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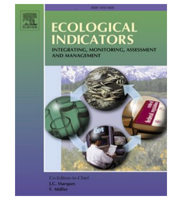

Indicators of ecosystem degradation along an elevational gradient in the Mediterranean Andes

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ABSTRACT

Successful restoration measures need a good understanding of how the composition, structure, and functioning of ecosystems change with degradation and what the best indicators of these changes are. To answer these questions, we worked on four ecosystem types in the Mediterranean Andes mountains in central Chile (from sclerophyllous forest to Andean shrublands), which represent an elevational gradient from 700 to 3,250 m. We sampled three plots on each of the three degradation levels (low, medium, and high) for each ecosystem at increasing distances from goat corrals. We measured 35 indicators that describe vegetation (14), soil (15), and ecosystem processes (6) for one growing season. Degradation caused a decrease in shrub cover, shrub productivity, the Normalized Community Structure Integrity Index ($CSII_n$), litter depth, total soil nitrogen and C/N ratio, and an increase in clay content. Plant species indicating low degradation were consistently native woody species. When comparing ecosystems (i.e., at different elevations) against the type of variable, process-based indicators showed more statistically significant differences. Based on their consistency across ecosystems and ease of measurement, we recommend using shrub cover and litter depth as indicators of degradation. Finally, we concluded that ecosystems are highly degraded when vegetation- and process-based indicators change ~ 60% or when soil indicators change ~ 25%. These results could also be used to set goals for restoration projects in these mountain ecosystems.

1. Introduction

Ecosystem degradation is defined as the loss of the original characteristics of an ecosystem in terms of its structure and functioning because of natural events and human activities (DeFries et al., 2012). The difference between the reference condition (usually assessed in an undisturbed site) and the current condition is used to design restorative measures and monitor their success (Moore et al., 1999). Therefore, identifying indicators of ecosystem degradation can aid in directing restoration proposals and supporting the effectiveness of those plans. Unfortunately, in areas with a long history of land use, it is hard to find undisturbed sites and the effects of degradation have often not been described.

Mountain ecosystems are important not only because they cover one-fifth of the terrestrial surface, but also because it is estimated that about 50% of the global human population depends on the ecosystem services they provide, water being the most relevant of these (Körner and Ohsawa, 2005; Martín-López et al., 2019). Mountain ecosystems are particularly fragile and subject to both natural and anthropogenic degradation drivers, including climate change (Nogués-Bravo et al., 2007), forest fires, wood harvest, and pasture practices (Körner and Ohsawa, 2005).

The Andes mountain range is also affected by degradation processes. In the tropical area of the Andes, land conversion over a 50-year period

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resulted in a 16% decrease in the overall landscape capacity to deliver ecosystem services, with the transformation of native forests to agricultural lands being the change that generated the largest decline in the provision of ecosystem services (Balthazar et al., 2015). In addition, urbanization has increased ecosystem degradation by fragmenting vegetation, leading to a decrease in the provision of ecosystem services and an increase in the frequency and magnitude of natural and anthropogenic hazards (Romero and Ordenes, 2004), effects that have been observed in other mountain ecosystems close to large cities in the Alps (Vigl et al., 2021) and central Chile (Alvarez-Codoceo et al., 2021).

The Mediterranean Andes Mountains in central Chile are part of an area that has been identified as a hotspot for the conservation of biodiversity, mainly because of its high levels of endemism and anthropogenic threat (Alaniz et al., 2016; Mittermeier et al., 2004). In the face of global warming, semi-arid temperate mountains might become increasingly important as refugia for native species (Millar et al., 2015; Muñoz-Sáez et al., 2021).

Ecological indicators enable the assessment of the condition of the environment and serve as an early warning against environmental problems (Niemi and McDonald, 2004). Although ecological indicators have been used to evaluate diverse ecosystems in Chile (Hernández et al., 2015; Steel et al., 2017; Weiland et al., 2011), their application to mountain ecosystems is scarce, despite the relevance of these environments throughout the Chilean territory. We studied the degradation generated by grazing and firewood extraction in four ecosystem types along an elevational gradient in the Mediterranean Andes in central Chile. The objectives of this study were: 1) to assess which vegetation, soil, and process indicators best differentiate the levels of degradation of four mountain ecosystem types; 2) to identify plant species as indicators of different levels of ecosystem degradation; and 3) to analyze whether elevation or the type of indicator (vegetation, soil, process) affects the magnitude of change in indicators of degradation.

2. Materials and methods

2.1. Study area and description of ecosystems

The study area is located in the Andes mountain range of the Metropolitan Region of Chile, between 700 and 3,250 m of elevation (Fig. 1). At this latitude (~33°40′), the climate in the valley is temperate Mediterranean, with precipitation concentrated in winter and a dry period of 6–8 months, typically from October to March. In the study area, however, the effect of elevation makes the climate cooler and more humid, with precipitation ranging from 660 to 1,340 mm (Uribe et al., 2012). At the highest elevation, the dry period is only 1–2 months, with most precipitation falling as snow, with a mean temperature in the coldest month (July) of −1.8 °C and 4.4 °C in the warmest (January).

The geological materials are volcanic sequences of lava and rocks of andesitic-basaltic materials from the Farellones Formation (SERNAGEOMIN, 2003), but the area falls outside of previous soil surveys, so there is no classification available at the soil series level (Casanova et al., 2013).

Four ecosystem types were studied, described by Teillier et al. (2011):

- Sclerophyllous forest (SF), found at elevations between 700 and 1,700 m, is dominated by *Quillaja saponaria*, *Kageneckia oblonga* and *Lithraea caustica*, whereas in wetter sectors *Cryptocarya alba* is the dominant species and on north facing slopes the succulents *Trichocereus chiloensis* and *Puya berteroniana* are representative. There is a heterogeneous shrub layer that dominates on disturbed sites, characterized by the presence of *Baccharis linearis* and *Muehlenbeckia hastulata*. An ephemeral herbaceous stratum grows during the winter and beginning of spring.
- Andean sclerophyllous forest (ASF) (1,650–2,000 m) is almost monospecific, dominated by *Kageneckia angustifolia*, with some presence of *Schinus montanus.* A tall shrub layer of *Colliguaja integerrima* dominates in steep-slope sectors, and *Guindilia trinervis* dominates in areas where trees have been cut or burnt. *T. chiloensis* and *P. berteroniana* also dominate on north-facing slopes, with *Escallonia myrtoidea* being found in more humid areas.
- Lower Andean shrubland (LAS) (1,950–2,800 m) is dominated by a shrub layer, frequently between 0.5 and 1.2 m tall, being mostly a perennial herbaceous stratum that cover about 30–50% of the soil. Dominant shrub species are *Tetraglochin alatum* and *Mulinum spinosum*, whereas in wetter areas *Discaria trinervis* dominates.
- Upper Andean shrubland (UAS) (2,500–3,250 m) is seldom taller than 0.5 m, composed of the shrub species *Berberis empetrifolia*, *Laretia acaulis,* and several species of the genera *Adesmia*, *Nassauvia,* and *Senecio*. There is also a herbaceous stratum in which *Poa holciformis* is consistently found.

2.2. Definition of degradation levels and selection of indicators

The areas selected to evaluate the degradation levels were located at the Colorado river valley (forest ecosystems, SF, ASF) and the Yeso river valley (shrub ecosystems, LAS, UAS) (Fig. 1). The SF site was located at an average elevation of 1,000 m, facing north, with a 31° slope; the ASF site was facing south-east, with an 11° slope and elevation of 1650 m; the LAS site was facing north-west, with a 52° slope and elevation of 2200 m; and the UAS site was located at 2850 m elevation, facing south-west, with a 28° slope.

In this area, degradation is caused by a combination of firewood extraction, occasional fires, and ongoing grazing. The identification of three degradation levels (low, intermediate, and high) was based on an expert appreciation of significant changes in the structural characteristics of vegetation and soil after observing the entire range of ecosystem conditions in the area. The high degradation plots of the four ecosystems were established close to goat corrals (<300 m). The intermediate and low degradation plots were located at increasing distances from the corrals but within comparable topography (i.e., aspect, slope, and position on the landscape). At each degradation level area, three plots were randomly located to sample vegetation, soil, and some process variables. The plot sizes were 20 × 20 m, 10 × 10 m, 4 × 4 m, and 4 × 4 m for the SF, ASF, LAS, and UAS ecosystems, respectively. All the field sampling was done between September 2012 and March 2013, moving upward as the weather became progressively warmer during the austral spring and summer seasons.

The search for indicators was designed to include those that represented the composition, structure, and functioning of biodiversity at the community-ecosystem level, as defined by Noss (1990). Many indicators were selected to explore which ones best represented the degradation at this elevational gradient and were classified as plant, soil, and ecosystem process indicators. The potential correlation between indicators was considered in the statistical analyses described below. The complete list of variables sampled and their abbreviations are presented in Table 1, and their definitions are provided together with the methods used to measure them in the following sections.

2.3. Sampling and analyses of vegetation variables

The structure and composition of the plant community were evaluated using the point-intercept transect method (Kent and Coker, 1992) over five transects equally spaced inside each plot, completing 100 points. At each point, the species found were identified and classified according to life form (tree, shrub, or herb) according to Rodriguez et al. (2018), while plant height and vertical length of green foliage for trees and shrubs were recorded (for the herbaceous plants these two parameters were the same). The plant cover was calculated as the relative abundance of herbs, shrubs, and trees (Cv_h, Cv_s, and Cv_t, respectively) and the total plant cover (Cv_{tot}) as the sum of the three strata. Similarly, the height of each life form was estimated (H_h, H_s, and H_t). Later, species

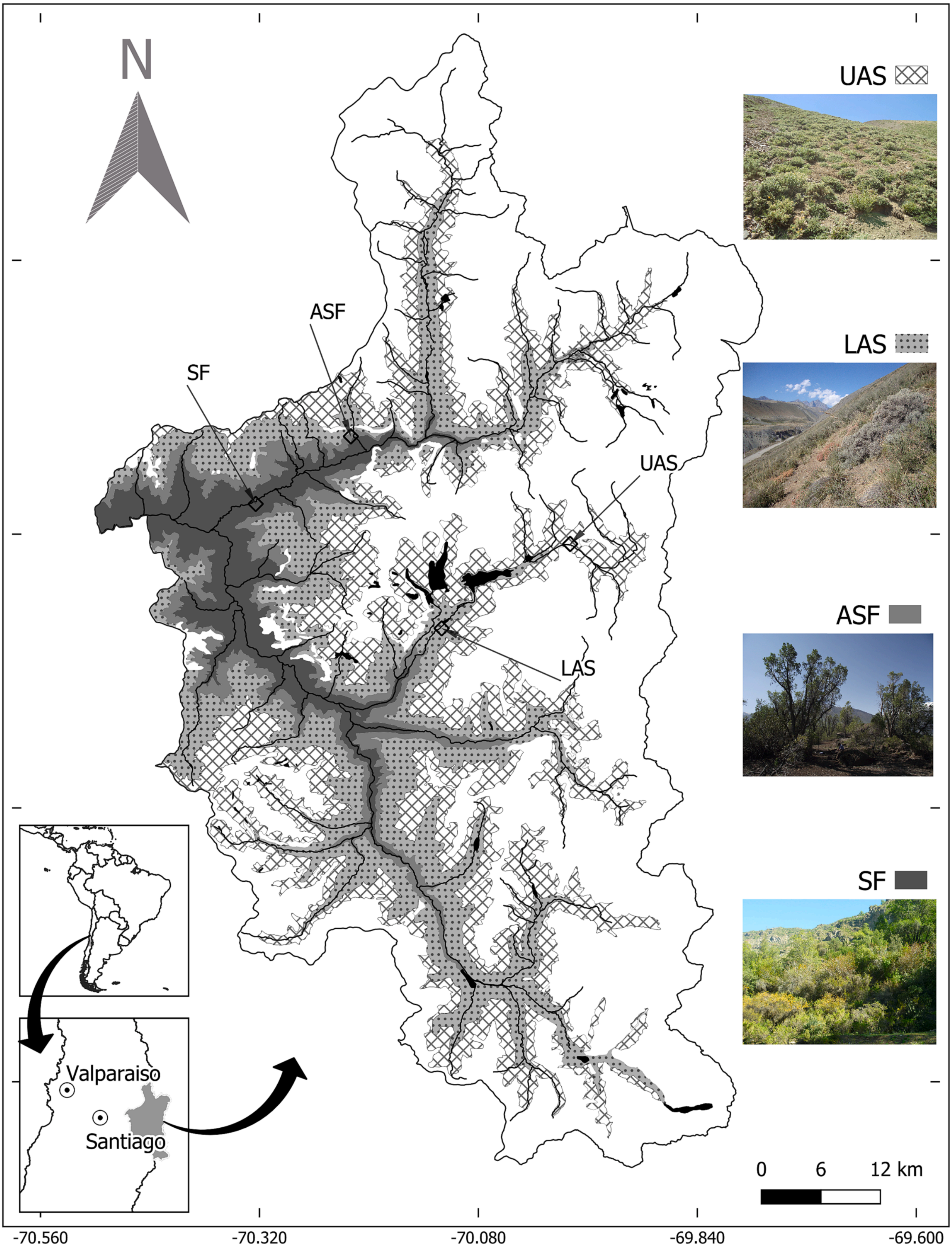

Fig. 1. Location of study areas in the San José commune. The four ecosystem types are sclerophyllous forest (SF), Andean sclerophyllous forest (ASF), lower Andean shrubland (LAS), and upper Andean shrubland (UAS). Black polygons and lines depict water bodies.

Table 1
List of abbreviations, definitions and units of variables sampled in this study.

Variable	Definition	Unit
Vegetation		
Cv_h	Relative cover of herbs	%
Cv_s	Relative cover of shrubs	%
Cv_t	Relative cover of trees	%
Cv_{tot}	Total cover of vegetation	%
$CSII_n$	Normalized community structure integrity index	0–1
D	Diversity (Shannon index)	–
H_h	Average height of herbs	m
H_s	Average height of shrubs	m
H_t	Average height of trees	m
PV_h	Phytovolume of herbs	$m^3\ m^{-2}$
PV_s	Phytovolume of shrubs	$m^3\ m^{-2}$
PV_t	Phytovolume of trees	$m^3\ m^{-2}$
PV_{tot}	Total phytovolume of vegetation	$m^3\ m^{-2}$
R	Species richness	Number of species
Soil		
C/N	Carbon-nitrogen ratio	–
Clay	Content of clay in the soil	% (w/w)
C_{tot}	Total carbon content of soil (top 10 cm)	% (w/w)
D_b	Bulk density of soil	$g\ cm^{-3}$
$D_{b\text{-}f}$	Bulk density of fine fraction of soil	$g\ cm^{-3}$
FC	Soil water content at field capacity	% (v/v)
L_b	Litter biomass	$g\ m^{-2}$
L_c	Litter cover	%
L_d	Litter depth	cm
N_{tot}	Total nitrogen content of soil (top 10 cm)	% (w/w)
Sand	Content of sand in the soil	% (w/w)
Silt	Content of silt in the soil	% (w/w)
S_t	Soil porosity	% (v/v)
Stones	Soil stoniness	% (w/w)
Texture*	Textural class	–
WP	Soil water content at wilting point	% (v/v)
Process		
P_h	Aboveground annual biomass productivity of herbs	$g\ m^{-2}\ year^{-1}$
P_s	Aboveground annual biomass productivity of shrubs	$g\ m^{-2}\ year^{-1}$
P_t	Aboveground annual biomass productivity of trees	$g\ m^{-2}\ year^{-1}$
P_{tot}	Total aboveground annual biomass plant productivity	$g\ m^{-2}\ year^{-1}$
R_{10}	Soil respiration, standardized at 10 °C	$g\ CO_2\ m^{-2}\ h^{-1}$
WIR	Water infiltration rate	$mm\ min^{-1}$

*Not included in statistical analyses.

origin was classified as native or exotic according to Zuloaga et al. (2008). Using the percentage cover and vertical length of green foliage, the phytovolume ($m^3\ m^{-2}$) was estimated for each life form (PV_h, PV_s, and PV_t) and the sum of the three strata (PV_{tot}).

Using plant species composition and relative abundance data from the point-intercept transect method, the species richness, Shannon's diversity index (*H*'), and the Normalized Community Structure Integrity Index ($CSII_n$, Jaunatre et al., 2013) were calculated. The $CSII_n$ index assigns an average value of 1 to reference communities (low degradation level in this study), whereas values close to 0 indicate that the communities being compared represent a small portion of such reference; therefore, it allows comparisons across ecosystems that, as is to be expected, differ in reference communities.

2.4. Sampling and analyses of soil variables

Two composite soil samples from the first 10 cm of soil depth were collected from each plot, one from under woody plant cover and the other from open spaces. Soil texture was measured using the Bouyoucos method (Gee and Or, 2002), separating the percentage of sand, silt, and clay. Based on the relative abundance of the three textural components, the textural class was defined according to the Soil Survey Staff (2006). Coarse material (>2 mm) was estimated in a shallow pit according to the method described by Schoeneberger et al. (2012). The total C and N concentrations in the soils (and the C/N mass ratio) were determined by means of flash combustion using a NA2500 Carlo Erba Element Analyzer in the Biogeochemistry Laboratory at the Pontificia Universidad Católica de Chile.

Plant litter cover (Lc) and depth (Ld) were determined based on the point-intercept transect method. The litter biomass (Lb) was estimated by harvesting 0.5 × 0.5 m quadrats, placing two replicates under woody plant cover and two in open spaces within each plot. The material collected was dried at 70 °C for 48 h.

To determine soil bulk density (D_b, g cm^{-3}), two samples per plot were collected with cylinders of known volume (137 cm^3), which were oven dried for 24 h at 105 °C (Grossman and Reinsch, 2002). The bulk density of the fine fraction (<2 mm, $D_{b\text{-}f}$) was calculated by subtracting the weight and volume of particles > 2 mm from the total sample mass and volume, assuming a particle density for mineral soils (D_p) equal to 2.65 g cm^{-3}, and then dividing the mass of the fine fraction by its volume (Hao et al. 2008). The soil porosity (S_t, %) was calculated as:

$$S_t = \left[1 - \left(\frac{D_b}{D_p}\right)\right] \quad (1)$$

The soil water retention was determined by the pressure chamber method, defining the water content at field capacity (33 kPa) and permanent wilting point (1500 kPa) (Reynolds and Clarke-Topp, 2008).

2.5. Sampling and analyses of process variables

To estimate the aboveground annual biomass productivity of herbs (Ph), the productivity biomass was harvested on four 0.35 × 0.35 m quadrats right after the plants completed fruiting, thus avoiding loss of biomass by grazing. In the case of the aboveground annual biomass productivity of shrubs (Ps), a similar number and size of quadrats were used to estimate the 'apparent' productivity by harvesting the fraction of the shoots generated during the current growing season, which was done at the beginning of autumn. Although there could have been some grazing before this, we observed that shrubs were grazed after the herbaceous stratum was depleted, which generally occurred by mid-autumn. To estimate the aboveground annual biomass productivity of trees (Pt), wood cores were collected from three individuals of each species per plot, which had a diameter at breast height close to the median. Using the diameter increase of the current season, the tree productivity was estimated based on allometric functions from Barriga (2012). By adding the productivity of the life forms, we obtained the total aboveground biomass productivity (Ptot).

The water infiltration rate (WIR, mm min^{-1}) of unsaturated soil surface was measured using a mini disk infiltrometer (Decagon Devices Inc., WA, U.S.A.), applying a constant suction of 3 cm (equivalent to a 0.3 kPa pressure) and recording the time that the soil took to absorb a known volume of water. With the sorption curve as a function of time, the saturated hydraulic conductivity (K) was calculated considering the A factor related to matric suction (Warrick, 2002). Two measurements per plot were performed, one under woody plant cover and one in an open space.

Soil respiration (R_s, soil CO_2 efflux) was estimated using the closed chamber technique connected to an infrared gas analyzer (model EGM-4, PP-System, Hitchin, United Kingdom). Two measurements per plot were performed, one under woody plant cover and one in an open space. R_s was standardized at a temperature of 10 °C (R_{10}, g $CO_2\ m^{-2}\ h^{-1}$) to take measurements comparable across plots using the formula (Lloyd and Taylor 1994):

$R_{10} = R_s\, Q_{10}^{\,(10 - Ts)/10}$ (2).

where R_s is the measured soil respiration, T_s is the soil temperature at the time of measuring R_s, and Q_{10} is a scaling factor for soil temperature. Soil surface temperature, T_s, was measured using an infrared thermometer (model 42530, Extech Instruments, Nashua, USA). A $Q_{10} = 2$

was assumed, which means that R_s doubles with a 10 °C increase in T_s, as suggested by Lloyd and Taylor (1994).

2.6. Statistical analysis and selection of the best indicators of degradation

An analysis of variance (ANOVA) was used to assess statistical differences between degradation levels at each ecosystem type for each indicator of degradation (vegetation, soil, and process variables). Variables were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Bartlett test) to check if they met the underlying statistical assumptions of linear models. When these assumptions were not met, a Kruskal-Wallis test was used, finding results similar to the parametric test in all cases. Therefore, based on the parsimony principle, all the *P* values reported are the results from the ANOVAs.

The Multiple Response Permutation Procedure (MRPP; Mielke, 1991; McCune and Grace, 2002) was used to assess the relative contribution of each indicator to classify degradation levels across ecosystem types. The MRPP is a multivariate non-parametric test of significant differences between groups within each individual variable. The MRPP provides change-corrected group agreement (*A*) and significance (*P*) values. A hypothetical value of $A = 1$ implies that an indicator thoroughly explains the variance between degradation levels; by contrast, a value of $A = 0$ means that the indicator does not explain the degradation levels. MRPP has shown robust results applied to biological and radiometric analyses (e.g., Lopatin et al., 2017); however, the potential synergies among multiple indicators are not considered in the indicator-wise MRPP-based analysis. Therefore, we considered these synergies among vegetation, soil, and process indicators by applying a partial least squares (PLS) discriminant analysis. We determined the contribution of each indicator to discern the level of degradation by applying a bootstrapping iteration procedure, where for each iteration (100) we:

1. Fitted a general model using all indicators and observations available and stored the overall Kappa (K_{all}) value;
2. Fitted indicator-wise partial models by randomizing the values of one indicator at a time in a stepwise procedure, storing one *K* value for each indicator replacement (K_i);
3. Estimated the relative contribution of each indicator by subtracting the indicator-wise partial model from the overall model (K_{all} - K_i), generating a delta Kappa per indicator (ΔK).

On average, 63% of the sample size was allocated for model training and 37% for validation during each iteration. We implemented a 5-fold cross-validation technique on the training samples to derive a test dataset and to fine-tune the optimal number of components. This approach was employed to mitigate overfitting and autocorrelation issues. The results of the 100 iterations were stored to present the distribution of ΔK and prevent stochastic biases (Kattenborn et al., 2019). The 'caret' and 'vegan' packages of the R statistical software (R Core Team, 2014) were used.

2.7. Identifying plant species as indicators of ecosystem degradation

Ordination transformations were used to depict the main floristic composition of the plot-by-species relative abundance matrices of the four ecosystem types (i.e., elevational gradient) using nonmetric multidimensional scaling (NMDS; Shepard, 1962). NMDS reduced data multidimensionality by creating a fixed number of components and summarizing the main data gradients. The final number of components was selected by keeping the model 'stress' values < 1.5 (using the best solution of 500 iterations; Paliy & Shankar, 2016). The Bray-Curtis dissimilarity distance was used because it is robust when dealing with an abundance of data with a significant presence of zeros (Shepard, 1962), even in small samples (e.g., Lopatin et al., 2022).

The indicator species were identified by depicting the NMDS coordinates closest to the degradation group centroids. The species with the highest relative abundance were preferred over less abundant species with similar coordinates. Finally, species occurring between two or more degradation centroids exhibit co-occurrences among degradation classes; hence, they were not considered adequate indicators of degradation.

2.8. Changes in indicators of degradation with elevation and type of indicator

The multivariate dispersion (variance) was examined for vegetation, soil, and process-based indicators of ecosystem degradation, relative to elevation or ecosystem types, using a principal coordinates analysis (PCoA) with the Gower dissimilarity distances. This approach has proven effective in efficiently representing hypervolumes of correlated variables, such as plant traits and characteristics (Carvalho and Cardoso, 2020; Mammola and Cardoso, 2020). To estimate if the dispersions (variances) of one or more groups were different, the distances of all PCoA group members to the group centroid were compared using ANOVA-like permutation tests (Legendre et al., 2011; α = 0.05) and the post hoc Tukey honest significant differences (HSD) test (Yandell, 1997).

For this same purpose, the absolute relative change (ARCh) of each indicator was estimated as:

$$ARC = \left| \frac{High\ degradation\ value - Low\ degradation\ value}{Low\ degradation\ value} \right| \tag{3}$$

The effects of ecosystem type (which are located at different elevations) and between types of indicators (i.e., vegetation, soil, or process) on the relative change of the indicators of degradation were evaluated using a two-sided ANOVA test (including the interaction effect) and post hoc Tukey HSD tests to assess for statistical significance (α = 0.05).

3. Results

3.1. Best vegetation, soil, and process indicators of ecosystem degradation

The results of the ANOVA analyses for the indicators that assess differences between degradation levels in all four ecosystem types are presented in Supplementary Material, Tables A1-A4. Of the 35 indicators, 6 showed significant differences in SF, 29 in ASF, 17 in LAS, and 20 in UAS.

Fig. 2 shows the relative importance of each indicator to predict ecosystem degradation according to their individual effect and incorporates synergies with other indicators. Among vegetation indicators, shrub plant cover (CV_s) and $CSII_n$ showed consistency among methods, while the total plant cover (CV_{tot}), tree cover (CV_t), the shrub phytovolume (PV_s), and diversity (D) depicted significant individual relative importance. Meanwhile, the herbaceous plant cover (CV_h) showed significant relative importance when also considering its synergies with other variables (ΔK). We found consistency in the soil-based indicators for litter depth (L_d), clay, total amount of nitrogen (N_{tot}), and the C/N ratio, while litter biomass (L_b) and total carbon (C_{tot}) depicted only individual relative contributions. Finally, only shrub productivity (P_s) depicted consistent relative importance in predicting ecosystem degradation among the process-based indicators, while soil respiration (R_{10}) showed individual importance, and tree productivity (P_t) showed important synergies with other variables.

3.2. Plant species indicators of ecosystem degradation

Fig. 3 shows the distribution of the most relevant indicator species in the two-dimensional space of the NMDS ordination algorithm. In this case, the species closest to the centroid coordinates of the low, medium, and high degradation classes indicate their suitability for using them as specific indicators of degradation classes. For example, the species *Kageneckia oblonga* and *Lithraea caustica* are robust indicators of low

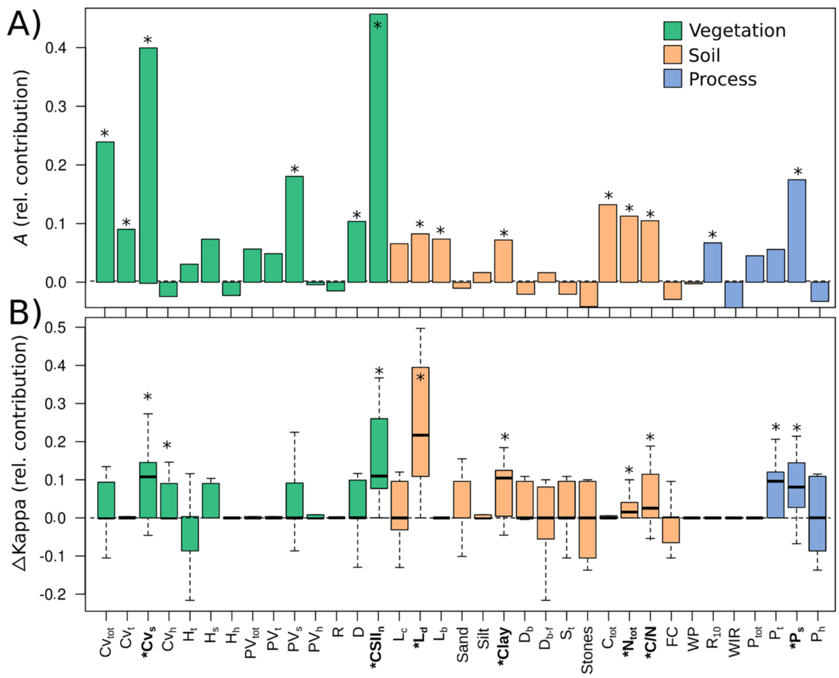

Fig. 2. Relative importance of indicators. A) shows the values of relative importance of individual vegetation, soil, and process indicators (A) in a barplot, using the Multiple Response Permutation Procedure (MRPP), and B) shows the relative importance incorporating synergies among multiple indicators in a boxplot, using ΔKappa according to a partial least squares (PLS) discriminant analysis. Significant variables are depicted by asterisks (*; $\alpha = 0.05$). Variable names in bold with asterisks indicate consistency between the two methods. Abbreviations of indicators are shown in Table 1.

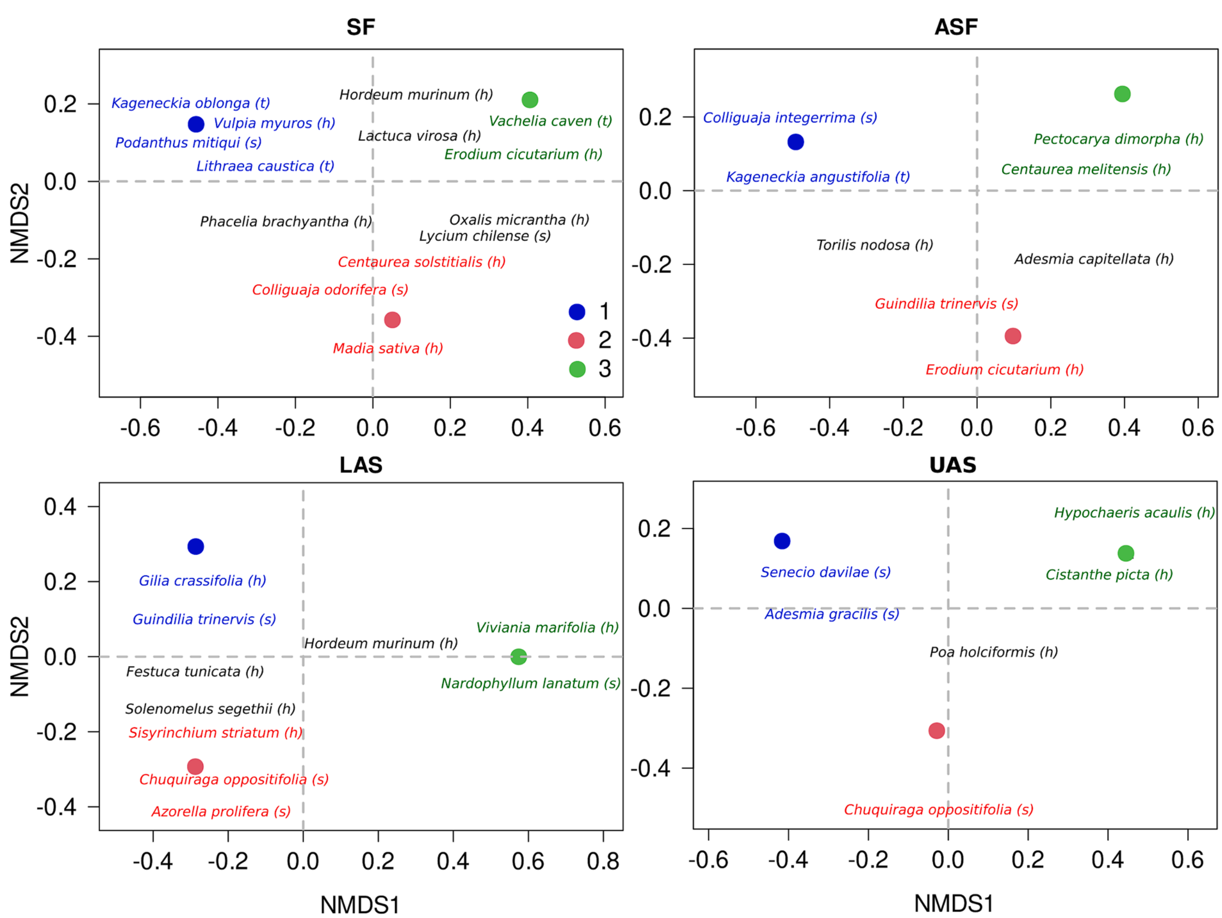

Fig. 3. Species-based main floristic gradients for sclerophyllous forest (SF), Andean sclerophyllous forest (ASF), lower Andean shrubland (LAS), and upper Andean shrublands (UAS) using NMDS. Blue, red, and green dots represent the centroid coordinates of the low, medium, and high degradation classes, respectively. Species of the same color as the centroids depict reliable indicators for that degradation level; names in black represent species that are shared between degradation classes. Letters in parenthesis are: t, tree; s, shrub; h, herb. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

degradation for Sclerophyllous forests (SF), while *Vachelia caven* indicates high degradation. The four ecosystem types, located at different elevations, have distinct species showing the three degradation classes. Meanwhile, species occupying intermediate coordinates between two or more degradation-class centroids are present in more than one degradation class and hence are unreliable indicators. For example, *Phacelia brachyantha* occupies coordinates between the low and medium degradation classes in SF, indicating near equal presence in both classes.

3.3. Changes in indicators with degradation and elevation

Fig. 4a depicts the multivariate dispersion of vegetation, soil, and process indicators of ecosystem degradation in relation to ecosystem types. Here, a principal coordinates analysis (PCoA) grouped observations according to their unique information in a two-dimensional space. The dispersions (variances) of one or more groups differ statistically in all cases using all eight PCoA dimensions ($\alpha < 0.001$). Fig. 4b shows the statistically significant differences between pairs of ecosystem types. Results show that UAS and LAS ecosystems cannot be statistically separated using vegetation, soil, or process indicators alone. However, all other combinations of ecosystem types can be statistically separated using only one indicator type. For example, SF and LAS ecosystems can only be separated by process-based variables, while ASF and UAS can be distinguished using only vegetation variables. Overall, the process variables were statistically significant in more cases than the vegetation and soil indicators.

Fig. 5 depicts the absolute relative change (%) of indicators according to degradation for ecosystems present at different elevations and for vegetation, soil, and process indicators. In this figure, the process indicators are the ones that show the greatest absolute relative change, followed by the vegetation indicators and finally the soil indicators. The vegetation and process indicators changed ~ 60% while soil indicators changed ~ 25%. We found no significant differences among ecosystems, showing that degradation affects overall statistically to the same degree through different elevations.

4. Discussion

4.1. Vegetation, soil, and process indicators of ecosystem degradation

Among the most consistent indicators of ecosystem degradation in the four Andes mountain ecosystems studied were shrub cover and shrub productivity. Both vegetation indicators exhibited the same pattern, consistently decreasing with degradation across all ecosystem types. Although working on a different spatial scale, Ferrara et al. (2012) also selected vegetation cover as one of four variables (out of 14) that provided the largest contribution to an index designed to monitor desertification. This can be partly explained by the relationship that shrub cover and its productivity have with degradation; shrub cover can have a facilitating effect on survival and the early stages of seedling establishment (Zhao et al., 2007; Perea and Gil, 2014), and an increase in aboveground C, total and organic C, total N, soil available P, and potential soil N mineralization (Zhao et al., 2007; Eldridge et al., 2011).

The similarity of species composition with the reference plots, expressed by the $CSII_n$ index, showed significant relative importance to explain degradation, suggesting that species composition drastically changes with degradation. This finding agrees with a study that examined the effects of grazing in remnant woodland vegetation in semi-arid

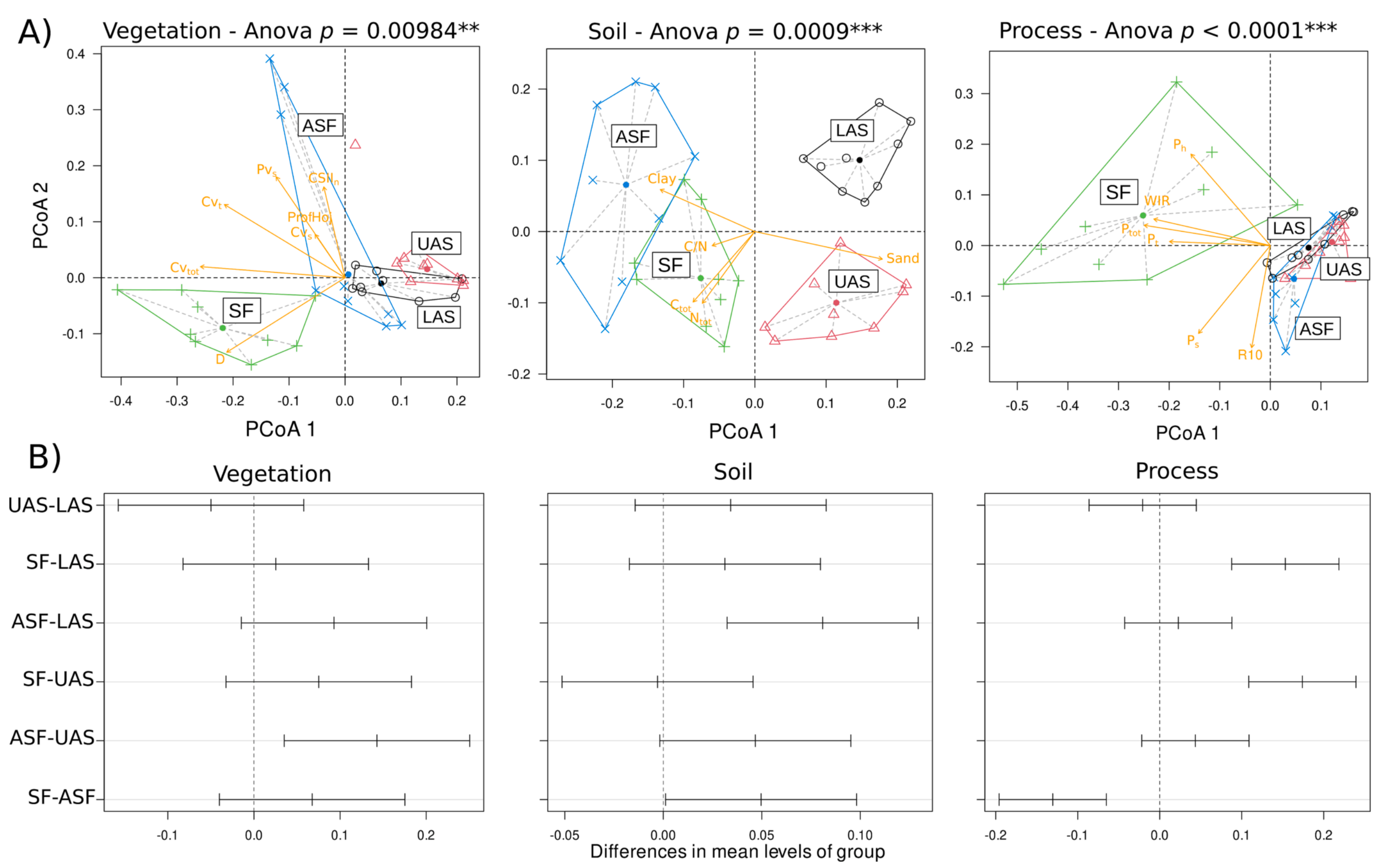

Fig. 4. A) Principal coordinates analysis (PCoA) showing how the vegetation, soil, and process-based indicators of ecosystem degradation can differentiate between vegetation types. Significant statistical differences between vegetation types were tested using one-tailed ANOVA models. Some statistical differences may not be visible because only two out of eight dimensions are shown. B) Tukey HDS post hoc test of significance ($\alpha = 0.05$). Ecosystem types are sclerophyllous forest (SF), Andean sclerophyllous forest (ASF), lower Andean shrubland (LAS), and upper Andean shrublands (UAS).

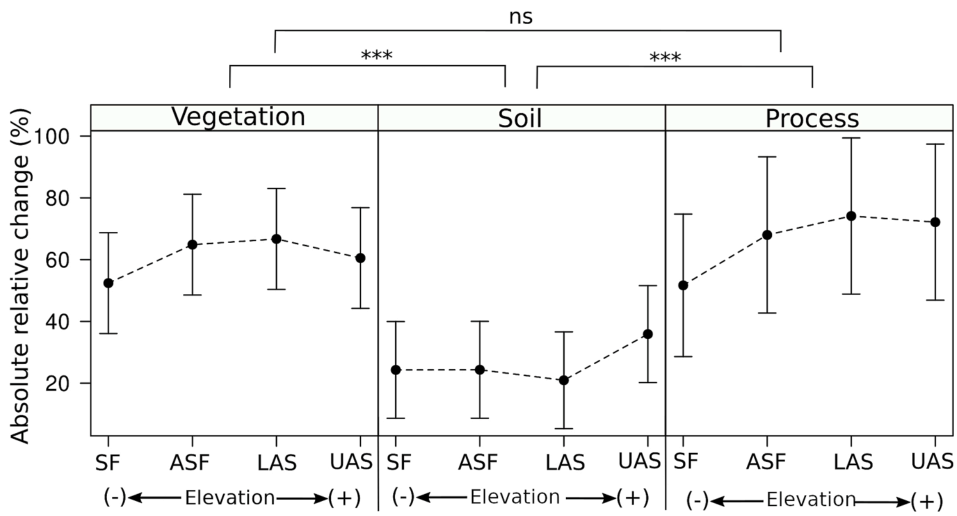

Fig. 5. Absolute relative change of indicators between low and high degradation levels for ecosystems present at different elevations and for type of indicator. Ecosystem types are sclerophyllous forest (SF), Andean sclerophyllous forest (ASF), lower Andean shrubland (LAS), and upper Andean shrublands (UAS). Bars on top show the significance of the ANOVA for the indicator types. The interaction between the ecosystem and the indicator type was not significant.

southwestern Australia, where species richness and diversity were reduced, while the proportion of exotic species increased (Pettit et al., 1995). Similarly, Yates et al. (2000) found a greater percentage cover of exotic annuals, a smaller percentage cover of native perennials, and no change in native annual cover between grazed and ungrazed fragmented woodlands in southwestern Australia. The proportion of exotic species consistently increased in degraded sites of our study across all ecosystem types (data not shown), except for the upper Andean shrubland, where no exotic species were found. Together with the change in plant species composition, evident decreases in species richness and diversity were observed. This is relevant because the loss of perennial shrubs and herbs and the invasion of exotic species may rapidly decrease the resilience of semi-arid ecosystems in central Chile (Holmgren, 2002; Becerra et al., 2020). This is consistent with the work by De Pietri (1992), who studied the combined effects of grazing and fire on North Patagonian forests in Argentina, finding three ecological indicators (key species compositional changes, plant cover, and phytovolume) that when used together explained degradation level. Such consistent trends, particularly changes in biodiversity with degradation, could also be used in the opposite way to monitor advances in restoration projects (Hobbs and Norton, 2004; Sasaki et al., 2015).

A relevant soil indicator of degradation was the litter depth, which decreased with increasing degradation, although this effect was more evident in the forest ecosystems. This is consistent with the literature, given its significant role in the nutrient and biogeochemical cycles in forest ecosystems (Giweta, 2020). In this sense, a greater presence of litter in forest ecosystems could trigger a greater diversity of entomofauna (Lindsay and Cunningham, 2009; Santonja et al., 2017), while in desert ecosystems with degraded soils, it would improve their structure, microclimatic conditions and encourage the appearance of herbaceous species (Chao Jia et al., 2018), contributing to the restoration of these ecosystems. The presence of leaf litter is related to other variables such as the C/N ratio, having a great potential to change soil carbon and nitrogen in forest ecosystems (Miao et al., 2019), in turn affecting soil microbial respiration (Fanin et al., 2011; Spohn, 2015).

Clay content was another soil indicator of high relative importance, as this increased with degradation consistently across all ecosystem types, whereas silt and sand contents did not exhibit a clear pattern. Since clay particles are smaller and tend to be more abundant in deeper soil layers of the Chilean Andes (Casanova et al., 2013), we believe that the sampling in degraded areas was actually at deeper layers of the original soil, exposed as a result of soil erosion, as was suggested by Seguel et al. (2015) in a granitic soil in central Chile.

Other important soil indicators of degradation were total nitrogen content and the C/N ratio. Both soil C and soil N in the first horizon strongly decreased with degradation consistently across ecosystems. The soil C/N ratio significantly decreased with degradation for all sites except the upper Andean shrubland ecosystem, where the C/N ratio was the lowest. Soil C and N were the most consistent soil properties decreasing with degradation, but also being greater in the two lower ecosystems compared to the two higher-elevation ecosystems. Bastida et al. (2008) highlighted the importance of soil C and N contents as indicators of soil quality, while Franzluebbers (2010) demonstrated the direct relation of C and N stocks with litter input, recommending that the cattle stocking rate be reduced to maintain soil functionality. Dale et al. (2008) found soil C to be the most relevant soil variable decreasing with disturbance regimes (i.e., reference, light-, moderate- and heavy-intensity training) in military training sites in Georgia pine forests, together with soil microbial activity and plant cover as relevant indicators. Jeddi and Chaieb (2010) found that excluding livestock for 6 and 12 years enhanced soil C, water infiltration rate, basal soil respiration, total plant cover, dry matter yield, the number of species per unit area, and the *H'* diversity index, in a degraded *Stipa tenacissima* steppe in southern Tunisia. Both studies (i.e., Dale et al., 2008; Jeddi and Chaieb, 2010) suggest that soil C can be used to track degradation as well as advances in restoration projects, mainly because this is related to the increase in organic matter and the consequent restoration of soil fertility and soil functions (Franzluebbers, 2010). Given the strong correlation between soil C and soil N contents ($r^2 = 0.94$, $P < 0.001$), choosing one would account for both.

4.2. Plant species that indicate the level of ecosystem degradation

The identification of indicator plant species has been used to determine degradation levels or restoration success in different types of ecosystems (Doren et al., 2009; González et al., 2013). Instead of using single species or only target species as indicators of conservation conditions of habitats, Helm et al. (2015) argue that this should be complemented by the information that both native (colonizer) and exotic (invasive) species provide. In our study, indicator species associated with low degradation levels for all ecosystems were almost entirely native species (e.g., *Guindilia trinervis, Lithraea caustica,* and *Kageneckia oblonga*). This is consistent with other studies where at lower levels of disturbance or degradation of the ecosystem there is a higher proportion of native plants (Arévalo et al., 2005; Moges et al., 2017; Roy et al., 2019). On the other hand, exotic species were not associated with any particular degradation level, although they appeared more frequently in ecosystems located at lower elevations (forests) than those at higher elevations (shrublands); this may be due to the proximity to urban centers and environmental stresses associated with elevation-related factors that act as a filter against alien plants at higher elevation (Arévalo et al., 2005). In this sense, the exotic species that appeared most frequently were *Centaurea solstitialis* and *Centaurea melitensis*, both of which are recognized as highly invasive in Mediterranean ecosystems (Dukes et al., 2011; Moroney and Rundel, 2013).

Even though there are species shared among different ecosystem types and levels of degradation, we found that indicator species tend to be specific for each combination of ecosystem and degradation level (Fig. 3). Regarding life forms, indicator species at low degradation levels are almost exclusively woody species, either shrubs or trees. In particular, the repeated presence of shrub species at levels of low degradation for the four ecosystems coincides with shrub cover being described before as an indicator of ecosystem degradation for these environments (Maestre and Cortina, 2004; Eldridge et al., 2013; Eldridge and Soliveres, 2015). By contrast, annual weeds are the most frequent life form at high levels of degradation.

4.3. Effects of elevation and type of indicator on the relative change produced by degradation

We sampled several vegetation (14), soil (15), and ecosystem processes (6) variables. When looking at the relative change in indicators (between low and high degradation levels), we found no differences between ecosystems located at different elevations (Fig. 5A). This means that most indicators not only showed a consistent direction of change caused by degradation, but also a similar quantitative effect, which argues in favor of using a limited number of indicators across ecosystem types.

By contrast, we found that process indicators showed more significant differences between ecosystem types, followed by vegetation and soil indicators (Fig. 5B). In other words, soil indicators showed the lowest relative change between the low and high degradation levels. Results showed that ecosystems are highly degraded when vegetation- and process-based indicators change ~ 60% or when soil indicators change ~ 25%. This is consistent with the theoretical model proposed by Whisenant (1999), which expects that degradation will first cause changes in the biotic components of ecosystems (and the associated processes), while the abiotic (soil) component will be affected at later stages of degradation.

4.4. Causes of degradation in mountain ecosystems and proposed indicators

Field observations show that grazing and firewood extraction were the main drivers of degradation in the forest ecosystems, while grazing was the most important one in the shrublands. Overgrazing has been related to ecosystem degradation, as in the study by López et al. (2013), who found that ecosystem functional integrity decreased because of the effect that grazing had on seedling emergence, recruitment, water infiltration, and nutrient cycling. Working on a larger spatial scale, Wessels et al. (2007) isolated the effects of rainfall and grazing over semi-arid rangelands in South Africa. They found that degradation caused by grazing had a significant effect on long-term vegetation productivity.

The use a reduced set of indicators has been recommended for mapping land degradation and desertification based on both quantitative data and expert opinions (Zucca et al., 2012). Furthermore, the combination of environmental and plant species indicators, like the ones presented in this study, better predict restoration success (González et al., 2014). Dale and Beyeler (2001) argue that ecological indicators may comply with several conditions: be easily measured, be sensitive to stresses on the system, predictably respond to stress, be anticipatory, predict changes that can be averted by management actions, be integrative, have a known response to disturbances, anthropogenic stresses, and changes over time, and have low variability in response. We believe all these conditions are met in this study by shrub plant cover and litter depth indicators. First, shrub plant cover and litter depth consistently decreased with degradation across all ecosystem (elevation) types, so we expect these variables will increase over time either if the ecosystem is left to rest or active restoration measures are carried out. Second, as previously discussed, these indicators are closely related to other indicators such as diversity, C/N ratio, and total C and N. Third, both variables are easily measured at a relatively low cost, which may allow for the prompt application of corrective actions. Finally, both indicators exhibit relatively low temporal variability compared to the process indicators.

5. Conclusions

We found significant changes in several vegetation, soil, and process indicators along an altitudinal gradient in the Mediterranean Andes. The original set of 35 variables can be narrowed down to two indicators, namely shrub cover and litter depth. These indicators were selected based on their consistency, ease of measurement and relatively low cost, for which they could be used as indicators of degradation and also to monitor advances in restoration projects. Additionally, indicator plant species that could be used for both purposes were consistently native woody species.

We propose that the relative change of indicators between the low and medium or high degradation levels may be more useful than the absolute values of the indicators, mainly because mountain ecosystems are highly variable. When comparing this relative change, we found that soil indicators varied significantly less than vegetation and process indicators and the effect of elevation, confirming that soil variables are affected by degradation later than vegetation and process variables.

CRediT authorship contribution statement

Jorge F. Perez-Quezada: Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Javier Lopatin:** Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **María R. Donoso:** Writing – original draft, Writing – review & editing. **Cristian Hurtado:** Investigation, Writing – original draft. **Ivan Reyes:** Investigation, Writing – original draft, Visualization. **Oscar Seguel:** Methodology, Resources, Writing – review & editing. **Horacio E. Bown:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, 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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110388.

References

Alaniz, A., Galleguillos, M., Perez-Quezada, J.F., 2016. Assessment of quality of input data used to classify ecosystems according to the IUCN Red List methodology: The case of the central Chile hotspot. Biol. Conserv. 204, 378–385.

Alvarez-Codoceo, S., Cerda, C., Perez-Quezada, J.F., 2021. Mapping the provision of cultural ecosystem services in large cities: The case of The Andean piedmont in Santiago. Chile. Urban For. Urban Green. 66.

Arévalo, J.R., Delgado, J.D., Otto, R., Naranjo, A., Salas, M., Fernández-Palacios, J.M., 2005. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspect. Plant Eco. Evol. Syst. 7 (3), 185–202.

Balthazar, V., Vanacker, V., Molina, A., Lambin, E.F., 2015. Impacts of forest cover change on ecosystem services in high Andean mountains. Ecol. Indic. 48, 63–75.

Barriga, C., 2012. Accumulation and carbon sequestration in Mediterranean forests of the national reserve Roblería del Cobre de Loncha: implications for its conservation. University of Chile, Santiago, Chile, Thesis, p. 37.

Bastida, F., Zsolnay, A., Hernández, T., García, C., 2008. Past, present and future of soil quality indices: A biological perspective. Geoderma. 147 (3-4), 159–171.

Becerra, P.I., Cavieres, L., Bustamante, R.O., 2020. Effect of the invasive exotic herb *Centaurea solstitialis* on plant communities of a semiarid ecosystem. Plant Ecol Divers. 13 (3–4), 267–275.

Carvalho, J.C., Cardoso, P., 2020. Decomposing the causes for niche differentiation between species using hypervolumes. Front. Ecol. Evol. 8, 243.

Casanova, M., Salazar, O., Seguel, O., Luzio, W., 2013. In: The soils of Chile. Springer, Madison, USA, p. 185 p.. World Soils Book Series.

Chao Jia, Z., Huang, Z., Miao, H.T., Lu, R., Li, J., Liu, Y., Weibo, S., Honghua, H., Wu, G. L., 2018. Litter crusts promote herb species formation by improving surface microhabitats in a desert ecosystem. Catena. 171, 245–250.

Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. Ecol. Indic. 1 (1), 3–10.

Dale, V.H., Peacock, A.D., Garten, C.T., Sobek, E., Wolfe, A.K., 2008. Selecting indicators of soil, microbial, and plant conditions to understand ecological changes in Georgia pine forests. Ecol. Indic. 8 (6), 818–827.

De Pietri, D.E., 1992. The search for ecological indicators: is it possible to biomonitor forest system degradation caused by cattle ranching activities in Argentina? Vegetatio. 101 (2), 109–121.

DeFries, R.S., Ellis, E.C., Chapin, F.S., Matson, P.A., Turner, B.L., Agrawal, A., Crutzen, P. J., Field, C., Gleick, P., Kareiva, P.M., Lambin, E., Liverman, D., Ostrom, E., Sanchez, P.A., Syvitski, J., 2012. Planetary opportunities: a social contract for global change science to contribute to a sustainable future. Bioscience. 62 (6), 603–606.

Doren, R.F., Volin, J.C., Richards, J.H., 2009. Invasive exotic plant indicators for ecosystem restoration: an example from the Everglades restoration program. Ecol. Indic. 9 (6), S29–S36.

Dukes, J.S., Chiariello, N.R., Loarie, S.R., Field, C.B., 2011. Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes. Ecol. Appl. 21 (6), 1887–1894.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol. Lett. 14 (7), 709–722.

Eldridge, D.J., Soliveres, S., 2015. Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. Aust. J Bot. 62 (7), 594–608.

Eldridge, D.J., Soliveres, S., Bowker, M.A., Val, J., Firn, J., 2013. Grazing dampens the positive effects of shrub encroachment on ecosystem functions in a semi-arid woodland. J Appl Ecol. 50 (4), 1028–1038.

Fanin, N., Hättenschwiler, S., Barantal, S., Schimann, H., Fromin, N., 2011. Does variability in litter quality determine soil microbial respiration in an Amazonian rainforest? Soil Biol. Biochem. 43 (5), 1014–1022.

Ferrara, A., Salvati, L., Sateriano, A., Nolè, A., 2012. Performance evaluation and cost assessment of a key indicator system to monitor desertification vulnerability. Ecol. Indic. 23, 123–129.

Franzluebbers, A.J., 2010. Achieving soil organic carbon sequestration with conservation agricultural systems in the Southeastern United States. Soil Sci. Soc. of Am. J. 74 (2), 347–357.

Gee, G.W., Or, D., 2002. Particle size analysis. pp: 255-293. In: Dane, J. H. and Topp, G. C. (Eds.) Methods of Soil Analysis. Part 4. Physical Methods. Soil Science Society of America Book Series No. 5. Madison, Wisconsin, USA. 1692 p.

Giweta, M., 2020. Role of litter production and its decomposition, and factors affecting the processes in a tropical forest ecosystem: a review. J Ecol Environ. 44 (1), 1–9.

González, E., Rochefort, L., Boudreau, S., Hugron, S., Poulin, M., 2013. Can indicator species predict restoration outcomes early in the monitoring process? A case study with peatlands. Ecol. Indic. 32, 232–238.

González, E., Rochefort, L., Boudreau, S., Poulin, M., 2014. Combining indicator species and key environmental and management factors to predict restoration success of degraded ecosystems. Ecol. Indic. 46, 156–166.

Grossman, R. B., Reinsch, T.G., 2002. Bulk density and linear extensibility. pp: 201-228. In: Dane, J. H. and Topp, G.C. (Eds.) Methods of Soil Analysis. Part 4. Physical Methods. Soil Science Society of America Book Series No. 5. Madison, Wisconsin, USA. 1692 p.

Hao, X., Ball, B.C., Culley, J.L.B., Carter, M.R., Parkin, G.W., 2008. Soil density and porosity. pp 743–759. In: Carter, M.R., Gregorich, E.G. (Eds.), Soil sampling and methods of analysis, 2nd Edition. Canadian Society of Soil Science, Boca Raton, Florida, USA, p. 1224.

Helm, A., Zobel, M., Moles, A.T., Szava-Kovats, R., Pärtel, M., Rejmanek, M., 2015. Characteristic and derived diversity: implementing the species pool concept to quantify conservation condition of habitats. Divers. Distrib. 21 (6), 711–721.

Hernández, A., Miranda, M., Arellano, E.C., Saura, S., Ovalle, C., 2015. Landscape dynamics and their effect on the functional connectivity of a Mediterranean landscape in Chile. Ecol. Indic. 48, 198–206.

Hobbs, R.J., Norton, D.A., 2004. Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. pp 72–95. In: Temperton, V., Hobbs, R.J., Nuttle, T., Halle, S. (Eds.), Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, USA, p. 441.

Holmgren, M., 2002. Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. Biol. Invasions. 4 (1), 25–33.

Jaunatre, R., Buisson, E., Muller, I., Morlon, H., Mesléard, F., Dutoit, T., 2013. New synthetic indicators to assess community resilience and restoration success. Ecol. Indic. 29, 468–477.

Jeddi, K., Chaieb, M., 2010. Changes in soil properties and vegetation following livestock grazing exclusion in degraded arid environments of South Tunisia. Flora. 205 (3), 184–189.

Kattenborn, T., Fassnacht, F.E., Schmidtlein, S., Nagendra, H., He, K., 2019. Differentiating plant functional types using reflectance: which traits make the difference? Remote. Sens. Ecol. Conserv. 5 (1), 5–19.

Kent, M., Coker, P., 1992. Vegetation description and analysis: a practical approach. Belhaven Press, London, p. 363.

Körner, C., Ohsawa, M., 2005. Mountain systems. Chapter 24. In: Hassan, R., Scholes, R., Ash, N. (Eds.), Ecosystems and human well-being: current state and trends, vol 1. Island Press, Washington, USA, Findings of the condition and trends working group of the Millennium Ecosystem Assessment, p. 948.

Legendre, P., Oksanen, J., ter Braak, C.J., 2011. Testing the significance of canonical axes in redundancy analysis. Methods Ecol. Evol. 2, 269–277.

Lindsay, E.A., Cunningham, S.A., 2009. Livestock grazing exclusion and microhabitat variation affect invertebrates and litter decomposition rates in woodland remnants. For. Ecol. Manag. 258 (2), 178–187.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Func. Ecol. 8 (3), 315.

Lopatin, J., Fassnacht, F.E., Kattenborn, T., Schmidtlein, S., 2017. Mapping plant species in mixed grassland communities using close range imaging spectroscopy. Remote Sens Environ. 201, 12–23.

Lopatin, J., Araya-López, R., Galleguillos, M., Perez-Quezada, J.F., 2022. Disturbance alters relationships between soil carbon pools and aboveground vegetation attributes in an anthropogenic peatland in Patagonia. Ecol. Evol. 12 (3).

López, D.R., Brizuela, M.A., Willems, P., Aguiar, M.R., Siffredi, G., Bran, D., 2013. Linking ecosystem resistance, resilience, and stability in steppes of North Patagonia. Ecol. Indic. 24, 1–11.

Maestre, F.T., Cortina, J., 2004. Insights into ecosystem composition and function in a sequence of degraded semiarid steppes. Restor Ecol. 12 (4), 494–502.

Mammola, S., Cardoso, P., 2020. Functional diversity metrics using kernel density n -dimensional hypervolumes. Methods Ecol. Evol. 11 (8), 986–995.

Martín-López, B., Leister, I., Lorenzo Cruz, P., Palomo, I., Grêt-Regamey, A., Harrison, P. A., Lavorel, S., Locatelli, B., Luque, S., Walz, A., Saunders, M.E., 2019. Nature's contributions to people in mountains: A review. PloS one 14 (6).

McCune, B., Grace., J. B., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

Miao, R., Ma, J., Liu, Y., Liu, Y., Yang, Z., Guo, M., 2019. Variability of aboveground litter inputs alters soil carbon and nitrogen in a coniferous–broadleaf mixed forest of Central China. Forests. 10 (2), 188.

Mielke, P.W., 1991. The application of multivariate permutation methods based on distance functions in the earth-sciences. Earth Sci. Rev. 31 (1), 55–71.

Millar, C.I., Westfall, R.D., Evenden, A., Holmquist, J.G., Schmidt-Gengenbach, J., Franklin, R.S., Nachlinger, J., Delany, D.L., 2015. Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California. USA. Quatern. Int. 387, 106–121.

Mittermeier, R.A., Robles Gil, P., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., da Fonseca, G.A., 2004. Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, Agrupación Sierra Madre, University of Virginia, Conservation International.

Moges, A., Beyene, A., Ambelu, A., Mereta, S.T., Triest, L., Kelbessa, E., 2017. Plant species composition and diversity in wetlands under forest, agriculture and urban land uses. Aquat. Bot 138, 9–15.

Moore, M.M., Wallace Covington, W., Fulé, P.Z., 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecol. Appl. 9 (4), 1266–1277.

Moroney, J.R., Rundel, P.W., 2013. Abundance and dispersion of the invasive Mediterranean annual, *Centaurea melitensis* in its native and non-native ranges. Biol. Invasions 15 (3), 495–507.

Muñoz-Sáez, A., Choe, H., Boynton, R.M., Elsen, P.R., Thorne, J.H., 2021. Climate exposure shows high risk and few climate refugia for Chilean native vegetation. Sci. Total Environ. 785.
Niemi, G.J., McDonald, M.E., 2004. Application of ecological indicators. Annu. Rev. Ecol. Evol. Syst. 35 (1), 89–111.
Nogués-Bravo, D., Araújo, M.B., Errea, M.P., Martínez-Rica, J.P., 2007. Exposure of global mountain systems to climate warming during the 21st Century. Glob Environ Change. 17 (3–4), 420–428.
Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conserv. Biol. 4 (4), 355–364.
Paliy, O., Shankar, V., 2016. Application of multivariate statistical techniques in microbial ecology. Mol Ecol. 25 (5), 1032–1057.
Perea, R., Gil, L., 2014. Shrubs facilitating seedling performance in ungulate-dominated systems: biotic versus abiotic mechanisms of plant facilitation. Eur. J. For. Res. 133 (3), 525–534.
Pettit, N.E., Froend, R.H., Ladd, P.G., 1995. Grazing in remnant woodland vegetation: changes in species composition and life form groups. J. Veg. Sci. 6, 121–130.
R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reynolds, W.D., Clarke-Topp, G., 2008. Soil water desorption and imbibition: Tension and pressure techniques. pp 981–997. In: Carter, M.R., Gregorich, E.G. (Eds.), Soil sampling and methods of analysis, 2nd Edition. Canadian Society of Soil Science, Boca Raton, Florida, USA, p. 1224.
Rodriguez, R., Marticorena, C., Alarcón, D., Baeza, C., Cavieres, L., Finot, V.L., Fuentes, N., Kiessling, A., Mihoc, M., Pauchard, A., Ruiz, E., Sanchez, P., Marticorena, A., 2018. Catálogo de las plantas vasculares de Chile. Gayana Bot. 75 (1), 1–430.
Romero, H., Ordenes, F., 2004. Emerging urbanization in the southern Andes - Environmental impacts of urban sprawl in Santiago de Chile on the Andean Piedmont. Mt. Res. Dev. 24 (3), 197–201.
Roy, M.C., Azeria, E.T., Locky, D., Gibson, J.J., 2019. Plant functional traits as indicator of the ecological condition of wetlands in the Grassland and Parkland of Alberta. Canada. Ecol. Indic. 98, 483–491.
Santonja, M., Fernandez, C., Proffit, M., Gers, C., Gauquelin, T., Reiter, I.M., Cramer, W., Baldy, V., McCulley, R., 2017. Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean oak forest. J. Ecol. 105 (3), 801–815.
Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M., Mori, A.S., 2015. Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. Ecol. Indic. 57, 395–408.
Schoeneberger, P.J., Wysocki, D.A., Benham, E.C., 2012. Field book for describing and sampling soils, Version 3.0. Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE.
Seguel, O., Farías, E., Luzio, W., Casanova, M., Pino, I., Parada, A.M., Videla, X., Nario, A., 2015. Physical properties of soil after change of use from native forest to vineyard. Agro Sur. 43, 29–39.
Sernageomin Mapa Geológico de Chile. Publicación Geológica N°4. Servicio Nacional y Geología y Minería, Gobierno de Chile 2003 Santiago, Chile 25 p.
Shepard, R.N., 1962. The analysis of proximities: Multidimensional scaling with an unknown distance function. I. Psychometrika. 27 (2), 125–140.
Soil Survey Staff, 2006. Keys to Soil Taxonomy, 10th ed. USDA-Natural Resources Conservation Service, Washington DC, USA, p. 333.
Spohn, M., 2015. Microbial respiration per unit microbial biomass depends on litter layer carbon-to-nitrogen ratio. Biogeosciences. 12 (3), 817–823.
Steel, Z.L., Steel, A.E., Williams, J.N., Viers, J.H., Marquet, P.A., Barbosa, O., 2017. Patterns of bird diversity and habitat use in mixed vineyard-matorral landscapes of Central Chile. Ecol. Indic. 73, 345–357.
Teillier, S., Marticorena, A., Niemeyer.,, H.,, 2011. Flora andina de Santiago: Guía para la identificación de las especies de las cuencas del Maipo y del Mapocho. Puntografix, Santiago, p. 478.
Uribe, J.M., Cabrera, R., de la Fuente, A., Paneque, M., 2012. Atlas bioclimático de Chile. Universidad de Chile, Santiago, p. 232.
Vigl, L.E., Marsoner, T., Schirpke, U., Tscholl, S., Candiago, S., Depellegrin, D., 2021. A multipressure analysis of ecosystem services for conservation planning in the Alps. Ecosyst. Serv. 47, 101230.
Warrick, A., 2002. Soil physics companion. CRC Press, Boca Raton, Florida, USA, p. 387.
Weiland, U., Kindler, A., Banzhaf, E., Ebert, A., Reyes-Paecke, S., 2011. Indicators for sustainable land use management in Santiago de Chile. Ecol. Indic. 11 (5), 1074–1083.
Wessels, K.J., Prince, S.D., Carroll, M., Malherbe, J., 2007. Relevance of rangeland degradation in semiarid northeastern South Africa to the nonequilibrium theory. Ecol. Appl. 17 (3), 815–827.
Whisenant, S.G., 1999. Repairing Damaged Wildlands: A Process-orientated, Landscape-scale Approach. Cambridge University Press, New York.
Yandell, B.S. (Ed.), 1997. Practical Data Analysis for Designed Experiments. Springer US, Boston, MA.
Yates, C.J., Norton, D.A., Hobbs, R.J., 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: Implications for restoration. Austral Ecol. 25, 36–47.
Zhao, H.L., Zhou, R.L., Su, Y.Z., Zhang, H., Zhao, L.Y., Drake, S., 2007. Shrub facilitation of desert land restoration in the Horqin Sand Land of Inner Mongolia. Ecol. Eng. 31 (1), 1–8.
Zucca, C., Peruta, R.D., Salvia, R., Sommer, S., Cherlet, M., 2012. Towards a world desertification atlas. Relating and selecting indicators and data sets to represent complex issues. Ecol. Indic. 15 (1), 157–170.
Zuloaga, F.O., Morrone, O., Belgrano, M., 2008. Catálogo de las plantas vasculares del cono sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). Pteridophyta, Gymnospermae. Monocotyledoneae. Monog. Syst. Botan. 107, 1–983.