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Reproductive traits variation in the herb layer of a submediterranean deciduous forest landscape

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Abstract In submediterranean ecosystems macroenvironmental stress gradients (winter cold stress and summer drought stress linked to elevation, slope aspect, and angle) affect forest distribution and composition. We hypothesized that in the herb layer of submediterranean deciduous woods (central Apennines), environmental stress gradients, jointly with overstory type, determine patterns of reproductive strategies, which are supported by different acquisitive/retentive traits. We used indicator species analysis, canonical redundancy analysis, and variance partitioning to identify the main gradients of trait variation, detect trait patterns, and assess the contribution of each environmental variable to the explanation of trait variability. Our results indicated that reproductive traits, related to resource acquisition and conservation strategies, showed a pattern mainly linked to the joint effect of altitude and overstory type and, second, to slope aspect. Species with both sexual and vegetative propagation, more abundant than those reproducing only sexually, did not show any trend. Below 1,000 m a.s.l. the long-lasting growing season favored traits aimed at efficient light and soil resource acquisition and space exploitation (e.g., persistent green leaves, runners, tap roots, medium sized seeds) that support a long reproductive cycle. Over 1,000 m a.s.l. the intense and long-lasting winter cold stress and the shorter growing period fostered traits aimed at fast growth and reproduction (e.g., self-pollination, low seed weight, spring and overwintering green leaves), and at stress tolerance (rhizomes, bulbils).

Keywords Acquisitive strategy · Clonality · Cold stress · Drought stress · Growing period · Retentive strategy

Introduction

Plant species differ in their adaptability to stress and disturbance, as their potential to establish or persist under any given set of environmental conditions is determined by their functional traits (McIntyre et al.

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1999; Díaz and Cabido 2001). Traits reflect plant adaptations to variation in the physical environment besides the trade-offs among different functions within a plant (Lavorel et al. 2007), and impact plant fitness indirectly via their effects on resource acquisition, growth, reproduction, and survival (Solbrig 1993; Grime 2006; Violle et al. 2007; Catorci et al. 2012a).

Trait-based approaches have improved the understanding of how forest ecosystems respond to environmental constraints and human impact (e.g., Nagaike et al. 2003; Verheyen et al. 2003; Decocq et al. 2004; Catorci et al. 2012b). It was demonstrated that species response to environmental perturbations or change often involves reproductive traits such as fecundity, regeneration, and dispersal (Weiher et al. 1999; Lavorel et al. 2007) and that stress and disturbance can directly influence the reproductive effort (Thompson and Stewart 1981; Campbell and Grime 1992). Moreover, Fu et al. (2010) argued that availability of resources affects the trade-off between sexual and vegetative reproduction. Indeed, clonal ability may be strengthened by both low and high levels of environmental resources and by low and high disturbance intensities (Eckert 2002; Klimešová and Pyšek 2011). In addition, clonal ability has an important role in the dynamic processes of plant communities (Prach and Pyšek 1994; Zobel et al. 2010). Concerning these issues, a knowledge gap about the submediterranean forest landscape needs to be filled. In fact, Díaz et al. (2002) argued that trait responses to disturbance and environmental constraints should be assessed in each climatic context to define a general framework.

Submediterranean ecosystems undergo alternations of winter cold stress and summer drought stress with different intensities, depending on the elevation gradient and land form factors such as slope aspect and angle (Rivas–Martínez and Rivas–Saenz 1996–2009). As these factors affect distribution and species composition of the submediterranean wood communities (Tardella et al. 2011; Arévalo et al. 2012), we hypothesized that: (1) environmental stress gradients affect reproductive strategies in the herb layer; (2) different reproductive strategies are supported by different acquisitive/retentive traits (i.e., traits that confer the ability to exploit or to retain resources). Moreover, since the dominant tree species in the forest canopy influence ecosystem processes changing light and water availability, litter accumulation, and soil nutrients content (Vivanco and Austin 2008; Blank and Carmel 2012), we hypothesized that (3) overstory type affects reproductive trait variation in the herb layer jointly with macro-environmental stress factors.

Materials and methods

Study area

The study area (central Apennines, Italy; coordinates range 43°34′–42°42′N; 12°41′–13°30′E) ranges from 200 to 1,800 m a.s.l. The forest landscape (over 20,000 hectares) is composed of woods, in which *Quercus pubescens* Willd. s.l., *Quercus cerris* L., *Ostrya carpinifolia* Scop., and *Fagus sylvatica* L. play a dominant or a codominant role.

The territory is characterized by calcareous substrata, on the border between the Temperate and Mediterranean bioclimatic regions. Below 1,000 m a.s.l. the main climatic features are: mean annual temperature of 12–14 °C; mean annual rainfall of 900–1,100 mm; one or 2 months with a mean minimum temperature below 0 °C; summer drought stress lasting from mid-July to the end of August; a vegetative period of 180–210 days. Over 1,000 m a.s.l. the main climatic features are: mean annual temperature of 8–11 °C; mean annual rainfall of 1,100–1,500 mm; 3–4 months with a mean minimum temperature below 0 °C; absence of summer drought stress; a vegetative period of 140–180 days (Orsomando and Catorci 2000).

The woods are managed as “coppice with standards” and are cut down every 25–30 years. Coppice with standards is a system of woodland management where trees are cut down (coppiced) to stimulate resprouting, except some of them, called “standards”, that are allowed to grow through two or more coppicing rotation cycles.

Sampling design

Using a random-stratified sampling method (Hirzel and Guisan 2002), first we selected coppiced woods in the second half of the regenerative cycle, to avoid the effects of regenerative processes. Then, using a geographic information system, we divided the altitudinal range into 200 m-wide classes; each class was further divided into 45°-wide aspect classes. As woods were not homogeneously distributed among classes (e.g., mountain woods on south-facing slopes were less represented) we used a proportional random-stratified instead of an equal random-stratified sampling method. Then, within each class we selected a priori a number of stands (surface area of 1 ha). The stand selection was based on a plant landscape geodatabase (Pesaresi et al. 2007). In each stand, one 20 m × 20 m plot was randomly placed (for a total of 226 plots). Tree layer cover, slope aspect and angle were homogeneous within each plot.

Data collection

For each plot we collected data on altitude (m a.s.l.), slope aspect (azimuth degrees), and slope angle (vertical degrees). Cover-abundance values of the species in the tree, shrub, and herb layers were assigned using the Braun-Blanquet scale (Braun-Blanquet 1964). Relevés were carried out from mid-May to mid-June (2010), to observe both the early spring and the late spring/summer flowering species.

As our aim was to assess the functional response of the herb layer with regard to plant reproduction, we considered the following traits linked to sexual and vegetative reproduction: occurrence of sexual and/or vegetative propagation and type of vegetative propagation; flowering period; pollen vector; seed weight. Since reproductive strategies also depend on the ability to retain resources and to exploit light, storage organs and leaf persistence traits were considered as well. We did not consider traits that may be influenced by the inter-annual climatic variability (e.g., SLA).

Bibliographic data on species traits (Pignatti 1982; Grime et al. 1988; Klotz et al. 2002; Klimešová and Klimeš 2006) were checked and supplemented by field observations. Flowering period and leaf persistence were checked during the year. Seeds were collected and weighed according to Cornelissen et al. (2003). Seed weight and flowering period were transformed into categorical variables, assuming that each category included the range of normal intraspecific variability of each species.

A description of each trait, with a list of the respective states and data sources, is reported in Online Resource 1.

Data elaboration

Following Warren (2008), aspect azimuth was first converted from the 0–360 compass scale to a linear (0–180) scale, giving northerly aspect a value approaching 0 and southerly aspect a value approaching 180. As south–south-west-facing slopes are the warmest aspect (Campetella et al. 2011), the aspect azimuth was shifted to a minimum on north–north-east slopes (22.5°) and a maximum on south–south-west slopes (202.5°).

To understand how gradients of environmental factors shaped the distribution and the species composition of wood community types, and to define the homogeneous groups of relevés needed to perform the following Indicator species analysis (Dufrêne and Legendre 1997), we processed the relevés by cluster analysis on a "sites-by-species matrix", using the complete linkage method, based on Chord distance. Preliminarily we transformed the Braun-Blanquet cover-abundance classes according to van der Maarel's scale which insures better classification results than those obtained with the presence/absence data or with an emphasis on dominance (van der Maarel 1979). To test their ecological consistency, relevé groups chosen from the dendrogram resulting from cluster analysis, were compared with regard to altitude, slope aspect, and slope angle (as indicated below), and formed the basis for the following elaborations.

Abundances of herb species were expressed in percent values using the average cover values of Braun-Blanquet classes (Podani 2007). Trait states the presence/absence data were transformed into quantitative data. For this purpose, the "relevés-by-herb species cover" matrix was multiplied by the "herb species-by-trait states" matrix to provide a "relevés-by-trait states cover" matrix, which formed the basis for the following analyses (Pakeman et al. 2009). To avoid having the different herb layer cover values of forest communities affect the assessment of trait trends, and to highlight the relations among trait states within each group of relevés, we calculated the mean relative abundance (Tr) of each trait state (percentage value) for each cluster using the formula $Tr = (Ta \cdot 100)/\sum_{i=1}^{n} Ta_i$, where Ta is the absolute abundance of a trait state in a relevé, and n is the number of trait states in a relevé (Catorci et al.

2012b). The *Tr* values, environmental variables and dominant tree species cover values were averaged for each cluster highlighted by the cluster analysis.

We assessed normality distribution and variance homogeneity of data using the Kolmogorov–Smirnov and Levene tests, respectively. Because data did not meet the assumptions required for parametric tests, we performed non-parametric Mann–Whitney *U*-tests to understand which relevés groups were significantly different ($P < 0.05$) from each other in relation to the response and explanatory variables (i.e., trait states relative abundance, topographic variables, and dominant tree species cover). We used a Holm adjustment for multiple comparisons of Mann–Whitney *U*-test results to avoid Type I error.

We performed Indicator species analysis (ISA) to highlight the trait response of the herb layer depending on the forest types identified by cluster analysis. ISA was run for each trait, on the "relevés-by-trait states" matrix (*Tr*, relative abundances) using groups of relevés highlighted by the cluster analysis as grouping variable, to highlight indicator trait states of each cluster. ISA is a non-parametric method for identifying those variables that show significantly preferential distribution (frequency and abundance) with respect to an a priori treatment group (McCune and Grace 2002). The statistical significance of the observed maximum indicator values for trait states was evaluated through the Monte Carlo test, based on 4,999 permutations, where samples are reassigned and recalculated. The number of randomized indicator values higher than the observed ones are used to calculate the probability value. Trait states with an indicator value greater than 20 were considered of interest.

To identify the main gradients of trait variation, the relations among traits, and between traits and environmental variables, we performed Canonical redundancy analysis (RDA) of the "relevés-by-trait states cover" matrix, constrained by the topographic variables (altitude, slope angle, slope aspect) and by the dominant tree species cover. Prior to RDA, the cover data matrix was Hellinger-transformed to avoid considering double absence as a resemblance between sites (Legendre and Gallagher 2001). This transformation expresses the data as relative abundances per site (Borcard et al. 2011).

To assess the contribution of each set of explanatory variables (topographic variables and dominant tree species cover) to the total variability of the trait data set, the total variance was partitioned into fractions explained by each set of the predictor variables by partial RDAs (Borcard et al. 1992; Borcard and Legendre 1994). Adjusted R^2 values ($R^2_{\text{adj}} = 1 - [(n - 1)/(n - m - 1)]\cdot(1 - R^2)$, where n is the number of objects and m is the number of explanatory variables) were calculated to produce unbiased estimates of the contributions of the independent variables to the explanation of the response variables (Peres-Neto et al. 2006). To test the significance of the adjusted R^2 (i.e., whether each independent fraction exhibits a significant influence on cover data), we applied a permutation test with 1,000 permutations, in accordance with Legendre and Legendre (1998). We used the same approach to detect the effect of dominant tree species cover on the variance explained by each topographic variable. First, we calculated the variance explained by each topographic variable. Variance partitioning was repeated adding dominant tree species cover to the explanatory variable data set. This made it possible to separate the independent fractions explained by altitude, slope aspect, and slope angle, from the proportion of variance explained by each of them jointly with dominant tree species cover.

To perform the statistical analysis we used the following softwares: SYN-TAX 2000 (Podani 2001); PCORD (version 5.0, MjM Software Design, Gleneden Beach, Oregon, US); SPSS (version 8.0, SPSS Inc., Chicago, Illinois, US); R (version 2.15.0, R Foundation for Statistical Computing, Wien, Austria. http://www.R-project.org), and *vegan* R-package (version 2.0–4; http://cran.r-project.org/web/packages/vegan).

Results

Cluster analysis highlighted three groups of relevés (Fig. 1). Cluster 1 grouped woods growing on north-facing slopes (400–1,000 m a.s.l.) and was divided in two subclusters: 1a (*Ostrya carpinifolia*-dominated woods spread at lower altitudes and on steeper slopes) and 1b (*Quercus cerris*-dominated woods of the higher altitudes and less steep slopes). Cluster 2 grouped *Fagus sylvatica* woods (950–1,750 m a.s.l.) and was divided into two subclusters: 2a (woods growing on north-facing slopes) and 2b (woods of the south-facing slopes). *Quercus pubescens* s.l. woods of south-facing slopes (200–950 m a.s.l.) were grouped in cluster 3.

The herb layer of *Ostrya carpinifolia*-dominated woods (subcluster 1a), particularly species rich, was mainly composed of *Sesleria nitida*, *Carex digitata*, *Luzula sylvatica*, *Hepatica nobilis*, *Primula vulgaris*, *Cyclamen repandum*, and *C. hederifolium*, while *Quercus cerris*-dominated woods (subcluster 1b) were characterized by *Festuca heterophylla*, *Luzula sylvatica*, and *Melica uniflora*. *Cardamine bulbifera*, *Corydalis cava*, *Galium odoratum*, and *Sanicula europaea* were the most widespread herb species in the understory of *Fagus sylvatica* woods (cluster 2). *Brachypodium rupestre* was the dominant herb species in *Q. pubescens* s.l. woods (cluster 3).

We detected significant differences in cover values of dominant tree species among clusters (Table 1). Moreover, clusters 1 and 2 differed significantly in all the examined variables, while cluster 3 differed from cluster 2 in altitude and aspect, and from cluster 1 in slope aspect and angle. Subclusters 1a and 1b differed significantly in altitude and slope angle, subclusters 2a and 2b in aspect and slope angle (Table 1).

The mean relative abundance values of trait states per cluster and subcluster, the related statistically significant differences and *P* values are indicated in Online Resources 2 and 3; mean absolute abundance values are shown in Online Resource 4. The most represented trait states in each wood type highlighted by cluster analysis are insect pollination, early summer flowering, and the possibility to accomplish both sexual reproduction and vegetative propagation (Online Resource 2). Table 2 shows the indicator trait states of each cluster and subcluster.

The total explained variance for trait data set, constrained by topographic variables and dominant tree species cover was 26.59 % (adjusted R^2). These two variable sets singly considered explained 4.04 and 7.39 % ($P = 0.001$) of the variability, respectively, while their joint effect accounted for 15.16 % of the variance. When variance was extracted from the trait data set using altitude, slope aspect, and slope angle as explanatory variables, altitude showed the greatest effect (adj. $R^2 = 0.1808$, $P = 0.001$), followed by aspect (adj. $R^2 = 0.0137$, $P = 0.001$), and slope angle (adj. $R^2 = 0.0068$, $P < 0.01$), while their joint effects were almost null (Table 3). The combination of altitude-dominant tree cover explained 15.12 % of the variance, while altitude considered singly explained 2.96 % ($P = 0.001$); all the other combinations had weaker or no significant effect (Table 3).

The first axis of RDA performed using altitude, aspect, slope angle, and the cover of the four dominant tree species as explanatory variables, explained 75.99 % of the constrained variance and was strictly linked to altitude and *Fagus sylvatica* cover (negative

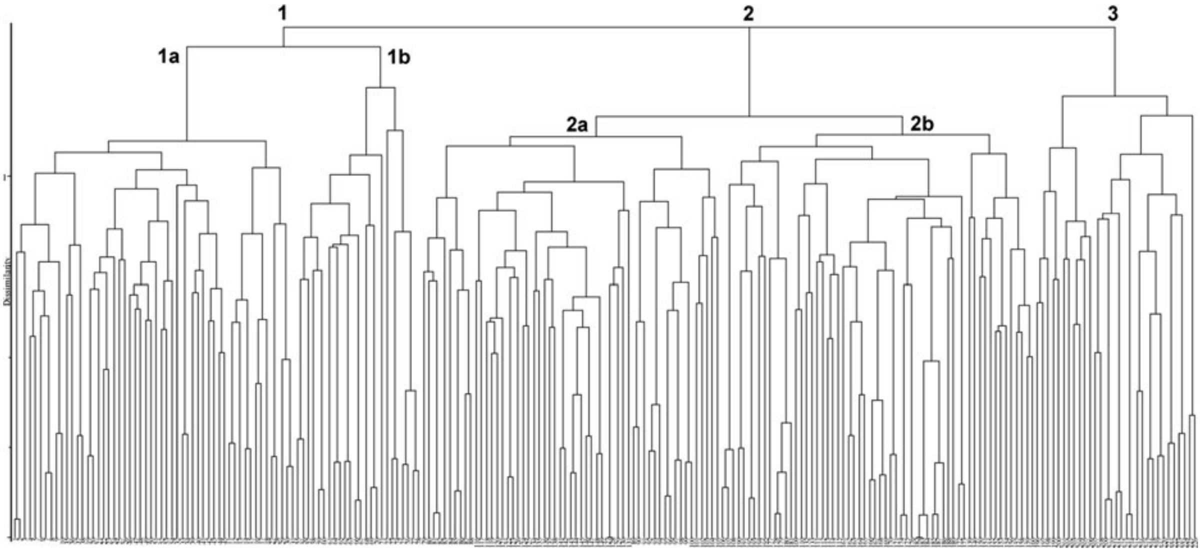

Fig. 1 Dendrogram of vegetation relevés of the study area (*1*: hilly woods of north-facing slopes; *1a Ostrya carpinifolia*-dominated woods, *1b Quercus cerris*-dominated woods, *2* mountain woods, *2a Fagus sylvatica* woods of north-facing slopes, *2b Fagus sylvatica* woods of south-facing slopes, *3 Quercus pubescens* s.l. hilly woods of south-facing slopes)

Table 1 Mean and median values of altitude, aspect angle, slope angle, cover of dominant tree species, followed, in parentheses, by standard deviation (normal font style) and interquartile range (italics), respectively

Env. variable/dominant tree	Statistics	Cluster			Subcluster			
		1	2	3	1a	1b	2a	2b
Altitude (m a.s.l.)	Mean	771.4 (149.5)	1.321.6 (205.9)	650.7 (239.3)	728.3 (132.9)	868.4 (141.4)	1.297.3 (216.6)	1.344.8 (194.2)
	Median	774.0^{a} (*212.5*)	1.300.0^{b} (*135.0*)	730.0^{a} (*480.0*)	730.0^{a} (*164.0*)	885.0^{b} (*97.5*)	1.290.0^{a} (*305.0*)	1.305.0^{a} (*187.5*)
Aspect (azimuth degree)	Mean	52.8 (47.8)	82.7 (66.0)	156.1 (19.2)	53.8 (49.7)	50.6 (44.1)	44.2 (48.5)	119.3 (59.5)
	Median	22.5^{a} (*45.0*)	67.5^{b} (*135.0*)	157.5^{c} (*0.0*)	22.5^{a} (*45.0*)	22.5^{a} (*67.5*)	22.5^{a} (*45.0*)	157.5^{b} (*78.8*)
Slope angle (vertical degree)	Mean	25.3 (10.3)	30.9 (11.1)	34.5 (15.1)	29.1 (8.9)	16.5 (7.7)	33.3 (11.0)	25.8 (10.8)
	Median	25.0^{a} (*10.0*)	30.0^{b} (*15.0*)	35.0^{b} (*20.0*)	27.0^{a} (*11.0*)	15.0^{b} (*10.0*)	30.0^{a} (*20.0*)	28.0^{b} (*10.0*)
Ostrya carpinifolia (cover %)	Mean	43.7 (31.1)	0.2 (0.61)	0.8 (1.2)	61.1 (19.1)	4.6 (9.0)	0.2 (0.8)	0.1 (0.4)
	Median	37.5^{a} (*87.5*)	0.0^{b} (*0.0*)	0.0^{c} (*0.5*)	62.5^{a} (*50.0*)	0.0^{b} (*3.0*)	0.0^{a} (*0.0*)	0.0^{a} (*0.0*)
Quercus cerris (cover %)	Mean	17.1 (24.3)	0.1 (0.4)	2.0 (5.1)	3.0 (7.2)	48.7 (18.7)	0.1 (0.6)	–
	Median	0.0^{a} (*37.5*)	0.0^{b} (*0.0*)	0.0^{c} (*0.0*)	0.0^{a} (*0.2*)	50.0^{b} (*25.0*)	0.0 (*0.0*)	–
Fagus sylvatica (cover %)	Mean	1.9 (4.0)	77.5 (17.4)	1.2 (6.7)	2.0 (4.7)	1.7 (1.4)	85.8 (4.6)	68.6 (20.4)
	Median	0.0^{a} (*3.0*)	87.5^{b} (*25.0*)	0.0^{c} (*0.0*)	0.0^{a} (*0.5*)	3.0^{b} (*3.0*)	87.5^{a} (*0.0*)	62.5^{b} (*25.0*)
Quercus pubescens s.l. (cover %)	Mean	4.8 (7.2)	–	52.0 (14.1)	6.3 (7.8)	1.5 (4.2)	–	–
	Median	0.5^{a} (*37.5*)	–	62.5^{b} (*25.0*)	3.0^{a} (*14.5*)	0.0^{b} (*0.4*)	–	–

Aspect angles were counted from north–north-east (the coldest aspect) to south–south-west (the warmest aspect). Equal letters indicate no statistically significant differences ($P \geq 0.05$) in the pairwise comparisons of clusters (1 vs. 2; 1 vs. 3; 2 vs. 3) and subclusters (1a vs. 1b; 2a vs. 2b) as determined by the Mann–Whitney *U*-test, after Holm correction for multiple comparisons (cluster and subcluster codes are the same indicated in Fig. 1)

values) and, secondarily, to *Quercus pubescens* s.l. and *Ostrya carpinifolia* cover (positive values); the second axis was related to *Ostrya carpinifolia* cover and explained 9.60 % of the variance, while the third, linked to *Quercus cerris* and *Fagus sylvatica* cover and to slope aspect, explained 5.78 % of the variance (Table 4).

The RDA ordination graph (Fig. 2) shows positive correlations of some trait states with the highest altitudes and *Fagus sylvatica* woods, i.e., self-pollination, both self- and insect pollination, light seeds (0.01–0.20 and 0.21–0.50 mg), vegetative propagation by rhizomes (also with storage function) and by bulbils, overwintering and spring green leaves. Instead, pollination by wind, vegetative propagation by runners, the absence of storage organs, and persistent green leaves were particularly related to the lowest altitudes. Tap root, seed weight ranging from 0.51 to 1.00 and from 1.01 to 2.00 mg, and vegetative propagation by rhizome fragmentation were related to north-facing slopes and *Ostrya carpinifolia* woods; flowering in spring and in early summer, seed weight ranging from 2.01 to 4.00 mg and greater than 10 mg were related to south-facing slopes and *Quercus pubescens* s.l. woods (Fig. 2).

Discussion

Our results highlighted that land form and tree dominant type had a joint effect in shaping the

Table 2 List of indicator trait states of clusters (1, 2, and 3) and subclusters (1a and 1b; 2a and 2b) indicated in Fig. 1, as performed by indicator species analysis (ISA) on the "relevés x trait state relative abundances" matrix

Trait	Trait state	Cluster		Subcluster			
		1–2–3		1a–1b		2a–2b	
		Max. cluster	Obs. I.V.	Max. subcluster	Obs. I.V.	Max. subcluster	Obs. I.V.
Flowering period	Spring	3	56.1^{*}	–	–	2b	56.9^{**}
	Early summer	3	54.5^{*}	–	–	2a	59.5^{***}
	Late summer	2	57.7^{***}	–	–	2b	54.3^{*}
Pollen vector	Selfing/insects	2	68.1^{***}	1b	64.3^{***}	–	–
	Insects	2	52.1^{*}	–	–	2a	52.1^{*}
	Wind	1, 3	58.7^{***}, 73.9^{***}	1a	62.2^{**}	2a	55.2^{***}
	Selfing	2	65.7^{***}	–	–	2b	64.2^{***}
Seed weight (mg)	0.01–0.20	2	52.6^{***}	1b	41.4^{*}	–	–
	0.21–0.50	2	51.7^{**}	1b	65.0^{***}	–	–
	0.51–1.00	1	51.2^{***}	–	–	–	–
	1.01–2.00	–	–	1a	63.5^{***}	–	–
	4.01–10.00	–	–	–	–	2a	49.6^{*}
	>10.00	3	46.7^{***}	–	–	–	–
Type of reproduction	Only sexual reproduction	–	–	1a	61.0^{**}	–	–
	Fragmentation/ rhizome°	–	–	1a	27.8^{**}	–	–
	Bulbil°	–	–	1b	20.8^{**}	2b	29.8^{**}
	Rhizome°	2	66.7^{***}	–	–	2a	53.0^{*}
	Runner°	1, 3	63.4^{***}, 68.0^{***}	–	–	–	–
Storage organs	Absent	1, 3	63.7^{***}, 71.0^{***}	1a	68.1^{***}	2a	58.8^{***}
	Bulb	–	–	–	–	2b	22.8^{*}
	Rhizome	2	60.4^{***}	1b	56.8^{*}	–	–
	Tap root	1	50.0^{***}	–	–	–	–
Leaf persistence	Overwintering green	2	55.0^{***}	1b	45.8^{***}	2b	68.2^{***}
	Spring green	2	39.7^{***}	1b	40.4^{***}	2b	57.3^{***}
	Summer green	2	53.1^{*}	–	–	2a	58.4^{***}
	Persistent green	1, 3	59.3^{***}, 56.3^{**}	1a	58.3^{***}	2a	54.6^{*}

Only trait states with $P < 0.05$ and indicator value >20 are reported (*Max. cluster/subcluster* cluster/subcluster with maximum observed indicator value, *Obs. I.V.* observed indicator value, P proportion of randomized trials with an indicator value equal to or exceeding the observed indicator value; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$)

(°) Type of vegetative propagation in addition to sexual reproduction

understory trait composition (Table 3; Fig. 2). In fact, the combination of altitude and overstory type explained the highest percentage of the constrained variance (57 %). Nevertheless, about half of the analysed traits were weakly affected by the considered environmental gradients and overstory type (Fig. 2). Most of them had low abundance, as did species having exclusively sexual reproduction (Online Resource 4), mostly annual and biennial species. Catorci et al. (2011) demonstrated that such species are linked to the first step of forest regeneration and tend to disappear in mature stands. Instead, the high abundance in any condition of species capable of both sexual and vegetative reproduction is consistent with Canullo et al. (2011) and Catorci et al. (2012b), who argued that vegetative propagation plays a key role in

Table 3 Results of partial redundancy analyses (adjusted R^2) performed using absolute abundance data of trait states (Hellinger-transformed), constrained by altitude, aspect, and slope angle (3rd column), and by altitude, aspect, slope angle, and dominant tree cover (4th and 5th columns). In the last case the contribution of only topographic variables (effect of dominant tree cover removed) was separated from the joint effects of topographic variables and dominant tree cover. Importance of both single and joint effects of topographic variables are shown

	Topographic variables	Adjusted R^2		
		Effect of dominant tree cover not removed	Effect of dominant tree cover removed	Joint effect topographic variable(s)-dominant tree cover
Single effect	Altitude	0.1808^{***}	0.0296^{***}	0.1512
	Aspect	0.0137^{***}	0.0085^{***}	0.0052
	Slope angle	0.0068^{**}	0.0020^{ns}	0.0048
Joint effect	Altitude and aspect	−0.0054	0.0001	−0.0055
	Slope angle and aspect	−0.0010	0.0000	−0.0010
	Altitude and slope angle	−0.0035	−0.0003	−0.0031
	Altitude, slope angle, and aspect	0.0006	−0.0001	0.0007
Residuals		0.8080		

Significance of the adjusted R^2 was tested with 1,000 permutations (*** $P = 0.001$; ** $P < 0.01$; *ns* non significant). The joint fractions and residuals could not be tested for significance. Negative values can be considered as null

Table 4 Results of redundancy analysis of plant trait states cover data (Hellinger-transformed), constrained by environmental variables (altitude, aspect angle, and slope angle) and by dominant tree species cover (*Ostrya carpinifolia*, *Quercus pubescens* s.l., *Quercus cerris*, and *Fagus sylvatica*). Scores (scaling 2) for explanatory variables are reported for the first three axes

Explanatory variables	Scores		
	Axis 1	Axis 2	Axis 3
Altitude	−0.8888	−0.2301	−0.1454
Aspect angle	−0.0334	0.1115	−0.7245
Slope angle	0.0011	−0.0764	0.3253
Ostrya carpinifolia	0.6178	−0.6476	0.2683
Quercus pubescens s.l.	0.6506	0.2930	−0.2994
Quercus cerris	0.0824	0.2129	−0.3487
Fagus sylvatica	−0.8148	0.1901	0.4418

managed woods. Silvertown (2008) indicated that clonality is not a substitute for sexual reproduction but helps to prolong the time a species can persist in ecosystems when sexual reproduction is hindered, for instance, by the periodic change in resources availability in managed forests (Rubio and Escudero 2003).

Trait states affected by the considered variables showed a pattern mainly linked to altitude, overstory type and, second, slope aspect (Fig. 2).

The indicator trait states of hilly woods growing below 1,000 m a.s.l., dominated by *Ostrya carpinifolia* and *Quercus cerris*, on northerly aspects, and by *Q. pubescens* s.l., on southerly ones (Table 1) were: the absence of storage organs, persistent green leaves, vegetative propagation by runners, and wind pollination (Table 2).

In the hilly forest landscape, drought stress is absent or moderate on north-facing slopes, and lasts about 1 month on south-facing ones (Orsomando and Catorci 2000); thus, the environmental constraints are not strong limiting factors for plant reproduction. In these conditions, plants do not need to store resources, but reproduction is mainly supported by slow resource exploitation throughout the year by a leaf type with a long life-span. Indeed, persistent green leaves produce higher photosynthetic returns than short-lived ones in ecosystems where water stress is not particularly severe (Chabot and Hicks 1982). Furthermore, long-lived leaves may store lipids and proteins that are translocated to the new leaves at the beginning of the growing season (Hadley and Bliss 1964), allowing an early flowering strategy (van Calster et al. 2008; Catorci et al. 2012a). In fact, as highlighted by RDA (Fig. 2), spring and early summer flowering strategies were positively related to persistent green leaves.

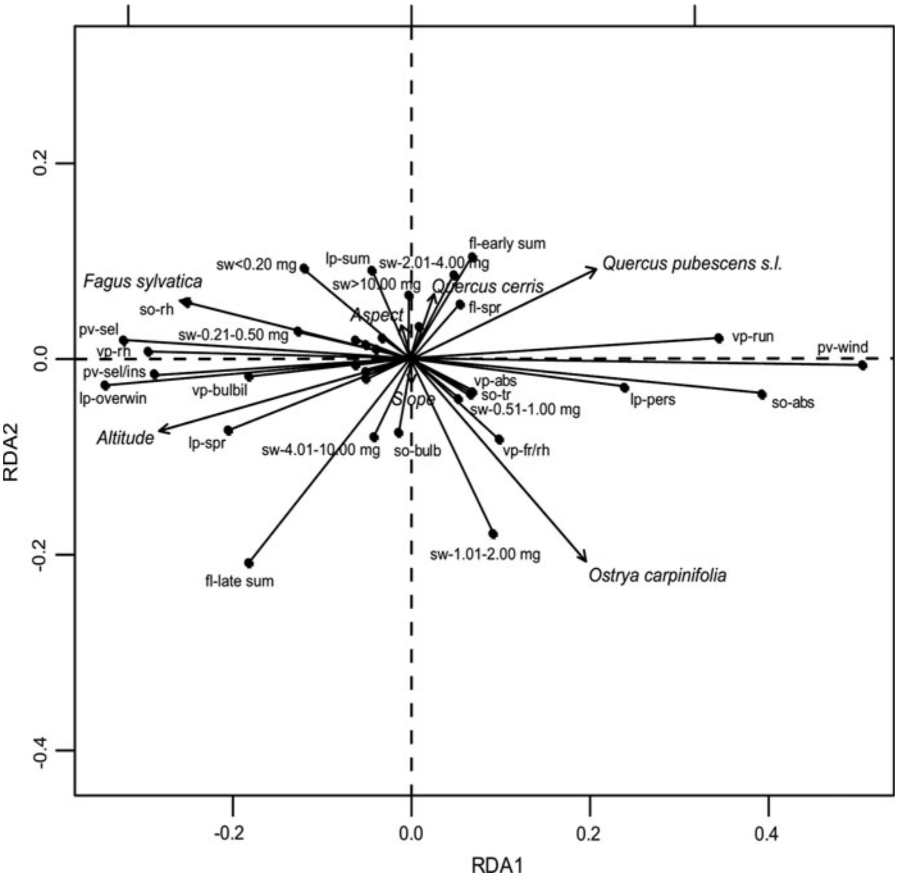

Fig. 2 Redundancy analysis ordination graph for plant trait data set, using altitude, aspect, slope angle, and the cover percentage of dominant tree species *Fagus sylvatica*, *Ostrya carpinifolia*, *Quercus cerris*, and *Quercus pubescens* s.l. as constraining variables. Labels of trait states falling next to the axes origin have been omitted (*abs* absence of the trait, *fl* flowering period, *fr* fragmentation, *ins* pollination by insects, *lp* leaf persistence, *pers* persistent green leaves, *overwin* overwintering green leaves, *pv* pollen vector, *rh* rhizome, *run* runner, *sel* self pollination, *so* storage organ, *spr* spring, *sum* summer, *sw* seed weight, *tr* tap root, *vp* vegetative propagation)

Vegetative spread by runners is a strategy aimed at maximizing the species competitive ability when resource availability is high (Grime 2001) and, in areas where resources are patchy distributed, enables plants to promptly exploit new niches (Tissue and Nobel 1988; Friedman and Alpert 1991).

As stated by Whitehead (1969) and Culley et al. (2002), pollination by wind can be regarded as a suitable strategy in relatively dry conditions (low air humidity and precipitation and high air temperature), such as those that occur in hilly woods during the summer period.

The above-mentioned resource acquisition strategies support a long reproductive cycle, as indicated also by the establishment of tap root and medium sized seeds, indicators of hilly woods of north-facing slopes (Table 2). Indeed, tap root allows plant to store resources and to reach the deepest soil layer, which is supplied with water even in summertime (Grime 2001). Thus, species adopting this strategy may have a late flowering period (Catorci et al. 2012a).

The presence of species with medium sized seeds has been attributed by some authors (e.g., Baker 1972; Catorci et al. 2012a) to the absence of intense stressing conditions and the availability of quite a long time to accomplish the reproductive cycle.

Spring and early summer flowering strategies, and seeds heavier than 10 mg were indicator trait states of woods spread on southerly slopes (Table 2). Indeed, on hilly south-facing slopes the reproductive periods are concentrated in spring and early summer because of the earlier start of the growing season and of the summer drought stress (Bonan 2008). The establishment of species with seeds heavier than 10 mg is consistent with Baker (1972), who associated larger seed mass with dry habitats and with decrease in altitude.

Over about 1,000 m a.s.l., the mountain forest landscape is dominated by *Fagus sylvatica* (Table 1); winter cold stress becomes increasingly intense and the growing season lasts less than 180 days (Orsomando and Catorci 2000). The indicator trait states of this forest type were: rhizome as storage organ and vegetative propagation mode; low seed weight (0.01–0.20 mg, 0.21–0.50 mg); self-pollination or pollination by insects; late summer flowering; overwintering, spring, and summer green leaves (Table 2).

The environmental constraints in mountain areas foster a strategy aimed at slow storage of resources in underground structures (rhizomes). These structures increase the likelihood that plants can establish themselves in stressful habitats (Grime et al. 1997), improving their uptake of water and nutrients (Newell and Tramer 1978).

Rhizomes also function as clonal growth organs and may be considered a tool to overcome sexual recruitment problems under unfavorable conditions. With regard to clonal propagation, we found a close positive relation between altitude and species with bulbils (Fig. 2). Bauert (1993) demonstrated that resource allocation to bulbils may be an adaptation to guard against worsened climatic conditions and unpredictable annual climatic fluctuations.

The short growing period available in mountain environment calls for a fast reproductive cycle that may be insured by the establishment of species with low seed weight (Bolmgren and Cowan 2008; Du and Qi 2010). Moreover, small seeds tend to show dormancy, an adaptation by which they can guard against the effects of winter cold stress (Venable and Brown 1988; Moles et al. 2000). Actually, our results are consistent with Baker (1972) and Bu et al. (2007), who found a negative correlation between seed mass and altitude.

The need for a fast reproductive cycle may also account for the self-pollination and self-pollination/insects pollination trait states (Gugerli 1998), which emerged as positively related to altitude (Fig. 2). Indeed, the decreased length of the growing season promotes adaptations for self-pollination (Bliss 1971), such as self-compatibility or homogamy (Richards 1986; Körner 2003).

Fast growth and reproduction are also supported by the mobilization of reserves stored in rhizomes during the previous growing season (Bolmgren and Cowan 2008); in fact, we found a positive relation between rhizomes and spring green/overwintering green leaves (Fig. 2). Indeed, spring green leaves and overwintering green leaves were the two main trait states for light acquisition in mountain woods. The former is generally linked to fast growing species with storage organs (Grime 2001), the latter allows resource acquisition and storage from autumn to spring and may support a very short reproductive cycle by exploiting the spring peak of photosynthetically active radiation (Graves 1990; Mitchell 1992).

The key role of the length of growing season also emerged from the comparison of the herb layer of mountain woods, spread on north- and south-facing slopes. On south-facing slopes, the higher radiation in summer dramatically reduces the soil water content (Joffre and Rambal 1993), posing an additional stress that plants have to face in mountain areas. These dry climatic conditions shorten the time available for plants to complete the vegetative cycle and in fact the indicator trait states of south-facing slopes (i.e., spring flowering, overwintering and spring green leaves, and self-pollination) mark the environmental differences between the warmest and the coldest aspects (Table 2). It is worthy to note that vegetative propagation by bulbils may be also considered a drought avoidance mechanism (Lee and Harmer 1980).

Conclusions

Our research demonstrated that the different reproductive strategies in the herb layer of submediterranean woods are filtered by environmental constraints that depend on the combined effect of land form and overstory type, and are related to specific resource acquisition and conservation strategies. The joint effect of different stress types, acting mainly on the length of the growing season, selects clusters of strategies aimed at slow or fast growth and reproduction by filtering different and synergic types of resource acquisition (leaf trait states), retention (storage organs), besides seed weight, and types of pollination. Thus, it is possible to assume that the combination of different environmental constraints filters different trait combinations devoted to plant reproduction rather than single traits. This means that the assessment of single traits and/or the evaluation of the simple gradient are not good tools to understand the understory species assemblage at the community level, especially in ecologically complex ecosystems as the submediterranean ones.

Moreover, the types of clonal growth organ have different ecological meanings and are filtered by the different stress types and intensities. They may confer high competitive ability where resources are not a limiting factor or are patchy distributed (e.g., runners) or insure stress tolerance (e.g., rhizomes; bulbils) where the ability to compete is likely to be of secondary importance to the capacity to tolerate stress.

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