AUCHENDRRHYNCHA / HOST PLANTS ASSOCIATIONS IN EAST MEDITERRAHEAN COMMUNITIES: A MULTIVARIATE APPROACH ON STRUCTURE AND SPECIFICITY 3

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ABSTRACT

We investigated the relations between fourteen Auchenorrhyncha species and the plants in an east mediterranean shrubland. We tried to reveal covariation patterns between biotope descriptive variables and insect species, abundances and preferences. We deviced a new quantitative approach to estimate preference. Insects niche parameters and overlaps were estimated and the niche structure in various seasons was compared to predictions of traditional niche theory. By using character set types in a conocharacter growth form system, instead of plant species, we discovered negative correlations between community diversities and temporal stability. stability.

KEYNORDS

Insect plant relationship, Niche structure, East Mediterranean, Multivariate techniques, Diversity.

INTRODUCTION

Plants give biotopes their characteristic configuration. In consequence, various aspects of them were quantified in an attempt the guiding forces of animal asseblages to be analyzed (MacArthur,1984; Andrzejewska,1985; James,1971; Shugart & Patten,1972; Roth, 1976; Blondel & Cuvellier, 1977; Rotenberry & Wiens, 1980; Mac Nally & Doolan, 1986). The selection of the critical variables to be measured, was based largely on the suspicion and the field experience of the investigator, on a particular group of animals. For this reason, the collected data sets contained an amount of extraneous information, as a result of the redundancy and the correlation of the selected variables (Mac Nally & Doolan, 1986).

To isolate this effect of variables, a reductionistic method was usually undertaken, and the original data set was reduced to a small set of orthogonal factors (Rotenberry & Wiens, 1988; Mac Nally & Doolan, 1986, among others). This reduction, made possible the quantification of the multidimensional Hutchinsonian niche, initially for molluscs (Green, 1971) and then for birds (James, 1971; Rotenberry & Wiens, 1988), for plants (Johnson, 1977a,b), for small mammals (Dueser & Shugart, 1978) and recently for cicadas (Mac Nally & Boolan, 1984). Doolan, 1986).

Through this approach and after the identification of the above MENTIONED axis, as resource axes, the niche parameters of each animal species were estimated, and the niche structure of the animal communities was sought, very often with obscured results, because of the inadequacies of the collected data (Pianka, 1975; Rotenberry & Miens, 1980). The problems associated with this unclear patterns, stemmed from three error sources.1) The scaling problem in the sampling design was not always taken in mind, and biotope descriptive variables were measured in incompatible scales than animal abundances (Petrakis & Catsadorakis, 1987 in press). 2) Data sets were collected from broad biogeographic regions and thus were largely inadequate to generalize interpopulation dynamics such as niche compressions or expansions (Cody, 1975; Rotenberry and Miens, 1988.3) To our knowledge, there is not any published work on the study of the niche space mobility within one year; the existing works (Wallof & Solomon, 1973; Morris, 1973; Gibson, 1976, among others), do not quantify niche space in the context of multivariate techniques.

In this paper, we analyze the relationships of Auchenorrhyncha niches with the habitat in an east-Hediterranean region on Kynosura peninsula, near Marathon village in Greece. Firstly we describe vegetation gradients with two alternative sets of variables. Then we estimate the niche parameters of insect species and their changes in three main seasons of the year. We then examine the relations of niches of the insect species and test the compatibility of this community patterns with predictions of niche theory.

PROCEDURES

Study area: The study was undertaken at a northeasternly exposed hillside on the base of Kynosura peninsula. Doainant vegetation is a Juniperus phoenicea and Olea europea codominated shrubland with openings dominated by annual and perennial herbs and low chamaephytes and hemicryptophytes. The depth of the soil is low (<= 5ca in many cases) and the parental material is usually exposed (Petrakis, 1904).

Sampling: The sampled sites are quadrats (10 x 10 mg), located at regular intervals along a transect strip descending the hillside from the top. Ten quadrats were sampled for insects at fortnight intervals with a sweep net by one person to reduce collector bias. Within a dudrat, the sweep net passed through every vegetation phase, readily distinguished by eye and the content of the net, was transferred in a plastic bag where insects were killed by ethyl acetate. This was considered as one sample. Two kinds of

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samples were taken from shrubs and low trees - trees with distinct trunk were rare in the broader region and absent from our transect. The first kind corresponded to the first one meter in the base of the plant where lower branches were intermingled with herbs grown under the shrub. The second kind corresponded to the rest of the shrub.

Plants were sampled for coverage, density and height. These parameters were selected because they provide the necessary plant parameters for the estimation of foliage value through the parabolic estimator formula: /2 (height)SDR(coverage), modified from whittaker (1961) without species corrections. Height was measured in the field and it is the mean value of all individuals of a plant species or a plant character set type (CST see below). Coverage was estimated by a photo-computational method (Petrakis, in prep). Five photographs of each quadrat were taken with a 17mmF optical lens and the transparency was then projected onto a board of a digitizing areometer connected serially to a computer. Rith an appropriate program (written by Petrakis) we then calculated the percentage of each species, or CST, with corrections for the parallaxis of the picture introduced by the lens. Although photo-computational methods require an appreciable amount of experience with the plant populations, they have been proved very accurate in estimating plant performance and abundance (Scots, 1979). This procedure was repeated twice, in February and in May and the data were pooled.

At the same time intervals we measured plant phenological parameters in a quantitative manner but these data are not incorporated into the subsequent statistical analyses, though they are taken into account in the discussion of results and will be reported in another paper.

Variables and statistical procedures: So far, in the literature, biotope descriptive variables fall into two broad categories. The first coaprises "coverage" variables and the second "structural" variables (e.g. Rotenberry & Aiens, 1980). Here we chose an alternative approach. Our first variable set included all plant species. Thirty plant species that had coverage in one site at least .5 a2 were included and 27 species were disregarded as rare. Iwenty two of the disregarded species had also very low weights in another study of Coleoptera plants associations in a neighboring site (Tselepatioti-Petraki unpubl.). Also we used an alternative set of variables, where plants are considered as CSI in a non taxonomic monocharacter growth fore system (MGFS) (Petrakis in prep.). In this classificatory scheee plants were assigned in 25 anatomical phenological and ecophysiological characters. This classification is proved here as a more powerful tool for variable set construction, since most characters in the scheme are insect oriented. In degraded Mediterranean plant formations, plants have evolved defending strategies to cope with grazing and drought. The morphological and phenological features of these adaptations are not discrete and unique, but they are performed in a variety of intensities not necessarily related to the intensity of the exerted pressure. For these reasons these two classifications produced two slightly different spaces as it can be seen in Fig. 1 and 2, the CSIs space being more easily explicable in the context of insect plant relationships.

For the estimation of insect niche parameters we took the multivariate approach, which reduces the dimensionality of the resource space with minimal information loss, and provides the possibility of tests for these parameters. The method was the principal components analysis (PCA), a robust technique in data bodies free of disjunctions and non-linearities (Bauch et al. 1977; Johnson, 1977b; Orloci, 1979; Gauch, 1982; Greig-Smith, 1983). Disjunction do not seem to exist, as it can be seen in the dendrogram of Fig. 2. To cope with the problem of non-linearities we transformed the original matrices to the octave scale (Gauch, 1982). A divisive classification (Lefkovitch, 1976) was applied on each FCA output to detect site groups along resource gradients. With PCA the diagnosis of resource gradients and the estimation of insect niche parameters became possible.

For the estimation of niche breadth (B) and overlap (O) a methodology compatible to that of Johnson (1977b) was adopted. Each principal resource axis was divided into five equally spaced intervals, and the abundance of each insect in the set of sites that felt in each interval was calculated. B was estimated by the formula Bipe 1/2 pijk(Hill, 1973) i=1,...,N; k=1,...,t; j=1,...,S; where Bij= breadth of the i-th species in the k-th resource axis, pijk = proportion of the i-th species in the j-th interval of k-th axis; N=total number of species; t=number of principal axes. O on a principal axis was measured by the formula: Oijk= Phik/Phik/Phik-Phik,h=1,...,N; j=1,...,S; k=1,...,t where Oik = overlap between i-th and h-th species on k-th principal resource axis (Levins, 1968; Planka, 1975). All these parameters were calculated in each of the three seasons in which the year was subdivided.

The maximum number of axes which accounted for the total trended variation in the data set was estimated by Anderson's (1963) criterion. All tests were performed at .05 probability level.

PCA was also used here as direct seeking method for site preference and as an indirect method for the detection of insect plant associations in a way similar to the indirect gradient analysis (Michols, 1977). We have extended this seeking approach to all the seasons and we have measured the "mobility" of the sites, by calculating the length of the trajectory of the site, regarded as a point in an insect variable sultidimensional space (Table 4 and Fig. 6). We feel that these mobilities are useful measures of the temporal association patterns of insects and plants, together with the possibility to probe the mechanisms through which biotope structural and temporal diversities affect these patterns.

To detect niche overlap relationships of insects in the three seasons, we submitted the matrix of insects by their niche overlap coefficients to a centroid clustering procedures (Orloci & Kenkel, 1985). The strategy was the minimization of group centroid distances measured by the Lance and Williams (1966) formula, since we intended to fuse into groups all species, according to their higher overlap. We have also manalyzed our original data eatrix of sites by plant species, to seek for floristic similarities among sites. The strategy was the minimization of between group sum of squares, and the algorithm was Orloci's (1967) 'sum of squares agglomeration' (SSA). Diversities were calculated by Simpson's and Shannon's formulas (Pielou, 1977).

RESULTS AND DISCUSSION

Axes description and resource axes derivation: Fourteen Auchenorrhyncha species were found in the set of ten sites. From the centered PCA by which the raw data matrix was analyzed in a space of plant species, it can be seen that site groups coincide with those formed by SSA clustering (Fig. 1 & 2). This implies that a contribution of plant species to the vegetative dissimilarity of sites is equal to their contribution to the separation of sites along the resource axes. Anderson's criterion predicted that maximum parsimony is attained at the first two principal axes (x² = 18.17, d²=27). The amount of trended variation accounted for by the first two principal axes is moderate (Fig.1). This may be a result of remaining non-linearities after octave scale transformation. Most surprising was that no plant species were significantly correlated to the third and subsequent axes. Nevertheless, these two axes are ecologically interpretable, though not fully. Shrubs and low trees in Mediterranean formations are well correlated to the first axis, not all of them however (Table 2). First principal axis (PA) therefore can be considered as a gradient from rocky soilless

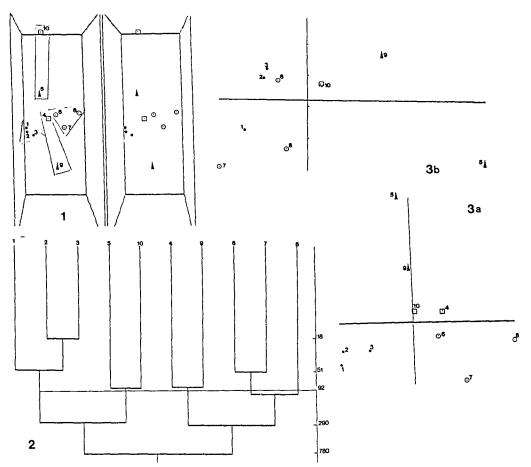


Table 31 Correlations of CSTs with the vagetation principal components. Only significant correlations are shown.

CSTs	Component Eigenvalue Cumulative% var	I 24.6 28.52	II 16.9 47.76	111 12.39 62.13		y 9.20 5.29
Juniphoel Jeniphoel Oleseurof Pistlent Pisttere Phlofrut Quercocc		47 .46 .66 .71	47 .47 49 48	.62	.56	.52
Prunwebb Euphacan Urgimari Eyclorae Avenbarb Knauinte Thapgarg		.46 .72 51 .76 93	.90 .41 .65	.02		.56
Anempayo Seladent		.42	-,62	64	.84	

Fig.1 Stereogram of the ordination of sites in a space of plant species foliage volume. Horizontal axis is 1-st PA, vertical axis is 2-d PA and depth axis is 3-d PA. Groups are marked by lines.

Fig. 2 Dendrogram of sites (SSA algorithm). Transverse line has been arbitrary drawn.

Fig. 3 Ordination plot of sites in a CSTs space. al Horizontal is 1-st PA, vertical is the 2-d PA. bl Horizontal is 2-d PA and vertical is 3-d PA.

openings (Cyclgrae is an indicator species of these biotopes) to mediterranean thermophilous shrublands. The high loading of A.barbata has an obscured basis while the correlation of K.integrifolia can be explained by its preference to grow under J.phoenicea shrubs. Second PA clearly reflects covariations in opening occupators -P.fruticosa is a phryganic element and O.europea is correlated to this PA because of its second low growth form which is a less efficient competitor to grasses and forbs. This aspect of O. europea will be clarified in the sequel.

The ordination of sites within a CST space is necessary if we are along to avoid such spurious correlations that were induced by the Latin bionys. 22 CSTs were recognized by allocating the plants into the MGFS characters. In the scattergram (Fig. 3) the groups are broadly the same as in Fig. 1 with one exception (sites 4 and 5). However the positions of sites and group centroids are guite different. Total

trended variation is 62.13% and is accounted for by the first 3 PAs (Anderson's x² =4.01 at df=27). By comparing the two ordinations it is easily seen that there exist more trended variation, though it is distributed in three orthogonal PAs. Also all three PAs are readily interpreted in terms of CSTs internally and diversity measures externally (Table 3). The first PA clearly represents covariations in the high shrub layer and a contrast between this phase and the opening occupators (E.acanthothamnos and C.graecum). The CST knauintegroup comprises of plants favored by the microclimate beneath shrubs — they possess thin and large leaves with thin palisade layer. This may explain their high loadings on the first PA. The negative correlation of J.phoenicea with this PA is a result of the reciprocity of the distributions of the two CSTs in which the plant was splitted. The second PA reflects variations in the herb layer. G.europea and G.coccifera are shrubs obviously associated with some herbs while P.terebinthus being a deciduous shrub, prevents the growth of the herb layers underneath as a result of the timing of the leaves shedding (Petrakis, 1984). The same holds for G.coccifera. An pavonina occupies usually small openings. The third PA is a contrast between G.coccifera and A.pavonina, a situation taking place from January to March. Fourth PA can be summarized under the label 'axis of S.denticulata'. This pteridophyte prevents soil from drought until May (Petrakis's, phenological observation). P.lentiscus is positively correlated to this PA as a result of its spatial cooccurrence with S.denticulata. Fifth PA can be labeled 'O.europea low trees and underneath herbs'. It is the macrophyllous form of this plant that allows sunlight to pass through its foliage in the winter and favors thus the growth of Knauintegroup CST. This effect was lost in the previous ordination.

Niche breadth: The meanings assigned to each vegetation PA, allowed for a consideration of these components as resource components (RC) and the estimation of Auchenorrhyncha species niche parameters. Possible values for B are 1.08 (for species occurring in only one plot, but not exclusively) to 5.00 (for species

recurring in all plots, but not exclusively). In Fig.4 can be visualized the temporal pattern of Bs. Because Resource axes (RA) are orthogonal the volumes of these 'boxes' are serving as estimates of Bs (Pianka,1975).

Several types of B can be recognized in Fig. 4 and one case is worth mentioned. While insects occurring in only one site have always B 1.00 the opposite is not always true. Absent species have 6 B. Ecological specialists and generalists can be diagnosed from this diagrams of Bs and these terms can be extended to include a temporal component. Generalists are expected to have a cubic niche space -e.g. 9.basininger in summer—while ecological specialists have niche dimensions elongated on one at least RA -e.g. P.spumarious in all seasons. The most striking case is B.maculipes. In spring it fed on 0.coccifera and 0.europea and other shrubs as well but few individuals were also accidentally found on nearby herbs. However in summer it abandoned 9.coccifera and migrated to other shrubs and herbs as well. D.maculipes had expanded its overall B in summer by restricting specialization that means, by restricting its B on 9.coccifera axis and dilated its B on the other 2 RAs. We accept this criticise that the same movements of niche dimensions on RAs may be artifacts of our procedure. In our procedure we have not weighted intervals by a resource utilization coefficient (Colvell & Futuyma, 1971), though we have included insect oriented biotope descriptive parameters (CSTs). For this reason an accidental finding of an insect normally foraging on shrub foliage, in herb layer, is equally weighted for the estimation of its B to an occurrence of this on a shrub for feeding or oviposition. Also a source of error is the host switches in the life stages of an insect. Insects D.maculipes and 0.basiniger are examples of such switches. Another type of error is the occurrence of an insect in a biotope because it prefers microclimatic conditions together with its feeding plant. M.macisumuri and P.spumarious exhibit such a behavior. While they are normal grass-forb feeders, they prefer to feed on plants growing underneath or nearby tall shrubs. Some individuals of these insects have been collected from the upper parts of shrubs while thei

Table 11. List of insect and plant species and codes discussed in this paper.+

Insects
1 Asicla Asiraca clavicornis (Fabr.) 5 Dicsp. Dictyophara sp. 9 Melmat Melillaia matsumuri (Metc.)
2 Balclu Balclutha saltuella (Kirsch.) 6 Empdec 7 Eupael Eupteryx melissae (Curt.) 11 Opssp. Opsius sp.
4 Dalmac Dalmatrium maculipes (Dlab.) 8 Harins Hardyopsis insularis (Rib)12 Penlep Pentastiridius leporinus (L.)
13 Phispu Philaenus spumarius (L.)

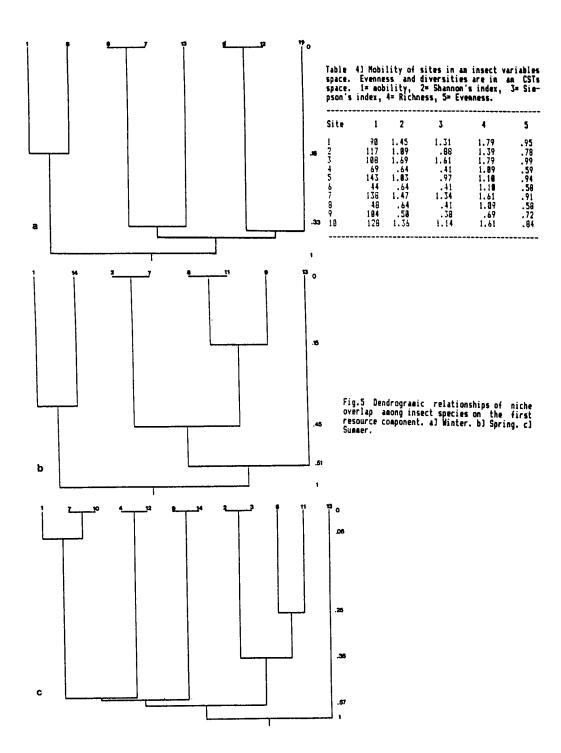
Plants
Junitarus phosnicea * Olea europea # Fistacia lentiscus # Pistacia terebinthus # Phlomis fruticosa
Guercus coccifera * Prunus webbii # Euphorbia acanthothamnos # Urginea maritiea * Eyrlamen graecum
Avena barbata # Knautia integrifolia # Crepis dioscoridis # Thapsia garganica # Anemonina pavonina
Seisginella denticulata # Crocus leevigatus * Ceterach officinarus # Asparagus aphyllus # Pimpinella cretica
Dactylis gloperata # Eynosunus echinatus # Trifolium stellatum # Smilam aspera # Clematis cirrhosa
Nigella damascena * Bromus hordeaceus # Lagurus ovatus # Prasium majus # Scandim pecten veneris

+ plant spacees codes are the first 4 letters of the genus and the species name.

to the other RAs can be explained by the diversity of CSTs highly loaded on these RAs. In general the trend of all insects to show reduced Bs on the second RA, can be explained clearly by the lower diversity of CSTs within the grass-forb layers. We have not yet found a sampling design to cope with these difficulties and may be it is impossible in monitoring studies, where the impact on the biotope must be minimal. We conclude from the B pattern that temporal niche allocation may be an important mechanism in reducing interspecific competition in these ecosystems and this is reflected even in seasons with severe environmental stress—winter and summer.

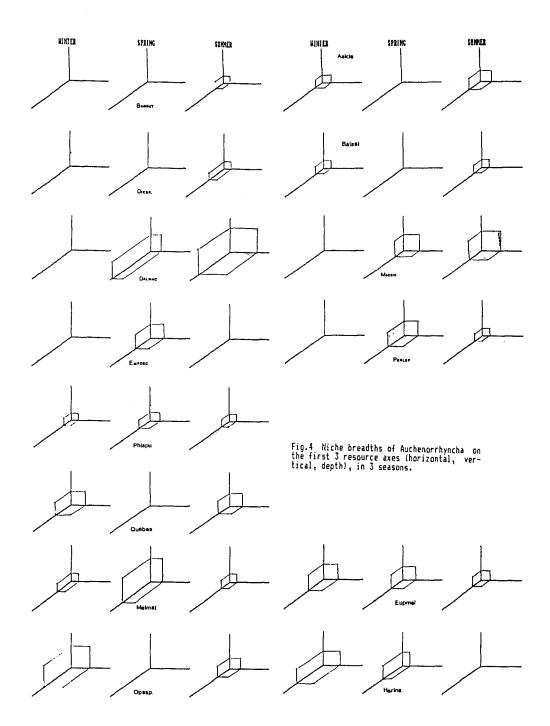
Hiche overlaps: We used niche overlap (0) as a measure of the degree of cooccurrence of insect species in the 5 intervals on the RAs. In Fig.5 the dendrograms of the Os relationships on the first RA are graphically summarized. At .5 0 the recognized groups are 3 in winter, 3 in spring and 5 in summer.

It can be shown that P.spumarious is not related with any other species while M.matsumuri is grouped with different species in each season. In the winter it is more related to H.insularis and Opsius sp. while in the summer it is grouped with O.basiniger. In spring it is related to P.leporinus. The degree in which these relationships include spatial cooccurrence was tested by correlating the overlap matrix to the initial matrix of occurrences. This yielded non significant correlations (r=.18).



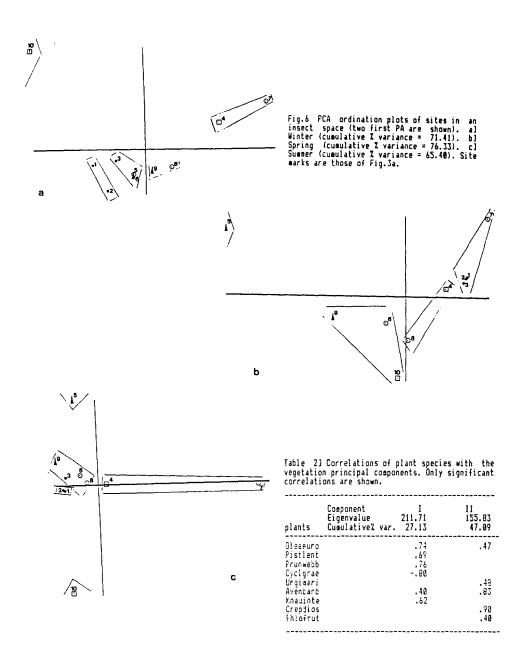
The O relationships we have found, support the first part of Pianka's (1974,1975) prediction that Os should very inversely with respect to diversity while they are contrary to the second part of the prediction, that Os remain more or less unchanged (Fig.4). In the summer when species diversity is high the O is reduced, as can be seen in Fig.5, while in the winter, when species diversity is low O is high.

Another prediction of current niche theory (Cody, 1975) that our findings do not support is the 'compensation hypothesis'. According to this hypothesis, high 0 between two species in one RA is compensated by reduced 0 on the second RA. We observed all the alternatives. For example, Opsius sp. and E.melissae overlap was .82 on the first RA in winter and .94 on the second while on the third axis was 8.88 -dendrograms on the overlaps on subsequent RAs beyond the first are not shown. This departure from traditional niche theory prediction seems to be a result of our different scale of approach to community



analysis. As Rotenberry and Hiens (1980) have pointed out 'most of the evidence offered to support those arguments came from comparative biogeographic studies' thus being inappropriate to analyze interactions between populations and individuals.

Mobility of sites: In Fig.6 it can be visualized the positions of ten sites in an insect abundance space. AII ordinations have efficiently concentrated the trended variation in two axes and this variation was surprisingly high (71.41%, 76.33% and 65.40%). In Table 4 are depicted the mobilities of the sites, their ranks and three aspects of the diversity (Pielou,1977), dominance or concentration was measured by Simpson's index, uncertainty was measured by Shannon-Weaver index and richness was measured as the logarithm of existing CSTs.



Although site groups, forced by ordinating sites in a CST space, are different than those presented in Fig. 6, the ordinations between seasons flow anoticeable similarity, in clustering sites. Summer and spring aspects of this insect community, are more similar than the winter aspect. Three sites (5,7 and 10) are located consistently at the pargins of the bidinensional space and these sites are the first three most mobile. It seems probable that the locations of these sites have caused the compression of the others around the origin at least in one axis. We accept this, since we intend to obtain an overall picture of the Auchenorrhyncha community. For all sites we calculated the Spearman's rank correlation coefficient to test the null hypothesis that site mobility is independent of site diversity and evenness. The test indicated that at all probability levels, there is an almost complete concordance between mobilities from one side and diversities and evennesses from the other, that is, the most diverse sites were preferred in various seasons by different Auchenorrhyncha species and abundances, in a strict accordance to their diversities in growth forms ($r_{1/2} = .918$; $r_{1/2} = .919$ and $r_{1/2} = .960$ all significant at P=.81). We tried also the same analysis with the site diversity measured in a plant species space. Although richness and evenness were significantly correlated to mobility - $r_{1/2} = .978$, P=.10; $r_{1/2} = .723$, P=.05 - their values are quite low to support any other discussion. In addition Shannon's and Simpson's diversities, were not significantly correlated to mobilities.

These results provide a clear answer to the question left open by Murdoch et al. (1972). Indeed the important relation is between plant structural diversities and insects and not between plant species diversities and insects. Since mobility is an appropriate estimate of site instability (though short termed), we can infer that not only the most diverse sites are not the most stable but the opposite is clearly true. Certainly this does not contradict the generalization drawn from a plenty of communities studied when they were in equilibrium. Nevertheless, we believe that between consecutive years variation must be studied in the context of this methodology in order this prediction to be testified.

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