

Chap. 1: Introduction – hypotheses on coexistence

“It was the variety of plants and animals which, without exception, first impressed naturalists in the tropics” (Lewinsohn et al. 1991). Tropical rain forests and coral reefs are usually regarded as the epitome of complexity and diversity (Connell 1979). The mechanisms, however, that allow so many species to coexist continuously, still need to be unraveled.

Several concepts on the maintenance of contemporary species rich communities are discussed by different authors (Pianka 1966, Linsenmair 1990 and 1995, Huston 1994, Putman 1994, Rosenzweig 1995). First, equilibrium or deterministic models (MacArthur 1972) assume a niche separation and specialization of species mainly by interspecific competition. Recently, specialization in phytophagous insects is also explained by several other mechanisms (Berenbaum 1996), for example as an effect of natural enemies (Bernays & Graham 1988), by physiological trade-offs, mating rendezvous, and optimal foraging (Futuyma & Moreno 1988, Jaenike 1990). Second, top-down regulation by predators or parasitoids can reduce herbivore populations below capacity limits and therefore enable coexistence of several species. For example Siemann et al. (1998) showed experimentally that the number of plant species significantly increased arthropod species richness, but that herbivore diversity was even more strongly correlated with parasite and predator diversity than with plant diversity. Third, more recently it has been argued that intermediate disturbances may prevent species saturation and thus no climax community will develop. Such stochastic or non-equilibrium models are characterized by broad niche overlaps of the species and an unpredictable community composition (Linsenmair 1990, 1995, Huston 1994). Such models have been found useful to describe the extremely species rich arthropod communities in tropical rainforest canopies or coral reef fish communities (Sale 1977, Floren & Linsenmair 1998).

Empirical evidence in temperate or arid regions supports several of the hypotheses mentioned above. Menge & Sutherland (1976) showed the importance of both competition and predation in maintaining high diversity in intertidal communities. Physiological trade-offs permitted coexistence in two species of mice mediated by inter-year variance in food and climate (Wolff 1996). Niche separation in time (season) occurred in coprophagous beetles (Sowig 1997). Resource partitioning in time or space allowed galling aphid species to coexist on the same host plant without competition (Inbar & Wool 1995). Finally spatial segregation permitted a community of leafhoppers on stinging nettles (Stiling 1980) as well as a

community of Pierid butterflies (Courtney & Chew 1987) to coexist in different shading levels.

The niche theory has a long tradition as a concept to describe community organization (Hutchinson 1957, Giller 1984), and still is appropriate in modern community ecology (Chesson 1991, Putman 1994). It explains how the community's members may be organized or 'packed' within resource space. Although the classical niche concept is similar to deterministic models and favors competition as the major structuring mechanism, information on the niche of a species has implication for both deterministic and non-equilibrium models. According to niche theory each resource is represented by an axis in a n-dimensional niche space (Hutchinson 1978). The position of any organism within a community can be defined by its pattern of utilization of any of these resources and its interaction with other organisms over shared resources (Putman 1994). Although the niche theory is applied to single species, it was particularly developed to explain community structure. Niche theory provides an approach to tropical biodiversity, as it explains how the diverse resources of the tropical primary producers are divided among phytophages: Are there small "resource-packages" and therefore small food niches which support a high proportion of specialists in the tropics, or does the majority of species consist of generalists coexisting in broadly overlapping niches (Linsenmair 1990)?

Mechanisms of coexistence should be examined where species interactions are strongest and species packing is highest. This is the case within a functional group or even more so among closely related species co-occurring in a guild. These are most likely to be very similar in resource use. In this study I examined a community of seven closely related leaf beetle species (Chrysomelidae: Cassidinae), feeding on a common host plant system, (Convolvulaceae) in a tropical savanna (Comoé-National Park, Ivory Coast). I tested resource utilization patterns in the shield beetle community in the framework of the niche concept. I investigated the three niche-dimensions: food, time, and space (Hutchinson 1957)(chap. 2-6). I examined predation and parasitism as further possible niche dimensions (enemy-free-space), as well as the general effect of natural enemies on the reduction of the beetle populations (top-down effects) (chap. 7). Finally a molecular phylogeny of the community was developed and compared to patterns of ecological resource use, and the evolution of host plant use within the beetle community was reconstructed (chap. 8). These results provide a basis to assess the relative importance of the mechanisms that maintain coexistence in the beetle community.