

PART V

Soil and Vegetation Monitoring

MONITORING TOOLS TO ASSESS VEGETATION SUCCESSIONAL REGRESSION AND PREDICT CATASTROPHIC SHIFTS AND DESERTIFICATION IN MEDITERRANEAN RANGELAND ECOSYSTEMS

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ABSTRACT

The relationship between grazing intensity and ecosystem performance is complex and can depend on the prevailing ecological conditions. Previous studies have revealed that, in traditional grazing ecosystems, grazing can reduce ecosystem diversity in poor soils, but increase diversity and productivity in rich ecosystems subject to moderate grazing pressure. We are interested in detecting long-term structural changes or drift in an ecosystem before it is too late to prevent irreversible degradation. We analyzed vegetation spatial patterns and complexities of four Mediterranean communities: Tihmadit Region (Middle Atlas, Morocco), Camiyayla (Namrum) Region (Taurus Mountain, Turkey), Sykia Region (south of the Sithonia Peninsula, Greece), and Cabo de Gata Nijar Natural Park, Spain. Grazing disturbance was most intense near shelter and water points, which lead to gradients in soil surface disruption, compaction, and changes in the composition and cover of perennial vegetation. Dense matorral was more resistant to species loss than were moderately dense and scattered matorral, and grassland. Information fractal dimension decreased as we moved from a dense matorral to a discontinuous matorral, and increased as we moved to a more scattered matorral and to a grassland, which resulted in two opposing processes (interaction declining with ecosystem development, and immigration increasing with degradation) in a common pattern, i.e., small patches homogeneously distributed in the landscape. Characteristic species of the natural vegetation declined in frequency and organization in response to higher grazing disturbance, while species of disturbed areas exhibited the opposite trend. Overall, the spatial organization of the characteristic plants of each

community decreased with increasing vegetation degradation, with the intensity of the trend being related to the species' sensitivity to grazing. Developmental instability analyses of key species were used to determine the sensitivity of dominant key species to grazing pressure. Palatable species, which are better adapted to being eaten, such as *Periploca laevigata*, *Phillyrea latifolia* and *Genista pseudopilosa*, were able to resist moderate grazing pressure, while species of disturbed, grazed sites did not change developmental instability in response to increasing grazing pressure, such as *Thymus hyemalis*, *Teucrium lusitanicum* and *Cistus monspeliensis*. The usefulness of these monitoring tools in preventing land degradation is discussed.

INTRODUCTION

Mediterranean ecosystems are characterized by highly heterogeneous and fluctuating environments where overgrazing and fires, together with episodic droughts, result in land degradation (DiCatri and Mooney, 1973; DiCatri *et al.*, 1981). Landscape preservation in such situations is complex and influenced by interactions among grazing pressure, rainfall, edaphic conditions and grazing history (Milchunas and Lauenroth, 1993). Climatic variability and grazing history are the principal forces affecting species composition and productivity (biodiversity and stability) in rangeland semi-arid ecosystems, which are concentrated on marginal areas where grassland productivity is relatively low. Nomadism and transhumance were the traditional ways of adapting to episodic drought in the Mediterranean region, which allowed an ecological balance between production and exploitation. But, transhumance has become more sedentary in many areas of the Mediterranean in recent decades (Aidoud *et al.*, 1998; Rebollo and Gomez Sal, 1998; Ruiz and Ruiz, 1986) and farmers use supplementary products from agriculture during periods of scarcity.

It is well accepted that many ecosystems will adapt to a disturbance if the disturbance persists over a long period and that it can be considered to be a part of the environment (Peterson, 2002), to a point where the absence of disturbance can become a disturbance in itself. Evolutionary changes observable over less than a few hundred years (contemporary evolution) are associated with the same factors that are driving current extinctions. Conservation efforts that ignore its implication will be less effective and even risk prone (Stockwell *et al.*, 2003). Recent simulation models show that, within the constraints of the external environment and the genetic potential of their biota, ecosystems can evolve to a state where they are highly resilient to perturbation (Cropp and Gabric, 2002). Thus, if contemporary evolution is an important source of ecological and co-evolutionary dynamics in natural biological communities, the preservation

of ecosystems will require the preservation of long-term evolutionary processes (Cardinale *et al.*, 2002).

In environments that have a long history of grazing, such as the Mediterranean ecosystem, grazing is considered essential to the maintenance of species diversity (Grime, 1979; Crawley, 1983; McNaughton, 1985; Milchunas *et al.*, 1988; Noy-Meir *et al.*, 1989), although high stocking rates or grazing in poor soils (arid or very saline) can decrease plant diversity (Milchunas *et al.*, 1988; Hobbs and Huenneke, 1992; Olf and Ritchie, 1998). In traditional grazing ecosystems, grazing can affect the system in two opposing directions: a) by reducing ecosystem diversity, especially in poor soils, and b) by increasing diversity and productivity of the ecosystem, particularly in natural ecosystems or under low grazing pressure in rich ecosystems. The relationship between grazing impact and ecosystem function is complex and not well understood. We need precise tools to determine when disturbance exceeds the threshold of tolerance (resistance and resilience), and thus drastically changes ecosystem structure and function causing it to switch from one steady state to a new one (Holling, 1973).

In this study, we assessed the effect of long-term grazing on vegetation by analyzing the disturbance gradient at increasing distances from the source. Disturbance is most intense near shelters and watering points, which produces a gradient of soil surface disruption, compaction, and changes in the composition and cover of perennial vegetation (Nash *et al.*, 1999). Our objective was to detect long-term structural changes or drift in the ecosystems by characterizing the parameters resulting from the dynamic variation of the system, before it is too late to prevent irreversible degradation.

Study Areas

Four characteristic ecosystems of the Mediterranean region were selected. In the shrubland of Greece, we selected the village community of Sykia (14 060 ha) on the Sithonia Peninsula (Greece). The climate is sub-humid Mediterranean with mild winters. The geological bedrock is mainly metamorphic rocks of the Mesozoic Era, with some sites covered by sedimentary rocks. The rangelands covered 11644 ha, with 9499 ha shrubland of broadleaved evergreen species or maquis dominated by *Pistacia lentiscus*, *Olea europea*, *Erica* spp., *Cistus* spp., *Quercus ilex*, *Q. coccifera* and *Arbutus unedo*.

A semi-arid matorral was selected in southeastern Spain in Cabo de Gata Natural Park (37 570 ha), where the elevation ranges between sea level and 493 m at El Fraile Peak. This area has been preserved since 1987. The climate is Mediterranean semiarid. The middle dense matorral of *Chamaerops humilis*, *Rhamnus* spp. and *Periploca laevigata* occupies 9332.41 ha (24.21% of the park area), and the Steppe grassland (*Stipa tenacissima* with *Phlomis*, *Thymus* and *Sideritis* as dominant species) occupies 10555.20 ha (27.4% of the park area). This study was performed in the middle dense matorral of the Sabinar-Romeral site.

In the high mountain grasslands located in the Çamliyayla (Namrum) Region of the Taurus Mountains, Turkey, we selected the Sigiryaylasi area located at 1300-1400 m a.s.l. It includes about 220-250 ha of pastureland and a typical temperate sub-humid Mediterranean climate. The characteristic vegetation is a low scattered matorral of *Phlomis* and grassland colonized by terophytic and ruderal plants.

Finally, we selected a high mountain grassland at Ait Beni Yacoub, Middle Atlas, Morocco, which occupies 13429 ha of rangelands. The characteristic vegetation is a low scattered matorral of *Genista* sp. and *Thymus* sp. colonized by *Poa* sp. grassland.

Livestock feeding habits and rangeland management

Grazing management in the dense matorral of the Sithonia Peninsula, northern Greece (Toroni, Chalkidiki) and in the semi-arid matorral of Cabo de Gata, Spain, involved use by individual shepherds holding grazing rights. The animals (goats in Greece and sheep and goats in Spain) moved daily from the shelter to different parts of the rangeland, which produced a gradient of soil and vegetation disturbance from the shelter to the periphery. The two high mountain grasslands in Ait Beni Yacoub, Middle Atlas, Morocco, and the Çamliyayla (Namrum) Region of the Taurus Mountains, Turkey, were nomadic and common lands.

Effective stocking rate (ind. ha⁻¹ year⁻¹) was calculated by direct observations (Table 1). Animal movements (sheep and goats) were located using GPS and transferred to a map in GIS format (Geographical Information System). Effective stocking rate was calculated by multiplying the average stocking rate by a correction factor of rangeland use. In the Turkish study areas, effective stocking rate was calculated based on biomass production in exclosures compared with the biomass outside the exclosures, and then compared with the average ingested feed of an adult sheep.

In each study area, a grazing gradient was established across increasing distances from a water point (for the nomadic herds) or from a shelter (for the established herds). In Sithonia (Greece) and Middle Atlas (Morocco), we identified three levels of grazing pressure (low, medium and high). In Cabo de Gata (Spain), a control (no grazing) treatment was also added. In the Taurus Mountains (Turkey) only medium and high levels of grazing pressure were observed.

GRAZING PRESSURE AND CHANGES IN PLANT DIVERSITY AND FREQUENCY

We recorded 96 vascular plant species in Sithonia, 144 in Cabo de Gata (at the Sabinar-Romeral site), 130 in the Taurus Mountains, and 95 in the Middle Atlas study area. At most sites, there was a significant decrease in the total number of species with an increase in grazing disturbance (Table 1), except in Sithonia shrubland, where there was non-significant variation in plant diversity because species sensitive to grazing disturbance (*Quercus coccifera*, *Olea europaea* var. *sylvestris*) were replaced by grazing-resistant species (e.g., *Plantago* spp. and *Poa bulbosa*). Overall, biodiversity decreased along the sclerophyllous Mediterranean ecosystems from the highly dense matorral to the low scattered matorral and to the xeric grassland, being more drastic towards the end of the regressive successional stage of each community (Figure 1). In addition, we observed that a diverse community also exhibits a high evenness index. Plants tended to be equally represented (larger evenness index) in the lightly grazed areas than in heavy grazed areas. Under heavy grazing pressure, a few species dominated the community according to the appearance of grazing-resistant species.

The increase in plant cover heterogeneity (low evenness) with increasing grazing disturbance confirmed the trend for an increase in grazing-resistant plants, which eventually become dominant. For example, cushion perennial grasses with underground stems (e.g., *Stipa tenacissima*) with their buried buds, are more protected from grazing than are shrubs. Thus, the Cabo de Gata middle dense scrubland of *Chamaerops*, *Rhamnus* and *Periploca* has transformed into *Stipa* steppe at the end of the regressive succession.

In the shrubland of the Sithonia Peninsula, where more species adapted to high disturbance (*Cistus monspeliensis*) than species that indicate pristine matorral, such as *Quercus coccifera* and *Olea europaea* var. *sylvestris*, that become very scarce as grazing pressure increases. Species

exhibiting grazing syndrome (prostrated or rosette twigs), such as *Plantago* spp., also became very frequent. In the Middle Atlas grassland, *Poa bulbosa* dominated under heavy grazing, while *Genista* sp. decreased. In the Taurus Mountains, grassland and shrubland differed significantly in bareground cover and species richness, although no significant difference were observed in proportional diversity indices.

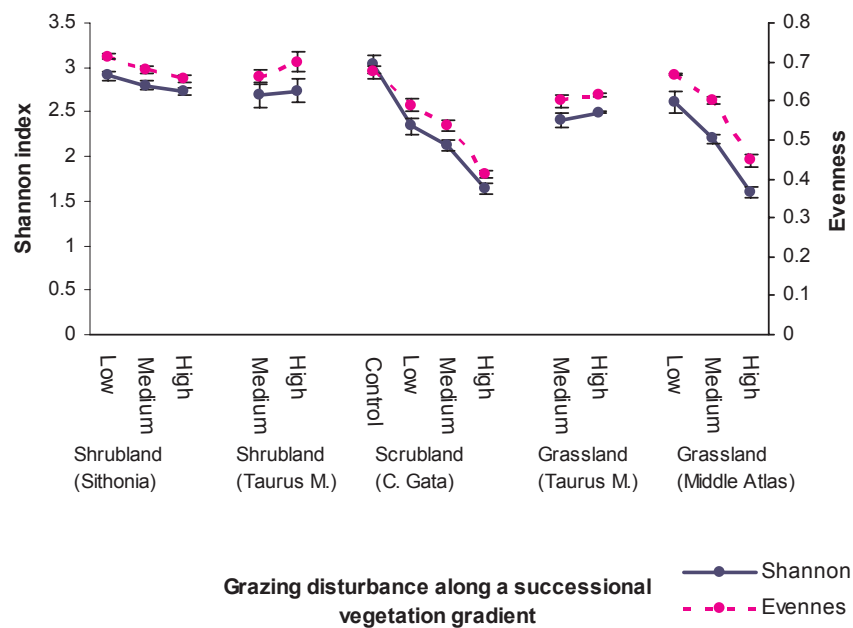


Figure 1. Changes in Shannon Diversity and Evenness indices along the grazing disturbance gradient in five Mediterranean ecological communities

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Table 1. Effective stocking rate (ind. ha⁻¹ year⁻¹ using the study area), richness (average number of species ± SE), percentage of bare-ground, and mean ± SE of the Inverse Simpson Index calculated from the presence of species along the three transects per test area. F values were calculated using a one-way ANOVA with grazing pressure as fixed-effect factors. * P < 0.05, ** P < 0.01, *** P < 0.0001.

Grazing pressure	Effective Stocking Rate	Richness	Bareground cover (%)	Inverse Simpson' Index
<i>Shrubland of Sithonia Peninsula (Greece)</i>				
Low	0.3	59±2.6	4.4	9.59±0.51
Medium	2.6	61.7±0.3	16.4	7.69±0.65
High	8.2	62.3±0.9	21.5	7.62±0.33
		F _{2, 6} = 1.18	G = 489.3***	F _{2, 6} = 4.73
<i>Scrubland of Cabo de Gata (Spain)</i>				
Control	0	89.7±4.5	20.9	9.25±0.50
Low	0.27	53±2.9	34.6	4.70±0.35
Medium	0.46	51.66±3.3	31.5	4.32±0.26
High	0.65	54±4.6	29.1	2.24±0.10
		F _{3, 12} = 22.52 ***	G = 115.9***	F _{3, 12} = 77.11***
<i>Grasslands of the Middle Atlas (Morocco)</i>				
Low	0.9	61.5±4.5	9.4	7.80±0.49
Medium	1.54	44.5±0.5	21	5.14±0.17
High	2.49	36±0.99	20	3.10±0.13
		F _{2, 4} = 33.38**	G = 171.9***	F _{2, 6} = 58.76
<i>Shrubland & Grassland of Taurus Mountains (Turkey)</i>				
Med_Grassland	4.4	59±2.1	11.1	5.94±0.50
High_Grassland	5.2	55.7±4.7	6.6	6.19±0.76
Med_Shrubland		58±5.3	32.3	7.16±0.81
High_Shrubland		50.7±3.3	35.9	8.78±1.51
		F _{3, 11} = 1.06	G = 1393.0***	F _{3, 11} = 1.06

Fractal Dimension of Plant Spatial Patterns

Spatial patterns have an important effect on ecosystem function. Soil erosion and runoff distribution is directly related to the spatial distribution of the vegetation (Cerdá 1997a, Sole Benet *et al.*1997, Martinez Mena *et al.* 2000).

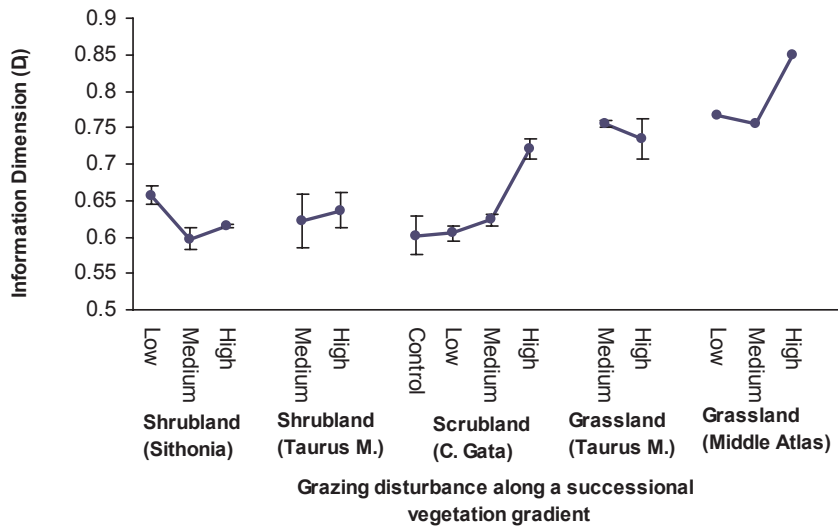


Figure 2. Changes in Information Fractal Dimension D_1 along the grazing disturbance gradient in five Mediterranean communities. The Information Fractal Dimension $D_1 \cong \lim_{\varepsilon \rightarrow 0} \frac{H'(\varepsilon)}{\ln 1/\varepsilon}$ (Alados *et al.* 2003) is calculated by regressing the Shannon Index $H'(\varepsilon)$ against the natural logarithm of window size ε . The slope of the line is the Information Fractal Dimension.

Plant spatial patterns can be quantified using the fractal dimension. In this study, we calculated the change in the Information Fractal Dimension along the regressive successional vegetation stages of different plant communities. The Information Fractal Dimension measures the complexity of a system, independent of the scale of observation, over a range of scales (Farmer *et al.*, 1983; Alados *et al.*, 2003). Changes in the fractal dimension indicate a substantial change in the processes that generate plant spatial

patterns (Krummel *et al.*, 1987; Li 2000) and can be used to measure the degree of regression of vegetation succession (Alados *et al.*, 2003, 2004). The Information Fractal Dimension provides a quantitative measure of the degree of patchiness of the plant community independent of scale. It increases with the degree of randomness (lack of spatial correlation).

We observed that the fractal dimension declined from a dense matorral to a discontinuous matorral, but increased from a discontinuous matorral to a scattered matorral, and kept increasing towards grassland. That change in the fractal dimension indicates a substantial change in the processes that generate plant spatial patterns. The “passage” from the matorral climax (high and dense) to low and discontinuous matorral occurs as a result of degradation, mainly due to overstocking, burning and cutting, and can be used to quantify degradation stages of the Mediterranean-type ecosystem.

Spatio-temporal heterogeneity is not the result of random processes; rather, it is a functional ecosystem property (Wu *et al.*, 1985, Couteron and Lejeune, 2001; Rietkerk *et al.*, 2002), that affects ecosystem functioning (Pickett and Cadenasso, 1985; Hutchings and Wijesinghe, 1997). To develop conservation strategies it is crucial to understand the self-organizing capacity of the system. Self-organized instability theory proposes that ecological complexity results from the interaction between the trend to increase diversity as the ecosystem develops and the negative feedback that arises from interactions among individuals (Solé *et al.*, 2002). That results in two opposite processes (interaction declining with ecosystem development, and immigration increasing with degradation) in a common pattern, i.e., small patches homogeneously distributed in the landscape (Alados *et al.*, 2004). In our study, we observed the same pattern in both extremes, the better preserved and most degraded, which confirmed previous hypotheses.

Since different species have different roles in ecosystem functioning, and not all of the species are expected to exhibit the same trajectory, we tested whether and how the spatial aggregation of each species' cover changed, independently of the scale of measurement. Detrended Fluctuation Analyses (DFA), developed by Peng *et al.* (1992), and applied to plant spatial analyses by Alados *et al.* (2003, 2004), can be used to quantify the degree of organization of each plant species. DFA corresponds to standard spectral analysis (Wilson and Francis, 2003). It measures the level of autocorrelation (α) of a random walk generated from the sequence of presence and absence intercepts per each species along the transect.

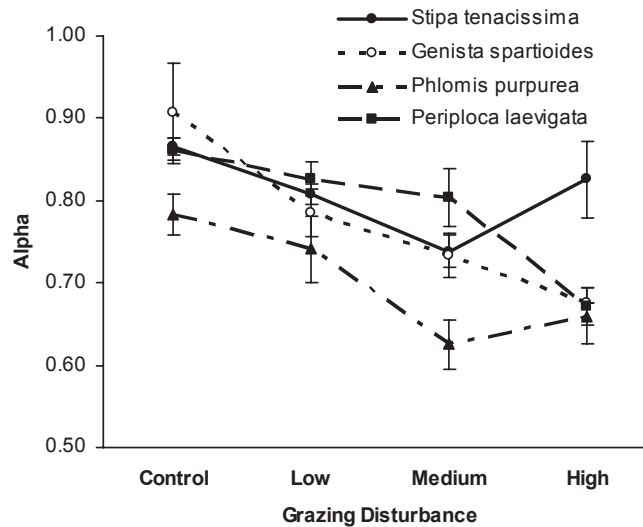


Figure 3. Changes in alpha exponent versus grazing disturbance for the characteristic species of Cabo de Gata NP. Alpha is calculated from the residual variance of the regression of $y_b(s)$ on s per non-overlapping boxes of size s from the N point contacts in the transect:

$$F^2(b) = \frac{\sum_{s=1}^N (y_b(s) - \hat{y}_b(s))^2}{N}$$

The slope of the line relating $F(b)$ to b determines the scaling exponent α : $F(b) \propto b^\alpha$. The scaling exponent alpha is inversely related to the fractal dimension

The extent to which plant spatial patterns depart from randomness is expected to increase with community age. During early colonization, the plant distribution is expected to be random (Kershaw, 1963; Fowler, 1990), then, the interactions among components increase and the system moves away from stochasticity and towards spatial organization. In our study, α was lower in the less competitive species (annuals) and larger in the more competitive species (shrubs), which suggests that the lower competitors are affected by the stochasticity of their colonization and mortality, in addition

to the stochasticity of the mortality of their best competitors (Alados *et al.* 2003, 2004).

We considered how the positive feedback from facilitation processes can lead to self-organized vegetation patterns in arid ecosystems as the ecosystem develops, as opposed to the random patterns that arise from competitive interactions of colonizing species in disturbed habitats. To that end, we analysed the change in spatial organization along a gradient of degradation. The spatial organization of the characteristic plants of each community increased in the best preserved areas (Figure 3 and 4). In contrast, as grazing pressure increased, those plants become more randomly distributed, except for species typical of perturbed ecosystems, whose spatial organization increased (e.g., the alpha autocorrelation parameter of *Euphorbia* in the Middle Atlas grasslands increased from 0.60 to 0.77; Alados *et al.*, 2004).

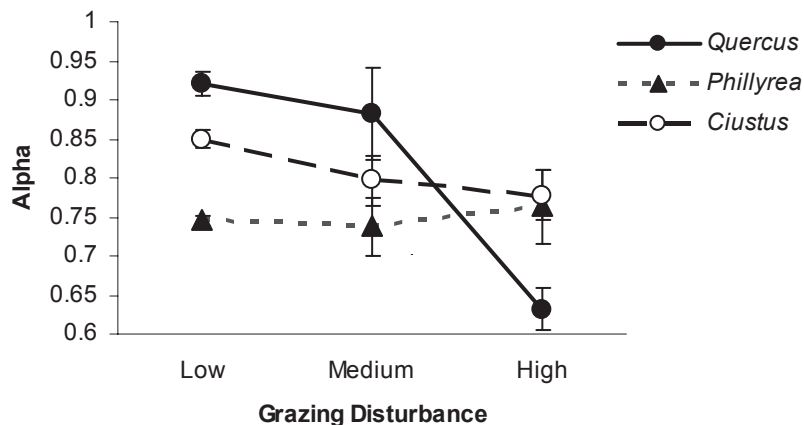


Figure 4. Changes in alpha exponent versus grazing disturbance for the characteristic species of Sykia shrubland (Greece)

In addition, the degree to which randomness increased with grazing disturbance was related to the sensitivity of the species to grazing. For example, *Chamaerops* declined in frequency, but its spatial organization did not change because its renewal buds are buried and not accessible to livestock. Similarly, the renewal buds of *Phillyrea latifolia* could not be accessed by the goats, so it was also very resistant to heavy grazing. *Stipa*

tenacissima has extensively branched rhizomes that fragment by withering and expand over large areas (Hessen 1999). The buried renewal buds of *S. tenacissima* cannot be reached by livestock and have a high capacity to retain soil and runoff, especially in fine material soils (Sánchez and Puigdefábregas, 1994; Cerdá, 1997b; Cammeraat *et al.*, 2002). In addition, the low palatability of *S. tenacissima* favours development under grazing pressure. We observed that the spatial organisation of *S. tenacissima* did not change with increased grazing pressure. On the contrary, the spatial organisation of sensitive species of the pristine matorral community, such as *Q. coccifera*, *O. europaea* var. *sylvestris*, *Erica. arborea*, *Phlomis purpurea* and even the grazing tolerant *Periploca laevigata* decreased drastically (Figures 3 and 4).

Thus, the degree of autocorrelation of plant spatial distribution at the species level, and the information dimension at the community level allowed us to quantify the degree of degradation of natural communities and to determine the sensitivity of key species.

PLANT POPULATION STRESS ASSESSMENT

The effect of grazing on vegetation can vary depending on plant strategy and available resources (i.e., plant physiological and evolutionary responses to water stress depend on the range of resources to which the plants are adapted). In addition, the relationship between stress and fitness is not expected to be linear. Plants that have previous exposure to a stress are expected to be better at resisting further stress. For example, plants that experience frequent periods of drought evolve a conservative strategy of reducing growth under severe drought while maintaining homeostasis of fundamental structures for fitness (Chapin, 1991). That conservative strategy has been called “stress resistance syndrome” (Grime, 1979; Chapin *et al.*, 1993) and it is frequently found among plants in dry areas (Edelin, 1977; Thomansson 1977). In contrast, plants living in more mesic habitats might have a more competitive strategy in which they allocate more energy to production, while still being able to maintain developmental stability (homeostasis) in growth structures, except in the face of occasional drought periods. Thus, if disturbance is a persisting part of the environment, the ecosystem might develop mechanisms of adaptation to prevalent conditions. For example, palatable plant species that are frequently grazed show lower stress under medium grazing than when not grazed (Escós *et al.*, 1997; Alados *et al.*, 1998, 2002). Those results are particularly important in

Mediterranean ecosystems, where sustainability depends on human impact and the history of adaptation (Milchunas and Lauenroth, 1993).

Developmental instability represents the cumulative effects of small, random developmental perturbations of environmental origin (Waddington, 1957). It is reflected by exaggerated intra-individual variation in repeated traits and patterns. Developmental instability has the advantage that, as a nonspecific measure of developmental disturbances, it can be used as an early indicator of anthropogenic impacts on animals and plants (Zakharov *et al.*, 1987; Graham *et al.*, 1993). Traditionally, developmental instability is assessed by measuring fluctuating asymmetry, random deviations from bilateral symmetry (Palmer and Strobeck, 1986). Most studies of plant developmental instability have measured the fluctuating asymmetry of leaves and flowers (see Møller and Shykoff, 1999, for review). Statistical noise in other allometric relationships can also be good indicators of developmental noise (Freeman *et al.*, 1993; Graham *et al.* 1993).

Allometric relationships between plant parts are maintained during growth so that the entire structure maintains its mechanical stability, and they are consistent within species (White, 1981; Weller, 1987). One of the most important allometries observed in plants is the arrangement of phyllotaxis around stems. Several studies have shown that the error in the curve-fitting accuracy between internode length (L) and node order (N) fits the equation $L = kN^a e^{-bN}$ (Alados *et al.*, 1994, 1998; Escós *et al.* 1995, 1997; Sherry and Lord, 1996; Anne *et al.*, 1998; Tan-Kristanto *et al.* 2003) and is a better indicator of developmental instability than is fluctuating asymmetry.

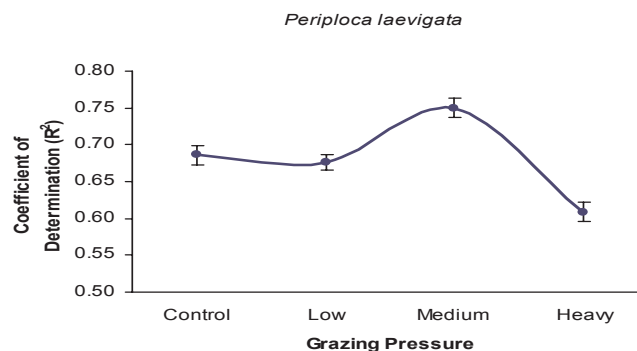


Figure 5. Developmental instability of shoots measures as R^2 of *Periploca laevigata*

In our study, we analyzed the change in developmental instability of the characteristic species of the community along the grazing intensity gradient. Two dominant shrub species (*Phillyrea latifolia* L., palatable, and *Cistus monspeliensis* L., unpalatable to domestic animals) were studied from Sykia (Sirkou *et al.*, 2002). Grazed *Phillyrea latifolia* was developmentally unstable compared to ungrazed because its degree of leaf fluctuating asymmetry was greater. That was particularly evident when we compared the upper part of shrubs (>1.50 m height) that could not be reached by goats and the lower, accessible area (<1.50 m height). Separate analyses of the upper and lower parts revealed that *Phillyrea* could compensate for the stress produced in the lower part by increasing growth and maintaining developmental stability in the upper, unreachable shoots (Sirkou *et al.*, 2002). The fact that grazing, even when it is quite intense, maintains the developmental stability of the top parts of *Phillyrea* shrubs, indicates that this species is very tolerant (even under heavy grazing pressure) and suggests that a compromise must be found between overgrazing and non-grazing in the pastoral management of this species. On the other hand, the translational asymmetry of *Cistus monspeliensis* did not vary significantly among different grazing treatments.

The development of *Periploca laevigata*, a high palatable species from Cabo de Gata (Spain), was more stable under medium grazing, as estimated by translational and floral asymmetry, than under heavier or lighter grazing (Figure 5). *P. laevigata* also responded to grazing pressure by accelerating growth at the beginning of spring, when grazing activity is concentrated in herbaceous plants, and finishing growth sooner than in the other grazing treatments (Alados *et al.* 2002). Indeed, plants with less translational asymmetry grew more and produced more flowers.

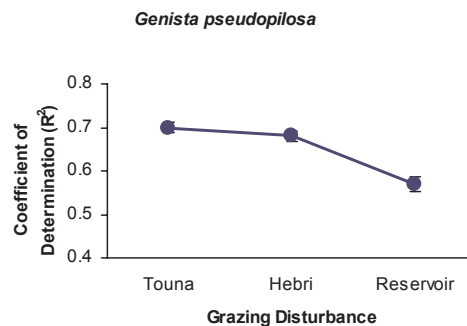


Figure 6. Developmental instability of shoots measures as R^2 of *Genista pseudopilosa*

Natural selection is expected to favor early growth and reproduction, such that plants phenologically escape herbivores that feed on the plant later in the season. Under high grazing pressure, it would be advantageous for *P. laevigata* to grow and establish reproductive structures before becoming a food source to sheep and goats. Higher photosynthetic activity during such a period would result in a higher capacity to construct carbon structures and permit faster growth. Early in the growing season, ungrazed *P. laevigata* had higher photosynthetic activity than did grazed plants, which suggests that the defoliated plants were still recovering from herbivore damage from the previous period (Castro *et al.* 2003). Later in the growing season, grazed plants had higher photosynthesis activity than did ungrazed plants, which suggests investment in chemical defences (Barroso *et al.*, 2003). In Cabo de Gata, *Sideritis osteoxylla* was favored by moderate grazing pressure, as indicated by the larger curve-fitting accuracy of the relationship between internode length and node order shown at intermediate grazing compared to lightly and heavily grazed areas. In contrast, grazing did not have a negative effect on *Thymus hyemalis* or *Teucrium lusitanicum*.

Grazing pressure at the Ait Beni Yacoub of Middle Atlas significantly ($F_{2,270} = 25.77$, $P < 0.0001$) increased developmental instability of *Genista pseudopilosa*, as measured by the curve-fitting accuracy of the relationship between internode length and node order (Figure 6), which indicates that the grazing pressure reached at this site significantly negatively affects the performance of this species. *G. pseudopilosa* functions as a nursery species by protecting underneath other species from grazing, and the decline of this species clearly is a threat to the maintenance of the diversity in the area.

CONCLUSIONS

Based upon the results of our study, we conclude that the impact of grazing on the preservation of vegetation depends on climatic conditions, soil properties, and vegetation cover. In Sykia (Greece), moderate grazing (2.5 goats ha⁻¹year⁻¹) seems to be the proper stocking rate because it combines increased productivity for goats with plant community stability and resilience. In the semi-arid land of Cabo de Gata (Spain), effective stocking rates above 0.5 sheep ha⁻¹year⁻¹ threaten the persistence of the tall-brush community and favor a posterior regressive stage in the vegetation towards tall-grass steppes. At Sigiryaylasi (Turkey), a grazing pressure of 4-5 sheep ha⁻¹year⁻¹ increased the risk of erosion on sloped terrain, but not in

flat areas. In the Ait Beni Yacoub (Morocco), if settlement on rangelands continues as it has in the last five years, grazing pressure will vary from 3.38 to 6.75 sheep ha⁻¹year⁻¹ in ten years, which will turn the vegetation into an impoverished grassland of *Poa* spp. and *Carex* spp.

In addition, fractal analysis of plant spatial patterns provided a quantitative characterization of vegetation dynamics in response to disturbance, which can help to predict the effect of grazing independently of scale and determines the sensitivity of key species to grazing disturbance. Drastic changes in the parameters that characterize vegetation spatial patterns revealed important changes in the processes driving the system. In addition, developmental instability analyses of target species will help to detect the effect of environmental stresses and to understand the alternative strategies of the species under specific circumstances.

REFERENCES

- Aidoud, A., Aidoud-Lounis F., Slimani, H. Effects of grazing on soil and desertification: a review from the southern Mediterranean rim. Pages 133-148. In: Ecological basis of livestock grazing in Mediterranean ecosystems (Papanastasis, V. P. & Peter, D. Eds.). European Commission EUR 18308. 1998.
- Alados, C. L., Escós J., Emlen J. M. Scale asymmetry: a tool to detect developmental instability under the fractal geometry scope. Pages 25-36. In: Fractals in the Natural and Applied Sciences. (MM Novak, Ed.). Elsevier, North-Holland. 1994.
- Alados, C. L., Emlen, J. M., Wachocki, B., Freeman, C. D. Instability of development and fractal architecture in dryland plants as an index of grazing pressure. *J. Arid Environ*, 1998; 38: 63-76.
- Alados, C. L., Giner, M. L., Dehesa, L., Escós, J., Barroso, F., Emlen, J. M., Freeman, C. D. Developmental instability and fitness in *Periploca laevigata* experiencing grazing disturbance. *Int J Plant Sci*, 2002; 163: 969-978.
- Alados, C. L., Pardo, Y., Giner, M. L., Navarro, T., Escós, J., Barroso, F., Cabezudo, B., Emlen, J. M. Quantitative characterization of plant spatial patterns by fractal analysis. *Ecol Model*, 2003; 163: 1-17.
- Alados, C. L., ElAich, A., Papanastasis, V. P., Ozbek, H., Navarro, T., Freitas, H., Vrahnakis, M., Larrossi, D., Cabezudo, B. Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. *Ecol. Model.*, 2004; 180: 523-535.
- Anne, P., Mawri, F., Gladstone, S., Freeman, D. C. Is fluctuating asymmetry a reliable biomonitor of stress? a test using life history parameters in soybean. *Int J Plant Sci* 1998; 159: 559-565.
- Barroso, F. G., Martínez, T. F., Paz, T., Alados, C. L., Escós, J. Relationship of *Periploca laevigata* (Asclepidaceae) tannins to livestock herbivory. *J Arid Env*, 2003; 53: 125-135.

- Cammeraat, L. H., Willott, S. J., Compton, S. G., Incoll, L. D. The effects of ants' nests on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. *Geoderma*, 2002; 105: 1-20.
- Cardinale, B. J., Palmer, M. A., Collins, S. L. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 2002; 415(6870): 426-429.
- Castro, H., Nabais, C., Alados, C. L., Freitas, H. Effects of cessation of grazing on leaf-level photosynthesis of *Periploca laevigata*. *Appl Veg Sci*, 2003; 6: 255-260.
- Cerdá, A. Soil erosion after land abandonment in a semiarid environment of southeastern Spain. *Arid Soil Res. Rehab.*, 1997a; 11 (2): 163-176.
- Cerdá, A. The effect of patchy distribution of *Stipa tenacissima* L. on runoff and erosion. *J. Arid Env.*, 1997b; 36: 37-51.
- Chapin, F. S. Integrated responses of plants to stress. *BioScience*, 1991; 41: 29-36.
- Chapin, F.S., Autumn, K., Pugnaire, F. Evolution of suites of traits in response to environmental stress. *Am Nat*, 1993; 142: S78-S92.
- Couteron, P., Lejeune, O. 2001. Periodic spotted patterns in semiarid vegetation explained by a propagation-inhibition model. *J Ecol*, 2001; 89: 616-628.
- Crawley, M. J. *Herbivory, the dynamics of animal-plant interactions*. Berkeley: University of California Press, 1983.
- Cropp, R., Gabric, A. 2002. Ecosystem adaptation: do ecosystems maximize resilience? *Ecology*, 2002; 83: 2019-2026.
- DiCstri, G., Mooney, H. A. *Mediterranean type ecosystems: origin and structure*. *Ecol. Stud* 7. Springer Verlag, Berlin, 1973.
- Di Castri, F., Goodall, D. W., Spetch, R. L. *Mediterranean-type shrubland. Ecosystems of the World*. Vol 11. Elsevier, Amsterdam, 1981.
- Edelin, C. *Images de l'architecture des coniferes. These de 3eme cycle*. VSTL. Montpellier, 1977.
- Escós, J., Alados, C. L., Emlen, J. M. Fractal structures and fractal functions as disease indicators. *Oikos*, 1995; 74: 310-314.
- Escós, J., Alados, C. L., Emlen, J. M. Grazing impact on plant fractal architecture and fitness of a Mediterranean shrub (*Anthyllis cytisoides*). *Funct Ecol*, 1997; 11: 66-78.
- Farmer, D., Ott, E., Yorke, J. A. The dimension of chaotic attractors. *Physica*, 1983; 7D: 153-180.
- Fowler, N. L. Disorderliness in plant communities: comparisons, causes and consequences. Pages 291-306. In: *Perspectives on plant competition* (Grace J.B., Tilman D., Eds.). Academic Press. Inc. San Diego, USA, 1990.
- Freeman, D. C., Graham, J. H., Emlen, J. M. Developmental stability in plants: symmetries, stress and epigenesis. *Genetica*, 1993; 89: 97-119.
- Freeman, D. C., Graham, J. H., Emlen, J. M., Tracy, M. A., Hough, R. A., Alados, C. L., Escós, J. Plant developmental instability: new measures, applications, and regulations. Pages 367-386. In: *Developmental Instability, causes and consequences* (Polak, M., Ed.). Oxford University Press, 2003.
- Graham, J. H., Freeman, D. C., Emlen, J. M. Developmental stability: A sensitive indicator of population under stress. Pages 136-158. In: *Environmental Toxicology and Risk Assessment*. ASTM STP 1179. (Landis W.G., Hughes J.S., Lewis M.A., Eds.). American Society for Testing and Materials, Philadelphia, 1993.
- Grime, J. P. *Plant strategies and Vegetation Processes*. John Wiley, New York, 1979.
- Hessen, I. Life strategies in a semi-arid grassland community mechanisms of dispersal and reproduction within *Lapiedro-martinezii-stipetum tenacissimae* (southeastern Spain). *Feddes Repertorium*, 1999; 110: 265-285.

- Hirata, M., Fujita, H., Miyazaki, A. Changes in grazing areas and feed resources in a dry area of north-eastern Syria. *J Arid Environ*, 1998; 40: 319-329.
- Hobbs, R. J., Huenneke, L. F. Disturbance, diversity, and invasion: Implications for conservation. *Conserv Biol*, 1992; 6: 324-337.
- Holling, C. S. Resilience and stability of ecological systems. *Annu Rev Ecol Syst*, 1973; 4: 1-23
- Hutchings, M. J., John, E. A., Wijesinghe, D. Towards understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology*, 2003; 84: 2322-2334.
- Kershaw, K. A. 1963. Pattern in vegetation and its causality. *Ecology*, 1963; 44: 377-388.
- Koehn, R. K., Bayne, B. L. Towards a physiological and genetical understanding of the energetics of the stress response. *Biol J Lin Soc*, 1989; 37: 157-171.
- Krummel, J. R., Gardner, R. H., Sugihara, G., O'Neill, R. V., Coleman, P. R. Landscape patterns in a disturbed environment. *Oikos*, 1987; 48: 321-324.
- Li, B. L. Fractal geometry applications in description and analysis of patch patterns and patch dynamics. *Ecol Model*, 2000; 132: 33-50.
- Martinez Mena, M., Rogel, J. A., Albaladejo, J., Castillo, V. M. Influence of vegetal cover on sediment particle size distribution in natural rainfall conditions in a semiarid environment. *Catena*, 2000; 38 (3): 175-190.
- McNaughton, S. J. Ecology of a grazing ecosystem: the Serengety. *Ecol Monogr*, 1985; 55: 259-294.
- Milchunas, D. G., Sala, O. E., Lauenroth, W. K. A generalized model of the effect of grazing by large herbivores on grasslands community structure. *Am Nat*, 1988; 130: 168-198.
- Milchunas, D. G., Lauenroth, W. K. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol Monogr*, 1993; 63: 327-366.
- Møller, A.P., Shykoff, J. A. Morphological developmental stability in plants: patterns and causes. *Int J Plant Sci*, 1999; 160 (6 Suppl): S135-S146.
- Nash, M. S., Whitford, W. G., Soyza, A. G., Van Zee, J. W., Havstad, K. M. Livestock activity and Chihuahuan desert annual-plant communities: boundary analysis of disturbance gradients. *Ecol Appl*, 1999; 9: 814-823.
- Noy-Meir, I., Gutman, M., Kaplan, Y. Responses of Mediterranean grassland plants to grazing and protection. *J Ecol*, 1989; 77: 290-310.
- Olf, H., Ritchie, M. E. Effects of herbivores on grassland plant diversity. *TREE*, 1998; 13: 261-265.
- Palmer, A. R., Strobeck, C. Fluctuating asymmetry: measurement, analysis, patterns. *Annu Rev Ecol Syst*, 1986; 17: 391-421.
- Peng, C. K., Buldyrev, S. V., Goldberger, A. L., Havlin, S., Sciortino, F., Simons, M., Stanley, H. E. Long-range correlations in nucleotide sequences. *Nature*, 1992; 356: 168-170.
- Peterson, G. D. Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems*, 2002; 5: 329-338.
- Pickett, S. T. A., Cadenasso, M. L. Landscape ecology: spatial heterogeneity in ecological system. *Science*, 1995; 269: 331-334.
- Rebollo, S., Gomez-Sal, A. Recent changes in transhumance systems: effects on mountain pasture management and conservation. Pages 312-317. In: *Ecological basis of livestock grazing in Mediterranean ecosystems* (Papanastasis V. P., Peter D., eds). European Commission EUR 18308, 1998.

- Rietkerk, M., Ouedraogo, T., Kumar, L., Sanou, S., Langevelde, F., Kiema, A., Van de Koppel, J., Van Andel, J., Hearne, J., Skidmore, A. K., De Ridder, N., Stroosnijder, L., Prins, H. H. T. Fine-scale spatial distribution of plants and resources on a sandy soil in the Sahel. *Plant and Soil*, 2002; 239: 69-77.
- Ruiz, J. P., Ruiz, M. Ecological history of transhumance in Spain. *Biol Conserv*, 1986; 37: 73-86.
- Sánchez, G, Puigdefàbregas, J. Interaction between plant growth and sediment movement in semi-arid slopes. *Geomorphology*, 1994; 9: 243-260.
- Sirkou, D., Alados, C. L., Papanastasis, V. P., Vrahnakis, M. S., Iovi, K., Ginner, M. L., Ispikoudis, I. Assessment of grazing effects on Mediterranean shrubs *Phillyrea latifolia* L. and *Cistus monspeliensis* L. with developmental instability and fractal dimension. *J Med Ecol.*, 2002; 3: 19-29.
- Sole Benet, A., Calvo, A., Cerdá, A., Lazaro, R., Pini, R., Barbero, J. Influences of micro-relief patterns and plant cover on runoff related processes in badlands from Tabernas (SE Spain). *Catena*, 1997; 31(1-2): 23-38.
- Solé, R. V., Alonso, D., McKane, A. Self-organized instability in complex ecosystems. *Phil Trans R Soc Lond B*, 2002; 357: 667-681.
- Stachowicz, J. J., Fried, H., Osman, R. W., Whitlatch, R. B. *Ecology*, 2002; 83: 2575-2590.
- Stockwell, C. A., Hendry, A. P., & Kinnison, M. T. Contemporary evolution meets conservation biology. *TREE*, 2003; 18: 94-101.
- Tan-Kristanto, A., Hoffmann, A., Woods, R., Batterham, P., Cobbett, C., Sinclair, C. Translational asymmetry as a sensitive indicator of cadmium stress in plants: a laboratory test with wild-type and mutant *Arabidopsis thaliana*. *New Phytol*, 2003; 159: 471-477.
- Thomansson, H. Ecomorphologie et port des végétaux . Exemple de quelques formations ligneuses de Madagascar. *Bulletin du Museum de la Historie Naturell Paris 3 sér.* N°460. Botanique, 1977; 31: 49-69.
- Turner, M. D. Spatial and temporal scaling of grazing impact on the species composition and productivity of Sahelian annual grasslands. *J Arid Env*, 1999; 41: 277-297.
- Waddington, C. H. *The strategy of genes*. Allen and Uniwinn, London, 1957.
- Weller, D. E. Self-thinning exponent correlated with allometric measures of plant geometry. *Ecology*, 1987; 68, 813-821.
- White, J. Allometric interpretation of the self-thinning rule. *J Theor Biol*, 1981; 89, 475-500.
- World Commission on Environment and Development. *Our Common Future*. Oxford University Press, Oxford, 1987.
- Wu, H., Sharpe, P. J. H., Walker, J., Penridge, L. K. Ecological field theory: a spatial analysis of resource interference among plants. *Ecol Model*, 1985; 29: 215-243.
- Zakharov, V. Animal asymmetry: populations phenogenetic approach. *Nauka*. Moscow, 1987.