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

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Abstract

The role of abiotic factors (soil, geology and climate) 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 pattern distributivi delle popolazioni vegetali sono ampiamente studiati. Si conosce meno, invece, riguardo agli effetti delle interazioni tra piante e tra piane e animali sulla dispersione dei semi, sull’emergenza e la sopravvivenza delle piante 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 chorologici e funzionali delle specie vegetali e animali nelle serie di vegetazione condizionano la dispersione dei semini, 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 mediterranea e submediterranea dominate da querce, in relazione al pascolamento.

Parole chiave: competizione, facilitazione, interazioni piante-animali, interazioni pianta-plant, 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 Annex 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 terracianoi Valsecchi, Euphorbia pithyusa L. and Helichrysum microphyllum (Willd.) Camb. subsp. tyrrhenicum Bach.., Bruullo & 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-Juniperetum turbinatae Σ, which is constituted by the natural potential vegetation of the Chamaeropo-Juniperetum turbinatae, shrub communities of the Pistacio-Chamaeropetum humilis, dwarf, spiny garrigue (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 rupeicolous 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 Criithmo maritimi-Limonietum nymphaei; 2) dwarf communities in flat summit areas with Astragalus terracianoi, 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 $\chi^2$ 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, Goeceano, 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 rhizolithic, schistic, and granitic substrata. Bioclimatic 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 phyto-climatic 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 sardoae-Quercetum ictis and of deciduous oaks with holly, Glechomo sardoa-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 monogyna-Aceretum monspessulani, and Crataego monogyna-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).
ANOVA s 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. *tyrrenicum* (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 phanerophytic microhabitat (*χ²* test, *P*<0.05).
No differences occurred in microhabitats dominated
by annual and perennial herbs (*χ²* 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 (*χ²* test,
*P*<0.05). No differences occurred in microhabitats
dominated by phanerophytes and on bare soil (*χ²*
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 (hemicyryptophytes + 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.

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.

References


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