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Functional indicators to explain the anthropic effects on community plant composition changes: The case of a temperate forest in Mexico

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A R T I C L E I N F O

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A B S T R A C T

In plant communities, changes in composition driven by the dominance of weed species have been used as ecological indicators to predict the anthropic impacts on these species. Nevertheless, anthropic disturbances do not act directly on species composition, but their effects depend on the species' functional responses. Hence, anthropic effects follow a logical sequence, in which disturbances act at different levels. In order to understand the sequence of the changes in the community there is a need to develop functional and compositional integrated indicators. In order to integrate them we suggest a method based on inference by abduction, to reduce the complexity in predicting the anthropic effects on species functional responses. With this method we develop functional indicators of responses to anthropic disturbances and the effect on composition changes. The method involves building structural equation models (SEMs), through which we evaluate the anthropic and environmental effects on the functional response of species and composition changes in an integral way. From these causal paths, we select the best-fitting model with plausible functional indicators to explain the anthropic effects, according to Akaike's information criterion (AIC). This research develops a methodological proposal to build up functional indicators with foliar attributes associated to resource acquisition and use strategies of herb and shrub species in the temperate *Abies religiosa* forest in the Magdalena river basin in Mexico City. The built indicators demonstrate for the first time and in a simultaneous way, that characteristic species (original component) and native weeds (component established under perturbation conditions) have different responses to anthropic perturbations as well as different contributions to community composition changes. This result represents a methodological contribution in the evaluation of anthropic impacts and the use of native weed species as functional indicators.

1. Introduction

At the global level, anthropic disturbances have modified the composition and function of plant communities at an unprecedented speed, a condition that has favored the establishment of weed species (Chapin et al., 2000). Weeds are native or introduced species that are highly competitive under certain regimes of anthropic disturbance, which can increase their abundances and can even inhibit the growth of some characteristic forest species (i.e., species that evolved originally in the site where they are) (Richardson et al., 2000; Drenovsky et al., 2012). As a consequence some composition indicators have been developed, for example Helm et al. (2015) and Santibáñez-Andrade et al. (2015) elaborated indicators based on the relation between characteristic and weed species abundance as a measure of the magnitude of anthropic disturbance and habitat change, however they did not consider the functional responses of species and the consequences of this at the compositional level in the community. Though there are currently different functional indicators that are based on a variety of biological attributes; they do not capture the causality of the anthropic effect at functional and composition levels, (review studies by Díaz et al., 2007; Duflot et al., 2014; and Capmourteres and Anand, 2016). Thus, functional indicators that enhance the understanding of anthropic

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effects on functional responses between characteristic and weed species need to be developed so that their differences and role as perturbation indicators are better understood (Drenovsky et al., 2012; Bruno, 2016).

Although composition indicators have demonstrated to represent the increase of anthropic activities (Helm et al., 2015), it is important to consider that anthropic disturbances do not act directly on species composition (Tilman et al., 1997; Song et al., 2014; Mayfield et al., 2010). First, continuous low-impact activities (chronic disturbances), such as constant livestock raising and the gradual loss of plant cover, cause environmental changes that intensify and/or modify preexisting environmental filters from local to microsite scales (Martorell and Peters, 2005; Martínez-Blancas et al., 2018). Thus, communities result from a hierarchy of successive filters, which select species with disturbance-tolerant attributes that frequently correspond to pioneer species and/or weeds (Richardson et al., 2000; Mayfield et al., 2010). Therefore, high intensities of anthropic disturbance and changes in composition will be promoted, which will favor a high abundance of weeds (Mouillot et al., 2013; Santibáñez-Andrade et al., 2015).

Due to the lack of functional indicators that consider the complexity of anthropic effects (Lavorel and Garnier, 2002; Lin et al., 2009; Mayfield et al., 2010), we present a methodological proposal for the development of indicators that evaluate, in an integral and simultaneous way, the anthropic effects on the functional responses of characteristic and weed species. The selection of functional indicators is performed through the inference of reasoning by abduction (Bigelow, 2010). This reasoning process allows in a practical way, through a group of previously selected variables, the detection of the most plausible indicators that connect causal pathways of the anthropic effect on the composition (Bigelow, 2010).

The aims of this study were (a) to corroborate through the application of SEMs whether the characteristic species and native weeds show similar functional responses to anthropic perturbations, due to their common adaptive history as we hypothesized or do they present different tolerance intervals, (b) to determine if the functional responses between characteristic species and weeds are the same in herbaceous and shrub species. We expect higher values of leaf area (LA) and specific leaf area (SLA) in herbaceous weeds than in shrub species due to resource acquisition strategy (Feng et al., 2008; Drenovsky et al., 2012). While shrub weeds will be associated with resource conservation strategy, attributes such as thick leaves with a high leaf dry matter content (LDMC) (Castro-Díez et al., 2002; Funk et al., 2016). Finally, (c) we evaluate the functional responses of characteristic and weed species and the implications of their use as anthropic perturbation indicators.

2. Materials and methods

2.1. Functional indicators method

2.1.1. Explanation of the inference by abduction method

The development of functional indicators represents an exhaustive task if we consider that there is a large number of available functional metrics (Mayfield et al., 2010; Mouillot et al., 2013). However, due to the logical sequence that the anthropic perturbations have on composition (Fig. 1), it is possible to use a logical reasoning of inference by abduction, which from a detected phenomenon (true premise), it is possible to give a causal probable explanation (probable premise) (Fitzhugh, 2008; Bigelow, 2010). This logical reasoning has been broadly used in medical and social sciences (Fitzhugh, 2008; Bigelow, 2010). In this study, inference by abduction is a logical process, which considers the anthropic and environmental effects on species function and composition as a premise (Fig. 1) and the anthropic effects on the functional response of species as a probable explanation (Fig. 1, B1-B4). Given the logical sequence of the anthropic effect on the functional response of the species (Fig. 1, B1-B4) and its subsequent effect on composition (Fig. 1, C1 and C2) (Lavorel and Garnier, 2002; Mayfield et al., 2010). From this reasoning, we used a two-step method to obtain

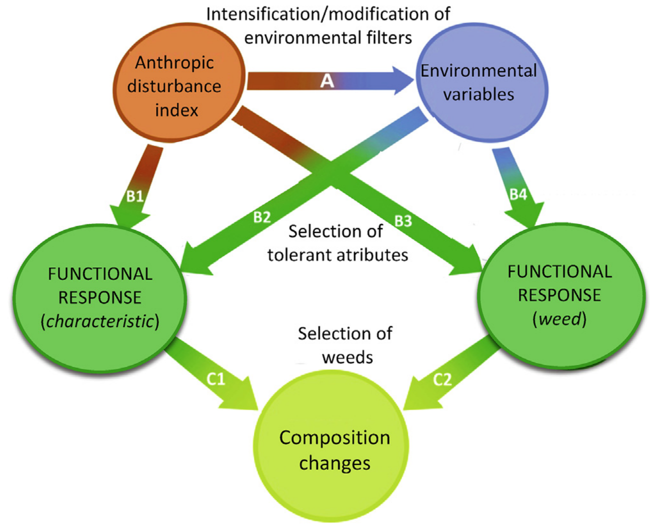

Fig. 1. Conceptual model of anthropic and environmental effects on species functional response and their effects on the changes in species composition of a community. Arrow A represents the effect of the anthropic disturbance agents in the intensification and modification of the environmental filters, through which the changes in environmental variables are promoted. Arrows B1, B2, B3 and B4 represent the effect of anthropic perturbations on the selection of attributes that confer tolerance to species; these are reflected in the functional responses of the species. Arrows C1 and C2 represent the effects of the functional responses on the probable selection of weed species that are represented in the composition changes.

functional indicators, which were used in our study system and further discussed. This method applied the inference by abduction through structural equation models (SEMs) to estimate the anthropic multiple effect causal pathways and to select functional indicators through Akaike's information criterion (AIC).

2.1.2. Step 1. Anthropic effect on the environment

Given that human activities can modify preexisting environmental filters, an initial step is to corroborate the anthropic effects on the environmental factors (Fig. 2, arrow A) (Díaz et al., 2007). For this, we suggest fitting the total set of potential linear models, thus evaluating all potential effects of the anthropic disturbance agents (explanatory variables; fixed effects) on the environmental variables (response variables). Depending on the nature of the data, different models can be included: linear models (LMs; fixed effects), linear mixed models (LMMs; fixed and random effects), generalized linear models (GLMs; error distributions different from Gaussian) and generalized linear mixed models (GLMMs; fixed and random effects, and error distributions different from Gaussian) (Bolker et al., 2009). Afterwards, we suggest the selection of the best-supported models through the smallest Akaike's information criterion (AIC), evaluating the difference in the AIC value of each model with respect to the best-supported model (ΔAIC) (Burnham and Anderson, 2002; Lefcheck, 2016; Fig. 2, Step 1). The selected models thus include the disturbance agent and the environmental variables that will be evaluated in the next step (Fig. 2, Step 1 towards Step 2).

2.1.3. Step 2. Inference by abduction

Based on the logic of the inference by abduction and taking into consideration as a true premise the causal web of the anthropic effects on composition (Fig. 2), the search for a functional indicator (Fig. 2, arrows B1-B4) represents a likely key link in this web. To determine functional indicators, we propose fitting the total set of potential structural equation models (SEMs), representing the web of effects of the disturbance agents (exogenous predictors) and the environmental variables (endogenous predictors) on the species functional responses

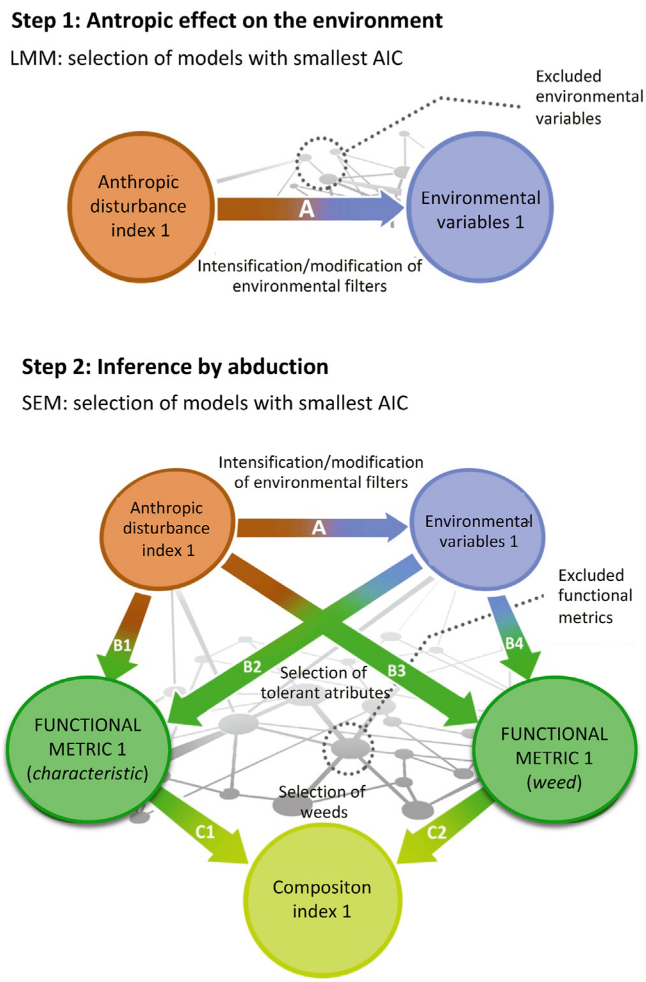

Fig. 2. Representation of the method for developing functional indicators of the response to disturbances and effect on composition changes. LMM = linear mixed model, SEM = structural equation model. AIC = Akaike's information criterion.

(endogenous responses) and the resulting changes in composition (exogenous composition response) (Fig. 2, Step 2). After estimating the total set of SEMs models, with different functional responses (attributes), the best -supported model would be selected through the AIC. In this way this model includes the functional response (attribute) that the functional indicator shows, and therefore that better explained the anthropic effect (Fig. 2, Step 2). SEM modeling can be performed with the statistical software piecewiseSEM (Lefcheck, 2016) on the statistical software R 3.5.2 (R Development Core Team, 2018). PiecewiseSEM allows to fit the models described in step 1 in a SEM context and to obtain AIC values from each SEM model, through nested comparison between models (including the missing functional metrics) (Lefcheck, 2016).

2.2. Application of the proposed method of functional indicators in the study system

2.2.1. Functional indicators method application

The application of the proposed method and the development of functional indicators was based on foliar attributes associated with the use and conservation of resources. This study was carried out in the understory community of an *Abies religiosa* forest. In the following paragraphs we describe the application of our proposed method.

2.2.2. Study site

The study was carried out in the temperate *Abies religiosa* forest in the Magdalena river basin, located southwest of the Valley of Mexico between 2900 and 3650 m a.s.l. and between 19° 13′ 53″, 19° 18′ 12″ N and 99° 14′ 50″, 99° 20′ 30″ W. The forest covers 3100 ha (Fig. 3, A and B) and adjoins a *Quercus* spp. forest at the lowest altitude (2700–2900 m s.n.m.), and at the highest altitudes, a *Pinus hartwegii* forest (Santibáñez-Andrade et al., 2015).

The *A. religiosa* forest has a temperate subhumid climate (C (w_2) (w) b(i′)) with temperatures of 6 °C to 20 °C and a mean temperature of 13 °C. The annual precipitation ranges from 950 to 1300 mm. The season with the highest precipitation is from June to October (rainy season) and the lowest precipitation occurs from November to May (dry season) (Dobler-Morales, 2010). The forest canopy is between 20 and 40 m high with *A. religiosa, Sambus nigra* subsp. *canadensis* and *Salix paradoxa* as dominant species, while the understory is 2 to 3 m high, with species of *Senecio, Acaena, Salvia* and *Ageratina*. This forest is part of the conservation area of Mexico City; however, it experiences constant disturbances such as deforestation, livestock raising and weeding as a silvicultural practice (Santibáñez-Andrade et al., 2015).

2.2.3. Selection of the study plots

In the *A. religiosa* forest of the Magdalena river basin, in June 2017, we selected 15 30 × 30 m plots (13500 m^2 total) (Fig. 3, A). These plots were distributed along an anthropic perturbation gradient at three altitudinal levels (high altitude = 2467–3449 m a.s.l. plots 1–5; intermediate altitude = 3202–3446 m a.s.l., plots 6–10 and low altitude = 3092–3122 m a.s.l., plots 11–15). The selection of these plots was based on the characterization of the study site made by Santibáñez-Andrade et al. (2015) and Tovar-Bustamante (2017), as well as on environmental anthropic disturbance information obtained in May 2017.

2.2.4. Characterization of the anthropic disturbance gradient

In June 2017, in each plot, we determined the intensity of 11 anthropic disturbances due to three factors: livestock raising (LR), human activities (HA) and habitat deterioration (HD) (Table 1). For LR, we quantified the number of square m with livestock dropping (livdro), livestock roads (livroa), branched plants (brapla) and soil compaction (soicom). This last measurement was determined through the apparent density, which refers to the reduction in soil pores per volume unit (g/cm^3) due to constant livestock trampling. In each plot, we randomly collected three soil samples with a cylinder (106.02 cm^3), and the samples were oven dried (105 °C) for 24 h and then weighed. The apparent density was obtained using Keller and Håkansson's (2010) equation:

$$AD = 100Ds/V, \quad (1)$$

where *AD* is the apparent density (g/cm^3), *Ds* is the dry soil weight (g) and *V* is the cylinder volume (cm^3).

For HD, we quantified the number of square meters that were subjected to weeding (weedin), deforestation (defore) and canopy openness (canope). The last factor was determined by 16 hemispherical photographs (digital camera Nikon D80, fisheye lens EX SIGMA4.5 2:28 DCHSM, Tokyo, JP). These were analyzed with the Gap Light Analyzer (GLA, 2.0) software, which quantifies the fraction of canopy openness (FAD) (GLA, 2.0; Frazer et al. 1999). For HA, we determined the presence of inorganic garbage (inogar), organic garbage (orggab) and the distance to roads (disroa). Distance to nearby roads was quantified through the inverse of the distance (m) between plots and the two nearest human roads.

2.2.5. Anthropic disturbance indexes

The indexes of anthropic disturbance (LR, HA and HD; Table 1) were obtained through dimension reduction with a principal component analysis (PCA), following the methods proposed by Martorell and

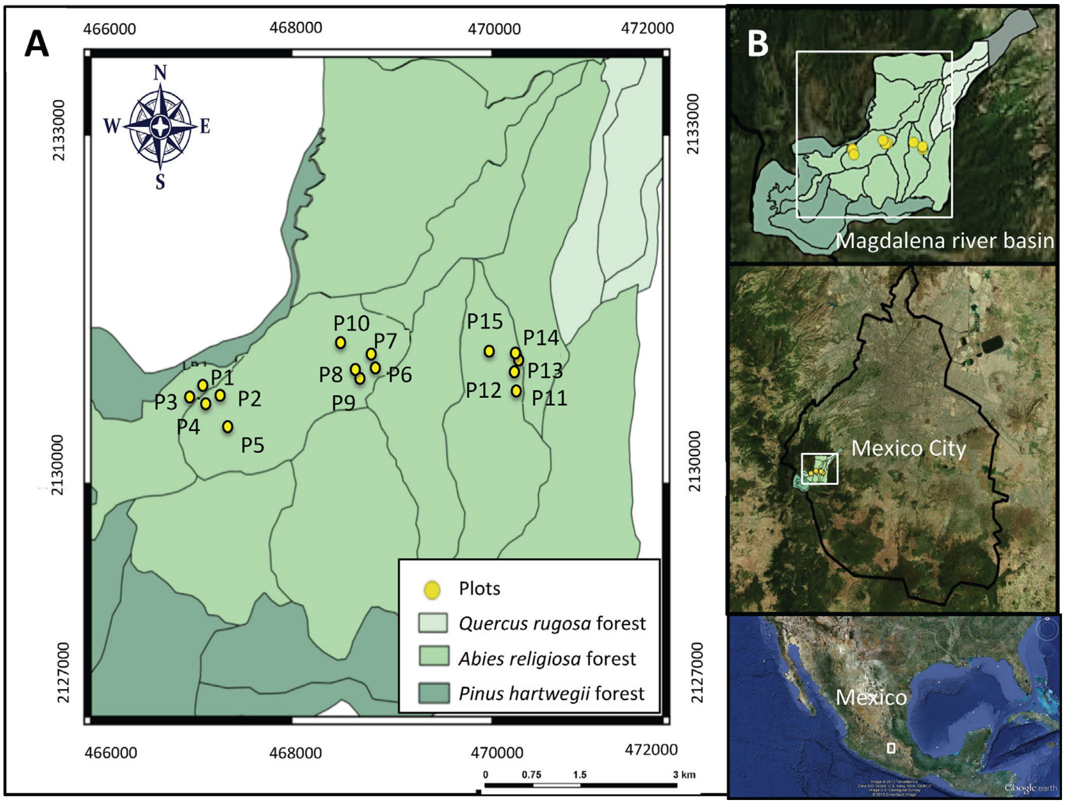

Fig. 3. Study plots (A) in the temperate *Abies religiosa* forest (B) in the Magdalena river basin, Mexico City, Mexico (D). Plots were set at three altitudinal levels (high altitude = 2467–3449 m a.s.l. plots 1–5, intermediate altitude = 3202–3446 m a.s.l., plots 6–10 and low altitude = 3092–3122 m a.s.l., plots 11–15).

Peters (2005) with the statistical software R (v. 3.5.2; R Development Core Team, 2018). From the addition of the scores of every agent in the first component, we obtained the index for each of them. With the addition of the three determined agents we obtained the disturbance index per plot (DI) (Table 1). Therefore, the model that integrates the considered variables to generate the anthropic disturbance index (DI) is the following:

$$DI = -0.036 livdro + 0.540 livroa + 0.275 \times brapla + 0.142 soicom + 0.521 \times weedin + 0.302 \times defore + 0.479 \times canope + 0.008 inogar - 0.085 orggar + 0.077 disroa, \quad (2)$$

2.2.6. Environmental variables

In each plot, the environmental variables were quantified in the dry season as well as in the rainy season during the study year (June 2017-June 2018). Temperature was registered continually with hobo data loggers (easy LogUSB-ONSET, Massachusetts, EUA). Light conditions were measured in each plot every two months through hemispheric photographs taken under overcast sky conditions at 8:00 am (digital camera Nikon D80, fisheye lens EX SIGMA4.5 2:28 DCHSM, Tokio, JP) (Table 1). The photographs were analyzed with the Gap Light Analyzer (GLA, 2.0) software to determine the global site factor (GSF), which is defined as the percentage of light (light moles transmitted per unit area) (GLA, 2.0; Frazer et al., 1999).

In both seasons, in each plot, we collected three combined soil samples for chemical analysis. The analyzed variables were pH through the relation of soil and water at 1:2, electric conductivity (EC) in water at a ratio of 1:5, and organic matter (OM) percentage obtained through moist digestion and Walkley-Black determination. The available inorganic phosphorus (P) concentration was determined through the extraction of $NaHCO_3$ 0.5 M (pH = 8.5) and colorimetric quantification (Table 1). Nitrogen (N) percentage was obtained through moist digestion with H_2SO_4 Kjeldahl distillation through steam drag and H_2SO_4 (0.05) (Table 1). In addition, three soil samples per plot were collected, weighed, oven dried (105 °C, 48 h) and weighed again to calculate the soil moisture (SM)percentage using the Reynolds (1970) equation:

$$SM = 100(Sf - Sd)/Sd, \quad (3)$$

where *SM* is the percentage of soil moisture, *Sf* is the soil fresh weight and *Sd* is the soil dry weight.

2.2.7. Vegetation sampling and determination of composition indexes

In each plot, we determined the understory species abundances (herbs and shrubs smaller than 3 m in height). For each species, we determined its status: native characteristic species, which are native plants that evolved originally in Mexico and that form part of temperate forests, and native weeds, which are species that evolved originally in Mexico and their establishment is favored by anthropic perturbations (Espinosa and Sarukhán, 1997; Richardson et al. 2000; Calderón de Rzedowski and Rzedowski, 2020; Vibrans, 2015). With the abundances of these two types of species, the indexes of favourable conservation status were determined for each plot, for herbs (FCS.herb) and for shrubs (FCS.shru) (Table 1), using the Helm et al. (2015) equation:

$$FCS = log(abuC/abuW), \quad (4)$$

where *FCS* is the index of favorable conservation status, *abuC* is the abundance of characteristic species and *abuW* is the abundance of native weeds. This index shows the proportion of the abundance of weed species in relation to the abundance of characteristic species.

2.2.8. Leaf attributes and determination of functional metrics

We randomly selected 10 individuals of each species and measured the following metrics for30 leaves of each individual: leaf area (LA; mm^2) with a foliar scanner (Area Meter AM300, ADC, Bio Scientific Ltd, Texas, EUA) and leaf dry matter content (LDMC; mg) through the ratio of the fresh leaf weight /dry leaf weight (oven dried for 48 h, 70 °C).

Table 1
Anthropic disturbance indices description, environmental variables, composition indexes and functional metrics; we present the abbreviations of the names used in the study and the units and scales of measure for the possible values for the variable.

Indicators	Abbreviation	Unit	Scale	Reference
Anthropic disturbance index				
Livestock raising index	LR	NA	$(-\infty, +\infty)$	Martorell & Peters (2005)[a,b]
Habitat deterioration index	HD	NA	$(-\infty, +\infty)$	Martorell and Peters (2005)[a,b]; Caviedes and Ibarra (2017)[a,b]
Human activities index	HA	NA	$(-\infty, +\infty)$	Martorell and Peters (2005)[a,b]
Disturbance index	DI	NA	$(-\infty, +\infty)$	Martorell and Peters (2005)[a,b]
Environmental variables				
Temperature	TEM	°C	−3 a 22	Wolff et al., (2018)[b]
Light	LIG	%	0.5 a 0.60	Théry (2001)[b]
pH	pH	NA	5 a 6.9	Santibáñez-Andrade et al., (2015)[b]
Electrical conductivity	EC	dS/m	0.03 a 0.17	Santibáñez-Andrade et al., (2015)[b]
Organic matter	OM	%	0.11 a 0.39	Santibáñez-Andrade et al., (2015)[b]
Phosphorus (available)	P	ppm	2 a 30	Barton et al., (2016)[b]
Nitrogen	N	%	0.5 a 0.65	Barton et al., (2016)[b]
Soil moisture	SM	%	0. 30 a 0.94	Odriozola et al. (2014)[b]
Composition Index				
Favorable conservation status	FCS	NA	$(-\infty, +\infty)$	Helm et al., (2015)[a,b]
Herbs	FCS.herb			
Shrubs	FCS.shru			
Functional metrics				
Community-weighted mean leaf area	CWM.LA	mm2	$(-\infty, +\infty)$	Violle et al., (2007)[a]; Sitzia et al., (2017)[b]
Characteristic herbs	CWM.LA.herb.C			
Weedy herbs	CWM.LA.herb.W			
Characteristic shrubs	CWM.LA.shru.C			
Weedy shrubs	CWM.LA.shru.W			
Community-weighted mean specific leaf area	CWM.SLA	mm2/mg	$(-\infty, +\infty)$	Violle et al., (2007)[a]; Sitzia et al., (2017)[b]
Herbs characteristic	CWM.SLA.herb.C			
Herbs weed	CWM.SLA.herbW			
Shrubs characteristic	CWM.SLA.shru.C			
Shrubs weed	CWM.SLA.shru.W			
Community-weighted mean leaf dry matter content	CWM.LDMC	mg	$(-\infty, +\infty)$	Violle et al., (2007)[a]; Sitzia et al., (2017)[b]
Herbs characteristic	CWM.LDMC.herb.C			
Herbs weed	CWM.LDMC.herb.W			
Shrubs characteristic	CWM LDMC.shru.C			
Shrubs weed	CWM.LDMC.shru.W			
Functional dispersion	FDis	NA	$(-\infty, +\infty)$	Laliberté and Legendre (2010)[a,b]
Herbs characteristic	FDis.herb.C			
Herbs weed	FDis.herb.W			
Shrubs characteristic	FDis.shru.C			
Shrubs weed	FDis.shru.W			

For the environmental variables, the scale takes into account the minimum and maximum values reported for the study site (Dobler-Morales, 2010; Santibáñez-Andrade et al., 2015; Bonilla-Valencia et al., 2017).
The scale of the functional metrics corresponds to a log transformation.
[a] Reference that shows its detailed construction.
[b] Reference that shows its application in the evaluation of perturbations.

Then, the specific leaf area (SLA; mm^2/mg) was obtained for each leaf through the ratio LA/LDMC.

For the four groups of species, characteristic herbs (herb. C), herbaceous weeds (herb. W), characteristic shrubs (shru. C) and shrubby weeds (shru. W), we calculated the community-weighted mean (CWM) for each attribute based on the quantification of the medium dominant value (Table 1) (Violle et al. 2007). With all the attributes determined, the index of functional dispersion (FDis), which reflects the variation in the weighted attributes in terms of the species abundances, was calculated (Table 1) (Laliberté and Legendre, 2010). Low values of FDis indicate the influence of environmental and disturbance filters that promote a high abundance of species with similar attributes (functional convergence), while high FDis values indicate the influence of interactions that promote the complementarity and dissimilarity of attributes (functional divergence) (Hernández-Vargas et al., 2019). These functional metrics were calculated with the attributes and abundance matrices of the species through the FD package (Laliberté and Legendre, 2010) in R software R (v. 3.5.2; R Development Core Team, 2018).

2.2.9. Application of the proposed method of functional indicators in the study system

In the first step of this method, we estimated the effect of the anthropic disturbance agents on the environmental variables (Fig. 2, Step 1), through the possible causal relations documented in the literature. Thus, we evaluated the effect of habitat deterioration (HD) and human activities (HA) on temperature (TEM) and light (LIG) and the effects of HD and livestock raising (LR) on soil moisture content (SM), pH, electric conductivity (EC), organic matter (OM), available phosphorous (P) and nitrogen (N) in the soil (Théry, 2001; Odriozola et al., 2014; Santibáñez-Andrade et al., 2015; Barton et al., 2016; Caviedes and Ibarra, 2017; Wolff et al., 2018). The causal relations were evaluated through LMMs with the lme4 package (Bates et al. 2014) in R software (v. 3.5.2; R Development Core Team, 2018). For the construction of these models, we assumed Gaussian distributions for the environmental variables TEM, pH, EC and P, and for the percentage variables we applied the logit transformation (LIG, OM, N, SM). Models included the random crossed effects of season (dry, rainy) and altitude (three levels). The altitude variation was considered as a random effect in the models, it is a variable that modifies the environment, but it doesn't have a direct relation with disturbance. We estimated the total set of potential models for each environmental variable, and the most plausible models were selected with the smallest AIC.

In the second step, we built the SEMs that evaluated the anthropic effects (exogenous predictors) as well as environmental effects (endogenous predictors) on the determined functional metrics (CWM. LA, CWM. SLA, CWM. LDMC and FDis; endogenous responses) and the effect of these metrics on the changes on the herb and shrub composition (FCS.her; FCS.shru; exogenous composition responses) (Fig. 2, step 2). The SEMs assumed a Gaussian distribution of the composition indexes (FCS.herb and FCS.shru) and functional metrics (under a log transformation). The inclusion of the LMMs in the construction of the SEMs was not possible due to convergence issues; thus, the SEMs were constructed with LMs, including only fixed effects (anthropic and environmental factors); with variance in the endogenous factors explained by the exogenous factors. For both herbs and shrubs, we selected as functional indictors the functional metrics that showed the smallest AIC.

3. Results

3.1. Anthropic disturbance indexes, of composition, environmental variables and functional metrics

The study plots showed different intensities of anthropic disturbance for the three disturbance agents (LR, Livestock raising HD, Habitat deterioration; and HA, Human activities) as well as for the general index of anthropic disturbance (DI) (Table 2). The disturbance agents with the highest intensity were LR and HD. Disturbance intensity of the three agents and the DI value were different among the three altitudes. Characteristic and weed species, shrub and herbs showed different abundances between plots with different disturbance intensities (Table 2). In Supplementary Material 1, the obtained values of the environmental variables are shown, as well as the index of favorable conservation status (FCS) for herbs (FCS.herb) and shrubs (FCS.shru) and the values of the determined functional metrics (CWM.LA, CWM.SLA, CWM.LDMC and FDis) for the four groups of species (herb.C, herb.W, shru.C and shru.W), with a total of 16 functional metrics for the plant communities.

3.2. Results of the proposed method

3.2.1. Step 1. Anthropic effect on the environment

Table 3; Step 1 show the AIC values of the anthropic effect on the environmental variables. According to the LMMs, only the models associated with phosphorus (P) and pH showed the smallest AIC values than the null model (Table 3; Step 1). For these models, we selected

Table 3
Step 1. Anthropic effect on the environment, **Step 2.** Inference by abduction. LMM = linear mixed model, SEM = structural equations model, ΔAIC = difference in the Akaike's information criterion and K = number of parameters. LR: livestock raising index, HD: habitat deterioration index, P: phosphorus available in soil, pH: pH of soil, CWM.LA: Community-weighted mean leaf area, CWM.SLA: community-weighted mean specific leaf area, CWM.LDMC: community-weighted mean leaf dry matter content, FDis: functional dispersion.

Step 1: Anthropic effect on the environment		
Predictor	Environmental response	ΔAIC (K)
LR	P	0 (5)
LR + HD		3.010 (6)
LR*HD		3.130 (7)
Null		7.420 (4)
HD		8.710 (5)
LR*HD	pH	0 (7)
HD		0.710 (5)
Null		2.310 (4)
LR + HD		3.250 (6)
LR		5.080 (5)

Step 2 Inference by abduction			
Exogenous predictor	Endogenous predictor	Functional response	ΔAIC (K)
Herbs models			
LR	P	CWM.LA	0 (15)
		CWM.SLA	24.015 (15)
		CWM.LDMC	38.057 (15)
		FDis	6.610(15)
LR*HD	pH	CWM.LA	0 (21)
		CWM.SLA	41.071 (21)
		CWM.LDMC	32.957 (21)
		FDis	21.184 (21)
Shrubs models			
LR	P	CWM.LA	4.670 (15)
		CWM.SLA	18.819 (15)
		CWM.LDMC	50.864 (15)
		FDis	0 (15)
LR*HD	pH	CWM.LA	2.355 (21)
		CWM.SLA	49.399 (21)
		CWM.LDMC	0 (21)
		FDis	9.285 (21)

Table 2
Anthropic disturbance indexes and total abundance of characteristic and weed species, herbs and shrubs in the study plot. Study plots are distributed at three altitude levels: (high altitude = 2467–3449 m a.s.l., intermediate level = 3202–3446 m a.s.l., and low altitude = 3092–3122 m a.s.l). C: characteristic species, W: weeds.LR: Livestock raising index, HD: Habitat deterioration index, HA: Human activities index, and DI: general disturbance index obtained from the addition of LR, HA and HD. Negative values indicate low disturbance intensity, positive values indicate higher disturbance intensity.

		Anthropic disturbance index				Abundance			
						Herbs		Shrubs	
Plots	Altitude	LR	HA	HD	DI	C	W	C	W
P1	High	−11,32	0,31	47,02	36,02	83	128	4	187
P2	High	−21,33	3,42	38,7	20,8	102	102	8	213
P3	High	−14,79	−5,52	0,93	−19,38	31	193	12	120
P4	High	5,56	−5,68	22,29	22,18	50	194	27	33
P5	High	−21,81	−3,44	−37,32	−62,57	14	112	61	87
P6	Intermediate	7,76	5,46	−26,2	−12,99	168	243	111	58
P7	Intermediate	49,02	5,34	−18,35	36	160	182	92	76
P8	Intermediate	50,67	0,39	42,11	93,17	232	132	31	55
P9	Intermediate	−4,03	−2,57	18,51	11,9	346	297	96	57
P10	Intermediate	−18,49	0,65	−27,48	−45,33	42	66	140	87
P11	Low	4,98	−0,24	−21,85	−17,11	104	46	111	56
P12	Low	−19,67	−3,56	−36,35	−59,58	61	31	72	113
P13	Low	−11,74	1,41	−2,46	−12,79	81	86	87	84
P14	Low	−16,78	2,19	−40,1	−54,7	131	80	60	94
P15	Low	21,96	1,85	40,56	64,36	81	77	59	88

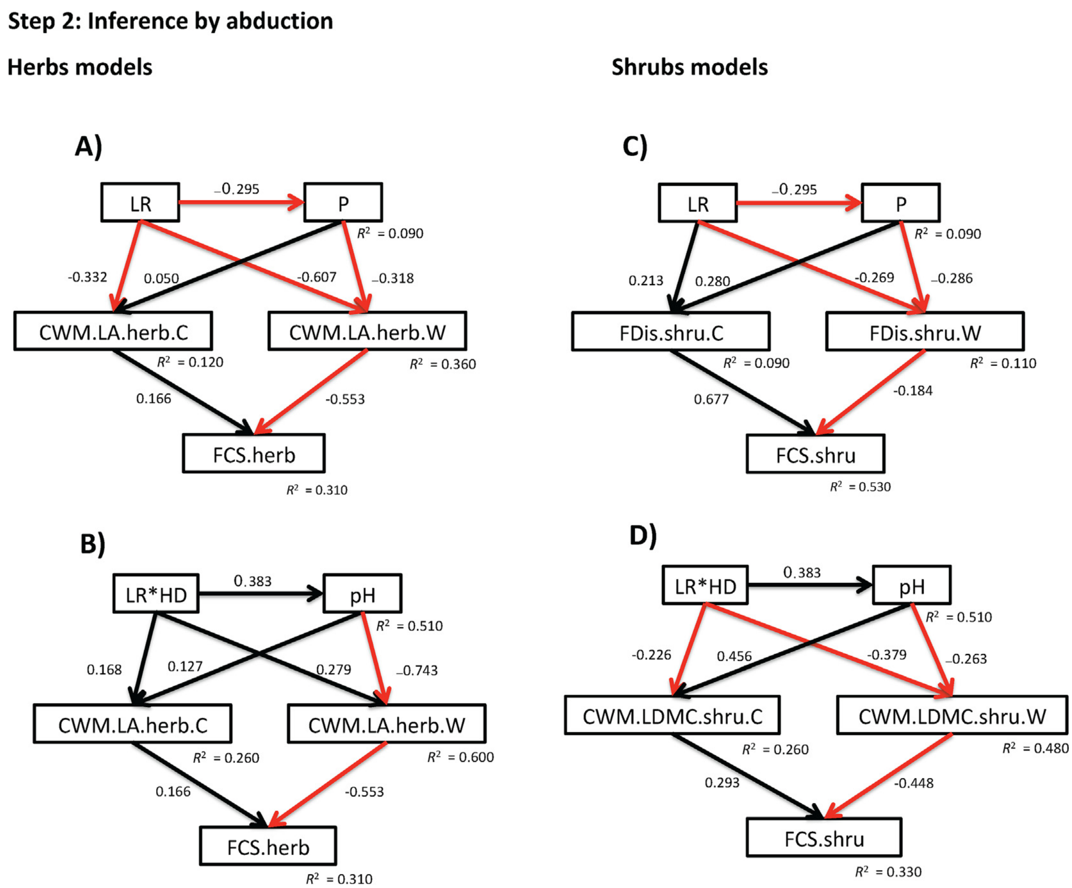

Fig. 4. Structural equation models selected according to the Akaike's information criterion (AIC). Models for herbs (A and B) and for shrubs (C and D). Red arrows represent negative effects, and black arrows represent positive effects. On the arrows, we show the standardized estimated values. The coefficient of determination (R^2) indicates the variance in the endogenous factors explained by the exogenous factors. LR: livestock raising index, HD: habitat deterioration index, P: available phosphorus in soil, pH: pH of soil, CWM.LA: community-weighted mean leaf area, CWM.LDMC: community-weighted mean leaf dry matter content, FDis: functional dispersion. FCS.her: index of favorable conservation status of herbs, FCS.shru: index of favorable conservation status of shrubs. Functional responses of characteristic species (C) and weed (W) species and herbs (herb) and shrubs (shru) species are included.

plausible LMMs with the smallest AIC (ΔAIC = 0; Table 3; Step 1).

3.2.2. Step 2. Abduction by inference

Table 3, Step 2 shows the AIC values of the functional responses. Particularly, for the herb and shrub species, we selected the best- supported SEMs with smallest AIC (ΔAIC = 0; Table 3; Step 2). For the herb species, the best-supported functional indicator was the community-weighted mean for leaf area (CWM. LA), and for shrubs, it was the functional dispersion (FDis) and community-weighted mean of the leaf dry matter content (CWM. LDMC) (Table 3; Step 2). These models show that livestock raising (LR) activities had a negative effect on soil P (Fig. 4; A and C). The interaction of LR with HD (habitat deterioration) showed a positive effect on soil pH (Fig. 4; B and D). Values higher than 0 were discarded because they did not represent the best supported model of the anthropic effect on the functional response.

3.2.3. Herbs models

The best-supported SEMs for herbs showed the negative effects of LR on the functional indicator of characteristic species (CWM.LA.herb.C) and weeds (CWM.LA.herb. W) (Fig. 4, A). The interaction of LR with HD showed positive effects for the functional indicator of characteristic species (CWM.LA.herb.C), as well as for weeds (CWM.LA.herb. W) (Fig. 4, B). In terms of the environmental variables, soil P and pH showed a positive effect on the functional indicators of characteristic species and negative effects on functional indicators of weeds (Fig. 4, A and B). Based on the effect of the functional indicators on composition, we observed positive effects of the functional indicator of characteristic species on FCS.herb and a negative effect of the functional indicator of weeds on FCS.herb (Fig. 4, A and B).

3.2.4. Shrubs models

The best-supported SEMs for shrub showed positive effects of LR on the functional indicator of characteristic species (FDis.shru. C), and negative effects on the weed indicator (FDis.shru.W) (Fig. 4, C). The interaction between LR and HD showed negative effects on the functional indicators of the characteristic species (CWM.LDMC.shru.C) and weeds (CWM.LDMC.shru.W) (Fig. 4, D). In terms of the environmental factors, soil P and pH showed positive effects on the functional indicators of the characteristic species and negative effects on the functional indicators of weeds (Fig. 4; C and D). Additionally, we found positive effects of the functional indicators of the characteristic species on FCS.shru and negative effects of the weed indicators on FCS.shru (Fig. 4, C and D).

4. Discussion

4.1. Implications of the development of functional indicators

Functional indicators are the key conceptual link to understanding the effect of anthropic activities on composition changes in communities (Tilman et al., 1997; Díaz et al., 2007; Mayfield et al., 2010; Song et al., 2014). Studies such as those by Lavorel and Garnier (2002) and Díaz et al. (2007) have proposed methodological strategies to determine the functional response of plant species, but few studies have applied such information in the development of functional indicators. To our knowledge, this study is the first to develop functional indicators that simultaneously respond to anthropic disturbance intensity and explain composition changes. Thus, the application of this method represents an excellent opportunity to understand the functional responses of weeds and to understand how their responses increase their establishment under anthropic perturbation conditions. This knowledge will improve predictions of anthropic effects at a functional scale (Funk et al., 2016).

The proposed method presents important theoretical implications. First, even though there is a common understanding in the scientific literature that anthropic disturbance modifies environmental variables, these modifications are rarely considered as change agents in species functional responses (Mayfield et al., 2010; Santibáñez-Andrade et al., 2015; Barton et al., 2016). Second, the anthropic effect on the functional response of species improve the resolution of functional indicators since the effect is quantified through the functional response of the species and not based on the categorization of composition (characteristic species and weeds) (Flynn et al., 2009; Mayfield et al., 2010). Finally, the development of functional indicators based on a causal path allows us to represent more accurately the complexity of the anthropic effect (Santibáñez-Andrade et al., 2015). Thus, it is possible to simultaneously determine the anthropic effect on the functional response of characteristic and weed species.

4.2. Functional indicators of a temperate forest

Over the last decades, the study of leaf attributes has allowed us to determine resource use strategies of species (Castro-Díez et al., 2002; Funk et al., 2017). Often, the success of the weed species under anthropic perturbation conditions has been related to a tendency to efficiently and rapidly acquire resources as represented by high values of leaf area (LA) and specific leaf area (SLA). These attributes allow high rates of nitrogen (N) assimilation during photosynthesis (Feng et al., 2008; Drenovsky et al., 2012). Nevertheless, most of this research has been conducted on herbaceous weeds, and very little is known about shrubby weeds (Funk et al., 2016). The results of this study are consistent with the empirical evidence since the indicator of herbs was the community-weighted mean of leaf area (CWM. LA). Additionally, in this study, we demonstrated that the functional response of shrub species is determined by the leaf dry matter content (CWM.LDMC). This scenario could be because shrub species have a slow life cycle that favors storing and conserving resources through thick leaves with a high content of dry leaf matter (Castro-Díez et al., 2002; Funk et al., 2016).

Under anthropic perturbations, weeds often show a higher variety of different functional responses than characteristic species (for example, a higher leaf and root area, Drenovsky et al., 2012; Ordoñez et al., 2010; Feng et al., 2008). Conversely in this study, livestock raising activities (LR) and habitat deterioration (HD) showed similar negative effects on the functional indicators of characteristic and weed species. This result matches the research reported for other temperate forests, where livestock raising activities and road establishment equally affect the establishment of characteristic and weed species (Ghazoul et al., 2015; Santibáñez-Andrade et al., 2015). However, it is important to note that the interaction of LR and HD had a positive effect on the functional indicators of herbs. This result was probably due to the synergistic effect of both activities in the promotion of vacant areas with a high availability of resources that are quickly used by understory species (Mihók et al., 2005).

At present, anthropic effects on the environment represent one of the main causes of plant diversity loss (Mayfield et al., 2010). In this study, we showed that LR and its interaction with HD promoted a reduction in available P and an increase in soil pH. This situation is most likely due to cation release during the mineralization of cattle manure, which increases soil pH and favors P precipitation in unavailable forms for plants (Dorrough et al., 2006; Trejo-Escareño et al., 2013). Additionally, the values of soil P and pH were similar to those reported in other disturbed areas of this forest (P; 2 a 30 ppm, pH; 5–6.9; Santibáñez-Andrade et al., 2015). Soil P and pH showed positive effects on the functional indicators of characteristic species, suggesting a tendency to maximize resource acquisition in herb species (higher LA) and to maximize resource conservation in shrub species (higher LDMC) (Feng et al., 2008). In contrast to what was expected, environmental modification of soil P and pH had negative effects on the functional tendencies of weeds. Similarly, several authors, such as Drenovsky et al. (2012), have proposed that the limitation of the leaf functional response of weeds can be compensated by the presence of deeper roots that favor nutrient absorption from soil.

Community assembly after an anthropic disturbance depends on characteristic species that survive as well as on the weeds that colonize the site (Burns, 2006; Mayfield et al., 2010). Thus, communities are integrated by species that are functionally similar, with attributes that allow them to cope with the conditions that are produced by anthropic disturbances (Hernández-Vargas et al., 2019). In this study, LR activities and changes in soil P promoted a decrease in the functional dispersion (FDis) of shrubby weeds. This result suggests a functional convergence effect and the selection of attributes that make species tolerant to perturbation (Richardson et al., 2000; Castro-Díez et al., 2012). However, LR and soil P had positive effects on the FDis of shrub characteristic species. This result suggests an effect of divergence and functional dissimilarity. Authors such as Liu et al. (2016) have demonstrated that the high leaf plasticity of characteristic species in temperate forests can promote a wide range of leaf variation even under perturbation conditions.

Functional attributes directly determine species fitness in a certain environment, which is why they directly contribute to community composition (Mayfield et al., 2010). In this study, we demonstrated in a simultaneous way that leaf functional responses of characteristic species contribute in a positive way with a favorable composition and that weed species contribute in a negative way with a favorable composition. In addition, it is possible that some changes are promoted in the representation of functional attributes due to weed colonization (Feng et al., 2008; Drenovsky et al., 2012; Helm et al., 2015).

4.3. Scope of the inference method by abduction and statistical methods

Authors such as Funk et al. (2017) have noted that the lack of functional indicators is a consequence of the absence of standardized methods capable of handling the complexity of the anthropic effects. Additionally, in different studies, research on functional responses has been an exhaustive and complex search (Niemeijer and de Groot, 2008; Lin et al., 2009). Thus, the main strength of the inference by abduction method is the integrated evaluation of anthropic effects and the practical detection of functional indicators. However, it is important to take into account that the selection of these indicators is based on preselected variables and attributes; thus, its application in future research requires previous knowledge of the study area. Inference by abduction only detects the functional indicators that connect the best causal path of the anthropic effects on composition; therefore, it is possible that other relevant attributes for survival and establishment of the species could remain unidentified.

This study demonstrated that structural equation models (SEMs) represent a good approximation to estimate the causal relations during the development of functional indicators. Similarly, several studies have demonstrated the application of SEM to evaluate causal relations of anthropic effects at the community level (Santibáñez-Andrade et al., 2015; Fan et al., 2016). Specifically, the piecewiseSEM package represents an adequate statistical tool because it allows modelling variables with a distribution different from the Gaussian (through generalized linear models, GLMs; Bolker et al., 2009; Lefcheck, 2016). In addition, this package allows the comparison and selection of models under the Akaike information criterion (AIC), thus avoiding the issues associated to the use of *P*-values (Burnham and Anderson, 2002). However, depending on the nature of the data, we recommend exploring other statistical tools, such as the Bayesian information criterion, which has also been demonstrated to evaluate successfully functional diversity in hierarchical structures (Funk et al., 2017), and the RLQ analysis, through which it is possible to evaluate causal relationships with categorical data (Dray et al., 2014).

4.4. Final considerations

We suggest applying the proposed method when changes in composition driven by the establishment of weeds are identified, since there are scenarios in which anthropic disturbances do not promote the establishment of weeds. This situation can occur when anthropic disturbances are recent or when they occur at a low intensity, similar to that of some natural disturbances, which allow the recovery of the system (Lin et al., 2009; Daehler, 2003; Niemeijer and de Groot, 2008).

It is important to mention that composition changes can be different among ecosystems. In temperate forests, it has been demonstrated that the anthropic effect on the changes of soil chemical properties promotes a high abundance of weeds (Bonilla-Valencia et al., 2017; Hernández-Vargas et al., 2019). In tropical forests, anthropic effects on light availability seem to affect increases in richness and diversity of weeds (Poorter et al., 2008; Lohbeck et al., 2013). The interpretations of the functional patterns can be different between ecosystems. For example, anthropic activities that cause a loss of soil moisture in temperate forests are the main factors that drive functional convergence (Hernández-Vargas et al., 2019). In dry ecosystems, such as xerophytic shrublands, low moisture regimes cause functional convergence, even in the absence of anthropic perturbation (Poorter et al., 2008; Lohbeck et al., 2013). Therefore, we suggest a rigorous interpretation of the functional indicators based on the study system.

5. Conclusions

The development of functional indicators by the method of inference by abduction allowed us to learn in a simultaneous way the functional responses of the characteristic and weed species under anthropic perturbation conditions. This method represents a methodological advance that will improve the prediction of the anthropic impact at the functional and composition levels. Through the suggested method and with the development of functional indicators, we demonstrated that the anthropic effects on soil P and pH act in different ways in characteristic and weed species in terms of leaf strategies for the acquisition and conservation of resources. The results of this study suggest that the functional responses of weeds are associated with acquisition strategies, while shrubby weeds favor the conservation of resources. This study also showed that the development of functional indicators allows improving our knowledge on the functional responses that promote the establishment of weeds under conditions of anthropic perturbation. This knowledge will allow the prediction of the colonization potential of weeds and their effects at a functional level.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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