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On the origin and evolution of the Mediterranean dry grasslands

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Abstract

A synthesis on the functional types of Mediterranean dry grasslands is outlined. Three different types are commented: wintergreen perennial dry grasslands, wintergreen ephemeral dry grasslands, summergreen perennial dry grasslands. The first type is the most primitive, including several relict species, often characterized by very disjoint, sometimes anfi-saharian distribution ranges. The second type is resulting from an evolutionary trend towards short-lived life strategy, triggered by climatic and topographic perturbations that affected the Mediterranean region in the Plio- and Pleistocene. The third type, only marginally occurring in the Mediterranean region, is deriving from Holarctic and Eurasian elements, that probably colonized the Mediterranean lands during the Pleistocenic dry interglacial periods. The evolutionary success of the Mediterranean dry grasslands have been ensured by the combination of high topographic diversity and multiple land-use patterns. Their existence is based on a dynamic long-term flow equilibrium, depending on cyclic perturbations, that let them to acquire a long-term evolutionary metastability.

Key words: Mediterranean Region, dry grasslands, adaptation, human impact, homeorhesis.

1. Introduction

Mediterranean people have been pioneers in the search of a balance between exploitation and conservation of natural resources. Their efforts have resulted in the domestication of livestock, the development of high-yield grains and the establishment of important cultivation techniques. While searching the best compromise between exploitation and conservation, the Mediterranean man was forced in many cases to migrate from his properties, as a consequence of the great decrease in land productivity due to the over-exploitation of natural resources. In every migration, the man left behind himself the traces of his mistakes but took with him his own heritage of experiences, knowledge, traditions. Proofs of this trend are well reflected by the Mediterranean dry grasslands, a living and highly changeable interface between abiotic and cultural matrices of the Mediterranean landscape.

In the Mediterranean region, three main structural types of dry grasslands can be recognized: those dominated by big caespitose hemicryptophytes (wintergreen perennial dry grasslands), those dominated by thermoxerophilous therophytes (wintergreen ephemeral dry grasslands), those dominated by relatively small chamaephytes and hemicryptophytes (summergreen perennial dry grasslands). All three kinds are occurring in the Mediterranean territories, especially in the most dry areas. Relevant physiognomic, adaptive and floristic differences are featuring the three mentioned typologies. Basing on literature and personal unpublished data, the main features of the three functional types are summarized in the following paragraphs and in Tab. 1, where the adaptations and functional consequences to environmental stresses of the plants growing in the Mediterranean dry grasslands are reported.

Tab. 1: Synopsis of the main adaptations to environmental stresses of the plants living in the Mediterranean dry grasslands (after RICHARDSON et al. 1986, modified).

Environmental stress	**Adaptation**	**Functional consequence**
Winter cold *	Winter dormancy	Tolerance to low temperatures
	Low stature of plants	Reduced physical stress and frost damage
Summer drought	Epidermal trichomes, waxes, thick cuticle	Reduced evapotranspiration
	Sunken stomata, conduplicate leaves	Increased boundary layer resistance
	Reduced leaf area	Reduced water loss
	Summer loss of the leaves	Reduced evapotranspiration
	High root/shoot ratio	Increased absorptive area
	Deep rooting	Access to perennial water
	Therophytic/Geophytic habit	Avoidance of extreme drought
Summer heat	Rapid root growth of seedlings	Adequate water supply
	Serotine germination	Avoidance of extreme temperatures
	Reduced leaves	Reduced heat loading
	Open canopy architecture	Sensible heat removal
	Epidermal trichomes, waxes, thick cuticle	Increased reflectance
Wildfires	Precocity / Serotiny	Fire avoidance
	Myrmechochory	Maintenance of viable populations
	Persistent, soil-stored seeds	Maintenance of viable populations
	Resprouting rootstocks	Vigorous post-fire regeneration
	Geophytic habit	Rapid re-establishment
Nutrient limitation	Bacterial symbioses	Facilitation of nutrient uptake
	Fungal symbioses	Facilitation of nutrient uptake
	Slow growth at maturity	Reduced nutrient requirements
	Cluster roots	Increased exchange surface
	Dense caespitose rootstocks	Nutrient sequestration
	Cumulative set of persistent seeds	Slow build-up of seed store
	Enthomogamy	Optimization of resources
	Rewardless pollination	Optimization of resources
Predation	Secundary aromatic/toxic compounds	Unpalatability
	Low seed set	Minimization of predator resource base
	Anemochory	Minimization of predator resource base
	Prolific seed set	Predator satiation
	Myrmechochory	Avoidance of post-fire predation
Wind	Reduced, slender leaves and stems	Reduced physical resistance and damage
	Low stature of plants	Reduced mechanical stress
	Anemochory	Optimal dispersal strategy

**Festuco-Brometea* only

2. Wintergreen perennial dry grasslands

Vegetation widely distributed in the most xeric habitats of the Mediterranean region (Fig. 1), finding its optimal ecological requirements on carbonatic or marly soils. With reference to the Rivas-Martínez's bioclimatic classification (RIVAS-MARTÍNEZ et al. 2002), these grasslands are chiefly linked to thermo-mesomediterranean thermotypes, with dry-subhumid ombrotypes. Perennial bunchgrasses, such as *Hyparrhenia hirta*, *Stipa tenacissima*, *Ampelodesmos mauritanicus* and *Lygeum spartum* are the most frequent and typical representatives of this vegetation, classified by phytosociologists within the class *Lygeo-Stipetea* Rivas-Martínez 1978 (= *Thero-Brachypodietea retusi* Br.- Bl. 1947 pro parte) (BRULLO et al. 1990, 1997, 2003, MINISSALE 1995, BACCHETTA et al. 2005). In the *Lygeo-Stipetea* vegetation, relictual floristic elements are frequently found, such as *Aristida adscensionis*, *Heteropogon contortus*, *Cenchrus ciliaris*, *Tricholaena teneriffae*, *Gypsophila arrostii*, currently having a very scattered distribution across the Mediterranean territories. Through ruderalization, the vegetation at issue becomes dominated by *Oryzopsis miliacea*, featuring a stepping stage towards *Brometalia rubenti-tectori* vegetation. The adventitious *Pennisetum setaceum* and *P. villosum* are also linked to this stage.

Fig. 1: Distribution range of the vegetation ascribed to the class *Lygeo-Stipetea*.

The *Lygeo-Stipetea* vegetation primarily colonizes rocky ledges and steep sunny slopes, where the edaphic and microclimatic conditions favour the vigorous growth of the perennial bunchgrasses. Grass-dominated plant communities promote fire and in many cases are also promoted by fire (MUTCH 1970), therefore a feedback switch becomes established, hampering the development of shrubberies.

Fire has been traditionally used by the Mediterranean shepherds to obtain grasslands on the cheap. Winter and early spring grazing, together with periodical summer burning, favours the settlement of *Lygeo-Stipetea* vegetation. Secondary dry grasslands obtained in this way are one of the most common elements of the Mediterranean landscape. They are characterized by more or less dense bunches of perennial grasses with interstitial space occupied by annual grasses.

The density of perennial vs. annual grasses is greatly influenced by the soil compaction: an excessive grazing pressure during the rainy season compacts the soil near the surface, which reduces infiltration, percolation, and water holding capacity, and concentrates roots near the surface (MENKE 1989). Soil compaction also impedes root elongation, placing deep rooted species, such as the perennial bunchgrasses, at a disadvantage during seedling establishment. Seeds of annuals germinate faster and earlier and the roots develop faster than those of the seedlings of perennial grasses. Differences in germination date and early seedling vigour may determine the competitive ability of one functional group (JOFFRE 1990, GARNIER 1992)

3. Wintergreen ephemeral dry grasslands

Pan-Mediterranean vegetation, sporadically spread, as well, in the temperate and Atlantic Europe, Macaronesia and Saharo-Sindic region (Fig. 2). It is dominated by poorly competitive annual grasses, colonizing nutrient-poor and seasonally dry soils. This vegetation is usually ascribed to the phytosociological class *Tuberarietea guttatae*

Br.-Bl. 1952 em. Rivas-Martínez 1978 (= *Thero-Brachypodietea retusi* Br.-Bl. 1947 p.p., incl. *Stipo-Trachynietea distachyae* Brullo 1985, incl. *Ononido variegatae-Cutandietea maritimae* de Focault & Géhu 1999) (RIVAS-MARTÍNEZ 1978, BRULLO 1985, DE FOUCAULT 1999). Through ruderalization, the *Tuberarietea guttatae*-vegetation may shift towards *Stellarietea mediae*.

Fig. 2: Distribution range of the vegetation ascribed to the class *Tuberarietea guttatae*.

Disturbances play a fundamental role in making or maintaining the site conditions suitable to the Mediterranean wintergreen ephemeral dry grasslands. Heavy grazing, long, dry summers and intense competition for limited soil resources favour the annual strategy (WESTOBY 1980), although frequent fires would favour the perennial bunchgrass establishment by reducing the chances of viable seed bank establishment for the therophytes.

Therophytic dry grasslands are the commonest and most diverse vegetation type in the Mediterranean region (Fig. 3), occurring on several soil types, from sands to marl and clay, ranging from the thermo- to the oromediterranean bioclimate. In spite of the high floristic richness, this vegetation is characterized by a very low resilience and functional stability, so that the species frequency and composition may change annually, in response to stochastic events, germination strategies and year to year fluctuations of the ecological factors determining the site conditions (HARPER 1977, NAVEH 1991, GUARINO et al. 2005). Most of the vegetation dynamics observed in Mediterranean therophytic dry grasslands cannot be predicted by the traditional linear succession model (NAVEH 1974, BARTOLOME 1989). A great part of the Mediterranean plant diversity is therefore precarious and ever-changing. In spite of this, Mediterranean therophytes play a relevant ecological role in most of the Mediterranean habitats: they prevent soils from rill erosion during the rainy season and are very important biomass producers, providing food to several seed eaters, pollinators and herbivores.

4. Summergreen perennial dry grasslands

Eurosiberian hemicryptophitic vegetation, stretching from the British Islands and Galicia (NW Spain) to the Central Siberia (ROYER 1991). The optimum for this vegetation is found on stony slopes and eroded soils, deriving from limestones and marls. The structure of this vegetation is given by the prevalence of caespitose grasses, such

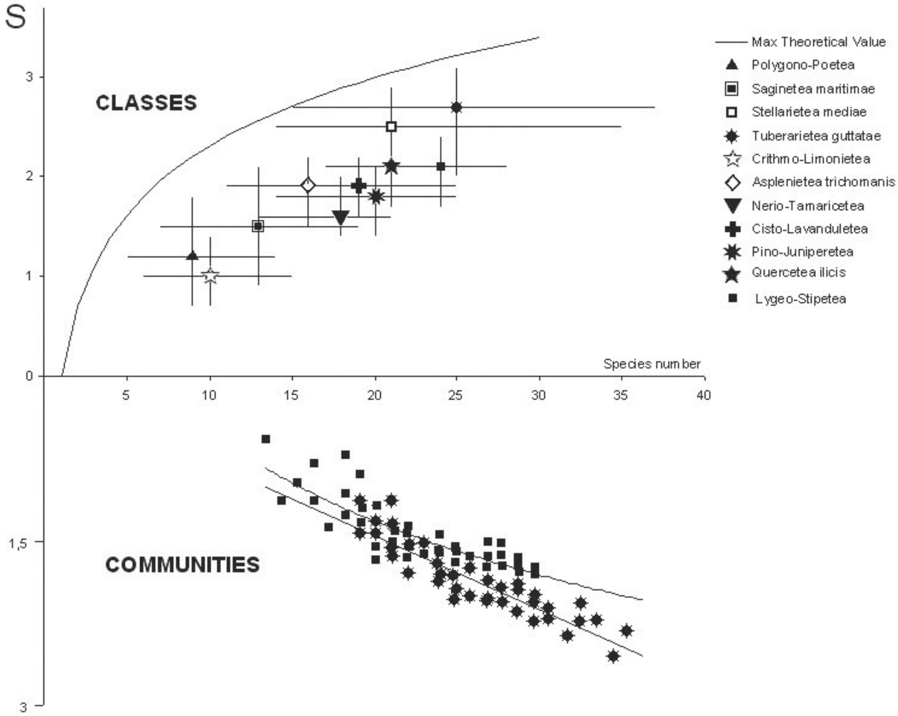

Fig. 3: Scatter diagrams of the average a-diversity (S) among different phytosociological classes (above) and (below) between two sets of 40 relevés each, taken in *Lygeo-Stipetea* (■)and *Tuberarietea* (✷) vegetation. The a-diversity is measured by the Shannon-Wiener index. Frequency values of a given species were obtained by discrete randomization, basing on the cover values assigned with the Braun Blanquet's scale. Processed relevés were sampled in Sardinia and Sicily.

as *Bromus erectus* and allied species, *Festuca valesiaca, Cleistogenes serotina, Koeleria macrantha, Carex humilis, Phleum phleoides, Chrysopogon gryllus*, *Botriochloa ischaemon*, characterizing the phytosociological class *Festuco-Brometea* Br.- Bl. & R. Tx. 1943 (incl. *Dactylo glomeratae hispanicae-Brachypodietea retusi* Julve 1993 non Br.-Bl. 1947) and subordinate syntaxa. The adaptation of *Festuco-Brometea* vegetation to short periods of intense heat and drought stress is remarkable. In the Southern Prealps, on steep stony slopes, the combined action of wind, solar radiation and limited water holding capacity of the soil imposes to the *Festuco-Brometea* vegetation thermic peaks up to 50° C and negative water balances up to –250 mm (LEDERBOGEN 1996).

In the Mediterranean region, this vegetation is limited to meso- and supramediterranean bioclimates (Fig. 4), with some relict outposts on the main elevations of the Iberian Massif, up to the Valencian territory (Serrania de Cuenca), on the Apennines (up to Mt. Pollino) and on the Balkans (up to Northern Greece) (RIVAS-GODAY & BORJA CARBONELL 1961, HORVAT et al. 1974, LOPEZ 1976, BIONDI & BLASI 1983, BIONDI et al. 1995, BRULLO et al. 2006). From north to south, at lower altitudes the *Festuco-Brometea* vegetation becomes progressively enriched in chamaephytes; when they become prevalent, the syntaxonomical treatment shifts towards the phytosociological classes of *Rosmarinetea officinalis* in the West- and of *Cisto-Micromerietea* in the East- Mediterranean region. On the high mountains, the *Festuco-Brometea* vegetation shifts towards the endemic-rich phytosociological classes grouping the Mediterranean orophilous dwarf-shrublands: from W to E, contacts occur with *Festuco hystricis-Ononidetea striatae* (Spain), *Rumici-Astragaletea siculi* (Calabria and Sicily), *Daphno-Festucetea* (Greece), *Astragalo-Brometea* (Turkey).

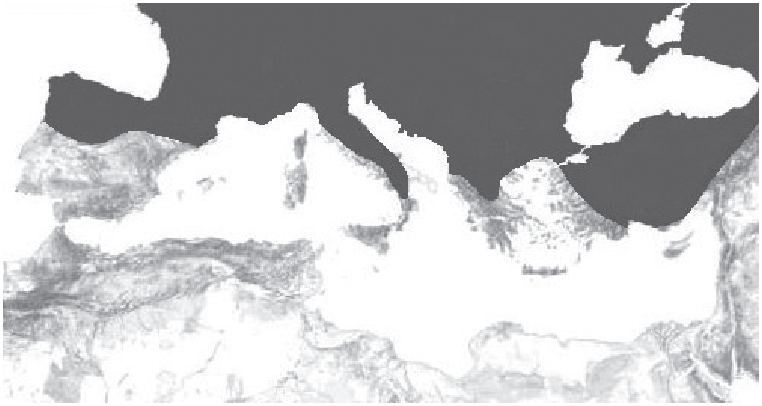

Fig. 4: Distribution range of the vegetation ascribed to the class *Festuco-Brometea*.

An extensive, moderate grazing pressure helps the ecological performance of *Festuco-Brometea* vegetation, that in the Mediterranean region was traditionally used as summer pastureland. Such traditional land-use has been greatly reduced in the last three decades, in response to the modernisation. In the past, to keep livestock in equilibrium with the grazing capacity of the summer pasturelands was an essential need and the Mediterranean *Festuco-Brometea* vegetation was rotationally burnt every 5-10 years, to control the density and spreading of the unpalatable chamaephytes. In recent year, large areas of the formerly used summer pasturelands have been abandoned and the subsidies provided by the EU to stop this trend are used by the local communities to make the mountain pasturelands more accessible, therefore facilitating shepherds to move from the pasturelands to the villages carrying hay and concentrates to feed their stocks during the critical periods, therefore turning an extensive production process into a more productive, but more restricted and intensive exploitation of the territory.

As a result, large parts of the Mediterranean *Festuco-Brometea* vegetation are nowadays shifting towards *Rhamno-Prunetea* vegetation, if abandoned, or towards *Onopordetea acanthii* and *Poetea bulbosae* vegetation through overgrazing.

5. Hypothesis on the origin and evolution of the Mediterranean dry grasslands

The differences in structure and floristic composition which are featuring the three above-mentioned kinds of Mediterranean dry grasslands are resulting from different events, that greatly influenced the current patterns of the Mediterranean biodiversity.

The origin of the species forming the Mediterranean dry grasslands can be viewed as a result of the gradual shifting from humid subtropical to seasonally dry climatic conditions, under evolutionary trends that probably begun during the meaningful gap represented by the Messinian disruption (MEDUS & PONS 1980, PONS & SUC 1980, SUC 1984, PONS & QUÉZEL 1985, QUÉZEL 1995).

The events associated to the Messinian age can be resumed as follows: starting from 5.8 Myrs. bp., due to the periodical obstruction of the Gibraltrar Strait, a great part of the Mediterranean Sea dried up and reflooded several times. In the most critical periods, the Mediterranean sea was up to 1250 m shallower than today. The continental scarps were almost completely emerged, and the bathyal floor turned into a patchy mosaic of sebkhas (i.e. salty deserts), saltmarshes and hypersalted, highly alkaline lakes, in depressions (HSÜ 1973). Erosion increased everywhere and diverse rocks were rapidly exposed. Moreover, the indirect uplift of the mountain ranges gave rise to huge rockfalls. The topographic diversity increased, and as mountain ranges were rapidly elevated, hundreds of new canyons and gorges were incised into them, steep slopes came into existence and divergent localised microhabitats developed everywhere. A lot of new ecological niches were ready to be colonized by pioneer plants with different adaptations (BERTOLANI-MARCHETTI & CITA 1975, BOCQUET et al. 1978).

As a consequence of the Messinian age and of the subsequent climatic changes, that increased the seasonal aridity on the Mediterranean lands, most of the ancestors of the Mediterranean plants passed through a new adaptive radiation.

The driving forces of this new speciation wave that still characterizes the Eu-Mediterranean flora are the following (RAVEN 1973):

- <u>Geographical segregation and appearance of new lands</u>: the most noticeable barrier to the free circulation of the Mediterranean terrestrial organisms is the sea, but the level of the Mediterranean sea ranged several times during the last 6 Myrs., as a consequence of the Messinian age and of the Pleistocenic glaciations. Several lands that currently are isolated have been connected to the mainland several times, in the past. Many plant species growing in the Mediterranean dry grasslands are neoendemics deriving from the splitting of a formerly continuous distribution range: some examples are provided by the phylogenetic groups of *Anthyllis vulneraria*, *Bromus erectus*, *Brachypodium pinnatum*, *Thymus serpyllum*, *Helianthemum nummularium, Stipa pennata*, *Centaurea deusta*, *C. jacea*.
- <u>Climatic variations</u>: The Mediterranean climate is not only depending on the latitude, but also on the cyclonic circulation of the oceanic air masses, whose position is ranging year by year. Annual climatic variations and major climatic changes may locally lead to the severe reduction and splitting of plant populations. Several noticeable disjunction in the distribution ranges of plant species growing in the Mediterranean dry grasslands can be attributed to these climatic changes: for example, the disjoint Sicilian populations of *Heteropogon contortus*, *Artemisia alba*, *Sesleria nitida* ssp. *sicula*, *Koeleria splendens*, *Helictotrichon convolutum*, have probably reached the island in the Pleistocene, during the dry interglacial periods. Moreover, long periods of high climatic variability favour an evolutionary trend towards the adoption of annual life strategies.
- <u>Rock heterogeneity</u>: In the Mediterranean lands, several rock types are represented. Because of the few or null frosty days, and because of the relatively scarce rainfall, the weathering of rocks is relatively slow and soils reflect with unusual fidelity the chemical composition of the mother rocks. Different soil chemistry and texture are selecting different floras, the most noticeable examples being the three orders belonging to the class *Tuberarietea guttatae*: *Tuberarietalia guttatae* on acidic soils, *Stipo-Trachynietalia distachyae* on basic-neutral soils and *Malcolmietalia* on sandy soils.
- <u>Rich fauna of pollinators</u>: The fauna of pollinators is richer in the Mediterranean region than in the neighbouring temperate and semiarid ones. We know that insects are quite precise in their flower-visiting habits and in the Mediterranean dry grass-

lands several examples of coevolution between flowers and insects are known, especially among representatives of the families *Fabaceae*, *Lamiaceae* and *Orchidaceae*.

- Short generation time (for therophytes): The short generation time and the intense gene flows characterizing the annual plants may easily segregate new homozygous races which can efficiently occupy new particular niches, that given to the patchiness of the Mediterranean environment are very common. Most of this inter- and intraspecific variability is still poorly investigated, but noticeable examples are provided by the groups *Silene* sect. *coloratae* (VALSECCHI 1995) and *Rumex bucephalophorus* (PRESS 1988).

With reference to the species growing in the Mediterranean dry grasslands, to the above mentioned speciation triggers, the following evolutionary trends can be associated (PIGNATTI 1978, 1979): from long-lived, big-seeded, monochorous plant species towards short-lived, small-seeded, polychorous species. Some examples of primitive plant species characterized by the above mentioned ancestral features are still found in the *Lygeo-Stipetea* vegetation of some isolated Mediterranean districts: *Astragalus huetii*, endemic to a small area of central Sicily, *Astragalus verrucosus*, endemic to a small area of SW Sardinia, *Asperula crassula* restricted to Crete. The three mentioned species are rare relicts, that not surprisingly are surviving in the most primitive kinds of Mediterranean dry grasslands, i.e. the wintergreen vegetation ascribed to the class *Lygeo-Stipetea*. Most of the species forming this vegetation derive from the paleotropic Tertiary flora and often are characterized by very disjoint, sometimes anfi-saharian distribution ranges. For example, it is highly probable that the *Lygeum spartum* vegetation of Southern Crete, i.e. the eastmost disjoint outpost of the *Lygeum spartum* distribution range, keeps isolated on that island since the Messinian age (BRULLO et al. 2002).

The *Lygeo-Stipetea* vegetation is probably originating from both Mediterranean and Mesogean elements. The Mediterranean elements may have differentiated *in situ*, on the continental tectonic microplates (Ibero-Mauritanic, Tyrrhenian, Cyrenaic, Balkanic, and Anatolian) after the onset of a seasonally dry-climate, while the Mesogean elements (such as *Astragalus*, *Artemisia*, *Aristida*) came into the Mediterranean region from the neighbouring Irano-Turanian and African regions, probably during the Messinian climatic worsening that allowed subcontinental drought-tolerant vegetation types to spread around the Mediterranean region, where they subsequently adapted to new climatic conditions at the end of the Messinian age.

The above mentioned speciation triggers and evolutionary trends, with a strong tendency towards therophytism through progressive reduction of the vegetative apparatus probably begun during the Messinian age. Since then, Mediterranean taxa increased their number as a result of the progressive adaptation to a very chageable climate and to the increased summer drought.

The already mentioned evolutionary trend towards short-lived life strategy goes often together with the tendency towards rewardless, species-specific pollination strategies (DAFNI 1987), and high investment in seed productivity. Obligate seeders have greater numbers of sexually produced generations, resulting in greater genetic recombination, which in turn contributes to more rapid speciation. This could explain why the Mediterranean region has such an high diversity of annual plant and insect species (MÉDAIL & QUÉZEL 1997).

Examples on how could have looked like the ancestors of the Mediterranean therophytes forming the *Tuberarietea guttatae* vegetation are quite rare in the perennial dry grasslands; yet grasslands are ruled by competition and intense dynamism. But ancestral life forms are found very frequently in the Mediterranean rupestrian flora: *Linum arboreum* looks probably quite similar to the ancestors of *Linum strictum*, *L. trigynum* and of other yellow-flowered annual flaxes; the same holds true for *Bupleurum dianthifolium* vs. *B. baldense, B. fontanesii* and allied taxa; *Tuberaria lignosa* vs. *T. guttata*, and many similar examples are reported by PIGNATTI (1979).

The evolutionary success of the Mediterranean therophytic dry grasslands have been ensured by the human interaction: the combination of high topographic diversity and multiple land-use patterns resulted in a patchwork of different annual plant communities that greatly contributes to the current Mediterranean biodiversity. We will go back to this topic in the next paragraph.

The *Festuco-Brometea* vegetation is deriving from Holarctic and Eurasian elements, that probably came into the Mediterranean region during the Pleistocenic glaciations, together with the herds of wild herbivores. During the glacial peaks, the North-Mediterranean territories had a non or feebly Mediterranean climate and they acted as a refuge for several species migrating from the north (POTT 1995). Huge migratory patterns of plants and animals along latitudinal gradients become established and new ecological niches become available for a new adaptive radiation. The Mediterranean patches of *Festuco-Brometea* vegetation are the last shreds of a vegetation type that was probably much widely distributed during the dry interglacial periods. In the Mediterranean region, this vegetation is nowadays restricted to the main mountain ranges of the Southern European countries, especially where the climatic mediterraneity is buffered by the condensation of orographic moisture, as it happens along the Apennines. In some cases, the post-glacial isolation of *Festuco-Brometea* species on the Mediterranean uplands originated new endemic taxa, such as *Phleum ambiguum, Sesleria nitida, Astragalus sirinicus*, *Crepis lacera*.

6. Trends associated to the human impact

As we have seen, the floristic richness of the Mediterranean dry grasslands is the result of plant migrations and adaptive radiations triggered by dramatic topographic, edaphic and climatic changes happened during the Pliocene and the Pleistocene. The importance of these changes must be particularly emphasized because a significant number of new taxa may not have appeared without them. Considering the relatively recent origin of these taxa, Mediterranean grasslands can be classified among the most dynamic and changeable biocoenoses in the world.

The great diversity of the Mediterranean dry grasslands has been influenced, as well, by the natural diversity and fragmentation of the Mediterranean landscape, that acted as a driving force not only on the species richness and genetic variability of their populations, but also on the human cultural diversity, which until now is one of the main features of the Mediterranean region.

The human land use increased everywhere the patchiness of the Mediterranean landscape, especially in the last twelve thousand years, as a consequence of the development of agriculture. The first agricultural practices arose from the periodical anthropogenic fires, that were used since many hundred thousands years (NAVEH 1998) to facilitate the growth of dry grasslands, where walking and hunting is easier and where it is possible to find several dry, durable seeds (grains and legumes), good for the human nutrition. The origin of agriculture probably occurred in a landscape that was already dominated by the Mediterranean dry grasslands since a very long time, as a consequence of anthropogenic fires, and where the domesticated livestock progressively took the place of the herds of wild herbivores.

The success of the Mediterranean dry grasslands, and particularly of those rich in thero-phytes have been boosted by a positive feedback switch with the human activity, that in the Mediterranean region begun in the Paleolithic. As we have seen, dry grasslands produce many food items for the humans (legumes, oily seeds, cereals, bulbs); moreover, they take advantage from the human disturbance, that increases the ecological fitness of these versatile but poorly competitive plant communities. The positive feedback switch settled down as follows: raised human population —> increased impact (clearings, fires, generic disturbance) —> decreased interspecific competitiveness —> increased ecological fitness of the ephemeral dry grasslands —> raised human population (PIGNATTI 1978).

This positive feedback led to the transition towards the Neolithic culture and the towards an extensive agro-pastoral landscape, that begun with the selection and domestication of the most productive breeds. This transition is wonderfully represented on one of the most outstanding archaelogical findings of the Sumerian civilisation: the Uruk-Warka vase: In the bas-relief decorating the vase, starting from the bottom one can see spikes (perhaps barley) and other grains, a flock of goats and sheeps, a file of servants bringing different food items and, at the top, a king and some officers accepting the food from the servants and storing it into the granaries.

This bas-relief is not only perhaps the first representation of a trophic chain, but also provides a direct proof that the transition from egalitarian tribal societies of gatherers and hunters to the social stratification of the civilized societies passed through the acquired ability of producing food through the agro-pastoral exploitation of the territory.

Therefore, the success of the Mediterranean dry grasslands is greatly depending on the cyclic human perturbation of their milieu, acting together with the climatic fluctuations and other natural perturbations that are affecting the Mediterranean ecosystem at different spatio-temporal scales, creating an highly dynamic and ever-changing natural ecosystem, where entropy let to the dry grasslands to acquire a long-term evolutionary metastability, far from an homeostatic equilibrium stage. The maintenance of a dynamic long-term flow equilibrium depending on perturbations has been defined *homeorhesis* ("preserving the flow"), and in thermodynamic terms it can be seen as a system depending on the existence of dissipative structures (perturbations) producing high internal entropy that impede to the system to achieve an homeostatic equilibrium (WADDINGTON 1975; NAVEH l.c.).

But if a perturbation-dependent system lasts in an homeorheic state of equilibrium for thousands years of human activity, the soil fertility may progressively be depleted, because a great part of the produced biomass is taken away by the agro-pastoral practices and used (directly or indirectly) to feed the human societies. This may lead to a decreased carrying capacity of the ecosystem, that imposes new conditions of homeostatic equilibrium, based on lower energetic inputs. This land degradation, also called "desertification", at present times affects large areas of the Mediterranean lands, as a result of a non well balanced land management. Preliminary results of a study carried out in Sardinia suggest that therophytic dry grasslands can be used to assess the threat of desertification in Mediterranean lands.

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