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The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*

Carlos Martorell [a,*], Edward M. Peters [b]

[a] *Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, México, DF 04510, Mexico*
[b] *Dirección General de Investigación de Ordenamiento Ecológico y Conservación de los Ecosistemas, Instituto Nacional de Ecología – SEMARNAT, Mexico*

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Abstract

Measuring how anthropogenic disturbance affects biological systems is crucial for conservation and management. However, it is often difficult to quantify disturbance when it occurs in a slow, long-lasting – or chronic – fashion. Because various human activities influence gradually an area, chronic disturbance must be measured on a continuous scale that accounts for different sources of disturbance. Here we propose a method to develop multimetric indices for chronic disturbance. The approach is exemplified by considering the effects of disturbance on the threatened cactus *Mammillaria pectinifera*. Fourteen indicators of three agents of disturbance (human activities, livestock raising and land degradation) were measured in 10 populations of *M. pectinifera*, and summarised through principal components analysis (PCA). An index for each agent was also developed. *M. pectinifera* achieved maximum density at intermediate values of the first PCA axis, which was related to disturbance intensity. Assessing only both extremes of the disturbance gradient, where density is low, would erroneously suggest that disturbance has no effect on this plant. The different disturbance agents act synergistically on *M. pectinifera*, and their combined effects are detrimental. Land degradation reduces plant density, while livestock enhances it. However, overgrazing promotes degradation, so maintaining appropriate livestock levels is critical for management. Our method allowed us to identify which agents have more impact on threatened species, and sets the basis to manage disturbance agents in a way compatible with conservation. The method proposed here can be easily modified for its use in other environments and to account for different forms of anthropogenic disturbance.

Keywords: Methods; Overgrazing; Land use; Land degradation; Density; Multimetric indices

1. Introduction

An understanding of anthropogenic disturbance and its effects on natural systems is needed in order to preserve wildlife (Phillips, 1997; Watt, 1998; Karr, 1999), restore communities (Cairns, 1987), and achieve sustainability (Kates et al., 2001). This is of especial relevance in regions where species replacement among sites (β-diversity) is so large that it is impossible to shelter all the taxa in protected areas (Toledo, 1988). In addition, there are several species endemic to small areas that are already exposed to human activities. As farther areas become disturbed, there appears to be no choice but to preserve diversity in the presence of man.

It is easy to tell a disturbed ecosystem when it has been turned into pasture for cattle or completely cleared; however, such utter transformations do not always take place. Several traditional forms of ecosystem management are based on the extraction of small amounts of resources at a time, and therefore they are not expected to

* Corresponding author. Tel.: +52 55 5622 4835.
E-mail address: martorel@miranda.ecologia.unam.mx (C. Martorell).

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inflict sudden and complete changes in the environment (Reichhardt et al., 1994; Toledo et al., 1994). This chronic form of disturbance has been acknowledged as the most widespread form of environmental destruction in developing countries, where it may be as destructive as other faster-acting forms of disturbance since its effects may be non-linear and cumulative (Singh, 1998; Rapport and Whitford, 1999; Gunderson, 2000). For example, chronic grazing has been found to set off catastrophic, irreversible shifts that result in barren lands (Van de Koppel et al., 1997; Scheffer et al., 2001).

The literature on the effects of human disturbance is vast, but a large proportion of it deals with acute (as opposed to chronic) forms of disturbance. These are more easily handled because they are readily detected and give way to a clear dichotomy between what is disturbed and undisturbed. Chronic disturbance, on the contrary, creates a gradient between pristine and heavily degraded sites, and therefore it needs to be measured on a continuous, rather than dichotomic, scale (Watt, 1998). There are three "types" of methods used to measure the amount of disturbance in a community:

A. *Expert-based methods* rely on the capability of the trained eye to assess the amount of disturbance experienced by a given area (Rawat, 1997; Eggleton et al., 2002; Bojórquez-Tapia et al., 2003). These methods frequently render binary (disturbed vs. undisturbed) or ordinal scales.
B. *Biotic indicators* measure disturbance through its effects on one species (e.g., Gill et al., 1996), a taxonomic group (Read and Andersen, 2000; Andersen et al., 2001; Hill et al., 2002), or on one attribute of the community (Hamer et al., 1997; Basset et al., 1998; Colville et al., 2002). Indices of Biotic Integrity and Authenticity are based on several metrics such as community composition and structure (Karr, 1999; Forest Innovations, 1999). These methods face limitations due to three inconveniences. First, different intensities, scales and kinds of disturbance are likely to have different effects on ecosystems (Mensing et al., 1998; Watt, 1998), thus the choice of certain biological indicators may set aside forms of disturbance that have a substantial impact on other components of the community. Second, they are not appropriate when the goal is to measure the effects of disturbance on some species or the community, since the effects themselves are already used as an estimator of the cause, leading to tautology. Third, in heterogeneous areas the biota responds to several factors besides disturbance, so the effects of both sources of variability become confused.
C. *Human activity indicators* are mainly represented by remote sensing techniques, which employ land use, fragmentation, or proximity to towns and roads as measurements of disturbance (e.g., Harding et al., 1998; Hill et al., 2002; Liley and Clarke, 2003; Crooks et al., 2004). Government statistics on population, agriculture, forestry, etc. have also been used as disturbance metrics (e.g., Ribic et al., 1998; Liley and Clarke, 2003). A few authors have used measurements of the factors causing disturbance in the field (Kaiser et al., 2000; Ramírez-Marcial et al., 2001; Williams-Linera, 2002; Bhuyan et al., 2003). This group of indicators overcomes most of the problems we have pointed earlier.

A type-B method is particularly unsuitable for drylands, which are quite heterogeneous environments. This is the case of the semi-arid Tehuacán Valley, Mexico. The area has a long history of human occupancy (Byers, 1967) and a large peasant population at present, resulting in a complex mosaic of differently disturbed patches. The main causes of chronic disturbance in the area are extensive grazing, agriculture, and extraction of uncultivated products. Such processes have menaced several unique communities and endemic species. Among the latter is the threatened globose cactus *Mammillaria pectinifera* (Anderson, 1990; Hunt, 1999; SEMARNAT, 2002; CITES, 2003).

Mammillaria pectinifera has suffered from looting for commercial purposes in the past. All of the sites where this plant grows are exposed to some degree of chronic disturbance, and some are very heavily degraded (Anderson, 1990). However, this cactus is frequently observed occurring in large numbers on lightly eroded soil patches at all sites, so that a moderate amount of disturbance may be beneficial to the species. *M. pectinifera* is therefore an interesting system for the study of the effects of chronic disturbance, both because of its status and its large range of exposure to human activities.

In this paper we will develop a type-C method for the measurement of chronic disturbance on a small enough scale comparable to the sizes of the populations of some endangered species. In the study area, disturbance involves multiple agents and the method accounts for them by yielding a multivariate index similar to IBIs and authenticity indices. We will also explore the adequacy of the index to reflect the condition of the populations of the threatened *M. pectinifera.*

2. Methods

All study sites were located in the northern portion of the Tehuacán Valley, State of Puebla, Central Mexico, on gently sloping areas at altitudes between 1740 and 2280 m. Climate is semi-arid, so all sites are susceptible to the cumulative effects of chronic disturbance. Vegetation was submontane scrub, a semi-evergreen community typical of cool, dry areas. The 10 sites where *M. pectinifera* was known to grow were sampled. All the locations, except Tecamachalco, El Riego and Texcala, were probably not known to looters. The areas where looting took place at these three sites are presently cornfields at El Riego, and devoid of plants at Texcala, so we worked in nearby areas of difficult access that were probably not previously known. This means that the effects of illegal extraction of plants are negligible in our study.

The areas of the 10 populations were delimited and sampled by means of randomly placed 100×1 m – transects. More transects were used when the total area was larger. All *M. pectinifera* individuals within the transect were recorded.

The most important disturbance agents in the area are livestock raising, diverse human activities, and land degradation. In order to measure the contribution of each agent to chronic disturbance, fifteen metrics were recorded at every site by means of six 50 m long transects at each site. Three of them were placed parallel and three perpendicular to the slope, forming three crosses. In the following list, metrics that were recorded in transects parallel to the slope are identified with an asterisk. The letters in parentheses will be used as the abbreviated names of each metric in the remainder of the paper.

Livestock raising

1. Goat droppings frequency (GOAT): Ten randomly chosen 1 m^2 squares along the transect were checked for goat dung. Frequency was defined as the fraction of squares with positive records.
2. Cattle droppings frequency (CATT): As GOAT, but recording bovine and equine dung.
3. Browsing (BROW): All shrubs and trees (except *Agave*) that were rooted within the transect were thoroughly examined for signs of browsing. The ratio of browsed to total plants was calculated as an index of browsing intensity. Since there are virtually no wild browsers in the area, most of the marks in the plants can be attributed to livestock.
4. Livestock trail density* (LTRA): Livestock uses well-defined trails to move while browsing. The number of these per meter along the transect was recorded.
5. Soil compaction (COMP): The constant trampling of livestock along tracks causes soil compaction, which affects water infiltration. A cylinder of 10.4 cm of diameter was driven 4 cm into the ground with the help of a hammer in a randomly chosen trail. 250 ml of water were then poured in the cylinder, and the time needed for complete infiltration was recorded. This procedure was repeated on a spot with no evidence of trampling. The degree of soil compaction was calculated as the ratio of the time recorded on the trail and in the untrampled terrain.

Human activities

6. Fuelwood extraction (FUEL): Peasants usually cut branches for their use as fuelwood. This metric was measured as BROW, but taking machete cuts into account.
7. Human trails density (TRAN): TRAN is measured as *LTRA*, but recording those trails that are used by people to travel. Livestock may use human trails too, but the opposite is infrequent.
8. Human trails surface* (TRAS): The trails more frequently used by people are usually wider, and therefore cover a larger fraction of the soil surface. This was measured by means of the line intercept method.
9. Settlement proximity (PROX): The areas far from human settlements are rarely visited, and therefore could be less disturbed. Proximity was defined as the multiplicative inverse of the distance to the closest towns in km.
10. Contiguity to activity cores (CORE): A core was defined as a place where human activities normally take place, such as houses, cornfields, mines or chapels. It is from these cores that the peasants may exert their influence on the environment. Contiguity was recorded at each transect if a core was less than 200 m away. The fraction of transects contiguous to a core was used as a metric. The same core was not counted twice, even if contiguous to two different transects.
11. Land use (LUSE): In several studies the percent of land cover devoted to agriculture, cultivated or induced pastures, or urban areas is used as a measure of disturbance. Here, the fraction of the study area used for these purposes was visually estimated.
12. Evidence of wildfires (FIRE): Most of these are initiated by people, either to clear an area, promote pasture growth for livestock, or accidentally. The presence or absence of evidence at a study site was recorded as one or zero.

Land degradation

13. Erosion (EROS): Overgrazing and human activities increase hydric erosion. Measuring it in the field is difficult, thus we only considered spots where the soil showed tracks of strong and frequent removal of material by water (such as ravines) as unequivocal evidence of erosion. Twenty points were selected randomly along the transect for its estimation, and the fraction of eroded spots was recorded.
14. Presence of soil islands (ISLA): When severe erosion takes place, soil is only held where large shrubs are rooted. As a result, a landscape of small

mounds can be observed. The presence or absence of these "islands" was recorded either as one or zero.

15. Totally modified surfaces (TOMS): Land may be so severely modified that measuring most of the previous metrics makes no sense, as it can happen on a paved road, a house, or on artificial waterways. When the transect crossed such surfaces, their cover was measured by means of the line intercept method.

Some of these metrics have been previously used to measure disturbance, such as LUSE (e.g., Harding et al., 1998; Hill et al., 2002; Liley and Clarke, 2003; Crooks et al., 2004), TRAN (Trombulak and Frissell, 2000; McGarrigal et al., 2001), FUEL, FIRE, CATT, and BROW (Ramírez-Marcial et al., 2001). The data were standardised and combined into a single index through a principal components analysis (PCA) performed on SPSS 9.0.

Prior to conducting the present study, each of the authors independently assigned an a priori, subjective measure of disturbance to each site in an ordinal scale. Ranks were assigned to each site, and when the opinions differed (as it happened in two pairs of localities) a tie was declared and the mean rank was assigned to the controversial sites. This subjective measurement was compared with the PCA scores by means of Spearman's rank correlation (Conover, 1980). This allowed us to verify if the resulting disturbance index had any agreement with the subjective appraisals characteristic of type-A methods.

A log-linear regression was performed on density (individuals per transect of 100 m^2) with PCA scores as independent variable. The data were collected in different months, so the number of seedlings may show strong variations as a result of seasonal recruitment and mortality. To avoid this problem, plants smaller than 4 mm were excluded from the analyses. The significance of a quadratic term was assessed in order to account for possible beneficial effects of moderate amounts of disturbance.

The PCA score of a site is a linear combination of the values recorded for each metric. This allows us to calculate an index for each disturbance agent by adding only the respective linear terms (see the above list). The sum of these indices equals the PCA score, so they reflect the contribution of different forms of disturbance in a location. *M. pectinifera* density was log-linearly regressed on these three indices along with their quadratic terms and interactions. We used the partial derivative of the fitted function with respect to each index as a measure of the sensitivity of *M. pectinifera* to different disturbance agents. The value of the three partial derivatives was calculated for each site and plotted against the PC1 to evaluate whether sensitivity changes with disturbance.

3. Results

All the metrics showed variation among sites, with the exception of FIRE. There was no evidence of wildfires except at one site. As we had no replicates, and the density at one site may be affected by a plethora of factors besides fire, this metric was considered uninformative and was excluded from the analysis.

Some degree of positive correlation was found among most metrics. However, it must be noted that several negative correlation coefficients were obtained from the data, especially when the variables CATT and COMP are compared to others (Table 1). Human activities had the lowest average correlation among them and with the other agents, while land degradation and livestock raising were more strongly correlated (Table 2).

The first two principal components accounted for 29.6% and 19.5%, respectively, of the total variance

Table 1
Correlation between individual metrics

	GOAT	CATT	BROW	LTRA	COMP	FUEL	TRAN	TRAS	PROX	CORE	LUSE	EROS	ISLA	TOMS
GOAT		*0.04*	*0.34*	*0.16*	*0.27*	*0.30*	*0.29*	*0.80*	*0.97*	*0.65*	*0.45*	*0.45*	*0.12*	*0.14*
CATT	−0.58		*0.67*	*0.85*	*0.11*	*0.10*	*0.70*	*0.80*	*0.27*	*0.12*	*1.00*	*0.24*	*0.06*	*0.32*
BROW	0.29	−0.13		*0.12*	*0.26*	*0.45*	*0.20*	*0.58*	*0.35*	*0.27*	*0.09*	*0.23*	*0.27*	*0.82*
LTRA	0.41	0.06	0.45		*0.45*	*0.72*	*0.97*	*0.97*	*0.95*	*0.58*	*0.62*	*0.62*	*0.30*	*0.02*
COMP	−0.33	0.46	−0.34	0.23		*0.20*	*0.34*	*0.45*	*0.07*	*0.04*	*0.07*	*0.65*	*0.60*	*0.26*
FUEL	0.31	−0.48	0.23	0.11	−0.38		*0.35*	*0.30*	*0.04*	*0.19*	*0.97*	*0.09*	*<0.01*	*0.18*
TRAN	−0.32	0.12	0.38	0.01	0.29	−0.28		*0.87*	*0.87*	*0.29*	*1.00*	*0.58*	*0.77*	*0.58*
TRAS	0.08	−0.08	0.17	−0.01	−0.23	0.31	0.05		*0.01*	*0.70*	*1.00*	*0.47*	*0.72*	*0.85*
PROX	0.01	−0.33	0.28	−0.02	−0.51	0.57	−0.05	0.67		*0.19*	*0.75*	*0.90*	*0.43*	*0.77*
CORE	0.14	−0.45	0.33	−0.17	−0.58	0.39	0.32	0.12	0.39		*0.30*	*0.80*	*0.19*	*0.45*
LUSE	0.23	0.00	0.49	0.15	−0.52	0.01	0.00	0.00	−0.10	0.31		*0.60*	*0.77*	*0.80*
EROS	0.23	−0.35	0.36	0.15	0.14	0.49	0.17	−0.22	−0.04	0.08	−0.16		*<0.01*	*0.11*
ISLA	0.45	−0.53	0.33	0.31	−0.16	0.77	−0.09	−0.11	0.24	0.39	−0.09	0.74		*0.06*
TOMS	0.43	−0.30	0.07	0.65	0.34	0.40	−0.17	−0.06	−0.09	−0.23	−0.08	0.46	0.53	

Numbers in romans are correlation coefficients, and significance is in italics.

Table 2
Average correlation coefficients within and among the three different agents of disturbance

	Livestock	Human activities	Land degradation
Livestock	0.38		
Human activities	0.13	0.18	
Land degradation	0.33	0.07	0.58

Table 3
Metric loadings for the first two principal components

	PC1	PC2
Livestock		
GOAT	0.64	−0.20
CATT	−0.72	−0.06
BROW	0.54	0.11
LTRA	0.32	−0.54
COMP	−0.52	−0.71
Human activities		
FUEL	0.83	0.01
TRAN	−0.12	0.07
TRAS	0.24	0.46
PROX	0.51	0.53
CORE	0.54	0.54
LUSE	0.21	0.34
Land degradation		
EROS	0.55	−0.52
ISLA	0.83	−0.35
TOMS	0.45	−0.76

and were significant (Jackson, 1993). The loadings of most variables for the first principal component were positive, with the exception of CATT, COMP and TRAN. The loadings for the second axis were negative for the metrics related with livestock and land degradation, but positive for human activities (Table 3). The scores of the sites were uniformly distributed on both principal components, without any strong discontinuity or clustering of sites (Table 4). The ordination of sites along the first principal component corresponded closely with that made a priori by the authors ($\rho = 0.980$).

Table 4
Scores of the sites on the first two principal components, and contributions of human activities (HA), livestock raising (LR) and land degradation (LD) to the first principal component

Site	PC1	PC2	HA index	LR index	LD index
Azumbilla	−0.75	0.30	−0.30	−0.25	−0.20
Coapan	1.15	0.75	0.59	0.13	0.43
El Riego	0.36	−0.44	−0.38	0.26	0.48
Frontera	−1.93	−0.22	−0.33	−1.13	−0.47
Nopala	−0.63	0.40	−0.07	0.02	−0.57
Tecamachalco	1.54	0.31	0.78	0.47	0.29
Teontepec	0.58	−2.60	−0.35	0.15	0.78
Teteletitlán	0.33	0.92	−0.05	0.75	−0.37
Texcala	−0.03	0.72	−0.05	−0.01	0.02
Zapotitlán	−0.63	−0.15	−0.37	−0.05	−0.22

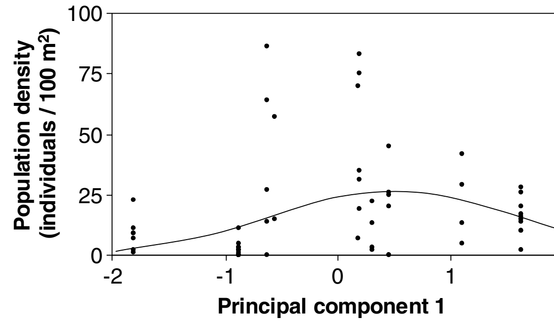

Fig. 1. Density of *Mammillaria pectinifera* as a response to PC1 ($R^2 = 15.32\%$).

Table 5
Log-linear regression of *M. pectinifera* density on the indices for the three disturbance agents

Source	χ^2	df	p	Variance explained
LR	41.01	1	<0.0001	23.97%
LR^2	15.97	1	0.0001	9.33%
HA^2	32.60	1	<0.0001	19.05%
LR × HA	31.47	1	<0.0001	18.39%
LD × HA	25.17	1	<0.0001	14.71%

Non-significant terms were dropped form the analysis. LR: livestock raising, LD: land degradation, HA: human activities. $R^2 = 53.06$.

Density of *M. pectinifera* responded to disturbance as measured through the first principal component (regression's $\chi^2 = 11.69$, $p = 0.0029$). The maximum density was recorded at a PC1 value of 0.519, and it decreased with lower or higher values (Quadratic term's $\chi^2 = 7.428$, $p = 0.0064$, Fig. 1). The three disturbance agents were found to affect significantly *M. pectinifera* density and to interact among them (Table 5). The fitted function was too complex and its shape changed strongly depending on slight shifts in the combination of different disturbance agents. However, within this variability surfaces with two maxima were frequent as a result of positive quadratic terms and negative interaction terms (Fig. 2). Large densities were commonly achieved when only one form of disturbance was present, but not when two or more occurred in large amounts.

Land degradation always had a negative impact on *M. pectinifera* density, with an average sensitivity of −3.30. On the contrary, livestock had a large beneficial effect (average sensitivity of 11.25). Human activities had both positive and negative impacts on cactus number (average sensitivity of 2.18). Sensitivity increased as disturbance grew, becoming more negative for land degradation ($R^2 = 0.684$) and more positive for livestock ($R^2 = 0.474$). No pattern was observed for human activities, whose impact over the whole disturbance gradient did not show any trend ($R^2 = 0.030$, Fig. 3).

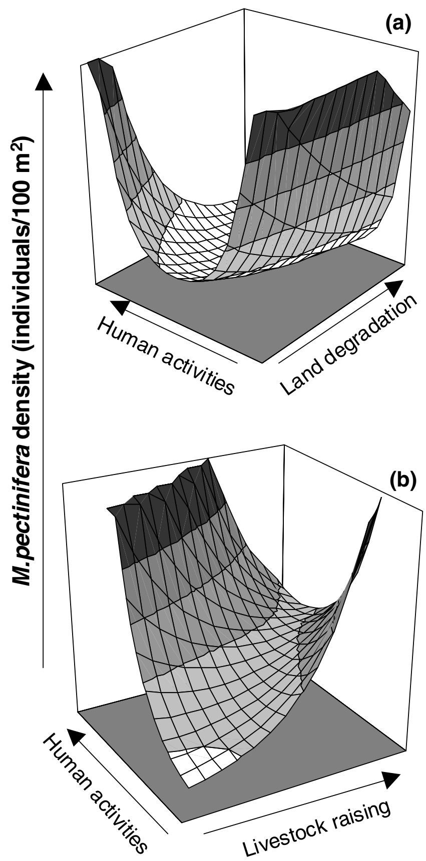

Fig. 2. Effect of the three disturbance agents on *Mammillaria pectinifera* density. Two examples of the form of the response surface under (a) heavy grazing and (b) without land degradation. Note that the axes are different for both graphs (R^2 = 53.06%).

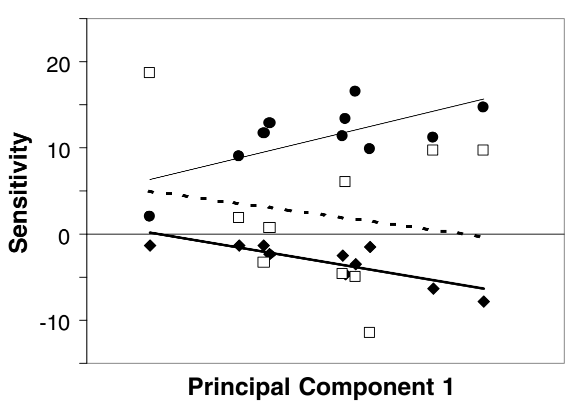

Fig. 3. Sensitivity of *Mammillaria pectinifera* to the different disturbance agents along PC1. - - -□- - - human activities, –●– livestock raising, –◆– land degradation.

4. Discussion

Most of the different metrics used in this study were positively correlated among them. This is in agreement with the concurrent nature of chronic disturbance agents proposed by Singh (1998), and suggests that metrics may be adequately summarised in a single index through PCA. However, the correlation coefficients were modest, revealing considerable independent variation among metrics. These were not redundant, and none was fully capable of reflecting the values of the remainder. This situation supports the idea that a multimetric index as the one proposed here is needed to describe correctly the status of the system.

Most loadings on the first principal component were large and positive, indicating that positive values on this axis corresponded to large values on most metrics, and therefore to high anthropogenic pressure. Larger PC1 scores corresponded to more disturbed sites. This is in agreement with the very high correlation between the site scores and our subjective, a priori disturbance appreciation. Therefore, throughout the following text we will refer to the score of each site on the first component as the disturbance index. The same reasoning applies to the indices of livestock raising, human activities, and land degradation.

The largest loadings corresponded to FUEL, ISLA, GOAT, EROS, BROW, CORE and PROX. These metrics represent the three agents of disturbance, stressing the importance of multiple factors in chronic disturbance. COMP and CATT had large negative loadings, maybe as the result of the practice of setting bovines and equines loose for months in remote areas with abundant vegetation. Thus, their presence is an indicator of relatively well-preserved areas. Cattle compact the soils more heavily than goats or sheep (Heady and Child, 1994), so COMP may be also an indicator of cattle presence. At heavily disturbed sites, livestock transit is diluted among several trails causing less compaction in each one. In both cases, COMP would be smaller under high disturbance regimes.

The two least disturbed sites according to the index, Frontera and Azumbilla, are areas with well-developed scrubs and native fauna such as deer. In contrast, the two sites with the largest disturbance indices have suffered urbanisation and replacement of scrubs by pasture in Tecamachalco, and the building of a city dump at Coapan.

The second principal component seems to be related to disturbance quality instead of quantity. As it can be appraised from the signs of the loadings, positive values correspond to human activities, and negative ones to livestock raising and the consequent land degradation. This agrees with the three disturbance agent indices. PC2 and the human activities index have a correlation of 0.45, while the correlation between PC2 and land degradation is −0.55.

Mammillaria pectinifera responded to disturbance intensity as measured through the multimetric index presented here. Density reached its highest values at sites with intermediate disturbance. A mere comparison of the least and the most degraded sites would not have shown any effect of disturbance on this plant, since densities are small at both localities (Fig. 1). The disturbance gradient must be sampled in order to appreciate fully the behaviour of *M. pectinifera* in the presence of man.

Our results suggest that *M. pectinifera* may only tolerate different agents of disturbance simultaneously if they are present in small amounts, but only one agent if it is severe (Fig. 2). The various disturbance agents act synergistically, so their combined effects are more detrimental than the sum of their individual influences (i.e., there are significant interactions between them, Table 5). The fact that *M. pectinifera* responded in a similar way to livestock and human activities, increasing its density at intermediate intensities, appears to be the result of some degree of equivalence between the two agents. Both of them reduce shrub cover, produce some erosion, affect the soil, and are related to trails. Because of the metrics we chose, the land degradation index connoted severe deterioration, so that its presence was always negative for *M. pectinifera*. However, these results must be interpreted carefully. Since we had only 10 populations, several of the possible combinations of the three disturbance agents were not observed in the field, and large portions of the fitted surface shown in Fig. 2 are extrapolations.

Our sensitivity analysis showed that *M. pectinifera* was affected in a different way by each disturbance agent. Land degradation was detrimental, but livestock increased cactus density. The fact that sensitivity to the land degradation index (i.e., the rate of change in density) increased with disturbance means that the effects of land degradation showed a non-linear, accelerating behaviour (Singh, 1998; Kercher and Zedler, 2004). Managers should be especially concerned about populations of *M. pectinifera* suffering erosion, since this process may lead to their rapid disappearance.

Livestock, on the contrary, was beneficial to *M. pectinifera*. This may be the result of the environmental requirements of this plant. Unlike other cacti, it is not associated to nurse plants (Rodríguez-Ortega and Ezcurra, 2001), but it occurs in soils covered by stones and gravel (Zavala-Hurtado and Valverde, 2003). Domestic animals may both reduce shrub cover and promote stoniness through increased superficial erosion. However, overgrazing seems to be closely related to land degradation as suggested by the loadings of PC2. Livestock may then have a negative indirect impact on *M. pectinifera* density if it is very intensive. The reason for the low densities of this plant when disturbance is absent may be low microhabitat availability, while intolerance to land degradation seems responsible for low densities under intense disturbance regimes.

This small cactus may be classified as a ruderal in the sense of a plant "living or thriving on disturbed sites" (Morris, 1992). This does not mean that it shares the life-history attributes of ruderals sensu Grime (1979), such as massive seed production and short life spans. However, within the Cactaceae, the population dynamics of *M. pectinifera* relies largely on reproduction as measured through elasticity. It nearly doubles the largest value reported for cacti (0.106 vs. 0.059 for *Coryphanta robbinsorum*, Godínez-Álvarez et al., 2003; Peters and Martorell, unpublished data). In the field we observed large numbers of seedlings. Also, globose cacti usually have shorter life spans than other plants in the same family. Thus it seems that *M. pectinifera* is closer to the corner of ruderals in Grime's triangle than other cacti, which has two important consequences for conservation:

First, the complete removal of human activities from the system is likely to reduce some of the populations of this species. Extreme disturbance, on the contrary, may lead to extinction. A rational form of use of the land is not only compatible with, but also desirable for the preservation of this threatened cactus. In particular, maintaining livestock numbers at an appropriate level seems crucial. We must bear in mind that wild ungulates were much more abundant in the past. If grazing is excessive and land degradation occurs, an accelerating reduction in this cactus density may initiate.

Second, while *M. pectinifera* may behave more ruderally than other cacti, it is still far from being a weed. This means that it may not respond to disturbance or colonise new areas as quickly. Xeric communities usually recover from disturbance at a slow pace (e.g. Belnap, 1995; Milton and Dean, 1995; Valone et al., 2002), so disturbed sites may remain available for larger periods. Under these conditions, plants adapted to disturbance would not necessarily be as short lived or make such large investments in reproduction as it happens in more mesic habitats. It has been argued that some traits of *M. pectinifera* may prevent fast, long distance dispersal (Zavala-Hurtado and Valverde, 2003). If so, this species may be unable to track properly the fast changes that characterise anthropogenic landscapes. If changes are too fast, a site suitable for this cactus may become inappropriate before it is colonised or before a viable population that serves as a source for the colonisation of other sites is established. Promoting colonisation of patches with the appropriate levels of disturbance should be priority in management practices.

It is common to presume that man has a negative effect on threatened species. While this assumption may be based on sound theory, it may not hold within certain disturbance-intensity ranges or under some disturbance regimes. Failing to recognise this may lead to unfit management decisions. A plan to preserve a ruderal plant should ponder which disturbance agents benefit the species, how they interact among them, and their impact on metapopulation dynamics. Some of the guidelines proposed here are examples of this approach. For non-ruderals, focus should be on their tolerance or susceptibility both to overall disturbance and to specific disturbance agents in order to direct conservation efforts more efficiently.

The regulation of disturbance is as important for conservation as the direct management of the species. Prescribed fire is an example of how such practices become essential for conservation. However, when it comes to anthropogenic disturbance its complete elimination is frequently the only management practice. Human influence may also be disguised in the shape of natural disturbance to minimise its impact (Hansen et al., 1991; Niemelä, 1999). It could be argued that livestock is beneficial to *M. pectinifera* because it resembles browsing by wild animals, but it is interesting to note that maximum densities of this plant are achieved under specific combinations of different disturbance agents which have no obvious natural counterparts. Such finding challenges some of the principles usually accepted in conservation practices, and opens the possibility for quite different forms of disturbance management. Studies like this one are a prerequisite to develop conservation plans in areas exposed to human activities.

The use of anthropogenic disturbance as a management tool to preserve a species should be cautious. *M. pectinifera* is favoured by livestock, but the rest of the vegetation may not. It has been found that this cactus grows in species-poor areas (Zavala-Hurtado and Valverde, 2003). Whether this is the natural condition of the habitat of this cactus, or if it is the result of an association between *M. pectinifera* and livestock, is still to be proved.

The effectiveness of our approach to measure disturbance on environments other than drylands can be evaluated by comparing with data from a montane rain forest (Ramírez-Marcial et al., 2001). Several metrics, among which were some indicators of disturbance, were analysed through PCA. The first axis was related to most disturbance metrics, and the authors interpret it as a disturbance axis despite the contribution made to it by other metrics such as altitude, slope or forest structure.

The data required for the calculation of the disturbance index developed here are easily and readily recorded at the field, and provide a repeatable, objective measurement of disturbance intensity. For the same region in the Tehuacán Valley, further research may use the same index simply by applying the formula:

$$\begin{aligned}D = {} & 0.1334\ \mathrm{GOAT} - 0.1631\ \mathrm{CATT} + 0.1334\ \mathrm{BROW} \\ & + 0.0799\ \mathrm{LTRA} - 0.1257\ \mathrm{COMP} + 0.1931\ \mathrm{FUEL} \\ & - 0.0231\ \mathrm{LTRA} + 0.0758\ \mathrm{TRAS} + 0.1389\ \mathrm{PROX} \\ & + 0.1371\ \mathrm{CORE} + 0.0929\ \mathrm{LUSE} + 0.1133\ \mathrm{EROS} \\ & + 0.1837\ \mathrm{ISLA} + 0.1009\ \mathrm{TOMS}.\end{aligned}$$

To obtain the index for individual disturbance agents, only the terms related to each one must be added. For example, the land degradation index is the sum of the last three terms in the equation. The method used for the derivation of the disturbance index may be tailored to any region or system by selecting a set of metrics that comprise the most important disturbance agents operating in the area. The metrics should be chosen having in mind that chronic disturbance is a multivariate, gradual process, and that no metric based on the effects of the agents on the biotic environment should be included in order to avoid tautology.

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