

## Chapter 4: Space - local species composition

### 4.1. Introduction

Predictability of a species community is generally seen as a property of deterministic or equilibrium systems which are mainly structured by biotic interactions (e.g. competition; Linsenmair 1990, Putman 1994). In contrast, communities with unpredictable species compositions can be found in stochastic or non-equilibrium systems where communities are subject to frequent (stochastic) disturbances (Putman 1994, Linsenmair 1990, 1995). In this model species are assumed to have broad niches and large niche overlaps. Stochastic communities were found, for example, in the extremely species-rich arthropod communities of tropical rainforest canopies (Floren et al. 1998, Floren & Linsenmair 1998).

Niche theory describes each organism's position within the community as its patterns of utilization of a range of resources and its interaction with other organisms over those same resources (Giller 1984, Putman 1994). Hutchinson (1959) suggested that there should be a limit to the ecological similarity of locally co-existing species in resource use (the principle of "limiting similarity") and postulated a difference in at least one dimension. The principle is still discussed recently (Leibold 1998). Putman (1994) present a number of examples where sets of species differ from each other primarily along one single dimension of the niche. However, extensive overlap in resource use in other examples seems more the rule than the exception (Putman 1994). Resource partitioning is known, for example, from a guild of specialist phloem feeding aphids which form galls on *Pistacia* trees. Most pairs of species were unlikely to compete for galling sites because their niches were separated either temporally or spatially, by attacking different sites on the tree, shoot or leaf (Inbar & Wool 1995). Up to 12 phytophagous insect species could coexist by resource partitioning in the flower heads of a single host plant species (for example *Centaurea solstitialis*) within the Cardueae (Fam. Asteraceae) (Sobhian & Zwölfer 1985, Zwölfer 1988).

Resources in natural ecosystems vary through time and space. Of the three main niche dimensions food, time and space (Hutchinson 1957), I examine in the next three chapters the spatial resource use of the beetle community. If a species community is predictable, the species composition of different sites should differ in a predictable way according to the spatial variation of important resources. Ten sites with host plant species available were investigated for their species composition of Cassidinae leaf beetles. With these data an correspondence analysis was conducted. Several habitat parameters were determined and their effect on the species composition assessed. Questions specifically investigated in this chapter

were: (1) Do species occur in a predictable way? (2) Which habitat parameter(s) determine(s) the species composition of a site? (3) Which habitat parameter(s) determine(s) the choice of a certain microsite within the habitat by a certain species?

## 4.2. Material and methods

### 4.2.1. *Spatial distribution of the beetle community between sites: correspondence analysis*

A correspondence analysis (type of ordination analysis) was used to investigate the spatial distribution of the beetle community. The analysis grouped sites and species in a way that reflected the similarity (or dissimilarity) of the species communities the sites supported. Only those first few largest factors (eigenvalues), for which the correlation between species values and site values were strongest, were used for the ordination (Jongman et al. 1995). The inventory of Cassidinae-species was determined on 1000 host plant leaves at each of the 10 sites in Nov./Dec. 1995. These data were used to set up a site-species matrix. With the program package MVSP (Kovach, 1993) a correspondence analysis (reciprocal averaging; detrended correspondence analysis) was performed and artificial factors created. The artificial factors were tested for correlation with empirically obtained habitat parameters.

#### *Methods used to determine different habitat parameters:*

Different methods were used to assess the habitat parameters. First, the leaf counting method was originally developed for the logistic regression analysis (see further below), but turned out to be more exact in describing two of the habitat parameters than the transect method. Second, most parameters were recorded with the transect method. Third, predator density could most easily be assessed by sampling with the beating tray.

- *Assessment of qualitative habitat characteristics*
- *Leaf counting:* I examined 1000 host plant leaves at each of ten sites. Plant individuals were chosen randomly. Of every 50<sup>th</sup> leaf different measures were taken (see also logistic regression). For the correspondence analysis only the parameters “direction of vines” and “microhabitat” were used.
- *Transect method:* Measures were taken along one or two parallel line transects (Krebs, 1989) at 10 sites. Transects in general were 60m long, except at one site, where the transect was 14m long. Each transect was partitioned in subunits of 1m<sup>2</sup> that served as sampling units.

- *Sampling with a beating tray*: Per site 6 samples of arthropods on the host plant were taken using a beating tray. The beating tray had an opening of 0,25m<sup>2</sup>. Each sample consisted of two positions (branches of vines) on which three strong beats were exerted. I examined the samples for the number of individuals per predator group (ants and spiders).

*Habitat parameters:*

- The factors “host plant species” (*Merremia hederacea*, *Ipomoea heterotricha*, *Ipomoea eriocarpa*), “host plant genera” (*Merremia*, *Ipomoea*) and “habitat” (river side, savanna) were used as categorical data and were assessed by direct observation.
- The factor “light intensity” was measured with a Luxmeter (INS DX-100 Digital Luxmeter) and expressed in Lux (transect method). Measurements were taken only in clear weather conditions. However, this measure is influenced by the time of the day, position of the instrument, and other variables, in a way that the total amount of radiation of a certain spot can hardly be estimated correctly by such a short-time measure.
- The factor “direction of vines” (assessed during leaf counting) was recorded in two classes, horizontally and vertically growing vines. Horizontally growing vines occurred mostly on rocks in the open sun whereas vertically growing vines climbed into shrubs or trees.
- The factor “microhabitat” (leaf counting) was categorized based on the degree of shade. I distinguished 8 classes depending on the structure that shaded a certain microsite. Additionally the shape and color of the leaves provided valuable information on the total amount of light the vine plant gets on this special microsite. The 8 microhabitat classes sorted after an increasing degree of shading were: rock sun, open sun, grass sun, shrub sun, tree sun, grass shade, shrub shade, tree shade (classes are described in more detail in chap.5).
- The factors “cover by vine, total”, “cover by vine, part.” and “cover by vegetation, part” were assessed with the transect method. Vegetation cover was determined after Braun-Blanquet in 5 classes (modified, Mühlenberg, 1989). The indices “r” and “+” were not used. Classes were: class 1: cover below 5%; class 2: 5-25%; class 3: 25-50%; class 4: 50-75%; class 5: 75-100%. In particular the term “cover by vine, total” estimates the mean cover by vine for all sampling quadrates per site. The term “cover by vine, part.” estimates the mean cover by vine only for the sampling quadrates where vines grow. The term “cover by vegetation, part” stands for the mean cover by vegetation for quadrates where

vines grow. Thus, except for the parameter “cover by vine, total” all measurements were restricted to quadrates where vines were actually growing.

- “density of vines” (2 classes: high density: above the mean of the range; low density: below the mean of the range; data were estimates)(transect method);
- density of vegetation (2 classes: high density: above the mean of the range; low density: below the mean of the range; data were estimates)(transect method)
- “vertical structure” (transect method): The presence of vines in different heights was registered in 5 height classes above ground for each quadrate (0-0,2; 0,2-0,5; 0,5-1; 1-2; >2m).
- The factors “ants”, “spiders” and “predators, total” are the numbers of individuals of the respective groups as assessed by sampling with the beating tray on each site.

#### 4.2.2. Spatial distribution of single species within a site: logistic regression

This statistical analysis was applied to investigate the relative importance of within-habitat parameters which determined the distribution of a certain species within a habitat. The logistic regression had the advantage that the x-variable could be a presence/absence-variable whereas y-variables could be metric or categorical. This analysis was only useful for species with a sufficiently high abundance at the time of the investigation (*A. quinquefasciata*, *C. opposita* and *A. indeterminata*).

Per site 1000 leaves of the host plant were investigated for beetle species (eggs, larvae adults). Within-habitat parameters of the occupied leaves were recorded. Habitat parameters, investigated, were: leaf age (3 classes: young, mature, senescent); leaf length; height above ground; microhabitat (8 classes; see above); plant structure (2 classes: high density: above the mean of the range; low density: below the mean of the range); vegetation structure (2 classes: high/low density; see above); direction of vines (2 classes: horizontal, vertical). Additionally, every 50<sup>th</sup> leaf was investigated for these habitat parameters, no matter if occupied by a beetle or not.

### 4.3. Results

#### 4.3.1. Spatial distribution of the beetle community

If all 10 sites (7 river side sites and 3 savanna sites) were included in the correspondence analysis, the parameter host plant species, host plant genera and habitat correlated highly significantly with factor 1 of the analysis ( $p < 0,001$ , oneway ANOVA, t-test)(Fig. 4.1, Tab. 4.1). This factors explained 60,71% of the variance in the observed distribution of the 7 species on the 10 sites. The 7 beetle species therefore could be divided into smaller subgroups by habitat and by host plant species.

Beside the three parameters above, also the habitat parameter “vegetation structure” correlated significantly ( $r_s = 0,7169$ ,  $p < 0,05$ ). This factor describes the density of the host plants in five different heights above ground.

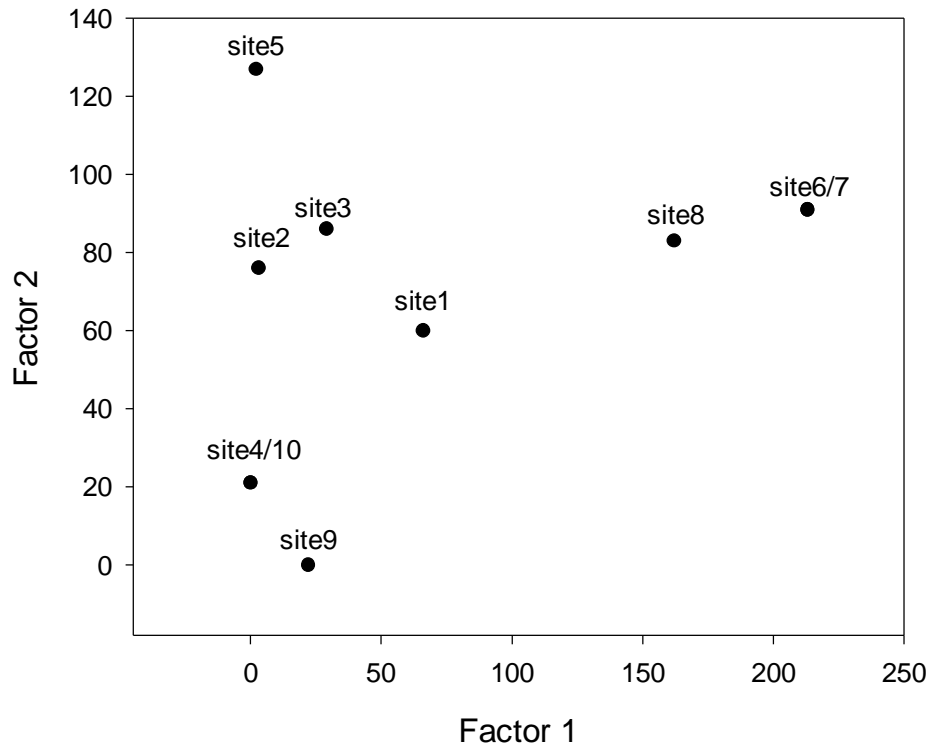


Fig. 4.1: Correspondence analysis for 10 sites/7species

Tab. 4.1: Relationship of factors 1 and 2 (correspondence analysis: 7species; 10 sites) with different variables; cover by vine, total=calculated from all squares; density of vine (of vegetation) (dense/not dense); cover by vine (vegetation), squ.w.v.=calculated only from squares with vines

	Factor 1	Factor 2
% Explanation of the model	60,7%	15,4%
Host plant species (1-3)	***	n.s.
Host plant genus (1-2)	***	n.s.
Habitat (1-2)	***	n.s.
Direction of vines (1-2)	n.s.	n.s.
Mikrohabitat (1-8)	( $r_s = -0,54$ ) n.s.	n.s.
Light intensity [Lux] (cont.)	n.s.	n.s.
Cover by vine, total (1-5)	n.s.	n.s.
Density of vines (1,2)	n.s.	n.s.
Density of vegetation (1,2)	n.s.	n.s.
Cover by vine, part. (1-5)	n.s.	n.s.
Cover by veget., part. (1-5)	n.s.	n.s.
Vertical structure	$r_s = 0,72$ *	n.s.
Ants	n.s.	n.s.
Spiders	( $r_s = 0,58$ ) n.s.	( $r_s = 0,55$ ) n.s.
Predators, total	n.s.	n.s.

Tests with oneway ANOVA (host plant species), t-test (host plant genus, habitat), rank correlation (spearman)(all other variables). \* =  $p < 0,05$ ; \*\* =  $p < 0,01$ ; \*\*\* =  $p < 0,001$ ;  $n = 10$ ;

In the second ordination analysis only the 7 sites which were located at the river side were included (Fig. 4.2, Tab. 4.2). In this analysis only one habitat parameter, microhabitat, correlated significantly with factor 1. Factor 1 explained 42,9% of the model ( $r_s = 0,76$ ,  $p < 0,05$ ). The microhabitat classes were investigated by the leaf counting method. The microhabitat was defined after the degree of shade under which the host plants grow (8 classes: rock sun, open sun, grass sun, shrub sun, tree sun, grass shade, shrub shade, tree shade). Other habitat parameters which had relatively high correlation indices ( $r_s$ ) but did not correlate significantly, were direction of vines, light intensity (lux) and spider density.

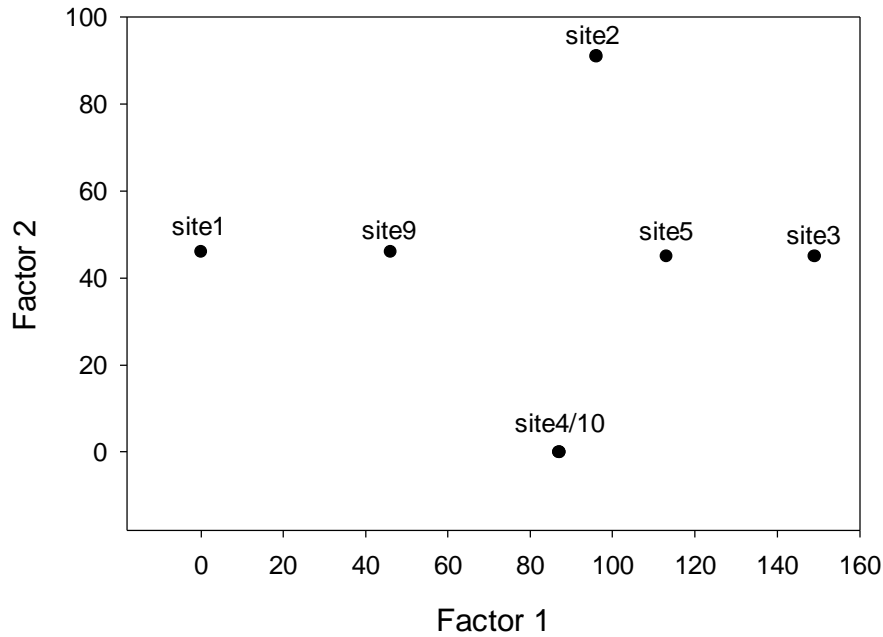


Fig. 4.2: Ordination for 7 sites/6 species at river side habitats

Tab. 4.2: Correlation of factors 1 and 2 (ordination analysis: 6species; 7 sites) with different variables; only sites at the river side were included;

	Factor 1	Factor 2
% Explanation of the model	42,9%	14,8%
Direction of vine (1-2)	( $r_s = -0,72$ ) n.s.	n.s.
Mikrohabitat (1-8)	$r_s = 0,76$ *	n.s.
Light intensity [Lux]	( $r_s = -0,71$ ) n.s.	n.s.
Cover by vine, total (1-5)	n.s.	n.s.
Density of vine (1,2)	n.s.	n.s.
Density of vegetation (1,2)	n.s.	n.s.
Cover by vine, part. (1-5)	n.s.	n.s.
Cover by veg., part. (1-5)	n.s.	n.s.
Vertical structure	n.s.	n.s.
Ants	n.s.	n.s.
Spiders	( $r_s = 0,70$ ) n.s.	( $r_s = 0,55$ ) n.s.
Predators, total	n.s.	n.s.

Test with spearman rank correlation;  $n=7$ ;

### 4.3.2. *Spatial distribution within sites*

For three of the beetle species several habitat parameters were examined which could correlate with their within habitat-distribution (logistic regression; stepwise forward inclusion of variables). Habitat parameters examined, were leaf age, leaf length, height above ground, microhabitat, plant structure, vegetation structure and direction of vines.

For *A. quinquefasciata* abundance was only significantly correlated with the habitat parameter microhabitat ( $R=0,0667$ ;  $p=0,046$ )(8 classes).

For *Ch. opposita* the regression showed a significant value only for the factor vegetation structure ( $R=-0,2299$ ;  $p=0,002$ )(2 classes; high and low vegetation density). The beetles were more abundant at places with higher vegetation density.

For *A. indeterminata* no factor correlated significantly with abundance.

## 4.4. Discussion

### 4.4.1. *Predictability of the species composition*

The question of this chapter was, whether the species composition of a certain site is predictable and which habitat parameter(s) is/are correlated with the species composition. Correspondence analysis was used to describe the relationship between species composition on a site and habitat parameters. In this study, two detrended correspondence analysis were conducted, the first including ten sites (seven river side sites and three savanna sites), the second including only the seven river side sites. For each of the two data sets, I could find at least one empirical habitat parameter which correlated with the most important factor of the correspondence analysis (Fig. 4.1 and 4.2, Tab. 4.1 and 4.2). The analysis mostly confirmed the observations which I had made before, during the regular abundance censuses in the field. Therefore, the existence of a habitat parameter which correlated with a high “eigenvalue” of the ordination analysis and which could explain the species composition on different sites in a logical way, strongly supported earlier results that the species composition of this tortoise beetle community is quite predictable.

The predictability of species communities (e.g. similar ecological conditions which always lead to similar species communities) is generally seen as a property of deterministic or equilibrium systems (Linsenmair 1990, Putman 1994). The system studied here might have been, therefore, on the scale between purely stochastic and purely deterministic systems more on the deterministic side. Final conclusions, however, have to be drawn with caution, with regard to two points: Results were based on rather small sample sizes of  $n=10$  and  $n=7$  sites.



Manly (1991), for comparison, used 16 sites for his detrended correspondence analysis, Jongman et al (1995) 20 sites. And second, predictability might be just one component of deterministic systems (see chap. 9: final discussion). Very stable species configurations among insect-plant systems, which move towards an equilibrium, have been found, for example, in the gall-forming fruit fly *Urophora* (Tephritidae) and its parasitoid community in temperate regions. From France to Japan similar niche structures could be observed in 24 associations of *Urophora* with its host plants and its parasitoid communities (Zwölfer & Arnold-Rinehart 1993, Zwölfer & Völkl 1993).

Herbivorous beetle communities on three tree species in the lowland rainforest of Kinabalu Park, on the other hand, showed quite different community patterns as compared to the savanna beetle community investigated in this study: Communities there seemed to be entirely unpredictable in their species composition and did –in recolonization experiments– not show any convergent community reorganization towards the original state (Floren et al. 1998).

#### 4.4.2. Correlation of the species composition with certain habitat parameters

In the first correspondence analysis both, savanna (3) and river side (7) habitats, were included in the analysis. Factor 1 could be grouped highly significantly for the habitat parameters **host plant species**, **host plant genus** and **habitat** (oneway ANOVA,  $p < 0,001$ ). The three habitat parameters showed the same grouping of the beetle community; they separated it in a savanna-group and a river side group. Because the host plant genera excluded each other almost completely, with *Merremia* growing exclusively at the river side and *Ipomoea* growing almost exclusively in the savanna, the effect of habitat and host plant genus on the beetle community could not be separated. The beetle community showed no such clear separation between habitats as the host plants. But with the exception of *Acrocassis roseomarginata* which was quite abundant in both habitats, all other beetle species had at least a clear preference for one habitat type. A further correlation of factor 1 with the habitat parameter “vertical structure” can be explained by differences in growth form between the plant genera. Whereas *Merremia* climbed high into the shrubs and trees at the river side, *Ipomoea* mostly grew horizontally on the ground, interspersed with grass patches in the savanna.

In the second analysis only the river side habitats were included, where the only host plant was *Merremia hederacea*. The only factor responsible for a differing community

compositions on the 7 river side sites was the “**microhabitat**” (explanation 42,9%)( $r_s=0,76$ ,  $p<0,05$ ) (Fig. 2, Tab.2). The microhabitat was defined on the basis of degree of shade on a certain microsite and categorized by direct visual assesment in eight classes: rock sun, open sun, grass sun, shrub sun, tree sun, grass shade, shrub shade, tree shade. Other habitat parameters like “direction of vines”, “light intensity [Lux]” and “number of spiders” also had relatively high, but not significant, correlation coefficients. The parameter “microhabitat”, sampled “by direct visual assessment”, seemed to represent better the light conditions of a certain microsite than measurements with a luxmeter for several reasons. The microhabitat was categorized by the degree of shading of the single host plants (e.g. on a rock in the open sun or beneath a tree). A microsite, therefore, was represented by a certain sum of light received by a plant over the day. A luxmeter, in contrast, measured only the light intensity of one moment. This changed profoundly by clouds, over the course of the day and throughout the year. Furthermore the leaf morphology/leaf form and leaf color of vines was known to be very variable under different light regimes (Lee & Richards 1991) and these properties of the host plant *Merremia* were typical and were also used to characterize a certain light condition. Leaves were deeply lobed and reddish in full sun and not lobed, thin and green in full shade. Since light intensity summed up over the day and over the season and was expressed in the observed parameters, a categorization in “microhabitats” seemed to be a more objective quantification of the light intensity than a short time measurement with an instrument like a luxmeter.

The habitat parameter microhabitat which was treated as one factor in this chapter includes several parameters, like plant quality, parasitism/predation and microclimate (temperature/humidity). Some of those could be responsible for the different spatial preferences of the beetle species. The influence of these factors on small scale distribution will be addressed in the following two chapters.

#### 4.4.3. *Habitat parameters responsible for the distribution of single species within one site*

Another way of addressing the problem of which habitat parameters influence community composition was, to examine the within site distribution for each species separately. In a logistic regression the presence-absence data of individuals of a single species were correlated with different habitat parameters which are added or removed by the procedure according to their rank of importance. Only for three beetle species abundances were high enough to perform the analysis. For *A. quinquefasciata* the factor microhabitat was correlated significantly with within habitat distribution. This is consistent with the results of the

---

ordination analysis. For *C. opposita* the factor vegetation structure showed a significant correlation.

In the logistic regression analysis the factor microhabitat correlated only in one of three species significantly with the within-habitat distribution. However, this analysis suffered from low abundance of the beetle species on the sites. The sample size of 1000 leaves per site should be increased when beetle abundances are that low. However, some sites consisted of only few small host plant patches and would not have allowed larger sample sizes.