Chap. 9: General discussion

Tropical ecology includes a wide range of non-rainforest environments, many of which are similarly threatened and interesting in their own (Price et al. 1991). In this study a tropical savanna herbivore-community was investigated and patterns of maintenance of coexistence tested in the light of classical niche theory. More recent theories on specialization of phytophagous insects and non-equilibrium models, however, are considered where appropriate.

A broad overlap in seasonal phenology of the leaf beetle species was contrasted by a marked niche differentiation in space. The beetle community could be separated in a savanna-group (host plant *Ipomoea*) and a river side group (host plant *Merremia*). A correspondence analysis showed that the beetle community of five species at the river side, which used *M. hederacea*, turned out to be predictable in their species composition by the factor microhabitat.

Tab. 9.1: Ecological properties of the single species within the beetle community, *Acrocassis roseomarginata (A.r.), Aspidimorpha quinquefasciata (A.q.), Aspidimorpha confinis (A.c.), Aspidimorpha submutata (A.s.), Chiridopsis opposita (C.o.), Aspidimorpha nigromaculata (A.n.)* and *Aspidimorpha indistincta (A.i.)*. Data on the geographical distribution from Borowiec (pers. communication).

Beetle species	**Host plant**	**Phenology**	**Habitat/ Microhab.**	**Oviposit.**	**Leaf side of larvae**	**Local density**	**Geogr. distrib.: Countries**
A.r.	*Merremia,* *Ipomoea*	Begin rainy season	River side/ sun Savanna	Single	Upper and lower side	High	6
A.q.	*M.* *(I.)*	Rainy season	River side/ light shade	Clutches	Lower side	Low	15
A.c.	*M.*	Rainy season	River side/ Shade	Single	Upper side	Rare!	24
A.s.	*M.*	Rainy season	River side/ Shade	Single	?	Rare!	15
C.o.	*M.*	Rainy season	River side/ shade	Single	Lower side	Rare!	4
A.n.	*(M.)* *I.*	Rainy season	Savanna	Single	-	Low	24
A.i.	*I.*	Rainy season	Savanna	Single	-	Low	13

The species could be separated according to the degree of shade in a certain microhabitat (chap. 4). However not all species were strongly separated by spatial resource use and some seemed to coexist basically in the identical food niche. *A. confinis, A. submutata* and *C. opposita* had a broad niche overlap in the microhabitat “shade” at the river side and *A. indistincta* and *A. nigromaculata* had an equally broad overlap in the microhabitat “light shade” in the savanna (Tab. 9.1).

Two questions follow from these results. First, why are *A. roseomarginata, A. quinquefasciata* and the three “shade”-species (see above) spatially separated at the river side? Second, why are the species in the microhabitat “river side shade” not separated?

This study investigated mainly the first question in field and laboratory experiments. Several factors which may influence the small scale spatial distribution of an insect, like interspecific competition, natural enemies, plant quality and microclimate were tested. A necessary consequence of classical niche theory should be that, by whatever mechanisms it is accomplished, overlap between adjacent species in resource space should be minimized in at least one resource dimension. Competition for any resource, however, (as the driving force for niche separation) will only occur when resources are limited (Putman 1994). An analysis of leaf damage in the field showed that food resources appeared to be not limited throughout the season and competition was therefore unlikely to be responsible for niche differentiation (chap.3). In replicated field experiments with *A. roseomarginata* and *A. quinquefasciata*, neither parasitism nor total mortality differed between sun and shade microhabitats. Thus, it was also unlikely that natural enemies were responsible for microhabitat-specialization (chap. 7). Plant quality and microclimate as strongly interacting factors were tested together and separately in field experiments. For all three beetle species tested, plant quality was significantly higher in the shade and consequently larvae performed better on shade plants. The microhabitat “shade” should therefore have represented the optimal habitat for all species. Beetle species differed, however, when the factor microclimate alone was tested (chap. 5). Laboratory tests confirmed that *A. roseomarginata* had a better tolerance towards high temperatures (40°C) than both *A. quinquefasciata* and *A. confinis*. Therefore *A. roseomarginata* was the only species that could survive in the microhabitats in the open sun at the river side where temperature maxima reached up to 50°C on the lower side of leaves (chap. 6).

According to optimality models organisms should prefer plant individuals with high quality that impart highest fitness gains to their offspring (Mayhew 1998). This was not the case in *A. roseomarginata*. Instead, a trade-off between microclimate, plant quality and occurrence in the season may best describe resource use of *A. roseomarginata*. Higher temperatures in the sun seemed to enhance larval development although plant quality was lower. *A. roseomarginata* was the first beetle species to occur in the season and started to oviposit on the seedlings in the sun directly after the onset of the first rains. Therefore it could profit of the high quality of the seedlings which might have made up for the in general lower quality of sun-plants. Because of its risk-spreading oviposition-behavior (one egg per seedling, Obermaier, unpubl. data) it might tolerate losses by the unpredictable first rains and the occasional desiccation of seedlings. Its occurrence only in the first period of the rainy season and its use of *Merremia*-plants that grew horizontally in full sun at the river banks, seemed to be well adapted to the fact that theses areas were permanently flooded later in the season. *A. roseomarginata* was the only species in the community using this resource space.

The other four beetle species, that used *Merremia* as host plant, all fed and oviposited on sites where *Merremia* was growing higher up into shrubs and trees. They occurred later in the year when the food was more predictable and used the high quality plants in the shade. *A. quinquefasciata* differed from the other species by microhabitat use (light shade), by its within-plant feeding site of the larvae and by ovipositing egg-clutches (all other species: single eggs). Over the season, along with decreasing temperatures, it showed a shift in microhabitat use from shade to light shade. Larvae of *A. quinquefasciata* and *A. confinis* had some overlap in microhabitat use, but differed with respect to the leaf sides they used (chap. 6).

A. confinis, A. submutata and *C. opposita* had very similar niches which suggests that competition between these three very rare shade-species was minimal or absent. No specific field experiments were performed on this subject. Here, I propose some hypotheses about reasons for rarity (and coexistence) in these species derived from field observations and experiments: First, a high mortality due to natural enemies and abiotic factors was generally expected according to the results of the field experiments on natural enemies (of 100 eggs laid by *A. roseomarginata* only 1,1 adults developed) (chap.7). Second, lifetime egg number might be lower in rarer species. However, fecundity was much higher in the rarer *A. confinis* than, for example, in *A. indistincta,* which was more abundant (chap. 6). Third, stochastic factors like flooding of the river bank might have severely reduced numbers of the river bank species each time with the consequence that competitive exclusion was permanently prevented (chap. 3). Such circumstances seemed to be important in the irregular flooding of a river bank in a study in Great Britain which resulted in the repeated elimination of a sub-population of *Gastrophysa viridula* (Chrysomelidae) depending on the time of the year the flooding occurred (Whittaker et al. 1979). If the populations in a community are frequently disturbed they might not reach the carrying capacity of the habitat and thus competitive exclusion will not appear (Putman 1994). Finally, differences between these species in thermal physiology or other life history traits might be quite small. Among the three “shade” species the effects of temperature and humidity on larval performance have been only tested for *A. confinis* in the laboratory. To find the reasons for rarity and coexistence of those species with a broad niche overlap, has to be left to future investigations.

A molecular phylogeny (mtDNA, COI-gene) was neither consistent with a phylogeny based on morphological data nor with a tree constructed on the basis of ecological criteria. Only in one of three closely related species pairs, species continued to use the same small-scale spatial niche. The other two pairs of species evolved divergently and showed different degrees of specialization or used different habitats.

Deterministic equilibrium systems and stochastic non-equilibrium systems have different, mostly opposing, ecological characteristics, however, different authors stress different characteristics to distinguish between the two alternatives. In this study, I referred to the definitions given by Linsenmair (1990), Huston (1994) and Putman (1994). In equilibrium systems a community structure is expected which is primarily determined by biotic interactions (competition and predation/parasitism). Species must be sufficiently ecologically distinct to coexist stable. Therefore, the degree of specialization should be high and niche overlap low. Community composition should be predictable and communities should be saturated with species. Non-equilibrium systems are expected to be structured by invasions. Their structure is far less influenced by biotic interactions, but instead organized primarily by independent interactions of species with abiotic factors. These communities are subject to frequent (intermediate) disturbance which prevent the formation of a climax community and species saturation. Community composition, finally, should be unpredictably and species should be little specialized and show broad niche overlaps.

There are, however, some difficulties involved with this classification. Phytophagous insect communities have some characteristics in common, which seem to classify them at once as non-equilibrium systems in spite of their sometimes evolutionary very stable and predictable three-trophic niche structure (Zwölfer & Arnold-Rinehart 1993). First, the existence of interspecific competition between phytophagous insects, a prerequisite of deterministic systems, is controversially discussed in the literature (Belovsky 1986, Denno et al. 1995, Stewart 1996) and denied at least by some authors (Strong et al. 1984). Second, many plant-insect systems seem to be unsaturated communities because of a large number of unused resources which are available for the evolution of new food niches of phytophagous insects (Price 1980, Lawton 1984, Zwölfer & Arnold-Rinehart 1993). Zwölfer & Arnold-Rinehart (1993) therefore cite that, “from an evolutionary point of view plant-insect communities are non-equilibrium communities”.

Tab. 9.2: Deterministic vs. stochastic characteristics of the tortoise beetle community. Arguments are listed below the respective model which they support. Description of the models after Linsenmair (1990), Huston (1994) and Putman (1994).

	Deterministic/ equilibrium models	**Stochastic/ non-equilibrium models**
Specialization	+ specialized in space + specialized, but only partly separated in food (oligophagous-monophagous)	
Niches	+ in general niche separation in space	+ 3 rare species little separated in microhabitat use at the river side shade; + broad overlaps in time and food
Biotic Interactions	+ high mortality by natural enemies	+ no interspec. competition, no resource limitation
Abiotic Factors		+ independent interactions of species with abiotic factors (temperature, humidity) + stochastic variations in abiotic factors: flooding, fire, unpredictable first rainfalls
Predictability	+ Species composition ± predictable (microclimatic conditions); River side sun: *A.r.* River side light shade: *A.r., A.q., A.s.* River side shade: *A.q., A.s., A.c., C.o.* Savanna: *A.r., A.n., A.i.*	

Tab. 9.2. lists characteristics of the tortoise beetle community that point either to a more deterministic or a more stochastic organization after Linsenmair (1990), Huston (1994) and Putman (1994). Although phytophagous insect communities might in general be unsaturated and interspecific competition rare (see above), the community investigated showed other important elements of equilibrium systems: i) a large impact of natural enemies (high larval mortality), ii) a relatively predictable species composition at different sites, and iii) a distinct spatial niche structure. Niche separation and specialization is, however, most probably not caused by interspecific competition, but by physiological trade-offs between plant quality and thermal tolerances of the single species. However, there are also characteristics that support

non-equilibrium systems. Abiotic factors, according to Putman (1994) an element of non-equilibrium systems, had a large influence on small-scale spatial niche separation. The broad niche overlap of the three species in the microhabitat shade at the river side also is a characteristic of non-equilibrium systems. In general the community shows more characteristics of deterministic equilibrium models, includes, however, also some elements of stochastic non-equilibrium systems.