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Abstract

Vegetation in high Mediterranean mountains usually consists of patchy communities. Patch structures have been interpreted as a result of the prevalence of facilitation phenomena in highly stressful environments. Several mechanisms have been proposed in order to explain the factors that control the existence of these clumped structures. However, they have not been evaluated in these mountains. Our hypothesis is that patchy structure in high mountain Mediterranean vegetation is a consequence of facilitative and competitive interactions in a very harsh environment which ultimately involve strong localized effects on soil properties. Our results show that levels of soil nutrients were higher under vegetation patches than in bare ground areas, confirming the hypothesis of an amelioration of soil resources under canopies. Pairwise associations and repulsions suggest the existence of two contrasting composition stages. Contrasting models relating patch species composition (cover and biomass) and soil resources indicated a weak relationship between species features and soil nutrient levels. Finally, structural modeling showed that patch size has a relevant but indirect effect on soil resource levels through grass and total biomass. We conclude that patch structure and dynamics in high Mediterranean mountain communities may be partly controlled by an endogenous process involving facilitation and competition for soil key resources. These interactions may operate through some community traits related to patch size but not to composition.

Introduction

Vegetation cover frequently occurs as relatively small patches embedded in a bare ground matrix in some alpine Iberian communities—cryoromediterranean belt sensu Rivas-Martínez (1987)—as well as in other mountain regions of the world (Komárková, 1979; Armesto et al., 1980; Kikvidze, 1993; Núñez et al., 1999). This spatial pattern has also been described in highly stressful habitats such as arid and semi-arid environments (Sala and Aguiar, 1996; Schlesinger et al., 1990), for which contrasting patch shaping factors have been extensively studied (see Aguiar and Sala, 1999). Composition, shape, and size of patches could be determined by the strength and direction of biotic interactions (Aguiar and Sala, 1999), which change over time and with environmental conditions (Callaway, 1997; Holzapfel and Mahall, 1999). In the case of nutrient-limited environments, facilitation will occur if benefits from an increase of nutrient levels within patches overcome other problems such as deterioration of light conditions within the vegetated patch (Holmgren et al., 1997). This positive biotic interaction may shift to competition as plants grow (Franco and Nobel, 1989; Escudero et al., 1999, 2000). In addition, patch structure and dynamics in stressful environments have been explained on the basis of a trade-off between facilitative and competitive interactions among plants (Fowler, 1986; Wu and Levin, 1994; Ludwig et al., 1994; Couteron and Lejeune, 2001).

Some authors have shown the existence of rather similar stressful environments and demonstrated positive biotic interactions in arctic (Carlsson and Callaghan, 1991) and alpine vegetation (Holtmaier and Broll, 1992; Kikvidze, 1993; Núñez et al., 1999; Callaway et al., 2002). However, there is a considerable lack of evidence on spatial structuring under the climate conditions of Mediterranean high mountains (but see Gavilán et al., 2002) because the large body of research available has

focused mostly on phytosociological and gradient vegetation analyses (Rivas-Martínez, 1963; Escudero et al., 1994). The extrapolation of arctic and alpine shaping factors to Mediterranean environments should be conducted with caution because high mountain Mediterranean plants face specific constraints such as the development of an intense water deficit during the short period in which temperatures are high enough to enable growth (e.g., Sierra Nevada site in southern Spain; Callaway et al., 2002).

Our hypothesis is that patch structure in high mountain Mediterranean vegetation is a consequence of facilitative and competitive interactions in a very harsh environment which ultimately comprise strong localized effects on soil properties. The importance of plant-created soil heterogeneity has been demonstrated in many types of ecosystems (Valiente-Banuet and Ezcurra, 1991; Facelli and Brock, 2000). Biomass tends to accumulate in soils beneath vegetation patches and modifies biogeochemical processes (Schlesinger et al., 1990), generating so-called islands of fertility (Jackson and Caldwell, 1993; Schlesinger et al., 1996; Kelly et al., 1996). Several plant species have been implicated in this process (Chen and Stark, 2000; Vinton and Burke, 1995), including some occurring in alpine systems (Onipchenko et al., 2000). However, to test this hypothesis under Mediterranean conditions, a specific study under the appropriate field conditions was needed.

Some papers have examined patch structures by analyzing species associations in several ways (Silvertown and Wilson, 1994; Gotelli, 2000; Haase et al., 1996), including in alpine systems (Kikvidze, 1993; Kikvidze and Nakhutsrishvili, 1998; Núñez et al., 1999; Gavilán et al., 2002). These studies have detected association and repulsion and therefore suggested the existence of biotic interactions, such as facilitation or competition (Freeman and Elmen, 1995; Vilá and Sardans, 1999; Callaway and Puignaire, 1999). In contrast, others have

focused mostly on the role of soil nutrients on patch formation and death (Tongway and Ludwig, 1994; Halvorson et al., 1995; Schlesinger et al., 1996). Here, we have conducted a study which includes both complementary approaches.

Specifically, we addressed the following questions: (1) Are nutrient levels different between skeletal bare ground surfaces and under vegetated alpine patches? (2) We hypothesized a monotonic improvement in soil conditions as the patch increases in size; hence, is there a positive relationship between soil nutrients and patch size? (3) We evaluated the relationship between species composition (through the species-wise biomass pool and the species-specific cover within a patch) and nutrient soil levels; so, could both traits control the resource level of each island of fertility? (4) Finally, several authors have shown the important role of grasses in patch dynamics (Sala et al., 1989; Aguiar and Sala, 1999); so, what is the relative importance of grasses (biomass and cover) on soil resource levels? This last question was approached by developing a causal aprioristic model which was assessed using structural equation modeling.

Methods

THE STUDY SYSTEM

The cryoromediterranean bioclimatic belt occurs in the Sierra de Guadarrama, a mountain range in the north of the province of Madrid, as a reduced set of conspicuous vegetation islands in the higher summits above 2200–2300 m. The Sierra de Guadarrama reaches its highest point at 2448 m at the peak of mount Peñalara. The dominant vegetation in snow-free zones such as windblown slopes and crests is an extremely short pasture (rarely exceeding 3 cm height) with several creeping chamaephytes, caespitosous grasses, and lichens but not mosses. Plants are organized in small ellipsoidal-shaped patches that usually do not surpass 50 cm in diameter (see Gavilán et al., 2002). From a phytosociological point of view the community has been denominated *Hieracio myriadeni–Festucetum curvifoliae* (Rivas-Martínez, 1963) and is endemic to the highest alpine islands of the Guadarrama sector of the Sistema Central in Spain (Rivas-Martínez et al., 1990). This community is particularly rich in endemics, such as *Festuca curvifolia*, *Hieracium vahlii* subsp. *myriadenum*, *Minuartia recurva* subsp. *bigerrensis*, and *Armeria caespitosa*, as well as in arctic and alpine relicts, such as *Agrostis rupestris* and *Phyteuma hemisphaericum*. The timberline is located between 1900 and 2100 m and is dominated by stunted pines (*Pinus sylvestris*), which appear interspersed in a shrub matrix characterized by *Cytisus oromediterraneus* and *Juniperus communis* subsp. *alpina*.

The study site is a well-conserved remnant of this community on Cerro de Valdemartín (Madrid province, 40°47′34″N, 3°57′10″W), where no evidence of intense anthropogenic disturbance due to human trampling or cattle grazing was found. It covers approximately 2.5 ha on gentle slopes (<10%) around the summit. Altitude ranges from 2240 m to 2279 m at the summit. About 60% of the ground is covered by pebbles or exposed gravel. There is a sharp ecotone with a *Nardus*-dominated community where snowpack is always higher. In the Navacerrada Pass (1890 m), located 2 km to the west, annual average air temperature is 6.3°C, whereas the mean monthly temperature ranges from −1°C in January to 16°C in July. Mean annual precipitation is 1330 mm with a very marked drought from May to October (<10% of the total annual rainfall) (Rivas-Martínez et al., 1990). At our study site, which is located more than 300 m higher, the climatic conditions should be more restrictive for plant growth.

OBSERVATIONAL STUDY

Transect lines running parallel to the maximum slope at 10 m intervals were established on the stand. Every patch of vegetation in contact with transect lines was marked, and 60 of them were randomly selected in late July (2001), during the period of maximum community vegetative activity. All patches were photographed with a digital camera at 1 m height and perpendicular to the ground surface. Digital images were analyzed with Olympus Micro Image version 4.0. Patch size, perimeter, and cover of each species including lichens were measured. Immediately after taking the digital photos, we collected all above-ground vegetation and necromass per patch and separated it species-wise in the laboratory. Biomass was measured by drying samples to 70°C for 48 h in a controlled oven and weighing them on a balance. Above-ground biomass is an accurate estimator of plant performance even for plants growing under stressful conditions. We also collected lichens because, in other fellfield communities, they are relevant elements of the community (Walker et al., 2001).

A 6-cm-deep soil core (6 cm in diameter) beneath the patches was collected immediately after plant sampling. It is worth noting here that smaller patches are present in the study area although they were not examined because soil sampling was not feasible. To compare the characteristics of soil under patches with those outside them, we collected 20 soil samples in bare surfaces interspersed among patches. These sampling points were located at least 15 cm away from any patch or plant. Soil samples were air-dried at laboratory temperature for approximately 1 month and then sieved. The mass of fine soil (<2 mm), fine-gravel (2–20 mm), and gravel (>20 mm) fractions of the soil samples was quantified and relative contributions calculated. Analyses of conductivity and pH were determined in the supernatant of a 1:2.5 soil-deionized water (v/v) suspension with glass electrodes. An estimate of moisture percentage was calculated gravimetrically after drying a subsample of the fine soil fraction at 105°C. Nitrogen was determined by semi-micro Kjeldahl procedure (Bremner, 1965). An acid (concentrated H_2SO_4) digestion was followed by a steam distillation, and NH_4^+ was evaluated by titration with 0.1 M H_2SO_4. The organic carbon was determined according to a modification of the Walkley and Black method (Walkley, 1946) as follows: 1 N $K_2Cr_2O_7$ and concentrated H_2SO_4 were added to a soil sample (<2 mm), and the dichromate excess was titrated after the addition of 10 ml of concentrated H_3PO_4 with 0.5 N $Fe(NH_4)_2(SO_4)_26H_2O$. Free iron was extracted with $Na_2S_2O_4$ at 3.5 pH and evaluated by titration with 0.05 N $K_2Cr_2O_7$ (Deb, 1950). We also determined carbon:nitrogen ratio, available phosphorous (extracted with acetic acid, sulfuric acid, and carbonates, pH 3.3 [Burriel and Hernando, 1950], and determined colorimetrically [DINKO, model D 105]) and available potassium (extracted with 1M NH_4Ac, pH 7) by flame photometry (Flame photometer JENWAY, model PFP7) (U.S. Salinity Laboratory Staff, 1954).

To conduct pairwise comparisons between species, we randomly selected and measured 200 additional multi-species patches. They were subjected to the condition of being within the size range of the 60 patches used for biomass estimation (37–160 cm of perimeter).

NUMERICAL ANALYSES

Previous to statistical analyses, variables were checked for normality, and transformations were performed when necessary. Differences in soil parameters between skeletal soils and beneath-patch soils were tested by means of one-way ANOVAs or Mann-Whitney nonparametric tests.

We tested the associations between species using contingency table analyses with Fisher's exact test and Phi coefficient on presence/absence data from all patches (N = 260).

An aprioristic structural modeling approach (SEM) was conducted to test the causal hypotheses for the nutrient level reached under each patch (see Mitchell, 1993; Iriondo et al., 2003). Although our model involves a very reduced set of explaining variables, we have
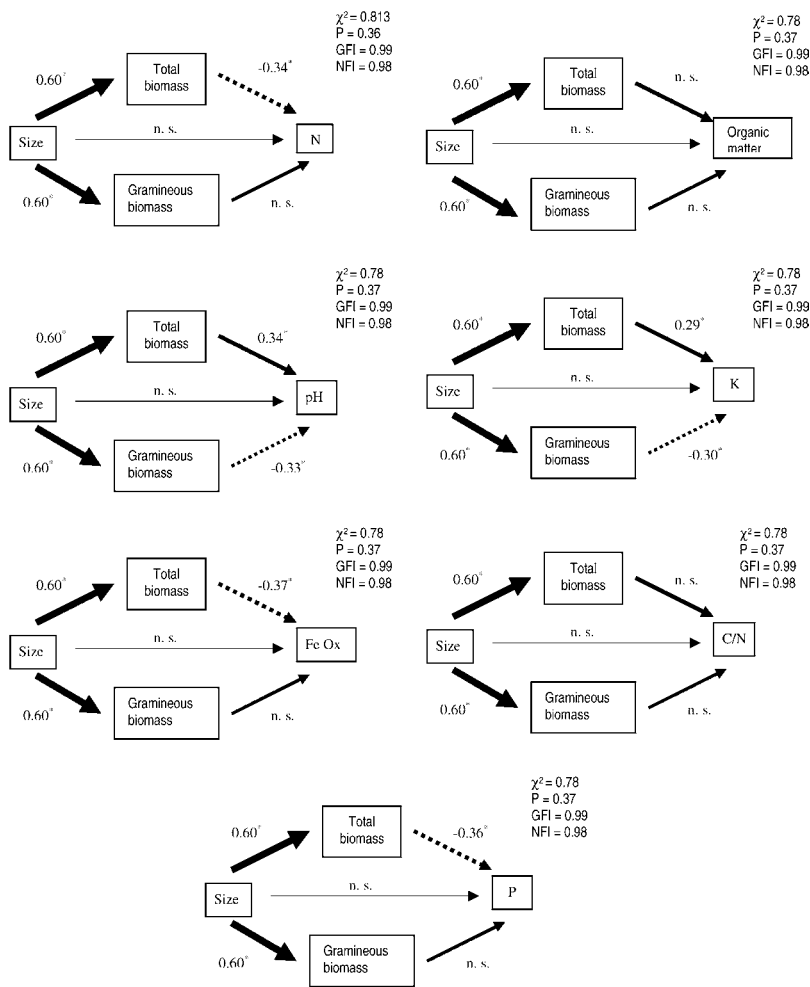
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FIGURE 1. Path models for the effects of patch size, total biomass, and gramineous biomass on mineral nutrient levels (N, P, K, and Fe), organic matter, pH, and C/N ratio. Width of each arrow is proportional to the standardized path coefficient, solid lines denote positive paths, and dashed lines denote negative paths. Asterisks indicate values significantly different from zero according to the Wald test ($p < 0.05$). GFI: Goodness-of-Fit Index; NFI: Normed Fit Index. NFI and GFI values above 0.95 along with a nonsignificant χ^2 indicate a good model fit.

preferred SEM over ordinary multiple regression because the SEM models, among other advantages, allow the estimation of indirect effects, which are usually eclipsed even in relatively simple models (Magnusson, 2002). Our causal model included the following relationships that were derived from our hypotheses and existing evidences: (1) the size of the patch positively affects nutrient levels, (2) the size of the patch positively affects grass biomass, (3) the size of the patch positively affects total biomass, (4) total grass biomass positively determines nutrient levels, and (5) total biomass affects nutrient levels (Fig. 1). We considered separately the total biomass effect from the grass component because there is evidence that both components have a primary role on high mountain vegetation processes (Grabherr, 1989). The null hypothesis of the model is that the observed and predicted covariances are equal. Standardized path coefficients were estimated by the maximum likelihood method. The degree of fit between the observed and predicted covariance structures was first examined by a χ^2 goodness-of-fit test. As this test may show inadequate statistical power (Mitchell, 1993), we used other fit indices such as the Normed Fit Index (NFI) and the Goodness-of-Fit Index (GFI). Both NFI and GFI range from 0 to 1, with values above 0.95 indicating a good fit (Tanaka, 1987). The significance of each individual path coefficient was assessed through multivariate Wald tests. Previously, we calculated the variance inflation factor for each variable to detect multicolinearity problems. Computation of the structural equation was performed using LISREL (version 8.51; Jöreskog and Sörbon, 1996).

We used constrained ordinations to examine the multivariate relationships between species biomass and cover, and soil nutrients (Legendre and Anderson, 1999; Rubio and Escudero, 2000). Our null hypothesis was that the influence of environmental variables (soil data set) on this multivariate data set (species biomass data matrix) was not significantly different from random. With this in mind a Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) with the biomass data set was conducted by detrending by segments and nonlinear rescaling of the axes, which has the property that the extracted axes are scaled in units of average standard deviation (Gauch, 1982). As the extracted gradients of the biomass data base were relatively short (standard deviation units $\approx$ 2), we conducted a Redundancy Analysis (hereafter RDA) which is a constraining ordination technique that assumes linear responses in relation to environmental variables. Using the soil variables as constraining matrix, the total variation explained (TVE) was calculated as the sum of all extracted canonical axes (Borcard et al., 1992). A Monte Carlo permutation test (1000 randomizations) was performed to determine the accuracy of the relationship between the two data sets, using the sum of all canonical eigenvalues or trace to build the F-ratio statistic (ter Braak, 1990; Verdonschot and ter Braak, 1994; Legendre and Anderson, 1999). If the RDA model was significant, a forward stepwise procedure was carried out to select a reduced model including only significant variables. We incorporated explanatory variables one at a time and step by step in the order of their decreasing eigenvalues after partialling out the variation accounted by the already-included variables. The process stopped when the new variable was not significant ($p > 0.01$). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 1000 randomizations. A similar approach was conducted using as the main matrix the specific plant

TABLE 1

Descriptive statistics of the vegetation patches (N = 60).

Variables	Min	Max	Mean	S.D.
Patch size (cm^2)	95	912	275	160
Patch perimeter (cm)	37	160	74	23
Total vegetation cover (%)	60	105	89	9
Total plant biomass (g)	3.5	21.8	9.7	3.9
Grass biomass (g)	0.7	17.2	3.8	3.0
Total number of species per patch	2	9	5.9	1.4
Vascular plant species per patch	2	8	4.6	1.3
Lichen species per patch	0	3	1.3	0.8

cover per plant data set. Multivariate analyses were conducted with CANOCO for Windows v. 4.0 (ter Braak and Smilauer, 1997).

Results

Patch size varied from 95 cm^2 to 912 cm^2. The total number of species in the 60 patches for biomass and soil analyses were 13 for vascular plants and 3 for lichens, whereas the average numbers of species per patch were 4.6 (range 2 to 8) and 1.3 (range 0 to 3), respectively (Table 1). The most important species in percentage of patch cover were *Festuca curvifolia* (100%), *Sedum brevifolium* (67%), *Jasione crispa* subsp. *centralis* (57%), and *Silene ciliata* subsp. *elegans* (45%). Among the lichens the most dominant species were *Coelocaulon aculeatum* (79%) and *Cetraria islandica* (38%). Using aboveground biomass, a rather different pattern emerges, *Silene ciliata* (5.1 g per patch on average), *Festuca curvifolia* (3.7 g), and *Minuartia bigerrensis* (3.1 g) being the main vascular plants, and *C. aculeatum* (0.5 g) the most important lichen species (Table 2).

As expected, a highly significantly positive correlation was found between total biomass and patch area (R = 0.472, P < 0.002). However, no correlation was found between total biomass and species richness (i.e., total number of species per patch including lichens; R = 0.213, P > 0.176).

As shown in Table 3, all soil variables apart from fine gravel and phosphorous content were significantly different between soil beneath patches and soil in skeletal zones. All nutrient levels were always higher under patches, the acidity was lower, and the fine-earth component contribution was greater.

We detected a reduced set of significant pairwise associations between plant species using the Fisher's exact test (P < 0.01). Only species occurring in more than 10% of samples were included (8 vascular plants and 2 lichens). From this subset we found 8 positive and 2 negative significant interactions.

Our causal model had a significant fit with the 7 soil parameters tested (Fig. 1). χ^2 goodness of fit showed P values above 0.1, indicating that predicted and observed covariances did not differ significantly. NFI and GFI were in all cases above 0.95, which is the standard threshold for not rejecting the models. The power of our model rests mainly on the important positive relationship between patch size and total biomass (standardized path coefficient of 0.60), and patch size and grass biomass (standardized path coefficient of 0.60). Surprisingly, there was no significant direct effect between patch size and any of the tested soil resources, but there was a considerable indirect effect through grass and total biomass. The direction and intensity of those effects were specific to each soil resource. Total biomass had a significant negative effect on nitrogen content (path coefficient –0.34), iron content (–0.37), and phosphorous (–0.36), but grass biomass had no effect. In contrast,

TABLE 2

Species (vascular plants and lichens) recorded in the patches sampled for biomass assessment. Additional vascular plants were found in the 200 patches surveyed for pairwise comparisons and are not included in the table: Armeria caespitosa, Biscutella gredensis, Festuca iberica, Koeleria caudate subsp. crassipes and Senecio boissieri. Mean aboveground biomass per patch and frequency of occurrence are shown. Life-form abbreviations are Hm—hemicryptophyte, HM cae.—caespitosous hemicryptophyte, Cs—cushion chamaephyte, L—lichen species.

Species	Life form	Mean Biomass (g)	S.D.	Frequency (%)
Festuca curvifolia Lag. *ex* Lange	Hm cae.	3.7	3.0	100
Jasione crispa (Pourret) Samp. subsq. *centralis* (Rivas-Martínez) Tutin	Cs	2.0	1.1	57
Jurinea humilis (Desf.) DC.	Hm	0.5	0.6	43
Thymus praecox Opiz subsq. *penyalarensis* (Pau) Rivas-Martínez, F. Fernández-Gonzalez and Sánchez-Mata	Ch	0.7	1.4	43
Phyteuma hemisphaericum L.	Hm	0.4	0.0	2
Hieracium vahlii Froel in DC. subsp. *myriadenum* (Boiss and Reuter) Zahn	Hm	0.2	0.1	24
Agrostis rupestris All.	Hm cae.	1.3	0.0	2
Poa cenisia All.	Hm	0.3	0.0	2
Deschampsia flexulosa (L.) Trin. subsp. *iberica* Rivas-Martínez	Hm cae.	1.0	0.1	5
Minuartia recurva (All.) Schinz and Thell subsp. *bigerrensis* (Pau) Rivas-Martínez, Fernández-Gonzalez and Sánchez-Mata	Cs	3.4	2.0	38
Sedum brevifolium DC.	Hm	0.2	0.3	67
Silene ciliata Pourret subsp. *elegans* (Link *ex* Brot.) Rivas-Martínez	Cs	5.1	3.8	45
Luzula hispanica Chrtek and Krisa	Hm	0.3	0.3	14
Coleocaulon aculeatum (Schreber) Link	L	0.5	0.6	79
Cetraria islandica (L.) Ach.	L	0.1	0.1	38
Cladonia ecmocyna Leight	L	0.5	1.0	14

potassium level and pH were positively affected by total biomass (0.34 and 0.29, respectively) but negatively by grass biomass (–0.33 and –0.30). Organic matter pools and C/N ratio showed no significant relationships with any of the biomass components.

When the species biomass matrix was constrained by the soil data set (9 variables), a significant model was obtained (Table 4), and TVE reached 33%. Following a forward stepwise procedure, only pH was selected from the soil matrix (Table 4). The RDA model with just this variable was highly significant, the drop in TVE with respect to the model with all soil variables being ca. 14%. The biplot of the reduced model including pH clearly shows that vectors for the biomass per patch of some species are arranged following acidity levels. *Silene ciliata* increases in biomass in those patches with higher levels of pH, whereas *Festuca curvifolia*, *Coelocaulon aculeatum*, and *Jasione crispa* perform better in patches with very acid soils (Fig. 2). The RDA model with the species cover matrix had no significant relationships with soil variables (Table 4).

TABLE 3

Mean and standard deviation of the edaphic variables measured below canopies (N = 60) and in bare soils (N = 20). Significant differences between samples were tested using one-way analysis of variance or Mann-Whitney U test (noted as U)

Edaphic variables	Soil beneath canopies Mean	S. D.	Bare soil Mean	S. D.	Statistic	Significance
Gravel (%)	31.23	13.65	41.07	12.81	7.300	0.009
Fine gravel (%)	13.78	6.17	17.26	8.08	3.493	0.067
Fine earth (%)	54.97	14.09	41.66	12.28	2.273	0.001
Moisture (%)	2.35	0.70	1.88	0.39	7.730	0.007
pH	5.13	0.20	4.94	0.18	13.331	0.001
Conductivity (S m^{-1})	0.039	0.023	0.029	0.006	253.0 (U)	0.007
Organic matter (%)	7.30	2.02	4.78	1.15	26.510	0.000
Nitrogen (%)	0.39	0.077	0.30	0.076	19.159	0.000
C/N ratio	10.52	1.53	8.50	2.31	16.595	0.000
Fe oxides (%)	1.10	0.33	0.93	0.40	235.5 (U)	0.005
Potassium (ppm)	142.86	38.58	92.90	67.25	13.810	0.000
Phosphorous (ppm)	219.92	154.47	169.60	82.72	402.5 (U)	0.792

TABLE 4

Results of RDA models between above-ground species biomass distribution and species cover matrices, with soil nutrients as constraining environmental matrix. λ$_1$, λ$_2$, λ$_3$ represent the eigenvalues of the corresponding extracted axes. Total Variation Explained (TVE) is the sum of all constrained axis eigenvalues. For the Monte Carlo test, F-ratio statistic was computed using the sum or trace of all canonical eigenvalues, and p is the significance of the model after 1000 randomizations. The forward stepwise procedure for the significant RDA model (biomass × soil) is shown below. Drop TVE represents the difference between the TVE of the model including all the variables and the TVE of the reduced model

RDA models	λ_2	λ_3	TVE (%)	Monte Carlo test F-ratio	p
Biomass distribution × soil nutrients	0.066	0.017	33	2.395	0.001
Species cover × soil nutrients	0.050	0.043	22.7	1.429	n.s.

Explanatory variables	F-ratio	p	Reduced model (biomass × soil) TVE (%)	Drop TVE (%)	p
Step 1 (pH)	5.53	0.003	18.3	14.7	0.001

Discussion

DIFFERENCES BETWEEN SOILS BENEATH CANOPIES AND IN BARE GROUND

Soils beneath patches in our study site are richer in nutrients than soils in surrounding open spaces. Our results seem to support the hypothesis that, under stressful conditions, biological activity results in the creation of high-nutrient patches in a low-nutrient matrix (Callaway et al., 1991; Belsky and Canham, 1994; Facelli and Brock, 2000; Hirobe et al., 2001). Enrichment of soil nutrients under perennials has been reported in many contrasting systems, particularly in semi-arid regions (Schmida and Whittaker, 1981; Callaway et al., 1991; Puignaire et al., 1996; Moro et al., 1997) but also in alpine and arctic environments (Chapin et al., 1994) and even under caulescent rosettes in tropical mountain Andean ecosystems (see Pérez, 1992, 1995). The potential mechanisms involved in this pattern may be related to the so-called "nutrient pumping" effect (Callaway and Puignaire, 1999; Titlyanova et al., 1999). Roots take up nutrients from deep stocks and deposit them on the soil surface. On the other hand, plants in patches may trap streamflow nutrient particles (Whitford et al., 1997; Garner and Steinberger, 1989), capture windblown materials (Coppinger et al., 1991), or even at a larger scale, capture particles through freeze-thaw cryopedogenic cycles (Johnson and Billings, 1962), which is the main disturbance factor in relatively snow-free alpine zones (Sakai and Larcher, 1987; Körner, 1999). Nitrogen atmospheric deposition may also be an important factor in mountain regions, especially in the vicinity of large urban areas (Sievering, 2001), as in our case (Madrid, a city with a population around 4 to 5 million people, is just 50 km away from our study site). This fact might be especially relevant because nitrogen is recognized as a limiting factor in cold environments (Bowman et al., 1993; Atkin, 1996), so levels of this nutrient may be at least partly responsible for patch dynamics (Bowman et al., 1996; Choler et al., 2001). Finally, patch formation and growth may also be shaped by intense summer droughts suffered in this Mediterranean mountain range, as shown in other water-limited systems (Aguiar et al., 1992; Aguiar and Sala, 1994). Recently, Núñez et al. (1999) highlighted the relevance of such a type of summer drought in the highest Andean communities of central Argentina. Under this constraint, patches would provide a suitable microenvironment to protect seedlings from desiccation, favoring recruitment within patches over bare areas in alpine and arctic communities (Bliss, 1971; Urbanska and Schütz,

1986). There is no doubt that the presence of plants drives amelioration processes in these high mountain environments (Körner, 1999), but, as posed by Chen and Stark (2000), could plants detect soil heterogeneity or existing fertility sources before patch construction? Our observational study was not able to give more information about this point, but the fact that soil resources in the 20 bare soil samples had nutrient levels lower than the soil beneath patches and that they showed very homogeneous levels for almost all soil parameters, suggests that the origin of these islands of fertility is exclusively plant-driven (Hirobe et al., 2001). In this sense, Grieve (2000) suggests that well-vegetated ground in alpine environments promotes and maintains soil nutrient enrichment, minimizing disturbance phenomena such as human trampling and cryoturbation processes.

SOIL AMELIORATION PROCESS AND SPECIES COMPOSITION

Usually, enrichment in soil resources is associated with changes in species composition interpreted as the result of biotic interactions (Callaway, 1995; Callaway and Walker, 1997; Holmgren et al., 1997). In this sense, there are numerous studies of spatial plant associations in arctic and alpine communities showing a large number of positive associations that have been interpreted as evidences of facilitation (Sohlberg and Bliss, 1984; Holtmaier and Broll, 1992; Kikvidze, 1993; Aksenova et al., 1998; Kikvidze and Nakhutsrishvili, 1998; Núñez et al., 1999). On the other hand, repulsions have been interpreted as a result of competitive exclusion and senility (Valiente-Banuet et al., 1991; Aguiar and Sala, 1994). Using contingency table analyses on presence/absence data we detect two contrasting stages (Fig. 3). One was comprised of pioneer plants such as *Jurinea humilis* and *Sedum brevifolium*, together with the two most abundant species (*Festuca curvifolia* and *Silene ciliata*), and the other was dominated by creeping chamaephytes such as *Thymus penyalarensis*. Similarly, Kikvidze (1993) explained the pattern of co-occurrences in the subnival-alpine limit of the Central Caucasus as comprising four dynamical steps based on the existence of pairwise positive and negative interactions. In contrast, Núñez et al. (1999) only found positive associations and noted an absence of replacement or species exclusion in a high-Andean community. The results presented here are partly in disagreement with those from our previous studies in central Spain (Gavilán et al., 2002),
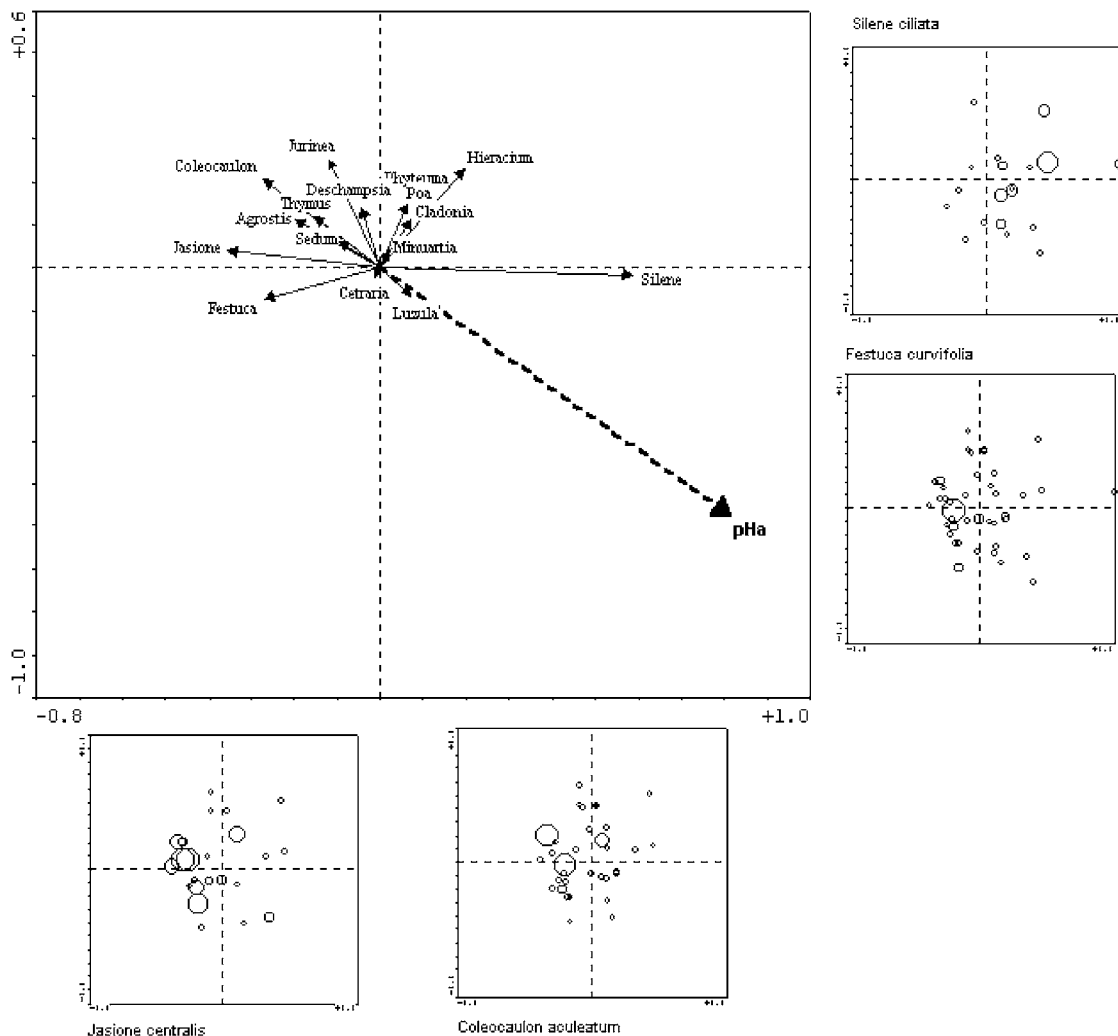
FIGURE 2.   Biplot (axes 1 and 2) of the reduced RDA model including only the pH variable. Vectors for the biomass of each species are included. Values of biomass per patch as proportional circles are represented for the four most outstanding species. Absences are not shown.

which showed different associations and repulsions. Those differences are probably related to the larger spatial scale approach followed in Gavilán et al. (2002), which included several types of Mediterranean high mountain communities within a wider geographical region.

Traditionally, patch dynamics have been considered a quasi-deterministic process in which benefactor species modify the environment through a wide variety of direct and indirect pathways to facilitate the recruitment, growth, and survival of the so-called beneficiary species (Callaway, 1995; Callaway and Puignaire, 1999; Tewksbury and Lloyd, 2001). However, we have detected an evident enrichment at soil resource levels not associated with the performance of any specific plant species, as shown by our RDA models. In addition, the way in which cover is distributed among species in a patch showed relatively short gradients not related to nutrient levels of soil beneath patches ($P > 0.10$). We expected plant species composition and structure to control local soil properties (Chen and Stark, 2000; Hirobe et al., 2001), but we only found a weak trend between biomass distribution among species and acidity (Fig. 2). Taking into account RDA modeling and pairwise comparison in combination, we suggest that the patch dynamic sequence (with at least two contrasting stages) is not coupled with soil amelioration but may be a response to other limiting factors. Our contingency table results suggest that graminoid *Festuca curvifolia* exerts a pioneer behavior probably related to its clonal growth. Positive interactions with lichens and with outstanding

pioneer crassulaceans such as *Sedum brevifolium* reinforce such interactions. On the other hand, negative associations frequently appear between plants with similar requirements or same functional groups, such as *Silene ciliata* and *Minuartia bigerrensis*, both cushion plants with roots that capture nutrients from relatively deep layers.

Although it has been demonstrated that individual alpine plant species can modify soil conditions under monoculture (Onipchenko et al., 2000), it is reasonable that under natural conditions, plant-specific effects may be overshadowed by those of the complete set of species, as shown in some semi-arid systems (Padien and Lajtha, 1992; Vinton and Burke, 1995).

PATCH AND SOIL DYNAMICS IN A HIGH MOUNTAIN MEDITERRANEAN FELLFIELD COMMUNITY

We hypothesized a linear enrichment in soil nutrients due to a direct effect of patch size (Kikvidze, 1993) and an indirect effect of size through two contrasting community traits: grass biomass and total biomass. However, our results do not support this expected direct effect for any of the modeled variables. Furthermore, the strength of the model is based on an indirect effect of size through total biomass and grass biomass. These findings agree with Chiarucci et al. (1999), who suggested that the most meaningful measure of abundance when exploring community structures is biomass.
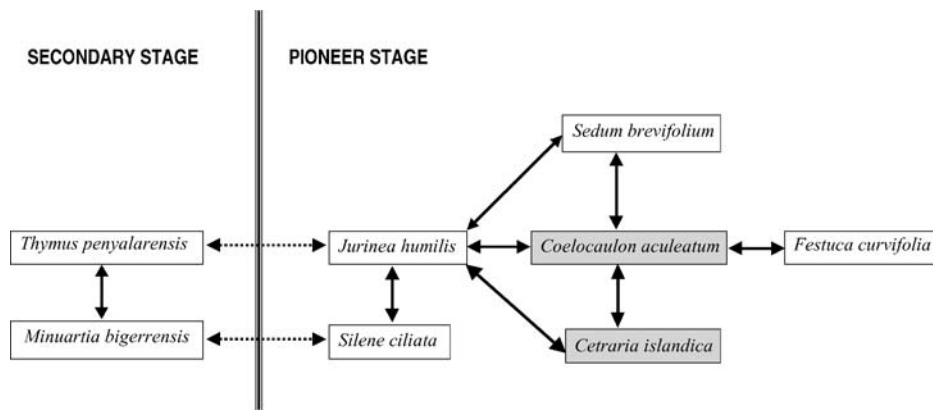
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FIGURE 3. Significant pairwise associations between plant species (P < 0.01). Solid lines indicate positive interactions, and dotted lines negative associations. Shadow indicates lichen species.

Our findings show the possible existence of senility processes coupled to a key soil resource such as nitrogen (Bowman et al., 1993), phosphorous, or iron content (Fig. 1). It is worth noting that this decay is mediated only by total biomass because grass biomass had no significant effects (Wald test), despite the existence of positive path coefficients. Facelli and Brock (2000) provided the first characterization of the development and decline of fertility islands in arid lands and demonstrated that it is an endogenous process. The main difference with our results is that there the process was controlled by a keystone species, *Acacia papyrocarpa*, whereas in our case it is not controlled by any particular species but by plant growth forms (grasses versus total vegetation) (see Aguiar and Sala, 1999). Thus, it can be concluded that although soil nutrient amelioration occurs after patch establishment, there is an endogenous process that determines the decomposition of the patch probably due to competition among plants when patches reach a limiting size. We have observed the loss of integrity and fragmentation once this size is reached.

At least for these key soil resources, our initial hypothesis needs to be reconsidered because patch size does not positively affect nutrient levels but instead determines a conspicuous decline through indirect effects mediated by total biomass (see Rehder, 1976). We propose a model for patch and soil dynamics (Fig. 4). This suggests an amelioration process through facilitation during the first steps of patch formation and a subsequent competitive decline by means of a unimodal

relationship between patch size—indirectly through total biomass or other noncontrolled community traits—and nutrient level. It has been shown previously that nutrient availability is higher in mid-successional stages, at least in forests (Walker, 1989; van Cleve et al., 1991; Chapin et al., 1994). We probably were able to fit significant linear models to our data because the smaller patches were not surveyed. They mainly reflect the right half side of the distribution of the redrawn model (Fig. 4). Nevertheless, we built models including quadratic transformations of variables, but this approach did not significantly improve the fit relative to the linear approach.

It is also worth noting that the effect of grass biomass significantly balances the positive effect of total biomass in the case of potassium content and acidity. This is in line with the complementary role of contrasting functional types in patch dynamics (Grabherr, 1989; Aguiar and Sala, 1999). Thus, facilitative recruitment in the so-called pioneer stage and the subsequent competitive exclusion to the secondary stage is not coupled to soil resources but to the total biomass and the balance with grass biomass. Finally, we did not detect any significant effect of grass biomass in organic matter and C/N ratio even though total soil N is usually a function of soil organic concentration (Rehder, 1976; Körner, 1999). Although some authors have highlighted the shift from competition to facilitation with abiotic stress (see Callaway et al., 2002), a temporal perspective at the scale of the patch suggests that competition may also play a key role in very stressful sites (Tielborger and Kadmon, 2000).

To conclude, our study shows that patch dynamics in high Mediterranean mountain communities may be controlled partly by an endogenous process involving soil key resources through facilitation and competition. These interactions may operate through some community traits related to patch size but not species composition. This process determines the existence of conspicuous islands of fertility interspersed in a bare ground matrix.

Acknowledgments

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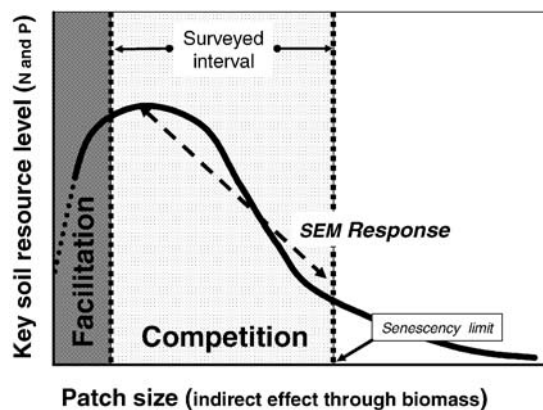

FIGURE 4. Hypothetical model indicating the effect of patch size upon key soil resource levels. In an initial stage consisting of small patches and probably isolated plants, resource level would increase with patch size, mainly due to facilitation. After a particular threshold for patch size, competition interactions would become increasingly more important and promote a decrease in soil resource levels as patch size increases. The negative effects of patch size on resource levels detected by our SEM models would lie on this competitive phase of the hypothetical model.

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