

Temporal and spatial distribution patterns of Collembola in a patchy environment

M. D. Argyropoulou, G. P. Stamou and G. D. Iatrou

Department of Ecology, School of Biology, Aristotle University, 54006 Thessaloniki, Greece.

Received May 27, 1993; accepted March 9, 1994.

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 on the microenvironmental conditions of the habitat.

Keywords: Community patterns, core-satellite, abundance, distribution, Collembola.

Modèles de distribution temporelle et spatiale de Collemboles dans un ensemble écologique en mosaïque.

Résumé

La distribution temporelle et spatiale des Collemboles dans un maquis pâturé a été étudiée. La saisonnalité du climat méditerranéen détermine la phénologie de la communauté des Collemboles dans la région étudiée, tandis que le gradient spatial principal le long duquel s'ordonne le peuplement va des sites ouverts vers les microhabitats abrités. La structure de la végétation, résultant de la pression due au pâturage, détermine la distribution spatiale des espèces de Collemboles, principalement par ses effets sur les conditions écologiques fines de l'habitat.

Mots-clés : Modèles de communauté, noyau-satellite, abondance, distribution, Collemboles.

INTRODUCTION

The effect of the temporal and spatial variations of the environment on the organization of animal communities has always been one of the main problems in ecology. 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). At this level, multivariate methods can be applied to summarize environmental variations, and correlate environmental and organismal heterogeneity (Downing, 1991).

The present paper deals with the temporal and spatial organization of a collembolan community in an evergreen-sclerophyllous formation with a patchy vegetation pattern, induced by prolonged grazing. In this attempt, a multivariate method has been adopted.

Nevertheless, although multivariate analyses are effective in revealing community gradients in patchy environments, they do not provide information on the community structure within a patch. For this purpose, we tested Hanski's (1982) "core-satellite" hypothesis, which was proposed to explain regional patterns of species' distribution. This model, based on the concepts of extinction and immigration of local populations, predicts bimodality of species'

distribution among the sites they occupy and a positive relationship between species' abundance and distribution. Thus, it discriminates between a group of high abundance, widely distributed, core species, and a group of low abundance, narrow distributed, satellite ones.

Up to now, the core-satellite hypothesis was tested on spatial scales larger than the one used in the present paper (Hanski, 1982; Collins and Glenn, 1990; Gaston and Lawton, 1990; Maurer, 1990) or over longer time periods (Gaston and Lawton, 1989). However, the predictions of Hanski's model are not unique to regional scale phenomena and can explain patterns of community structure on several spatial scales (Collins and Glenn, 1990). Moreover, there might be several other reasons, than the ones conceived by Hanski, leading to a core-satellite pattern (Gotelli and Simberloff, 1987). Indeed, in this study we will try to explain the observed community patterns not in terms of Hanski's model, that is immigration-extinction dynamics, but on the basis of the activity and population dynamics of the component species.

THE STUDY SITE

The study site is a gentle slope at the foot of Mt. Hortiatís, 20 km east to Thessaloniki, at about 400 m a.s.l. and has a north-eastern orientation. It is a typical mediterranean formation dominated by evergreen sclerophyllous *Quercus coccifera* shrubs, with a few randomly dispersed "cushion-formed" *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 by Graminae species. Thus, grazing forms a gradient of adjacent microsites from the center of the *Q. coccifera* shrubs to the open sites.

MATERIALS AND METHODS

Sampling design

Six microsites were distinguished and sampled for Collembola; the 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) near the shrubs and the lichen patches (LC). From October 1987 to September 1988, at monthly intervals, five randomly distributed samples were taken inside each microsite (30 monthly samples), with a steel cylinder of 5 cm diameter. Animals were extracted by means of a Berlese-Tullgren apparatus and collected in a 3:1 solution of 70% ethyl alcohol and glycerin.

Data analysis

The temporal pattern of the collembolan community as well as the between microsites spatial pattern were explored by means of Detrended Correspondence Analysis (Hill and 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.

The core-satellite hypothesis was tested in order to explore the community structure among the samples within the different microsites. By the term "distribution", we name the proportion of samples from the whole experimental year, which are occupied by the species, while by the term "abundance", we name the mean density of each species in the samples it occupies. Thus, a bimodal species' distribution among the proportion of occupied samples and a positive abundance-distribution relationship would mean that the component species of the community occur either in almost all samples within a microsite, in large assemblages (core species), or in very few samples with small numbers (satellite species).

We should note that bimodality of species' distribution has been criticized as a sampling artefact (Brown, 1984). The inclusion in the abundance-distribution analysis of species, which are recorded on habitat patches on an accidental basis, inflates the number of satellite species, resulting in a dubious community pattern, which does not require an ecological explanation (Nee *et al.*, 1991). In order to avoid this mistake, in this paper we excluded from the analyses all the species, which appeared irregularly in samples over time, and we considered only the species with interannually stable populations in the study area (Stamou *et al.*, 1993).

RESULTS

The ordination of monthly samples and Collembola species is depicted in figure 1. The first 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. Thus, there is a clear distinction between the dry and the wet period of the year. Minor changes can be observed along the second axis, corresponding to the transition from autumn to winter and to spring.

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

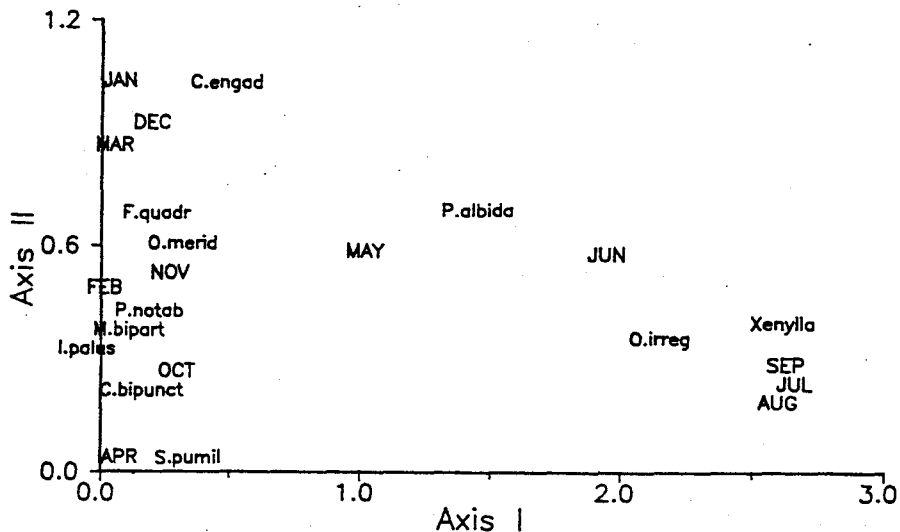


Figure 1. - Ordination of monthly samples and collembolan species on the plane of the two first axes of DCA.

I. palus: *Isotomurus palustris*, F. quadr: *Folsomia quadrioculata*, S. pumil: *Sphaeridia pumilis*, P. notab: *Parisotoma 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*.

which corresponds to a transition from the open microsites of lichens (LC) and gramineae (GR) to the sheltered ones of humus, litter and the cushion-formed *J. oxycedrus* (HM, LT, JO). Moss (MO) seem to have an intermediate species composition. Regarding the second axis (12% contribution, length = 0.96 sd), the humus (HM) and litter (LT) microsites 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 the 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.

In order to illustrate the succession pattern of the epiedaphic and euedaphic Collembola along the environmental gradient represented by the first 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 successional from *Isotomurus palustris*, which has the mode of its distribution in lichens (LC), to *Pseudosinella albida*, which has the mode of its distribution in *J. oxycedrus* (JO). As regards the euedaphic species, there is a succession from *Onychiurus meridiatus* to *Xenylla* sp. The only species which have a discontinuous appearance in microsites, and are therefore excluded from this graph, are *Orchesella irregularilineata*, which is almost absent in (HM) and (LT), and *Ceratophysella engadinensis* which displays high densities in (GR), (HM) and (LT), but not in moss (MO). Therefore, these species are ordinated almost in the center of the DCA plane, giving the false impression of a wider habitat selection, compared with the rest collembolans. Furthermore, in this graph we can see that more species

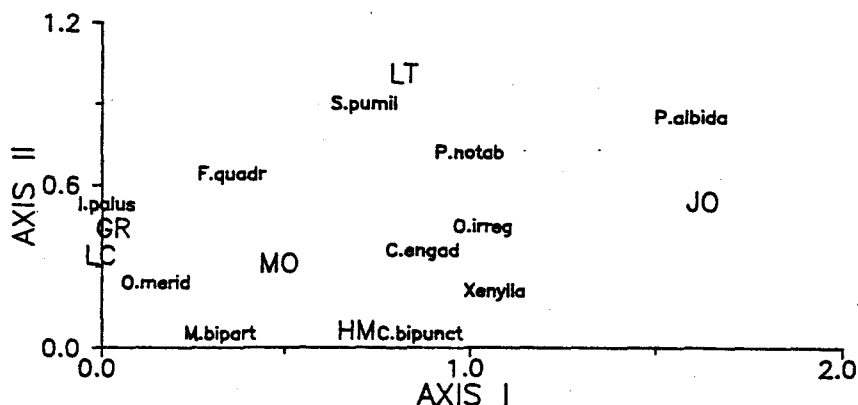


Figure 2. - Ordination of microsites and collembolan species on the plane of the two first axes of DCA (for microsite codes see text).

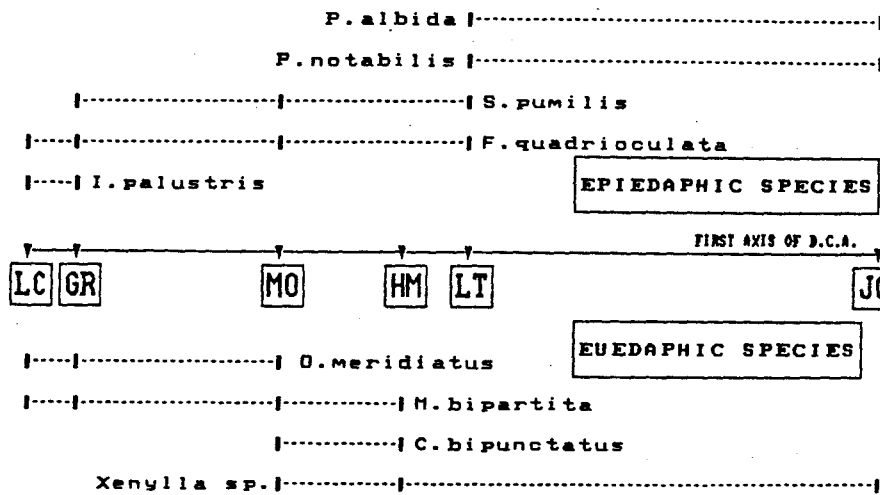


Figure 3. – Succession pattern of the epiedaphic and euedaphic collembolan species along the environmental gradient represented by the 1st axis of DCA. Species are ordered according to their microsite preferences.

display high densities in the center of the *Q. coccifera* shrub (HM, LT) than in its adjacent microsities, while *J. oxycedrus* is the less preferred site.

Species' distribution among samples within each microsite is depicted in figure 4(A). A linear regression line is fitted to abundance-distribution data (fig. 4B). Since the litter (LT) and humus (HM) microsities 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 we consider the samples from the whole experimental year and 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 abundance indicates a core species. The analysis conforms to the predictions of the core-satellite hypothesis within the lichen microsite (LC); species' distribution among the proportion of occupied samples is bimodal and the abundance-distribution relationship is positive. The same holds in gramineae (GR), although bimodality is less obvious. Neither a bimodal species' distribution nor a significant relationship between local abundance and distribution exists in moss (MO) and *Q. coccifera* (QC), where community structure appears more homogenous; species display intermediate abundance and/or intermediate distribution, while no species occupies less than 20% of the samples. In *J. oxycedrus* (JO), although there is a positive correlation between abundance and distribution, the slope of the regression line ($b=4.1$) is lower than the one in (LC) or (GR), while species' distribution is unimodal with a peak close to zero. We should note that species which are core in other microsities, e.g. *Folsomia quadrioculata* or *O. meridiatus* in (LC) and (GR), switch to the satellite status here. The inverse happens in the case of *P. albida*.

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 of the year. Besides demographic characteristics (e.g. aestivation in the form of eggs), the animals' ability to alter their physiological status (e.g. anhydrobiosis; Poinso-Balaguer and Barra, 1978) or their ability for vertical and horizontal movements towards protected microsities (e.g. beneath stones; Sgardelis and Margaris, 1993) could be of considerable importance, regarding those changes. In any case, the species composition of the community in summer is entirely different from that of the rest of the year, so that we would rather speak of a bipolarity, than of a community gradient in time.

As regards the spatial pattern of the collembolan community, the vegetation structure, which results from grazing pressure, forms a gradient from open microhabitats to sheltered ones, along which the species are more or less evenly distributed. This gradient has often been reported as an ecological factor, which influences the collembolan populations and, consequently, contributes to an ordination of their communities (Poza, 1986; and references therein). Furthermore, it determines also the structure of the oribatid mite community in our study area (Asikidis and Stamou, 1991).

The effect of habitat structure on the communities of the associated organisms may be either direct, through mechanical effects regulating the distribution of resources, or indirect, via microclimate (Brown, 1991). Microarthropods in Hortiatias display a high degree

of food specialization (Asikidis, 1989; Argyropoulou, unpubl.), feeding mainly on the epiphytic lichens, which grow on the *Q. coccifera* branches and constitute a great part of the *Q. coccifera* litter. Thus, the spatial distribution of the species does not seem to result from the partitioning of food resources. These are in accordance with the results reported by Ponge (1993), who found no direct influence of vegetation on the spatial distribution of a collembolan community

in a temperate ecosystem. Moreover, our laboratory cultures did not provide any evidence that other biological processes, such as mating or egg-laying, of Collembola are related to structural properties of the habitat.

The changes along the open-sheltered microsite gradient do not only refer to the succession of the species, but to the community structure as well. In *J. oxycedrus* (JO), the low slope of the abundance-

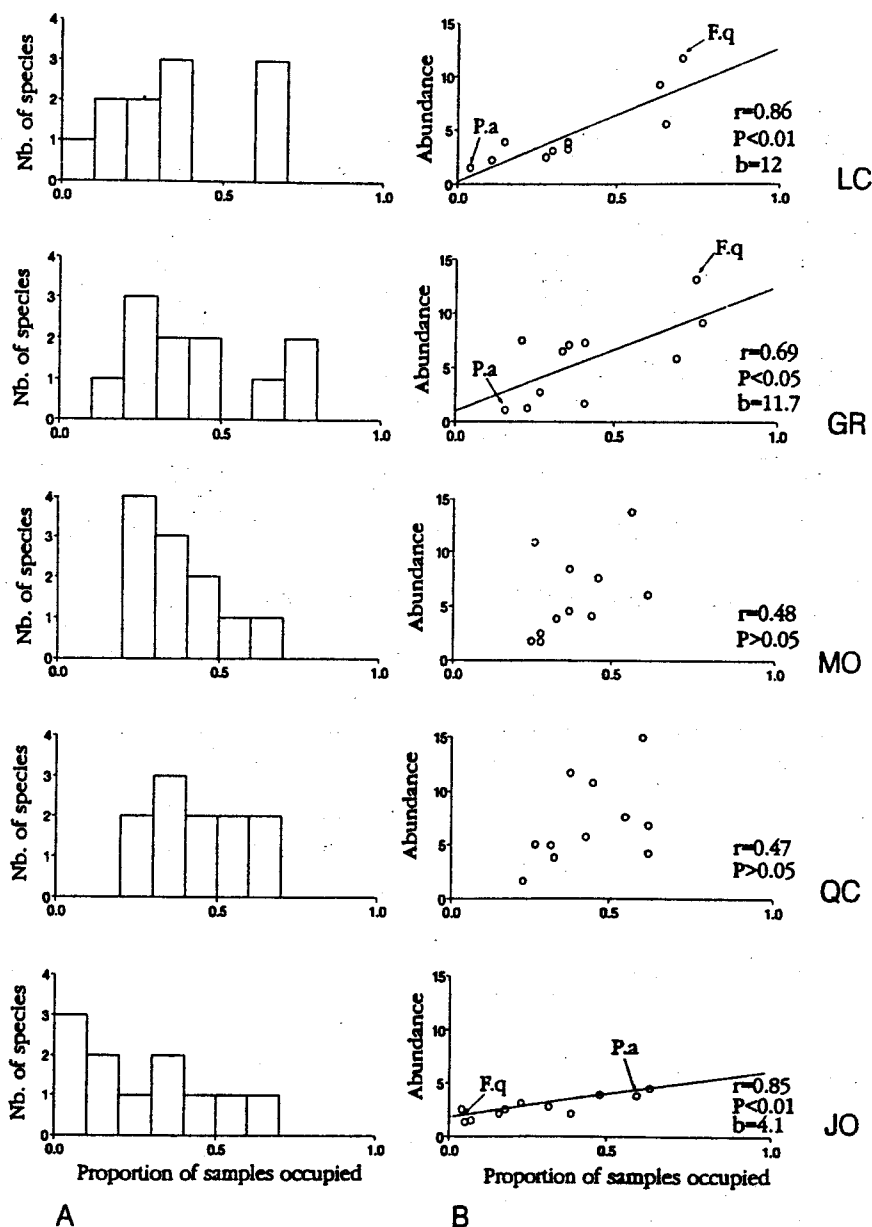


Figure 4. - (A) Distribution of 11 collembolan species among proportions of occupied samples within the different microsites.

(B) Relationship between distribution (proportion of samples occupied by the species) and abundance (mean density in the occupied samples), for 11 collembolan species. Arrows indicate examples of core-satellite switching (F. q: *Folsomia quadrioculata*, P. a: *Pseudosinella albida*).

distribution regression line indicates a relatively simple environment with only a few kinds of resources available (Maurer, 1990). Given that the lichens which constitute the greatest part of the microarthropod diet are absent in this microsite, we would suggest that this might be the only case where food resource partitioning results in spatial separation of niches. As regards *Q. coccifera* and its vicinity, the collembolan community is homogeneous in the sheltered microsites (QC, MO), while in the exposed sites (LC, GR) a species occurs either in many large assemblages (core) or in few small ones (satellite).

We should note here that, since in the analysis of abundance-distribution data we consider the samples from the whole experimental year, the results actually reflect the space-time interaction. However, the core species of the exposed sites do not have a wider temporal distribution than the satellite ones and, moreover, there is a core-satellite "switching" among the different microsites, which can only be attributed to the habitat properties and not to differences in the temporal distribution of the species.

On the other hand, a bimodal species distribution may be the result of the heterogeneity within a site (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. In stable environments, biotic factors could play a more direct role in regulating the population numbers (Joosse, 1981), but in an exposed and unstable environment, species ought to adapt themselves in order to face the oscillations of the abiotic variables. Ponge (1993) suggested that ecophysiology could be more adequate for explaining the adaptations of species to the constantly changing environmental conditions of the open sites. Indeed, *O. meridius*, which is a core species in both the open sites of lichens and graminiae (LC, GR), is a wide temperature selected animal (Argyropoulou and Stamou, 1993). The fluctuations of temperature have a stimulating effect on its metabolism, preventing the arrest of its life-cycle development during winter. Therefore, this animal has a competitive advantage over the satellite species in the exposed sites. From the above, we could suggest that it is mainly the microenvironmental conditions of the habitat and their fluctuations in time, which determine the spatial pattern of the collembolan community.

Sgardelis and Margaritis (1993) report that in a typical mediterranean phryganic ecosystem the effect of seasonality on the microarthropod community structure is greater than that caused by human intervention (fire). The same seems to hold also in the case of our maquis formation, where seasonality results in a bipolar species distribution in time, while grazing in a microsite gradient, along which species are evenly

distributed. The community structure within each microsite is mainly determined by the microclimate.

REFERENCES

- Argyropoulou M. D. and Stamou G. P. (1993). – Respiratory activity of the collembolan *Onychiurus meridius*. *J. Insect. Physiol.*, **39**, 217-222.
- Asikidis M. D. (1989). – *Dynamics and activity of oribatid mites (Acari: Cryptostigmata) in an evergreen-sclerophyllous formation (Hortiatias)*. PhD Thesis, Univ. of Thessaloniki (in Greek with an English summary).
- Asikidis M. D. and Stamou G. P. (1991). – Spatial and temporal patterns of an oribatid mite community in an evergreen-sclerophyllous formation (Hortiatias, Greece). *Pedobiologia*, **35**, 53-63.
- Brown J. H. (1984). – On the relationship between abundance and distribution of species. *Am. Nat.*, **124**, 255-279.
- Brown V. K. (1991). – The effects of changes in habitat structure during succession in terrestrial communities. In: S. S. Bell, E. D. McCoy and H. R. Mushinsky (eds.). *Habitat Structure; the physical arrangement of objects in space*. pp. 438. Chapman and Hall.
- Collins S. L. and Glenn S. M. (1990). – A hierarchical analysis of species' abundance patterns in grassland vegetation. *Am. Nat.*, **135**, 633-648.
- Downing J. A. (1991). – The effect of habitat structure on the spatial distribution of freshwater invertebrate populations. In: S. S. Bell, E. D. McCoy and H. R. Mushinsky (eds.). *Habitat Structure; the physical arrangement of objects in space*. pp. 438. Chapman and Hall.
- Gaston K. J. and Lawton J. H. (1989). – Insect herbivores on bracken do not support the core-satellite hypothesis. *Am. Nat.*, **134**, 761-777.
- Gaston K. J. and Lawton J. H. (1990). – Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos*, **58**, 329-335.
- Giller P. S. (1984). – *Community Structure and the Niche*. pp. 176. Chapman and Hall.
- Gotelli N. G. and Simberloff D. (1987). – The distribution and abundance of tallgrass prairie plants: A test of the core-satellite hypothesis. *Am. Nat.*, **130**, 18-35.
- Hanski I. (1982). – Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, **38**, 210-221.
- Hanski I. (1991). – Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, **42**, 17-38.
- Hill M. O. and Gauch H. G. J. (1980). – Detrended correspondence analysis: An improved ordination technique. *Vegetatio*, **42**, 47-58.
- Joosse E. N. G. (1981). – Ecological strategies and population regulation of Collembola in heterogeneous environments. *Pedobiologia*, **21**, 346-356.
- Maurer B. A. (1990). – The relationship between distribution and abundance in a patchy environment. *Oikos*, **58**, 181-189.
- Nee S., Gregory R. D. and May R. M. (1991). – Core and satellite species: theory and artefacts. *Oikos*, **62** (1), 83-87.

- Poinsot-Balaguer N. and Barra J. A. (1978). – Adaptation de certains collemboles à la sécheresse: l'anhydrobiose. *Bull. Soc. Ecophysiol.*, 3, 56-58.
- Ponge J. F. (1993). – Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems. *Pedobiologia*, 37, 223-244.
- Pozo J. (1986). – Ecological factors affecting collembola populations. Ordination of communities. *Rev. Ecol. Biol. Sol*, 23(3), 299-311.
- Sgardelis G. P. and Margaritis N. S. (1993). – Effects of fire on soil microarthropods of a phryganic ecosystem. *Pedobiologia*, 37, 83-94.
- Stamou G. P., Asikidis M. D., Argyropoulou M. D. and Sgardelis S. P. (1993). – Ecological time versus standard clock time: the asymmetry of phenologies and the life history strategies of some soil arthropods from Mediterranean ecosystems. *Oikos*, 66, 27-35.