a	19.58 b
FL-EF	31	5.22 b	0.74 b	23.85 a	4.97 b	8.87 a	22.08 a	0.42 a	14.66 ab
FL-OF	29	4.63 b	0.77 b	20.47 a	5.02 b	6.70 a	16.70 a	0.39 a	13.13 a
<i>F</i>		5.55	21.15	29.19	7.83	37.06	37.09	56.51	4.31
(<i>p</i>)		(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(0.002)
(B) Grazing impacts									
OL-LG	12	2.29 a	0.35 a	116.83 c	4.92 bc	20.73 c	51.56 c	1.19 c	15.67 ab
OL-HG	42	3.45 ab	0.65 b	52.03 b	4.58 a	12.66 b	31.49 b	0.73 b	13.78 a
FL-LG	61	4.61 b	0.71 bc	25.25 a	5.18 c	7.82 a	19.49 a	0.41 a	18.31 b
FL-HG	50	4.74 b	0.81 c	21.52 a	4.81 b	7.43 a	18.51 a	0.40 a	14.34 a
<i>F</i>		4.23	17.44	24.05	20.73	16.80	16.82	26.32	2.77
(<i>p</i>)		(0.006)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(0.043)
(C) Harvesting and fire impacts									
FL-UH	57	5.21	0.72	26.07	5.01 ab	7.97	19.84	0.40	17.77
FL-LH	15	4.53	0.82	21.54	4.92 ab	7.42	18.50	0.40	16.74
FL-HH	9	3.44	0.84	19.03	4.68 a	7.98	19.88	0.47	11.31
FL-F	30	4.08	0.77	21.20	5.17 b	7.04	17.56	0.40	15.62
<i>F</i>		1.70	2.05	2.63	2.98	0.37	0.37	1.74	1.63
(<i>p</i>)		(0.171)	(0.111)	(0.053)	(0.034)	(0.771)	(0.771)	(0.162)	(0.186)

F = Fisher's test; (*p*) = significance level. Values followed by different letters were significantly different with Tukey's test at $p < 0.05$.

When we analyzed the forest structure values (Table 1B), the grazing impacts showed significant differences between land types (FLs and OLs), but not between intensity types. However, we found differences for both dimensions when we analyzed the topography and soil properties (Table 2B). The slope was higher on the FLs than OLs, but the grazing intensity increased at higher slopes. Additionally, livestock generated significant impacts on the soil bulk density and significantly increased the values on both OLs and FLs. Livestock also influenced the other studied soil properties, reducing the values according to the impact intensity (low > high) and environment type (FLs and OLs). Some values were higher for OLs (SM, SOC, SOM, and SN), while the pH and SP depended on the combination of both variables (e.g., these variables were higher at FL-LG and minimum at OL-HG).

The harvesting and fire impacts significantly influenced the forest structure variables and were slightly influenced by the topography and soil properties (Tables 1C and 2C). High harvesting (CC = 35.5%, HD = 7.4 m, BAmax = 13.3%) and fires (CC = 38.1%, HD = 7.6 m, BAmax = 20.4%) showed the lowest values in the forest structure variables, while low harvesting presented higher values (CC = 77.3%, HD = 8.8 m, BAmax = 60.8%) due to the secondary forests presenting abundant advanced regeneration. The unharvested stands presented medium values due to mature and old-growth forests presenting open

canopies and trees growing at different development and decay stages (Table 1C). Only one soil property showed significant differences, where fires increased the values (pH = 5.2) and harvesting decreased (pH = 4.7–4.9) the values compared to the unharvested stands (pH = 5.0) (Table 2C).

3.3. Vegetation Cover

The understory vegetation cover showed significant differences among different environment and impact types (Table 3). Three variables presented the highest values in dry grassland areas (OL-G), including bare ground (BG = 16.1%), bryophyte cover (BR = 2.3%), and native dicot cover (DICO = 16.8%). Native monocot cover showed the highest values in the wet grasslands (MONO = 67.0%) and showed the lowest values in closed forests (MONO = 25.1%). The exotic species cover (MONO-E and DICO-E) increased with the tree crown cover (closed > edge > open forests) as well as at different land types (forests > open lands), where closed forests presented the highest values of exotic monocot (MONO-E = 26.5%) and exotic dicot cover (DICO-E = 18.7%). The dry grasslands showed the lowest values of exotic species cover, which indicates the greater ecosystem integrity of their original species assemblage. Finally, as expected, closed forests presented the highest cover of debris (DC = 4.7%), and open forests presented the highest cover of regeneration (RC = 5.5%) (Table 3A).

The grazing intensity increased the bare ground, both at open lands and forest lands. Also, debris cover was higher in the high grazing areas, which was probably related to the impacts of grazing in the forest (e.g., harvesting generates higher debris and open canopies, which promotes higher grass development). In open lands, grazing also occurred in areas with greater bryophyte cover (e.g., more humid areas) and higher native dicot cover. Additionally, in open lands, a higher exotic species cover was found in areas with low grazing pressure, maybe because they are preferred for livestock during foraging. In the forest lands, a higher grazing pressure was found in areas with higher exotic monocot covers (pastures) but lower native dicot covers (Table 3B). Fires promote a higher native monocot cover, but with a lower exotic monocot cover, while light harvesting generates better conditions for exotic species cover (MONO-E and DICO-E) and lower native monocot cover. Finally, high harvesting areas promote more bryophyte cover (BC = 1.8%) than the other treatments (Table 3C).

3.4. Degradation Indicator Plant Species

Four degradation indicator plant species showed significant differences by considering different environments and impact types (Table 4). The two species, *Achillea millefolium* (ACMI) and *Rumex acetosella* (RUAC), did not differ across the types of environment, grazing, and harvesting or fire regimes, but the general trends were higher in the forest lands. As expected, *Azorella caespitosa* (AZCA) and *Bolax gummifera* (BOGU) showed the highest values of cover in open lands. However, AZCA was higher in wet grasslands (3.0%), while BOGU was higher in dry grasslands (3.4%). AZCA greatly decreased with the grazing intensity (6.1% to 1.6%) in open lands, while BOGU insignificantly increased with grazing in both open lands and forest lands (1.7% to 2.3% and 0.06% to 0.12%, respectively). *Azorella trifurcata* (AZTR) naturally grows in open lands, but our samplings showed a higher abundance in open forests (FL-OF and FL-EF > FL-CF and open lands). This species decreased with grazing in both land types (6.7% to 3.9% in open lands and 14.0% to 9.9% in forest lands). Additionally, AZTR significantly increased in highly impacted forests (e.g., FL-F reaching to 22.5% cover). Finally, *Hieracium pilosella* (HIPI) increased from wet to dry grasslands (1.1% to 2.6%) and when the tree canopy cover decreased (from 1% in CF to 7.1% in OF). However, the different impact types did not significantly influence its cover. The trends showed marginal increases associated with grazing (1.0% to 2.1% in open lands and 2.0% to 4.1% in forest lands), where maximum covers were found at high harvesting stands (7.9%).

Table 3. One-way ANOVAs of understory cover considering open lands (OL) and forest lands (FL) analyzing (A) different environment types considering dry grasslands (OL-G), wet grasslands (OL-W), closed forests (FL-CF), edge forests (FL-EF), and open forests (FL-OF); (B) grazing impacts considering open lands with low grazing pressure (OL-LG), open lands with high grazing pressure (OL-HG), forest lands with low grazing pressure (FL-LH), and forest lands with high grazing pressure (FL-HG); and (C) harvesting and fire impacts in forest lands considering unharvested areas (FL-UH), low harvested stands (FL-LH), high harvested stands (FL-HH), and stands with fire impacts (FL-F) as main factors, along with bare ground (BG, %), debris cover (DC, %), regeneration cover (RC, %), bryophyte cover (mosses and liverworts) (BC, %), monocot plant cover (MONO, %), monocot plant exotic cover (MONO-E, %), dicot plant cover (DICO, %), and dicot plant exotic cover (DICO-E, %). Number of plots are indicated for each category (n).

	n	BG	DC	RC	BC	MONO	MONO-E	DICO	DICO-E
(A) Environment types									
OL-G	29	16.13 b	2.00 ab	1.72 ab	2.34 b	47.93 b	2.07 a	16.75 b	2.20 a
OL-W	25	4.32 a	0.00 a	0.00 a	0.32 a	67.04 c	8.08 ab	9.28 a	6.64 ab
FL-CF	51	5.52 a	4.66 b	2.35 ab	0.19 a	25.09 a	26.50 c	13.14 ab	18.70 c
FL-EF	31	6.00 a	1.80 a	4.51 ab	0.64 a	41.67 b	13.61 b	10.32 ab	10.84 b
FL-OF	29	4.55 a	1.79 a	5.51 b	1.03 ab	44.41 b	5.65 ab	14.96 ab	4.41 a
<i>F</i>		12.30	5.42	3.39	6.75	226.41	25.81	2.77	26.43
(<i>p</i>)		(<0.001)	(<0.001)	(0.010)	(<0.001)	(<0.001)	(<0.001)	(0.029)	(<0.001)
(B) Grazing impacts									
OL-LG	12	5.16 a	0.00 a	0.00	0.33 a	65.50 b	5.50 ab	10.83 ab	5.50 ab
OL-HG	42	12.24 b	1.38 a	1.19	1.71 b	54.28 b	4.66 a	14.00 ab	3.90 a
FL-LG	61	3.94 a	2.78 ab	4.06	0.52 a	36.22 a	14.65 bc	15.21 b	13.96 c
FL-HG	50	7.20 a	3.52 b	3.44	0.56 a	33.00 a	20.88 b	9.92 a	11.32 bc
<i>F</i>		9.92	2.88	2.59	3.91	17.04	11.76	2.92	10.68
(<i>p</i>)		(<0.001)	(0.040)	(0.055)	(<0.001)	(<0.001)	(<0.001)	(0.035)	(<0.001)
(C) Harvesting and fire impacts									
FL-UH	57	5.19	2.56 a	4.10	0.28 a	34.35 b	20.98 bc	11.64	12.56 a
FL-LH	15	6.93	6.00 b	1.46	0.13 a	18.00 a	28.00 c	10.93	24.13 b
FL-HH	57	8.00	1.55 a	3.33	1.77 b	34.00 ab	8.66 ab	19.11	8.44 a
FL-F	30	4.27	3.20 a	4.46	0.86 ab	44.20 b	8.13 a	14.13	8.80 a
<i>F</i>		1.39	5.02	0.78	3.71	7.84	9.15	1.81	8.98
(<i>p</i>)		(0.248)	(0.002)	(0.507)	(0.014)	(<0.001)	(<0.002)	(0.149)	(<0.001)

F = Fisher's test; (*p*) = significance level. Values followed by different letters were significantly different with Tukey's test at $p < 0.05$.

3.5. Relationship among Environmental Variables and Impact Types

The PCA showed different ordination patterns depending on the variables used to characterize the sampling plots based on the environment or impact types (Figure 4). The environment types were clearly split along the first axis, explaining 31.5% of the variation, whereas the second axis separated within forested or open land types, explaining 19.0% of the variation. The forest lands (CF, EF, OF) were slightly overlapped with less dispersion than open lands (Figure 4A). However, the open forests and wet grasslands presented some overlap, generating a continuous gradient across the environment types. These dispersion trends can be associated with a CC gradient. As was expected, closed forests (green dots) were positively related to the forest structure variables (CC, BAm_{ax}, and DH), but also to two soil properties (pH and SP) and three understory cover variables (DC, DICO-E, and MONO-E). Additionally, two soil properties (SLO and SBD) and two understory cover variables (RC and DICO) were associated with edge (grey dots) and open forests (pale blue dots), and they shared some variables (TR, BG, and BC) with wet grasslands (orange triangles).

Table 4. One-way ANOVAs of indicator species cover considering open lands (OL) and forest lands (FL) analyzing (A) different environment types considering dry grasslands (OL-G), wet grasslands (OL-W), closed forests (FL-CF), edge forests (FL-EF), and open forests (FL-OF); (B) grazing impacts considering open lands with low grazing pressure (OL-LG), open lands with high grazing pressure (OL-HG), forest lands with low grazing pressure (FL-LH), and forest lands with high grazing pressure (FL-HG); and (C) harvesting and fire impacts in forest lands considering unharvested areas (FL-UH), low harvested stands (FL-LH), high harvested stands (FL-HH), and stands with fire impacts (FL-F) as main factors, along with *Azorella caespitosa* (AZCA, %), *Bolax gummifera* (BOGU, %), *Azorella trifurcata* (AZTR, %), *Hieracium pilosella* (HIPI, %), *Achillea millefolium* (ACMI, %), and *Rumex acetosella* (RUAC, %). Number of plots are indicated for each category (n).

	n	AZCA	BOGU	AZTR	HIPI	ACMI	RUAC
(A) Environment types							
OL-G	29	2.31 ab	3.37 b	4.62 a	2.62 ab	0.03	4.07
OL-W	25	3.00 b	0.84 a	4.44 a	1.12 a	0.08	1.92
FL-CF	51	0.06 a	0.00 a	1.80 a	1.00 a	0.54	3.54
FL-EF	31	0.41 ab	0.12 a	16.64 b	2.32 ab	0.25	5.06
FL-OF	29	1.34 ab	0.20 a	25.45 b	7.10 b	0.17	4.14
<i>F</i>		3.54	14.43 (<0.001)	14.26 (<0.001)	3.41 (0.010)	0.62	1.41
(<i>p</i>)		(0.008)				(0.652)	(0.234)
(B) Grazing impacts							
OL-LG	12	6.08 b	1.75 ab	6.75 ab	1.00	0.00	2.08
OL-HG	42	1.64 a	2.33 b	3.90 a	2.19	0.07	3.35
FL-LG	61	0.67 a	0.06 a	13.95 b	2.03	0.39	3.22
FL-HG	50	0.28 a	0.12 a	9.90 ab	4.10	0.34	5.24
<i>F</i>		8.87 (<0.001)	11.44 (<0.001)	2.93	0.94 (0.423)	0.45	2.15
(<i>p</i>)				(0.035)		(0.718)	(0.096)
(C) Harvesting and fire impacts							
FL-UH	57	0.38	0.12	10.05 ab	3.35	0.19	5.14
FL-LH	15	0.06	0.00	0.66 a	1.00	1.60	3.86
FL-HH	9	0.55	0.00	9.66 ab	7.88	0.11	4.11
FL-F	30	0.90	0.10	22.53 b	1.73	0.16	2.36
<i>F</i>		0.97	1.04	5.82	1.42 (0.240)	2.27	1.84
(<i>p</i>)		(0.408)	(0.376)	(<0.001)		(0.084)	(0.145)

F = Fisher's test; (*p*) = significance level. Values followed by different letters were significantly different with Tukey's test at $p < 0.05$.

Four soil properties (SM, SOC, SOM, and SN) and one understory variable (MONO) were associated with dry grasslands (orange triangles). Pairwise comparisons among treatments through MRPP showed significant differences among all groups ($p < 0.01$). The grazing impacts also split the environment types (OL in purple triangles and FL in blue dots) (Figure 4B), but the level of grazing impacts was overlapped among the treatments. Some variables can be associated with grazing impacts; (i) the forest structure (CC and BAm_{ax}), soil (SP and pH), and understory cover (DICO-E and MONO-E) can be related with low grazing in FLs (light blue dots), while most of the understory variables (DC, RC, DICO, BG, and BC), two soil properties (SLO and SBD) and one forest structure (DH) can be associated with areas with high grazing in FLs (blue dots). Finally, BC, TR, and MONO can be related to areas with high grazing in OLs (purple triangles), while only soil properties (SOC, COM, SM, and SN) can be related to areas with low grazing in OLs (light purple triangles). Pairwise comparisons among treatments through MRPP showed significant differences for most of the groups ($p < 0.01$), except between grazing levels in OLs ($p = 0.09$) and FLs ($p = 0.07$). In these two analyses (Figure 4A,B), axis 1 (Eigenvalue = 6.305, explained variance = 31.5%) was mainly influenced by CC, BAm_{ax}, TR, DH, SOC, SOM, SN, and MONO (Eigenvectors of 0.33, 0.30, −0.32, 0.31, −0.29, −0.29, −0.27, and −0.31, respec-

tively). Axis 2 (Eigenvalue = 3.976, explained variance = 19.9%) was mainly related with SBD, SP, and BG (Eigenvectors of -0.31 , 0.32 , and -0.32 , respectively). The Eigenvalues in the PCA for axes 1 and 2 were both significant (both presented $p < 0.01$).

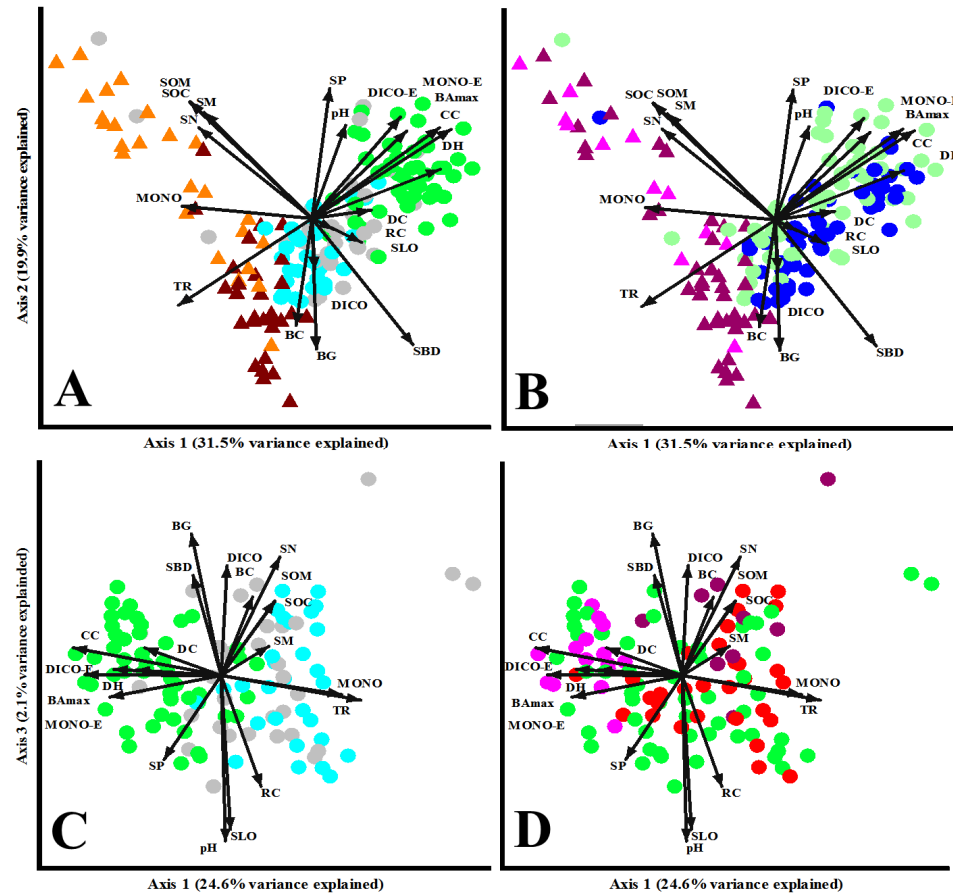


Figure 4. Principal Component Analysis (PCA) of plots showing the incidence of the forest structure, soil properties, and understory variables in open lands (OLs—triangles) and forest lands (FLs—circles). Plots were shaped and colored by considering (A) environment types classified as dry grasslands (brown), wet grasslands (orange), closed forests (green), edge forests (grey), and open forests (pale blue); (B) grazing impacts classified as open lands with low grazing pressure (light purple), open lands with high grazing pressure (purple), forest lands with low grazing pressure (light blue), and forest lands with high grazing pressure (blue); (C) forest lands classified as closed forests (green), edge forests (grey), and open forests (pale blue); and (D) harvesting and fire impacts in forest lands classified as unharvested areas (green), low harvested stands (light purple), high harvested stands (purple), and fire impacts (brown red). The vector length and direction indicate the magnitude of the correlation of the employed variables (see acronyms in Tables 1–3) with PCA axes (1 and 2).

The PCA that analyzed forest land types split the closed forests (green dots) with edge forests (grey dots) and open forests (pale blue dots) that presented high overlapping (Figure 4C). Closed forests can be related to the forest structure (CC, DH, and BAm_{ax}) and understory cover variables (DC, DICO-E, and MONO-E), while edge and open forests can be related to greater total direct radiation at ground level (TR) and total monocot plant cover (MONO). The pairwise comparisons among treatments through MRPP showed significant differences for all groups ($p < 0.01$). The PCA that analyzed the harvesting and fire impacts showed some trends, but with high overlapping among treatments (Figure 4D). Unharvested forests (green dots) and fires (red dots) presented great dispersion at both axes, while some soil properties (SOC, SOM, SN, and SBD) and understory variables (BC, BG, and DICO) could be related with high harvested stands (purple dots), and some

forest structures (CC, BAmax, and DH) and understory variables (DC, MONO-E, and DICO-E) can be associated with low harvested stands (light purple dots). The pairwise comparisons among treatments through MRPP showed significant differences for most of the groups ($p < 0.01$), except for fires and heavy harvesting stands ($p = 0.18$). In these two analyses (Figure 4C,D), axis 1 (Eigenvalue = 4.915, explained variance = 24.6%) was mainly influenced by CC, BAmax, TR, MONO, MONO-E, and DICO-E (Eigenvector of $-0.41, -0.38, 0.39, 0.33, -0.31$, and 0.30 , respectively). Axis 3 (Eigenvalue = 2.068, explained variance = 10.3%) was mainly related with SLO, pH, SN, RC, and DICO (Eigenvectors of $-0.40, -0.43, 0.31, -0.29$, and 0.29 , respectively). The Eigenvalues in the PCA for axes 1 and 3 were significant (both presented $p < 0.01$).

The PCA showed different ordination patterns depending on the variables used to characterize the sampling plots based on degradation indicator plant species cover (Figure 5). The environment types were clearly split between OLs and FLs, but with high overlapping among the types (Figure 5A). Two indicator plant species (BOGU and AZCA) can be related to dry and wet grasslands, while the other species can be related to a wide range of forested environments. Pairwise comparisons among treatments through MRPP showed significant differences for most of the groups ($p < 0.01$), except between grassland types ($p = 0.44$) and edge and open forests ($p = 0.64$). The grazing impacts also split the different environment types (OL in purple dots and FL in blue dots) (Figure 5B), but once again, the level of grazing impacts was strongly overlapped among treatments. No clear associations were found between indicator plant species and grazing levels. Pairwise comparisons among treatments through MRPP showed significant differences for most of the groups ($p < 0.01$), except between the grazing levels in OLs ($p = 0.34$) and the grazing levels in FLs ($p = 0.09$). In these two analyses (Figure 5A,B), axis 1 (Eigenvalue = 1.568, explained variance = 26.1%) was mainly influenced by AZTR, BOGU, and AZCA (Eigenvectors of $0.70, -0.49$, and -0.42 , respectively). Axis 2 (Eigenvalue = 1.320, explained variance = 22.0%) was mainly related with RUAC and AZCA (Eigenvectors of 0.67 and -0.44 , respectively). The Eigenvalues in the PCA for axes 1 and 2 were non-significant. However, axis 2 presented marginally significant differences ($p = 0.12$ and $p = 0.06$, respectively).

The PCA that analyzed forest land types related to degradation indicator plant species cover showed that closed forests (green dots) presented greater homogeneity compared to edge forests (grey dots) and open forests (pale blue dots), which presented a high dispersion (Figure 5C). Some species showed relationships with the closed forests (ACMI and HIPI), but the other species were related to particular canopy conditions of the open forests. Pairwise comparisons among treatments through MRPP showed non-significant differences ($p > 0.05$), except between landscape types (OLs and OFs, $p < 0.01$). The PCA that analyzed the harvesting and fire impacts showed some trends, but with high dispersion among treatments (Figure 5D), e.g., burnt stands showed a greater relation with AZTR. In these two analyses (Figure 5C,D), axis 1 (Eigenvalue = 1.73, explained variance = 28.9%) was mainly influenced by AZTR, RUAC, and BOGU (Eigenvectors of $0.61, -0.56$, and -0.49 , respectively). Axis 2 (Eigenvalue = 1.24, explained variance = 20.8%) was mainly related with AZCA and BOGU (Eigenvectors of 0.79 and 0.43 , respectively). Pairwise comparisons among treatments through MRPP showed that half of them showed significant differences ($p < 0.01$), and half showed non-significant differences, including closed forests compared to high ($p = 0.92$) and low harvested stands ($p = 0.09$), and between low and high harvested stands ($p = 0.21$). The Eigenvalues in the PCA for axes 1 and 2 were non-significant. However, axis 1 presented marginally significant differences ($p = 0.08$ and $p = 0.36$, respectively).

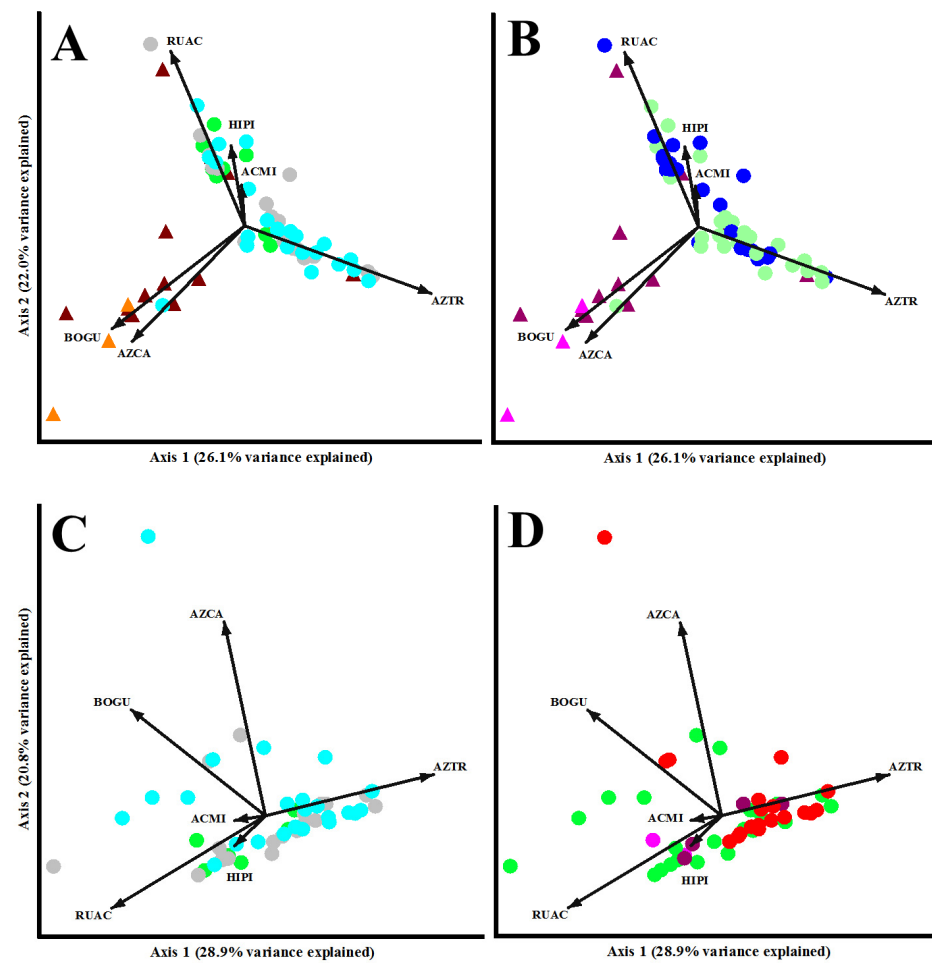


Figure 5. Principal Component Analysis (PCA) ordination of plots according to degradation indicator plant species cover in open lands (OLs—triangles) and forest lands (FLs—circles). Plots were shaped and colored considering (A) environment types classified as dry grasslands (brown), wet grasslands (orange), closed forests (green), edge forests (grey), and open forests (pale blue); (B) grazing impacts classified as open lands with low grazing pressure (light purple), open lands with high grazing pressure (purple), forest lands with low grazing pressure (light blue), and forest lands with high grazing pressure (blue); (C) forest lands classified as closed forests (green), edge forests (grey), and open forests (pale blue); and (D) harvesting and fire impacts in forest lands classified as unharvested areas (green), low harvested stands (light purple), high harvested stands (purple), and fire impacts (brown red). The vectors' length and direction indicate the magnitude of the correlation of the indicator species with PCA axes (1 and 2): *Azorella caespitosa* (AZCA), *Bolax gummifera* (BOGU), *Azorella trifurcata* (AZTR), *Hieracium pilosella* (HIPI), *Achillea millefolium* (ACMI), and *Rumex acetosella* (RUAC).

The relationships between crown cover (CC) and animal density (SE, livestock, and guanacos) were synthesized in the univariate and multivariate analyses (Figure 6), highlighting the coincidences between these major studied impacts (with CC as a proxy of harvesting, and SE as proxy of animal use). The environment type comparisons showed a gradient of CC, where FL-OF and FL-EF were closer to open lands than FL-CF, and SE was not greatly changed, except for FL-EF, which presented higher average values (Figure 6A). Interestingly, the lower and higher grazing intensities occurred at similar crown covers (Figure 6B). When we analyzed the impacts of harvesting and fires, it was expected that there would be a clear trend between CC and SE, when CC increases and SE decreases, e.g., these trends can be observed between harvested and unharvested forests (FL-HH > FL-UH > FL-LH from higher values of SE to higher values of CC). Fires presented lower values of CC, but also presented lower values of SE. Fires and FL-HH presented similar CC values;

however, the harvesting areas presented higher SE levels. These differences probably showed some degradation processes (Figure 6C). Finally, the degradation indicator plant species showed a clear relationship between CC and SE (from lower to higher values), where BOGU < AZCA < HIPI-AZTR < RUAC < ACMI (Figure 5D).

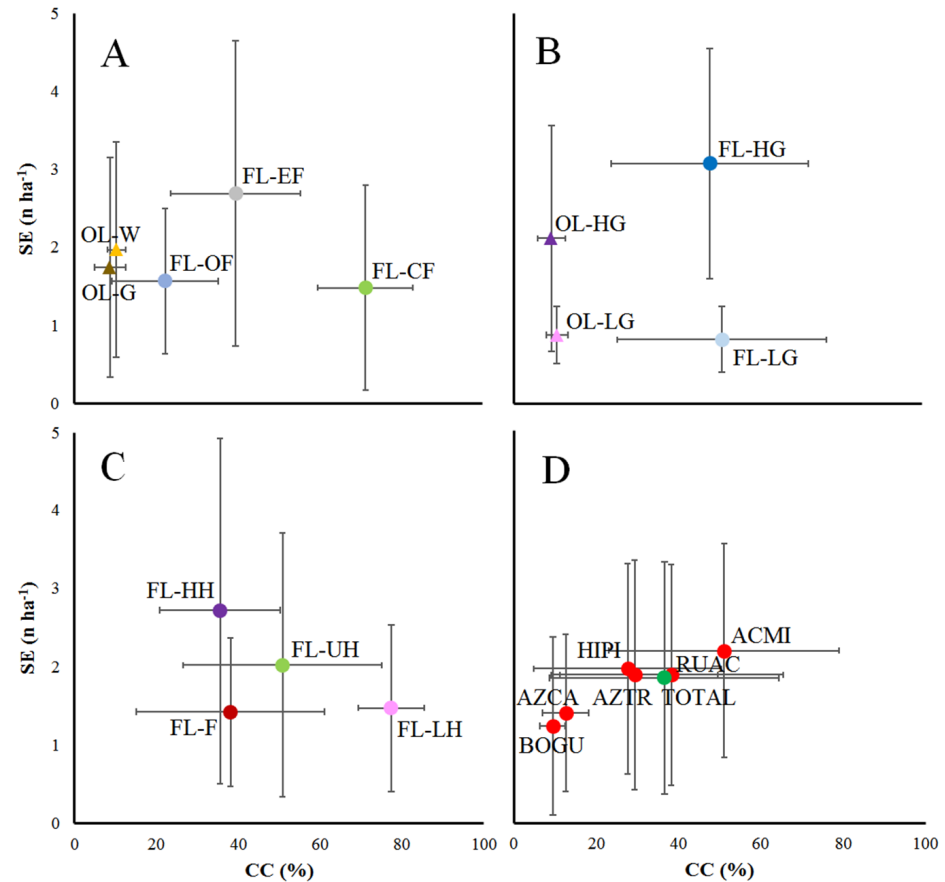


Figure 6. Relationship between crown cover of the overstory (CC, %) and animal density (livestock + guanaco) expressed as sheep equivalents (SE, n ha⁻¹) analyzing open lands (triangles) and forest lands (circles) according to (A) environment types classified as dry grasslands (OL-G, brown), wet grasslands (OL-W, orange), closed forests (FL-CF, green), edge forests (FL-EF, grey), and open forests (FL-OF, blue); (B) grazing impacts classified as open lands with low grazing pressure (OL-LG, light purple), open lands with high grazing pressure (OL-HG, purple), forest lands with low grazing pressure (FL-LG, light blue), and forest lands with high grazing pressure (FL-HG, blue); (C) harvesting and fire impacts in forest lands classified as unharvested areas (FL-UH, green), low harvested stands (FL-LH, light purple), high harvested stands (FL-HH, purple), and fire impacts (FL-F, brown red); and (D) indicator species cover (red dots) considering *Azorella caespitosa* (AZCA), *Bolax gummifera* (BOGU), *Azorella trifurcata* (AZTR), *Hieracium pilosella* (HIPI), *Achillea millefolium* (ACMI), *Rumex acetosella* (RUAC), and the average for all of the measured plots (TOTAL, green). Dots show averages, and lines represent standard error on both axes.

4. Discussion

4.1. Changes in Forest Structure, Soil Properties, and Understory Cover

A mosaic of vegetation types characterizes the ecotone of Southern Patagonia, where *N. antarctica* forests often intermingle with diverse landscapes, including grasslands. Those landscapes are characterized by several environmental factors and the availability of different natural resources [8]. Our sampled plots were distributed throughout different environments that represent this landscape. Our approach considered both natural conditions, such as transition zones and soil moisture levels, and human influences, like extensive

grazing, which often lead to additional activities like harvesting and fire, which are aimed at enhancing forage availability in forested areas [26].

The differences in the forest structure attributes were directly related to transition zones. Open and edge forests exhibited lower canopy cover and higher levels of total radiation in the understory, while closed forests presented a higher site quality, as was described for other *N. antarctica* forests [51]. This direct relationship showed the importance of transition zones, where changes influence the availability of critical resources (e.g., light and moisture) for understory plant growth. Although we anticipated that these differences in forest structure might induce changes in soil properties, we found that the most significant fluctuations occurred primarily in wet grasslands, characterized by high soil moisture conditions, organic carbon, and organic matter, and clearly distinguishing them from other natural areas. While most soil properties remained relatively consistent across the different forest structures [56,65], our study revealed that the pH and soil phosphorus levels increased with crown cover. Additionally, the availability of limiting resources significantly affected the understory species cover. The impact of these factors was significant, where the soil properties and forest structure played crucial roles in shaping the sampled plant community. These findings align with previous research that underscores the influence of environmental factors and resource availability on the establishment and persistence of plant species [66,67]. In our study, we found that grasslands were better preserved than forests, showing the highest cover values for native species and bryophytes. Additionally, consistent with the findings of other studies, our results also revealed a correlation between changes in forest structures, soil phosphorus availability, and the increase in exotic species cover [14].

4.2. Environmental Changes and Indicator Plants Related to Anthropogenic Impacts

In ecosystems under the pressure of anthropogenic impacts, new environmental conditions and resources pose novel challenges for both resident and invading species. The establishment and expansion of plant species depend on how closely these new conditions align with historical baselines [68]. Several studies have demonstrated how harvesting and fire impact light availability, and how grazing affects soil resources, which, in turn, can influence the cover of understory plant species [8,26]. Our study revealed that a high grazing pressure significantly affected soil properties, leading to increased soil bulk density and reduced soil carbon, organic matter, nitrogen and pH across the different land types [69]. Consequently, grazing had a substantial influence on species cover, resulting in decreased native species cover in open lands and forests, while the response of exotic species cover varied based on different combinations of factors. On the other hand, harvesting and fire significantly increased solar radiation, while fire directly affected soil conditions, raising pH levels [70]. These impacts facilitated the establishment of exotic and native understory species that increased under similar conditions to those found in more open forested areas [8,51,70].

Understanding how human impact modifies natural structures that facilitate the invasion of understory species is critical to assess the magnitude of these impacts, especially in ecosystems where productivity and ecological resilience are highly affected [52]. In fact, the early detection of indicator species is crucial for mitigating the long-term impacts of new species introductions or the expansion of already established species [14,37]. In *N. antarctica* forest lands, several studies have linked the presence of specific native and exotic plant species to human impacts, making them excellent indicators of environmental and forage productivity degradation [42,51]. Two native species of our study, *Bolax gummifera* and *Azorella caespitosa*, were more prevalent in open lands, particularly in dry grasslands. Grazing intensity significantly influenced the presence of these species, where *A. caespitosa* decreased with a higher grazing intensity, while *B. gummifera* increased when the soil became more acidic. Additionally, *A. trifurcata*, primarily associated with open lands, showed increased cover in open forests and high-impact forested areas [40,52]. The increases in *B. gummifera* and *A. trifurcata* are associated with soil erosion conditions [42]. In fact, *A.*

trifurcata displayed grazing response characteristics, such as rosette growth forms, which are more tolerant to trampling compared to erect forms, leading to increased competition for resources and space [71].

Despite the changes in local factors, landscape-level factors such as fragmentation also played a role in facilitating the invasion and establishment of invasive species [21]. In the context of *N. antarctica* forests, human land use (e.g., grazing and harvesting) increases landscape fragmentation, making these ecosystems more susceptible to invasions [19,20,37]. Our results showed an increase in exotic species cover in forests subjected to high pressures of grazing and harvesting. Most of those species were intentionally introduced to improve native grasslands (e.g., *Rumex acetosella*) over a century ago [72]. However, their cover increased after disturbances, particularly with fire and overgrazing in forest areas [73]. Moreover, *Hieracium pilosella* varied with wetness and tree canopy cover, where invasion cover increased as areas became drier (e.g., dry grasslands) and had reduced tree canopy cover (e.g., open forests). Although this species is considered the most significant threat to profitable livestock farming [50,51], our study did not find significant differences in the species cover in response to the impacts analyzed across different environments.

4.3. Relation between Invasive Understory Species and Forest Harvesting

To effectively address the challenge of mitigating the ecological and economic consequences of species invasion, it is imperative to gain a deep understanding of the resilience thresholds within natural ecosystems and how these thresholds are altered by human activities. This knowledge forms the foundation for developing more sustainable forest management and conservation strategies. Although invasive plant issues are often experienced by many landowners and managers at the regional level, the practical management of invasive plants typically takes place at the stand scale [12]. In this context, the development of early detection tools becomes crucial, as they can assist owners and forest managers in identifying alien plants in their early stages of establishment [74]. This approach is particularly important for species that are recognized as invasive in other countries, such as *Hieracium pilosella* in Europe. Additionally, adaptive management practices in the framework of SPS can be effectively employed to regulate inter-species competition. These systems help to reduce the establishment of invasive species while promoting the growth of native species [26,30]. The removal of disturbances (e.g., reducing animal density) is known to benefit native species and results in a gradual reduction in invasive species succession over time [12]. However, it is essential to recognize that the trajectory of plant community succession can follow multiple paths when disturbances and invasive species play significant roles [75]. In this context, the long-term monitoring of plant invasions in forests becomes a necessary tool to unravel the patterns of invasion longevity (stage) and the factors influencing the direction of these changes [12]. In future research, better landscape control must be explored (e.g., rainfall patterns) to determine if the studied exotic species or another one (e.g., impacts associated with the exotic species *Castor canadensis*) [76] can have an influence in the same direction and magnitude. Additionally, data independence in the landscape must be considered [53] while avoiding imbalance among the sampling plots of the treatments.

5. Conclusions

We can conclude that *N. antarctica* forest landscapes involve the interaction of many factors, including environmental characteristics, species distributions, and their ecological interactions, alongside the effects of both natural and anthropogenic disturbances. We found a considerable variation in forest structure, soil properties, and vegetation cover across different environments at the landscape level. Human impacts exhibited profound effects on different variables and land types, emphasizing the importance of managing intensities. The use of indicator plant species allows us to identify potential ecological thresholds related to human impacts and establish species linked to ecological and economic degradation; e.g., *Bolax gummifera* and *Azorella trifurcata* were associated with high grazing

pressures in grasslands and fire in forested areas, while *Rumex acetosella* and *Achillea millefolium*, typically associated with forested areas, were related to high harvesting pressure and fire impacts. Although the influence of these impacts is well documented, our study provides a deep understanding of the environmental patterns at the forest landscape level and how human impacts can alter these factors affecting understory cover and facilitating the establishment of invasive species. Our results can contribute to designing better management and conservation practices to reduce exotic species invasion and maintain the resilience of natural ecosystems.

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