



Relationship between degradation and the structural-functional complexity of subtropical xerophytic forests in the Argentine Wet Chaco

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ABSTRACT

Globally, forests are severely compromised by land use change and anthropogenic degradation. Forests' structural and biotic homogenization leads to the loss of ecosystem processes that sustain their functionality and determine their contributions to people. Resilience is a key property that expresses the capacity of an ecosystem to tolerate, recover, and/or adapt to disturbances without drastically changing its structure or ecological functions. Once this capacity is exceeded beyond the threshold limit, resilience is lost, and degradation occurs. The Structural – Functional of State and Transition Models (SFSTM) provide a conceptual framework to address ecosystem resilience and the identification of degradation thresholds. In this work, we sought to describe and quantify structural degradation and its relationship between vegetation structural complexity, proxies of ecological processes, and species composition of the quebrachales, a threatened xerophytic subtropical forest of great environmental and socio-economic value in the Wet Chaco of Argentina. For this purpose, a set of forest sites were selected to represent the different histories of uses, where vegetation and soil samplings were carried out. A Structural Degradation Index (SDI) was constructed based on a set of structural variables using multivariate techniques, and the sites were ordered and classified into two structural groups. Linear (generalized) and segmented models were performed to analyze the responses of vegetation heterogeneity and proxies of ecosystem process to structural degradation and to identify thresholds. In addition, species composition was analyzed based on comparing the coefficients of beta diversity, nestedness, and concordance between sites. The structural degradation of the quebracho forest was negatively related to vegetation complexity and ecological processes, and there were breakpoints or non-linear responses between structural groups. Biological diversity was negatively related to anthropogenic degradation due to an increase in beta diversity between structural groups, as well as a process of species divergence between degraded sites. This work shows a clear approach to studying the resilience of subtropical xerophytic forests with concrete results on structural homogenization, loss or decrease of ecological processes, and biotic simplification due to anthropogenic degradation of these ecosystems. In the context of global climate change and rapid human-induced alterations, addressing forest ecosystem resilience from a structural and functional perspective could be a novel approach to its medium- and long-term management.

1. Introduction

Global forest cover is seriously threatened by changes in land use and anthropogenic degradation (Hansen et al., 2013; Watson et al., 2018; FAO, 2020). The causes of degradation are manifold and not independent, including fires, agriculture, livestock expansion, urbanization, and

over-extraction of raw materials (Hosonuma et al., 2012; Global Forest Watch, 2020). From 2001–2020, a total of 411 million hectares (Mha) of forests have been lost worldwide (Global Forest Watch, 2020). Although the global annual loss rate has decreased from 7,8 Mha in the 1990–2000 period to 4,7 Mha in the 2010–2020 period, South America still has the second highest annual deforestation rate in the world, with

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approximately 2.6 Mha (FAO, 2020).

Many forest degradation definitions have been proposed, but consensus remains elusive (Simula, 2009; Putz and Redford, 2010; Vázquez-Grandón et al., 2018). Each definition emphasizes specific properties of interest and aims to identify indicators to measure it and a forest site for comparison, either a conserved one or a benchmark, where these properties are as little modified as possible (Morales Barquero et al., 2014; Gobbi et al., 2022). A comprehensive definition proposed by the FAO (2020) is that forest degradation encompasses changes that negatively affect its structure and function and thereby decrease the provision of goods and services to people. In this study, we want to emphasize structural degradation, which describes the loss of structural attributes and triggers the loss of ecosystem functions (Gobbi et al., 2022). When the degradation process affects key variables (structural and functional), the forest loses its resilience to anthropogenic and/or natural factors of disturbances that impede the natural recovery to its previous state (Gunderson, 2000; Ghazoul et al., 2015; Vázquez-Grandón et al., 2018; Nikinmaa et al., 2020; Falk et al., 2022). In a broad sense, resilience is the capacity of an ecosystem to tolerate, recover, and/or adapt to a disturbance without drastically changing its structure and/or ecological functions (Holling, 1973; Walker, 2020). Sufficiently large changes, that irreversibly alter the structure and composition of species, trigger the loss of ecosystem processes that sustain ecosystem functioning (López et al., 2011; Morales-Barquero et al., 2014). The tipping points at which a steep change in ecosystem properties triggers large changes in its structure and process, and exceeds its resilience, are called thresholds (Groffman et al., 2006). Beyond these breakpoints, the ecosystems become degraded and therefore, their identification constitutes a key point in studying its resilience (Suding and Hobbs, 2009; Briske et al., 2010; Standish et al., 2014; Bestelmeyer et al., 2017). Measuring the resilience of an ecosystem is not an easy task, but it can be addressed indirectly from the study of the behavior of some indicators (e.g. compositional, structural, or functional slow variables) to degradation (Carpenter et al., 2001).

Vegetation heterogeneity is an attribute of the spatial structure closely related to ecosystem resilience (Virah-Sawmy et al., 2009; Senf et al., 2020) that expresses the variability and the structural-functional complexity of vegetation in space (Li and Reynolds, 1995; Pélissier and Goreaud, 2001; Ghazoul et al., 2015; Ehbrecht et al., 2021). There is evidence that anthropogenic management for productive purposes and/or high disturbance rates tend to homogenize forest vegetation structure (Kuuluvainen et al., 1996; Senf et al., 2020). Ecological processes, in turn, result from the structural configuration of ecosystems and determine the contributions of nature to people (*sensu* Díaz et al., 2018), such as primary productivity, CO₂ fixation, regulation of biogeochemical cycles in general, key species regeneration rate, among others (Franklin et al., 2002). In structurally degraded forests, ecological processes are lost or altered and thus provide fewer ecosystem services. Therefore, the structural and functional degradation of forest ecosystems will negatively influence their resilience (Seidl et al., 2016).

On the other hand, biodiversity is closely related to the structure and ecological functions of ecosystems and thus, is a fundamental component of resilience (Thompson et al., 2009; Willis et al., 2010; Oliver et al., 2015). Numerous studies have demonstrated a positive association between biodiversity and ecosystem processes mediated by morphological and functional traits of species, e.g. variability of responses to disturbances (Carpenter et al., 2001; Díaz et al., 2004; Laliberté et al., 2010). However, anthropogenic pressure on forests significantly affects species composition and leads to biotic homogenization of these ecosystems (Johns, 1988; Kumar and Shahabuddin, 2005; Klanderud et al., 2010; Baiser et al., 2012; Clark and Covey, 2012). For these reasons, analyzing the species diversity of a community is important to understand its resilience and different approaches have been proposed (Whittaker, 1972; Anderson et al., 2011; Baselga, 2010; Podani and Schmera, 2011). The conceptual framework developed by Podani and collaborators (2013) is particularly interesting for the

analysis of the species composition of a set of communities in different structural degradation states within an ecosystem. It allows comparing these communities, based on quantitative data (e.g. abundance), by extracting the coefficients of beta diversity, nestedness, and species concordance. From these coefficients, it is possible to understand how structural degradation affects diversity patterns and processes, for example, if there is an impoverishment or a total change of species.

Resilience has become a focal point for the conservation and sustainable management of ecosystems in general, and specifically in the development and application of the State and Transition Models (STM) (Westoby et al., 1989; Bestelmeyer et al., 2009; Walker, 2020). The Structural-Functional approach (Structural-Functional State and Transition Models, SFSTM) constitutes an alternative to the previous model STM, that considers the functional variations of the ecosystems (e.g. ecological processes) based on their structural changes (e.g. vegetation and soil) (López et al., 2011, 2013) to quantify the states, transitions, and thresholds. These models propose a theoretical and methodological framework to address the sustainable management of ecosystems. For a given ecosystem they recognize an Ecological Site characterized by a reference (or potential) state and multiple alternative states with dynamic transitions of degradation or restoration between them. These changes could be natural (e.g. floods, fires) or anthropogenic (e.g. cattle ranching, deforestation, etc.) disturbance factors, as well as regeneration and other ecological processes that affect each state (López et al., 2011; Bestelmeyer et al., 2017). Negative transitions between states involve profound transformations, on both vegetation and abiotic factors (e.g. soil loss) and lead to a decrease or loss of resilience of the current state and push the ecosystem to cross one or more thresholds, to one or more degraded states (structurally and functionally). Often such negative transitions are irreversible or hardly reversible (unlikely positive transitions) without anthropogenic intervention (López et al., 2013; Bestelmeyer et al., 2017). In turn, within each state, it is possible to identify one or more plant communities, called phases, with a dynamic of temporary vegetation changes between them, which correspond to minor modifications, mainly related to the vegetation (i.e. the state maintains its resilience) (Bestelmeyer et al., 2017).

Forest ecosystems represent a challenge when studying their resilience, mainly due to the slow response times to changes compared with the quick and drastic human-induced ecosystem transformations (Seidl and Turner, 2022). To overcome this problem, structural degradation gradients are used as an indirect approach, as they recreate the degradation process. This allows addressing the relationship between structural degradation with ecosystem functions (e.g. forest recruitment processes) and/or spatial patterns associated with key ecological processes (e.g. with soil erosion, diversity), and with slow variables indicating state changes (e.g. soil carbon stock, forest biomass stock) (Pickett, 1989; Walker et al., 2010; Cavallero et al., 2015). Dry forests are spread worldwide, and they are highly threatened by anthropogenic activities (Sunderland et al., 2015). Particularly, in the Wet Chaco ecoregion of Argentina, there are heterogeneous xerophytic forests ("quebrachales" of *Schinopsis balansae* Engl.) of hardwood species, which constitute an interesting scenario for the application of SFSTMs since these forests have historically been affected by simultaneous activities (e.g. timber, firewood, charcoal extraction, and extensive cattle ranching), generating a mosaic of woody communities in different structural degradation states (Zarrilli, 2018).

The objective of this work was to describe and quantify the structural degradation and its relationship with vegetation structural complexity, ecological processes, and species composition of xerophytic forests in the Wet Chaco, as an approach to estimate their resilience, following the theoretical framework of SFSTM. Thus, we wonder (1) how the structural degradation of these xerophytic forests affects their vegetation structural complexity, ecological processes, and species composition, and (2) whether there are structural and functional thresholds that differentiate alternative states of degradation in quebracho forests.

2. Materials and methods

2.1. Study area

The Gran Chaco region is a large plain of about 1000000 km², most of which is in the central north of Argentina and the rest occupies northwest of Paraguay, a small area in the south of Brazil, and the southeast of Bolivia. This huge region is divided into two ecoregions: Dry Chaco in the west and Wet Chaco in the east (Fig. 1a). In both ecoregions, there is a marked seasonality with dry-cold winters and wet-hot summers. Probably the annual precipitation gradient is the environmental factor that most affects vegetation communities between Dry and Wet Chaco, ranging from 1300 mm in the east to less than 500 mm in the southwest part (Prado, 1993). Despite that, its vegetation shows some similarities. Broadly speaking, forest physiognomy dominated by species of the genus *Schinopsis* is the most widespread land cover, but savannas are common too (Prado, 1993). Several other woody genera, like *Prosopis*, *Vachellia*, *Celtis*, *Schinus*, and *Aspidosperma*, are present in both Chaco ecoregions, with many species in common.

The Santa Fe Forest Wedge is the southern portion of the Wet Chaco, and its plant communities are arranged following a topographic gradient. In the lowest parts, there are hygrophilous communities ('esteros' or 'cañadas'), whereas, at intermediate levels, there are 'algarrobales' of *Neltuma nigra* var. *ragonesei* (Griseb.) C.E. Hughes & G. P. Lewis or palm savannas of *Copernicia alba* Morong. Further up in the topographic gradient, the 'quebrachales' of *Schinopsis balansae* Engl. (quebracho forest) show their greatest development, and finally at the top of the elevation gradient the 'bosque fuerte' or mixed dense forests are established (Lewis and Pire, 1981; Lewis, 1991; Lewis et al., 1994).

The 'quebrachales' are xerophytic forests with great environmental and physiognomic heterogeneity due to the interaction of biotic and abiotic factors (Barberis et al., 1998, 2002). The climate is temperate-humid to warm, with a mean annual temperature of 20 °C and a mean annual precipitation of 1000 mm distributed between spring and summer. The soils are halo-hydromorphic (typical or albic natra-cualfs, Morrás, 2017). The topography is flat, with a pronounced micro-relief (Barberis et al., 2002), resulting from water dynamics (e.g. erosion and floods) and large anthills of leaf-cutter ants (*Atta vollenweiderii* Forel) that create zones with elevations and depressions of varying areas. Elevations are well-drained, characterized by a high density of woody individuals with continuous woody cover (vegetation 'patch'), and have typically three strata. The upper stratum is about 8–12 m tall, dominated by *S. balansae*, and accompanied by *Aspidosperma quebracho-blanco* Schldl., *Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn., *Myrcianthes cisplatensis* (Cambess.) O. Berg, and *Neltuma* spp. The middle stratum consists of woody species of slightly shorter height, ranging from 2–7 m. This layer is typically inhabited by shrubs such as *Achatocarpus praecox* Griseb, *Schinus fasciculata* (Griseb.) I.M. Johnst., *Maytenus vitis-idaea* Griseb., *Celtis pallida* Torr., among others (Ragonese and Covas, 1940; Lewis and Pire, 1981; Lewis et al., 1997). The herbaceous stratum of these patches is dominated by colonies of the spiny bromeliads *Bromelia serra* Griseb. and *Aechmea distichantha* Lem. (Marino and Pensiero, 2003; Barberis et al., 2005), but a diversity of grasses and herbs can also be found. In contrast, depressions have poor drainage, are temporarily flooded in the summer, and are characterized by a savanna physiognomy with a low density of woody species (generally a single stratum) and a continuous herbaceous stratum. The woody species that thrive in these conditions are *S. balansae*,

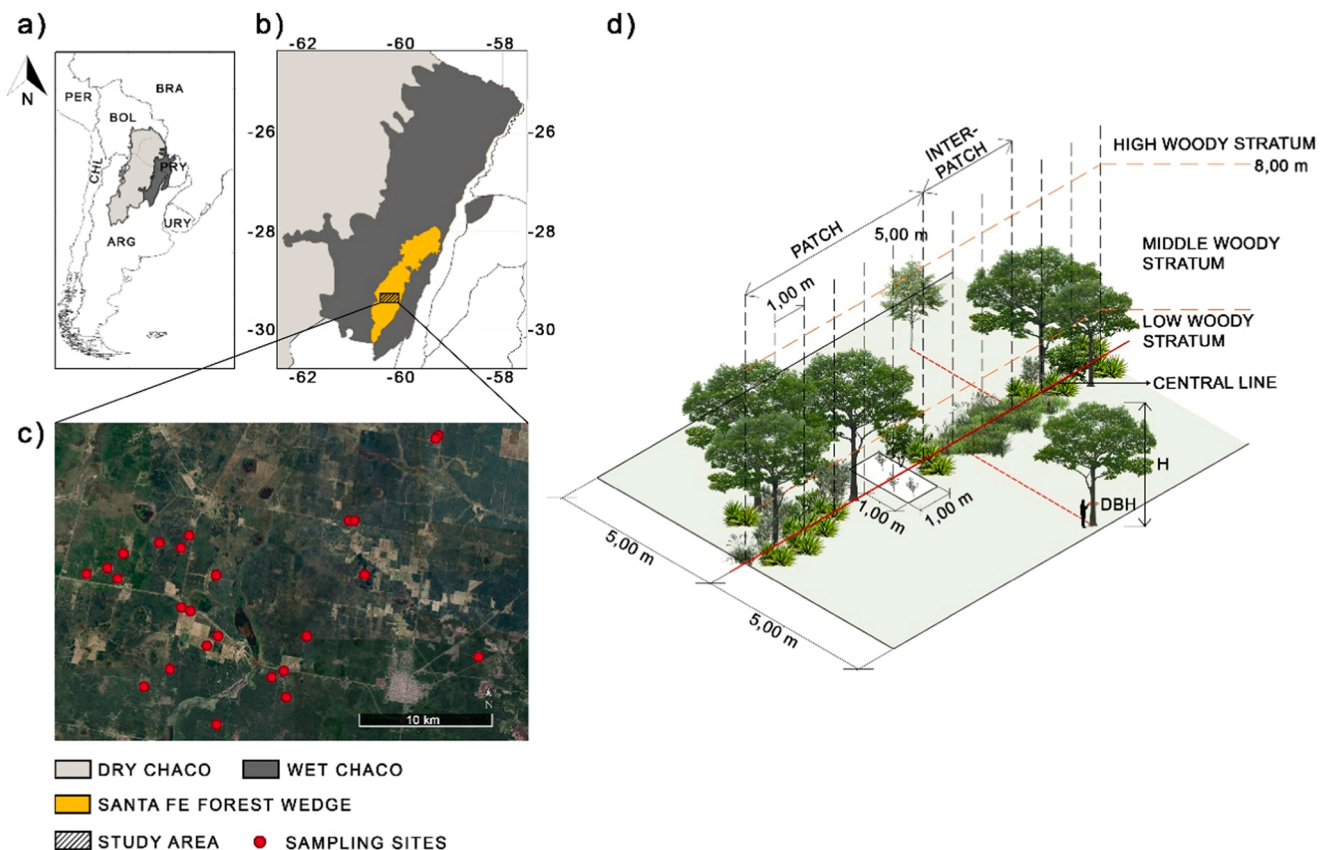


Fig. 1. a) Distribution of the Gran Chaco region divided into Dry (light gray) and Humid (dark grey) Chaco in South America. Country codes: ARG = Argentina, BOL = Bolivia, BRA = Brazil, CHL = Chile, PRY = Paraguay, PER = Peru, and URY = Uruguay. b) Study area located in the Santa Fe Forest Wedge of the Argentinean Wet Chaco. c) Sampling site distribution into the study area. d) Illustrative diagram of the survey methodology in a rectangular plot of 2500 m² (250 m × 10 m), divided by a 250 m long central straight line (red transect). The maps were modified from Morello et al. (2012) and the satellite image was extracted from Google Earth Pro.

Neltuma spp., *Vachellia caven* (Molina) Seigler & Ebinger, and *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart. Herbaceous species of the genera *Leersia*, *Luziola*, *Panicum*, and *Cyperus*, among others, dominate these humid areas (Lewis and Pire, 1981; Marino and Pensiero, 2003).

2.2. Survey design

For this study, we selected an area of about 500 km² of quebracho forests within the Santa Fe Forest Wedge (Fig. 1b). Using satellite images from Google Earth Pro software (<https://www.google.com/intl/es/earth/versions/#earth-pro>), we identified several potential sampling sites within the study area that *a priori* were in a similar topographic position, and soil type (Cruzate et al., 2023), but presented different physiognomies. Besides, before the selection of the sites, we read and talked with experts from the study area about the degradation processes (particularly Simón et al., 1997, 2003) and then, we visited all these pre-selected sites to request access permission, learn about their management history, and determine their usefulness for the work. This information indicates that differences between selected sites were related to anthropogenic activities and that environmental factors are similar between them. Finally, we selected 25 sampling sites associated with different histories of use and different structural degradation levels constituting a gradient of vegetation physiognomies (associated with different use histories) ranging from the best-preserved quebrachal (or reference forest, i.e. mature forest) to the most structurally degraded ones (i.e. areas transformed into grasslands, savannas, or open forests with tree or shrub patches, intended mainly for livestock production) (Fig. 1c). As the reference sampling site, we selected a 20-ha plot located in the “Santa Felicia Forestry Operating Center”, a natural reserve, without forest exploitation (Bullo et al., 2016). We carried out vegetation samplings during the growing seasons (spring and summer) from 2019 to 2021. In each sampling site, we established one rectangular plot of 2500 m² (250 m × 10 m), crossed by a 250 m long central straight line (transect) (Alaggia et al., 2020).

We divided the vegetation sampling at each plot into two parts: the plot area and the central line. Across the entire plot area, we recorded the number and species identity of all woody individuals (shrubs and trees). For those with a DBH above 10 cm, we also measured the height (m), and diameter at breast height (DBH) (cm). At every meter along the 250 m central line, we recorded the tallest species covering the point in each stratum (herbaceous, low woody: 0–2 m, middle woody: 2–8 m, and high woody: > 8 m) using the point intersection method (Muel-ler-Dombois and Ellenberg, 1974). Besides, every five meters, we measured the maximum height of the species recorded in each vegetation stratum (that of the individual who dominates the stratum at the intersection point), and the number of seedlings (0–30 cm height) and saplings (30–150 cm height but < 10 cm DBH) in a subplot of 2 m² (Alaggia et al., 2020) (Fig. 1d).

To characterize the soil, we sampled the percentage of organic carbon with a CSP SR20 soil auger. We took a composite sample of 10 subsamples at two depths (0–10 cm and 10–30 cm), along the transect and sent them to analyze by the dry combustion method with a LECO CR-12 automatic carbon analyzer. Also, we sampled the bulk density with a 170 cm³ cylinder. We took two single samples, one from 0–10 cm depth and the other from 10–30 cm depth. Then, we dried the samples in an oven at 60° C until constant weight (ASPEN EK3052 digital balance; Max. = 2 kg, d = 1 g).

Finally, we used the Sentinel 2 MultiSpectral Instrument (MSI), Level 2 A (Copernicus Sentinel data 2022, processed by ESA) satellite images to calculate the Normalized Difference Vegetation Index (NDVI) values for each plot (250 m × 10 m) for the years in which the field vegetation surveys were carried out, including two previous years (i.e. 2017–2021). As the plots were located in a homogeneous vegetation area and the selected images had a spatial resolution of 10 m for the spectral bands used, the surrounding noise was reduced and the NDVI calculation was representative of the plots. We used the free software Google Earth

Engine (GEE, <https://earthengine.google.com>).

2.3. Data processing

2.3.1. Derived variables

Based on the vegetation survey, we calculated several derived variables to describe patches, inter-patches, and other structural characteristics of each site. We defined a “patch” as the space where the soil surface is completely covered by woody individuals, while the “inter-patch” is the space without woody cover between two patches (could or could not have herb cover).

We derived the following structural variables: total and per stratum (low, middle, and high) woody vegetation cover (number of points covered along the transect), total mean and per stratum woody patch size (average length in meters of segments with continuous woody species cover), total mean and per stratum inter-patch size (average length in meters of segments on each transect that do not record woody species cover), number of patches and inter-patches, coefficient of variation of the patch and inter-patch size, number of strata per point, mean height per stratum (m), and mean height of trees in the whole plot (m).

2.3.2. Structural vegetation indices

For each sampling site, we calculated the Structural Degradation Index (SDI) as a measure of structural degradation, and the Horizontal and Vertical vegetation Heterogeneity Indices (HHI and VHI) as measures of vegetation structural complexity (López et al., 2011, 2013; Cavallero et al., 2015; Ehbrecht et al., 2021).

Construction of the SDI of any ecosystem requires selecting those structural variables that describe the most important ecological characteristics of the ecosystem (i.e. vegetation and soil). Particularly for a forest ecosystem, woody structural variables, such as woody cover and tree height, are very important, as well as a measure of the key species' importance (FAO, 2023; Martínez Pastur et al., 2023). For the selection of the structural variables of the SDI, first, from a set of variables describing forest physiognomy and species composition, we chose those not considered as response variables in the study. Then, with the pre-selected variables, successive Principal Component Analyses (PCA) were performed to choose those that explained the greatest variability of the data with the least possible collinearity between them. Based on these analyses, we selected a set of physiognomic and floristic variables that best described the structural degradation of the quebrachales: the woody species cover (%), the herbaceous species cover (%), the bromeliad (*A. distichantha* and *B. serra*) cover (m), the average tree height measured in the plot area (m), the bare soil proportion and the density of woody species (sum up of the density of the following eight key woody species (abundance.ha⁻¹): *S. balansae*, *Neltuma* spp., *M. cisplatensis*, *Senegalia praecox* (Griseb.) Seigler & Ebinger, *M. vitis-idaea*, *A. praecox*, *Coccoloba argentinensis* Speg., and *S. fasciculata*) (Figure A.1, Appendix A). From the last performed PCA we used the site scores to calculate a matrix of Mahalanobis distances (MD) between them (De Maesschalck et al., 2000). As the PCA axes are orthogonal, there is no collinearity between variables. Finally, we extracted the distances between each sampling site and the reference sampling site (previously selected). We calculated the SDI as follows: $SDI_i = [(MD_i \times 100) \times (MD_{max})^{-1}]$, where MD_i is the MD between the *i*-th sampling site and the reference sampling site. The MD_{max} corresponds to the maximum value of MD, based on which all MD values were standardized, such that the SDI varied between 0% and 100%. The higher the value of this index, the greater the structural vegetation degradation.

For each stratum, we calculated HHI using the following formula: $HHI = (\sigma_{PL} / \mu_{PL}) \times \text{No. of patches} + (\sigma_{IPL} / \mu_{IPL}) \times \text{No. of inter-patches}$, where PL is the patch length of woody species in each stratum, IPL is the inter-patch length in each stratum, “ σ ” is the standard deviation, and “ μ ” is the average. Then, we summed the three strata to obtain a total value. This index varies between 0 and $+\infty$, and the closer

to zero it is, the more homogeneous the distribution of woody vegetation cover. We followed a similar procedure to calculate the total VHI, using the following formula: $VHI = (\mu_{LS} \times \sigma \times LS_{prop}) + (\mu_{MS} \times \sigma \times MS_{prop}) + (\mu_{HS} \times \sigma \times HS_{prop})$, where “ μ ” is the average height, LS is the low stratum, MS is the middle stratum, HS is the high stratum, and “prop” indicates the proportion of woody vegetation cover. The higher the value of this index, the greater the variability in the height of each stratum, conferring greater heterogeneity to the vertical structure. Studying these structural properties is of great ecological interest as they are tightly related to key ecosystem functions like soil erosion or habitat diversity (Hutchings et al., 2000; Briske et al., 2005; Bestelmeyer, 2006; López et al., 2013; Cavallero et al., 2015).

2.3.3. Functional variables estimators

We used the numbers of seedlings and saplings as estimators of the recruitment process of woody individuals (Cavallero et al., 2018; Alaggia et al., 2020), the average NDVI for the period 2017–2021, as a measure of photosynthetic activity (Σ NDVI 2017–2021/ Σ days with valid records) directly related to aerial net primary productivity (ANPP), the coefficient of variation of NDVI for the same period mentioned, as a proxy of the system’s capacity to buffer climate temporal variability (intra and inter-annual) on ANPP (cvNDVI), the basal area ($m^2 \cdot ha^{-1}$) as an estimator of wood supply, the equivalent number of species ($D = e^{H_{shannon}}$ where $H_{shannon}$ is the Shannon-Weaver diversity of the woody species cover along the transect) as a measure of community diversity, and the soil organic carbon stocks (SOC $g \cdot m^{-3}$) at two different depths (SOC₁₀ = 0–10 cm and SOC₃₀ = 10–30 cm) as estimators of the capacity of soil carbon storage. We calculated the SOC stocks according to the equation: $C \times BD_d$ where C is the concentration of SOC (g) and BD_d is the bulk density ($g \cdot m^{-3}$) at a certain depth (0–10 or 10–30 cm).

2.4. Statistical analysis

2.4.1. Sites grouping according to their structural degradation state

To group the sampling sites according to their physiognomic degradation condition (i.e. structural groups), we performed a non-hierarchical, non-agglomerative, and non-divisive kmeans clustering, with 10000 initial configurations, which seeks the best combination of sampling sites for a given number of groups that has the least intra-group variation (Palacio et al., 2020). The clustering was done using the scores of the sites resulting from the PCA ordination analysis carried out previously to select the variables used in the calculation of the SDI (Section 2.3.2). Two structural groups were obtained from the analysis: Group I with 16 sites and Group II with 9 sites (Figure A.1, Appendix A).

2.4.2. Relationship between forest structural degradation, vegetation structural complexity and forest functioning

To understand the response of structural complexity and the functional variables (i.e. functions and services) to forest structural degradation and to detect the breakpoints (τ) associated with this process, we used linear (or generalized linear), polynomial, and segmented linear regression models (Ficetola and Denoël, 2009; Clements et al., 2010). The structural complexity response variables were the HHI and the VHI. The functional response variables were the proxies associated with forest ecosystem processes: regeneration of woody species by size classes, average NDVI and its coefficient of variation, basal area per hectare, diversity (equivalent number of woody species), and SOC stocks. In all cases, we used the SDI as an explanatory variable. To test if there were differences between structural groups for all the variables considered, we performed non-parametric Mann-Whitney tests (Legendre and Legendre, 2012).

2.4.3. Groups specific composition analysis and its relationship with forest structural degradation

For the structural group compositional characterization, we

performed a Species Indicator Value analysis for the woody species (Dufréne and Legendre, 1997; Borcard et al., 2018; Legendre and Legendre, 2012). This value is the result of the product of two components: specificity and fidelity. The first refers to the probability that a given sampling site belongs to a group of sampling sites, given the fact that the woody species has been found in that sampling site. In contrast, the second component refers to the probability of finding a given woody species at the sampling sites belonging to a group of sampling sites. We constructed a phytosociological table (Table A.2, Appendix A) with the site structural groups and the information generated from the Species Indicator Value analysis (specificity and fidelity).

We followed the conceptual framework proposed by Podani et al. (2013), to identify the underlying patterns in the compositional data of forest structural degradation through the comparison between the reference sampling site and the other sampling sites, considering the structural group of belonging. This analysis is based on the comparisons of the importance values of woody species (e.g. cover in this case), between pairs of sampling sites, to estimate three relative indices, whose values vary between 0 and 1: difference (D), replacement (R), and similarity (S) in species composition. The first index expresses the differences in woody species identity and total cover between sampling sites. The replacement index considers that a given amount of cover at one sampling site is replaced by the same amount but of different woody species, at the other sampling site. Finally, similarity refers to the coincidence between the woody species composition of the sampling sites compared. These indices, in turn, constitute the components of the coefficients of beta diversity (D + R), nestedness (D + S), and concordance (R + S). From this analysis, two sets of comparisons were constructed. The first set comprised comparisons between sampling sites of each group with the reference site ($n = 15$ for Group I, and $n = 9$ for Group II), whereas the second set comprised comparisons between sites of the same group ($n = 120$ for Group I, and $n = 36$ Group II).

To know the response of the indices and coefficients to the SDI as explanatory variables, we fitted linear, polynomial, and segmented models with the comparisons between each sampling site and the reference sampling site. In addition, to know if there were differences between the structural groups for the coefficients obtained from the comparisons of sampling sites of the same group, we performed non-parametric Mann-Whitney tests (Legendre and Legendre, 2012).

2.4.4. Statistical models and software used

For the linear, polynomial, and segmented models, we used normal (Gaussian) or Poisson error distributions (with identity or log linkage function, respectively), depending on whether the response variables were continuous or discrete, and negative binomial for those discrete variables with overdispersion. For each variable, we ran the three types of models and selected the one with the lowest AIC (Akaike Information Criterion) value (Crawley, 2007).

All the analyses were performed with the free software R 4.3.2 (The R Core Team, 2023). We performed the PCA with the PCA() function of the factominer package and the classification with the kmeans() function of the stats package. For linear (or generalized linear) and polynomial models, we used the functions lm() and glm(), both from the stats package. For the segmented linear models, we used the segmented() function from the segmented package. For non-parametric comparisons between groups, we used the wilcox.test() function from the coin package. We performed the analysis of the indicator value of the species with the multipatt() function of the indicspecies package. Finally, we analyzed the compositional data structure using the freely available program "The Simplex method for abundances (SDR-abunSimplex)", developed by Podani J. (<http://podani.web.elte.hu/SYN2000.html>).

3. Results

3.1. Relationship between forest structural degradation and vegetation structural complexity

The structural degradation of the quebrachal was associated with a simplification of the vegetation physiognomy (Fig. 2). Both the horizontal and vertical heterogeneities of the vegetation decreased linearly with forest structural degradation (Fig. 2).

For both types of heterogeneity, sampling sites of the first structural group were more heterogeneous than those from the second one. This is due to differences between the structural groups for the variables that make up the heterogeneity indices. For HHI, the total and per stratum average patch lengths were higher for sampling sites from Group I (Figure A.2 a, d, g, j, Appendix A), while the total and per stratum average inter-patch lengths were higher for sampling sites from Group II (Figure A.2 b, e, h, k, Appendix A). For VHI, total and per stratum heights were greater for sampling sites from Group I (Figure A.2 c, f, i, l, Appendix A).

3.2. Influence of structural degradation on forest functional proxies

The abundance of seedlings (< 30 cm height) showed a high dispersion between Group I sites, with very high values for some of them and low for others, whereas Group II sites had all lower values (Fig. 3a). The number of saplings (30 cm height to < 10 cm DBH) decreased with structural degradation (Fig. 3b). The photosynthetic activity of forests responded negatively to structural degradation. NDVI showed a decrease in its mean towards the most degraded sites where it stabilized and slightly increased after a breakpoint ($\beta_{1 \text{ NDVI}(\bar{x})} = -0.002$, $\beta_{2 \text{ NDVI}(\bar{x})} = 0.0007$) (Fig. 3c). On the contrary, its variation showed an increase with forest structural degradation until reaching a point after which decreased to the more degraded sites ($\beta_{1 \text{ NDVI}(cv)} = 0.0005$, $\beta_{2 \text{ NDVI}(cv)} = -0.0004$) (Fig. 3d). The SOC stock in the top 10 cm of soil was greater than in the next 20 cm ($t = 7.32$, $df = 22$, $P < 0.001$). There were also differences in the response to structural degradation at different depths. Surface SOC stock increased for sites with intermediate structural degradation but decreased in heavily degraded sites ($\beta_{1 \text{ SOC}_{10}} = 35.537$, $\beta_{2 \text{ SOC}_{10}} = -41.301$), while deep SOC stock tended to decrease linearly with structural degradation, but not significantly (Fig. 3e, f). Finally, both the diversity and the basal area decreased with increasing the SDI. The former did it linearly and the latter showed a breakpoint from which the slope of the response changed ($\beta_{1 \text{ BA}} = -1.262$, $\beta_{2 \text{ BA}} = -0.159$) (Fig. 3g, h). Statistically significant differences between structural groups were observed for almost all variables analyzed, except for SOC

stock which showed no differences for any of the depths despite finding a breakpoint between structural Groups (Fig. 3).

3.3. Comparative analysis of woody species composition between structural groups and its relationship with forest structural degradation

As SDI increased, the difference index (D) also increased but the similarity and replacement indices (S and R) decreased. Due to the behavior of their components, beta diversity (D + R) and nestedness (S + D) increased, while concordance (R + C) decreased (Fig. 4). Significant differences were found between structural groups for all indices and coefficients ($P < 0001$). Breakpoints were found around 50% of SDI, where the indices and the coefficients tend to stabilize.

The average beta diversity among sampling sites from Group II was 1.3 times greater than that of sampling sites from Group I (0.87 – 0.63, respectively). On the contrary, the average concordance among sampling sites from Group I was 1.5 times greater than that of sampling sites from Group II (0.86–0.55, respectively). For nestedness, there were no significant differences between groups (Fig. 5).

4. Discussion

In the present work, the structural and functional response of xerophytic subtropical forests to anthropogenic degradation was evaluated using the Structural-Functional State and Transition Models as a conceptual framework, with the contribution of the species characterization of the communities under study. The results indicate that structural degradation, mediated by anthropogenic activities, negatively affects the vegetation structural complexity and the ecological processes of forests, with significant differences and breakpoint responses between structural groups for some variables. In addition, degradation would simplify species composition through the loss and replacement of species with higher cover.

4.1. Relationship between forest structural degradation and vegetation structural complexity

This work reports a positive association between physiognomic homogenization and structural degradation (Fig. 2). Vegetation homogenization is manifested when structure differences are eliminated, both between patches and inter-patches (for the HHI) and between the heights of the different strata (for the VHI), either because woody species of a certain diameter and height are extracted, one or several woody strata are reduced or eliminated, or the entire area is cleared (Figure A.2, Appendix A). These disturbance processes lead to patch's degradation,

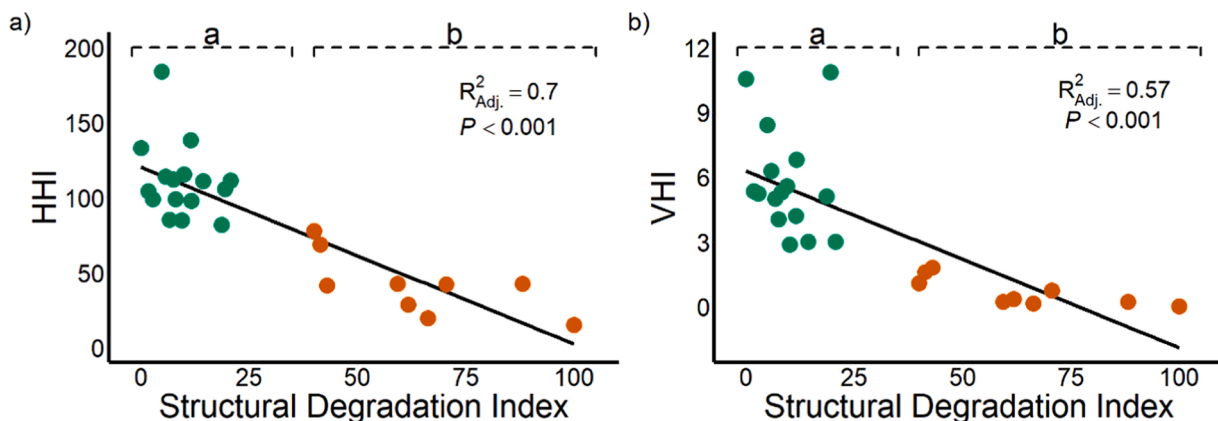


Fig. 2. Estimated responses of a) Horizontal (HHI) and b) Vertical (VHI) Heterogeneity Indices to the Structural Degradation Index. Regressions report the adjusted coefficient of determination ($R^2_{Adj.}$) and the P value. Green dots correspond to sampling sites from Group I ($n = 16$) and orange dots to those from Group II ($n = 9$) (Section 2.4.1). Letters report the result of the Mann-Whitney comparative analysis between structural groups. Different letters indicate significant differences ($P < 0.05$).

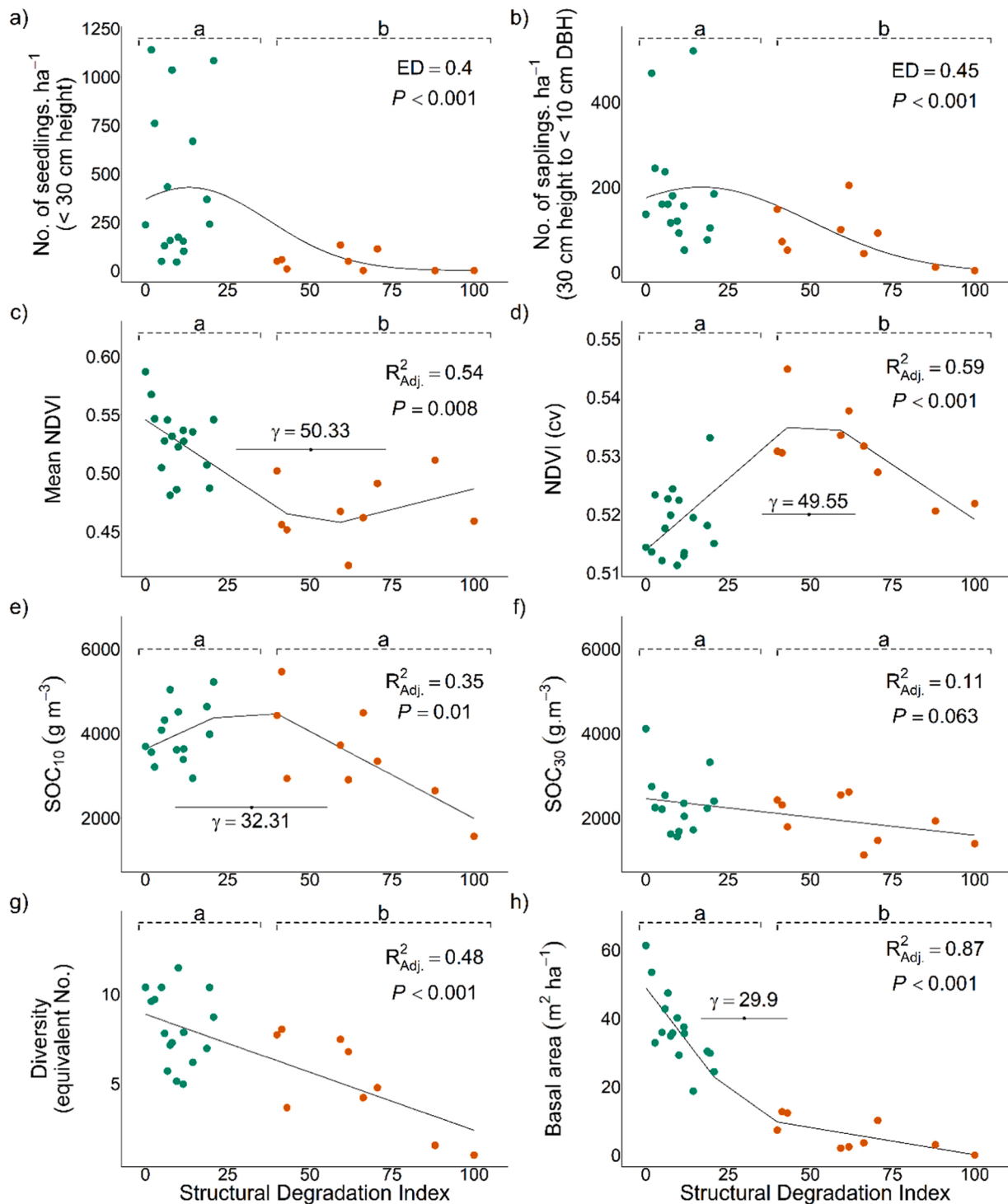


Fig. 3. Estimated responses of forest functions proxies to the Structural Degradation Index. Regressions report the adjusted coefficient of determination ($R^2_{Adj.}$) or explained deviance (ED), the P value, and the inflection point (γ) value with its confidence interval, when applicable. Green dots correspond to sampling sites from Group I ($n = 16$) and orange dots to those from Group II ($n = 9$) (Section 2.4.1). Letters report the result of the Mann-Whitney comparative analysis between structural groups. Different letters indicate significant differences ($P < 0.05$).

losing woody cover (i.e. making them more similar to the inter-patches) and causing the homogenization of the forest vegetation. These results are consistent with other works that report that mature, non-degraded forests have greater structural vegetation complexity (Franklin and Van Pelt, 2004; Schulte et al., 2007; Cavallero et al., 2015; Senf et al., 2020; Gobbi et al., 2022; De Marzo et al., 2023).

Despite not finding any breakpoint, changes in heterogeneity are reflected in the structural groups, which show a clear difference

(Figures A.1 and A.2, Appendix A). Sampling sites from Group I show varied forest physiognomies, but in all cases, with clear differences between patches and inter-patches and height variability. Sites from Group II, on the other hand, show a very simplified physiognomy, such as very degraded shrublands, savannas with widely scattered trees of similar size, and, in the worst cases, sites with grassland appearance. Savanna or grassland physiognomies are maintained by the cattle rancher, who constantly eliminates the regrowth of woody plants and shrubs, while

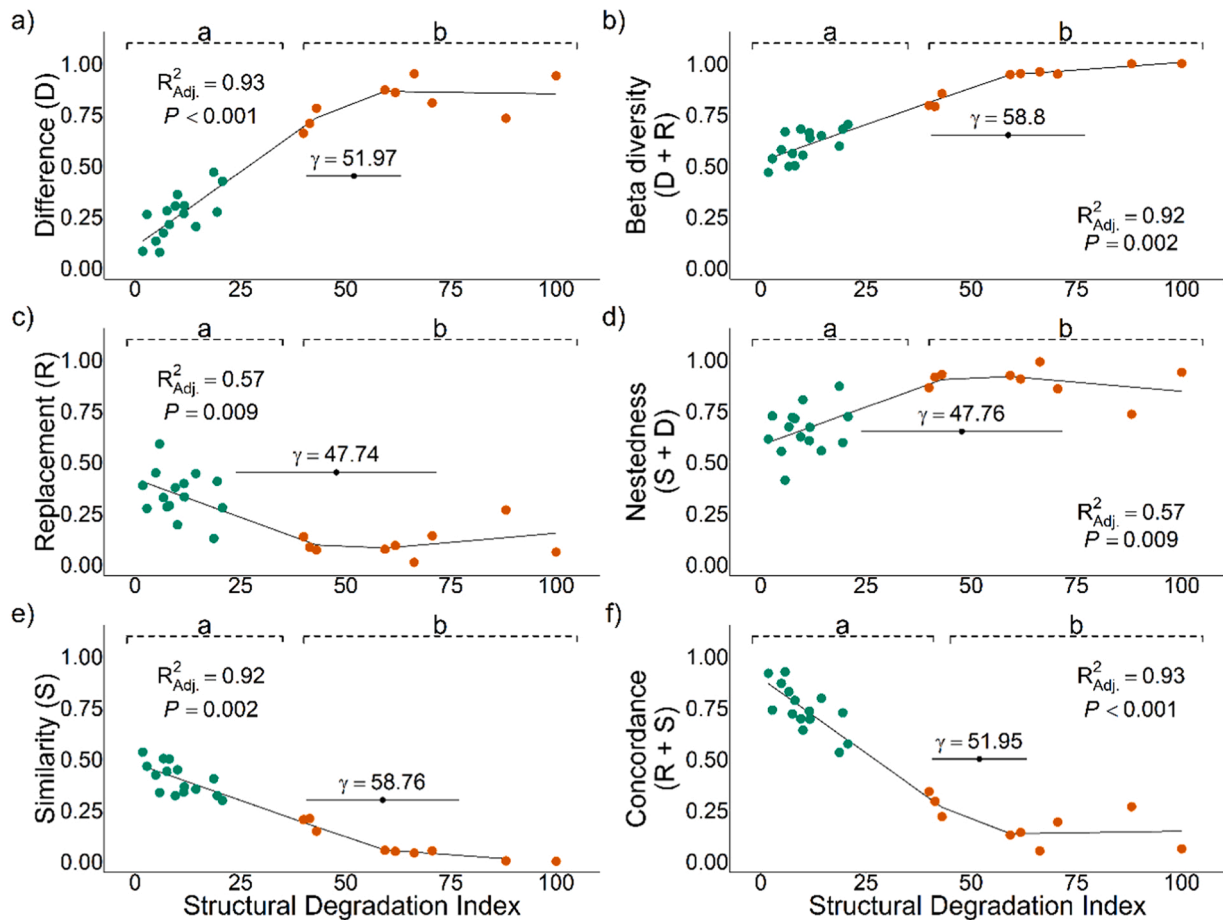


Fig. 4. Estimated responses of difference (D), replacement (R), and similarity (S) indices (a, c, e), and beta diversity, nestedness, and concordance coefficients (b, d, f) to the Structural Degradation Index. Regressions report the adjusted coefficient of determination ($R^2_{Adj.}$), the P value, and the inflection point (τ) value within its confidence interval, when applicable. Green dots represent the comparisons of sampling sites from Group I against the reference sampling site ($n = 15$) and orange dots represent the comparisons of sampling sites from Group II against the reference sampling site ($n = 9$). Letters report the result of the Mann-Whitney comparative analysis between structural groups. Different letters indicate significant differences ($P < 0.05$).

the shrubland usually originates after the abandonment of these communities. A study carried out in the same Ecological Site (i.e. quebrachal) reports that shrublands are of anthropogenic origin and generally result from the degradation of different quebrachal communities that converge towards the same physiognomy dominated by a few shrub species (Simón et al., 2003). This shrub encroachment has been reported in many communities around the world (Eldridge et al., 2011; Anadón et al., 2014; Mariani et al., 2022) and in other Chaco communities. For example, the invasion of “vinal” (*Prosopis ruscifolia* Griseb.) C. E. Hughes & G.P. Lewis in areas of the Dry Chaco of Formosa and Chaco provinces (Morello et al., 1971; Astrada and Adámoli, 2004), or in pastures of the Wet Chaco of Formosa (Cabral et al., 2003).

Few works have studied the influence of anthropogenic disturbances on the plant communities of the Argentine Wet Chaco and even fewer have on quebracho forest communities. Most of the work was carried out in the Dry Chaco ecoregion, with a predominance in the Semi-arid Chaco (Barberis et al., 2021). In this sense, the present work constitutes an important contribution of evidence to the knowledge of the influence of anthropogenic degradation in communities of the Chaco region, particularly in the quebracho forests of the Santa Fe Forest Wedge.

4.2. Influence of structural degradation on forest functional variables

The response of the functional characteristics to structural degradation was variable, although negative effects were observed at high levels of degradation for all of them (Fig. 3). Regeneration decreased

towards high structural degradation sites for both size categories. Despite the large variation between Group I sites, there were significant abundance differences between structural groups for both regeneration size classes (Fig. 3a, b). The site dispersion found in Group I could be associated with mature forests. In these mature and well-preserved forests, the limitations to regeneration would be given by biotic and abiotic factors imposed by the community itself, such as resource competition between saplings and grasses or shrubs, allelopathy, or shading from the upper strata canopy (Brokaw, 1983; Royo and Carson, 2006; Liira et al., 2011). In mature quebracho forests, two terrestrial bromeliads (*A. distichantha* and *B. serra*) dominate the understory (Barberis et al., 2014), and affect woody species regeneration by intercepting a large proportion of propagules in their canopy tanks (Barberis et al., 2011; Klekailo, 2019). On the contrary, in very degraded and homogeneous forests, the regeneration of woody species would present limitations in the production, dispersal, recruitment, and establishment of propagules (Elgar et al., 2014). The lack or the presence of a few isolated adult trees would hinder pollination and other processes related to reproduction, resulting in none or low (and poor quality) seed production. Propagule dispersal by animals would also be affected in degraded areas because of a lack of food or safe sites for seed dispersers. In addition, recruitment of seedlings and their subsequent establishment would be limited by the stressful abiotic conditions that usually occur in degraded areas (high temperature and humidity fluctuations, soil loss, etc.) and by the management pressure (e.g. livestock grazing) sustained in these areas (Jordano et al., 2008; Elgar et al., 2014; Cavallero et al.,

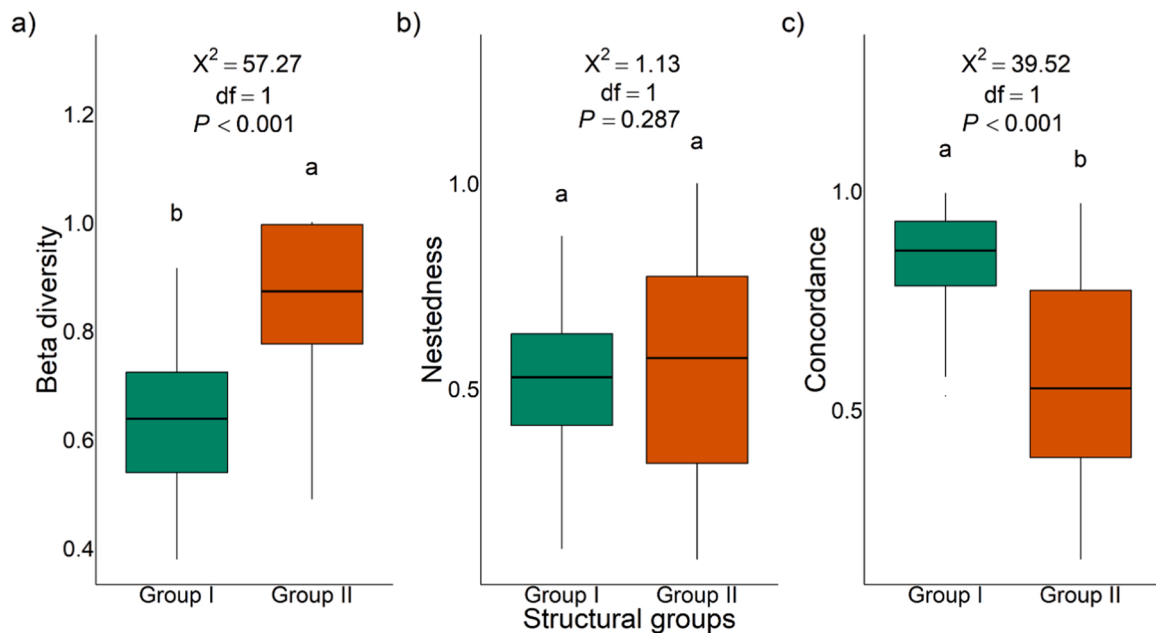


Fig. 5. Boxplots showing the differences between structural groups for the coefficients of (a) beta diversity, (b) nestedness, and (c) concordance. Each boxplot results from comparisons between sites within the same group. Green boxes correspond to Group I ($n = 120$) and the orange boxes to Group II ($n = 36$). For each plot, the χ^2 , the degrees of freedom (df), and the P values are reported.

2019).

Primary productivity was higher and more stable in less degraded sampling sites, decreasing and becoming more variable as structural degradation increased (Fig. 3c, d). In mature forests, the NDVI pattern would be related to the vegetation biomass and the heterogeneity of its distribution in patches and inter-patches. The greater amount of biomass from different growth forms, widely distributed in space, would sustain a high ANPP and reduce the inter-annual variations caused by adverse abiotic conditions. In degraded sites, it is worth noting that the average NDVI increased a little bit after the breakpoint, while the coefficient of variation showed a decrease. This pattern seems to be associated with a variability in vegetation cover in degraded sites. For example, we found that there were structural degraded sites with low NDVI (those sites next to the breakpoint) that had a high proportion of bare soil and very few trees and shrubs, but there were also structural degraded sites that showed a small increase in NDVI, perhaps because they had a very high grass cover throughout the analyzed years. The decreasing NDVI trend toward structural degraded sites found in this work coincides with other studies conducted in different regions of the Chaco (Volante et al., 2012; Landi et al., 2021; Bigerna et al., 2022) and the world (Amiro et al., 2000; Hicke et al., 2003; Basuki et al., 2019). In the Dry Chaco and Yungas regions, cleared sites presented lower mean annual NDVI values and higher seasonal coefficient of variation than the better-conserved ones. Additionally, the greater the change in vegetation structure (e.g. woody cover replaced by herbaceous crops), the greater the change in functional processes, particularly in the ANPP (Volante et al., 2012). A similar pattern was observed in the Dry Chaco in a study associated with burned forests, where sites with greater physiognomic changes (e.g. from forest to shrubland) had greater percentage differences in NDVI for unburned than burned sites (Landi et al., 2021). Finally, in the Wet Chaco, the most structurally complex woody communities are those with the highest NDVI values (Bigerna et al., 2022).

The first 30 cm soil depth showed a decreasing trend in SOC stock at high levels of structural degradation but with varying initial responses (Fig. 3e, f). The superficial SOC stock showed a breakpoint occurrence between structural groups at intermediate structural degradation levels, whereas deep SOC stock showed a non-significant linear decrease. The observed pattern of SOC stock reduction is an expected result, since

globally, there is evidence that forest ecosystem land use change reduces SOC stocks, particularly from forest to plantations, crops, or pastures (Guo and Gifford, 2002; Don et al., 2011; Jackson et al., 2017; Eze et al., 2023). The increase in surface organic carbon towards sites with intermediate structural degradation (breakpoint < 35 of SDI, Fig. 3e) may be related to the increase in root density of herbaceous species associated with those degraded sites. SOC stock constitutes a slow variable (i.e. slow dynamic) that affects fast variables, such as productivity, so it is a good indicator of state changes (Carpenter and Turner, 2000; Walker et al., 2012). A meta-analysis for tropical regions shows that primary forest soils retain greater carbon stocks than secondary forest soils and even more than grassland or crop soils (Don et al., 2011). In the Dry Chaco ecoregion, numerous works highlight that forest degradation by different anthropogenic activities (e.g. cattle ranching, forest logging, and clearing) significantly reduces SOC stocks (Abril and Bucher, 2001; Villarino et al., 2017; Osinaga et al., 2018; Baldassini and Paruelo, 2020). For the Wet Chaco forests, there is little evidence of the response of SOC stocks to changes in land use, but a report by Peri et al. (2022) showed that under different land uses, primary forests (or natural vegetation) would have higher carbon stocks than forest plantations and other alternative uses.

Species diversity declined markedly with the degradation index, and there were differences between structural groups (Fig. 3g). Despite very little information about this relationship in the Wet Chaco, some studies in the Dry Chaco found a decrease in woody plant diversity with forest degradation (Aguilar et al., 2018; Magnano et al., 2023). Studies in different forest types around the world also report a similar trend (Halpern and Spies, 1995; Gibson et al., 2011; Clark and Covey, 2012).

Basal area showed an initial abrupt reduction concerning structural degradation, perhaps indicating that very few forest sites were not logged (Fig. 3h). The decreasing response showed could be related to the selective extraction of bigger timber trees, used for anthropogenic use (Echeverría et al., 2007; Osazuwa-Peters et al., 2015; Tallei et al., 2023). Similar results were reported when comparing mature forest sites against degraded or secondary forest sites (Táلامo and Caziani, 2003; Bonino and Araujo, 2005; Sebbenn et al., 2008; DeArmond et al., 2023). The threshold response to structural degradation is a critical finding as this variable has a double function as carbon storage and timber

provision. Moreover, it is also considered a slow variable since its recovery takes a long time, so its reduction by anthropogenic activities implies a loss of ecosystem processes (LaRue et al., 2023; Mills et al., 2023).

4.3. Comparative analysis of woody species composition between structural groups and its relationship with forest structural degradation

Our results show a process of simplification of woody species composition evidenced by an increase in beta diversity and nesting and a decrease in concordance concerning the reference sampling site (Fig. 4). It is worth noting that the three coefficients showed breakpoints at intermediate levels of SDI. This is because degradation by anthropogenic activities eliminates woody species or decreases their cover due to selective extraction, forest clearing, livestock introduction, and/or other management activities, thus increasing beta diversity and nesting processes and decreasing the importance of the concordance between them. For example, sampling sites from Group II were characterized by the presence of a shrub species (*L. boerhaviaefolium*) and two small, heliophilous trees species (*V. aroma*, and *V. caven*), while sampling sites from Group I had the typical species of the quebrachal (e.g. *S. praecox*, *M. cisplatensis*, *A. praecox*, etc.) (Figure A.3, Table A.2, Appendix A). The woody species found in each group have been reported for degraded sites (Cabido et al., 1994; Astrada, 2013; Marquez et al., 2019) and conserved sites (Ragonese and Covas, 1940; Lewis et al., 1997), respectively. Likewise, several studies carried out in the Dry Chaco ecoregion pointed out that woody species assemblages differed between conserved sites and degraded sites under anthropogenic management (Loto and Bravo, 2020; Lipoma et al., 2021), even more so if the disturbance is so intense as to modify forest physiognomy (Tálamo et al., 2012). Further studies should analyze the change in the species composition of the herbaceous community along the degradation states of quebracho forests to generate a more holistic understanding of this system. In this sense, an interesting study in the Wet Chaco proposes states and transitions of woody and herbaceous communities, highlighting the effect of cattle ranching on changes in the herbaceous communities, although without analyzing their species composition (Astrada, 2013).

Another process identified in this work is the divergence in woody species composition between structural degraded sampling sites, possibly because of the differential effects of disturbances on the species assemblages or the environment (Fig. 5) (Laurance et al., 2007; Solar et al., 2015). For example, a forest used for extensive cattle ranching will have fewer changes in plant species composition than another site that was also used for selective logging, especially if the extraction was focused on certain woody species. Another common practice is to clear the understory (shrubs and spiny bromeliads) leaving only isolated big trees of a few species or clear the whole forest. When these sites are abandoned, the mentioned shrub encroachment takes place. All these degradation forms would also explain why the Species Indicator Value index did not significantly associate any species with Group II (Table S1).

Biological diversity is associated with many aspects that confer resilience to ecosystems, such as functional redundancy and diversity of responses to disturbances (Laliberté et al., 2010). Thus, in the face of a disturbance or long-term abiotic variations (i.e. climate change), the possibility of having species with similar ecological roles to replace those that were affected or the ability to respond differently to the changes produced by disturbances confers resilience to the ecosystem (Hobbs et al., 2007; Laliberté et al., 2010; Sasaki et al., 2015; Correia et al., 2018). The loss of the representative woody species implies the loss of ecosystem structure and key ecological processes, deleting its characteristic appearance and breaking its functioning (Ellison et al., 2005). In the quebracho forest, this role is mainly played by *S. balansae* accompanied by other tree species such as *M. cisplatensis* or *S. praecox* and shrubs such as *A. praecox*, *C. argentinensis* or *M. vitis-idaea* (Lewis and

Pire, 1981). This background would indicate that the loss of biodiversity observed among the structural groups of the present work could be interpreted as a loss of resilience among them.

4.4. Structural – Functional State and Transition Model hypothesis: an approach to quebracho forests

Measuring resilience is a difficult task due to its many definitions and the difficulty of quantifying it, so several approaches have been proposed to do it (Baho et al., 2017; Yi and Jackson, 2021; Cantarello et al., 2024). In this work, we proposed to address the resilience of quebracho forests by studying the behavior of their compositional, structural, and functional components through the use of STM. The development of STM for ecosystems is a complex process since it involves disciplines related to ecology, but also includes social aspects (i.e. socio-ecosystems) (Bestelmeyer et al., 2009). The first step for the construction of conceptual STMs is the systematization of the historical use of the ecosystem under study and the possible transitions between plant communities (i.e. potential alternative states), associated with an Ecological Site, by conducting workshops with experts and producers (Bestelmeyer et al., 2010, 2017). Although such valuable information is not available in this work, we sought to study the ecology of quebracho forests under anthropogenic use, and its influence on resilience by the analysis of biotic and abiotic characteristics, looking for inflection points that determine thresholds between degradation states (Briske et al., 2006; Sasaki et al., 2015). In this regard, we were able to establish a clear difference between two groups of sampling sites and to determine non-linear responses to structural degradation for biotic (woody regeneration, mean and coefficient of variation of NDVI, basal area, species composition) and abiotic (surface SOC stock) variables, some of which showed breakpoints. Their identification is very important for management purposes, so many studies have reported the occurrence of thresholds in forest vegetation characteristics to different disturbances: herbivory (Augustine et al., 1998; Hester, 2000; Tremblay et al., 2006), deforestation and fragmentation (Bodin et al., 2006; Arroyo-Rodríguez et al., 2008, 2009; Digiovinazzo et al., 2010), selective logging (Furukawa et al., 2011), and invasion of exotic species (Gooden et al., 2009).

The breakpoints identified in this work, coupled with the non-linear response of some variables and the statistical differences between groups, constitute strong evidence to suggest that sampling sites from Groups I and II correspond to different degradation states associated with an SDI threshold near 50%. Transitions between them would be mediated by losses in vegetation structure complexity, functions, and species composition, which would trigger the loss of resilience (slow variables *sensu* Carpenter et al., 2001). In addition, there seems to be intra-group variability (particularly in Group II) which could indicate the presence of different phases in the same state (phases and state concepts *sensu* Bestelmeyer et al., 2009, 2017). While phase changes within the same state imply less intensive disturbances, such as extensive cattle ranching with low animal density or the selective extraction of some tree species regulated by low-scale management plans (i.e. farm or smallholder) in Group I sites, transitions between states involve intense disturbances or combinations of them (Table A.1, Appendix A; Simón et al., 2003). For example, a study conducted in quebrachales showed that *S. balansae* seedlings were highly selected by cattle among other woody species when the stocking rate per hectare was high, even when the available herbaceous biomass was also high (Simón et al., 1997). That work demonstrates the impact of grazing on one of the representative species of the quebracho forest. Besides, it is very common to clear the understory, sow forage species, and then introduce cattle, leaving only the largest trees or none of them (i.e. savanna or grassland physiognomies). These new plant communities have the support of the cattle rancher who controls shrub establishment, but when this management is abandoned, these sites are colonized by small trees or shrubs, generally endozoochorous (e.g., dispersed by cattle) and heliophilous species, such as *V. caven* or *V. aroma*, and anthills are also

established (Cabral et al., 2003; D'Odorico et al., 2011; Eldridge et al., 2011; Sala and Maestre, 2014). This degraded community differs from the previous ones both in plant structure (typically stunted trees and shrubs due to constant browsing) and in its specific composition. Commonly, natural (e.g. prolonged droughts) and anthropogenic disturbances occur simultaneously, increasing the potential damage to forest structure. These events indicate the partial or total destruction of the forest structure and the elimination of entire populations of certain woody species (i.e. biotic threshold: local extinction of species), which then remain in a degraded state by livestock grazing feedback. These changes imply that the transitions between the two states are naturally irreversible, so active positive management would be necessary for eventual forest recovery, involving the exclusion of livestock from certain areas, the reintroduction of species (herbaceous and woody), or other activities (Simón et al., 2003). Future studies should sample more sites and conduct workshops with local experts and landowners to identify the possible degradation pathways of these forests and the ways of recovering them (i.e. hysteresis). From a larger number of sites and taking into account the different transition mechanisms and degradation pathways, more than one segmented regression should be fitted to obtain a more complete picture of the quebrachal state and transition model (López et al., 2011; Standish et al., 2014; Peri et al., 2017). Likewise, it would be important to be able to install cattle or logging enclosures in the degradation gradient sites, follow them over time through regular monitoring, and observe the direction of vegetation changes in the long term.

5. Conclusion

In the context of global climate change and rapid human-induced alterations, addressing forest ecosystem resilience from a structural and functional indicator perspective could be a novel approach to its medium- and long-term management. In this sense, using the Structural-Functional State and Transition Models plus the species composition characterization of the xerophytic subtropical forest communities of the Wet Chaco allowed us to answer the questions posed. Based on a set of structural characteristics and the abundance of the most representative woody species of the quebrachal, we constructed a structural degradation gradient of quebracho forest sites and classified them into two structural groups. According to our results, we proposed that the structural groups correspond to different states of degradation of quebracho forests, mediated by transitions of an anthropogenic origin of different intensity (cattle ranching, forest logging, and clearing, etc.) in combination with natural disturbances (e.g. prolonged droughts) and separated by biotic and abiotic thresholds. In conclusion, the sustainable management of forest ecosystems could be addressed from the SFSTM approach, so that identifying and describing the different Ecological Sites, their states (reference and alternative ones), and the threshold between them become an essential contribution. Moreover, future studies at a landscape level are necessary to identify the interactions between different forest types (i.e. Ecological Sites).

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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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121957.

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