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## TEMPORAL STABILITY OF COMMUNITY STRUCTURE OF THE PARASITIC HYMENOPTERA IN A BEECH FOREST ON LIMESTONE

**ABSTRACT:** The stability of the community structure of the parasitic Hymenoptera of a beech forest on limestone (northern FRG) was studied. The annual number of species was around 350 to 450 with a high degree of species turnover. In a comparison of the study years the species identity of the abundant species turned out to be low and their dominance rank order was highly variable. The yearly sequence of emergence appeared to be constant. Density fluctuations of the species were high and positively correlated with mean density and negatively with the weight of the species. No clear common temporal trends in density could be detected. Host guild, stratum of host attack or number of generations did not detectably influence the degree of density fluctuations of the species. The findings are discussed in the context of concepts of stability and classifications of communities and it is concluded that this hymenopteran community is best described as non-interactive and non-stable.

**KEY WORDS:** Hymenoptera, parasitoids, community, stability, beech forest, density fluctuation.

### 1. INTRODUCTION

Stability of communities has been defined in various ways and several definitions and measures have been proposed in the ecological literature (Holling 1973, Connell and Sousa 1983, Williamson 1987): Holling (1973) emphasized long term persistence (resilience) of a system in the presence of perturbations which may be measured by the probability of local extinction. Lawton (1984) focused on the predictability in species abundance and constancy in dominance rank order. The most often used concept of stability is that of Connell and Sousa (1983) who defined stability as the ability of a population

to return to a certain range of densities after disturbance.

The concept of stability can be linked with a classification of ecological communities. Lawton and Gaston (1989) classified communities into four basic models, depending upon the underlying population dynamics: their first type contains assemblages of species with unpredictable population dynamics, frequent local extinctions and immigrations, and little influence of density dependence. In the second type density dependent processes regulate component populations and the populations will have predictable relative popu-



lation sizes. Interspecific competition is scarce or absent. Delayed density dependence controls the populations of the third type. The populations have predictable relative population sizes and interspecific competition may occur during peak densities. Assemblages of the fourth type are governed by interspecific competition. They are saturated with species and have predictable structures.

Cornell and Lawton (1992) classified communities into two basic types defining the ends of a continuum: interactive and non-interactive. Interactive communities are characterized by strong interactions (interspecific competition), species saturation, and density dependence. Non-interactive communities, on the other hand, are not saturated with species. Interspecific competition is low and local colonizations and extinctions as well as population dynamics of the species are environmental driven processes and independent of the other species.

Non-interactive communities and type 1 communities can hardly be classified as stable. Their structure is by definition not predictable and random extinctions and immigrations contradict

the concept of resilience. Populations with environmentally driven (often random) density fluctuations may fulfill the stability criterion of being buffered against disturbances (returning to a certain range of densities) if there are certain outer limits outside which the species return and a band of 'normal' densities inside which no density regulation happens. The results of Ulrich (1999a) indicate that such a type of regulation may occur in the parasitic Hymenoptera. At the other extreme are interactive and type 4 communities which have to be, by definition, more or less stable under all of the above criteria.

The present study investigates the temporal variability of the parasitic Hymenoptera of a beech forest in northern Germany. In doing so it deals with species turnover, species composition, dominance rank order, seasonal entry into the community, and density fluctuations (density dependence could not be studied due to the too small number of sampling years). It then compares the findings with the above described concepts of stability and community classification and argues that this community is best classified as non-interactive and non-stable.

## 2. MATERIALS AND METHODS

### 2.1 STUDY SITE

The studies were undertaken between 1980 and 1987 at a chalk plateau in a mixed beech forest (420 m altitude, roughly 120 years old) on limestone near Göttingen (FRG). Eggert (1985), Schaefer (1990) and Ulrich (1988, 1998a) gave detailed descriptions of the study area. Dierschke and Song (1982) characterized the vegetation as a Melico-Fagetum subassociation *Lathyrus vernus*. The herbaceous flora mostly consists of

spring-geophytes that to a great extent disappear in the summer months. Most abundant are *Allium ursinum* and *Mercurialis perennis*.

Between 1981 and 1987 samplings were taken using ground-photo-electors. A detailed description of the sampling program is already given in Ulrich (1988, 1998a), Schaefer (1990) and Hövemeyer (1985, 1992). Each year between 5 (1985) and 24 electors of



0.25 m<sup>2</sup> (1984, 1985) or 1m<sup>2</sup> (other years) sampling area were used. The traps were checked weekly or every two weeks. To sample crown living species yellow traps

were installed on a 40 m high tower for ecological studies (at 10, 20, and 30m). The sorting of the species into ecological guilds is the same as in Ulrich (1998a).

## 2.2 STATISTICAL METHODS

To compare the annual numbers of species it is necessary to use extrapolations of the species numbers found in the yearly samples. There is a growing literature on this subject (Palmer 1990, 1991, Bunge and Fitzpatrick 1993, Solow 1994, Colwell and Coddington 1994, Tackaberry *et al.* 1997, Keating 1998, Ulrich 1999b) but up to now none of the various parametric and non-parametric tests had been fitted to larger natural animal assemblages.

Ulrich (1999b) compared various methods using large model assemblages. He found that a corrected second order jackknife estimator performed best if more than 67% of the total species number was already represented in the sample (estimate = real number  $\pm$  10%). Loglinear models also gave sufficiently good estimates (real number  $\pm$  20%) even if only 30% of the total species number was found. In the present study I use two corrected loglinear models and the second or-

der jackknife for estimating annual species numbers (S) of the beech forest:

$$\text{LOGLIN 1: } S = a (\ln(\text{area}))^b + c \quad (1)$$

and

$$S_{\text{real}} = 0.8 [S + S (0.5 (\log_2(\text{SD}) - 1)] \quad (2)$$

$$\text{LOGLIN 2: } S = a (\ln(\text{area}))^b \quad (3)$$

and

$$S_{\text{real}} = 0.8 [S + S (0.5 (\log_2(\text{SD}) - 1)] \quad (4)$$

a, b, c are the constants of the species accumulation curves, 'area' refers to total area for which S has to be computed. SD denotes the standard deviation of log<sub>2</sub> species densities. The formulas, the derivation of the correction factors and the performances are discussed in detail in Ulrich (1999b). In Table 1 the LOGLIN 1 estimator and the mean of LOGLIN 1 and 2 are used. As a bias correction for the second order jackknife the formula in

Table 1. Estimates of annual numbers of hymenopteran species in the beech forest 1981, 1982, 1983, and 1986

N: number of traps. The estimators LOGLIN 1 and 2 were computed using formulas (1) and (2) in the methods section. The jackknife estimator was corrected using formula (3). Because only 30 to 50% of the yearly species numbers were found the jackknife estimator is negatively biased and gives too low estimates (Ulrich 1999b)

| Year | N  | Total No. of species found | Mean No. of species found per m <sup>2</sup> | Corrected LOGLIN 1 | Mean of corrected LOGLIN 1, 2 | Corrected second order jackknife |
|------|----|----------------------------|--|--------------------|-------------------------------|----------------------------------|
| 1981 | 12 | 163                        | 34   | 436                | 348                           | 277                              |
| 1982 | 12 | 151                        | 36   | 347                | 303                           | 247                              |
| 1983 | 8  | 216                        | 55   | 355                | 296                           | 267                              |
| 1986 | 8  | 313                        | 76   | 637                | 509                           | 374                              |



Anderson and Burnham (1994) was included:

$$\text{Corr} = 2(K+1)(K+2)/(n-K-2) \quad (5)$$

with  $n$  the number of traps and  $K$  the number of free parameters. For the second order jackknife  $K$  becomes 3.

The most common estimate of variability (temporal or spatial) is the standard deviation (SD) of  $\ln$  (density) (Williamson 1984). Wolda (1983) and McArdle *et al.* (1990) found that this estimate (and also the transformation  $\text{SD } \ln(N+1)$ ) is strongly biased at low densities if many zero counts are included. To overcome this problem only those species were included when estimating temporal variability which were found at least in 6 of the 7 study years. One zero count is tolerable

and has, of course, also an ecological meaning.

The appearance of species in the community (its place in the sequence of emergences) was determined by the time of peak of emergence. Only those species were considered which were found in at least 6 of the sampling years and of which such a peak could be clearly recognized. This was the case in 39 of the 720 hymenopteran species. Of course, the control dates of the traps varied from year to year (the traps were checked once a week). Therefore, the exact dates of sampling were not used but it was determined whether the peak occurred in the first or in the second half of a month. These lumped data were taken to establish sequences of appearance.

### 3. RESULTS

#### 3.1. VARIABILITY IN SPECIES NUMBERS

Table 1 shows estimates of total species numbers of the beech forest for 1981, 1982, 1983 and 1986 (the sampling programs of the other study years do not allow reliable estimates to be made). Even if one takes the high variance of the estimators into account marked differences in species numbers between the years appear. 1983 was a species poor year with probably only 300 to 350 species. In 1981 and 1982 around 350 to 450 species occurred and in 1986 even more than 500. The mean annual species numbers were 350 to 450 species. These data suggest yearly fluctuations in species numbers up to 40%.

After 7 years of study 720 different species of Hymenoptera were actually found in the Göttingen beech forest (Ulrich 1998a). A method to assess the annual species turnover is to compute the minimum species number that would be

necessary to arrive at 720 species after 7 years given a certain degree of turnover. If  $S_0$  denotes the species number in the year  $t_0$ , the cumulative number of species in  $t_1$  is

$$S_1 = S_0 + xS_0 (S_{\text{regional}} - S_0)/S_{\text{regional}} \quad (6)$$

$(S_{\text{regional}} - S_0)/S_{\text{regional}}$  is the proportion of species of the regional species pool not present in  $t_0$  and  $x$  denotes the annual species turnover. The regional species pool comprises all the species which have the ability to colonize a certain habitat, in this case the beech forest under study.

After  $i$  generations the cumulative number of species is

$$S_i = S_{i-1} + xS_{i-1} (S_{\text{regional}} - S_{i-1}) / S_{\text{regional}} \quad (7)$$

In formula (7) it is implicitly assumed that each species of the pool has the same chance to immigrate. If the species which



had just become extinct have a greater chance to invade again a second correction term has to be introduced. This would reduce the number of new immigrants and therefore  $S_i$ . If the regional species pool is large in comparison to the local species number this latter term can be neglected and formula (7) can be solved. In the case of the Hymenoptera, however, the local species numbers reach high percentages of the species pool (between 10% and 20%: Ulrich 1998a) and the recursive formula (7) has to be computed numerically. In the case of the Hymenoptera of the Göttingen forest the regional species pool comprises up to 3200 species (as estimated from species accumulation curves; see Ulrich 1998a).

### 3.2. VARIABILITY IN SPECIES COMPOSITION OF THE MOST ABUNDANT SPECIES

Species turnover and density fluctuations result in a variation in species composition. How large is this variation in the most abundant species (that means the species which were sampled)? Fig. 1A shows the values of Jaccard's index of similarity (comparing all the years) for the top 10, 20, 30 and 50 ranking species (for all species the value would range between 0.85 and 0.9 when assuming 10% species turnover per year). The index-values are rather stable and range between 0.25 and 0.55. No decline in value could be detected when comparing more distant years (Fig. 1A and B). That means that only around 25% to 55% of the species abundant in one year are also abundant in another year. Only 20 of the 669 parasitoid species (3%) were found in all of the study years (Table 2; see also Ulrich 1998a). Interestingly, the mean degree of density fluctuation of these 20 species is not lower

With annual species numbers between 350 and 450 and using formula (7), annual species turnover rates between 10 and 15% result in 720 species after 7 years of study. For the more abundant species of the forest Ulrich (1998a) found turnover rates between 5 and 10%. The present result therefore indicates higher species turnover rates in the less abundant species.

During the study period there were great differences in species density (mean number of species  $m^{-2}$ ) (Table 1). In 1981 and 1982 only 34 to 38 species per  $m^2$  occurred. In 1986 the species density doubled to a value of 76 species  $m^{-2}$ . The mean species density was 50 species  $m^{-2}$ . Species density and total species numbers were not correlated.

but even slightly higher than the mean of all species (1.49 to 1.39).

Such comparisons have to be tested against null-models and randomization tests are required to evaluate whether observed differences are larger or smaller than expected just by chance (Phillippi *et al.* 1998). Ulrich (1999a) showed that the Hymenoptera of the beech forest can be described by a normal species – weight distribution with a mean of 8.5 (from 16 weight classes) and a variance of 0.52. The density – weight distribution of the species had a slope of  $-0.84$ . With these values null-model assemblages were constructed (669 species each) using the program 'community model' (a FORTRAN program that constructs model assemblages out of basic underlying species – weight distributions; for a detailed description of the program see Ulrich 1999b). Random density fluctuations of these model species resulted in mean similarity indices of



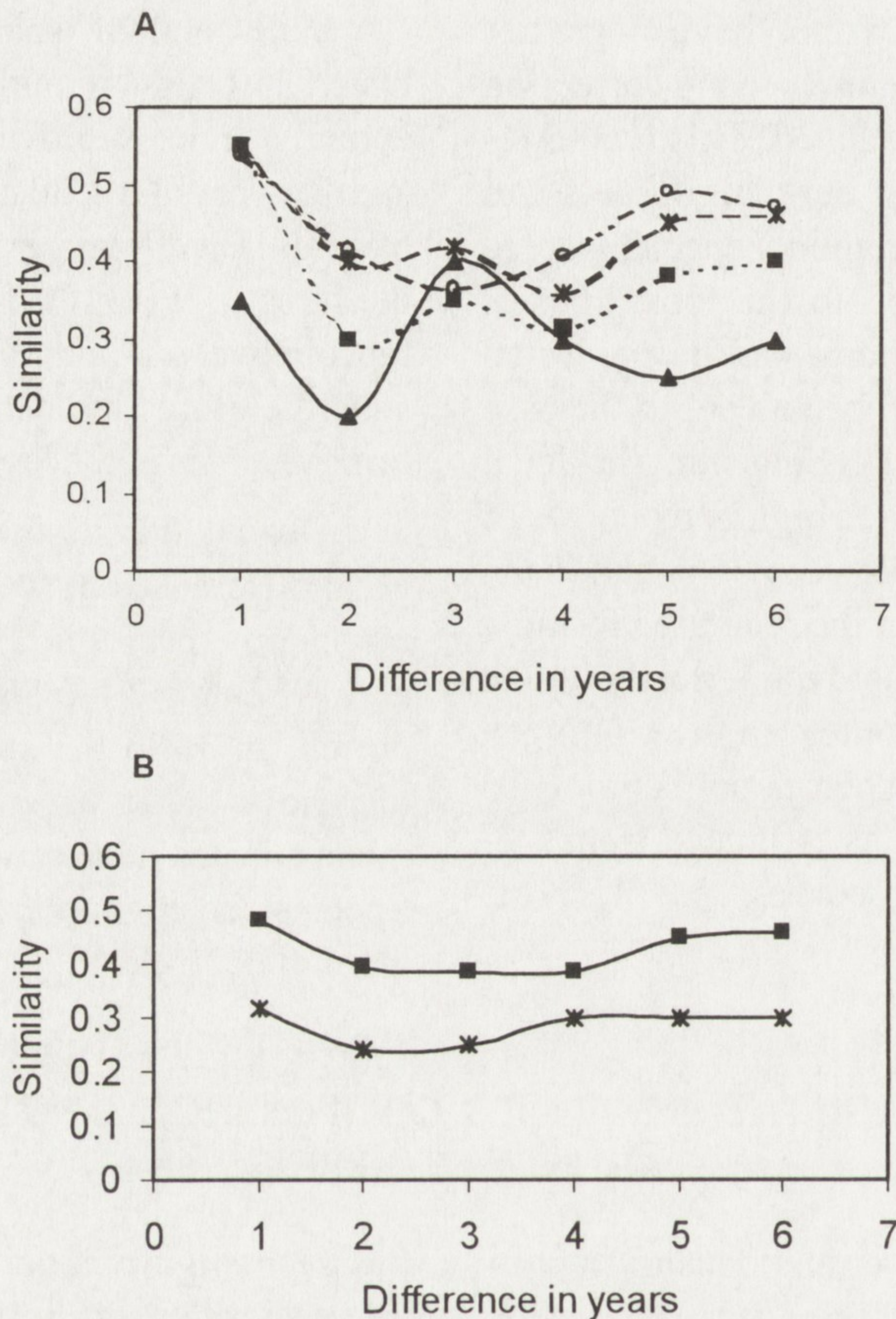


Fig. 1. Jaccard's index of species similarity of the Hymenoptera of the beech forest.

A: Temporal trend given as means of pairwise comparisons between 1981 and 1982 (1 year difference), '83 (2 years) ... '87 (6 years), and 1987 and 1986 (1 year), '85 (2 years) ... '81 (6 years). Such a forth and back computation reduces the variance of only one time series. ▲ – first 10 ranking species of each year. ■ – first 30 species. \*: first 50 species. ○: all species found per year.

B: Mean index values of all combinations of years: mean of 6 index value for 1 year difference up to only 1 value in the case of 6 years difference. \*: first 10 ranking species of each year. ■ – first 50 species.

0.27 (top 10 species; 10 replicates), 0.34 (top 30), 0.37 (top 50), and 0.46 (top 100). These model values are very similar to the observed ones [0.28 (top 10); 0.38 (top 30); 0.43 (top 50)]. Of course, the index values of the model assemblages are sensitive to the initial settings. However, it was interesting to see that the best fit to the observed values was obtained using the real parameter values of the Hymenoptera

which are given above. Different parameters (especially in the case of the slope of the density – weight distribution) resulted in lower or much higher values of Jaccard's similarity index than observed (data not shown). The above result, therefore, cannot rule out the possibility that the observed pattern in species similarity between the study years is simply the outcome of random density fluctuations of the species.



Table 2. Densities (ind. m<sup>-2</sup> yr<sup>-1</sup>) and density fluctuation (SD ln (densities)) of all hymenopteran species of the beech forest which had been found in all of the study years. GW and number refers to the species list in Ulrich (1998a)

| Species                         | Host guild  | Max. density | Min. density | SD   |
|---------------------------------|-------------|--------------|--------------|------|
| <i>Aclastus micator</i>         | Eggs        | 2            | < 1          | 0.88 |
| <i>Anacharis eucharoides</i>    | Predators   | 4            | < 1          | 1.37 |
| <i>Anaphes dorcas</i>           | Eggs        | 10           | < 1          | 1.89 |
| <i>Aphelopus melaleucus</i>     | Sap-suckers | 15           | 1            | 1.46 |
| <i>Aphelopus serratus</i>       | Sap-suckers | 2            | 1            | 1    |
| <i>Aspilota</i> GW"2"           | Saprophages | 27           | 1            | 1.64 |
| <i>Aspilota</i> GW23            | Saprophages | 7            | < 1          | 0.36 |
| <i>Aspilota</i> GW5             | Saprophages | 14           | < 1          | 2.14 |
| <i>Eustochus atripennis</i>     | Eggs        | 36           | 1            | 1.71 |
| <i>Basalys abrupta</i>          | Saprophages | 2            | < 1          | 0.89 |
| <i>Basalys pedisequa</i>        | Saprophages | 38           | 1            | 2.09 |
| <i>Ceraphron</i> GW2            | ?           | 1            | < 1          | 0.93 |
| <i>Chrysocharis prodice</i>     | Miners      | 9            | 1            | 1.17 |
| <i>Cleruchus</i> GW1            | Eggs        | 50           | 1            | 2.16 |
| <i>Gastrancistrus walkeri</i>   | Gall-makers | 39           | 1            | 1.34 |
| <i>Platygaster</i> GW2          | Gall-makers | 19           | 1            | 1.39 |
| <i>Stilpnus</i> GW1             | Saprophages | 2            | < 1          | 0.82 |
| <i>Tetrastichus brachycerus</i> | Gall-makers | 83           | 1            | 1.51 |
| <i>Tetrastichus</i> GW1         | ?           | 8            | < 1          | 2.19 |
| <i>Tetrastichus luteus</i>      | Gall-makers | 19           | 1            | 2.04 |

### 3.3. VARIABILITY IN DENSITY RANK ORDER OF THE SPECIES

Figure 2 shows that the rank order of species densities (all species with more than 1 ind. m<sup>-2</sup> yr<sup>-1</sup>) changed remarkably from year to year. In the mean, Spearman's rank correlation coefficient was only 0.26 (ranging from 0.09 to 0.61 when computed separately for all guilds) and only 6 out of a total of 21 correlations were statistically significant at the 5%-level. There was a slight – but statistically not significant – trend to a lower correlation coefficient when comparing more distant years. These low correlations show the

high degree of annual variability in dominance order.

Again one has to compare this result with the one expected from the null-model assemblages described above. Using the top 50 species (a similar number to the one in Fig. 2) Spearman's rank correlation gave a mean value of 0.2 (ranging from 0 to 0.56) and 2 out of 21 correlations were significant ( $P < 0.05$ ). Again, the result of the null model is similar to the observed pattern and random density fluctuations may cause this pattern.



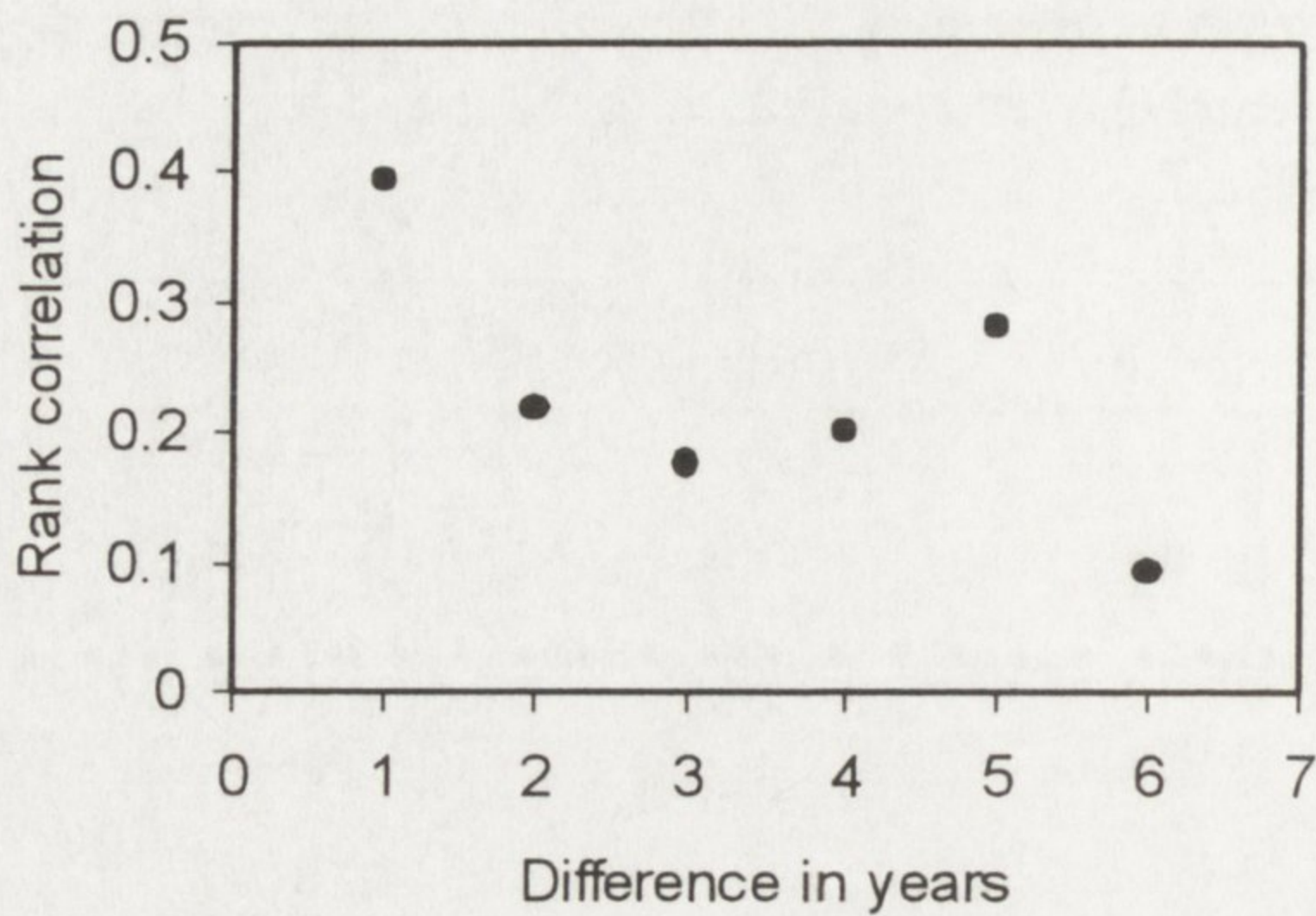


Fig. 2. Spearman's rank correlation between the yearly dominance rank orders of all species with more than 1 ind.  $m^{-2} yr^{-1}$ . As in Fig. 1B the plot gives mean values of all combinations of years.

### 3.4. ANNUAL CHANGES OF APPEARANCE

Lawton and Gaston (1989) focused on another aspect of temporal predictability, the sequence of emergence. A community may be called temporarily stable if the yearly appearance (the time of emergence) has the same sequence. Figure 3 analyzes the parasitoids of the beech forest in this respect. The sequence of entry into the community proved to be highly predictable: Spearman's rank correlation gave in all of the cases values above 0.87.

However, as in the case of the species rank order, the coefficients were highest if adjacent years were compared. The larger the distance between the compared years, the lower the correlations were (Fig. 3). Although the community appears to be stable when looking only at the correlation coefficients, such a trend indicates again long term changes in community structure: in this case at a phenological level.

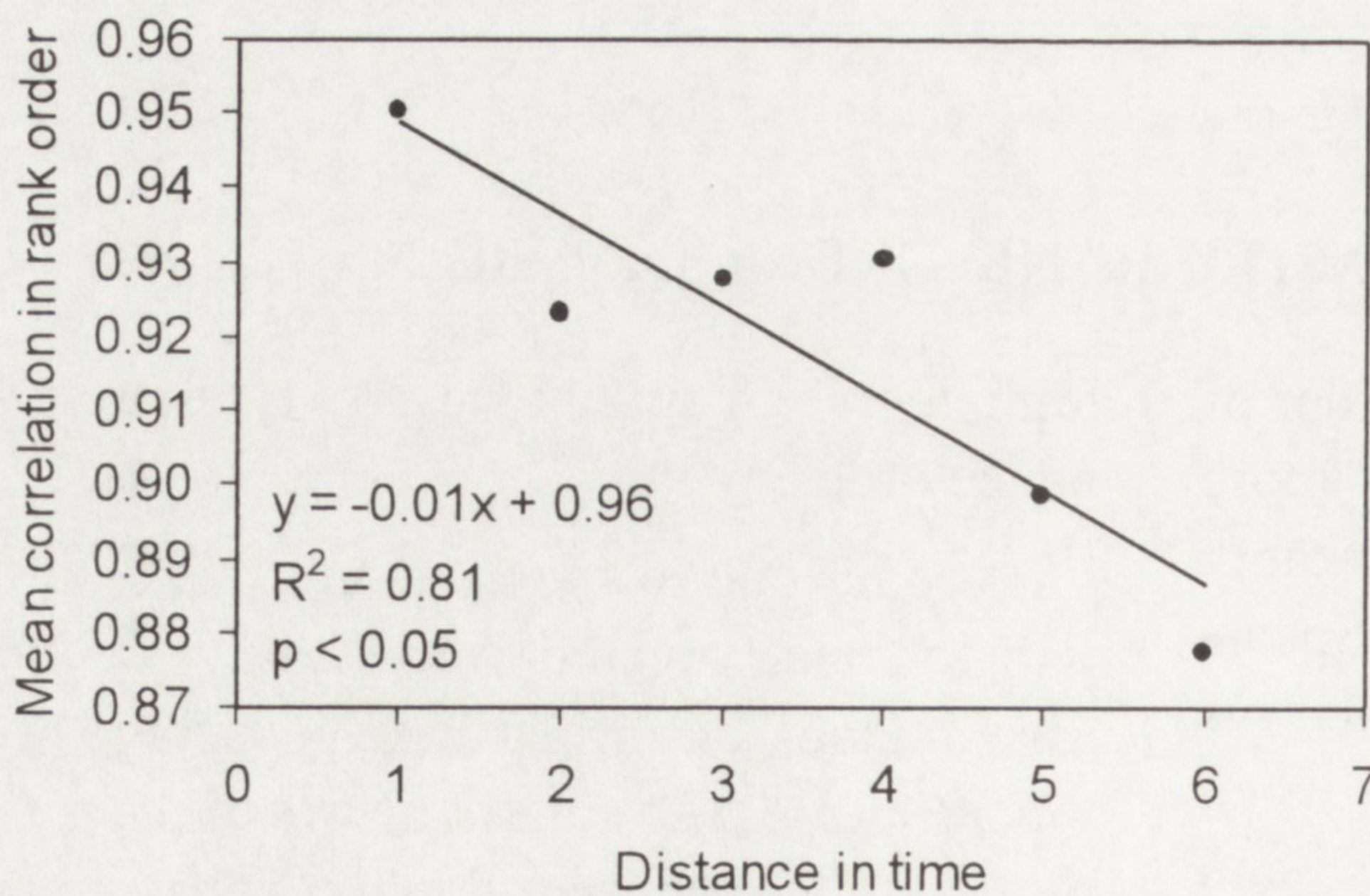


Fig. 3. Yearly entry sequence (sequence of emergence) into the parasitoid community of the Hymenoptera of the beech forest (first generation only). Data from 39 species which were found in at least 6 of the study years and which showed clear peaks in emergence. As in Fig. 2 the plot gives all combinations of Spearman's rank correlations between the study years.  $R^2$ : variance explanation, distance in time: years.

### 3.5. DENSITY FLUCTUATIONS

The density fluctuations of each of the abundant hymenopteran species of the

Göttingen forest is already given in Ulrich (1998b).



The temporal variability of the species is positively correlated with the mean density of the species (Fig. 4). Species with higher mean densities tended to have lower density fluctuations. This is of course expected if one assumes that Taylor's power law (the correlation between mean and variance in spatial distribution) also holds for temporal variations. On the other hand, the temporal fluctuations of the species were negatively correlated with weight. The larger the species the more stable were the populations (Ulrich 1999c; Fig. 4).

Table 3 tests whether the density fluctuations can be related to ecological factors. An ANCOVA detected no differences in fluctuations between host guilds, taxa, strata, type of hibernation and number of generations. Only the parasitoid type may have a small influence. Idio-biontic species (mostly egg- and pupal-parasitoids) fluctuated to a slightly larger extent than koinobiontic (mostly larval endoparasitoids) species. Thus, species of all ecological types may have larger density fluctuations.

Do the parasitoid species fluctuate independent of one another or were there common trends in density? To answer this question I compared the densities of the

most common species (37 species of which the first generation had been found in at least 6 of the 7 study years) in each of the study years. The densities of each species (first generation only) were ranked and the mean rank of all species combined was plotted against the year (Fig. 5). The Figure shows that in the parasitoids of gall-makers and the species which appear late in the summer (September to beginning of October) the plot indeed hints to a common trend in density fluctuation. The results of an ANOVA showed in both cases significant deviations from the mean. In all other species no such deviation could be detected.

In the case of the parasitoids of gall-makers this trend is made by 4 parasitoids of *Contarinia fagi* which had extraordinary high and parallel density fluctuations (Ulrich 1987). The detected trend may therefore be caused by density fluctuations of the common host. The parasitoids which emerged in late summer (*Gastrancistrus autumnalis*, *Eumacepolus grahami*, *Omphale aetius*, *Tetrastichus fagei*, *T. luteus*, *Tetrastichus* sp., *Stilpnus* sp., *Trioxis bicuspis*, *Acoelius erythronotus*) showed a rise in density from 1982 to 1986. Because the first 5 species again are parasitoids of gall-makers and probably all associated with beech leaves again the

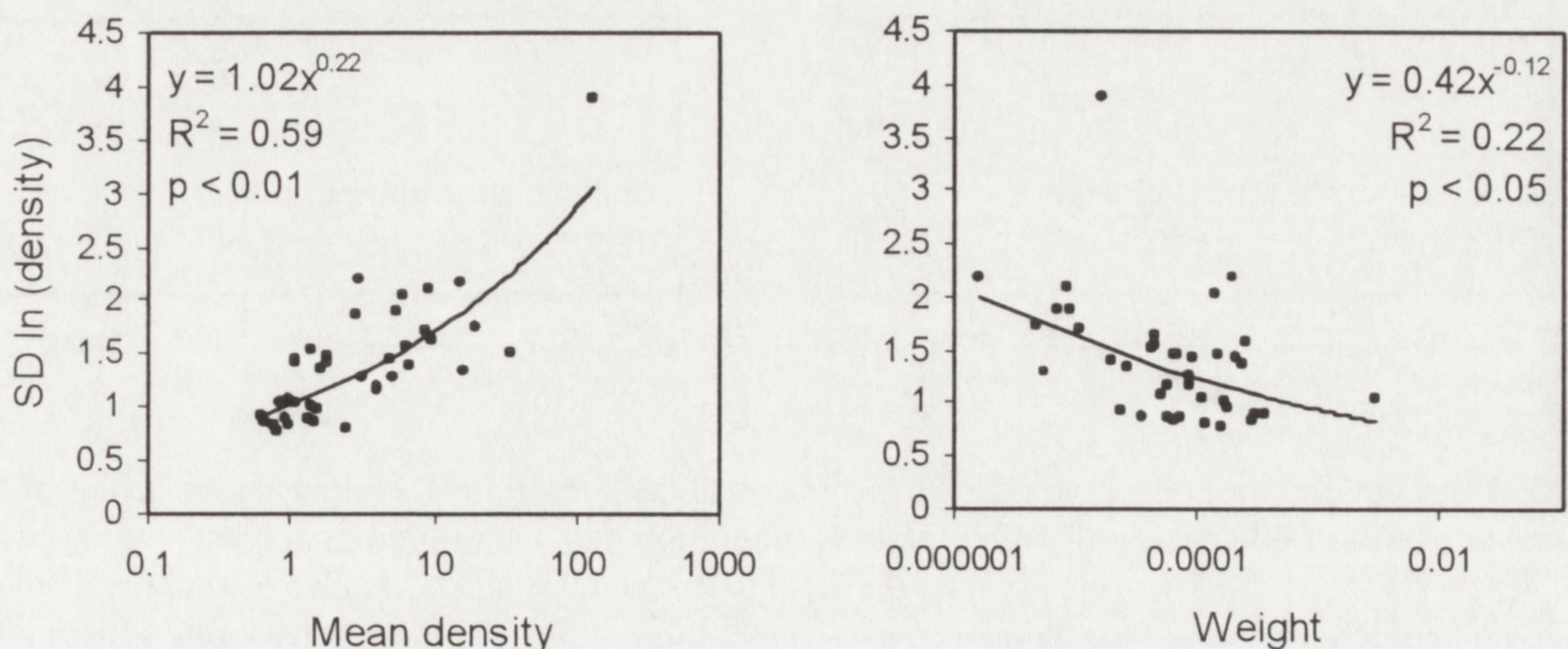


Fig. 4. Density fluctuations of the Hymenoptera of the beech forest (SD ln(density)) plotted against their mean density (ind. m<sup>-2</sup>) and their mean weight (g). Included are all species which had been found in at least six of the seven study years (total of 39 species)



Table 3. Dependence of density fluctuations [SD ln(density)] of parasitic Hymenoptera on various ecological factors. Analysis of covariance with mean density as covariate. Species as in Fig. 4. On the right side are given the SD's for the two parasitoid types (koinobiontic and idiobiontic) for which the ANCOVA gave a significant difference

| Factor                | <i>F</i>         | <i>P</i> |   |
|-----------------------|------------------|----------|---|
| Host guild            | $F(27;7) = 0.55$ | 0.79     | <b>Idiobiontic species</b><br>SD ln(density) $1.52 \pm 0.48$  |
| Host taxon            | $F(25;8) = 0.38$ | 0.92     |   |
| Stratum               | $F(30;3) = 0.61$ | 0.61     | <b>Koinobiontic species</b><br>SD ln(density) $1.30 \pm 0.42$ |
| Type of hibernation   | $F(37;1) = 0.21$ | 0.65     |   |
| Number of generations | $F(30;1) = 0.08$ | 0.77     |   |
| Parasitoid type       | $F(34;1) = 4.75$ | 0.04     |   |

density fluctuation of their hosts may have been responsible for the common trend in density.

Another method to reveal common trends in density is to correlate the densities of all species. A preponderance of

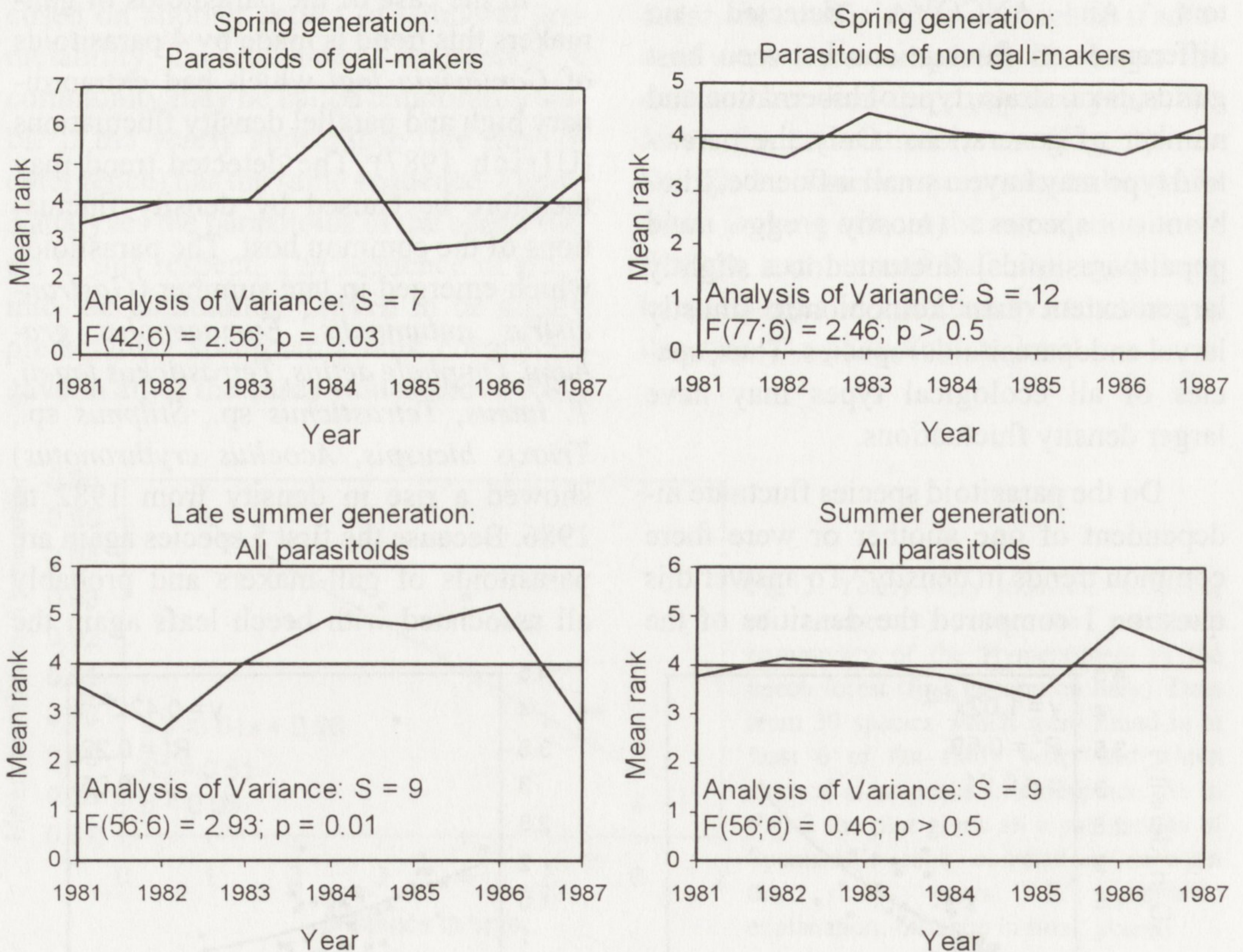


Fig. 5. Trends in densities of the parasitic Hymenoptera of the beech forest. Plotted are the means of the ranked densities of 37 species of which the first generation had been found in at least 6 study years (because in 1984 and 1985 for some species the second generation was not sampled quantitatively these data were omitted). Given are the data for species emerging in spring (April to June: spring generation), late summer (September, early October: late summer generation), and summer (August: summer generation). The results of an ANOVA are given to show whether the yearly mean ranks deviate more from the mean than expected by chance



positive correlations would indicate a common trend. Such a computation with the same data set as in Fig. 5 and the same seasonal differentiation gave a total of 79 positive and 80 negative correlations. This result does not point to common trends in

densities of the parasitoid species. An exception were again the species which appeared late in the summer: 24 of the pairwise correlations between these species were positive, 12 negative.

#### 4. DISCUSSION

The results presented in this paper are largely negative. The parasitoid species were characterized by a fairly high species turnover, low species identity when comparing different years, unpredictable dominance rank orders and detrended density fluctuations. I could not identify regular patterns in species identity, dominance rank order and density fluctuations. The results are consistent with the hypothesis that the densities of species fluctuated independently and at random. Only the seasonal entry into the community (the sequence of emergence) was constant.

The only other study in which total annual numbers of hymenopteran species were estimated is the work of Hilpert (1989) who estimated 366 species per year in a mixed oak forest near Freiburg (FRG) a value which is in good agreement with the present estimate.

Hilpert (1989) also estimated turnover rates. His estimates (between 10 and 15% for the Hymenoptera of the oak forest he studied) are in line with the estimates presented here. In a study on carabid beetles, Den Boer (1985) reported turnover rates of up to 8% year<sup>-1</sup> in an old forest habitat and mean survival rates of a species of 10 to 40 years. Dempster *et al.* (1995) reported immigration rates between 9 and 14% per year at patches of flowerheads.

The species densities reported here are higher than in other species rich taxa of the same forest. Hövemeyer (1992) re-

ported for the Diptera species densities of 30 (1981) to 60 (1987) species m<sup>-2</sup>. Winter (1985) found 53 species of Lepidoptera pointing to species densities of less than 30 species m<sup>-2</sup>. The data in Stippich (1986) and Schaefer (1991) also indicate less than 30 species m<sup>-2</sup> for the Araneae and Coleoptera. However, the species densities of the Hymenoptera of the beech forest are even low when compared to an open landsite habitat. At the dry meadow Drakenberg 191 hymenopteran species m<sup>-2</sup> were found (Ulrich 1999d).

Testing for species saturation requires sufficiently complete data sets (Cornell and Lawton 1992) and the sampling methods used for this study do not allow definite answers to be given. However, judged from the high amount of species turnover and especially from the annual differences in species numbers it seems not very probable that the hymenopteran community of the Göttingen beech forest is saturated in species. This conclusion is in line with various studies which failed to detect saturation (Lawton 1984, Cornell 1985, Hawkins and Compton 1992, Hugueny *et al.* 1997). However, non-saturation is much easier to detect than saturation (Cornell and Lawton 1992) and the prevalence of failures to detect saturation may just be an outcome of these difficulties.

The findings about dominance rank orders contrast with various studies on herbivorous insect communities. Law-



ton (1984), Joern and Pruess (1986), Evans (1988), Lawton and Gaston (1989), Owen and Gilbert (1989), Root and Cappuccino (1992) reported remarkable predictability and constancy in dominance rank order. Data on parasitic Hymenoptera however are missing.

From the above results it is concluded that the parasitic Hymenoptera of the Göttingen beech forest are characterized by a highly unpredictable community structure. Due to the low number of study years the existence of density dependent regulation could not be studied in detail but from the available data density dependence seems to be at least not important. The data are more consistent with random density fluctuations. Furthermore, Ulrich (1999e) could not detect interspecific competition between parasitoids of soil living necrophagous parasitoids. From these results it is concluded that the parasitic Hymenoptera of the forest under study are best described as non-interactive community in the sense of Cornell and Lawton (1992) or as a type 1 community according to Lawton and Gaston (1989).

This also implies that the community have to be called non-stable by the first two of the criteria mentioned in the Introduction. Whether the populations were buffered against disturbances remains unclear. Ulrich (1999a) when studying

density – weight distributions in the Hymenoptera of the Göttingen beech forest found evidence that there were upper density boundaries above which the species always returned to densities well below their boundaries. For small species (0.01 mg dry weight) this boundary was around 55 times of the mean density of a species (boundary:  $45 \text{ ind. m}^{-2} \text{ yr}^{-1}$ ), for medium sized species (0.1 to 1 mg dry weight) around 27 times (boundary:  $5 \text{ ind. m}^{-2} \text{ yr}^{-1}$ ), and for large species (1 mg dry weight) around 5 times (boundary:  $0.4 \text{ ind. m}^{-2} \text{ yr}^{-1}$ ) (Ulrich 1999a and unpublished). For densities below these boundaries no density regulation could be detected. Only 25 of the 720 species (3.5%) reached in one of the study years densities above their boundary density. In half of these cases this was followed by a collapse of the population (Ulrich 1999a). Therefore, true density dependent regulation may be a rather seldom phenomenon although the species are kept inside a range of stable densities.

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## 5. SUMMARY

The stability of the community structure of the parasitic Hymenoptera of a beech forest on limestone (northern FRG) was studied.

The annual number of species was around 350 to 450 species (Table 1) with a high degree of species turnover. In a comparison of the study years the species identity of the abundant species turned out to be low (Fig. 1) and their dominance rank order was highly variable (Fig. 2). On the other hand, the yearly sequence of emergence appeared to be constant (Fig. 3).

Density fluctuations of the species were high (Table 2) and positively correlated with mean density and negatively with the weight of the species (Fig. 4). No clear common temporal trends in density could be detected (Fig. 5). Density fluctuations were not dependent on host guild, stratum or the number of generations (Table 3).

Judged by concepts of stability and classifications of communities it is concluded that this community is best described as non-interactive and non-stable.



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