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Seed bank composition and above-ground vegetation in response to grazing in sub-Mediterranean oak forests (NW Greece)

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Abstract We investigate the persistent soil seed bank composition and its relation to the above-ground flora of grazed and non-grazed sub-Mediterranean deciduous oak forests of NW Greece. Twenty-eight taxa were recorded in the soil seed bank and 83 taxa (70 taxa in plots of seed bank sampling) in the above-ground vegetation. The dominant tree species and many woodland species found in the above-ground vegetation were absent from the soil seed bank. Similarity between the soil seed bank and the above-ground vegetation decreased with grazing, and grazing led to a decrease of species richness in above-ground vegetation and soil seed bank. Beta diversity of vegetation among grazed and among non-grazed plots did not differ, but was significantly higher between grazed and non-grazed areas. Beta diversity of the soil seed bank declined with grazing. When applying classification tree and logistic regression analyses, non-grazed forest sites are clearly differentiated by the presence of *Phillyrea latifolia*, *Euphorbia amygdaloides* and *Brachypodium sylvaticum*. PCA ordination of above-ground species composition reflected a gradient from sites grazed by ruminants to non-grazed sites, but no clear structure was detected in the seed bank.

Keywords Soil seed bank · Wood pasture · Grazing · Browsing · Deciduous oak forests · Greece · Wild boar · Ruminants

Introduction

The composition of a seed bank depends on present and former above-ground vegetation (Rice 1989) and seed rain from adjacent areas (Hutchings and Booth 1996). The historical composition of above-ground vegetation has often been identified as a key factor determining seed bank composition (Bekker et al. 1998). Soil seed bank composition is also influenced by the surrounding vegetation and former

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successional stages (Falinska 1999; Godefroid et al. 2006) and can undergo significant changes depending on the management applied (Wellstein et al. 2007). However, there is still considerable lack of knowledge on the seed bank characteristics of many species, including typical forest species (Bossuyt and Hermy 2001), and seed viability in forest soils (Grandström 1987; Thompson et al. 1997).

Mediterranean environments have undergone many changes due to human disturbances, such as sylvopastoralism (Le Houérou 1990). The effects of herbivory vary due to parameters such as intensity, plant taxa and soil properties. Species composition in European beech forests grazed by high densities of *Cervus elaphus*, *Cervus dama*, *Capreolus capreolus*, *Ovis musimon* and *Sus scrofa* has been significantly determined by two pathways: dispersal in time by a persistent seed bank, and dispersal in space using ungulates (Naaf and Wulf 2007). In the agricultural landscape of central Europe wild boars epizoochorously transport large amounts of seeds due to their fur characteristics, behaviour (wallowing and rubbing on trees), large local population size and general abundance (Heinken et al. 2006).

Ungulate species such as *Cervus elaphus*, *Capreolus capreolus* and *Sus scrofa* affect natural regeneration of forests throughout Europe. Selective browsing promotes changes in forest tree composition (Kuiters and Slim 2002). However, boars have different grazing behaviour from ruminants. Wild boars prefer acorns as a food source (Jedrzejewska et al. 1997), and forage on germinating oak seedlings, saplings and roots by digging, thus affecting both regeneration and soil properties (Groot Buinderink and Hazebroek 1996). Ruminants such as *Capreolus capreolus* and *Cervus elaphus* browse on seedlings, leading and lateral shoots causing structural changes (Pépin et al. 2006) and rub trunks resulting in tree damage (Ramos et al. 2006).

The role of browsing and grazing in woodland regeneration, and the long distance dispersal of seeds has been studied extensively. However, the impact of ruminant and boar grazing on soil seed bank composition, and its similarity to above-ground vegetation has received less attention. In different types of grasslands, grazing increases (Bakker and de Vries 1992; Ungar and Woodell 1996), decreases (Jutila 1998) or has no effect on (Peco et al. 1998) the similarity of seed banks and above-ground vegetation (Osem et al. 2006). For forests, discrepancies between above-ground vegetation and soil seed banks have been recorded (Thompson and Grime 1979; Bossuyt et al. 2002; Forrester and Leopold 2006; Roovers et al. 2006) and attributed to disturbance (Olano et al. 2002; Godefroid et al. 2006).

Earlier studies have investigated the seed bank composition of either undisturbed forests (Warr et al. 1994; Kjellsson 1992), or the relationship between seed bank composition and land use (Bossuyt and Hermy 2001; Brown and Oosterhuis 1981). Few studies on soil seed banks have investigated the impacts of differences and changes in management practices (Wellstein et al. 2007) and none, to our knowledge, have researched the impacts of overgrazing and different grazing regimes in sub-Mediterranean oak forests.

In the present study, we examine the hypothesis that long-term (more than 30 years) overgrazing affected not only the above-ground vegetation but also the seed bank of the seeds accumulated in the soil. A secondary goal of this study was to test the hypothesis that ruminant and non-ruminant grazers affect the soil seed bank and the above-ground vegetation in different ways. Above-ground vegetation and soil seed bank were analysed at the levels of species composition and richness (alpha diversity), and species turnover (beta diversity). The practical application of these findings is in the field of restoring heavily grazed woodlands in the Mediterranean region. Therefore, our results are discussed from the restoration point of view, to assess the potential role of soil seed banks in contributing to vegetation restoration after the cessation of overgrazing pressure.

Materials and methods

Study site

The research area is a deciduous mixed broad-leaved forest in north-western Greece (Bourazani area, municipality of Konitsa, Epirus), close to the Albanian border (40°02′ N, 20°38′ E). The forest was coppiced until a few decades ago. It consists of chiefly deciduous sub-Mediterranean thermophilous tree species with high proportions of *Quercus frainetto*, *Q. pubescens*, *Carpinus orientalis* and *Fraxinus ornus*, and scattered *Quercus cerris* and *Q. trojana*, while *Q. coccifera*, *Phillyrea latifolia*, *Cotinus coggygria* and *Juniperus oxycedrus* are common in the shrub layer (Tsaliki et al. 2005). The forests represent subtypes of the south-western Balkan association Verbasco glabrati-Quercetum frainetto (Quercion frainetto, Quercetalia pubescentis) (Bergmeier and Dimopoulos 2008).

The substrate is flysch locally substituted by limestone. The soils are shallow (15–30 cm) or of medium depth (30–60 cm). The topography of the study sites is hilly to mountainous (400–700 m a.s.l.). The climate is classified to sub-Mediterranean with a 4-month-long dry period (end of May to September) and about 700 mm average annual precipitation. Mean monthly temperatures range between 5°C in winter and 24°C in summer. Mean monthly rainfall ranges between 12 mm in July and 135 mm in December (Tsaliki et al. 2005).

The study site includes (A) a fenced, private wooded area (112 ha) grazed continuously since 1974 by ruminants and wild boar (*Sus scrofa*) in high but varying population densities, and (B) a non-fenced and non-grazed forest.

Site A, the fenced forest area (112 ha), was further subdivided into site A1 (26 ha) that was continuously grazed by wild boar and site A2 (86 ha) that was grazed by ruminants: *Dama dama*, *Cervus elaphus*, *Capreolus capreolus*, *Ovis musimon* and *Capra hircus cretica*. This subdivision and grazing practice precede our study by at least 30 years. As a result of over-grazing, the herb and litter layer of the oak woodland has almost completely vanished, soils are bare, compressed and eroded, and tree roots protrude from the ground.

Site B is adjacent to site A. During our study period, its vegetation cover and other ecological characteristics were similar to those of site A; however, the site was not systematically grazed. Therefore, samples from site B were used as controls (i.e. ungrazed sites) in the present study. This combination of overgrazed forests adjacent to undisturbed forests of identical climatic, geological and topographical conditions allows us to study the effect of grazing independently of other environmental parameters and is unique in the wider region.

Sampling

Above-ground vegetation was investigated in 42 permanent plots of 150 m^2. The plots were established in both grazed (22 plots, of which nine were grazed by wild boar and 13 by ruminants) and non-grazed (20 plots) forest sites.

In each plot, plant species composition (alpha diversity) was recorded twice: during spring-summer of 2004 and autumn of 2005. The data were combined into one data set so that the maximum number of species occurring in the above-ground vegetation of each plot is taken into account.

Of the 42 permanent vegetation plots, six plots were selected to sample the seed banks, and 20 sample soil cores were taken from each plot. The six plots were classified into the three types of grazing regime as follows:

Type 1: grazing by ruminants (R: ruminant regime sampled at two plots in site A2);
Type 2: grazing by wild boar (B: non-ruminant regime, sampled at one plot in site A1);
Type 3: no grazing by ruminants or boars (C: control, i.e. no grazing, sampled at three plots in site B).

As our research focused on the effects of grazing, our sampling scheme comprised three grazed plots (site A) and three ungrazed control plots (site B). In the grazed treatment there were two discrete sub-areas grazed by different species. In addition to the main research topic (grazed versus non-grazed), we regarded the two grazing treatments as well.

To assess the persistent seed bank composition, we collected soil samples at the end of May 2004, when germination had ended and before any new seeds were dispersed. Soil cores were sampled at two depths: 0–5 cm (upper layer) and 5–10 cm (deeper layer). In each plot we collected twenty soil samples, 10 for each depth (i.e. a total of 120 soil samples for the six plots studied). The quantitative and qualitative composition of the seed bank was investigated using the seedling emergence method (Thompson et al. 1997) and with the additional prior application of a 3-month period of artificial stratification, the soil samples were stored wet in a refrigerator, in the dark (3–5°C). The seedling emergence method, although laborious, is considered more reliable than elutriation for determining the species composition of the seed bank of a plant community (Gross 1990). Emerging seedlings were counted at regular intervals and, at a later developmental stage, identified to the closest taxonomic level possible (about 80% of the soil seed bank taxa were identified to the species level).

Data analysis

Similarity in species composition between seed bank and above-ground vegetation under different grazing regimes was assessed by Sørensen's qualitative similarity index (Kent and Coker 1994; Magurran 2004). We compared the values of the similarity index using the Mann–Whitney test. To measure the effect of grazing on the species richness of our samples, we used the Kruskall–Wallis test.

In order to descriptively display a structure of species composition possibly related to the grazing regimes, the indirect linear response model was used. Explorative ordinations (Principal Component Analysis, PCA) were carried out on the soil seed bank and above-ground vegetation species data, using CANOCO for Windows (ter Braak and Šmilauer 2002). All analyses were scaled on inter-species correlations and species-centred by dividing species scores by their standard deviation to obtain correlation matrices. Community parameters such as total cover were not taken into consideration, since our interest was focused on the presence of species with respect to possible grazing effects.

To test if the grazing regimes affect the species composition, we compared the samples from the different grazing regimes using two statistical methods: logistic regression and classification tree analysis. Classification trees have recently been applied to the analysis of ecological data (e.g. De'ath and Fabricius 2000; Kallimanis et al. 2005, 2007). They predict the value of a response variable (grazing regime in this study), from the values of a set of explanatory variables, which may be either numerical or categorical (Witten and Frank 2005). The basic assumption of this method is that the functional dependency among system variables is not uniform in the whole domain, but can be approximated as such on smaller sub-domains. Classification trees are induced by recursively dividing the data set to more homogeneous subsets. At each repetition, the most informative attribute is identified, and the data set is divided according to the values of that attribute. This process is repeated for each subset until pure datasets (i.e. datasets where all examples have the same value) or datasets that cannot be divided further are reached. Those datasets are the terminal "leaves" of our tree.

Species turnover (beta diversity) analysis

Beta diversity represents the spatial turnover of species and is a measure of changes in the species composition between two assemblages. There is a lack of agreement in the literature as to the feature of the pervasive spatial turnover in the identities of species that beta diversity is intended to capture, therefore there are several indices of beta diversity (see Koleff et al. (2003) for an extensive review on the subject). In this study, we estimated beta diversity according to the Colwell and Coddington (1994) index, which was calculated with the formula:

$$\beta = \frac{1}{n}\sum_{i=1}^{n}\left(1 - \frac{a_i}{b_i}\right)$$

where for every pairwise comparison i we estimated the number of species simultaneously present in both plots (a_i) and the total number of species recorded in the two plots (b_i), and n the total number of pairwise comparisons.

We analysed the species composition of six plots (three grazed and three ungrazed). To compare the patterns of beta diversity of seed bank and the patterns of beta diversity of vegetation, we used the same six plots for both analyses. Among those six plots there are a total of 15 possible pairwise comparisons. Three of these comparisons are among grazed plots and represent the beta diversity within grazed plots; three comparisons are among the ungrazed plots and represent the beta diversity within ungrazed plots. The nine remaining pairwise comparisons among grazed and ungrazed plots represent the beta diversity of the transition among grazed and ungrazed areas, i.e. between grazed and ungrazed treatments. Beta diversity was estimated for both above-ground vegetation and the soil seed bank.

Results

Effect of grazing on seed bank-vegetation similarity

The above-ground vegetation under different grazing regimes comprised 83 taxa, of which 70 taxa occurred in the above-ground flora of the six seed bank sampling plots; only 30% of these (21 taxa) were represented in the persistent soil seed bank, in which a total of 28 taxa were recorded (Table 1). Thus, 75% of the species found in the seed bank were also observed in the above-ground vegetation.

When comparing alpha diversity estimated as species richness of the samples (number of species per sample) from different grazing regimes, i.e. the species richness at the finest scale, we found that the difference was significant for both the above-ground vegetation (Kruskal Wallis $P < 0.0001$) and the soil seed bank ($P = 0.0003$). In the samples from control (non-grazed) plots more species were observed than in the samples from the grazed plots. Species richness in samples from the two grazing regimes did not differ significantly.

Next we analysed the extent of overlap between the species composition of the above-ground vegetation and the seed bank flora in each plot, i.e. how many of the species in the above-ground vegetation were present as seeds in the soil seed bank of each plot. Similarity of the above-ground vegetation with the seed bank flora varied considerably among the different plots (Table 2): it was higher in the non-grazed areas, and significantly lower in the grazed ones (Mann–Whitney $P = 0.046$ for the soil seed bank). In the grazed areas, similarity between above-ground vegetation and seed bank did not exceed 19%, and in the plots grazed by wild boar the similarity was 0%. In the non-grazed areas the similarity index reached 29%. Higher similarity was observed between ruminant and wild boar sites in above-ground vegetation (Table 2).

By applying logistic regression and classification tree analyses, we analysed the effect of grazing regimes on the species composition of the above-ground vegetation and the soil seed bank. Both approaches yielded similar results. Above-ground vegetation was clearly distinguished with small misclassification errors (12% for the tree model and 19% for the logistic regression) and high kappa statistic (0.8 and 0.7, respectively). The absence of *Phillyrea latifolia* indicates grazing by ruminants, while its presence in combination with the absence of *Euphorbia amygdaloides* and *Brachypodium sylvaticum* indicates grazing by wild boar (Fig. 1). The combined presence of *Phillyrea latifolia* and either *Euphorbia amygdaloides* or *Brachypodium sylvaticum* or both indicates non-grazed control plots. Contrary to the above-ground vegetation, seed bank

Table 1 Taxa found in three grazing regimes (R: ruminant, B: boar, C: control, i.e. non-grazed) for above-ground vegetation and soil seed banks in the six sampling plots

	Grazing regime		
	R	B	C
Taxa found only in the above-ground vegetation			
Acer campestre L.			×
Acer monspessulanum L.	×		×
Arbutus unedo L.			×
Aremonia agrimonoides (L.) DC.			×
Asparagus acutifolius L.		×	×
Bituminaria bituminosa (L.) C. H.Stirt.			×
Brachypodium sylvaticum (Hudson) Beauv.			×
Clematis vitalba L.			×
Clinopodium vulgare L.			×
Colutea arborescens L.			×
Cornus mas L.			×
Corylus colurna L.	×		×
Cotinus coggygria Scop.		×	×
Crocus chrysanthus (Herb.) Herb.			×
Cyclamen hederifolium Aiton			×
Echinops ritro L.			×
Epipactis microphylla (Ehrh.) Swartz			×
Galium lucidum All.			×
Geranium brutium Gasp.			×
Geranium purpureum Vill.			×
Hedera helix L.			×
Helleborus odorus subsp. *cyclophyllus* (A. Braun) Strid	×	×	
Juniperus oxycedrus L.			×
Lapsana communis L.			×
Lathyrus niger (L.) Bernh.			×
Lathyrus nissolia L.		×	
Melittis melissophyllum L.			×
Muscari neglectum Ten.	×		×
Osyris alba L.			×
Phillyrea latifolia L.		×	×
Poa trivialis L. subsp. *sylvicola* (Guss.) Lindb. fil.	×		
Potentilla micrantha DC.			×
Quercus cerris L.	×	×	×
Quercus coccifera L.			×
Quercus frainetto Ten.	×	×	×
Quercus pubescens Willd.	×	×	×
Quercus trojana Webb	×	×	×
Rosa gallica L.			×
Ruscus aculeatus L.			×

Table 1 continued

	Grazing regime		
	R	B	C
Sorbus domestica L.			×
Sorbus torminalis (L.) Crantz		×	×
Tamus communis L.			×
Tanacetum corymbosum (L.) Schultz Bip.			×
Thymus longicaulis C. Presl			×
Torilis arvensis (Hudson) Link			×
Trifolium ochroleucon Hudson			×
Trifolium pallidum Waldst. & Kit.			×
Trifolium tenuifolium Ten.			×
Vicia sativa L.			×
Number of taxa in each grazing regime	9	10	45
Total number of taxa in category: 49			
Taxa common to the above-ground vegetation and soil seed banks			
Campanula spec.	+		×
Carex flacca Schreb.	×	+	+/×
Carpinus orientalis Mill.		×	+/×
Cercis siliquastrum L.		×	+
Crataegus monogyna Jacq.		×	+/×
Dactylis glomerata L.	+		+/×
Dorycnium hirsutum (L.) Ser.			+/×
Euphorbia amygdaloides L.	+		+/×
Fraxinus ornus L.	×	×	+/×
Galium aparine L.			+/×
Gramineae			+/×
Inula salicina L.			+/×
Lathyrus laxiflorus (Desf.) O. Kuntze			+/×
Luzula forsteri (Sm.) DC.	+		+/×
Medicago lupulina L.			+/×
Silene italica (L.) Pers.	+		+/×
Trifolium arvense L.		+	+/×
Trifolium campestre Schreb.	+/×		×
Trifolium physodes Bieb.	+/×	×	+/×
Veronica chamaedrys L.	+/×	×	+/×
Viola alba Besser	+		+/×
Number of taxa in each grazing regime	11	8	21
Total number of taxa in category: 21			
Taxa found only in the soil seed banks			
Caryophyllaceae		+	
Parietaria judaica L.		+	
Petrorhagia cf. *saxifraga* (L.) Link	+		
Rubus sanctus Schreb.			+
Solanum nigrum L.			+
Sonchus asper (L.) Hill	+		+
Vicia cassubica L.			+
Number of taxa in each grazing regime	2	2	4
Total number of taxa in category: 7			
Total number of taxa in each grazing regime	21	19	70
Total number of taxa in Table: 77			

+ Indicates presence in the soil seed bank and × indicates presence in the above-ground vegetation

Table 2 Sørensen similarity index (%) between soil seed bank and above-ground vegetation in different grazing regimes

Type	Ruminant	Boar	Control
Ruminant	**19sv**	36v	23v
Boar	0s	**0sv**	24v
Control	32s	13s	**29sv**

v, Similarity among different types of above-ground vegetation; s, similarity among different soil seed banks; sv, similarity between soil seed bank and above-ground vegetation of the same type

Bold values represent the seed bank-vegetation similarity of the same type of grazing regime (i.e. between ruminants, between boar, between control plots)

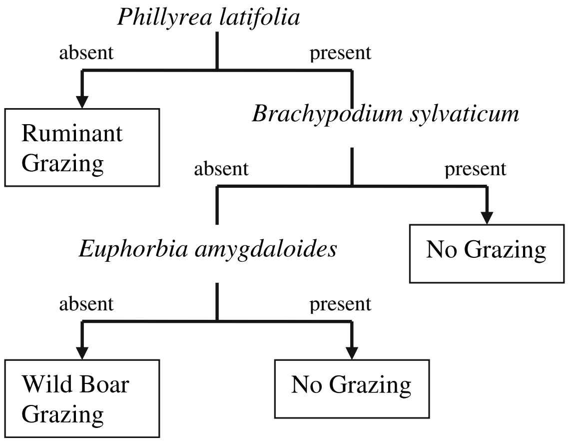

Fig. 1 Classification tree of the grazing regimes (ruminant, boar and no-grazing) on the basis of indicator plants. Each "leaf" is labelled according to presence-absence of the species *Phillyrea latifolia*, *Brachypodium sylvaticum* and *Euphorbia amygdaloides* in the above-ground vegetation. The misclassification error was minor (12%)

Table 3 PCA analysis on the above-ground vegetation; eigenvalues from ordination of plots for axes 1–4

Axes	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.249	0.107	0.083	0.066
Cumulative percentage variance of species data	24.9	35.6	43.9	50.5
Total inertia: 1.000				

species composition was not distinguishable by either logistic regression or classification tree analyses.

Examining the presence of particular species of the seed bank in more detail we find that frequent species like *Cotinus coggygria*, *Juniperus oxycedrus*, *Phillyrea latifolia*, *Quercus frainetto* and *Q. pubescens* are absent from the soil seed bank of the study area. Other less frequent species like *Hedera helix*, *Clematis vitalba* and *Lapsana communis* were also absent from the seed bank of the study area. On the other hand, some of the above-ground woody species *Carpinus orientalis*, *Cercis siliquastrum*, *Crataegus monogyna*, *Fraxinus ornus* and *Rubus sanctus* were found in the soil seed bank.

Ordinations of above-ground vegetation and soil seed banks

PCA ordinations were performed on the species presence data of the above-ground vegetation and soil seed bank separately. The first two PCA axes of the data set of the above-ground vegetation account for 36% of variance (see Table 3), a relatively low proportion that reflects a heterogeneous vegetation gradient structure. The first axis explains 25% of the variance reflecting a gradient of grazing intensity from the plots under heavy grazing conditions (left side of the diagram) to the non-grazed plots (right side of the diagram) (Fig. 2).

PCA on the soil seed bank composition did not reveal a clear structure of the identified species in relation to the differently grazed forest sites. In the ordination diagram of soil seed bank (not shown), species of grazed plots (left part along the first axis) were separated from species of non-grazed plots (right part along the first axis). The first two axes explained the bulk of the variance (31%) compared to the total variance of 49% explained by the first four axes (eigenvalues for the first four axes: 0.158, 0.150, 0.097 and 0.083, respectively).

Species turnover (beta diversity)

For the above-ground vegetation beta diversity among grazed plots did not differ significantly from beta diversity among non-grazed plots. However, the species turnover between grazed and non-grazed plots was significantly higher than the beta diversity within both grazing regimes (Kruskal–Wallis $P = 0.006$).

For the soil seed bank the differences in beta diversity were found to be statistically significant (Kruskal–Wallis $P = 0.005$). More precisely, beta diversity of grazed plots was significantly higher than that of non-grazed plots. Beta diversity between grazed and non-grazed plots was of intermediate value.

Discussion

Seed banks and above-ground vegetation compared

Approximately two-thirds of the taxa found in the vegetation did not occur in the soil seed bank of the study area; on the other hand, three-quarters of the soil seed bank taxa were found in the above-ground vegetation. This confirms the generally low similarity between above-ground vegetation and persistent soil seed bank floras in forest ecosystems, and that the above-ground vegetation does not necessarily reflect the soil seed bank composition (Olano et al. 2002). To our knowledge, this dissimilarity is reported for the first time in a sub-Mediterranean woodland. As expected, small-seeded species dominate the seed bank flora, while large-seeded species dominate the woody above-ground vegetation of the studied forest. Roovers et al. (2006) observed a similar pattern in a temperate mesophilous deciduous forest.

Looney and Gibson (1995) report that only few tree taxa of the above-ground vegetation were found in the soil seed bank, a fact attributed to animal predation and dormancy (Shen et al. 2007). Similarly, in our study some of the most frequent species like *Cotinus coggygria* (anemochorous), *Juniperus oxycedrus*, *Phillyrea latifolia* (both zoochorous), *Quercus frainetto* and *Q. pubescens* (both dispersed by gravity) are absent from the soil seed bank of the study area (not surprising of course for the latter two species, well known to bear recalcitrant seeds). Other species like *Hedera helix* are absent from the seed

Fig. 2 Ordination (PCA) species-samples diagram (species data set of 42 above-ground vegetation plots) along axes 1 and 2 (eigenvalues for the first two axes 0.249 and 0.107, respectively). The species are labelled by the first three letters of the generic name and the first three letters of the species epitheta (see Table 1 for full names). Plots are displayed as: ● boar-grazed plots; × ruminant-grazed plots; ■ control (i.e. non-grazed) plots

bank since they rarely produce seeds in shady habitats (Buckley et al. 1997). Another group of species with *Clematis vitalba* and *Lapsana communis* were absent from the seed bank of the study area, although they were found in seed banks of woody and disturbed habitats elsewhere (Roovers et al. 2006).

Some of the above-ground woody species were found in the soil seed bank: *Carpinus orientalis*, *Cercis siliquastrum*, *Crataegus monogyna*, *Fraxinus ornus* and *Rubus sanctus*. *Fraxinus ornus* and *Carpinus orientalis* are common tree species in the study area with noticeable regeneration in the sapling layer, thus contradicting Forrester and Leopold's (2006) observation that most of the dominant canopy species appearing in the soil seed bank are absent from the sapling and shrub layer of deciduous forests.

Effect of grazing on seed bank-vegetation similarity

In the studied sub-Mediterranean forest, grazing reduced the similarity between seed bank and above-ground vegetation. Especially in sites with wild boar, there were no common species between seed bank and vegetation. This finding is consistent with the general pattern of decreasing similarity between seed bank and vegetation under grazing (Marage et al. 2006; Haretche and Rodriguez 2006). In temperate forests, Heinken et al. (2006) found large numbers of seeds of chiefly non-forest species and others which occur both in forests and open habitats near trees rubbed by wild boar, and concluded that most plant species were dispersed epizoochorously by *Sus scrofa*. In our study, the wild boars were restricted inside the fenced area and it was therefore impossible for them to serve as long-distance vectors of diaspores (from outside the forest).

Effect of grazing on species richness

The impact of grazing on seed bank species richness and composition has been studied mainly in grasslands and to a lesser extent in forests, scrub and rangelands. In most studies species richness was found to decrease with grazing pressure (Marage et al. 2006; Miller 1999). However, two studies geographically close to our own (Heinken et al. (2006), temperate forest in Germany; and Malo et al. (2000), Mediterranean dehesas) showed the opposite, i.e. increase in the seed bank diversity under grazing. In our study, we found that species richness of the above-ground vegetation and the soil seed bank declined with grazing, thus confirming the general trend. We presume that contradictory statements in literature might be due to different grazing intensities and duration. Furthermore, our results indicate that long-term over-grazing as such is the determining factor and not the particular species of mammal, as the effects of ruminants and boars did not differ significantly.

Effects of grazing on beta diversity (species turnover)

The effect of grazing on beta diversity has recently attracted the interest of researchers, but presently no clear picture emerges from the literature. Although most studies found no effect (see Harrison 1999; Zhang 1998; Alrababah et al. 2007; Robson and Clay 2005), a few studies demonstrate increase (e.g. Bakker and Ruyter 1981) and others decrease (e.g. Chaneton et al. 2002) of beta diversity with grazing.

Our results show different effects of grazing on the beta diversity of the vegetation and the seed bank. Above-ground vegetation displayed no significant difference in the beta diversity among grazed and among non-grazed plots, but beta diversity was significantly higher between grazed and non-grazed plots. This finding and our community analysis results indicate that grazed and non-grazed plots are characterized by distinct species assemblages. Although the grazed plots had fewer species, these were not characterized by higher species turnover compared to the control plots. So our finding contradicts other studies that report increased beta diversity in areas with decreased alpha diversity (Kallimanis et al. 2008; Lennon et al. 2001).

Results for soil seed bank reflect a different picture, since species turnover was significantly higher in the grazed plots and our statistical analysis failed to identify distinct communities in the different grazing regimes, despite the existence of such communities in the above-ground vegetation. It is also indicative that the species turnover in the seed bank between grazed and non-grazed plots is lower than the respective one in the grazed plots. This discrepancy might indicate that the main seed dispersal mode is related to animals. This observation allows us to suggest that the zoochorous mode of dispersal and its role in shaping seed bank communities under grazing should be the focus of further study in the future.

Seed bank and restoration implications

Soil seed bank appeared consistent with the conclusion of Godefroid et al. (2006) that there is no close relationship between the species composition of the seed bank and that of the established vegetation. Thus, the seed bank is ‘capable’ of restoring the studied forests only to a limited extent. Studies on the restoration of forests through diaspores stored in the soil have also been carried out by Oke et al. (2006) and Warr et al. (1994), and the potential contribution of the soil seed bank to restoration of temperate deciduous forests has been recently investigated by Roovers et al. (2006).

Difficulties in the restoration of forests by soil seed banks are to be expected when the similarity between the above-ground species composition and that of the seed bank proves to be poor. Most of the dominant or frequent species of the herb layer rarely or never emerged from the soil samples of our forest, or from temperate forests with *Fagus sylvatica*, *Quercus robur* and *Pinus sylvestris* (Godefroid et al. 2006). Our study suggests that ruderal species in forest soil seed banks increase with grazing and typical non-weedy forest species decrease.

The potential of seed banks to restore communities is rather limited when many species of the community are either absent from the persistent seed bank or are not even able to create any seed bank at all (Handlova and Münzbergova 2006). The use of seed bank as a tool for restoration depends strongly on which taxa retain seeds able to recruit in degraded environments. The results presented in this study have implications on the restoration of heavily disturbed forests and are useful for the conservation management of over-grazed sub-Mediterranean forest types.

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