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PLANT CO-EXISTENCE MECHANISMS RELATED TO STRESS AND DISTURBANCE INTENSITIES IN SUB-MEDITERRANEAN AND SUB-DESERTIC GRASSLAND SYSTEMS

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1. SCIENTIFIC BACKGROUND

Plant species co-existence (Fig. 1) may depend upon a complex chain of events involving competitive ability (Navas & Violle 2009), complementarity (Fridley 2001) and facilitation (Callaway & Pugnaire 2007) between plants and numerous interactions with herbivores, pathogens, soil features, fauna and micro-organisms (Grime 2001). The co-existence of species in herbaceous vegetation is possible for the presence of factors that limit the expression of the dominance of plants. This limitation may operate through stress or disturbance or by a combination of them, and its effect is usually to debilitate the potential dominants and to allow plants of smaller stature to regenerate and to co-exist with them (Grime 2001). Species co-existence can reflect niche partitioning at several spatial and temporal scales. The functional strategies avoiding the temporal and/or spatial overlapping of the neighbouring individuals are key factors in the niche partitioning inside the plant community, so that species do not exclude each other by competition (Harris 2001).

Stress and disturbance

Grime (1973, 1974, 1977) put forward a model that describes some of the major factors which influence the species composition of herbaceous vegetation. The model suggests that it is useful to classify the external factors, which affect vegetation, into two broad categories: stress and disturbance. Their effects change according their intensity.

Stress includes factors which restrict the photosynthetic production such as:

- shortage of light;
- shortage of water (drought stress);
- shortage of mineral nutrients;
- thermal stress (cold stress).

Plant biomass production in vegetation is subjected to a variety of environmental constraints, the most frequent of which are related to shortages and excesses in the supply of solar energy, water, and mineral nutrients. In order to accommodate its diverse forms, stress will be defined simply as the external constraints which limit the rate of dry matter production of all or part of the vegetation.

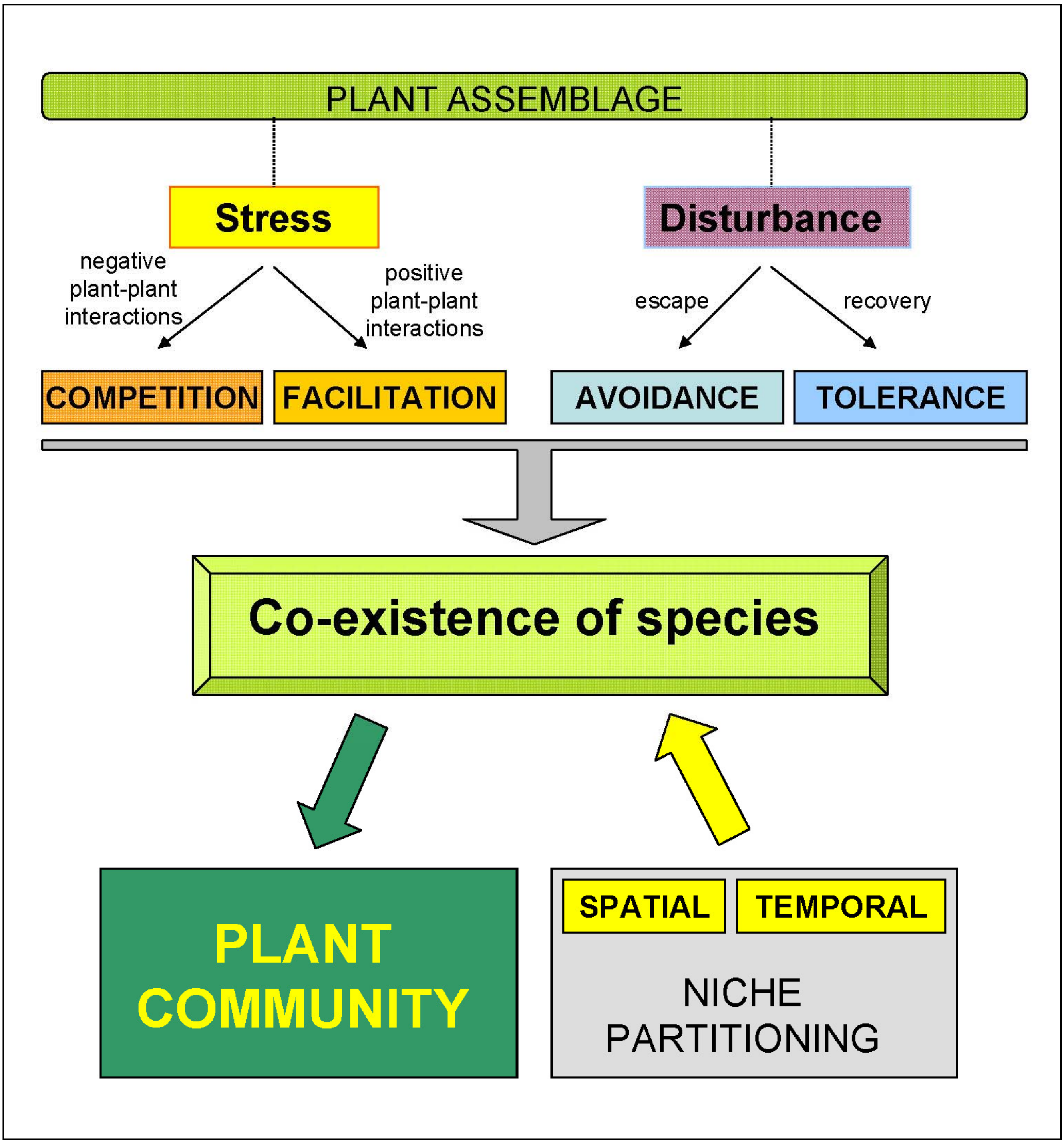

Figure 1. Factors acting on species co-existence and consequently on the assemblage of the plant community.

Disturbance consists of factors which cause the partial or total removal of the vegetation such as:

- grazing;
- mowing;
- forest cutting;
- soil erosion;
- fire.

Disturbance includes mechanisms which limit the plant biomass by causing its partial or total destruction. Whilst the effects of herbivores and decomposing organism tend to be restricted to the living or the dead material, respectively, certain phenomena, e.g. fire, may affect both components of the vegetation. Among the forms of disturbance which affect living components, a distinction may be drawn between mechanisms which involve the immediate removal of plant structures from the habitat (e.g. grazing, mowing) and those in which plant material is killed but remains *in situ* (e.g. frost, drought, application of herbicides).

Competition and facilitation

Vegetation composition and species distribution may be influenced by negative processes (competition) and positive interactions (facilitation).

Darwin (1859) defined competition as “the struggle for existence”. Grime (1979) defined competition as the tendency of neighbouring plants to utilise the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space. Competition refers exclusively to the capture of resources and is only part of the mechanism whereby a plant may suppress the fitness of a neighbour by modifying its environment (Grime 2001).

Competition shows a maximal intensity in habitats with high productivity and low disturbance (Newman 1973; Huston and Smith 1987; Tilman 1988), while this phenomenon completely disappears under conditions of low productivity or intense disturbance.

In order to obtain a more complete assessment of the role of these factors on species density, it is necessary to consider the rather different circumstances which arise when the intensities of stress and/or disturbance become severe. In these harsh habitats the intensities of stress and/or disturbance experienced by herbaceous vegetation are sufficient not only to eliminate potential dominants, but also to produce local environments that are inhospitable to all except a few specialised plants.

As a general ecological process inherent plant community dynamics, the interspecific competition strongly affects plant growth and phenology (Lemaire and Chapman 1996).

Where plants are exposed to extreme stress, such as in desiccated open habitats, it is frequently observed that seedling establishment is promoted under the canopies of established vegetation (Franco and Nobel 1989; Carlsson and Callaghan 1991; Aguiar and Sala 1994). The process of facilitation is a positive plant interaction in which some plants benefit from closely associated neighbours (Padilla and Pugnaire 2006).

Facilitative interaction is a form of commensalism in which plants (known as facilitators, benefactors, or nurse plants) create more favourable micro-habitats than those available in their surroundings for the germination, establishment, and survival of other plants (Valiente-Banuet et al. 1991; Tewksbury and Lloyd 2001).

The mechanisms implicated in these various examples of facilitation include reduced water stress in the shade of nurse plants, avoidance of heat stress, and protection against herbivory. Facilitation occurs widely but is more frequently documented in unproductive habitats (Grime 2001).

The balance between negative and positive interactions should shift along environmental gradients, with competition prevailing under environmentally benign conditions and positive interactions dominating under harsh conditions (Tielborger and Kadmon 2000).

Niche partitioning

The term niche partitioning (synonymous with niche segregation, niche separation and niche differentiation), as it applies to the field of ecology, refers to the process by which natural selection drives competing species into different patterns of resource use or different niches. This process allows two species to partition certain resources so that one species does not out-compete the other as dictated by the competitive exclusion principle; thus, coexistence is obtained through the differentiation of their realized ecological niches. Niche partitioning may not occur if there is sufficient geographic and ecological space for organisms to expand into. In most cases, niche partitioning has created a relationship between two species where competition is small or non-existent.

Niche partitioning is a process which occurs through several different modes and on multiple temporal and spatial scales (Grime 2001).

Spatial heterogeneity

Spatial resource partitioning occurs when two competing species use the same resource by occupying different areas or habitats within the range of occurrence of the resource. Spatial partitioning may occur at small scales (microhabitat differentiation) or at large scales (geographical differentiation). Microhabitat differentiation occurs when two competing species with overlapping home ranges partition a resource.

Even in apparently uniform terrain, most vegetation samples include a complex mosaic of micro-habitats. These arise from such factors as edaphic variation, interactions between micro-topography and climate, selective predation, local disturbance of the soil, and redistribution of nutrients by animals. To these must be added spatial differences in environment arising from the activity of the plants themselves.

These include variation in nutrient availability (Snaydon 1962), water supply (Silvertown et al. 1999), degree of shading, accumulation of litter and organic toxins, and modification of the soil micro-flora.

It is the task of the plant ecologist to identify the circumstances in which this small-scale spatial variation is sufficient to initiate or to maintain conditions favourable to the co-existence of different species.

Temporal heterogeneity

Some coexisting species reduce overlap by using different seasons (Loreau 1989). Temporal resource partitioning occurs when two species eliminate direct competition by utilizing the same resource at different times. This can be on a daily scale or on a longer, seasonal scale. Close scrutiny of small samples of vegetation often reveals situations in which species of contrasted ecology are growing in intimate association and in which it is difficult to explain their co-existence in terms of spatial heterogeneity in environment. In many of these cases, it is apparent that the species concerned have different seasonal patterns of shoot expansion and flowering and are adapted to different parts of the annual climatic cycle. Differences in response to seasonal variation in day length and temperature are particularly important as determinants of the timing of growth, flowering, and vegetative reproduction. Where co-existence involves plants which grow in quite different season of the year, widely contrasted physiologies may be brought together in the same habitat (Grime 2001).

Functional strategies avoiding the temporal and/or spatial overlapping of the leaves of neighbouring individuals are key factors in the niche partitioning inside the plant community, so that species do not exclude each other by competition (Harris 2001). In a pasture, competition for light principally involves differences in the ability of plants to place their leaves above those of adjacent plants or to avoid the shadowing of neighbouring individuals. It is vital, because if a plant has a high proportion of shaded leaves, its net gain of energy by photosynthesis may be less than the respiratory energy it requires for maintaining the tissue (Pugnaire and Valladares 2007).

Avoidance and tolerance

The concept of grazing resistance describes the relative ability of plants to survive and grow in grazed systems (Briske, 1991). The level of resistance is often determined by qualitative and/or quantitative expression of the attribute(s) conferring resistance to the plant (e.g. specific trait approach) (Simms 1992).

In fact, pasture plants do not undergo herbivory passively, but react to defend themselves against grazers by means of two strategies that enable them to survive and grow in grazed systems, namely, avoidance and tolerance.

Avoidance mechanisms are composed of architectural attributes, mechanical deterrents and biochemical compounds which reduce tissue accessibility and palatability. Tolerance mechanisms are composed of the availability and source of residual meristems and physiological processes capable of promoting re-growth of plant tissues (Briske 1996).

In particular, the avoidance strategies are adaptations enabling plants to minimise the damaging effects which grazing directly inflicts on them. Avoidance mechanisms therefore correspond to active-means of plant defence or escape. Some example are indicated below:

- Mechanical defences (prickles, stings, hairs, spines, leaf texture and toughness). Leaf toughness is regarded as among the most important mechanical attributes influencing grazing by both vertebrate and invertebrate herbivores (Theron and Booysen 1966; Coley 1983). Animal preferences and/or accessibility to live biomass within large plants is restricted by the accumulation of culms and senescent leaf material (Norton and Johnson 1983; Ganskopp et al. 1992). When these deterrents are removed, grazing intensity becomes proportional to the canopy volume of plants. Small plants may not be grazed proportionally because herbivores are less likely to locate them within the community (Feeny 1976; Norton and Johnson 1983).

- Chemical defences (unpalatable smell and taste or toxicity due to the presence of specific chemicals). Biochemical compounds are substances capable of deterring herbivores (Mc Naughton 1983; Briske 1991). For example, alkaloids may reduce sheep (Simons and Marten 1971) and cattle preference (Marten et al. 1976). The occurrence of phenolics, cyanide and cyanogenic glycosides as well as condensed tannins deterred grazing (Georgiadis and McNaughton 1988; Redak 1987; du Toit et al. 1991).

- Escape mechanisms (prostrate habit, dormancy, species associations, frequency and distribution). Spatial avoidance mechanisms influence the vertical and horizontal distribution of plant canopies to limit herbivore accessibility. Many species are capable of developing a prostrate decumbent architecture in response to frequent, intensive defoliation. Decumbent canopies are better able to resist grazing because less biomass is accessible to herbivores (Stobbs 1973; Hofmann 1988) and a greater amount of photosynthetic and meristematic tissues remain to facilitate growth following grazing (Detling and Painter 1983; Carman and Briske 1985). Grazing-induced selection primarily affects architectural attributes of plants, rather than physiological processes (Detling and Painter 1983). The associations of less palatable species with more palatable species may also influence the relative frequency and intensity of grazing (Hay 1986). The protection afforded to grasses growing within the canopy of low-growing shrubs is a widely observed example (Jaksić and Fuentes 1980). The benefits derived from associative defences is based on the assumption that the growth reduction resulting from competition with unpalatable plants is less than the growth reduction resulting from severe grazing (Hay 1986).

Tolerance mechanisms are adaptations which enable plants having survived the damaging impact of herbivory, to secure and utilise the resources needed for replacing lost tissue as quickly as possible. Tolerance strategies are therefore mechanisms that promote growth following defoliation. With these strategies the plants seek to recover after the damage. Examples include:

– Meristems (the number and location of growing points from which to replace grazing damage, as the tiller buds on grasses).

– Seeds (the number and viability of seeds from which to replace mortality losses from the population).

– Physiology (compensating mechanisms for restoring levels of production, as photosynthetic ability, uptake of nutrients via roots).

Plant-herbivore interaction

Herbivory is currently defined as the interaction that results when an animal consumes the live tissues of a plant, usually without causing the plant’s death (Crawley 1983). It is an antagonist interaction, in which the animal gets food whereas the plant loses live tissues (Baraza et al. 2007).

Grazing is a major disturbance, which often causes extensive changes in plant richness and composition (Bakker 1998). Watkinson and Ormerod (2001) suggest, variations in the density or seasonality of grazing are key factors in understanding how grazing impacts on plant community composition.

Extensive or semi-intensive grazing has a positive effect on biodiversity (Isselstein et al. 2005, Tallowin et al. 2005). Extensively managed pastures and meadows are of crucial importance for grassland biodiversity across Europe. Unfortunately, biodiversity of such biocenoses is currently threatened either by intensive use or by abandonment (Dolek and Geyer 2002; Poschlod and Wallis de Vries 2002). In many areas of Europe, low grazing pressure leads to the creation of unexploited areas that are progressively covered with shrubs (Bailey et al. 1998). The result is a succession of undesirable plant communities leading to a biodiversity decline (Metera et al. 2010).

On the contrary sub-desertic pastures of Latin America nowadays, as in the past, are subjected to a high disturbance. In fact many grasslands, especially near the villages, are managed by traditional practices of grazing, and burning of the dominant coarse bunchgrasses every 2-5 years to renew forage for livestock (Catorci et al. 2011).

Grazing animals can affect an ecosystem through defoliation, treading and leaving excreta (Warda and Rogalski 2004; Duncan 2005; Wasilewski 2006). The transport of seeds is another significant way in which grazers can influence plant diversity (Olff and Ritchie 1998). Natural fertilization and transport of nutrients in animals' excreta is also important for grassland and adjacent biocenoses which may be used by herbivores for feeding and resting. It may be assumed that wild plants are adapted to herbivores since they have evolved together. However, the intensity of defoliation, treading and natural fertilization in farming landscapes may exceed the levels occurring in natural systems, thus adversely affecting grassland biocenoses (Metera et al. 2010).

Defoliation is the main way in which herbivores affect plant communities. Periodic defoliation is vital for controlling succession of plants (Rook et al. 2004). Intensive defoliation, on the other hand, inhibits the development of trees and shrub seedlings and supports mass growth of grasses (van Braeckel and Bokdam 2002).

Herbivores usually defoliate selectively. Selective defoliation encourages the growth of unpalatable tall plants and supports the creation of a mosaic landscape structure (Warda and Rogalski 2004). Rook et al. (2004) concluded that the main mechanism through which grazing animals influence pastures is their dietary selection, which in consequence creates and maintains the structural heterogeneity of pasture swards.

Treading can have both a positive and negative effect on pasture soil. Treading or trampling creates gaps in the sward and has a positive effect on the establishment of annual, bi-annual species and weeds. (Van Braeckel and Bokdam 2002; Kiss et al. 2011).

The extent of that impact depends largely on the size of grazing animals and the number of individuals per surface area (Isselstein et al. 2007). Bartoszuk et al. (2001) suggest that heavy animals prevent the growth of weeds by trampling and disturbing the soil with their hoofs. According to Vavra (2005), grazing animals can protect specific plant seeds by churning the soil and creating mulches which cover them. On the other hand, trampling may reduce stream bank stability and increase soil erosion (Kauffman et al. 1983; Vavra 2005). The risk of erosion increases when a soil is wet, when animals cut the canopy very short (less than 20 mm) or when stocking rate is too high (Russell et al. 2001).

In addition overgrazing affects soil properties resulting in reduced water infiltration, less soil moisture and fertility. It changes microbiological activity and increases soil erosion (Thurow 2005). High grazing pressure decreases plant diversity, changes the botanical composition of the sward and can lead to the invasion of undesirable plant species. For example, when grazing is intensive, bunch grasses tend to be eliminated. Intensive grazing leads to an increase of short grasses and annuals, which do not stimulate soil maintaining because of their poor root system.

Animal manure plays an important role in creating and preserving biological diversity. The excreta produced by herbivores during grazing act as a natural fertilizer and influence seed distribution. Manure is a rich source of nutritive substances essential for green biomass growth. The dispersal of faeces results in species and structural diversity of flora (Peco et al. 2006). However, intensive grazing can also cause over-fertilization of pastures, disturbing organic matter and the nutrient circulation balance, thus negatively influencing the biodiversity of a whole ecosystem.

Undergrazing can be equally harmful for biodiversity as overgrazing. Undergrazing leads to less stimulation and gradual loss of grazing-dependent endemic grasses and legumes. It was found that long-term grazing abandonment can result in the loss of more than 60% of grassland species (Peco et al. 2006).

The effect of grazing on the ecosystem depends on its intensity, and particularly on livestock density, and the herbivores behaviour has profound effects on plant communities. In fact, the way in which herbivores utilize plants differs between species. This is demonstrated by the different browsing strategies and preferential grazing of different plant species. When the sward is rich in diverse species of flora, animals tend to choose plants which meet best their nutritional requirements. Due selective biting some species decrease and/or disappear, while other plant increase their abundance.

In most habitats, plants are abundant, and therefore food quantity is, in principle, not a problem for herbivores. However, plants are not a highly profitable food because they bear compounds of low nutritive value (high content in cellulose and low in proteins) and substances that reduce digestibility, thus hampering the herbivore's nutrient acquisition (Hartley and Jones 1997). When the sward diversity is smaller, animals start to graze less selectively (Metera et al. 2010). Consequently, there are many ways which plants use to avoid or tolerate herbivores.

Plant traits and functional responses

Milchunas et al. (1988) have hypothesized that the relative importance of plant strategies diverges with increasing primary production that, in turn, is related to environment stress intensity (Tilman 1987; Sala et al. 1988; Berendse 1994; Silvertown et al. 1994). Bullock et al. (2001), affirm that this dichotomy may be simplistic. They assert that response mechanisms can vary, even within the same grassland, depending on the type of grazing animals. In fact, grazers choice is connected to a wide range of factors, including animal condition, season, breed and gender of herbivore (Illius & Gordon 1993; Hulme et al. 1999; Sebastià et al. 2008).

Some plant traits may reflect selection by herbivores, while others are likely to be by-products of selection for other ecological functions (Rosenthal and Kotanen 1994). The former group of traits, involved in the avoidance and tolerance strategies, are mostly related to life history, palatability, features determining the availability of the stored resources for herbivores or to reproductive traits (Briske 1996; Skarpe 2001).

A useful tool to understanding how disturbance acts on plant community assemblage is offered by the analysis of plant functional traits (Lavorel et al. 1997, McIntyre et al. 1999, Pillar 1999, Díaz and Cabido 2001, Hunt et al. 2004, McGill et al. 2006). Plant functional traits are defined as biological characteristics of plant species responding to the dominant processes in an ecosystem (Keddy 1992, Kelly 1996, Gitay and Noble 1997, Lavorel et al. 1997, Kahmen and Poschlod 2008). The advantage of dealing with traits instead of species is that different vegetation types or even floras may be compared and general trends may be exposed (Diaz et al. 2001). Therefore, functional trait responses give information about the mechanisms of processes like management treatments (Gillison and Carpenter 1997, Diaz et al. 1999, Bullock et al. 2001), allowing the assessment of functional differences and shifts acting in complex ecosystems. The comprehension of these mechanisms enables to predict vegetation changes induced by different management types (Noble and Gitay 1996, Roberts 1996, Kleyer 1999, Pausas 1999).

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2. RESEARCH AIM

The research aim was to assess how different types and intensity of disturbance affect species and functional composition of sub-Mediterranean and sub-desertic grassland systems, also in relation with environmental stress. Consequently, the specific research goals were to:

- identify changes in species and functional trait composition and in diversity of plant communities, under different disturbance types (grazing vs. mowing; mown vs. unmown meadows; grazed vs. ungrazed pastures; sheep grazing vs. horse grazing);
- identify coenological and functional responses of grassland to intensity of stress and intensity and timing of disturbance, by analysing the plant functional traits, that are expression of competitive ability, facilitation, co-existence, avoidance and tolerance strategies;
- identify plant-plant spatial interactions, i.e. whether species have species-specific spatial associations, especially in harsh environments; understand how disturbance intensity affect species co-occurrence.

3. STUDY AREAS

Two study areas were considered: sub-Mediterranean grasslands of Umbria-Marches Apennine (central Italy) and the sub-desertic rangelands of southern Peruvian Andes (Peru).

Sub-Mediterranean grasslands (central Italy)

The study site belongs to semi-natural grasslands at altitudes ranging from 800 to 1500 m a.s.l., in the Sibillini Mountains National Park and neighbouring areas, along the mountain ridge of Umbria-Marches Apennine (central Italy) (Fig. 2). It is characterized by limestone substratum and belongs to the upper mesotemperate, lower and upper supratemperate bioclimatic belts (Biondi and Baldoni 1995, Catorci et al. 2009) within temperate region (Rivas-Martinez 2004). The main bioclimatic characteristics of this study site are shown in table 1. Grasslands are subjected to 2-4 months with mean minimum temperatures below 0 °C, with possibility of strong frosts from October to the end of March. There is a short period of water scarcity (drought stress) in late summer, with high temperatures, low rainfall and a very low above-ground phytomass with a lack of re-growth of plant tissues (Fig. 3). Winter cold stress alternates with summer drought stress.

The study area has been marked by traditional pastoral practices for centuries, such as mowing (once a year at the end of June or in early July) and grazing by sheep, cattle and horses. As in the whole Europe, the semi-natural calcareous grasslands are in strong decline in extension and threatened by abandonment. In the last decades these practices underwent a collapse thus often abandoned grasslands occur.

Bioclimatic belt	Altitudinal range (m a.s.l.)	Average annual (T °C)	Average annual (P mm)	N° of months with annual T<10 °C	N° of months with tmin<0 °C	Thermotype	Ombrotype	Drought stress N° months	Cold stress N° months	Length of growing period (N° days with tmin>6 °C)
Upper Mesotemperate	450-1000	11-13	850-1100	5-6	1-2	Upper Mesotemperate	Lower Humid	0	6-7	180-210
Lower Supratemperate	1000-1450	9-11	1100-1300	6-7	2-3	Lower Supratemperate	Upper Humid	0	7-8	150-180
Upper Supratemperate	1450-1900	7-9	1300-1500	7-8	3-4	Upper Supratemperate	Lower Iperhumid	0	8-9	120-150

Table 1. Main bioclimatic characteristics of the study area.

Figure 2. Study area concerning the sub-Mediterranean grasslands in the Sibillini Mountains National Park along the mountain ridge of Umbria-Marches Apennine (central Italy).

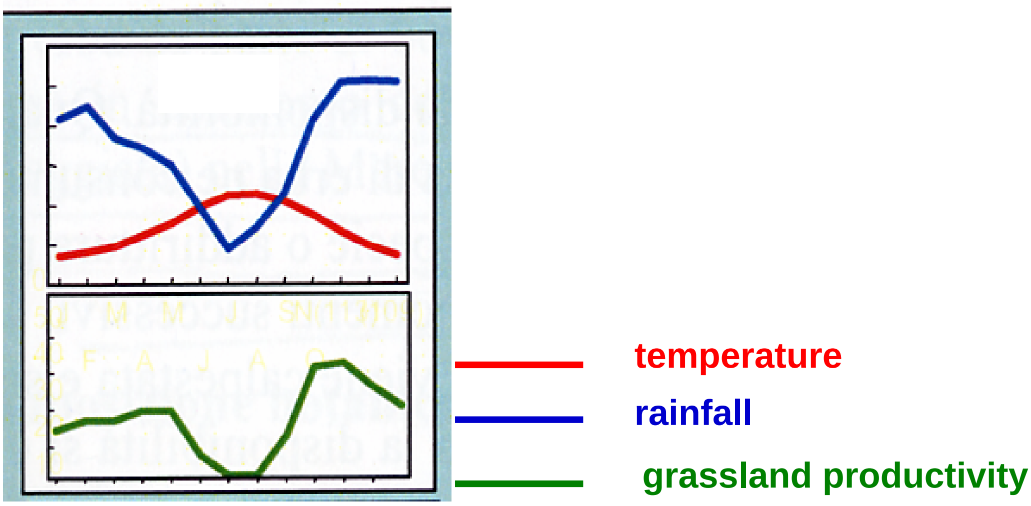

Figure 3. The seasonal trend of temperature, rainfall and productivity in Sub-Mediterranean grasslands (from Pardini 2006).

Sub-desertic grasslands (southern Peru)

This study area belongs to semi-natural rangelands of Salinas and Aguada Blanca National Reserve (RNSAB) within Arequipa and Moquegua Departments at about 3500-5000 m a.s.l (Fig. 4). This protected area is sited in the Southern Peruvian Andes and represents a typical dry Puna landscape of Latin America (Zeballos et al. 2009). From geomorphological viewpoint, this area is characterized by volcanic structures covered by saline soils and deposits of volcanic ash. From bioclimatic point of view this area is included in Neotropical Kingdom, Andean Subregion, Puna Region and in upper mesoandean, lower highandean and upper highandean bioclimatic belts (Rivas-Martínez & Tovar, 1982). The mean annual temperature range is 2-8 °C with sharp diurnal and annual variations, from freezing to temperatures of more than 30 °C. Rainfall is concentrated in a rainy season (from December to March), with annual precipitation ranging between 200 and 600 mm, while during the other months this ecosystem is affected by water shortage and cold stresses with absence of grassland productivity (Fig. 5); soil moisture ranges from 0 (dry season) to below 10% in the rainy season (Montenegro et al. 2010). Thus, this study site is subjected to a short and hot rainy season alternated with a long and cold dry season.

Grasslands of study area are grazed by camelids livestock (lamas, vicunas, alpacas) and sheep. This pastoral practice represents an essential livelihood resource for the people living in the reserve, whom exploited very intensively these pastures, especially those in the surroundings of farms and villages. Furthermore, throughout the Peruvian dry Puna, there is the widespread practice of burning to renew forage for livestock (Garcia and Beck 2006). Overgrazing in combination with burning causes different environmental damages as soil erosion, accelerating desertification process.

Figure 4. Study area concerning the sub-desertic grasslands located in the Salinas and Aguada Blanca National Reserve (southern Peruvian Andes).

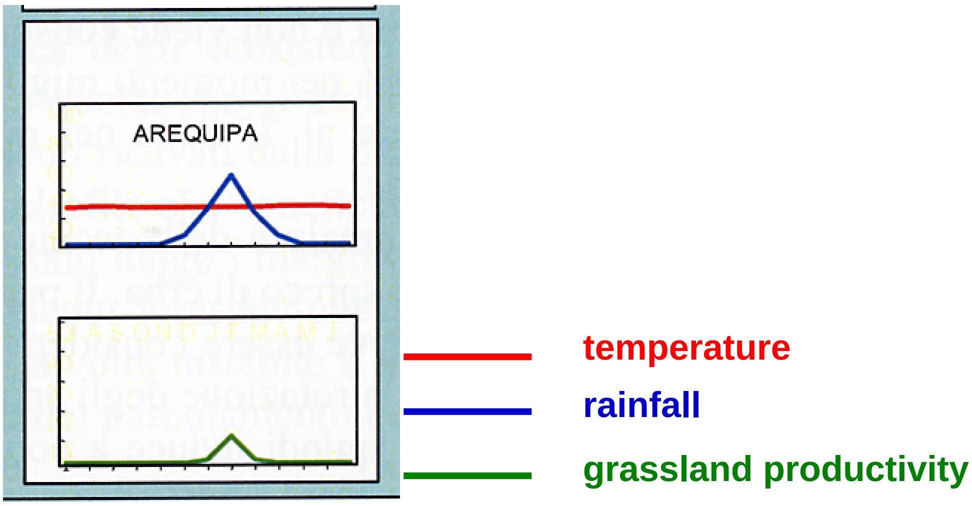

Figure 5. The seasonal trend of temperature, rainfall and productivity in Sub-desertic grasslands (from Pardini 2006).

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4. WORKING PLAN

In order to achieve the research goals, in sub-Mediterranean and sub-desertic grasslands, the research project started with the literature search and study of papers and scientific publications focused on the grassland biodiversity conservation. In addition, issues on the effects of environmental stress and disturbance gradients on plant communities, grassland management, plant-plant interactions and plant functional traits differentiation were consulted.

Considering the above-mentioned subjects, data were collected and statistical analysis was performed, following this working plan.

Sub-Mediterranean grasslands

- **I year (2009): Forage resources modelling at a large scale in the pastoral systems of the Umbria-Marches Apennine (central Italy)**
  - Phytosociological analysis
  - Agro-zootechnical analysis (productivity, pastoral value, bromatological composition, carrying capacity)

- **II year (2010): plant community differentiation assessment by means of floristic and functional analysis**
  - Analysis of spatial and temporal patterns of stress and disturbance intensities in a sub-Mediterranean grassland landscape
  - Functional differentiation assessment of central Apennine grasslands under mowing and grazing disturbance regimes
  - Long-term pattern of floristic, functional and phytosociological changes under different management conditions in Apennine meadows and xeric grasslands

- **III year (2011): Effects of selective defoliation and of different behaviour of grazers on plant community**
  - Analysis of horse and sheep grazing effects on grassland composition

Sub-desertic grasslands

- **I year (2009): Plant landscape assessment of Salinas and Aguada Blanca National Reserve**
  - Floristic, phytosociological and ecological analysis
  - Plant community description and ecology

- **II year (2010): Facilitation processes in *Festuca orthophylla* plant community**
  - Identification of the nurse and beneficiary species
  - Assessment of plant-plant spatial interactions
  - Functional analysis of indicator plant traits

- **III year (2011): Stress and disturbance effects on floristic and functional composition of Dry Puna landscape**
  - Overgrazing and fire effects analysis
  - Floristic and functional differentiation assessment of grasslands subjected to different disturbance regime intensity
  - Co-occurrence individuation between potential nurses and beneficiary species

5. RESEARCH ACTIVITIES

Sub-Mediterranean grasslands

<u>**I YEAR**</u>

Forage resources modelling at a large scale in the pastoral systems of the Umbria-Marches Apennine (central Italy).

During the first year, the phytosociological study combined with the analysis of agronomic parameters (pastoral value, seasonal productivity, coefficient of theoretical use of phytomass, theoretical carrying capacity and bromatological characterization) of the Umbria-Marches Apennine pastoral systems was performed. This study showed that each *syntaxon* is characterized by different agronomic parameters. In addition, the comparison between theoretical carrying capacity and real carrying capacity allowed to know the disturbance condition (overgrazing, undergrazing or the optimal number of herbivorous grazing in the pastoral system).

This approach allowed to obtain the forage resources modelling at a large scale in a pastoral system, to define the optimal management and decision making aimed on biodiversity conservation.

The analytical process is based on correlation between phytosociological and agro-zootechnical analysis. This approach allows to extend any type of data (provided this is in any way correlated to the intrinsic characteristics of the plant community) to the whole polygon and therefore to all polygons referring to the same phytosociological unit. In terms of planning and application, the results of phytosociological modelling are much more useful when integrated in a database (GIS), in which the different information levels, based on hierarchical criteria, are simulated in multiple polygon segmentations. In particular, this method allows to obtain a first general overview of the forage resource using the theoretical data linked to the phytosociological interpretation of the territory. Subsequently, this overview can be enhanced with actual quantitative data, offering also a qualitative dimension coming from the phytosociological aspects.

Scientific papers:

1) ***Cesaretti S., Castagna S., Montenegro B., Catorci A. 2009.*** Zootechnical characterization of grassland vegetation in a pastoral system as a tool for biodiversity conservation: A case study of Umbria-Marches Apennine. **INFORMATORE BOTANICO ITALIANO 41 (2): 247–258.**

2) ***Catorci A., Cesaretti S., Gatti R. 2009.*** Biodiversity conservation: Geosynphytosociology as a tool of analysis and modelling of grassland systems. **HACQUETIA 8 (2): 129–146.**

II YEAR

Plant community differentiation assessment by means of floristic and functional analysis.

The second year of research involved the investigation of the effect of spatial and temporal patterns of stress and disturbance intensities, focusing on the floristic and functional changes owing to different management type (mowing and grazing). Furthermore, grassland changes due to abandon effects were examined (mown *versus* abandoned meadows; grazing *versus* abandoned grassland).

Spatial and temporal patterns of stress and disturbance intensities.

It has been examined a sub-Mediterranean pastoral system with a long history of grazing, where winter cold stress is alternated with summer drought stress. Considering the variations in density or seasonality of grazing as key factors to understand how grazing impacts on plant community composition.

Scientific paper:

Catorci A., Ottaviani G., Vitasović Kosić I., Cesaretti S. 2011. Effect of spatial and temporal patterns of stress and disturbance intensities in a sub-Mediterranean grassland. **PLANT BIOSYSTEMS. DOI:10.1080/11263504.2011.623192 (in press).**

Research aim: The research goals were to ascertain whether different floristic structures correspond to different stress conditions (xeric and semimesic), and whether peculiar functional plant traits (such as avoidance and tolerance mechanisms) respond to stress/disturbance intensities, and understand how vegetation reacts to changeable livestock pressure (through floristic and plant trait variations).

Study area: Pian della Cuna - Visso (Macerata province, Marches Region) located along the mountain ridge of Umbria-Marche Apennine (central Italy) between 1100 and 1360m a.s.l.

Data collection: integrating soil data, plant diversity data, disturbance intensity, environmental constraints and effects of herbivorous forage selection.

- Plant community survey using Braun-Blanquet method (1964)
- Soil features (texture, depth and N content)
- Thermo-pluviometric data
- Aboveground phytomass productivity
- Plant functional features
- 10-m transects in grazed and ungrazed patches

Data analysis: Cluster analysis using Syntax 2000 Software; Independent t-test, Multivariate discriminant function analysis (DFA) and Pearson correlation analysis using SPSS 13.0 software.

Results: Stress and disturbance intensity affect plant community functional response and can also lead to changes in plant community structure. Patches formation occurs in semisemic grassland where a brief period of overgrazing occurs in late summer. These spiny cushions are dominated by spiny species as *Astragalus sempervirens* and *Eryngium amethistinum* and by species with tough and silica-rich leaves (unpalatables) as *Brachypodium rupestre*, as consequence of herbivorous selection and facilitation processes.

Both the studied plant communities are strongly marked by historical grazing, because all the collected species show one or more avoidance/tolerance strategies.

DFA showed as the most relevant plant traits in xeric grassland are hairs and leaf texture, representing mainly plant adaptations to environmental constraints (water shortage). They could play a double role because can lower the evapotranspiration and render the leaves less palatable to grazers.

In semimesic condition either avoidance mechanisms (leaf distribution, chemical substances, spines, prostrate form and unpalatability) and tolerance strategies (re-growth capacity) occur.

Conclusion: Stress and disturbance levels act in concert in the definition of the winner strategies within the plant community, showing a direct relationship between stress/disturbance intensity and the strength of plant strategy response. Best practices for management were identified. In xeric conditions, it is advisable that the intensity of disturbance be lessened, while in semimesic grassland overgrazing should be forbidden during the dry period, because it could facilitate the development of spiny patches, and subsequent spread of *Brachypodium rupestre*.

Functional differentiation under mowing and grazing disturbance regimes.

It has been studied the functional differentiation of grasslands potentially developing the same vegetation type because sited in the same environmental contest (bioclimate, substratum, soil, slope, altitude) but under diverse management regimes (grazing and mowing) for many decades.

Scientific paper:

Catorci A., Ottaviani G., Ballelli S., Cesaretti S. 2011. Functional differentiation of central Apennine grasslands under mowing and grazing disturbance regimes. **POLISH JOURNAL OF ECOLOGY 59(1): 115–128.**

Research aim: The aim of this work was to understand if and how different disturbance types affect floristic compositions and plant functional traits set, thus the ecological functions, in central Apennine grasslands.

Study area: Mown and grazed grasslands located at 1500m a.s.l.,inside Sibillini Mountains National Park along the mountain ridge of Umbria-Marche Apennine (Central Italy).

Data collection: To compare grasslands with the same stress intensities but subjected to different disturbance (grazing and mowing), the following data were collected:

- Soil features
- Plant diversity using point quadrat method
- Plant functional features

Data analysis: Principal coordinates analysis (PCoA) using Syntax 2000 Software; Independent t-test, One-way ANOVA, Multivariate discriminant function analysis (DFA) and Pearson correlation analysis using SPSS 13.0 software.

Results: This research demonstrated how different disturbance types lead the separation of floristic composition and that late-mowing favours a higher species richness, life forms and functional strategies; grazing is a more selective disturbance regime than mowing. Species having different functional adaptations (as represented by traits combinations) are advantaged by the system. Grazing favours grasses (especially *Poaceae* species) while mowing advantages tall species. Mowing favours the affirmation of species equipped with dominant strategies (*Brachypodium genuense* and *Carex macrolepis*) that probably are not under control in late mowing managed grassland, having involvement for species richness and distribution responding to Grime's hump-back model (2001). This could highlight that probably in central Apennine grasslands only mowing cannot ensure the long-term maintenance of the floristic peculiarities, thus it should be suitable an integrated management strategy, planning a late mowing followed by a moderate grazing.

Conclusion: Both grazing and mowing provoke aboveground phytomass remove but act in different ways on plant community: grazing is a selective pressure, while late-mowing gives to all the species the same development chances. Hence, it is understandable that convergent strategies within the two systems are possible and frequent. Finally this study has confirmed how disturbance represents the main environmental driver for plant community differentiation, either at floristic and functional traits level, in central Apennine landscape too.

Mowing and grazing, mowing alone, and abandonment: functional and coenological changes under different long-term management conditions in Apennine meadows.

In seeking to understand plant community shifts due to management modification, simple measurements of species richness may lead to misleading conclusions for conservation issues; to avoid such pitfalls, species grouping by social behaviour type (SBT) can be useful for understanding ecosystem dynamics and properties.

The theoretic framework follows Grime's theory about the correlation between species richness and disturbance intensities.

Scientific paper:

Catorci A., Ottaviani G., Cesaretti S. 2011. Functional and coenological changes under different long-term management conditions in Apennine meadows (central Italy). **PHYTOCOENOLOGIA 41: 45–58.**

Research aim: the research aim was to understand long-term change patterns in Apennine meadows due to management modification. Hence the research goals were to characterize physiognomic and coenological changes, identify floristic shifting (species richness and turnover), formulate an ecological and functional interpretation of floristic change, and detect threatened species.

Study area: Sub-Mediterranean meadows, namely "Prati di Ragnolo" subjected to three kinds of management entailing different disturbance intensities, located in the Sibillini Mountains National Park at about 1450 m a.s.l.

Data collection: Phytosociological relevés were carried out in three different management-disturbance situations, namely mowing and grazing, mowing alone, and abandonment. Plant functional traits, social behaviour types and bioindication values were considered.

Data analysis: MRPP and ISA elaborations were executed using PCOrd 5.0 software while the Independent t-test and the Mann-Whitney U-test were performed using SPSS 13.0 software.

Results: The three identified plant communities corresponded to three different disturbance intensities, and that species richness was comparable between high disturbance situation and those of void disturbance, whilst it considerably decreased under intermediate disturbance. High disturbance condition vs. void disturbance comparison showed the higher differences regarding: species turnover (57% of Sørensen similarity index and 45 differential species), light request and pH soil reaction. Hemicryptophytes, fringe social behaviour type (SBT3), upright forbs, clonal ability, late flowering period emerged as differential traits and species height increases moving to undisturbed situation. Other important evidences concern avoidance strategies which are favoured by mowing and grazing, whereas species equipped with late flowering period and clonal ability are advantaged under intermediate and void disturbance conditions.

Conclusion: Grazing cessation but mowing maintenance lead to slight functional and floristic differences, and allow the conservation of the main plant community characteristics. Mowing alone does not ensure long-term control of dominant species. Abandonment drastically changes the plant community composition and ecology; in this case many grassland and meadows species disappeared while generalist species, mostly living in open woods or fringe habitats, become very numerous and abundant. With the aim of biodiversity conservation, hay cutting every two or three year probably being sufficient to prevent local extinction of threatened species.

Mown *versus* abandoned meadows: abiotic and biotic changes due to spread of *Brachypodium genuense*(DC.) Roem. & Schult. in sub-Mediterranean meadows under different management type.

Semi-natural calcareous grasslands threatened by the abandonment of traditional management practices were studied. In fact, as a consequence of pasture abandonment, tall grasses tend to dominate the plant community through specific plant traits such as tall canopies, extensive lateral spread, litter deposition, and capacity to project shoots through litter and herbaceous cover thus influencing the availability of soil nutrients and light at ground level. For this reason, the impact of the invasive species *Brachypodium genuense* in central Apennine meadows was studied.

Scientific paper:

Catorci A., Cesaretti S., Gatti R., Ottaviani G. 2011. Abiotic and biotic changes due to spread of Brachypodium genuense (DC.) Roem. & Schult. in sub-Mediterranean meadows. **COMMUNITY ECOLOGY 12(1): 117–125.**

Research aim: the research evaluated abiotic and biotic changes due to the cessation of management in sub-Mediterranean mountain meadows.

Study area: The study compared meadows of the "Prati di Ragnolo" located at about 1450 m a.s.l. in the Sibillini Mountains National Park, but subjected to different management types (mown *versus* abandoned).

Data collection: five patches that are mown once a year and five abandoned patches (for 20 years) were chosen. In these patches the following data were collected:

- *B. genuense* above-ground productivity and litter production
- Soil features
- Species cover value (%) and the number of flowering shoots of each species in bloom (six spatial scales were examined, as were five dates)

Data analysis: the species richness and floristic diversity of the mown and abandoned conditions, Shannon-Wiener diversity (H') and Evenness (E) indices, and Sørensen index of community similarity were evaluated.

Independent t-tests and Mann-Whitney U-tests were performed using SPSS 13.0 software,while PCAwas performed using the SYN-TAX 2000 package.

Results: *B. genuense* spread in the abandoned condition alters the ecological status of the site. It lowers soil temperature, moisture and pH, while it increases soil C/N ratio and litter production. In terms of biotic features, phenological analysis indicated that the abandoned condition is less rich in flowering species and individuals in each analysed date. We observed a less affected temporal niche (during the first phase of *B. genuense* leaf growth) and two strongly influenced phases (in early spring and in correspondence with phases when *B. genuense* flowers and has full growth of leaves). Functional trait analysis indicated that species with runners, ability to form patches, and late flowering strategies benefit from *B. genuense* spread, whereas species marked by storage organs, small size, and early flowering strategies benefit in the mown condition. However, it seems that only low frequency species are heavily threatened, while the others can remain inside the plant community by shelter niche occupation.

Conclusion: Hay cutting every two or three years should be sufficient to prevent local species extinction and to foster biodiversity conservation. This kind of management, in fact, should preserve enough temporal and spatial niches for subordinate and accidental species.

Abandonment and spring grazing effect on dry grasslands.

In this study case, grasslands grazed by sheep in late winter and spring until 1980 were investigated. Nowadays, the site is abandoned.

Scientific paper:

CatorciA., Cesaretti S., Gatti R. Effect of long-term abandonment and spring grazing on floristic and functional composition of dry grasslands in a central Apennine farmland. **ACTA BOTANICA CROATICA (Submitted).**

Research aim: The aim was to assess plant community changes due to abandonment and the effect of spring grazing in sub-Mediterranean dry grasslands, focusing on the plant functional traits set involved in this turnover.

Study area: Abandoned grasslands located in the central Apennines between 700 and 850 m a.s.l characterized by alternation of winter cold stress and summer drought stress.

Data collection: We compared two groups of 30 relevés performed with the Braun-Blanquet method (1964) in 1976-1980 (grazed pasture) and again in 2010 (abandoned pasture). To detect plant community functional composition and shifts in ecological needs, the plant functional traits and bioindication values were considered.

Data analysis: PCoA was run using the Syn-tax 2000 package, ISA elaboration using PCOrd 5.0 software and Mann-Whitney U-test using SPSS 13.0 software.

Results: Results indicate that abandonment leads to the increase of species richness. The indicator functional traits were therophyte for the grazed pasture, and geophytes, flower palatability, and early flowering strategy for the abandoned ones.

Traits related to low levels of stress (tolerance strategies) are heavily reduced in grazed systems, and thus the plant community functional composition is mostly characterized by traits related to drought stress. In abandoned condition a higher number of species can co-exist thanks to the micro-scale variation of soil features, particularly soil water availability and the low cover value of tall dominant grasses that were able to spread only in niches with deep soil.

Conclusion: Assessment of grazing timing emerged as a key factor for understanding changes of plant functional trait along disturbance gradients. It is possible to state that comparisons among different grassland communities have to consider not only site productivity, intensity, and kind of grazer, but also the timing of grazing; without the latter factor, comparison of different sites could give erroneous results and lead to incorrect predictive models and biodiversity conservation planning.

III YEAR

Effects of selective defoliation and different behaviour of grazers on plant community

In the third year the research project has been focused on the functional plant traits response of pastures grazed by different herbivores, considering the level of primary production, the intensity of defoliation, and the foraging behavior of grazers. In particular horse and sheep grazing effects on grassland composition were analysed.

Scientific paper:

Catorci A., Gatti R., Cesaretti S. Effect of sheep and horse grazing on species and functional composition of sub-Mediterranean grasslands.

APPLIED VEGETATION SCIENCE (Accepted).

Research aim: How does horse or sheep grazing affect species richness, diversity and functional composition of plant communities in sub-Mediterranean grasslands? How do these different types of grazing management influence species conservation?

Study area: Pastures dominated by *Bromus erectus* grazed by sheep or by horses in the Umbria-Marches Apennines (central Italy) were compared.

Data collection: We examined grasslands at altitudes ranging from 1000 to 1200 m a.s.l., on north-facing slopes and with slope angle of 20-40°. In 20 plots of 1 m^2 for each management type, canopy height and aboveground phytomass were recorded. In 120 plots (60 for each management type) of 1 m^2 the cover value of each species was recorded. Floristic diversity and community similarity of the sheep- and horse-grazed conditions were compared. Functional plant traits and strategies or ecological needs were also evaluated.

Data analysis: Species richness, Shannon-Wiener, Evenness, Sørensen and Simpson diversity indexes, Functional diversity. Mann-Whitney U-test and Pearson Correlation Analysis by SPSS 13.0 Software; Multi-Response Permutation (MRPP) and Indicator Species Analysis (ISA) by PCOrd 5.0 Software; Canonical Redundancy Analysis (RDA) by R software.

Results: Sward canopy height and aboveground phytomass had lower values in the horse-grazed area. The sheep- and horse-grazed areas had similar floristic diversity. Accidental species emerged as the species most affected. Plants with low nutrient needs spread in horse-grazed pasture. Functional differentiation caused a diverse cover value of species whose combination of functional traits is filtered by the system. In the horse-grazed area, plants require a strong defence strategy (avoidance and tolerance) to grow leaves when horses are not grazing, and to have clonal growth. In the sheep-grazed area, a higher level of selective defoliation and a delayed start to the grazing period promoted species with low palatability, a late flowering strategy, and those intolerant of trampling by large herbivores (chamaephytes). The forage feed value was slightly higher in horse-grazed pasture. Grazing of horses emerged as more effective for controlling dominant unpalatable tall grasses.

Conclusion: In terms of biodiversity conservation, horse grazing may be considered as useful as sheep grazing, but only if managed at optimal stocking rates, because the increase of short grasses and annuals, species with poor root systems, does not ensure maintenance of soil on steep slopes.

Sub-desertic grasslands

<u>I YEAR</u>

Plant landscape assessment of Salinas and Aguada Blanca National Reserve.

During the first year in order to define the main plant communities of the study area, floristic data, phytosociological relevés, ecological and soil features were collected. The aim is to achieve the knowledge about plant communities floristic structure, distribution and site ecology with stratified sampling by morphological, aspect and altitudinal features assessment. In addition, *Festuca orthophylla* plant communities were analysed with more attention. In fact this species with its large distribution characterizes the "Pajonal" that is the vegetation type which occupies the greater part of grassland surface (61%)of Salinas and Aguada Blanca National Reserve.

This vegetation is characterized by big *Poaceae* with tough leaves as *Festuca orthophylla* and *Stipa plumosa*. In the first research step, different Pajonal types were preliminarly described from a physiognomic and ecologic point of view.

1) Low dry Pajonal, extended at lower altitudes of Western Andean ridge, is composed by a lot of *Poaceae* dominated by *Festuca orthophylla* or *Stipa plumosa.*
2) Middle slope Pajonal, with low floristic richness and characterized by *Festuca orthophylla* and *Lupinus saxatilis.*
3) High slope Pajonal, extended near the Hemicryptophytes upper limit of distribution, where *Festuca orthophylla* and *Calamagrostis mexicana* are the most important species.
4) Very dry Pajonal, where *Festuca orthophylla* and pulvinate or plate forms species are dominant.

The first and the fourth plant comunities seem to develop following a drought stress gradient; on the other hand, the second and the third seem to be related to a tempeature (altitudinal) gradient. In the first case, catenal contact is with high Andean semidesert plant community (Confital), while in the second case the contact is with Yaretales one.

Publications:

1) ***Cesaretti S., Velásquez J.L., Zeballos H., Catorci A., 2009.*** Geosynphytosociological landscape analysis of Salinas and Aguada Blamca National Riserve as a tool for actual plant mosaic understanding. **ABSTRACT OF INTERNATIONAL CONGRESS SISV & FIP, Cagliari 22-24 giugno 2009. pp. 140.**

2) ***Cesaretti S., Zeballos H., Velásquez J.L., Catorci A., 2009.*** Preliminary analysis of overgrazing effects on floristic structure in tropical subdesertic grasslands (Peru). **ABSTRACT OF INTERNATIONAL CONGRESS SISV & FIP, Cagliari 22-24 giugno 2009. pp. 139.**

The preliminary scheme (Fig. 6) of Salinas and Aguada Blanca National Reserve (RNSAB) landscape particularly focused on *Festuca orthophylla* plant community (dry Puna landscape and desertic Puna landscape unit) is illustrated below.

QUECHUA LANDASCAPE UNIT

It covers the territory between 2300 and 3500-3700 m a.s.l. It is the most populated region of the Sierra and the origin of the Andean culture. The inter-Andean valleys and the most important Andean cities, like Arequipa, are placed in this region.

SUNI (YALCA) LANDASCAPE UNIT

It is the highest level where agriculture is possible and where are present the last fragments of *Polylepis rugolosa* woods, that extends into the western side of the Andean chain.

***Polylepis rugolosa* wood series (Queñuales)**
Head series:
- *Polylepis rugolosa* community (Queñua woods) from 3500- 3700 to 4000-4200 m a.s.l.
Replacement stage:
- *Stipa plumosa* grassland community
- *Festuca orthophylla* and *Poa pearsonii* grassland community

DRY PUNA LANDASCAPE UNIT

It is the most widespread landscape unit and includes the dry Andean steppe.

***Parastrephia* sp. pl. shrubs series (Tolares)**
Head series: *Parastrephia lepidophylla* and *Parastrephia phyllicaeformis* community (Tola shrubs) from 4000-4200 to 4400-4600 m a.s.l.
Replacement stage:
- *Calamagrostis breviaristata* and *Festuca orthophylla* grassland community
- *Festuca orthophylla and Lupinus saxatilis* grassland community
- *Festuca orthophylla and Stipa depauperata* grassland community

***Distichia muscoides* mesohygrophilous grass series (Bofedales)**
It ranges from 3900 to 4900 m a.s.l. and is characterized by very palatable species typical of humid environment, like *Distichia muscoides, Werneria orbignyana* and *Alchemilla diplophylla.*

JANCA (NIVAL) LANDASCAPE UNIT
It is the Andean peacks landscape.

***Festuca orthophylla* and *Calamagrostis mexicana* grass series**
It ranges from 4400-4600 to 5000-5200 m a.s.l.. Represents the primary grassland; landscape is characterized by *Festuca orthophylla* and *Calamagrostis mexicana* with *Azorella yarita* community.

***Azorella yarita* grass series (Yaretales)**
It ranges from 5000-5200 to 5400-5600 m a.s.l. on a very rocky area where only *Azorella yarita* and few species can live in adverse climatic conditions.

Glacial desertic zone
It is included between 5400-5600 m a.s.l. and the mountains peak. Bare rocks and glaciers characterize the landscape.

DESERTIC PUNA LANDASCAPE UNIT

***Pycnophyllum molle* grass series (Semi-desierto)**
It ranges from 4400-4500 to 4800-4900 m a.s.l on hilly top. Is characterized by pulvinate plant as *Pycnophyllum molle* where other species grow like *Azorella* sp., *Calamagrostis* sp., *Distichia muscoides*.

***Calamagrostis curvula* grass series (Césped de Puna**)
It ranges from 4400-4500 to 4800-4900 m a.s.l. on depressions (U-shaped). Typical plant structures are pulvinate forms, low flat rosettes and small dimensions. The main species are *Calamagrostis curvula, Pycnophyllum molle, Azorella compacta, Carex ecuadorica, Nototriche longisima, Poa spiciegera, Muhlenbergia peruviana* and *Poa horridula*.

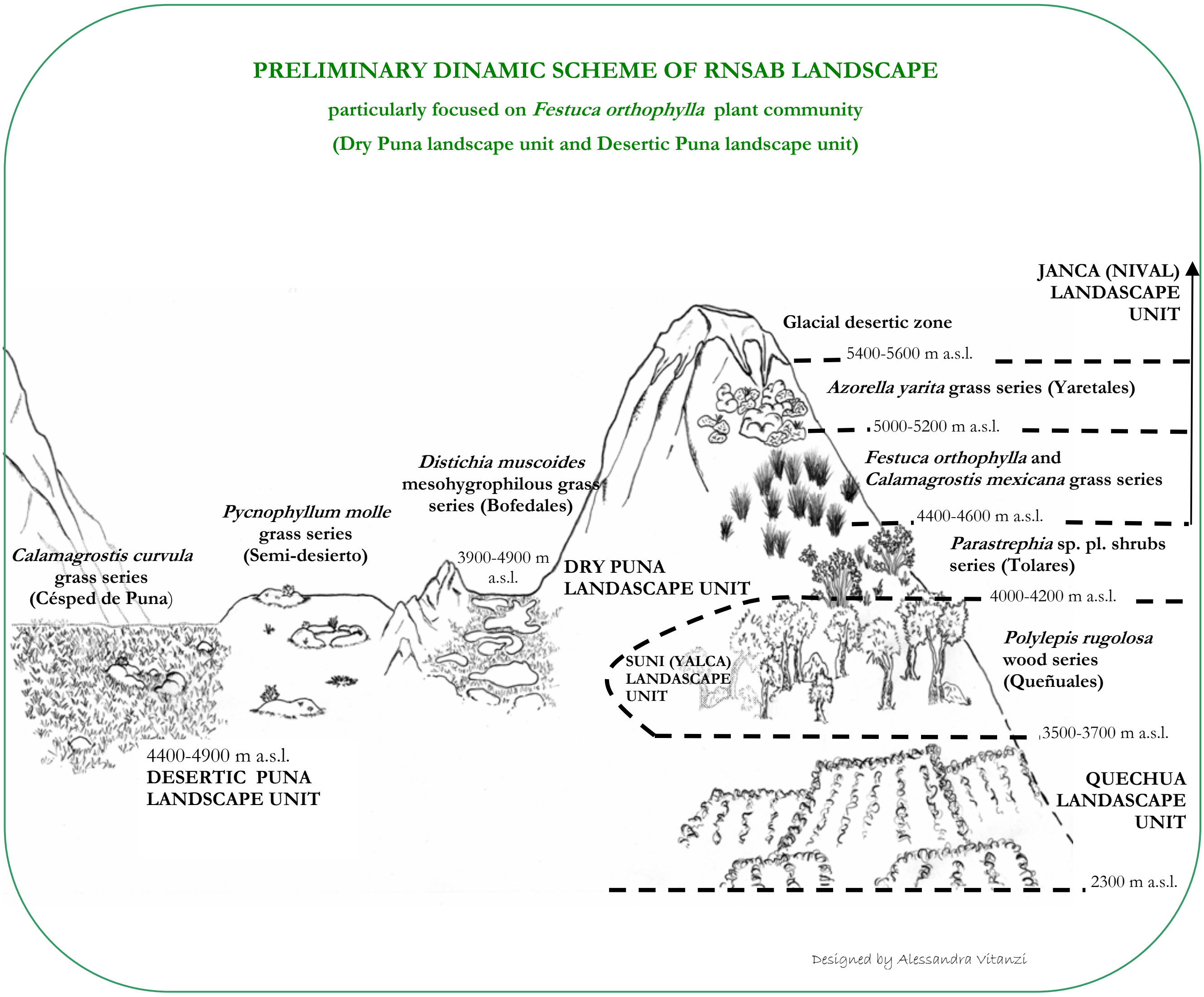

Figure 6. Preliminary scheme of Salinas and Aguada Blanca National Reserve (RNSAB) landscape.

<u>II YEAR</u>

Facilitation processes in *Festuca orthophylla* plant community.

In the Andean region, several studies have focused on cushion nurse species but little is known about the spatial associations in communities dominated by tall grasses such as those found in the dry Puna. This type of vegetation is widespread in a very arid and harsh environment, so that positive plant–plant interactions are expected to play a key role. Considering this lack of knowledge, during the second year the plant–plant interactions regulating the assemblage of *Festuca orthophylla* community were investigated.

Scientific paper:

Catorci A., Cesaretti S., Velasquez J.L., Zeballos H. 2011. Plant-plant spatial interactions in the dry Puna (southern Peruvian Andes). **ALPINE BOTANY 121(2): 113–121. DOI: 10.1007/s00035-011-0097-1.**

Research aim: The research aim was to ascertain whether spatial plant–plant interactions act in the dry Puna, in order to determine whether beneficiary species have species-specific spatial associations with certain nurse plants; how the spatial interactions affect the species distribution, richness and the biodiversity conservation at local scale.

Study area: *Festuca orthophylla* grassland (dry Puna) of Salinas and Aguada Blanca National Reserve, in the southern Peruvian Andes.

Data collection: Plots in grasslands with the same altitude (4400–4600), aspect (south-facing), slope (10–20°) and disturbance intensity and type (moderate grazing by camelids) were considered. 20 linear transects, each 10 m long and divided into 20 plots (50 cm x 50 cm), were randomly laid out (the distance between the transects was never less than 500 m). Nurse species cover values (cm^2), the occurrence of beneficiary species and the different spatial interaction types (SIT) were recorded in every plot.

Data analysis: linear regression analysis was performed using the SPSS 13.0 software package; Principal component analysis (PCA) by the Syn-tax 2000 package; Indicator species analysis (ISA) by PCOrd 5.0 software.

Results: the most important nurses were the tall tussock species. A direct correlation was observed between the dimension of the *F. orthophylla* tussocks and the number of beneficiary species. Twelve species were closely associated with nurse species; five occurred in relation with nurse plants but without any preference for one of them; four species grew both isolated and in relationship with nurse plants and six species mostly grew isolated on bare soil.

Conclusion: Because of the impact of grazers, some plants cannot grow on open ground; in fact, the species most in need of spatial interactions are those without avoidance strategies and/or with broad leaves. *F. orthophylla* is the core of a clumped spatial pattern of vegetation. The importance of spatial interactions for biodiversity conservation seems to be closely related to environmental amelioration and to grazer activity because plants of low palatability often serve as biotic refuges for palatable plants. Thus, the management of this species should be viewed as a key factor for dry Puna biodiversity conservation.

III YEAR

Stress and disturbance effects on floristic and functional composition of Dry Puna landscape.

To define management guidelines for biodiversity conservation of dry Puna, it is basic to know the trade-offs between burning/grazing and plants interactions, and functional response. To achieve this topic during the third year, study sites with different disturbance conditions were analysed in harsh environments, where inappropriate land use practices lead to a soil features change and species richness collapse. The excessive grazing and uncontrolled fire, are the fundamental causes of the loss of plant species and consequently of land degradation that amplifies the impact of climatic change.

Scientific paper:

Catorci A., Cesaretti S., Velasquez J.L., Burrascano S., Zeballos H. Effects of different disturbance regimes on plant community functional composition and plant-plant spatial interaction in the dry Puna (southern Peruvian Andes). **JOURNAL OF ARID ENVIRONMENTS (Submitted).**

Research aim: The research aim was to assess the difference in species composition, plant-plant spatial interactions, and functional composition between grasslands with low and high disturbance.

Study area: Grasslands with the same lithotype (volcanic ash), altitude (4000-4100), aspect (north-facing), and slope (< 10°), but different disturbance regimes placed in the Salinas and Aguada Blanca National Reserve (Peruvian Andes). The low disturbance site was mainly grazed by wild camelids; the high disturbance site was grazed by domestic camelids and sheep, and burned every 2-5 years.

Data collection: Species cover percentage in 40 vegetation surveys (10 x 10 m) were listed. 10 soil samples were collected to measure the content of organic matter (%), carbon/nitrogen ratio (C/N), and K (ppm). To detect the plant-plant spatial interactions, four linear transects (two for each disturbance regime) 50 m long and divided into 1,000 plots of 5x5 cm, were randomly laid out. Species occurrence and information about presence/absence of bare soil were recorded in every 5x5 cm plot. Plant traits were checked by field observation and consultation of the herbarium collection.

Data analysis: Independent t-tests and Mann-Whitney U-tests were performed using SPSS 13.0 software. PCoA and PCA by Syntax 2000 package. MRPP and ISA were executed using PCOrd 5.0 software. Co-occurrence analysis by EcoSim 7.0.

Results: the two main types of differences between the analysed treatments were soil features and the cover values of potential nurse species. The high disturbance site had lower floristic richness, less diversity, and a less equal distribution of species. Furthermore, several traits are linked to the high disturbance condition such as annual leaf history, non-graminoid and dwarf shrub plant forms, tap root, and spinescence. The main traits associated to low disturbance site were perennial leaf history, graminoid, tall shrub and cushion plant forms, top inflorescence, and roots with little starch content.

Conclusion: The effects of combined overgrazing and fire lead to the collapse of the clumped spatial structure of the dry Puna, with a consequent decrease of tall species such as *Festuca orthophylla* and increase of dwarf and spiny shrubs *Tetraglochin cristatum*. In high disturbance condition this species acts as a nurse plant, but it is less efficient, than other nurses like tall shrubs and tall grasses, probably owing to its small dimensions. Thus, the reduction of nurse cover value leads to the decrease of facilitative interactions and consequently to a reduction of species richness in such a management condition.

PhD scientific papers list

Sub-Mediterranean grasslands

1) ***Cesaretti S., Castagna S., Montenegro B., Catorci A. 2009.*** Zootechnical characterization of grassland vegetation in a pastoral system as a tool for biodiversity conservation: A case study of Umbria-Marches Apennine. **INFORMATORE BOTANICO ITALIANO 41 (2): 247–258.**

2) ***Catorci A., Cesaretti S., Gatti R. 2009.*** Biodiversity conservation: Geosynphytosociology as a tool of analysis and modelling of grassland systems. **HACQUETIA 8 (2): 129–146.**

3) ***Catorci A., Ottaviani G., Vitasović Kosić I., Cesaretti S.*** 2011. Effect of spatial and temporal patterns of stress and disturbance intensities in a sub-Mediterranean grassland. **PLANT BIOSYSTEMS. DOI:10.1080/11263504.2011.623192 (in press).**

4) ***Catorci A., Ottaviani G., Ballelli S., Cesaretti S. 2011.*** Functional differentiation of central Apennine grasslands under mowing and grazing disturbance regimes. **POLISH JOURNAL OF ECOLOGY 59(1): 115–128.**

5) ***Catorci A., Ottaviani G., Cesaretti S. 2011***. Functional and coenological changes under different long-term management conditions in Apennine meadows (central Italy). **PHYTOCOENOLOGIA 41: 45–58.**

6) ***CatorciA., Cesaretti S., Gatti R., Ottaviani G. 2011.*** Abiotic and biotic changes due to spread of Brachypodium genuense (DC.) Roem. & Schult. in sub-Mediterranean meadows. **COMMUNITY ECOLOGY 12(1): 117–125.**

7) ***CatorciA., Cesaretti S., Gatti R.*** Effect of long-term abandonment and spring grazing on floristic and functional composition of dry grasslands in a central Apennine farmland. **ACTA BOTANICA CROATICA (Submitted).**

8) ***Catorci A., Gatti R., Cesaretti S.*** Effect of sheep and horse grazing on species and functional composition of sub-Mediterranean grasslands. **APPLIED VEGETATION SCIENCE (Accepted).**

Sub-desertic grasslands

1) ***Catorci A., Cesaretti S., Velasquez J.L., Zeballos H. 2011.*** Plant-plant spatial interactions in the dry Puna (southern Peruvian Andes). **ALPINE BOTANY 121(2): 113–121. DOI: 10.1007/S00035-011-0097-1.**

2) ***Catorci A., Cesaretti S., Velasquez J.L., Burrascano S., Zeballos H.*** Effects of different disturbance regimes on plant community functional composition and plant-plant spatial interaction in the dry Puna (southern Peruvian Andes). **JOURNAL OF ARID ENVIRONMENTS (Submitted).**

6. CONCLUSION AND IMPLICATION FOR GRASSLAND MANAGEMENT

Competition in sub-Mediterranean grasslands

In the studied sub-Mediterranean grasslands of Umbria-Marches Apennine (central Italy) the competition among species may be extremely intense. In fact, competition plays a key role especially in dense and more productive grasslands, where the co-existence of plants is mainly linked to the competitive exclusion.

Because of this, in these plant communities the species co-existence is driven by a specific functional plant trait pattern that ensures foliage expansion affording a competitive advantage. Furthermore, clonal growth forms and vegetative propagation modes that imply horizontal space occupation, can be interpreted as a strategy aimed at maximizing the species competitive ability when there is higher exploitation of soil resources, allowing individuals to explore the neighbouring area and find unexploited soil niches (Tissue and Nobel 1988; Friedman and Alpert 1991). This helps to avoid competition for soil resources with the dominant species (Grime 2001).

Accordingly, the plant functional composition also affects the competitive ability in relation to the stress and the disturbance intensity. In the studied sub-Mediterranean grasslands, drought stress cause a complex trait response, and both stress and disturbance can determine a dual function of plant traits. For instance, in xeric condition hairs and leaf texture can confer resistance to drought stress reducing evapotranspiration and at the same time render the leaves unpalatable to grazers. This kind of trait is strongly fostered in dry habitat that undergo a high disturbance intensity (Peltzer and Wilson 2001). Dry grassland system is very poorly productive in summer, when a quite strong drought stress influences the plant communities. Species with tolerance strategies are strongly affected by the intensity and timing of grazing, because tissue re-growth after the herbivorous bite is not possible in summer time (Catorci et al. 2011). It can be hypothesized that, especially in the most stressed habitats, such as the south-facing slopes, spread of grasses and of other not stress tolerant species is favoured by the absence or the low intensity of herbivory. Stress can drive the functional composition in the abandoned dry grasslands when the disturbance is absent after livestock grazing has ceased. Drought stress tolerant species with strong avoidance ability and species with tolerance strategy and with high soil resources needs can co-exist thanks to the micro-scale variation of soil features, particularly soil water availability. The impossibility of dominant species to spread after the abandonment, owing to the high level of drought stress (Grime 2001), plays an important role in biodiversity conservation after grazing cessation as well. Since dry grasslands are more resistent to vegetation change (Bennie et al. 2006; Vitasović et al. 2011), they tend to preserve plant biodiversity; on the contrary, mesophilous meadows are less resistent and hence more vulnerable to the loss of floristic diversity when grasslands are abandoned (Bonanomi et al. 2009). In fact, the absence of disturbance in more productive grasslands favours dominant species like *Brachypodium genuense*, that increase its cover value, aboveground phytomass, and litter deposition in the abandoned meadows. The spread of dominant species alters the ecological status of the site, it lowers soil temperature, moisture and pH, and increases soil C/N ratio and litter production. Dominance of tall grasses alters the light intensity at ground level (Hurst and John 1999), and the intensified competition for light (Abrams 1995) drives the competitive exclusion of small species (Grime 2001).

B. genuense invasion also enables some traits to flourish while it reduces the expression of others. Species with runners, ability to form patches, and late flowering strategies benefit from *B. genuense* spread, whereas species marked by storage organs, small size, and early flowering strategies benefit in the mown condition. However, it seems that only low frequency species are heavily threatened, while the others can remain inside the plant community by shelter niche occupation.

The abandonment does not lead to the reduction of species richness but notable floristic changes were observed along the disturbance intensity gradient. In fact, different disturbance intensity leads to plant communities with different phytosociological placement, and a turnover between pasture/meadow species and the fringe/open wood ones is underway in abandoned meadow. Abandonment drastically changes the plant community composition and ecology; many pasture and meadow species disappeared, while generalist species, mostly living in open woods or fringe habitats, become very numerous and abundant.

Grazing cessation but mowing maintenance lead to slight functional and floristic differences, and allow the conservation of the main plant community characteristics; in fact, only species strongly affected by the grazer bite and with very low average cover become scarce or disappear.

In meadows dominant species such as *Brachypodium genuense* and *Carex macrolepis* increase their average percentage cover value, consequently it can be stated that mowing alone does not ensure long-term control of dominant species. In fact, the comparison of grazing and mowing management regimes, indicated how different disturbance types lead the differentiation of floristic composition. Moreover, late mowing (meadows are mown at the end of June or early July) favours a high species richness, high number of life forms and functional strategies. Grazing favours grasses (especially *Poaceae* species) while mowing advantages tall species. Mowing favours the affirmation of species equipped with dominant strategies (*Brachypodium genuense* and *Carex macrolepis*) that probably are not under control in meadow managed with late mowing. This study has confirmed how disturbance represents a significant environmental driver for plant community differentiation, either at floristic and functional traits level. Both grazing and mowing provoke aboveground phytomass removal but act in different ways on plant community: grazing is a selective pressure, while late-mowing gives to all the species the same development chances.

The grasslands studied belong to the habitat 6210 of the 92/43/EEC Directive and require management plans, in order to control the floristic and ecological transformations due to abandonment and changes in mowing/grazing practices. For this reason and with the aim of biodiversity conservation, hay cutting every two or three years probably is sufficient to prevent local extinction of threatened species. Finally, our findings show that well-informed interpretation of pastoral landscapes requires knowledge about management (mowing, grazing, or abandonment) and the kind of herbivores (sheep, horses, cattle).

Different grazers exert selective pressure on plant species, related to their browsing strategies and foraging behaviour (Dumont et al. 1995; Grant et al. 1996). It is therefore hypothesized that different grazer types acting in pastoral systems (with the same environmental features) could lead to floristic differentiation of the plant community.

For instance, sheep are intermediate forage selectors because their narrow mouth enables them to eat very selectively (Hofmann 1989). They will ingest single leaves, flowers or shoots from a sward, biting them off close (2-3 cm) to the ground (Phillips 1993). By contrast, horses have teeth that point slightly forward and can graze as close to the ground as rabbits, but they are less selective, especially in overgrazed systems. In fact, they can eat weed species, branches of shrubs and trees, and less palatable plants such as sedges. Sheep and horses also differ in the selection of grassland patches, as the former prefer steep slopes and the latter prefer gentle slopes and flat areas (Crofts and Jefferson 1999).

Our findings showed that if the disturbance intensity is optimal, horse grazing is not harmful. Indeed, functional distinction due to different management only causes a change in the pool of accidental species and a difference in the cover value of species whose combination of functional traits is filtered in different ways by the system. For instance, in horse-grazed systems, plants need a strong escape strategy (low stature or prostrate form), to grow leaves when horses are not grazing, and to possess clonal ability because flowers and leaves are eaten and trampled. In sheep-grazed system, the higher level of selective defoliation and the delayed start of the grazing period enhanced species with low palatability, late flowering strategy, and those that cannot tolerate the trampling of large herbivores (chamaephytes).

On the other hand, exclusive grazing by sheep does not seem to inhibit the spread of dominant species such as *Brachypodium rupestre*, which in turn threaten grassland biodiversity (Bonanomi and Allegrezza 2004). Hence, in terms of biodiversity conservation, horse grazing is as useful as sheep grazing, but only if managed at optimal stocking rates. Indeed, the increase of short grasses and annuals does not ensure soil maintenance because these species have poor root systems (Metera et al. 2010). Thus the intensity of disturbance should be planned both in respect of grassland carrying capacity and slope angle to avoid the soil erosion (Russell et al. 2001).

The relationship between stress and disturbance intensity affects the functional response of plant communities, but can also lead to changes in plant community structure, favouring the creation of patches dominated by unpalatable species (i.e. *Astragalus sempervirens, Brachypodium rupestre* and *Eryngium amethystinum*). Sheep can choose single leaves or shoots from the sward, biting them close to the ground level. Young leaves of *B. rupestre* are eaten by sheep (Ellenberg 1988); thus, inside *A. sempervirens* cushions (via facilitation mechanisms), small and young individuals can establish themselves and grow undisturbed, thereby becoming dominant and replacing the smaller spiny species to form bigger patches. The spread and fusion of two or more patches allow the affirmation of the *B. rupestre* community. This species has dominant features (*sensu* Grime 2001).

In order to preserve biodiversity, an alternative management solution could be mechanical removal (mowing) of *A. sempervirens* patches or late summer grazing by very low selective herbivores, such as donkeys or horses (Hofmann 1989; Crofts and Jefferson 1999). The problems linked to the expansion and management of the dominant species *B. rupestre* are not related to conditions of undergrazing only, but also to changes in livestock composition. In fact, traditionally (until the 1950s), the grazers in the study area were sheep, goats, mules and/or horses, a situation that made it impossible for one or several poorly palatable species to predominate (Crofts and Jefferson 1999).

Highlights

In terms of biodiversity conservation, the research outputs represent an advance in the understanding of the ecological processes involved at plant community level as well as at landscape scale. Some plant traits may reflect selection by herbivores, while others are likely to be by-products of selection for other ecological functions (Rosenthal and Kotanen 1994). Plant traits may have a dual role; for instance, hairs and leaf texture reduce evapotranspiration and at the same time render the leaves unpalatable to grazers. The study findings allow to highlight a general scheme, in which the stress intensity filters the pool of traits at landscape scale while the disturbance intensity leads to the distribution, occurrence and abundance of single traits at plant community level.

1. Stress intensity (drought stress) selects the trait composition of the plant community at a landscape scale. Thus, traits and associated plant species are distributed at landscape scale depending on stress intensity.
    - xeric grassland: stress tolerance and avoidance strategies by hairs and leaf texture determining low evapotranspiration and poor palatability are widespread. Therophyte and chamaephyte life forms are fostered.
    - semimesic condition: either avoidance mechanisms (rosette form, chemical substances, spines and prostrate form) or tolerance strategies (re-growth capacity)

occur as well as late flowering and tall species (upright forbs, tall tussock grasses). More productive environments develop more functional types and, thus, a higher floristic richness.

2. Disturbance intensity (number of herbivores), type (mowing or grazing, and the different livestock type) and timing act as driving forces in promoting or suppressing the plant functional traits expression. The pool of traits is filtered in different ways by the system.
   - High intensity of disturbance: avoidance strategies (i.e. prostrate form, rosette forbs, hairs) and vegetative reproduction (clonal ability) are favoured.
   - Intermediate disturbance: largest pool of traits that allows maximum floristic richness. The co-existence of species is promoted by the avoidance and tolerance strategies co-existence, due to the possibility to use the maximum number of spatial (micro-scale) and temporal niches (change in sward structure during the growing season).
   - Low intensity of disturbance and abandonment: tolerance strategies and dominant species are promoted; on the contrary, the low statured (rosette and prostrate form), accidental and subordinate species are disadvantaged.
   - Large herbivores: increasing of short grasses, sedges, rosette forbs and annuals (growth forms with poor root systems). These plants do not ensure the maintenance of soil on steep slopes.
   - Small herbivores: upright forbs, dominant unpalatable tall grasses (*Brachypodium rupestre*) and chamaephyte species are promoted by selective defoliation of sheep. Facilitative interactions between palatable and unpalatable species were observed.
   - Grazing in springtime: negatively affects the early spring flowering species of mid/tall dimensions and relevant species such as orchids. This is an issue for biodiversity conservation.

Facilitation in sub-desertic grasslands

Bertness and Callaway (1994) hypothesized that the importance of facilitation in plant communities increases as abiotic stress or herbivorous pressure intensify, whilst competition is more important in environmental conditions that allow rapid acquisition of resources (e.g. high soil moisture and nutrients in conditions of full light). Facilitation processes are positive interactions in which some plants benefit from closely associated neighbours; this phenomenon is essential for plant community diversity and dynamics in harsh environments. Castro et al. (2002) demonstrated that seedling survival is higher in shadier positions under the canopy of nurse plants and their establishment may be influenced by the nurse plant's canopy structure, particularly in relation to shade intensity and rainfall interception (Padilla and Pugnaire 2006). Distance from the nurse plant is an important factor as well; in fact, it has been shown that amelioration of negative conditions and improved availability of resources decreases from the canopy centre outwards (Moro et al. 1997; Dickie et al. 2005).

Therefore, in habitats with harsh conditions or with a large number of herbivores, nurse species may provide refuge to other plants, which otherwise might fail to establish (Ellner and Shmida 1981; Flores and Jurado 2003; Padilla and Pugnaire 2006). Recent studies (e.g. Pugnaire and Luque 2001; Callaway et al. 2002; Flores and Jurado 2003) revealed an increase in positive plant-plant interactions with increasing environmental stress.

The research findings highlight the strong importance of plant–plant spatial interactions in the Peruvian dry Puna. In this harsh environment many species need some kind of facilitative interaction with nurses (mainly with tall grasses, shrubs or cushion plants). Tall grasses (mainly *Festuca orthophylla*) are the most important nurse species because they have the highest number of spatially associated plants. Monteiro et al. (2011) demonstrated that *F. orthophylla* tussocks ameliorate local environmental conditions in a number of ways (e.g. temperature, soil moisture, litter deposition). This species also provides protection from herbivorous bite (Callaway et al. 2000; Milchunas and Noy-Meir 2002; Rebollo et al. 2002), because in grazed systems palatable forbs only survived when nested in the rigid, tall *F. orthophylla* tussocks or in thorny shrubs (Patty et al. 2010). It is possible to state that these poorly palatable plants act in the systems by creating shelter or regenerative niches for less stress-tolerant or more palatable species, especially during the wet season and in not overgrazed pastoral systems (such as the study area). This could explain why the *F. orthophylla* cover value increase was related to the increase of the number of spatially associated species. In fact, when the cover of nurse plants increases, the number and the size of the shelter and regenerative niches increase as well (Bruno et al. 2003; Baumeister and Callaway 2006). Furthermore, Walker (1994) argued that a high density of nurse species may stabilize soil and increase soil organic matter, moisture, and nutrients more powerfully than isolated or dispersed individuals, thus better facilitating the growth of less stress-tolerant species. For these reasons, our findings seem to corroborate the hypothesis of Callaway and Walker (1997) that in stressful habitats facilitation increases in intensity with nurse plant size. *F. orthophylla* forms the core of the facilitation-shaped community structure. Thus, the management of this species should be viewed as a key factor for dry Puna biodiversity conservation. In fact, as camelids prefer the fresh, regrown leaves of *F. orthophylla* that resprout after burning (Monteiro et al. 2011) throughout the Peruvian dry Puna, there is the widespread practice of burning these plant communities to renew forage for livestock. Furthermore, after the burn, the juvenile leaves of *F. orthophylla* are eaten by domestic and wild camelids (Genin and Tichit 1997), and thus subsequent to burning, shelter and regenerative niches are probably few and small for some years. For this reason, species with strong spatial relationship with *F. orthophylla* could be threatened with local extinction, especially in conditions of overgrazing.

Our findings highlighted a change in soil features and a decrease of cover values of potential nurse species. Burning and the consequent reduction of plant cover leads to loss of nutrients as well (Ares et al., 1990). Bret-Harte et al. (2004) and Brooker (2006) stated that the loss of soil nutrient availability can contribute to the lower cover value of graminoids. The potential nurse species *F. orthophylla* had a very low cover value in the high disturbance condition, while the poorly palatable shrubs *Tetraglochin cristatum* was the dominant species. This dwarf shrub has spines that protect flowers (with intermediate position) and leaves (with an intermediate palatability) against the herbivorous bite, while the presence of tap root allows this species to survive in environments poor in soil nutrients and water. In the overgrazed area palatable species without avoidance strategies can save themselves only under biotic refuges, as seen with the *Tetraglochin cristatum* patches. Moreover, dwarf shrub spread does not ensure the maintenance of such facilitative interactions in the high disturbed condition, because of the small dimensions of *Tetraglochin cristatum*. Consequently, the species richness and diversity was lower in such a management condition. On the other hand, the reduction of below ground competition for soil resources and the greater availability of space enable annuals and small statured species with strong avoidance strategies to spread in high disturbed condition. Inappropriate land use practices (excessive grazing and uncontrolled fire) are the fundamental causes of land degradation. It should be kept in mind that an abundance of tall grasses and shrubs counters soil erosion by wind, and reduction of their cover value could lead to increased soil loss. This could contribute to desertification more than climatic change, or contribute to a cumulative process that amplifies the impact of climatic change (Le Houérou 1996).

Finally, the very low soil nutrient values caused by inappropriate management of dry Puna may well prevent floristic and functional recovery of the plant community long after livestock grazing has ceased. Indeed, this lack of nutrients could prevent the spontaneous growth and spread of graminoids such as *Festuca orthophylla* tussocks. Thus it can be stated that management plans must be carried out very carefully, especially in protected areas or in those with systems of high economic value, for example, those devoted to the production of such high quality fibers as Alpaca wool.

Highlights

Plant–plant interactions play a key role in regulating the composition of communities and ecosystems. Besides controlling the biodiversity of plant communities they also have widespread impact on ecosystems, for instance through their effects on resource availability and habitat structure. However, impacts of plant–plant interactions can be altered by external drivers (both natural and anthropogenic) such as climatic conditions or nutrient availability. The research outcomes can be summarized in the following highlights:

1. The importance of facilitative processes increases with increasing environmental stress and with the increasing of harsh abiotic conditions.
    - Environmental amelioration: nurse plants act as 'fertile islands' in which seedling of protégé plants (also known as beneficiaries, target or facilitated species) can benefit

from environmental amelioration (e.g. buffer temperature, less evaporation, higher soil moisture, more nutrients).

- Distance from the nurse plant: the establishment of beneficiary species may be influenced by the canopy structure of the nurse plant, particularly in relation to shade intensity and rainfall interception.

2. Disturbance drives the facilitative processes increasing positive spatial relations among species, in habitats with equal harsh conditions (equal intensity of stress) but with a large number of herbivores.
   - Plants of low palatability often serve as biotic refuges for palatable plants. For instance, spines, leaf toughness, resins, were typical plant traits of nurse species.

3. Very heavy disturbance (excessive grazing and uncontrolled fire) contribute to the desertification amplifying the impact of climatic change.
   - Decrease or loss of some types of nurses, such as the tall species.
   - Increase of dwarf and spiny shrubs as nurses but less efficient owing to the small dimensions than tall nurse species.
   - Increase of soil loss owing to the decrease of tall species that counter soil erosion by wind.
   - Decrease of plant richness and consequently biodiversity conservation problems.

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