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Patterns of plant population spatial variability in relation to vegetation dynamics: vegetation series matter.

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Abstract

The role of abiotic factors (geology and climate) and human activities in shaping the spatial variability and distribution patterns of plant populations are widely studied. Less is known on the effects of plant-plant and plant-animal interactions in determining the dispersal, establishment and performance of plant species propagules and therefore in conditioning plant population spatial variability.

Plant and animal species composition can be considered constant within a vegetation series in a discrete biogeographical and bioclimatic area: structural and functional traits of communities are therefore biotic factors that play a major role in determining the fate of populations.

Here we analyze how the chorological and functional traits of plant and animal species within vegetation series affect seed dispersal, recruits performance and population fluctuations of some case-study plant species. Comparison of the performance of plant populations among vegetation series is of great interest to understand mechanisms of plant-plant and plant-animal interaction.

Two case study are presented: temporal analysis of the population dynamics of an endemic dwarf plant (*Centaurea horrida* Badarò), living in coastal, thermomediterranean, juniper vegetation series, under different types of land use, and the spatial analysis of the population structure of a temperate, relic tree (*Taxus baccata* L.), within different types of Mediterranean and sub-Mediterranean oak-dominated series, in relation to browsing.

Keywords: competition, facilitation, plant-animal interactions, plant-plant interactions, Sardinia, secondary succession.

Abstract

Il ruolo dei fattori abiotici (geologici e climatici) e delle attività antropiche nel condizionare la variabilità spaziale e i patterns distributivi delle popolazioni vegetali sono ampiamente studiati. Si conosce meno, invece, riguardo agli effetti delle interazioni tra piante e tra piante e animali sulla dispersione dei semi, sull'emergenza e la sopravvivenza delle plantule e quindi sulla variabilità spaziale delle popolazioni vegetali.

La composizione delle specie animali e vegetali può essere considerata costante in una serie di vegetazione all'interno di un'area biogeografica e bioclimatica discreta: le caratteristiche strutturali e funzionali delle comunità sono pertanto fattori biotici che giocano un ruolo decisivo nel determinare il destino delle popolazioni vegetali.

In questo contributo si analizza come i caratteri corologici e funzionali delle specie vegetali e animali nelle serie di vegetazione condizionano la dispersione dei semi, il reclutamento e le fluttuazioni di popolazione in alcuni casi di studio. La comparazione dello stato delle popolazioni vegetali tra serie di vegetazione può permettere di comprendere i meccanismi delle interazioni tra piante e tra piante e animali.

Vengono presentati due casi di studio: 1) l'analisi temporale delle dinamiche di popolazione di una pianta endemica suffruticosa (*Centaurea horrida* Badarò), che vive nell'ambito degli stadi di degradazione di una serie costiera, termomediterranea, del ginepro turbinato, in differenti tipologie di uso del suolo; e 2) l'analisi spaziale della struttura delle popolazioni di un albero caratteristico dei climi temperati, a distribuzione relittuale (*Taxus baccata* L.), nell'ambito di diverse serie di vegetazione mediterranee e submediterranee dominate da querce, in relazione al pascolamento.

Parole chiave: competizione, facilitazione, interazioni piante-animali, interazioni pianta-pianta, Sardegna, successione secondaria.

Introduction

The role of abiotic factors (soil, geology and climate) in shaping the spatial variability and distribution patterns of plant populations are widely studied (Biondi *et al.*, 2004; Escudero, 1996; Zuccarello *et al.*, 1999). Less is known on the effects of plant-plant and plant-animal interactions in determining the dispersal, establishment and performance of plant species propagules and therefore in conditioning plant population spatial variability. Plant and animal species composition can be considered constant within a vegetation series in a discrete biogeographical and bioclimatic area: structural and functional traits of communities are therefore biotic factors that play a major role in determining the fate of plant populations. Within a given vegetation series, a fundamental dynamic role is that of shrub communities: these are ecotones with high specific diversity (Hansen *et al.*, 1988), that in Mediterranean environments are able to colonize wide open areas swiftly after disturbance. In many Mediterranean regions shrub communities substitute forests (Quézel & Médail, 2003) and are thus of considerable biogeographical significance (Thompson, 2005). Therefore, in the Mediterranean basin, shrub groves are substitution communities, that in the long run, if not disturbed (e.g. by bushfires, grazing, etc.), are inevitably replaced by potential forest vegetation. Furthermore, they play an important ecological role by way of their facilitation of the renewal of many tree species (García *et al.*, 2000). As a consequence, shrub communities can be competitors of herbs and dwarf species and at the same time nurse species for trees. Their role of colonizers and/or nurse species is often mediated by animals as herbivores and seed dispersers.

Facilitation among plants takes place when the recruitment and survival of one species is enhanced by another, as a consequence of their spatial association (Bruno *et al*., 2003; Callaway, 1995; Callaway & Walker, 1997). Facilitation occurs through direct and indirect interaction. In the former case the nurse plant (Tewksbury & Lloyd, 2001) facilitates the other by making the physical-chemical environment under its canopy better than the nearby areas. In the latter the positive interaction between two species is mediated by a third organism: as for example, when frugivores are attracted by shrubs and disperse seeds of tree species (disperser-mediated facilitation: shrubs become thus dispersal foci for trees, see Verdú & García-Fayós, 2003) and when shrubs protect tree propagules from herbivores (herbivore-mediated facilitation, see Farris & Filigheddu, 2008; García *et al*., 2000). Disperser-mediated facilitation and herbivore-mediated facilitation can occur together, for example when a shrub acts as a dispersal focus for a tree and subsequently protects its propagules against herbivores (Verdú & García-Fayós, 2003).

The composition of the plant and animal community involved in a given vegetation series is therefore of great importance in determining the interactions among species and consequently the performance of a plant population in the long term. Despite the large amount of information available on the structural diversity of shrub communities (Biondi *et al*., 2002; Blasi *et al*., 2002; Farris *et al*., 2007; Poldini *et al*., 2002), there is a paucity of data regarding their functional diversity from both a biogeographical and an ecological perspective. With the aim to clarify their role in the dynamics of vegetation series, here we analyze: 1) how the proceeding of a secondary succession can affect the performance of a threatened dwarf plant; and 2) how the shrub species can facilitate tree propagules in relation to dispersers and herbivores. Two case study will be presented: 1) temporal analysis of the population dynamics of an endemic chamaephytic dwarf plant (*Centaurea horrida* Badarò), living in coastal, thermo-Mediterranean, juniper vegetation series, under different types of land use (Farris *et al*., 2009); and 2) the spatial analysis of the population structure of a temperate, relic tree (*Taxus baccata* L.) under different types of herbivore pressure (Farris & Filigheddu, 2008).

Materials and methods

Case study 1

Centaurea horrida (Asteraceae) is a sea cliff species listed with priority status in the Annexe II of the EU 43/92/EEC Directive, that has been recently classified as ‘endangered’ (EN) following the IUCN criteria (Pisanu *et al*., 2009). This species is a spiny dwarf chamaephyte, defined as narrow endemic, because it grows only along the coasts of Northern Sardinia (Valsecchi, 1977).

This study was carried out on two populations of *C. horrida*, located at Cala della Barca (40°36’N/8°09’E) and Marina di Lioneddu (40°37’N/8°09’E) respectively, in the Capo Caccia Peninsula (NW Sardinia, Italy). The bioclimate is of the Oceanic Pluviseasonal Mediterranean type: the study area falls in the upper thermo-Mediterranean phytoclimatic belt, with an upper dry ombrotype (Biondi *et al*., 2001). This area was managed as penal colony from 1939 to 1961. It was acquired by the Forestry Board of Sardinia in 1967-68 and included in the Porto Conte Regional Park in 1999. Until 1968 the deep soils were used to grow cereals, while the stony areas were used for the traditional husbandry of sheep and goats. To this aim, fire was often used as a management practice. Dwarf vegetation with *C. horrida*, *Astragalus terraccianoi* Valsecchi, *Euphorbia pithyusa* L. and *Helichrysum microphyllum* (Willd.) Camb. subsp. *tyrrhenicum* Bacch., Brullo & Giusto Nyman was widespread (Desole, 1956). After 1968, the deeper soils were planted with allochthonous tree species such as *Pinus halepensis* Mill., *Cupressus sempervirens* L., *Acacia saligna* (Labill.) H.L. Wendl. and *Eucalyptus camaldulensis* Dehnh., while in the stony ground grazing activity ceased (Farris *et al*., 2009).

Centaurea horrida takes part in the Sardinian, thermo-Mediterranean, edapho-xerophilous series of the *Chamaeropo-Junipero turbinatae* Σ, which is constituted by the natural potential vegetation of the *Chamaeropo-Juniperetum turbinatae*, shrub communities of the *Pistacio-Chamaeropetum humilis*, dwarf, spiny garrigues (phrygana) of the *Centaureetum horridae*, perennial herb communities of the *Anthyllido vulnerariae-Kundmannietum siculae*, and annual herb communities of the *Bupleuro fontanesii-Scorpiuretum muricati* (Bacchetta *et al*., 2009; Biondi *et al*., 2001).
At present *C. horrida* grows in different communities (Biondi *et al*., 2001): 1) halophilic rupicolous communities dominated by chamaephytes, on the higher front of sea-cliffs, with other endemic sea-cliff species of the genus *Limonium* Miller, referred to the association *Crithmo maritimi-Limonietum nymphaei*; 2) dwarf communities in flat summit areas with *Astragalus terraccianoi*, *Euphorbia pithyusa* and *Helichrysum microphyllum* subsp. *tyrrhenicum*, ascribed to the association *Centaureetum horridae*

and 3) *Juniperus phoenicea* L. subsp. *turbinata* (Guss.) Nyman scrub communities, of the association *Chamaeropo-Juniperetum turbinatae*, also in flat summit areas.

First, to detect changes in the structure of vegetation cover at Cala della Barca, we carried out photointerpretation of aerial photographs taken during 1951 and 2001, by using ArcView GIS 3.2 software.

Second, to detect how the community structure can affect the population structure of *C. horrida*, two 1 hectare plots were randomly established at Cala della Barca, one in the *Chamaeropo-Juniperetum turbinatae* and one in the *Centaureetum horridae*, respectively. All the individuals of *C. horrida* within each plot were assigned to one of three different life stages: seedlings, saplings and adults (reproductive individuals). The individuals belonging to each life stage were counted. The structure of the *Centaureetum horridae* and the *Chamaeropo-Juniperetum turbinatae* was described in terms of plant species cover. Since cover data coming from the application of the phytosociologic method were already gathered (Biondi *et al*., 2001), in this study plant species composition was assessed along five 50 m long transects (Bullock, 1996), that were randomly placed within each plot. The identity of plant species was recorded at points located every 50 cm along the transect (N = 100 points per transect). Nomenclature of taxa follows Conti *et al*. (2005). Within each association we distinguished the following five microhabitats: phanerophytic, chamaephytic, perennial herbs (hemicriptophytes and geophytes), annual herbs (terophytes) and empty spaces (rocky, stony and bare ground). Finally, each individual of *C. horrida* was assigned to a microhabitat within each plant community. In order to verify whether the spatial distribution of the individuals of *C. horrida* was dependent on the availability of the microhabitats, a χ^2 test was carried out to compare the observed distribution of the individuals with the expected distribution, representing a random distribution where the occurrence of individuals was proportional to microhabitat availability within each association.

Case study 2

Taxus baccata (Taxaceae) is a long-living tree species, the occurrence of which is progressively decreasing all over Europe (Thomas & Polwart, 2003). Previous reports have suggested that *T. baccata* regeneration depends on the facilitative effects of shrubs (García & Obeso, 2003; Hulme, 1996), especially in systems wherein the browsing pressure is high (Farris & Filigheddu, 2008; García *et al*., 2000).

This study was conducted on *T. baccata* populations at six localities of Northern Sardinia, in the subregions of Gallura, Goceano, Marghine and Montiferru. The study sites had similar altitude (870-1100 m a.s.l.) and soil, because *T. baccata* stands grow all on acidic soils that have developed on rhyolitic, schistic, and granitic substrata. Bioclimate is similar as well, being of the Oceanic Temperate type in the sub-Mediterranean variant: the study sites are all included in the upper mesotemperate – lower supratemperate phytoclimatic belts, with a humid ombrotype.

All the yew populations studied were included within woods composed mainly of *Quercus* gr. *pubescens* Willd., *Q. ilex* L., *Acer monspessulanum* L., and *Fraxinus ornus* L. *Ilex aquifolium* L. was also present at all the sites. These woods are the natural potential vegetation of Sardinian, sub-Mediterranean, acidophilous, climacic and mesophilous series of the holm oak with holly, *Saniculo europaeae-Quercetum ilicis* and of deciduous oaks with holly, *Glechomo sardoae-Quercetum congestae* associations (Bacchetta *et al*., 2009). Shrubby patches are found in the wood understory, dominated by *Rubus ulmifolius* Schott. Other less frequent shrubs are *Crataegus monogyna* Jacq. and *Rosa canina* L. Shrub communities are referred to the *Clematido vitalbae-Maletum pumilae*, *Crataego monogynae-Aceretum monspessulani*, and *Crataego monogynae-Pyretum amygdaliformis* associations (Farris *et al*., 2007). The main yew-seed dispersers at these sites were frugivorous birds such as *Turdus merula*, *T. philomelos*, and *T. viscivorus*; however, *Vulpes vulpes* and *Martes martes* also have been observed to eat arils from the ground (personal observations of the authors).

The sites considered for this study differed in their types of uses (three were grazed by livestock and three were not). Livestock was composed of sheep and cattle, whereas wild ungulates were absent, with the exception of *Sus scrofa* that was present at all the studied sites.

The vegetation structure of the studied woods was described as the prevalence (%) of each habitat at each site and was determined by means of 5 transects 100 m long (Bullock, 1996) randomly located at each site. At each meter along the transect, the habitat was qualitatively recorded so that at each site a total of 500 samples were gained. Plant names have been provided following Conti *et al*. (2005).

To estimate the spatial distribution of juveniles, 3 ungrazed and 3 grazed sites were selected. At each site, five habitats were identified: 1) areas under the canopy of reproductive females of *T. baccata*, 2) areas under the canopy of reproductive females of *I. aquifolium*, 3) areas under the canopy of adult non-fleshy-fruited trees (mainly oaks and maples), 4) areas below the shrubs, and 5) open areas, always forest gaps with herbaceous species cover.

Ten quadrats, 2 x 2 m in size, were randomly chosen for each combination of site x habitat, so that, overall, 300 quadrats were sampled for the complete experiment. Two response variables were considered: seedling abundance and sapling abundance.

ANOVA was used to test the differences between the abundances of the seedlings and saplings with reference to the type of land use (grazed versus ungrazed), sites (3 levels), and habitats (5 levels). Land use was considered as a fixed factor, site as random and nested within land use, and habitat as fixed and orthogonal. Before proceeding with the analyses, the homogeneity of variances was tested by Cochran's *C*-test and, whenever necessary, data were appropriately transformed. Student-Newman-Keuls (SNK) tests were carried out to compare the mean values of all significant factors (Underwood, 1997). ANOVAs were conducted using the GMAV5 software package (University of Sydney).

Results

Case study 1

The only association that remained constant in terms of surface cover between 1951 and 2001 was the *Crithmo maritimi-Limonietum nymphaei,* because it is an azonal community living on the cliffs facing the sea, and therefore is not involved in the secondary succession process. The plateau area was entirely occupied by the *Centaureetum horridae* in 1951 (56 hectares) but only 6 hectares were still occupied by this association in 2001. About the 88.5% of the cliff plateau under study was occupied by the *Chamaeropo-Juniperetum turbinatae* association in 2001: this juniper scrub community was not present in 1951.

The density of *C. horrida* in the two associations was found 5 times higher in the *Centaureetum horridae* than in the *Chamaeropo-Juniperetum turbinatae*. Furthermore, no seedlings were found in the *Chamaeropo-Juniperetum turbinatae*.

The structure of the two associations was dominated by the phanerophytic microhabitat (65%) in the juniper scrub and by bare soil, stones and rocks in the *Centaureetum horridae* (35%) (Fig. 1). The more abundant species in the *Chamaeropo-Juniperetum* were *Pistacia lentiscus* L. (27%), *Juniperus phoenicea* subsp. *turbinata* (25%), and *Brachypodium retusum* (Pers.) P. Beauv. (5%), whereas the prevalent species in the *Centaureetum horridae* were *Helichrysum microphyllum* (Willd.) Camb. subsp. *tyrrhenicum* (14%), *Brachypodium retusum* (8%), and *Euphorbia pithyusa* (6%).

In the *Chamaeropo-Juniperetum turbinatae*, there were more individuals of *C. horrida* than expected in the chamaephytic microhabitat and in the bare soil, whereas there were less individuals than expected in the phanaerophytic microhabitat (χ^2 test, $P<0.05$). No differences occurred in microhabitats dominated by annual and perennial herbs (χ^2 test, $P>0.05$). In the *Centaureetum horridae*, there were more adult individuals of *C. horrida* than expected in the chamaephytic microhabitat and more juveniles in microhabitats dominated by annual herbs, whereas there were less individuals than expected in the microhabitats dominated by perennial herbs (χ^2 test, $P<0.05$). No differences occurred in microhabitats dominated by phanaerophytes and on bare soil (χ^2 test, $P>0.05$). The majority of juveniles were found in empty spaces (Farris *et al*., 2009).

Case study 2

The prevalent habitat at all the studied sites is constituted by areas under the canopy of adult non-fleshy-fruited trees, followed by open areas, shrubs, areas under the canopy of reproductive females of *I. aquifolium,* and areas under the canopy of reproductive females of *T. baccata* (Fig. 2).

A higher mean density of seedlings was observed at the grazed sites than at ungrazed sites. Higher density of seedlings was measured under canopies of reproductive female *T. baccata* and *I. aquifolium*. No seedlings were found in open habitats. Seedling density was significantly affected by the interaction between the types of land use and habitat. The density of seedlings was lower at the ungrazed sites in *Taxus* and *Ilex* habitats but no differences were observed for other habitats. Seedling density at the ungrazed sites was in the order *Ilex* > *Taxus* > shrubs = non-fleshy-fruited trees > open, whereas the same was in the order *Taxus* > *Ilex* > shrubs = non-fleshy-fruited trees > open at the grazed sites (SNK test, $P<0.05$).

Conversely, the sapling density was greater at the ungrazed sites than at the grazed sites. The habitats containing higher sapling density were areas below the shrubs. Also the sapling density was significantly affected by the interaction between the types of land use and habitats. The sapling density was lower at the grazed sites. Sapling density at the ungrazed sites was:

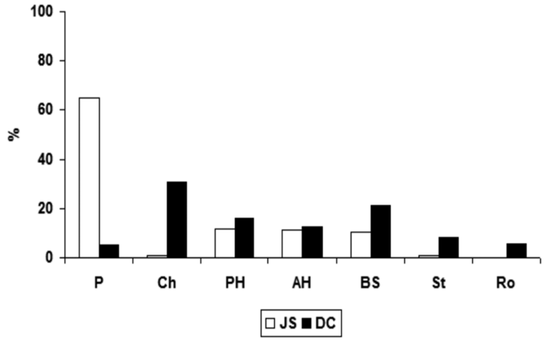

Fig. 1 - Habitat composition (% cover) of the two communities under study. JS = juniper scrub; DC = dwarf community; P = phanaerophytes; Ch = chamaephytes; PH = perennial herbs (hemicryptophytes + geophytes); AH = annual herbs (therophytes); BS = bare soil; St = stones; Ro = rocks.

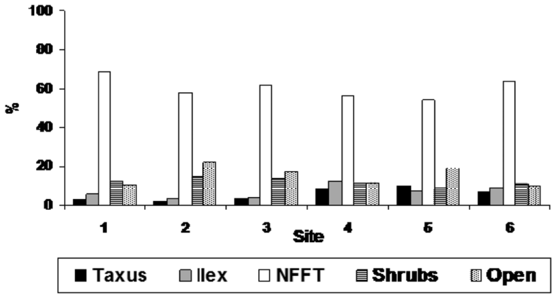

Fig. 2 - Vegetation structure as percent cover of the habitats at each site. NFFT = non-fleshy fruited trees.

shrubs > non-fleshy-fruited trees > *Ilex* = *Taxus* > open, whereas the order of sapling density at the grazed sites was shrubs > *Ilex* = *Taxus* = non-fleshy-fruited trees = open (SNK test, P<0.05) (Farris & Filigheddu, 2008).

Discussion

The differences in density and population structure of *C. horrida* seem to be linked to the spatial variations of the different microhabitats. The spatial distribution of the individuals of *C. horrida* was not homogeneous, because they were concentrated in open microhabitats, hence explaining the lower density in the juniper scrub, a community characterised by a lower percentage of open microhabitats. The juvenile individuals preferred bare soil and annual herb microhabitats, as confirmed by seeding experiments (Farris *et al*., 2009). This finding, together with the information about land cover change (1951-2001), is evidence of a process of secondary succession (Pickett *et al*., 1987), which favoured *J. phoenicea* subsp. *turbinata* and led to the disappearance of *C. horrida*. Our data show that *C. horrida* is a species linked to the initial stages of soil development, when bare soil is available, but it is non-competitive with the late-succession species of *Chamaeropo-Juniperetum turbinatae*.

The second case study shows that the density of *T. baccata* seedlings was higher at the grazed than the ungrazed sites in all shaded habitats. However, the density of saplings was higher at the ungrazed rather than the grazed sites in all habitats. The density of *T. baccata* recruits was particularly affected by the habitat with respect to land use; conversely, no significant effect was apparent due to the differences among the sites within the same type of land use. Other studies highlighted that browsing of saplings caused a significant increase in the risk and intensity of herbivory (Farris & Filigheddu, 2008).

The current study highlights the contrasting effects of browsing on *T. baccata* regeneration. Browsers probably had positive effects on seed germination through their trampling and resulting scarification. Subsequently, the most important effects of browsing are the sharp decrease in the total density of saplings, their concentration in the shrubby habitats, and their nearly complete extinction in non-shrubby habitats. Moreover, these data confirm the essential role of shrubs in the regeneration of *T. baccata* as mechanical protection in the presence of browsing, as already highlighted by applicative studies on the use of shrubs as nurse plants for forest species (Gómez-Aparicio *et al*., 2004).

Our case study 1 demonstrates that the institution of protected areas is necessary to protect coastal species that are subject to increasing pressure due to tourism, but should take spontaneous vegetation succession into particular account (Romero-Calcerrada & Perry, 2004). In many areas of the Mediterranean Basin active management practices have recently been proposed, such as the removal of forest species for the conservation of herb species linked to open habitats (Andrieu *et al*., 2007) and the use of fire for the conservation and sustainable management of tree species (Fernandes & Rigolot, 2007). The case of *C. horrida* is likely to be representative of the need for such management also for other cliff species, at least for those of particular conservation value within protected areas.

The second case study highlights the importance of shrubs and the need to preserve shrubby patches in the vicinity of reproductive female *T. baccata* and *I. aquifolium* for the regeneration of *T. baccata* in the presence of browsing (Farris & Filigheddu, 2008), and is in accordance to previous reports that, in dioecious species, the act of attracting frugivorous birds by reproductive females and the improvement of environmental conditions beneath tree canopies were the factors mainly responsible for variation in juvenile density (Montesinos *et al*., 2007).

The two case studies herein presented, well illustrate how the fate of plant populations is linked to the role of shrub communities within vegetation series. In particular, when the secondary succession process takes over, shrubs can be strong competitors against herbs and dwarf plants; on the other hand, when disturbance is present (as browsing caused by domestic livestock), shrubs can act as nurse species for tree propagules. This study strongly emphasizes the urgent need to take vegetation series into account, in particular for conservation purposes.

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