

Empirical guild analysis of forest litter linyphiids

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Recent work suggests that guild structure could be adequately represented as an inverse linear relationship between the habitat specialization of each species of the guild and the variability in its habitat choice. The microhabitat preferences of the main species of forest litter linyphiids found at one 4-ha deciduous forest site show such a linear relationship. Thus, immature linyphiids (a composite group) and *Lepthyphantes* sp. (mainly *Lepthyphantes flavipes*) seemed to be generalists, *Microneta viaria* a specialist and *Centromerus serratus*, *C. aequalis* and *C. dilutus* to be in intermediate positions.

1. Introduction

In this paper, we look for occurrence of sheet-web spider species in quadrat samples from a deciduous forest litter. Each sampling field location is described by an array of presumed microhabitat variables and by an array of species occurrences. Microhabitat variables are transformed by principal component analysis into a small number of factors: thus each location is associated with a point in the factor (habitat) space. Points near the space origin represent common microhabitats; points farther away from the origin represent uncommon microhabitats. The null hypothesis is that sheet-web spider species are distributed randomly in this habitat space. We tested this hypothesis by applying the empirical method of Mac Nally & Doolan (1986). The alternative hypothe-

sis then becomes that the size of the factor space region occupied by a species (species microhabitat breadth) will linearly decrease with the species mean distance from the origin of factor space (species microhabitat position). In other words, the litter sheet-web spider guild under study would be a mixture of generalist and specialist species similar to those found by Post & Riechert (1977) but structured by some process to be discussed later.

2. Methods

The study was undertaken at the Station Biologique de Foljuif, 80 km south of Paris, France, in a 4-ha mixed forest plot. Dominant species are oak (*Quercus sessiflora*), hornbeam (*Carpinus bet-*

ulus) and pine (*Pinus sylvestris*). Details on climate, vegetation structure and litter can be found in Blandin et al. (1980).

We have used the method proposed by Mac Nally & Doolan (1986) but restricted it to analyses of microhabitats within a single macrohabitat; thus, sheet-web spider species may occur in the different litter microhabitats of the experimental plot. These microhabitats are assumed to be correctly described by some subset of an array of variables (Table 1) related to vegetation structure (Stevenson & Dindal 1982, Bultman & Uetz 1982, Hatley & MacMahon 1980, Robinson 1981) and litter abundance and structure (Duffey 1975). Subset selection (see results) is independent of species occurrence. 72 sampling field locations were randomly located over the study area. At each location, microhabitat variables were evaluated and a 1/16 m² litter sample collected and put in extraction (March 17–18, 1987). Spider identification was made at the species level for all adults. Immature *Lepthyphantes* (probably a majority of *L. flavipes*) were pooled. Other immature linyphiids (probably a majority of *Macrargus rufus*) were put in a single group.

Statistical analysis was initiated with the completion of a principal component analysis (Norusis 1986) of microhabitat variables. The next step was the calculation of factor scores for each sampling field location. Microhabitat mean position and breadth of each spider species were then calculated using the mean and variance of factor scores of the sampling points where the species occur. For details of statistical analysis and neutral model procedure, refer to Mac Nally & Doolan (1986).

3. Results

A first principal component analysis revealed that high partial correlations, varying between 0.6 and 0.8, exist between homologous variables estimated at different scales (Table 1) while these are assumed to be uncorrelated in the principal component model (Norusis 1986). We retained only the small scale (1/16 m²) member of the partially correlated variable pairs. Other variables, TRUNK, WSPRIG, WLITTER, WDEBRIS, BRANCH16, COVER and TREE were dropped because they had insuffi-

cient sampling adequacy (below 0.6, see Norusis 1986). By dropping these variables, one can produce a habitat description which conforms to the mathematical model. The second model includes just five variables (LITTER16, SHOOT16, LEAF16, SPRIG16 and MOSS). Though the two models give similar results, we present only the second more parsimonious model.

The first two principal components (axis) explain about 72% of the total variance and are readily interpreted in terms of the five initial variables (Fig. 1). The first axis (50% of the variance) is a function of litter abundance and, to a lesser degree, sprig abundance. At the places where the litter is shallow, moss becomes important. The second axis (22% of the variance) is a function of leaf and shoot abundance. Each field sampling location can be mapped in this factor space by linear transformation of the initial 5 microhabitat variables into factor scores (coordinates in factor space).

Table 1. Microhabitat variables. Most variables (LITTER1 to COVER) were evaluated by 1–5 (rare-abundant) abundance classes. SHOOT1 to LEAF16 refer to live undergrowth (mainly ivy). SPRIG (diameter less than 5 mm) and BRANCH (diameter 5 mm and more) refer to dead wood found in litter. TRUNK and TREE are evaluated in meters. WSPRIG, WLITTER and WDEBRIS are weights in grams of extracted dried material. WLITTER and WDEBRIS are separated by a 1 cm sieve.

Variable	Description	scale (m ²)
LITTER1	litter abundance	1
LITTER16	litter abundance	1/16
SHOOT1	number of shoots	1
SHOOT16	number of shoots	1/16
LEAF1	number of leaves	1
LEAF16	number of leaves	1/16
SPRIG1	sprig abundance	1
SPRIG16	sprig abundance	1/16
BRANCH1	branch abundance	1
BRANCH16	branch abundance	1/16
MOSS	moss abundance	1
COVER	tree abundance	16
TRUNK	distance to nearest dead trunk	16
TREE	distance to nearest tree	16
WSPRIG	weight of extracted sprig	1/16
WLITTER	weight of extracted litter	1/16
WDEBRIS	weight of extracted debris	1/16

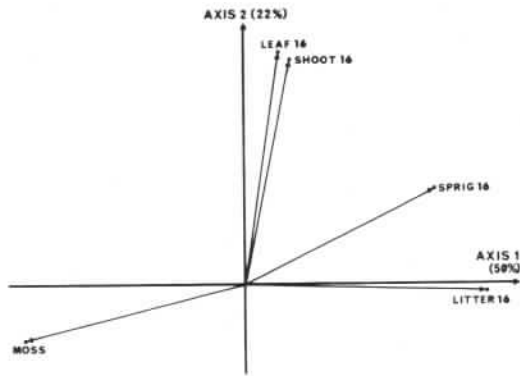


Fig. 1. Projection of the five microhabitat variables (model 2) in the principal component space (first two axes, with percentage of variance explained). Variables are described in Table 1.

The four main species of adult spiders were *Centromerus serratus* (mean and variance for 1/16 m²: 0.6, 0.8), *C. aequalis* (0.5, 0.9), *C. dilutus* (0.3, 0.3) and *Microneta viaria* (0.3, 0.3). Two immature groups were added: *Lepthyphantes sp.* (0.6, 0.6) and other immature linyphiids (1.0, 1.8). Immature linyphiids and *Lepthyphantes sp.* seemed to be generalists, *Microneta viaria* a specialist and *Centromerus serratus*, *C. aequalis* and *C. dilutus* to be in intermediate positions (Fig. 1). Each of these categories occurs in a particular subset of the 72 sampling locations which can be mapped in the factor space, allowing calculation of mean and variance (breadth).

There is an inverse linear relationship between breadth and mean position of the six main categories of spiders (Fig. 2). A regression analysis gives:

$$\text{breadth} = 0.86 - 0.28 \times \text{position.}$$

with $r = -0.92$. The regression coefficient, -0.28 , is significantly different from zero ($P < 0.05$). It has been argued that such a relationship is a mathematical artifact of principal component analysis (see Mac Nally & Doolan 1986 for a discussion). To test this possibility, we made a neutral model analysis by randomly reshuffling species occurrences over sampling points, creating a random subset of field sampling locations

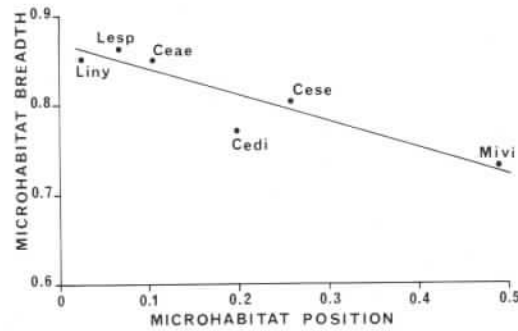


Fig. 2. Microhabitat breadth as a function of microhabitat position of the six main categories of spiders found during spring at Foljuif. Mivi = *Microneta viaria* (adult), Cese = *Centromerus serratus* (adult), Ceae = *C. aequalis* (adult), Cedi = *C. dilutus* (adult), Lesp = *Lepthyphantes sp.* (immature), Liny = other Linyphiidae (immature).

for each species and destroying the presumed relation between microhabitat position and breadth. We have calculated the equation with these pseudodata 1000 times and never found a degree of linearity (pseudo $r = -0.03$; $SD = 0.46$) as high as in the real data relation so the latter can be considered to indicate a real guild pattern.

4. Discussion

We found that species do not occur randomly in the habitat factor space but follow the inverse linear relationship described in the alternative hypothesis. This is possible only if initial microhabitat variables used to build habitat space by principal component analysis are relevant to litter spider ecology. As we have selected variables related to vegetation and litter structure and abundance (see methods), our results are a confirmation of their importance in litter spider guilds.

The inverse linear relationship (Fig. 2) is possible if each species has an optimal microhabitat. If there is no optimal microhabitat, then the observed partitioning would be caused by inter-specific competition in which dominant species

displace others into the more variable marginal microhabitats, generating a positive rather than a negative relation between microhabitat breadth and position in the factor space.

Microhabitat specialization can enhance each species' fitness while avoiding interspecific competition (Rosenzweig 1981). It is predicted to occur, at fixed densities of competing species, when a species density is low enough to maintain a higher fitness in its preferred microhabitat. Field experiments indicate that litter spider densities are probably low relative to web site availability at the study site (in prep.). Rosenzweig's theory also predicts that specialization is a local phenomenon. Specialist spider species in a given habitat were found to be generalist in different nearby habitats (Post & Riechert 1977).

Non-competitive models of microhabitat specialization should also be considered because the role of interspecific competition is far from clear in spider communities (Wise 1984). Other information, to be analysed elsewhere, shows that the guild under study is probably not structured by competition. For instance, the three *Centromerus* species are hypothesized to be ecologically equivalent (Blandin 1986). Toft (1987) has found such equivalence between two species of *Linyphia*. As a non-competitive model, we suggest that the predation risk for spiders moving from one web site to another is greater than for spiders resting on a web. Such a process could favor site tenacity in optimal microhabitat and could possibly explain the observed partition.

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