

TEMPORAL AND SPATIAL PATTERNS OF A COLLEMBOLAN COMMUNITY IN A MAQUIS FORMATION (HORTIATIS, MACEDONIA, GREECE)

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Abstract

The temporal and spatial distribution of collembolans in a grazed maquis formation was studied. The seasonality of the mediterranean climate determines the temporal pattern of the collembolan community in the study area, while the main spatial gradient, along which the community is ordinated, is from open to sheltered microhabitats. The vegetation structure, resulting from grazing pressure, determines the spatial distribution of the collembolan species, mainly through its effect in the microenvironmental conditions of the habitat.

Key words: collembola, maquis formation, habitat

Περίληψη

Το θέμα αυτής της εργασίας αφορά τη διανομή στο χρόνο και στο χώρο των Κολλειμβόλων, σε ένα βοσκημένο σύστη αιφύλλων-σκληροφύλλων. Η εποχιακότητα του Μεσογειακού κλίματος καθορίζει το σχέδιο διανομής στο χρόνο της βιοκοινότητας των Κολλειμβόλων, ενώ το πρότυπο διανομής στο χώρο ακολουθεί το αντίστοιχο της βλάστησης, που επάγεται από τη βόσκηση. Η δομή του ενδιαιτήματος επηρεάζει την οργάνωση της βιοκοινότητας, κυρίως διαμέσου των μικροκλιματικών συνθηκών.

Introduction

Ecologists have often been concerned with the effect of the temporal and spatial variations of the environment on the organization of animal communities. Although community structure reflects the adaptations of the component species, studies on the behaviour and population dynamics of individual species have not always been a very fruitful approach at the community level (Giller, 1984). Thus, a holistic approach has often been used, focusing on the overall aspects of community structure.

The work presented here is part of a wider project concerning the dynamics and activity of soil Collembola in a Mediterranean ecosystem. The study site is a gentle hill at the foot of Mt. Hortiatis dominated by *Quercus coccifera* shrubs, with a few randomly dispersed *Juniperus oxycedrus* shrubs. The area is subject to grazing by goats, resulting in the creation of pathways in between the stands. The discontinuous canopy cover provides a mosaic of microhabitats for the soil fauna; a narrow mossbank borders the *Q. coccifera* shrubs, while soil lichen patches are dispersed within the open sites, which are covered mainly by Graminae species. Our aim is to explore the patterns of changes in the structure of the collembolan community over time and space, in relation to changes in habitat structure.

Materials and methods

Six microsites were distinguished and sampled for Collembola; Humus (HM) and litter (LT) layers of *Q. coccifera*, the organic horizon of *J. oxycedrus* (JO), the zone of moss (MO), the

rhizospheres of the Graminae species (GR) and the lichen patches (LC). From October 1987 to September 1988, at monthly intervals, five randomly distributed samples were taken inside each microsite, with a steel cylinder of 5cm diameter. Animals were extracted by means of a Berlese-Tullgren apparatus.

The temporal pattern of the collembolan community as well as the between microsites spatial pattern were explored by means of Detrended Correspondance Analysis (Hill & Gauch, 1980). In order to study the temporal pattern, samples from all microsites were glued together for each month, while the combination of the monthly samples from the whole experimental year for each microsite was used for the examination of the spatial patterns.

In order to examine the community structure within the different microsites, we tested the core-satellite hypothesis (Hanski, 1982), which was proposed to explain local patterns of species' distribution. This model predicts bimodality of species' distribution among the proportion of occupied samples, with peaks close to unity and zero, and a positive abundance-distribution relationship. Thus, the species components of the community will either occur in almost all samples within a microsite, being locally abundant (core species), or in very few of them, being locally rare (satellite species).

Results

The ordination of monthly samples and Collembola species is depicted in Fig. 1. The 1st DCA axis accounts for 82% of the total data variability, representing a longer community gradient than the second one ($\text{length}_1 = 2.67\text{sd}$, $\text{length}_2 = 1.01\text{sd}$). Major changes in community composition occur along this axis, corresponding to the transition from spring to summer and then again to autumn. Minor changes can be observed along the 2nd axis, corresponding to the transition from autumn to winter and to spring.

Fig. 1 Ordination of monthly samples and collembolan species on the plane of the two first axes of DCA. I.palus: *Isotomurus palustris*, F.quadr: *Folsomia quadrioculata*, S.pumil: *Sphaeridia pumilis*, P.notab: *Parisetoma notabilis*, P.albida: *Pseudosinella albida*, O.merid: *Onychiurus meridiatus*, M.bipar: *Metaphorura bipartita*, C.bipun: *Cryptopygus bipunctatus*, Xenylla: *Xenylla sp.*, O.irreg: *Orchesella irregularilineata*, C.engad: *Ceratophysella engadinensis*.

The spatial organization of the collembolan community is depicted in Fig. 2. The ordination scores of the microsites and consequently their species composition differentiate mainly with respect to the 1st DCA axis (87% contribution, $\text{length} = 1.64\text{sd}$), which corresponds to a transition

from open microsites (LC, GR) to sheltered ones (HM, LT, JO). Regarding the 2nd axis (12% contribution, length= 0.96sd), the microsites (HM) and (LT) occupy the opposite end points of it, while the rest microsites are ordinated close to the middle. Thus, this axis can be related to the depth of microsite organic layers. Indeed, the epiedaphic collembolan species are ordinated at the upper half of the DCA plane, while the euedaphic ones at the lower half.

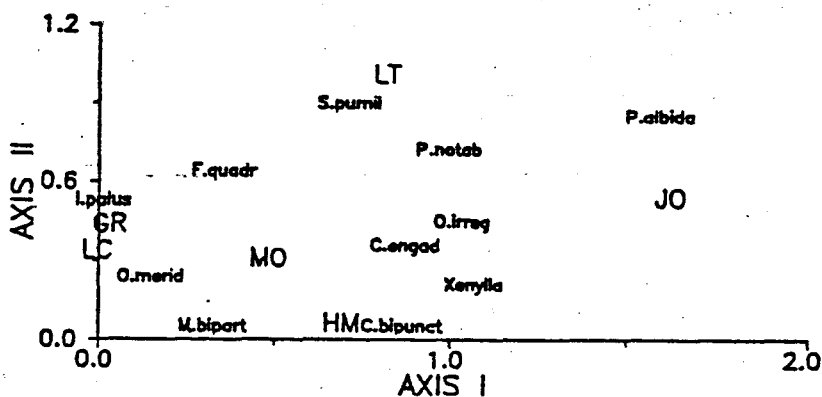


Fig. 2 Ordination of microsites and collembolan species on the plane of the two first axes of DCA (for microsite codes see text).

In order to illustrate the succession pattern of the epiedaphic and euedaphic Collembola along the gradient represented by the 1st DCA axis, we considered the microsites where each species displays a density higher than its mean overall (Fig. 3). The occurrence of the epiedaphic species in microsites changes successionaly from *I. palustris*, which has the mode of its distribution in (LC), to *P. albida*, which has the mode of its distribution in (JO). As regards the euedaphic species, there is a succession from *O. meridiatus* to *Xenylla* sp. The only species which have a discontinuous appearance in microsites, and are therefore excluded from Fig. 3, are *O. irregularilineata*, which is almost absent in (HM) and (LT), and *C. engadinensis* which displays high densities in (GR), (HM) and (LT), but not in (M). Therefore, these species are ordinated always in the center of the DCA plane, giving the false impression of a wider habitat selection, compared with the rest of the species.

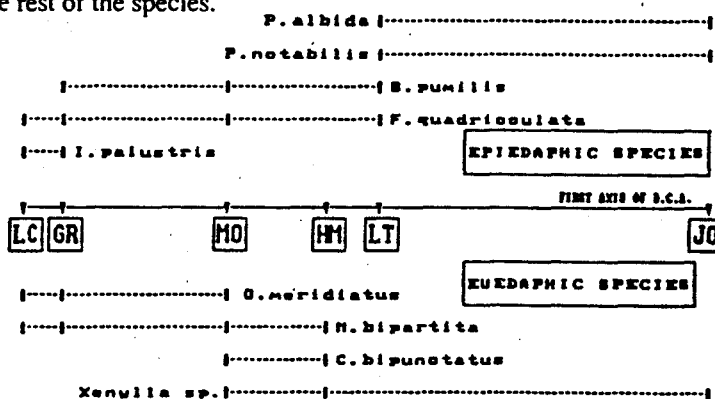


Fig. 3 Succession pattern of the epiedaphic and euedaphic collembolan species along the environmental gradient represented by the 1st axis of DCA. Species are ordered according to their microsite preferences.

Species' distribution among samples within each microsite is depicted in Fig. 4(A). A linear regression line is fitted to abundance-distribution data (Fig. 4B). Since (LT) and (HM) microsites are separated only vertically, in this analysis they are considered as one microsite, named *Q. coccifera* (QC). No site has a mode of species' distribution near unity. This is due to the dynamics of each population, since almost no species is active the whole year round in the study area (Stamou et al., 1993). Thus, a site occupancy over 50% coupled with a high local abundance corresponds to a core species. The analysis conforms to the predictions of the core-satellite hypothesis within the (LC) microsite. The same holds for (GR), although bimodality is less obvious. Neither a bimodal species' distribution nor a significant relationship between local abundance and distribution exists in (MO) and (QC), where community structure appears more homogenous; no species occupies less than 20% of the samples and high abundances are recorded. In (JO), species' distribution is unimodal with a peak close to zero. Although there is a positive correlation between abundance and distribution, the slope of the regression line is low ($b=0.4$) (Fig. 4B), indicating a relatively simple environment with only a few kinds of resources available (Maurer, 1990). Furthermore, *P. albida* and *Xenylla* sp., which are the core species in (JO), the most protected site, are mainly "summer" species.

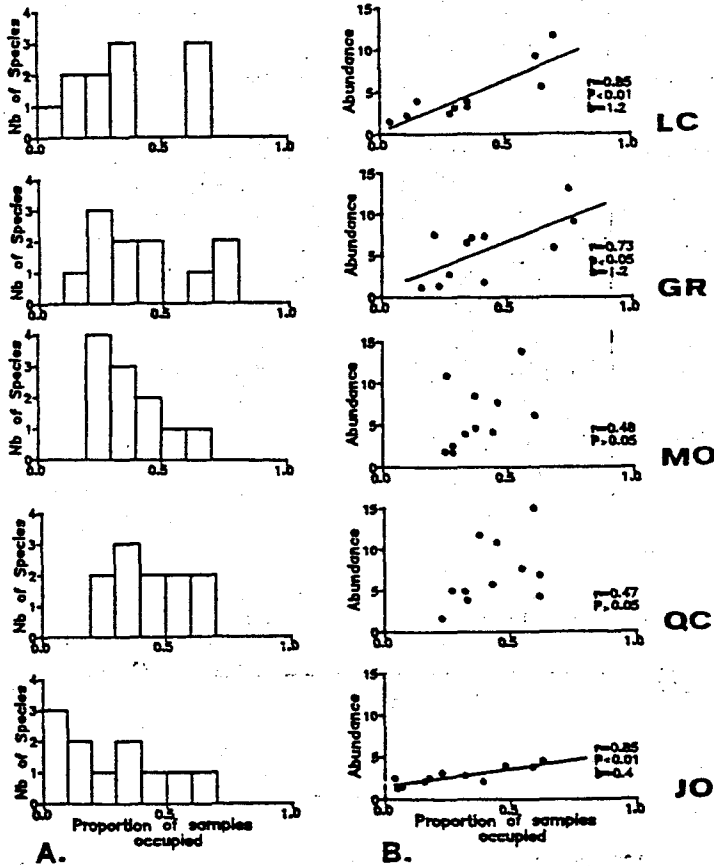


Fig. 4 (A) Distribution of 11 collembolan species among proportions of occupied samples within the different microsites.
 (B) Relationship between distribution (proportion of samples occupied by the species) and abundance (mean density in the occupied samples), for 11 collembolan species.

Discussion

According to our results, the species composition of the collembolan community changes before and after the dry period of the year, responding to the seasonality of the mediterranean climate. Indeed, rapid changes in the population size of each component species occur either at the beginning or at the end of summer (Stamou et al., 1993), which is considered the adverse period.

The main spatial gradient, along which the collembolan community is ordinated in the study area, is from open to sheltered microhabitats. Thus, the vegetation structure, resulting from grazing pressure, determines spatial distribution of the species. This effect may be indirect, via microclimate (Brown, 1991). In the study area, the collembolan community structure is homogenous in the sheltered microsites, while in the exposed sites a species occurs either in many large assemblages (core) or in few small ones (satellite). Heterogeneity within a site may give rise to a bimodal species' distribution (Hanski, 1991). Indeed, the fluctuations of the environmental variables, namely air-temperature and humidity, are more severe in the exposed sites, creating an heterogeneous microenvironment in time, while the canopy cover over the microsites seems to create a more moderate environment for the settlement of populations.

From the above, we could suggest that the microenvironmental conditions of the habitat determine the spatial pattern of the collembolan community between, as well as within the different microsites. Moreover, the fact that (JO) provides shelter for the "summer" species in the study area implies a possible relation between the temporal pattern of the community and habitat structure.

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