Trophic interactions and population structure of the large blue *Maculinea nausithous* and its specialist parasitoid

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1 Introduction

1.1 Trophic interactions in parasitic large blues

Food webs depict the feeding relationships in ecological communities. For a long time, two-species approaches have dominated research on ecological interactions. However, focussing on two species interactions has been shown to be too simplistic in many cases. A multi-trophic approach often addresses the complexity of food webs more realistically (Tscharntke and Hawkins 2002). Holt (1977; 1997) introduced the concept of community modules as an alternative approach to understand species interactions. Community modules are groups of closely interacting species, whose dynamics can be understood separated from the surrounding community. Familiar community modules include simple food chains (Oksanen *et al.* 1981; Post 2002), exploitative competition (Mac Arthur and Levins 1967; Amarasekare 2003), shared resources (Tilman 1982), and shared predation (Holt and Lawton 1993).

Within the module of shared predation, two species have a common natural enemy. Shared predation between a plant species and an ant species is the basic community module of the food web surrounding the lycaenid butterfly genus *Maculinea*. Most species of the family Lycaenidae are characterised by an ant-associated life-history (Fiedler 1991; Pierce *et al*. 2002; Weeks 2003). These butterfly-ant interactions, which are termed “myrmecophily”, are mutualistic in most cases (Pierce 1987; Fiedler 1991). Caterpillars secrete substances that attract and appease ants and in return gain ant protection against predators and parasitoids. In order to produce these secretions, caterpillars must feed on high quality food plants or nitrogen-rich parts of plants such as flowers. Parasitoids are thought to be major selective factors that shaped the variety of ant-butterfly interactions and ant-exclusion experiments showed increased parasitism (Box 1; Pierce and Mead 1981, Pierce and Eastal 1986, Weeks 2003). Relationships between myrmecophilous caterpillars and ants range from loose, facultative interactions in which larvae are tended occasionally by several species of ants to highly specific and obligate associations in which a larva is always tended by ants, often by only a single species (Fiedler 1998; Pierce *et al.* 2002). However, in some lycaenid species the mutualistic relationship with ants evolved to a predatory (Thomas and Wardlaw 1992; Pierce 1995) or parasitic relationship (Pierce 1995; Thomas and Elmes 1998) leading to the severe exploitation of ant nests (reviewed by Fiedler 1998). The caterpillars of parasitic lycaenids such as *M. nausithous* lay their eggs on specific food plants. The young larvae feed on the flowers and seeds, quickly developing through three larval instars, but gaining comparatively little weight. At this point, they undergo a dramatic life history change: Caterpillars leave the food plant and drop to the ground. Once found by foraging *Myrmica* workers they are adopted and brought into the ant nest where they feed until the following summer (Fiedler 1990; Thomas and Elmes 1998). Because the mobility of lycaenid caterpillars is restricted, both food resources have to be present on the local oviposition site to ensure development. The ant and plant resources of *M. nausithous* reach highest densities in different habitat types. In a small intersection of ant and plants habitat types, *M. nausithous* is able to reproduce successfully. There is no doubt that adult *Maculinea* efficiently locate their food plant. However, it is unclear, whether females are able to detect the presence of the host ant species (Fiedler 1998). The mobility of lycaenid caterpillars is strongly limited. It is thus expected that adults gain fitness benefits if they deposit eggs on food plants

Box 1. Life history of parasitoids

Parasitoids are insects that lay their eggs in or on the body of a single immature host. Depending on the species, a single (“solitary parasitoids”) or several (“gregarious parasitoids”) emerge from the host. Parasitoids are estimated to constitute up to 25% of all insects in the world (Godfray 1994). Overall, they kill more herbivores than do either predators or pathogens (Hawkins *et al.* 1997) and have thus been subject to numerous studies investigating trophic level interactions (e.g. Price 1980; Tscharntke and Hawkins 2002), host-parasitoid population dynamics (e.g. Hassell 2000), and biological control (e.g. Wajnberg and Hassan 1994). Here, key issues of parasitoid life history and parasitoid evolution are described that is relevant to chapters 4 and 6 of this thesis.

Host location

The process of host selection of insect parasitoids is commonly divided into three main steps (Vinson 1976, Vinson et al. 1998). Females have to 1) initially find the host habitat patch, i.e. the plant the host feeds on (host habitat location); 2) locate the host within the patch (host location); and 3) identify hosts that are profitable for the development of offspring.

Host discrimination

In order to avoid intra-specific competition, many parasitoid species are able to discriminate parasitised from healthy hosts. Some parasitoids mark parasitized hosts or the substrate of the host. Since the haemolymph of parasitised hosts differ from the haemolymph of unparasitised hosts, especially hymenopteran parasitoids have evolved the ability to probe hosts. Hosts are stung without oviposition to obtain information on previous parasitism (Quicke 1997).

Feeding strategy

Parasitoid species that spend the larval stage inside the host are called endoparasitoids. Species that live outside the host species, but imbide nutrients from the host are called ektoparasitoids. Koinobiont parasitoids allow their host to continue to feed and grow in size, whereas idiobiont parasitoids kill or paralyze their host (Haeselbarth 1979; Askew and Shaw 1986). The host range of koinobiont parasitoids is much more restricted than the host range of idiobiont parasitoids. In order to persist inside a live foreign organism, parasitoids have to deal with the immune system of the host species (Vinson 1990; Pennachio and Strand 2006).

Superparasitism

In solitary parasitoids, one host produces one parasitoid. The decision to superparasitise, i.e. to add an additional egg, can be adaptive for the individual (van Alphen and Visser 1990, but see Reynolds and Hardy 2004). In most cases, supernumerary larvae are killed by competitors (contest competition) or limitation of resources leads to reduced overall survival or smaller body size (scramble competition).

Co-Evolution

Co-evolution is the process of reciprocal evolution of interacting species (Thompson 1999). In host-parasitoid interactions, it creates an evolutionary arms race in modifying levels of parasitoid virulence and host resistance (Vinson 1975). Parasitoids are selected for manipulation of the host immune system, whereas the successful encapsulation of parasitoid eggs or parasitoid larvae enhances host fitness (Godfray 2000).

growing in the vicinity of host ant colonies. While there is evidence for the use of host ant cues for oviposition in mutualistic lycaenids (Atsatt 1981; Fiedler and Maschwitz 1989; Wagner and Kurina 1997), there is no sound evidence for such behaviour in parasitic lycaenids, such as *M. nausithous*.

The dependency of *M. nausithous* on two different food resources poses the question, whether the food plant or the host ant species limit the density and population growth of this butterfly. All populations, if left unchecked, have the potential to grow exponentially (Malthus 1798). Density-dependent processes, that may limit exponential growth, have two facets: temporal and spatial (e.g. Hassell 1987). Temporal density dependence describes how, as a population increases over time, its mortality changes for a single point in space. Spatial density dependence describes how, as average prey density varies among patches, prey mortality changes for a single point in time (Stewart-Oaten and Murdoch 1990). As the butterfly *M. nausithous* is highly endangered in Europe (Thomas and Settele 2004), spatial density-dependence of this species is of high practical relevance to habitat conservation strategies. Food limitations caused by the host ant may result in different management regimes than food limitations caused by the food plants due to different habitat requirements of both species (Seifert 1996, Musche *et al.* 2006).

Despite of the association with protective ants, many lycaenid blues are attacked by parasitoids. Insect parasitoids exhibit most complex adaptations to locate hosts and to successfully live inside a foreign body (Box 1). In fact, there is evidence that the proportion of parasitised lycaenid caterpillars increases with increasing degree of myrmecophily (Seufert and Fiedler 1999; Thomas *et al*., unpublished data). Three arguments were proposed for this counterintuitive finding: First, certain parasitoids use ants as cues to locate their hosts (Pierce *et al*. 1987; Nash 1989). Second, obligate myrmecophiles may provide particularly rewarding targets for parasitoids because the use of myrmecophilous hosts may provide enemy-free space for both host and parasitoid. Third, the association of lycaenid caterpillars with ecologically dominant ant species constitutes a predictable and clumped resource (Seufert and Fiedler 1999).

1.2 Species interactions in space

The natural habitat of a species is defined as “an area with the combination of resources and environmental conditions that promotes occupancy by individuals of a given species and allows those individuals to survive and reproduce” (Morrison *et al.* 1992). Most habitats exhibit a varying degree of heterogeneity so that the habitat is divided into distinct habitat patches (Hanski and Gilpin 1997; Hanski 1999). Many species are thus believed to live in metapopulations, with populations being connected by limited migration. The local extinction of populations is counter-balanced by local colonisations and enables the metapopulation to persist in the long term. The most prominent issue of space in ecology is the ecological consequences of fragmentation of species habitats. The effects of habitat fragmentation can be mainly assigned to three processes: reduction of total habitat area within a region, loss of area within each single habitat, and increase of isolation between habitat patches (Andrén 1994; Kruess and Tscharntke 2000). Holt (2002) suggested that strongest evidence for the influence of space on food chain length, e.g. the occurrence of parasitoids, may be found in community modules or guilds. The number of species in a community module is expected to increase with habitat area and to decrease with isolation. There is ample evidence of impoverished species diversity as a consequence of changes in the spatial configuration of species' habitats (e.g. Tscharntke and Brandl 2004; Fahrig 2003). Loss of species may lead to changes in ecosystem function such as pollination (Steffan-Dewenter and Tscharntke 1999; Dupont and Nielsen 2006), decomposition (Burkey 1997), and parasitism (Komonen *et al.* 2000). However, most studies are based on species numbers and less is known about the functional processes such as the damage caused by herbivory or mortality caused by parasitoids (Tscharntke and Brandl 2004). According to the trophic rank hypothesis, susceptibility to habitat fragmentation should amplify in species from higher trophic levels (Didham *et al.* 1996; Holt *et al.* 1999; Kondoh 2003; Henle *et al.* 2004). While this is probably true, it is not always the case (van Nouhuys 2005). Species attributes that affect their sensitivity to habitat fragmentation like feeding type, dispersal ability, reproductive potential, and rarity may not necessarily correspond to trophic level. Beneath a decrease of individuals in isolated populations, the genetic structure of populations may be affected by spatial isolation. The advent of large-scale genotyping methods such as microsatellite markers (simple sequence repeats) facilitates the assessment of isolation effects on the genetic diversity and structure of insect populations.

1.3 Population structure and gene flow

Knowledge of the genetic structure of populations is important for the understanding of their ecology and evolution. The ability of a population to adapt to unique local conditions is not solely determined by the strength of natural selection, but countering effects of genetic drift and gene flow (Slatkin 1973; May *et al.*1975; Endler 1977). Gene flow among populations is a fundamental evolutionary force that can determine the geographical spread of novel adaptations, and therefore the potential for local adaptation and speciation (Fisher 1930; Mayr 1942; Mayr 1963; Ehrlich and Raven 1969). Elucidating the factors that influence the spatial extent of gene flow and the genetic structure of populations is fundamental in understanding species persistence. Various environmental factors such as geographical distance (Wright 1943; Kimura and Weiss 1964; Peterson and Denno 1998), habitat persistence (Roderick 1996; Peterson and Denno 1998), habitat patchiness (King 1987; Roderick 1996; Peterson and Denno 1998), physical barriers (Hartl 1980; Gerlach and Musolf 2000; Keller and Largiadèr 2003), and the frequency of extinction/colonization events (Whitlock and McCauley 1990; Hastings and Harrison 1994; Harrison and Hastings 1996) can promote gene flow and hence the relative isolation of populations. In addition, some intrinsic life history or ecological traits such as dispersal ability (Peterson and Denno 1997) and phenological asynchrony (Wood and Guttman 1982; Runyeon and Prentice 1996) are expected to have significant effects on gene flow and the genetic structure of populations.

The frequency of alleles with the same fitness will change at random through time. These random changes between generations are called genetic drift, or simply drift (Ridley 1996). Drift has important consequences for the random substitution of genes and the Hardy-Weinberg equilibrium (Hartl and Clark 1997). The rate of change of gene frequency by drift depends on the size of the population.

The most obvious source for intraspecific variation in gene flow is the decline of gene flow with geographic distance (Wright 1943; Peterson and Denno 1998), known as genetic isolation by distance (hereafter IBD). The IBD model is based on a stepping stone model of population structure among organisms whose dispersal ability is constrained by distance such that gene flow is most likely to occur between neighbouring populations (Hutchison and Templeton 1999). As a result, more closely situated populations are genetically more similar. A pattern of IBD results from the changing relative influence of gene flow and drift as populations become geographically more separated (Hutchison and Templeton 1999). At increasing geographic distances, the relative influence of drift increases and gene frequencies within populations fluctuate to a certain degree.

A way to unravel the relative influence of extrinsic and intrinsic factors on the spatial structure of insect species is to develop a parallel study on different taxa. Comparing the population genetic structures of closely interacting species inhabiting the same landscape may provide valuable insights, because potential differences in population genetic structure may be due to the ecological properties of the species. Two species linked by a mutualistic or parasitic relationship may evolve correlated population differentiation if there is long-term continuity between specific partners (Dybdahl and Lively 1996). For example, if the scale of gene flow is similarly restricted in both species, then random population genetic differentiation may evolve in parallel in both species according to an IBD model (Slatkin 1993; Parker and Spoerke 1998). An absence of correlated genetic variation implies that dispersal and population extinction proceeded largely independent in each organism. Population genetic variation, genetic diversity and IBD represent powerful tools to compare the spatial structure of a large blue butterfly and its specialist parasitoid.

1.4 Butterfly mimics of ants: Ecology of *Maculinea* large blues

Maculinea nausithous and its associated species constitute and ideal system for the study of community modules. Among the community modules of shared predators it has the least diffuse interaction scheme due to restriction to one specific food plant and one specific host ant species (Holt and Lawton 1994).

The life history of the butterfly genus *Maculinea* is characterized by a phase as an herbivore, followed by a predatory development inside *Myrmica* ant nests. Eggs are laid around the flower buds of their food plants. Caterpillars then feed on the immature seeds where they quickly develop to the fourth final instar. At this stage, caterpillars expose themselves to the foraging workers of *Myrmica* ant species. Once found by *Myrmica* worker ants, *Maculinea* larvae are adopted after a complex pattern of caterpillar-worker interaction (Fiedler 1990; Elmes *et al.* 1991a, b). They are brought into the ant nest where they are placed among the ant grubs. Inside the ant nest, *Maculinea* caterpillars feed in two different ways. Predatory *Maculinea* species, like *M. nausithous*, move into safe chambers of the ant nest, returning periodically to feed on the ant brood (Thomas and Wardlaw 1992). Caterpillars of the “cuckoo-type” remain among the ant brood and are fed by “nurse ants” (Elmes *et al.* 1991b). After obtaining more than 98% of their final mass inside the ant nest, adult *Maculinea* leave host ant nests (Elmes *et al.* 2001). Chemical mimicry is the key for the social integration of *Maculinea* caterpillars into *Myrmica* ant nests. Elmes and co-workers (2002) could show that there is a consistent similarity of cuticular hydrocarbon surfaces between *Maculinea* caterpillars and their specific host ant grubs to explain the specificity of European *Maculinea* butterflies. Thus, successful development of *Maculinea* caterpillars is restricted to specific *Myrmica* species (Thomas *et al.* 1989).

Box 2. Life history of *Maculinea* butterflies

(1) *Maculinea nausithous* oviposits on flower buds of *Sanguisorba officinalis*; (2) Adoption of *M. nausithous* caterpillar by workers of *Myrmica rubra;* (3) *Maculinea* caterpillars inside brood chamber of *Myrmica* host ants; small picture: *Maculinea* caterpillar is fed by worker ants; (4) *Maculinea* pupae inside *Myrmica* ant nest; (5) Emergence of adult *Maculinea* butterfly from the host ant nest.

The host ant species can vary locally (Als *et al.* 2002), ranging from one host ant species in *M. nausithous* across Europe to four host ant species in *M.* rebeli/alcon. Feeding on the ant brood like the "predatory" species *M. teleius*, *M. nausithous*, and *M. arion* is less efficient than feeding on the regurgitations of the ants. Consequently, predacious *Maculinea* often cause the extinction of the local ant nests. In contrast, *Maculinea* species of the "cuckoo" type (*M. rebeli*/alcon) experience contest competition inside the ant nest because worker ants select the largest caterpillars. A small proportion of *Maculinea* caterpillars take two years until emergence as an adult butterfly. This "biennialism" is known from "cuckoo"-*Maculinea* and predatory *Maculinea* (Thomas *et al.* 1998; Witek *et al.* 2006). According to the bet-hedging hypothesis, species with unpredictable resources may benefit from this strategy (Hopper 1999).

The life history of the predatory *Maculinea nausithous*, which is in the focus of this study, is described in box 2. Female *M. nausithous* deposit their eggs on the closed inflorescences of *Sanguisorba officinalis* (Rosaceae). Caterpillars hatch and bore into single florets where they feed until they drop to the ground. Unlike other *Maculinea* species, successful development of *M. nausithous* is restricted to the red ant *Myrmica rubra* (Fiedler 1990; Thomas and Elmes 1998; Stankiewicz and Sielezniew 2002). This red ant is a common holarctic species that can be found in a variety of habitats (Seifert 1996). Recently, it was suggested that *M. nausithous* may currently evolve towards a cuckoo-feeding *Maculinea*. It is a predator, but has some attributes of cuckoo-feeders and achieves some social integration (Als *et al.* 2004; Thomas and Settele 2004).

1.5 Specialists attack specialists: Ecology of *Neotypus* and *Ichneumon* parasitoids

Insect social parasites such as *Maculinea* are extremely specialised to enter the nutrient-rich, but fiercely protected ant nests. However, the natural enemies of *Maculinea* are not far behind. Though spending a long time of their development inside ant nests, all *Maculinea* species are attacked by specific solitary Hymenopteran parasitoids (Thomas and Elmes 1993; Anton *et al.*, unpublished; Box 3). For example, the predatory *M. teleius* is parasitised by three parasitoid species, each specialised on a specific larval instar feeding outside or inside of ant nests. The highest degree of specialisation is found in parasitoids attacking the cuckoo feeder *M. alcon/rebeli*. *Ichneumon eumerus* enters ant nests to oviposit *M. alcon* caterpillars. In order to reach host caterpillars, this wasp releases chemicals to induce in-fighting between worker ants (Thomas *et al.* 2002). While the ant nest is unprotected, the parasitoid enters the brood chamber and oviposits into the *Maculinea* caterpillars (Box 3). According to Thomas and Elmes (1993), this strategy is only warranting when there is a high survival rate of host caterpillars inside ant nests. Predatory *Maculinea*, such as *M. nausithous*, often cause the extinction of host ant nests due to overexploitation (Thomas and Elmes 1998) resulting in starvation of *Maculinea* caterpillars. Therefore, predatory species of *Maculinea* were suggested to be parasitised while feeding on the food plant, because it is simple and safe to do (Thomas and Elmes 1993). However, excavations of numerous ant nests across Europe showed that predatory *Maculinea* are victims of parasitoids twice: they are attacked while feeding on the feed plant and while feeding inside ant nests (Anton *et al.*, unpublished).

Box 3. Parasitoids attacking *Maculinea* butterflies

1) *Ichneumon fulvicornis* inside nest of *Myrmica rubra;* (2) *Maculinea alcon* is attacked by the same parasitoid as *M. rebeli* (*Ichneumon eumerus*); (3) *Ichneumon eumerus* first locates *Myrmica schencki* nests by their odour, but enters only those nests that also contain *M. rebeli* caterpillars, (4) *Neotypus melanocephalus* attacks concealed feeding *Maculinea nausithous* caterpillars.

1.6 Structure of this thesis

This thesis is concerned with trophic interactions and spatial patterns of interacting species. While there is plenty of information about the complex interactions in community modules of cuckoo - *Maculinea*, less is known about trophic relationships and parasitism in predatory *Maculinea*, such as *M. nausithous*. The small number of studies that previously dealed with the population ecology of *M. nausithous* was restricted to a small number of populations providing low statistical power (Binzenhöfer *et al.* 2000; Pfeiffer *et al*. 2000; Nowicki *et al.* 2005). *Maculinea nausithous* is listed in Annex II of the Habitats Directive (van Helsdingen *et al*. 1996) and vulnerable on the European Red List (van Swaay and Warren 1999). Causes of spatial density-dependence and the consequences of population isolation will also provide valuable information for conservation of this target flagship species. Moreover, this work is the first to analyse the behaviour and population ecology of parasitoids attacking predatory *Maculinea*. These parasitoids are expected to be even more endangered than their host species.

Chapter 2 focuses on the spatial density dependence of *M. nausithous* larval stages and its two resources, the initial food plant *Sanguisorba officinalis*, and the host ant *Myrmica rubra*.

Chapter 3 investigates the ability of *M. nausithous* females to use ant odours as oviposition cues. This ability of *Maculinea* butterflies has gained large interest and was subject of long discussion. Until today, there is no consensus about host ant dependent oviposition in the genus *Maculinea* (van Dyck *et al.* 2000; Thomas and Elmes 2001; Wynhoff 2001).While previous studies on oviposition choice in *Maculinea* were descriptive (van Dyck *et al.* 2000, Thomas and Elmes 2001, Küer and Fartmann 2004, Nowicki *et al.* 2005), an experimental approach is used in this dissertation: food plants were contaminated with odours from ant nests to test if female *M. nausithous* prefer food plants carrying ant cues.

Chapter 4 aims to investigate the behavioural adaptations of specialised parasitoids and to analyse patterns of parasitism on the population level. To reveal these, may provide important insights into the behavioural ecology and population ecology of parasitoids attacking highly specialised hosts.

Chapter 5 provides the prerequisites for the population genetic study presented in chapter 6: nine polymorphic microsatellite loci isolated from the parasitoid *Neotypus melanocephalus*. This tool enables spatial genetic analyses and analyses of genetic richness.

Chapter 6 compares the effects of population isolation on the population density and genetic population structure of both the host species *M. nausithous* and the parasitoid *N. melanocephalus*.

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2 Myrmica host ants limit the density of the large blue *Maculinea nausithous*

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Abstract

Butterflies of the highly endangered genus *Maculinea* are parasites of red *Myrmica* ants. Prior to the adoption by *Myrmica* worker ants *Maculinea* caterpillars feed on a specific food plant. This study aims to answer the question whether the density and distribution of the food plant *Sanguisorba officinalis* or the density of the host ant *M. rubra* limit the density of *M. nausithous* egg, larval and adult stage. In a field study on 33 sites we found egg density and adult butterfly density of *M. nausithous* to be positively correlated with the density of the host ant. The density of *M. nausithous* caterpillars did neither correlate with ant density, nor the density of the food plant. This study suggests that the density of *M. nausithous* is limited by the density of the host ant *M. rubra*. We conclude that habitat management for *M. nausithous* should focus on the maintenance of habitats that hold both resources, but that enable high densities of *M. rubra*. In addition, it is discussed why high densities of host ants may be more important in predatory than in cuckoo-feeding *Maculinea*.

Keywords: Habitat conservation, *Myrmica rubra*, spatial density-dependence.

3 No experimental evidence for ant related oviposition in a parasitic butterfly

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Journal of Insect Behavior (2006) **19**, 631-643.

Abstract

The ability of adult butterflies of the genus *Maculinea* to locate their host ants prior to oviposition has been the subject of much discussion. We studied the egg laying behavior of the dusky large blue Maculinea nausithous whose larvae parasitize colonies of the ant Myrmica rubra. Flowerheads of the initial food plant were sprinkled with soil from ant nests, which contain chemicals involved in the nest recognition behavior of ants. The experiment was conducted to determine whether ant-released chemicals may act as oviposition cues and whether intraspecific competition for suitable plants may force female butterflies to alternative decisions. Host plant choice was not influenced by the presence of nest-derived host-ant cues. Density dependent shifts to less suitable host plants could not be ascertained nor changes in egg laying behavior across the flight period. The observed egg distribution could be primarily explained by host plant characteristics and environmental variability among sites. The result confirms the theory that host ant dependent oviposition appears to be a disadvantageous strategy in the face of resource limitation within ant colonies and the immobility of caterpillars.

Keywords: *Maculinea nausithous*, myrmecophily, oviposition, social parasite.

4 Spatial patterns of host exploitation in a larval parasitoid of the large blue *Maculinea nausithous*

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Basic and Applied Ecology (2007) **8**, 66-74.

Abstract

The foraging behaviour of the parasitoid wasp *Neotypus melanocephalus* and factors affecting parasitism at the population level was studied. This specialised parasitoid attacks caterpillars of the butterfly *Maculinea nausithous* which sequentially feed on the plant *Sanguisorba officinalis* and specific red *Myrmica* ants. Among *M. nausithous* populations, there is considerable variation in caterpillar densities. At low *M. nausithous* densities, foraging may be time-consuming for *N. melanocephalus.* High host densities may not always be advantageous to foraging parasitoids due to the caterpillars' frequent overexploitation of ant resources and subsequent density-dependent mortality. In order to disperse progeny we hypothesised that *N. melanocephalus* should search in a non-random way at the level of the micro-habitat, i.e. single flower heads of *S. officinalis*. Our analysis of 32 natural populations in the Upper Rhine valley in Germany did not show a density-dependent relationship between *M. nausithous* caterpillars and parasitism. Furthermore, habitat parameters like patch size and density of the host's food plant did not affect the parasitism rate. Foraging *N. melanocephalus* females preferred to search on large flower heads. They probed host-occupied flower heads only, visiting non-host-exploited flower heads only briefly. Time spent on a flower head was independent of the number of caterpillars per flower head. This study indicates that *N. melanocephalus* increases its foraging efficiency by preferring large flower heads which were previously shown to contain more host caterpillars than small flower heads. Furthermore, oviposition increases the likelihood of continuing to search on a flower head, which is an adaptive strategy for parasitoids foraging for aggregated hosts. However, many host occupied flower heads were not probed by *N. melanocephalus*. We discuss the possibility that temporal host refuges of *M. nausithous* caterpillars may contribute to heterogeneity of parasitism, and why spreading offspring may constitute a suitable strategy for a parasitoid of an ant-parasitic butterfly.

Keywords: Foraging behaviour, host refuge, *Neotypus melanocephalus*, patch size, population density.

5 Nine polymorphic microsatellite loci for the parasitic wasp *Neotypus melanocephalus*

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Molecular Ecology Notes (2006) **6**, 399-401.

Abstract

Nine polymorphic microsatellite loci were isolated from *Neotypus melanocephalus* (Gmelin), a parasitoid of the parasitic large blue butterfly Maculinea nausithous. Allelic diversity and heterozygosity were quantified in samples from the Upper Rhine valley in South West Germany.

Keywords: contemporary gene flow, *Maculinea*, microsatellite, *Neotypus*, population genetics.

6 Population structure of a large blue butterfly and its specialist parasitoid in a fragmented landscape

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Molecular Ecology (2007), **16**, 3828-3838.

Abstract

Habitat fragmentation may interrupt trophic interactions if herbivores and their specific parasitoids respond differently to decreasing connectivity of populations. Theoretical models predict that species at higher trophic levels are more negatively affected by isolation than lower trophic level species. By combining ecological data with genetic information from microsatellite markers we tested this hypothesis on the butterfly *Maculinea nausithous* and its specialist hymenopteran parasitoid *Neotypus melanocephalus*. We assessed the susceptibility of both species to habitat fragmentation by measuring population density, rate of parasitism, overall genetic differentiation (θ ST), and allelic richness in a large metapopulation. We also simulated the dynamics of genetic differentiation among local populations to asses the relative effects of migration rate, population size, and haplodiploid (parasitoid) and diploid (host) inheritance on metapopulation persistence. We show that parasitism by *N. melanocephalus* is less frequent at larger distances to the nearest neighbouring population of *M. nausithous* hosts, but that host density itself is not affected by isolation. Allelic richness was independent of isolation, but the mean genetic differentiation among local parasitoid populations increased with the distance between these populations. Overall, genetic differentiation in the parasitoid wasp was much greater than in the butterfly host and our simulations indicate that this difference is due to a combination of haplodiploidy and small local population sizes. Our results thus support the hypothesis that *Neotypus* parasitoid wasps are more sensitive to habitat fragmentation than their *Maculinea* butterfly hosts.

Keywords: Host-parasitoid interaction, isolation, *Maculinea*, metapopulation, population genetics, spatial structure.

7 Synthesis

7.1 Main results

This dissertation was involved in the European research project *MacMan* (MACulinea Butterflies of the Habitats Directive and European Red List as Indicators and Tools for Habitat Conservation and MANagement, supported by the European Commission under the fifth framework program). The work presented here aimed to investigate the trophic relationships in the community module of the predatory large blue *M. nausithous*.

The density of the egg and adult stages of *M. nausithous* is limited by the density of the host ant *Myrmica* rubra (chapter 2). However, ant-released chemicals do not act as oviposition cues for female *M. nausithous*. The observed egg distribution was primarily explained by host plant characteristics and environmental variability among sites (chapter 3). For the first time, quantitative data on parasitism by specific larval parasitoids of large blues were gained. The butterfly *M. nausithous* itself is host to the parasitoid wasp *Neotypus melanocephalus*. The analysis of field populations did not show a density-dependent relationship between *M. nausithous* caterpillars and parasitism. Habitat parameters like patch size and density of the host's food plant did not affect the parasitism rate. Female *N. melanocephalus* parasitoids increased foraging success by preferring to search on large flower heads and probed host-occupied flower heads.

Nine dinucleotide microsatellite DNA loci were described to analyse the population genetic structure of the parasitoid *N. melanocephalus* (chapter 5). By combining ecological data with genetic information from microsatellite markers I assessed the susceptibility of both host and parasitoid to habitat fragmentation by measuring density, parasitism, overall genetic differentiation, and allelic richness in a large metapopulation. This dissertation shows that the overall genetic differentiation across local populations is moderate in the butterfly *M. nausithous* and strong in the specialised parasitoid *N. melanocephalus*. Genetic differentiation across parasitoid populations increased with distance to the nearest *M. nausithous* host population and decreased with host population size. However, genetic differentiation did not result in reduced allelic richness of isolated populations in either species. In fact, population specific allelic richness in the parasitoid increased with the adult population size of the host. A pattern of isolation by distance was found in the butterfly host, but was absent in the parasitoid. Parasitism rates were reduced in isolated populations, but host density was not affected by population isolation (chapter 6).

7.2 Is *Maculinea nausithous* top-down or bottom-up limited?

Terrestrial communities are comprised of decomposers plus three trophic levels: plants, herbivores and predators (or parasitoids, pathogens; Hairston *et al.* 1960). In insect parasitoids, we can occasionally find a fourth trophic level. Hyperparasitoids are recognised as higher-order predators (Rosenheim 1998, Sullivan and Völkl 1999). Since the initial work by Lindemann (1942) there has been a controversial debate on the question whether resources (bottom-up) or natural enemies (top-down), or both, determine the abundance of insect herbivore populations (e.g. Hairston *et al.* 1960; White 1978). The influential paper by Price *et* *al*. (1980) represented the departure from this dichotomy by considering that three trophic levels strongly interact in many terrestrial systems. Though this dissertation does not enable to answer the question whether the density of *M. nausithous* is bottom-up or top-down-limited, it gives some valuable insights. The field study presented in chapter I shows that a potential bottom-up limitation of *M. nausithous* is restricted to *Myrmica* host ants. Walker and Jones (2001) suggest that herbivores may be bottom-up limited if plant populations have low colonization rates and high extinction risks. *Sanguisorba officinalis*, the food plant of *M. nausithous*, is a perennial plant and shows very low levels of genetic differentiation in the study area (Musche, unpublished). Though significant proportions of seed set are destroyed by *M. nausithous* larvae (Musche, unpublished), the clonal reproduction effectively enables this plant to persist. The second resource of *M. nausithous*, the red ant *M. rubra*, is very common in numerous habitat types (Seifert 1996). Though there are frequent extinctions of local ant nests due to over-exploitation by *M. nausithous* (Thomas and Elmes 1998), the rapid re-colonisation from surrounding areas may prevent long-term absence from sites (Singer 2006, Loritz, unpublished). The limiting (bottom-up-) role of *M. rubra* ant density for *M. nausithous* population density may be accompanied by top-down effects of parasitism (Fig. 1). The parasitoid *N. melanocephalus* appears to be not attacked by hyper-parasitoids. The absence of a fourth trophic level may suggest that the density of *N. melanocephalus* is exclusively limited by the density of *M. nausithous* host caterpillars and that *Neotypus* parasitoids may thus have a significant top-down impact on *M. nausithous*. However, according to Hassell (2000), density-dependent parasitism is an important hint for top-down control of herbivores by parasitoids. The absence of such a relationship in *M. nausithous* (chapter 3) supports the idea that *M. rubra* plays a dominant role in determining population density of *M. nausithous*.

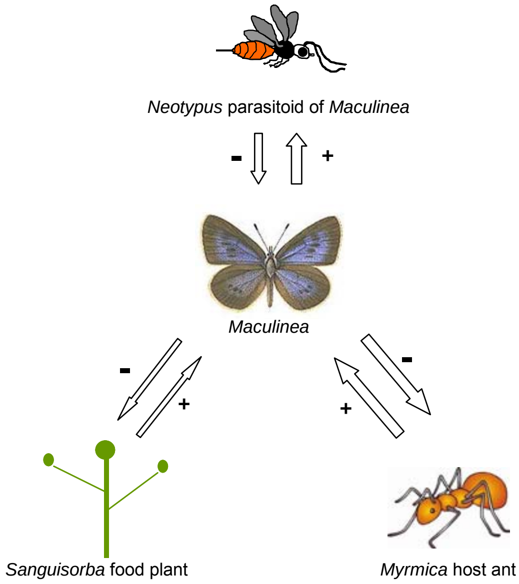

Fig. 1 Trophic relationships between *M. nausithous, Neotypus* parasitoids, *M. rubra* host ants and *S. officinalis* food plants. The strength of the arrow indicates the strength of the interaction between species.

7.3 Decreasing levels of gene flow with increasing trophic level

The solitary parasitoid *N. melanocephalus* (global genetic differentiation θ_{ST} =0.12) has lower levels of gene flow than its butterfly host *M. nausithous* (θ_{ST} =0.07, chapter 6). The butterfly host itself has an intermediate position concerning gene flow, because its food plant shows very low genetic differentiation in the study area (θ_{ST} = 0.008, Musche, unpublished). Because of the frequent occurrence of *Myrmica rubra* in numerous habitat types (Seifert 1996), the host ant of *M. nausithous* is expected to show similar levels of gene flow. The trophic cascade of energy loss through trophic levels may thus be accompanied by decreasing levels of gene flow in this system. Here, decreasing levels of gene flow with increasing trophic level may not be caused by limited absolute dispersal ability of the species (which may e.g. be greater in the parasitoid *N. melanocephalus* than in the large blue *M. nausithous*), but caused by small population size of increasingly fragmented populations. Such cascades of gene flow, however, may be restricted to community modules of closely interacting species.

7.4 What happens to community modules if top-species are removed?

Neotypus melanocephalus, which is specific to the butterfly *M. nausithous*, shows decreased levels of parasitism in isolated butterfly populations and diminished levels of gene flow in the study area (chapter 6). Thus, this parasitoid may reach the threshold of local extinction sooner than its butterfly host. Habitat fragmentation being continued, the top level species of the *Maculinea* community module is threatened to extinction in the long term.

Non-density-dependent parasitism is expected to stabilise host population dynamics (Anderson and May 1978). The simplest qualitative prediction of food chain models is that the addition or removal of top predators can cause dramatic changes in species abundances at lower trophic levels (Power 1992; Spiller and Schoener 1994; Holt 1997). The short-term response of *M. nausithous* to extinction of local *N. melanocephalus* populations may be an increase of local population capacity. Subsequently, *M. nausithous* populations are expected to overexploit local host ant resources leading to local butterfly extinctions. The amplitude of population fluctuations is thus expected to increase as known from simple predator-prey dynamics (Lotka 1925; Volterra 1926).

7.5 Co-evolution of *Maculinea* host and *Neotypus* parasitoid?

Co-evolution happens when two or more species influence one another’s evolution (Ridley 1999). It should be distinguished from sequential evolution where a change in one species selects for changes in a second species, but not the reverse. In host parasitoid systems, co-evolution is the interaction between host resistance and parasitoid virulence. Resistance describes the ability of the host to destroy parasitoid eggs and virulence the ability of the parasitoid to overcome host defences (Godfray 2000). Due to the high specificity between *M. nausithous* hosts and *N. melanocephalus* parasitoids, the strength of co-evolutionary interaction should be equal for both species. Theoretical studies predict that species with higher gene flow are locally more adapted (Gandon and Michalakis 1996; Gandon *et al*. 1998). High levels of gene flow distribute a variety of genotypes that may lead to local fitness increase. Lower parasitism rates in isolated host populations and the genetic structure of *N. melanocephalus* populations suggest that this parasitoid has lower levels of gene flow than its butterfly host. Because of the limited dispersal of *N. melanocephalus* the evolution of counter defences is expected to lack behind the ability of the host to encapsulate parasitoid eggs.

7.6 Conclusion

This dissertation provides insight into the population ecology and behaviour of parasitoids attacking predatory *Maculinea* species. The parameters gained in the behavioural study allow the incorporation of parasitoids in theoretical studies on *Maculinea* population dynamics. Such modelling studies that involve three trophic levels and four species were done for the cuckoo-species *M. rebeli/alcon* (Hochberg *et al.* 1996), but are still lacking for predatory *Maculinea*, such as *M. nausithous*.

A key finding of practical relevance in this dissertation is the sensitivity of *Neotypus* parasitoids to habitat fragmentation. The demographic and genetic analyses presented in this study suggest that *Neotypus* parasitoids are more sensitive to population isolation than their butterfly host. Thus, the equilibrium of local population extinction and colonization of *Neotypus* parasitoids may be endangered in the long term. Hochberg (2002) stressed that the incredible diversity of insect parasitoids discounts the concept of their conservation despite of their important ecosystem function and Shaw (2006) showed that habitat conservation for parasitoids is still in his infancies. This dissertation suggests that the *Maculinea-Neotypus* system is still functioning in the Upper Rhine valley. Facing the ongoing intensification of land use in the Upper Rhine valley (Loritz, unpublished), fragmentation might interrupt trophic interactions soon. Therefore, small habitat patches like waysides and fallow land become increasingly important for this butterfly. In order to maintain high local butterfly densities (and accordingly stepping stone populations for *N. melanocephalus*), habitat management efforts should aim to increase the local densities of *Myrmica* hosts. Host ant-oriented management of the above mentioned habitat types and specific mowing regimes in agriculturally used grasslands (Johst *et al*. 2006) may enable the survival of this fascinating host-parasitoid system.

7.7 References

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8 Zusammenfassung

In dieser Dissertation wurden die Nahrungs-Beziehungen in einem so genannten *community module* analysiert. In solchen Modulen können Nahrungsbeziehungen in einer kleinen Gruppe von Tier- und Pflanzenarten untersucht werden, da deren Dynamik losgelöst von weiteren Arten der Lebensgemeinschaft verstanden werden kann. Als Modellsystem für diese Arbeit dient der Dunkle Ameisenbläuling *Maculinea nausithous*. Hauptmerkmal der Bläulinge (Lycaenidae) ist die mit Ameisen verbundene Lebensweise. In den meisten Fällen sind diese Beziehungen mutualistisch, dass heißt der Kontakt geschieht zum gegenseitigen Vorteil. Die Bläulingsraupen sondern aus einer speziellen Drüse am Rücken Sekrete ab, die von den Ameisen aufgenommen werden. Im Gegenzug schützen die Ameisen die Raupen vor Fressfeinden wie zum Beispiel parasitischen Wespen. Der Selektionsdruck durch Schlupfwespen gilt als die wichtigste Ursache für die enge Beziehung zwischen Bläulingen und Ameisen. Die Vielfalt der Beziehungen von Bläulingen mit Ameisen reicht hierbei von gelegentlichen Kontakten mit mehreren Ameisenarten bis zu obligaten Beziehungen mit nur einer einzigen Ameisenart, ohne die sich der Bläuling nicht entwickeln kann. In wenigen Arten hat sich der Ameisenkontakt weg von einer mutualistische Beziehung hin zu einer parasitischen Beziehung entwickelt, die zum Nachteil der Ameisen verläuft. Exemplarisch für diese Lebensstrategie steht die Bläulingsgattung *Maculinea*. Die Raupen dieser Gattung verbringen den Großteil ihrer Larvalentwicklung räuberisch in Ameisennestern. Zuvor fressen sie jedoch für eine kurze Zeit auf bestimmten Futterpflanzen und entwickeln dort den trickreichen Mechanismus, der sie ins Ameisennest einschleust: chemische Mimikry. Mit Hilfe stickstoffreicher Futterpflanzenbestandteil ist die Bläulingsraupe nach etwa zwei bis drei Wochen in der Lage, auf ihrem Rücken chemische Stoffe zu produzieren, die denen der Ameisenbrut gleichen. Trifft eine Arbeiterin der spezifischen Wirtsameise auf eine solche Raupe, hält sie diese für ihre eigene Brut. Damit ist der Weg frei ins Ameisennest, dessen Eingänge für Eindringlinge sonst nur schwer zu durchdringen sind. Die Arbeiterin trägt die Raupe ins Nest, wo diese sich bis zum nächsten Sommer räuberisch ernährt und teilweise sogar gefüttert wird.

Im Zentrum dieser Arbeit steht die Lebensgemeinschaft um den Ameisenbläuling *M. nausithous*. Nach der Eiablage auf den Blüten des Großen Wiesenknopfs fressen die Jungraupen versteckt in den Samenanlagen. Nach etwa zwei Wochen lassen sich die Raupen von der Futterpflanze fallen. Stoßen Arbeiterinnen der Roten Knotenameise (*Myrmica rubra*) auf Raupen von *M. nausithous*, werden diese nach einem aufwändigen Ritual „adoptiert“ und zur Ameisenbrut in die Kolonie getragen. Im folgenden Sommer schlüpft aus dem Ameisennest der fertige Falter. Trotz ihrer verborgenen Lebensweise in Blütenköpfen haben die Raupen von *M. nausithous* einen natürlichen Gegenspieler. Die hoch spezialisierte Schlupfwespe *Neotypus melanocephalus* parasitiert die Bläulingsraupen, während diese im Blütenkopf fressen. Kurz vor dem Abschluss der Metamorphose im Ameisennest tötet der so genannte Parasitoid seinen Wirt: Aus der Puppenhülle schlüpf statt des Schmetterlings die adulte Schlupfwespe.

Der erste Teil dieser Arbeit (Kapitel 2-4) beschäftigt sich mit den Nahrungsbeziehungen zwischen *M. nausithous*, seiner Wirtsameise, seiner Futterpflanze und dem Parasitoiden. In Kapitel 2 beantworte ich die Frage, ob die

Futterpflanze oder die Wirtsameise die Populationsdichte von *M. nausithous* limitieren. Während die Dichte der Eier und der adulten Falter mit der Häufigkeit der Wirtsameise korrelierten, bestand zwischen der Raupendichte und beiden Nahrungsressourcen kein Zusammenhang. Da der Große Wiesenknopf und die Knotenameise *M. rubra* ihre höchsten Dichten in sehr unterschiedlichen Habitaten erreichen, ergeben sich aus diesem Resultat wichtige Hinweise für den Naturschutz dieser gefährdeten Bläulingsart. Da die Wirtsameise die limitierende Ressource für *M. nausithous* ist, sollten sich Habitaterhaltungs-Maßnamen an dem Ziel orientieren, lokal eine hohe Dichte der Wirtsameise zu ermöglichen. Je nach Produktivität des lokalen Standorts sollte eine regelmäßige Mahd das Verbuschen der Wiesen verhindern.

Im Zentrum des dritten Kapitels dieser Arbeit steht eine Frage, die in den vergangenen Jahren in internationalen Zeitschriften kontrovers diskutiert wurde: Können *Maculinea*-Weibchen bei der Eiablage die Anwesenheit der Wirtsameise feststellen? Zur Beantwortung dieser Frage wurde mit dieser Arbeit erstmals ein experimenteller Ansatz gewählt. Während der Flugzeit von *M. nausithous* wurde ein Teil der Blüten des Großen Wiesenknopfs mit Erde aus Wirtsameisennestern beimpft. Die Erde diente als Trägerstoff für die charakteristischen Duftstoffe der Knotenameisen. Nach zweiwöchiger Beimpfung zeigte sich, dass Blüten, die den Ameisenduftstoff tragen, nicht bei der Eiablage bevorzugt wurden. Stattdessen bestimmten Pflanzenmerkmale wie Blühstadium und Blütenkopfgröße sowie Habitatparameter die Zahl abgelegter Eier.

Aufgrund der hoch spezialisierten Lebensweise haben Bläulinge der Gattung *Maculinea* nur sehr wenige Fressfeinde. Kapitel 4 liefert erstmals Einsichten in die Populationsökologie und das Verhalten der Schlupfwespe *Neotypus melanocephalus*. Im Zentrum des populationsökologischen Teils stand die Frage, welche Faktoren die lokalen Parasitierungsraten dieses Parasitoiden beeinflussen. Der Anteil parasitierter Raupen wird weder von der Raupendichte noch von Habitatparametern wie der Futterpflanzendichte des Wirts oder der Größe des Habitats (als Annäherung für die Wirtspopulationsgröße) beeinflusst. Bei der Suche nach Wirtsraupen gehen die Parasitoidweibchen jedoch nicht unsystematisch vor: sie bevorzugen großen Blütenköpfe, die kurz vor dem Verblühen stehen. In diesen Köpfen ist die Wahrscheinlichkeit nachweislich am größten, Larven von *M. nausithous* anzutreffen. Ist das Weibchen beim Betrommeln der Blütenköpfe nicht nach einer bestimmten Zeit fündig geworden, verlässt es diesen. Blütenköpfe, die Wirtsraupen enthalten, werden deutlich länger abgesucht als Köpfe, in denen sich keine Raupen befinden. Während der Wirtssuche entscheiden sich die Wespen frühzeitig, wie viel Zeit in einen Blütenkopf investiert wird und können auf diese Weise auch Habitate mit geringer Wirtsdichte ausbeuten.

Im zweiten Teil dieser Arbeit untersuchte ich die genetische Populationsstruktur von *M. nausithous* und *N. melanocephalus*. Neun molekulargenetische Marker wurden entwickelt, um mit diesen selektionsneutralen „Mikrosatelliten“ die Populationsstruktur von *N. melanocephalus* zu analysieren (Kapitel 5). Anschließend wurde mittels eines Vergleichs untersucht, ob sich die Theorie bestätigt, wonach Arten aus höheren trophischen Ebenen empfindlicher auf die Isolation von Populationen reagieren als Arten niedriger trophischer Ebenen. In diesen Vergleich wurden neben dem Grad der genetische Differenzierung und der genetischen Diversität auch demographische Daten wie Schmetterlingsdichte und

Parasitierung miteinbezogen. Populationen von *N. melanocephalus* zeigten eine deutlich stärkere genetische Gesamtdifferenzierung als die Populationen von *M. nausithous*. Um den Effekt der unterschiedlichen Fortpflanzungssysteme abzuschätzen (Diploidie beim Wirt *versus* Haplodiploidie bei der Wespe), wurde der Genfluss in einer Metapopulation simuliert. Die Haploidie der Hymeopteren-Männchen hatte einen signifikanten Einfluss auf die Populationsstruktur der Wespen. Das Fortpflanzungssystem allein konnte jedoch nicht die starke genetische Differenzierung der Parasitoid-Population erklären. Die reduzierte Populationsgröße der Parasitoide hatte ebenso einen großen Einfluss. Aus den Simulationen wurde die Erkenntnis gewonnen, dass eine haploide Art mit geringerer Populationsgröße als die Wirtsart sehr ausbreitungsstark sein muss, um diesen Effekt auszugleichen. Die Differenzierung der Parasitoid-Populationen nahm mit der Entfernung zur nächsten Population zu, was auf einen reduzierten Genfluss hindeutet. Gleichzeitig hatten Parasitoid-Populationen aus großen Wirtspopulationen eine höhere genetische Diversität. Der gleiche Effekt hat sich bei der genetischen Differenzierung gezeigt. Parasitoid-Populationen in großen Wirtspopulationen waren genetisch weniger differenziert, was auf eine bessere Vernetzung von und einen intensiveren Genfluss zwischen großen Populationen hinweist. Die Analyse demographischer Daten in Bezug auf die Isolation der Habitate unterstützte die Hypothese, dass Parasitoide empfindlicher auf Habitatfragmentierung reagieren als ihre Wirtsarten: Während die Parasitierungsraten in isolierten Populationen abnehmen, zeigte sich bei den Ei-, Raupen-, und Adultstadien des Falters keine solche Beziehung.

Abschließend lässt sich für den Naturschutz aus dieser Dissertation die Erkenntnis gewinnen, dass der natürliche Gegenspieler des Dunklen Ameisenbläulings gefährdeter ist als seine Wirtsart. Bei fortschreitender Intensivierung der Landnutzung und der daraus resultierenden Fragmentierung der Lebensräume von *M. nausithous* ist zu befürchten, dass die Wespenart *N. melanocephalus* früher als der Bläuling einen Schwellenwert erreicht, ab dem das Gleichgewicht zwischen dem lokalen Aussterben von Populationen und der Wiederbesiedelung von Habitaten gestört ist. Für eine funktionierende Metapopulation beider Arten ist ein dichtes Netz aus Teilpopulationen notwendig. Diese Arbeit zeigt, dass die lokalen Populationsdichten des Dunklen Ameisenbläulings von seiner Wirtsameise bestimmt werden und Naturschutzmaßnahmen sich an diesem Ziel orientieren sollten.

9 Danksagung

Mein herzlicher Dank gilt Josef Settele für die engagierte Unterstützung und die exzellenten Rahmenbedingungen in seiner Arbeitsgruppe. Walter Durka danke ich für die Einführung in die Populationsgenetik und dafür, mir bei allen Problemen und Fragen immer mit großem Engagement geholfen zu haben. Robin Moritz gilt mein Dank für die freundliche Bereitschaft, meine Dissertation an der Uni Halle-Wittenberg zu betreuen.

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Vielen Dank für die in den jeweiligen Kapiteln genannte Mithilfe an Oliver Boßdorf (Kapitel 2), Daniela Faust (2 & 6), Maria Filowa (2 & 6), Sarah Gwillym (5), Klaus Horstmann (4), Hannelore Jany (2 & 4), Holger Loritz (2 & 5), Christof Manhart (3), Martin Musche (5), Daniel Prati (3), Karsten Schönrogge (4), Christian Stettmer (3), Vicky Temperton (2 & 4), Palle Villesen (5) und Dana Weinhold (2 & 6).

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10 Appendix

10.1 Curriculum Vitae

Name	Anton
First name	Christian
Date of birth	1973-09-27 in Freudenberg (Westfalen)
Adress	Fichtestraße 4, 06114 Halle

Education/Jobs

Scientist Helmholtz-Center for Environmental Research, January 07-
PhD student UFZ, March 02-September 05
Research stay at Copenhagen University, 06- 20 May 2003
PEER Course in **Ecological Modelling**, Großbothen, March 2003
Diploma thesis “Host selection and performance of the parasitoid *Cotesia melitaearum* in a tri-trophic context”. Supervision: Saskya van Nouhuys (Metapopulation Research Group, University Helsinki), Wolfgang W. Weisser (Institute of Ecology, University of Jena)
University of Jena, 1997-2001, Diploma in biology with a major in ecology and minors in Botany, Zoology and Law
University of Helsinki, June-September 2000, Research stay for Diploma thesis (data gathering)
University of Osnabrück, 1993-1997, Studies of biology
Ev. Gymnasium Siegen-Weidenau, 1993, Abitur

10.2 Publications

Anton C, Musche M, Hula V & Settele J (2007) Myrmica host ants limit the density of the large blue Maculinea nausithous.
Journal of Insect Conservation (in press).

Anton C, Zeisset I, Musche M, Durka W, Boomsma J & Settele J (2007) Population structure of a large blue butterfly and its specialist parasitoid in a fragmented landscape.
Molecular Ecology 16, 3828-3838.

Anton C, Musche M & Settele J (2007) Spatial patterns of host exploitation in a larval parasitoid of the predatory Dusky Large Blue, *Maculinea nausithous*. Basic and Applied Ecology 8, 66-74.

Anton C, Settele J & Durka W (2006) Nine polymorphic microsatellite loci for the parasitic wasp *Neotypus melanocephalus* (Hymenoptera: Ichneumonidae). Molecular Ecology Notes 6, 399-402

Musche M, Anton C, Worgan A & Settele J (2006) No experimental evidence for ant-dependent oviposition in an ant-parasitic butterfly. Journal of Insect Behavior 19, 631-643.

Anton C, Arlt D & Schurr F (2000) Einfluss von *Bromus erectus* auf *Brachypodium pinnatum* und die Vegetation von Halbtrockenrasen.
Beiträge zur Ökologie 4, 55-62.

10.3 Contributions of co-authors

The following table shows the contributions of co-authors to the original articles.

	CA (%)	JJB	WD	BG	WH	MM	JS	AW	IZ
Chapter 2	**90**								
Idea	x					x	x		
Empirical data gathering Maculinea field	x				x	x			
Emp. data gathering Maculinea lab	x					x			
Emp. data gathering ant determination	x								
Analysis	x								
Manuscript	x								
Chapter 3	**10**								
Idea	x					x	x		
Empirical data gathering field	x					x		x	
Emp. data gathering lab									
Analysis						x			
Manuscript						x			
Chapter 4	**95**								
Idea	x						x		
Empirical data gathering field	x					x			
Empirical data gathering lab	x								
Analysis	x								
Manuscript	x								
Chapter 5	**80**								
DNA extraction	x								
Cloning				x					
Raw data handling of 96 sequences	x								
Primer design	x								
Test for polymorphism/multiplex	x		x						
Analysis	x		x						
Manuscript	x								
Chapter 6	**80**								
Idea	x	x					x		
Emp. data gathering field	x					x			
Extraction/PCR Neotypus	x								
Extraction/PCR Maculinea									x
Analysis	x		x						
Manuscript	x								
CA=Christian Anton, JB=Jacobus Boomsma (Professor), WD=Walter Durka (Scientist), BG=Barbara Gautschie (Postdoc), WH=Wladimir Hula (Field assistant), MM=Martin Musche (PhD student), JS=Josef Settele (Scientist), AW=Andrew Worgan (Scientist), IZ=Inga Zeisset (Postdoc)									

10.4 Declaration of self-contained work

Herewith I affirm that I composed the dissertation “Trophic interactions and population structure of the large blue butterfly *Maculinea nausithous* and its specialist parasitoid” single handed without utilising illegitimate resources. I used no other than the cited references and facilities. This work has not been previously handed in to another university and was not subject to miscellaneous examinations.

Halle, 18.03.2007 Christian