Analysing effects of spatiotemporally distributed species interactions in Maculinea systems

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Contents

Part I

Introduction

Introduction

Ecological multi-species systems are driven by many spatially distributed processes. There is no general theory on the interplay of small scale ecological processes and how they affect dynamics at larger scales (e.g. Levin, 2000; Wootton, 2001; Green et al., 2005). Nonetheless, conservation of species communities in order to preserve biodiversity requires understanding the complex systems of many interacting species (Poiani et al., 2000; Ebenman & Jonsson, 2005, and references therein). But, for a particular conservation action, it is sufficient to develop landscape management measures, which are suitable for the community under consideration. Having in mind a concrete case study, it is easier to recognise processes and their effects on performance of species (Shrader-Frechette & McCoy, 1993; Krause & Ruxton, 2002; Crowley et al., 2005).

In this thesis, we present an analysis framework for complex systems of interacting species. It is orientated at a central objective of nature conservation: the persistence of species in a habitat. By means of a simulation model, a multitude of scenarios is tested for their suitability to sustain species communities. Knowledge on suitability helps to detect which properties of the scenarios noticeably affect species survival. In this context, a method for the evaluation of landscapes is suggested, which accounts for species behaviour and ecological processes. In more detailed investigations on few strongly influencing scenarios, mechanisms are analysed which provoke the effects.

Following the concept, we study the influence of spatiotemporal host distribution and species interaction on survival of Maculinea populations on isolated habitat sites.

Parasitic butterflies of genus Maculinea live in close relation to their specific obligatory host plants and host ants of genus Myrmica (Weidemann, 1986; Thomas et al., 1998a; Wynhoff, 2001). There are five European Maculinea species (but see Als et al., 2004; Thomas & Settele, 2004). Each of them is restricted to one or two host plants and several Myrmica host ant species, depending on the geographical region (Thomas et al., 1998a; Tartally & Varga, 2005; Thomas et al., 2005; Witek et al., 2005). The narrow interaction in Maculinea species communities, where only few species are strongly involved, make them a perfect study system. All five European Maculinea species are listed as nearly threatened or vulnerable in the IUCN red list (IUCN, 2004). They are listed in Annex B of the EU's Habitats Directive. Because some of the species are endemic, Europe has an increased responsibility for their conservation. This for example expresses in the installation of the EU research project MacMan[1] (Settele et al., 2002, 2005). This thesis has arisen from the project.

In this work, we aim to reveal, how spatially distributed parasitism of Maculinea on its hosts

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[1] Maculinea Butterflies of the Habitat Directive and European Red List as Indicators and Tools for Habitat Conservation and Management

affects population dynamics of the species and in consequence persistence of the butterfly population. From our findings, we can give advises for the management and evaluation of closed habitat sites. But, with our generic approach we do not restrict to the case study of one Maculinea species. Observations on transient behaviour or host-parasite-mechanisms of the Maculinea system are relevant in a broader context of interacting species systems.
A major part of the thesis is dedicated to the development of new methods. With analytical and numerical calculations, we enhance a recently by Wissel & Stöcker (1991); Stephan (1992); Stephan & Wissel (1994b); Wissel et al. (1994); Stelter et al. (1997); Frank et al. (2002); Grimm & Wissel (2004) suggested approach for population viability analysis (PVA) on single species, and make it applicable for interacting species systems. Further, we suggest a method for landscape evaluation which takes into account species perception of the spatial structure. These methods should open new paths in community and landscape ecology.

The thesis consists of three parts. The first part is dedicated to a short introduction of the ecological system and development of a simulation model. In the first chapter, development of the stochastic spatially explicit rule-based simulation model Macu is presented.
The second part deals with non-spatial analysis of the system. An overview on host-parasite-dynamics calculated by the Macu model is given in chapter two. The third chapter provides the theoretical foundation for population viability analysis (PVA) on interacting-species systems, while in the fourth chapter, the method is tested assessing persistence of Maculinea populations. Results of both chapters provide new interesting insight to extinction dynamics of interacting species systems.
In the third part of the thesis spatiotemporal species interactions are taken into account. Initially, in chapter five, a method is developed which evaluates landscape structures according to species demands. In chapter six, this method is extensively applied to investigate influence of host plant and host ant distribution on persistence of Maculinea butterflies. Guided by earlier results, in the seventh chapter, we enter deeper into the complex spatiotemporal dynamics of the system and work on the development of a spatial index for habitat suitability. Finally, in the eighth chapter, we give a preview on model simplification and approximation with some preliminary results.
Each chapter in this thesis is a closed entity and can be read independently of the others. This structure in few occasions leads to short repetitions of earlier results. However, this form of presentation is advantageous, as it allows to entirely expose one topic after the other. The sequence of the chapters follows the order of investigations.

Part II

Ecology and Model

Chapter 1

Development of the Macu simulation model

1.1 Introduction

Spatially heterogenous habitat distribution can promote coexistence of interacting species for different reasons; for example different dispersal abilities of species (Holyoak & Lawler, 1996; Holyoak, 2000; Ellner et al., 2001), refuges from predation (Huffaker, 1958; Amezcua & Holyoak, 2000; Poggiale & Auger, 2004), small probability of encounter (Hassell et al., 1991; Cuddington & Yodzis, 2002) or self-organised pattern formation (De Roos et al., 1998). For a brief review on literature see Hosseini (2003, and references therein).

The Maculinea system can be considered as a model system to study effects of spatial habitat structures on coexistence of parasitic Maculinea butterflies, their obligatory initial host plant and the Myrmica host ants which are obligatory hosts for the 4th instar larvae until eclosion. Because, first the system is mainly restricted to these species due to their close interaction. Second, the distribution of initial host plants spatially structures a Maculinea habitat site. The spatial distribution of these oviposition plants can be considered as a heterogeneous landscape for a local Maculinea system. Third, Maculinea systems are well studied in respect to population ecology by field, laboratory and model investigations. In particular spatiotemporal dynamics of Maculinea butterflies and hosts are currently studied in field investigations (Glinka or Witek, priv. comm.).

In this chapter, we develop a rule-based spatially explicit stochastic simulation model to analyse effects of spatial host plant distribution (landscape structure) and spatiotemporal dynamics of host ants on the persistence of Maculinea butterflies. This so called Macu model is based on the HCET model for Maculinea rebeli populations (Hochberg et al., 1994; Clarke et al., 1997, 1998). In simulation experiments, using the mainly validated (Elmes et al., 1996) quite realistic HCET model, effects of spatial distribution of hosts on performance of Maculinea populations are found. However, different processes can contribute to these effects. Their relative influence is not clear.

In contrast, the Macu model is designed for investigations of effects of spatiotemporal interactions of hosts and parasite species, in particular. This concept is expected to provide general new insight into theory of spatial host-parasite dynamics and species coexistence. Nevertheless, results are supposed to be embedded and interpretable in the context of natural Maculinea systems.

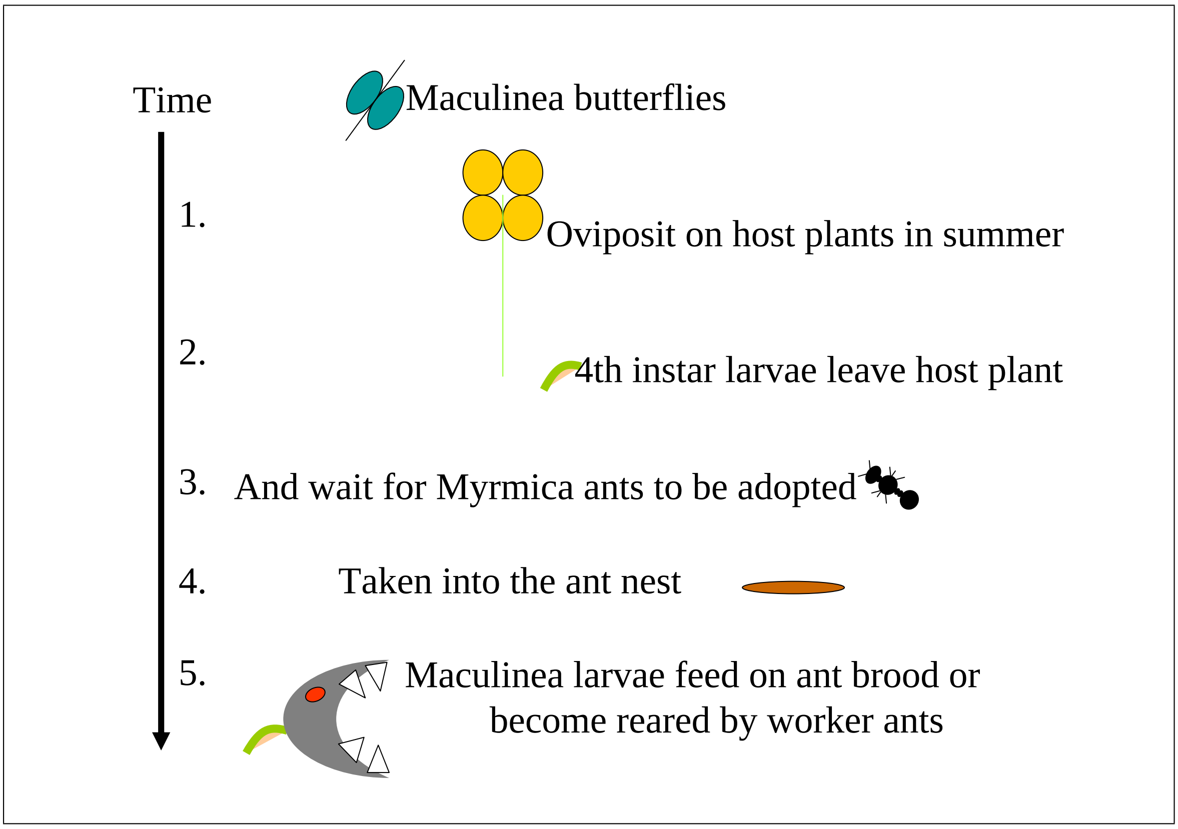

Figure 1.1: Simplified life cycle of Maculinea

1.2 Ecology of Maculinea systems

In this description of Maculinea ecology, we restrict to general processes which allow understanding of the model definition in sec. 1.3. For further details on the Maculinea system refer to the following literature: An overview on population dynamics in systems of Maculinea can be found in Thomas et al. (1998a); Nowicki et al. (2005). Elmes et al. (1998) summarise relevant facts about the ecology of Myrmica ants concerning their interaction with Maculinea species. An overview on ecology of Myrmica ants is given in Elmes (1991). The book by Settele et al. (2005) provides comprehensive material on recent scientific results about Maculinea systems.

1.2.1 Maculinea

A quick overview on the life cycle of Maculinea species is given in fig. 1.1. Adult Maculinea butterflies fly in summer. During the flight period, the butterflies lay eggs on the flowers of their host plants. Oviposition is restricted to one or two host plant species. An overview on host plants of each Maculinea species is given in Thomas et al. (1998a, tab. 11.1). Maculinea females distribute their eggs (about 50-75 eggs per M. arion female (Thomas et al., 1998a), but can be higher (Hochberg et al., 1992, 1994)) on several host plant individuals. Usually only one egg is deposited on a flower head (Thomas et al., 1991). This finding is supported for Maculinea teleius (Wynhoff, 2001)[p. 25]. Thomas et al. (1991) on average have found about

3 to 10 eggs per host plant for four different Maculinea species, whereas maximum number of eggs per plant is about 5 times higher. For Maculinea rebeli, they give an average value of 59.3 and a maximum of 304 eggs per host plant. They indicate, that the host plant species of M. rebeli (Gentiana) typically grows in lower densities than host plants of other Maculinea species.

During the first three larval stages, Maculinea caterpillars stay and feed on the plant. Only about 1% of entire body mass of the adult Maculinea specimen is gained during that initial period on the host plant (e.g. Thomas et al., 1991). These young larvae undergo density independent and density dependent mortalities caused e.g. by predation or starvation (Hochberg et al., 1992). Wynhoff (2001, p. 24) reports a 50% survival for Maculinea teleius and a 47% survival for Maculinea nausithous on plants (from the egg to 4th larval instar). Thomas et al. (1998a) reviews earlier investigations. They find a larval mortality of $20-40\%$ including failure of adoption (see below). However, they point out, that inside an ant nest (see below) Maculinea experience higher mortality rates of $80-90\%$.

Fourth instar larvae leave their host plants. For Maculinea rebeli, it is observed, that larvae leave the plants in the early evening which coincides with foraging time of Myrmica ants (Elmes et al., 1991a). On the ground, Maculinea caterpillars stay in vicinity of their initial host plants. They wait until they are found and adopted by Myrmica ants. Elmes et al. (1991a) observe a maximum distance of movement of 6cm. Thomas (2002) reports that in the wild Maculinea arion larvae, after leaving their initial food plant, do not disperse. Although in laboratory experiments, Maculinea larvae were observed to follow ant trails. Myrmica worker ants do not necessarily adopt every Maculinea larva, they find. Sometimes, an ant carries a larva a short way and then drops it again (Thomas, priv. comm.). But in general, it is said, that once a caterpillar is found and adopted, more worker ants return to the finding place and adopt other larvae from there. Therefore it is assumed, that Maculinea caterpillars are accumulated in Myrmica nests, which are neighbouring to host plants, where a large amount of Maculinea caterpillars grew up (Elmes et al., 1991a). If a Maculinea caterpillar is not found by host ants within one or two days, it dies (Settele et al., 1995, and references therein).

Inside ant nests, Maculinea larvae can benefit from many advantages. Only slightly varying climatic conditions (e.g. during hibernation) and protection against predators (Elmes et al., 1991b). But, most important is feeding. There are two different life styles for Maculinea larvae (Elmes et al., 1991a; Thomas et al., 1991, 1998a; Wynhoff, 2001). So called 'predator species' (or primitive parasites Thomas & Wardlaw, 1992) feed directly on Myrmica brood. During most time, they stay apart of main ant activity and only approach for feeding (Wynhoff, 2001, p. 26; laboratory studies: rearing experiments). So called 'cuckoo species' (advanced predators according to Thomas & Wardlaw, 1992; Elmes et al., 1998) mimic ant brood and therefore are fed and cared by worker ants.

Differences in life styles lead to different forms of intraspecific competition for Maculinea caterpillars in ant nests. If there are too many predacious Maculinea caterpillars in an ant nest, they generally eat all ant brood in the nest and thereupon all butterfly caterpillars die (scramble competition). However sometimes, they can be rescued, if the depleted nest is taken over by an offshoot from neighbouring nests (Thomas & Wardlaw, 1992). In contrast, worker ants select which of the highly abundant cuckoo caterpillars in a nest they are rearing. Thus, in nests, which are overcrowded by cuckoo larvae, a part of these larvae survive (contest competition) (Elmes et al., 1991b; Wynhoff, 2001).

Effectively, both life styles weaken rearing capacity of a Myrmica nest. From laboratory experiments it is known, that about 50 workers of Myrmica schenckii (a cuckoo species) are needed to sustain one caterpillar of Maculinea rebeli. The result is supported by field observations (Hochberg et al., 1994). In contrast, a predatory Maculinea arion caterpillar needs about 230 Myrmica sabuleti larvae until it pupates (Thomas & Wardlaw, 1992). Summarising, Thomas et al. (1998a, and references therein) estimate that about 350 Myrmica ant workers are needed to rear a predacious Maculinea, whereas only 50 workers can rear a cuckoo species caterpillar. This corresponds to estimations, that Myrmica nests of the same size can support about 6 to 7 times more cuckoo species than predacious species (Thomas et al., 1991; Thomas & Wardlaw, 1992)

Therefore, it depends on ant nest size and life style of Maculinea caterpillars, how much butterfly offspring can be reared within one nest. It is mentioned that the number of caterpillars of Maculinea teleius (predacious) in a host ant nest of Myrmica scabrinodis is low, rarely exceeding one individual (Thomas et al., 1998c). In nests of Myrmica rubra, which are larger than M. scabrinodis nests a higher number of Maculinea nausithous larvae can be supported, basing probably on a mixed predacious and cuckoo life style (Wynhoff, 2001, and references therein). In a modelling study for Maculinea rebeli, Hochberg et al. (1992) report adoption rates of 37.6 caterpillars into nests; 5.4 of them emerge. This result is contrasted in a further study (Hochberg et al., 1994), where about 16 caterpillars are adopted and about 2.3 of them emerge. In field studies, 3.5 emerging butterflies are counted (Hochberg et al., 1994, tab. 3).

It is assumed, that Maculinea larvae have their highest impact on development of Myrmica nests during spring time, when food is in shorter supply. 'They are fed in preference to the workers' own overwintered brood, which may starve or even be fed to the caterpillars' (Hochberg et al., 1994). In contrast, Myrmica larvae, which develop already in autumn, are not affected by inter-specific competition with Maculinea caterpillars. It is found, that about 50% of Myrmica brood develops already in autumn ('rapid brood'), whereas the other part is delayed to spring of next year ('diapause brood'). Hence, ant nest damage by Maculinea is reduced, because rapid brood is saved (Elmes et al., 1991b,a; Hochberg et al., 1994; Elmes et al., 1998).

After about 9 months, adult butterflies leave their nests. There is evidence that, at least for Maculinea rebeli, some caterpillars stay in the nest for another year. One year and two year developers can be distinguished by weight and size (Weidemann, 1986; Elmes et al., 1991b; Thomas et al., 1998b).

Parasitoids of genus Ichneumon or Neotypus predate on different species of Maculinea (Anton, priv. comm.).

1.2.2 Host plants

Host plants are necessary for oviposition and serve as habitat and food resource for young caterpillars. Kery et al. (2001) analyse the impact of herbivorous Maculinea rebeli on populations of Gentiana cruciata. They find that larger populations of Gentiana cruciata are more likely infested by Maculinea rebeli. However, genets in larger populations have more flowers. Both effects seem to compensate each other. Therefore, number of developed seeds is neither influenced by plant population size nor by herbivory. This corresponds to results from Thomas et al. (1998a), that host plant populations (Thymus and Gentiana cruciata) are stable in space and time on their Maculinea rebeli study site. (Musche, priv. comm.) assumes, that spatial distribution of Sanguisorba officinalis (host plants of Maculinea nausithous and teleius) does change only slightly from one year to the other.

Interaction of Myrmica ants and host plants is not clear, but also not suspected.

1.2.3 Myrmica ants

During most of their life cycle, Maculinea individuals live in nests of Myrmica ants (see sec. 1.2.1). Therefore it is important to have a closer look on the ecology of these ants.
Species distribution of Myrmica follows a gradient of soil temperature and soil moisture (Elmes et al., 1998, fig. 1). Several Myrmica species might co-occur within one site. There is evidence for high turn-over of nest sites between conspecifics (Elmes & Wardlaw, 1982b,a).
Species distribution of Myrmica ants is important for occurrence of Maculinea, because each Maculinea species depends on special host species of Myrmica. In Thomas et al. (1998a, tab. 11.1) some host ants are listed for different species of Maculinea. However, discussion on host-specificity of Maculinea butterflies is ongoing. New results show geographical variation (Stankiewicz et al., 2005; Tartally & Varga, 2005; Thomas et al., 2005; Witek et al., 2005).
According to Elmes et al. (1998), Myrmica host ants are best described at colony level, when considering their influence to local Maculinea populations. Abundance and size of Myrmica colonies on a site depend on the number of potential nest sites and food availability (Elmes, 1991).
Consequently, the growth of Myrmica nests is density dependent; it can be described by a logistic equation (see Elmes et al., 1998, and references therein). The growth rate is determined by habitat conditions within the foraging area of the nest. Host ant nests usually survive for about 10 years, if they are not infested by Maculinea (Thomas et al., 1998a)
Colony foundation in Myrmica species is realised either by mated queens or by fragmentation of existing colonies (see Elmes, 1991; Elmes et al., 1998). On habitat sites with an established Myrmica population, success of queen foundation is unlikely. Due to high competition for space, these small nests are either destroyed by existing congeneric colonies or taken over by conspecific colonies. For this reason, Myrmica ant dispersal mainly happens on a small spatial scale via the so called budding mechanism (fragments of existing nests bud to empty nest sites; see Hochberg et al., 1994).

1.2.4 Local interaction and spatial distribution of species

Parasitism of Maculinea butterflies on Myrmica ant brood happens on a small spatial scale, because 4th instar Maculinea larvae, after leaving their initial host plant, do not move away. Instead, in close vicinity to the plant, they wait for adoption by Myrmica host ants from a nest in the neighbourhood. Therefore, Maculinea individuals can complete their life-cycle only, if the eggs are laid on host plants, which are situated within the foraging area of a Myrmica ant nest. Foraging area of host ants is estimated to range from about $1m^2$ to $11m^2$, depending on the Myrmica ant species (Elmes & Wardlaw, 1982b; Hochberg et al., 1994; Clarke et al., 1997, 1998). Obviously, parasitism of Maculinea on Myrmica host ants is spatially restricted to areas with host plants, within a habitat site.
Clarke et al. (1997, 1998) show, that spatial distribution of host plants and spatial distribution of host ant habitat both influence population size and persistence of Maculinea rebeli populations.

1.2.5 The HCET model

For their studies, Clarke et al. (1997, 1998) used the HCET model, which was first described in Hochberg et al. (1994). The HCET model is a rule-based spatially explicit stochastic population dynamical simulation model for systems of Maculinea rebeli. It was originally developed and parameterised for a Maculinea rebeli population at Panticosa in the Spanish Pyrenees, including as well results from an earlier so called HTE model (Hochberg et al., 1992). The HCET-model was validated by successfully predicting dependency of sizes of Maculinea rebeli populations and its Myrmica schencki host ant populations on densities of the initial food plant Gentiana cruciata at 13 other sites in the French Alps and Spain (Elmes et al., 1996).

The HCET model simulates the life-cycle of Maculinea: oviposition on host plants, adoption, caterpillar rearing in ant nests, finally pupation and development to adult butterflies. There are different reasons for mortality of caterpillars. Density independent mortality on host plants and inside nests. A risky adoption process, when caterpillars either might not be found or not adopted. Inner-specific contest competition of Maculinea caterpillars is assumed on host plants and inside the ant nest. And Maculinea caterpillars might be attacked by Ichneumon eumerus parasitoids.

Spatial distribution of host plant Gentiana cruciata is assumed to be constant in time, according to field observations (Hochberg et al., 1994). Plant and their tillers are not randomly distributed.

The Myrmica ant population is modelled individual-based, Each ant nest represents an individual. Within nest dynamics as well as short-range colonisation (budding to neighbouring cells) is implemented. Two types of Myrmica ants are implemented: Myrmica schencki (host ants of Maculinea rebeli) and other Myrmica non-host species (which might adopt Maculinea rebeli but do not rear them sufficiently). There is competition for nest places between these types of Myrmica ants. Quality of nest places is heterogeneous throughout the simulation area.

For the Maculinea model, influence of spatial host distribution on performance of Maculinea butterflies was found. Strong focus was laid on analysing effects of spatially varying host ant habitat quality (Hochberg et al., 1994; Clarke et al., 1997, 1998). In another study, Thomas et al. (1997, 1998a) found apparent competition of the initial food plant Gentiana cruciata on Myrmica ants due to localised parasitism of Maculinea butterflies. An effect of host plant clumping on population size of Maculinea rebeli populations was detected (Clarke et al., 1998, and see as well ch. 2).

1.3 Model development

1.3.1 Motivation of model design

We aim to understand the effect of spatial host distribution and dynamics on the persistence of parasitic Maculinea butterfly populations. In particular, we are interested how localised parasitism in ant nests affects performance of the whole Maculinea population on a site. This is a central question for all systems of Maculinea.

For this purpose, we construct the simulation model 'Macu'. We use the HCET model as basis for model development, which gives us two advantages. First, we gain realism by employing tested and validated processes of the HCET model. Second, we profit from results of simulations of the HCET model, concerning functioning and relevance of processes. This allows to design a model specifically tailored to answer our questions.

To emphasise effects of localised parasitism of Maculinea caterpillars on host ant nests, inner-specific competition of young butterfly larvae on host plants is ignored. Hence, ant-butterfly interactions are pronounced.

With the objective to analyse effects of spatial host distributions, we exclude non-host ants from the model. Host ant habitat is homogeneously distributed on the site. By this step, spatial host distributions arise only from host and parasite dynamics. These distributions are expected to depend on dispersal ability of species. For this reason, we include a flexible mechanism of host ant dispersal (budding to empty nest sites), which gives us external control of dispersal range. Flexible host ant budding is a key factor of the Macu model. On the one hand it can be used to test effects of queen dispersal, which is expected to be important for some Maculinea systems. On the other hand is dispersal shown to influence coexistence of interacting species (e.g. Ellner et al., 2001), hence it touches our main question.

In the following, we describe the model. Thereafter we explain details of the implementation, which are important for the management of data in respect to analysis of spatial distributions and population viability.

1.3.2 Model description

1.3.2.1 Actors and processes in the system

In fig. 1.2 a causal diagram of the system is depicted. Species (actors) and their relevant properties are drawn as boxes. Rhombs indicate processes.

We start the description of the diagram with the process of oviposition. Adult Maculinea distribute eggs on host plants. The amount of eggs depends on Maculinea population size. Their spatial distribution is restricted to the spatially distributed host plants. This process results in a spatial distribution of Maculinea eggs and -after hatching- in a distribution of Maculinea caterpillars.

These caterpillars, after adoption feed in nests of Myrmica ants. The size of a nest (where 0 ants implicitly mean an empty nest site) influences the amount of butterfly caterpillars, which can develop into adults. Parasitism of ants, however, reduces nest size. Hence, development of Maculinea caterpillars feeds back on Myrmica ants.

The remaining three processes are part of the host ant dynamics. Growth of an ant nest depends on nest size. In particular, if there are no ants, there is no nest growth. Such empty nest sites can be colonised (budded) by a sprout from an existing nest, depending on its size and its distance to the empty site. This process influences spatial ant nest distribution and nest sizes. Extinction of an ant nest depends on the size of a nest. Small nests go extinct frequently. Extinction changes spatial nest distribution and size of the local nest, because ants and nest vanish.

From the graph, it becomes obvious that dynamics of host ants and butterflies is coupled. In contrast, host plants are not affected by any process. For this reason, host plants can be considered as an external factor for the system. Their spatial distribution forms the landscape, in which adult butterflies oviposit.

1.3.2.2 State variables of the model

We use variables $Z_i(t)$, $P_i(t)$ for numbers of ants and butterflies at position i at time t. Morphological state of butterflies and ants is always given by the state reached at time t

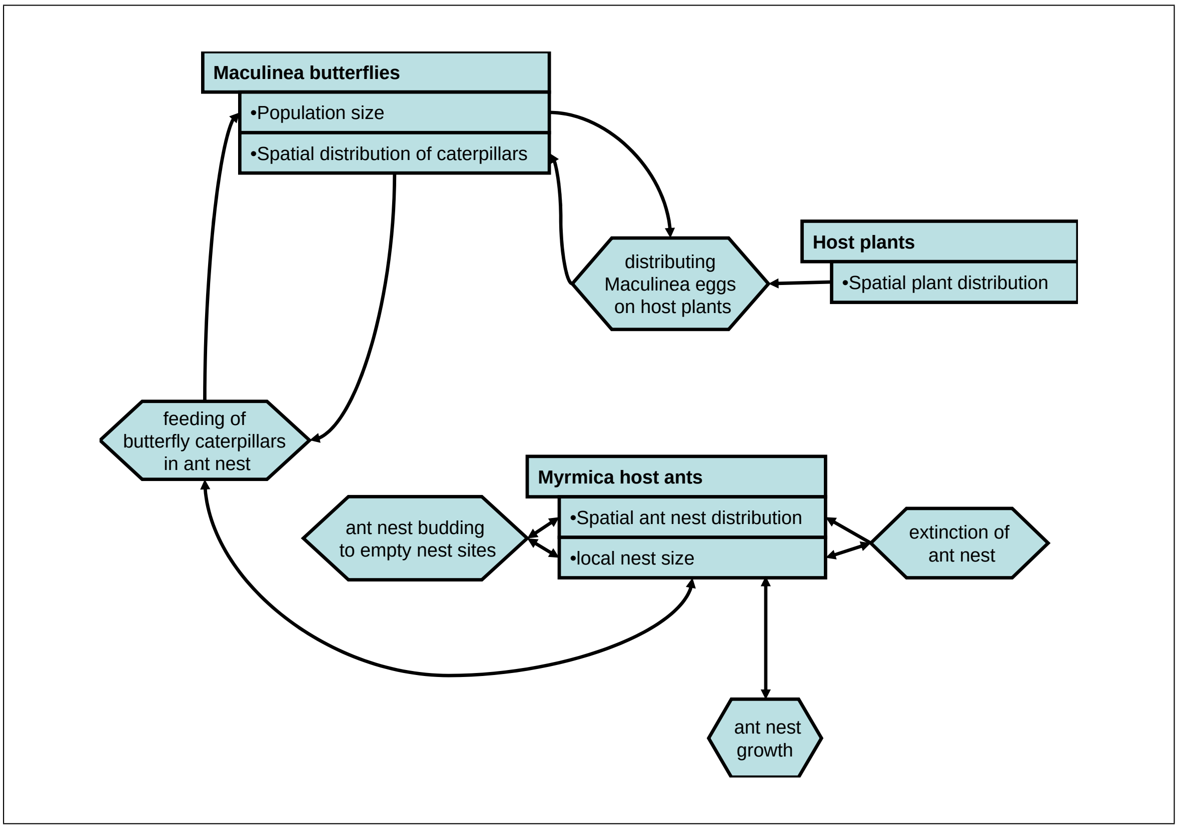

Figure 1.2: Schema of causal links between actors/components (boxes) and processes (rhombs). Arrows indicate directions of influences.

within the life cycle. $P(t)$ is the total number of butterflies.
$Z_i(t)$ is given in units of caterpillar equivalents (Hochberg et al., 1994). 1 caterpillar equivalent is the amount of worker ants lost by rearing one Maculinea caterpillar. In the system of cuckoo species Maculinea rebeli one caterpillar corresponds to about 50 Myrmica schencki worker ants. In contrast, in systems of predacious Maculinea one caterpillar equivalent corresponds to much higher numbers of worker ants. The unit 'caterpillar equivalent' is useful to adapt the model to different Maculinea systems.
According to findings from field investigations (sec. 1.2.2) and description in sec. 1.3.2.1, we ignore dynamics of host plants in the model. Spatial host plant distribution is handled as a temporally constant external factor.

1.3.2.3 Discretisation of space and time

The model is discrete in space and time. We use naturally given scales to define discretisations.

Spatial grid The model is grid based. Grid shape is rectangular. Cell size corresponds to the foraging radius of ant nests. It is assumed, that neighbouring ant nests do not interfere (Hochberg et al., 1994).

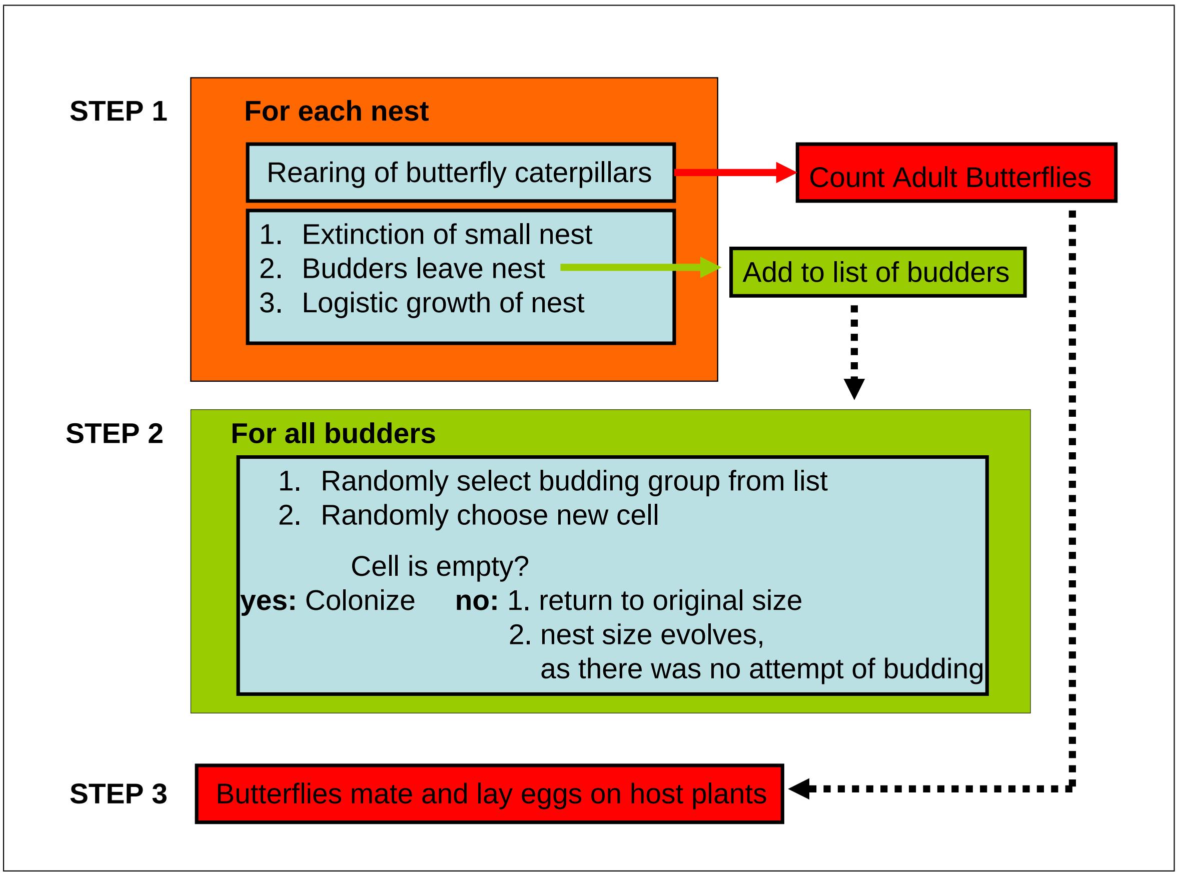

Figure 1.3: Schema of program steps during one generation

Time order in a simulation step The model is discrete in time. One time step corresponds to one year, which is the length of one generation of Maculinea butterflies (sec. 1.2.1). A brief overview on a single simulation step is given in fig. 1.3. We keep the order of processes close to the order used in the HCET model (Hochberg et al., 1994). Modifications are due to different included processes. In comparison to the HCET model, our model starts each generation in spring time, which allows to speed up the simulation. Temporal order of steps:

1. Interaction of Maculinea larvae and ants in ant nests (rearing of butterfly caterpillars)
2. Hatching out of butterfly pupae → adult butterflies
3. Internal ant nest dynamics (ant nest growth, extinction, ants leave their nest attempting to colonise an empty nest site)
4. Ant colonisation of empty cells (budding)
5. Distribution of Maculinea eggs on plants

These processes are described below in more detail.

1.3.2.4 Ant-butterfly-interaction

We simulate behaviour of a cuckoo species according to Hochberg et al. (1994) with corrections from the appendix in Clarke et al. (1998). The number of emerging adult butterflies from nest i is

$$P_i(t+1) = \min\{P_i(t), \mathrm{trunc}(mZ_i(t))\} \tag{1.1}$$

whereas the remaining ant nest size (reduced by parasitism) is

$$Z_i(t+1) = Z_i(t) - \min\{P_i(t), mZ_{\mathrm{i}}(t)\} \tag{1.2}$$

The mathematical operation $\mathrm{trunc}(x)$ returns the integer part of a float value x (e.g. $\mathrm{trunc}(7.2324) = 7$). Parameter m ($0 \leq m \leq 1$) is the fraction of ant brood that develops in spring. This ant brood is mainly affected by Maculinea caterpillars because in spring less food is available for the host ants. Hence, the ant brood is in competition to Maculinea caterpillars in the nest (sec. 1.2.1). m regulates the strength of competition between Maculinea caterpillars and ant brood. ($m = 1 - \alpha$, where α is the corresponding parameter of the HCET model. See Hochberg et al. (1994, tab. 2) for further details.)

Equations 1.1 and 1.2 can be interpreted as follows: if there are only few caterpillars in a nest (less than $mZ_i(t)$), these caterpillars are successfully reared by the nest, which costs an equivalent number of worker ants. However, if the nest adopts too many caterpillars (more than $mZ_i(t)$), pressure to the nest is too high. Maculinea caterpillars compete for food with the ant brood in spring. The maximal number of caterpillars, the nest can support, is $mZ_i(t)$. If there are more caterpillars in the nest, only $mZ_i(t)$ caterpillars are reared, due to inner-specific contest competition between Maculinea larvae. Rearing costs the equivalent number of worker ants.

1.3.2.5 Internal ant nest dynamics

Using the foraging range as the spatial scale of the model is an easy way to implement competition for food and for nest sites between host ant nests. In the model, ants from one ant nest are restricted to forage within one cell. Each cell contains at most one ant nest.

For this reason, most host ant nest dynamics take place within the cell, where it is located. The only process which affects other cells is dispersal (or budding) of host ants from an ant nest to another cell (see p. 23).

Simulation of the processes is mainly according to the HCET-model (Hochberg et al., 1994). The processes are split into three subsequent steps.

extinction Below a threshold of Z_T, an ant nest goes extinct (i.e. $Z_{\mathrm{i}}(t+1) := 0$) with probability

$$p_i^{ext} = 1 - \frac{Z_i(t)}{Z_T}$$

In contrast to HCET, if an ant nest goes extinct, the cell can be recolonised within the same year. In this case, Maculinea larvae are rescued, else they would be lost. This model rule is a compromise to incorporate different types of Maculinea butterflies. At least for predating species, the rule is fulfilled (Thomas & Wardlaw, 1992; Thomas et al., 1998a). It is implemented in a derivative of HCET for species Maculinea arion (Clarke et al., 2005).

Clarke et al. (1997) included a further 8% density-independent ant colony mortality.

However, in Clarke et al. (1998) this mortality is not mentioned. In the present thesis, density-independent mortality of ant colonies is not implemented.

budding The ant colonisation mechanism of the Maculinea model differs substantially to the nearest neighbour budding process implemented in the HCET model (Hochberg et al., 1994). Budding is restricted to next neighbouring cells. In our model we allow more flexible budding. This change allows to analyse the role of dispersal distance as a central factor for the formation of spatial host ant distribution patterns (sec. 1.3.1)

It is clear that host ant dispersal is a species trait and, as such, a fixed process to any modelling attempt. However, we construct a general model for Maculinea systems, which involves behaviour of different host ant species. Broadening the range of possible ant dispersal in our model allows to represent a larger variety of species. For example in the system of Maculinea arion another dispersal mechanism seems to become relevant. Colonisation by queens of Myrmica sabuleti is assumed to influence system dynamics (Thomas, Clarke, pers. comm.).

Now we explain the steps of budding, as implemented in the Macu model:

1. A fraction of size *ratio_ of_ budders* splits from an existing ant nest with probability

$$p_i^{\mathrm{bud}} = \min(\Gamma Z_i(t), 1) \tag{1.3}$$

   where Γ is a constant.

   These colonising ants of one nest build a budding group.

   Clarke et al. (1997) suggested another more realistic function for budding probability $p_i^{\mathrm{bud}} = \frac{2Z_i(t)}{\epsilon - 1}$ for the system of Maculinea rebeli. We, however, keep to the older eqn. 1.3 suggested by Hochberg et al. (1994). We assume that the additional parameter Γ allows easier adaptation of the model to other Myrmica systems. Comparing both suggested functions for the standard parameter set of our model in tab. 1.1, we receive that budding probability from eqn. 1.3 is about $\frac{1}{10}$ of that calculated with the newly suggested function. Hence, in our model the chance of budding is clearly reduced. However, budding is not seldom in the Macu model (unpublished data).

2. According to a spatially discrete dispersal kernel (p. 27), a cell in the surrounding of the original nest is selected.

3. If the cell, selected for colonisation, is already occupied or is situated outside the grid, the colonising group is treated as not having left its original nest. If the cell is empty, the group settles and builds a new nest. This nest will not grow in the year of colonisation. However, the original nest (because it is smaller) will undergo a higher effective population growth according to logistic growth of ant nests described in step 'Ant nest growth' below. Hence, a successful budding process leads to a higher total number of ants.

Ant nests bud stochastically independent from each other.

Ant nest growth Like in the HCET model, Myrmica ant nests grow according to density regulated almost logistic growth.

$$Z_i(t+1) = R\frac{Z_i(t)}{1 + \Theta Z_i(t)} \tag{1.4}$$

would be ant nest size after one year, if no further processes would take place. Θ is a 'within nest competition constant'. It is a species constant (see Elmes et al., 1998). Logistic growth of Myrmica ant colonies is reported in Elmes et al. (1998); Hochberg et al. (1994, and references therein). The growth rate of an ant nest R is a function of nest site quality. It combines physical characteristics of the site and resources in the surrounding foraging territory (see Elmes et al., 1998, and references therein). In contrast to the HCET model, which was used to analyse effects of varying ant habitat quality, R in this model is kept spatially constant over the whole grid.
From eqn. 1.4 equilibrium nest size in absence of Maculinea predation can be derived as (see Hochberg et al., 1994; Elmes et al., 1998)

$$\epsilon = \frac{R-1}{\Theta} \tag{1.5}$$

1.3.2.6 Butterfly reproduction and spatial egg distribution

The total number of adult butterflies

$$P(t) = \sum_{\text{all nests}} P_i(t)$$

is multiplied by the mean fraction of females (ω) in a population and the mean number of eggs a female deposits (λ_f), in order to obtain the number of Maculinea eggs at time t. It is $\omega \cdot \lambda_f \cdot P(t)$. The number of Maculinea eggs is a scalar, which has lost all spatial information about the position of nests, where adults emerged from. This follows the assumption, that adult butterflies within a habitat site are spatially unlimited.
All Maculinea eggs are distributed uniformly in a random process over all plants (i.e. each plant has an equal probability to receive the next Maculinea egg).
In the model, we ignore mortality of Maculinea eggs and young caterpillars. Up to their third instar, caterpillars do not undergo density dependent or independent mortality. But see theoretical studies of Hochberg et al. (1992, 1994); Griebeler & Seitz (2002); Mouquet et al. (2005), where effects of intra-specific competition of butterfly caterpillars on host plants are thoroughly studied.
The assumption of ignoring mortality to early stages of Maculinea individuals has important consequences for the model: Effectively, all eggs laid on a plant survive to fourth larval instar. The capacity of larvae on the plant is unlimited.
Further, we follow the assumption, that 4th instar caterpillars are only adopted, if they are located within the foraging range of an ant nest (sec. 1.2.1). Grid cells are defined to correspond to the foraging range of ants. Therefore all eggs laid on a plant are adopted by the ant nest in the same cell, provided, there is one. Hence, the number of eggs on a plant is effectively the number of fourth instar larvae that can be adopted by host ants.
Summarising, the rule for adoption of caterpillars is as follows: If there is a host plant and a host ant nest within the same cell, all eggs $P_i(t)$ oviposited on the plant are adopted by the nest. If there is no nest, all caterpillars die.
Therefore, ignoring intra-specific competition on host plants in our model, leads to a pronounced interaction of parasitic butterflies and their host ants. Maculinea eggs are spatially distributed according to the distribution of host plants. The complete amount of developed fourth instar larvae undergoes the adoption process and further potential rearing within the nests.

1.3.3 Stochasticity of the model

Stochastic processes are implemented into the model at different steps. The Maculinea population is stochastically affected by randomly distributing eggs to host plants (sec. 1.3.2.6). Survival of an egg depends on the presence of a host ant nest and subsequently on inner-specific competition within the nest. Fate of Myrmica ant nests depends on stochastic processes, too. They are affected by random extinction events and by random budding (sec. 1.3.2.5). In particular, a budding process is randomly released. Afterwards, selection of an empty nest again is a random event.

The described processes influence the system by demographic stochasticity. That is, the fate of each butterfly individual and host ant nest is decided independently of the fate of others (Wissel, 1989). Especially, in situations when population size of Maculinea is small, by chance each of the eggs might be laid on a host plant without an ant nest nearby. Hence, the butterfly population goes extinct (see sec. 2.3.2).

External random processes are not implemented in the Macu model. Effects of for example rainy summers, which negatively influence flying and oviposition activity of the whole population (see e.g. Pfeifer et al., 2000), are ignored for simplicity. It could be interesting to include such environmental stochasticity. However, Clarke et al. (1997, 1998) find only minor effects, when they allow stochastic temporal fluctuations in host ant habitat.

1.3.4 Parameterisation

A summary of the model parameters is given in tab. 1.1. All parameters have a standard value. According to the idea of only varying parameters, which directly influence the spatial host distributions, many of these parameters are never changed. Hence, they do not build a degree of freedom to the model. Several parameters and standard values are transferred without change from the HCET model (see Hochberg et al., 1994; Clarke et al., 1998, for further explanation). In the following, we discuss some parameters of the Macu model:

1.3.4.1 Grid size

In the model, we used parameters *field_ x* and *field_ y* to define the size of the grid in number of cells, where the number of cells in x-direction has to be equal or higher than number of cells in y-direction. The analyses in this thesis are performed on a square grid of 30 cells times 30 cells. The parameter *cell_ length* denotes dimension of one cell side in reality. We choose $cell\_length = 2m$, however different estimates can be found in literature (see caption of tab. 1.1).

1.3.4.2 Host plant distribution and initial host ant distribution

In this thesis, we used 687 different patterns of spatial host plant distributions and 1130 initial host ant distributions. These distributions are characterised by different spatial indices (Stoyan & Stoyan, 1992; Baddeley et al., 2005; Baddeley & Turner, 2005). Different degrees of clumping are found on different scales (up to the 10^{th} order of neighbours; see p. 27). Hence we assume that these distributions represent a good section of the 2^{900} possible plant or host ant nest distributions.

Table 1.1: Parameters of Maculinea simulation model and standard values.

Parameter[!]	Description	Standard
Output management		
index_file	process protocol	index.txt
OutputFileName	name pattern of output files	
save_first	number of stored runs of population dynamical data	3
Initial values		
NumberOfEggs	number of initial Maculinea eggs	50[*]
ant_cell_file	file name of initial ant distribution	
field_x, field_y	number of cells in x and y direction (first line in ant_cell_file)	30
Simulation grid		
plant_index_file	file name of initial plant distribution	
cell_length	real size of one cell	2m[*][2]
Simulation parameters		
NumberOfRuns	number of simulation runs	50000 / 300[*][1]
NumberOfIterations	max. number of generations per run (time horizon T_H)	5000
Myrmica population dynamics		
R	growth rate of ant nests	1.27[*]
Theta (Θ)	within nest competition constant	0.025[*][H]
ZT (Z_T)	maximum nest size at which a nest might go extinct	4[*][H]
Gamma (Γ)	factor regulating probability that an ant nests starts to bud	0.025[*][H]
ratio_of_budders	fraction of worker ants leaving nest for colonising a new one	0.5[*][H]
Myrmica nest dispersal		
kernel	dispersal kernel for ant nest budding (for other kernels see tab. 1.2)	Gauss2d[*]
sigma (σ)	width of Gaussian dispersal kernel	8
highest_order_of_neighbours	longest dispersal distance in units of neighbouring cells	100[*]
integration_precission	accuracy of numerical integration to calculate discretised dispersal kernel; A value of 0.01 means that $\frac{1}{0.01} \cdot \frac{1}{0.01} = 100 \cdot 100 = 10000$ sample points are used to calculate probability of reaching one cell	0.01[*]
Maculinea species traits		
EggsPerFemale (λ_f)	effective number of offspring per female reaching 4th larval instar	8[*]
SexRatio (ω)	mean fraction of females in population	0.5[*][H]
Maculinea species traits		
m	strength of parasitism (fraction of ant brood attacked)	0.5[*][H]

[!] Abbreviations from the mathematical description (sec. 1.3.2) are given in brackets.

[*] Values are never changed within this thesis. They can be considered as constants.

[H] Values are transferred from the HCET model (see. tab. 2 in Hochberg et al. (1994) and Clarke et al. (1998, appendix) for corrections).

[1] Two values are given for *NumberOfRuns*: In ch. 2 and ch. 4, calculation of extinction dynamics is based on 50000 simulation runs to achieve high accuracy. In ch. 5 and ch. 6 analysis of spatial patterns is based on 300 simulation runs.

[2] We assumed cell length of 2m, according to estimates of ant foraging range given in Thomas et al. (1998a) and (Glinka, pers. comm.). However, in HCET roughly foraging range of a large Myrmica schencki is indicated to be 11.11m^2 Hochberg et al. (1994); Clarke et al. (1997, 1998). Therefore, they assume a cell length 3.3m. Griebeler & Seitz (2002) build a model for Maculinea arion with grid cell size 1m^2 which corresponds to foraging area of M. sabuleti workers (Elmes & Wardlaw, 1982b). *cell_length* and *sigma* can be adjusted to values in HCET by rescaling with factor $\frac{2}{3.3}$.

Table 1.2: Dispersal kernels implemented in Macu program.

kernel	description	parameters
mean_field	no colonisation of ant nests	
Gauss2d	normal distribution[1]of dispersal distances	width: *sigma*
uniform	uniform distribution[1]of dispersal distances	equal probability p to reach a cell
neg_binom	negative binomial distribution[1]of dispersal distances	probability of success A; if r is number of successes and x is random number: $B = \mathrm{x} + \mathrm{r}$

Dispersal kernels are discretised according to the underlying grid. Parameter *integration_precission* is the resolution for numerical integration of probability distributions. Dispersal is spatially limited by a parameter *highest_order_of_neighbours*, which describes the maximum distance to which the dispersal kernel is evaluated in units of next neighbouring cells. In this thesis dispersal kernel Gauss2d is uniquely used.

[1] see McLaughlin & McLean (1999)

1.3.4.3 Growth rates

Our model as many population models is especially sensitive to the growth rate of species. In simulations ignoring ant nest dispersal[1], we adjusted standard values for parameter λ_f and R. According to the purpose of the model (sec. 1.3.1), we selected parameter values for growth rates, which allow to pronounce impact of Maculinea parasitism on Myrmica ants (unpublished data). Resulting population dynamics show predator-prey-cycles (see ch. 2).

It is difficult to compare the adjusted value of parameter λ_f to reproduction rates found in other studies. In HCET (Hochberg et al., 1994; Clarke et al., 1998) and HTE models (Hochberg et al., 1992), modelled female Maculinea rebeli butterflies lay about 120 to 160 eggs, Griebeler & Seitz (2002) assumed average values of 54 hatched eggs per female Maculinea arion butterfly in a modelling study. However, egg and early larval mortality is different in these models in comparison to the Macu model suggested here. In particular these earlier models included, effects of non-host ants which reduce the number of host ant nests on a site. Therefore, risk of dying of a caterpillar after adoption is higher in these models than in the Macu model. The adjusted value for ant reproduction R corresponds to a low growth rate of M. schencki in the HCET-model: at $j \approx 13$ in the habitat gradient. (Hochberg et al., 1994, fig. 2 and eqn. 5).

1.3.4.4 Budding

As mentioned on p. 23, host ants leave an existing nest, to colonise (bud) another cell. This cell is selected according to a dispersal kernel. To analyse effects of different dispersal mechanisms, several discretised dispersal kernels are implemented (see tab. 1.2). All these kernels work in the same way. First, the distance of a cell from the original cell is determined on the scale of next neighbours. The central cell has next neighbour order 0. The four adjacent cells have next neighbour order 1, the diagonally adjacent cells are of order two and so on. Relevant for determination of the order is the distance of the central points of the cells. Second, the continuous probability distribution function is discretised by calculating the probability

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[1] set model parameter *kernel*: mean_field. The mean field kernel is a program option which ignores dispersal.

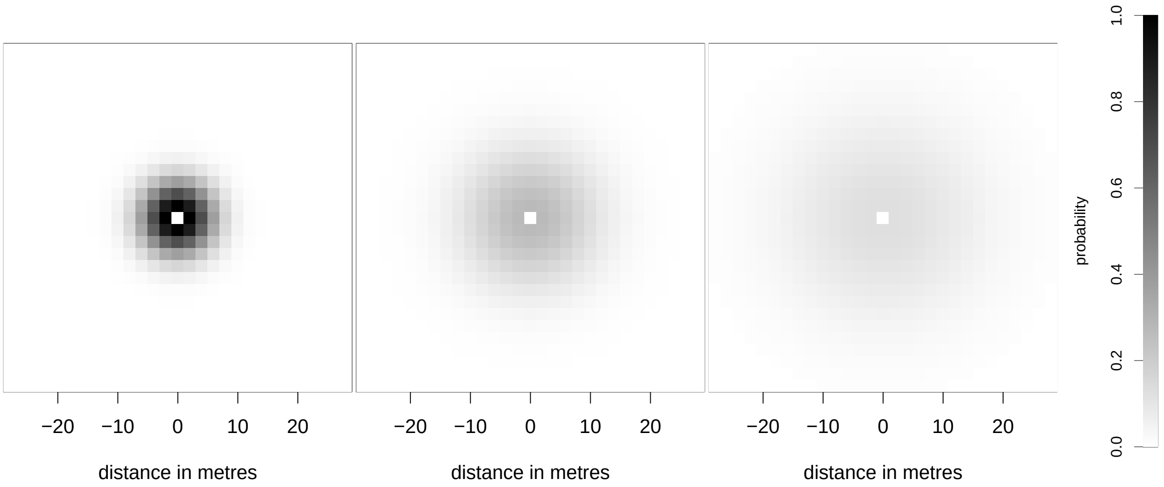


Figure 1.4: Budding range of a Myrmica nest for $\sigma = 4m, 8m, 12m$. Different grey values correspond to different probabilities to select the cell for budding. The centre cell is marked white because it cannot be chosen for budding. Cell length is 2 m.

that a cell in a particular next neighbour order is reached. The discretisation is performed by numerically integrating the probability to reach points in the cell. Accuracy of the integration procedure is determined by parameter *integration_precission* (tab. 1.1). Third, the probability distribution is truncated. The lower limit is set to the first order of next neighbours. This setting avoids, that ants try to bud their own nest. The upper limit is set by the parameter *highest_order_of_neighbours.* Afterwards, the resulting probability distribution is normalised. Fourth, a random number for budding distance of host ants (in units of next neighbour order) is taken from this distribution. The direction is determined by randomly selecting one of the cells with corresponding next neighbour order.

In this thesis, only a Gaussian kernel is used, i.e. distance of budding is selected from a Gaussian distribution with mean 0 and standard deviation σ. In the following, parameter σ is called 'budding range'. Fig. 1.4 displays the two-dimensional probability distributions for distances from the central cell disperses to another cell (from left to right: budding ranges $\sigma = 4m, 8m, 12m$). According to the Gaussian dispersal kernel, probability declines with increasing distance. It has to be noticed, that for budding range $\sigma = 12m$ ants from a central cell on the grid can reach all other grid cells with almost equal probability.

1.3.5 Implementation of the model

In this section, we give details on the implementation of the model outlined in sec. 1.3.2. On the one hand, we want to give a guideline for using the model. On the other hand, we want to present a model design, which is oriented to the task of this thesis – analysing the influence of spatial distributions of hosts on persistence of Maculinea.

Idea of the analysis is, to perform a parameter variation on parameters, which directly influence the spatial distribution of hosts, whereas other parameters are kept constant (see ch. 5). In particular, we are going to vary host plant distribution, initial host ant distribution and budding range (dispersal) of colonising host ants (ch. 6). Other parameters of the model are set to a standard value. The effects of different spatial host distributions on persistence of the butterfly population will be assessed by population viability analysis (ch. 3, ch. 4 and ch. 5). Complexity of the planned analysis requires a framework for data processing, which allows flexible access to data structures at differently aggregated levels. In the following we describe how the model is organised to meet this requirement.

1.3.5.1 Software package Macu

The package consists of the main c++ program code and two versions of executables. One of them (Macu_gui) is equipped with a user-friendly graphical user interface. This version is helpful to observe behaviour of the model for single scenarios. A help file and example scenarios are provided. The other version of the program is a command line application, which reads in a specified parameter file. Advantage of this version is that it is faster and that it can process many scenarios sequentially. Thus it is especially useful for parameter variations.

Both programs are compiled from the same model source code file. For this reason, changes in the model are effective in both versions, after simple recompilation. Hence, it is secured that both programs run with the same model version.

To run the simulation model, three input files are required, which are described in the following.

1.3.5.2 Main input file

The main input file (extension '.txt') contains all settings that are necessary to define scenarios. The file is organised in table form. The first line specifies parameter names. Each of the following lines specifies one complete scenario. The parameters are explained in sec. 1.3.4.

The main input file is used to set up parameter variation experiments. The different parameter values are easy to be surveyed. Arrangement of parameters in table form makes the file compatible for the use with relational databases (ch. 5 and ch. 6).

Two additional input files for spatial host distributions are specified in the main input file. They are described now.

1.3.5.3 Host plant file and initial host ant file

Each spatial pattern of host plants or initial host ants is saved in a single file. Hence they are available for several simulations with different parameter sets and for further analysis e.g. in ch. 6 and ch. 7.

Positions of plants are stored in a subsequent line. Plant position (x, y) is stored as $y * x\_length + x$ in the plant file (Plant file extension: '.pla'.). x_length is the length of the grid in x direction in number of grid cells (see p. 25) There is only one plant per cell. In contrast to the HCET model (Hochberg et al., 1994), there is no subdivision on buds or tillers.

We can simplify description of spatial host plant distribution to a presence-absence representation, because we ignore density-dependent mortality of caterpillars on a plant (see sec. 1.3.2.6).

The initial host ant distribution is saved in a matrix, where each cell contains the number of ants per nest (ant file extension: '.ant').

1.3.5.4 Organisation of the simulation program

Every simulation experiment consists of several simulation runs with equal parameter sets and equal initial conditions. Hence, results of one simulation build a sample of independent simulation runs. The sample size is controlled by the input parameter *NumberOfRuns*. Each simulation run consists of a repetition of simulation steps describing Maculinea life cycles (see fig. 1.1). Each life cycle lasts for one year and includes a complete Maculinea generation. A simulation run ends either after extinction of butterfly or ant population or when the predefined time horizon T_H of the simulation (program input parameter *NumberOfIterations*) is reached.

1.3.5.5 Model output

The purpose of the model, to analyse persistence of Maculinea under conditions of spatial host distributions, implies that full insight into all spatiotemporal processes must be possible. The disadvantage: having all information does not mean to understand it. You can't see the wood for the trees. Therefore, the simulation program provides the data aggregated to different levels:

Times to extinction: Highly aggregated statistical data, which give the number of generations, populations of Maculinea butterflies and Myrmica ants survive in each simulation run. This data is used for population viability analysis (PVA) in ch. 3 and ch. 4. (Compiler option *ext*). Result file extension: .ext

Population sizes: Time series on population sizes of Maculinea butterflies and ants, as well as the number of ant nests are recorded. This data gives an overview on spatially aggregated population dynamics. (Compiler option *pop*). Result file extension: .pop

Spatial host ant dynamics: In each simulation step, ant distribution on the grid is recorded. This data is used to analyse spatial effects on population dynamics. (Compiler option *ant*). Result file extension: .ant

These levels of aggregation allow an hierarchical approach for data analysis (sec. 5). Input parameter *save_first* gives control on the number of completely stored time series of population dynamics. $save\_first = 3$ produces 3 pop-files or 3 ant-files.
Population size and spatially explicit host ant distributions are calculated synchronised for butterflies and ants before the first process in each generation.

1.4 Summarising remarks

With our Maculinea model, we keep close to the HCET model (Hochberg et al., 1994; Clarke et al., 1998) which was developed for a Maculinea rebeli (Hir.) population at Panticosa in the Spanish Pyrenees. By basing model development on processes and parametrisation of the HCET model, we relate the Macu model to the natural system.
Additionally, we can profit from results of HCET model studies, which indicate functioning of processes in the system. This knowledge is used to determine, which mechanisms and parameters might be relevant for our study. These factors are the temporally constant spatial host plant distribution, which can be considered as a landscape for oviposition of Maculinea, the initial Myrmica host ant distribution, and the budding of empty nest sites by host worker

ants (a dispersal mechanism).

To investigate the influence of spatial host distributions on persistence of Maculinea populations, we will perform parameter variation experiments and evaluate them by population viability analysis (ch. 4, 5 and 6). This methodology is already reflected in the implementation of the model. With the Macu model, it is easy to simulate population dynamics of the Maculinea system for many different scenarios of spatial host distributions. The flexible output of simulation results supports analysis at different levels of complexity.

The model presented in this chapter is developed for analysis in the frame of Maculinea systems. However, due to its particular tailoring, it can be applied more generically to give insight to effects of host distribution in parasitic systems. This flexible level of abstraction is achieved by increasing generality, coming from a concrete complex case study. The special power of this model is, that on the one hand, it is abstract enough to be comprehensible, on the other hand it is embedded in the context of natural Maculinea systems.

Part III

Observing temporal dynamics

Chapter 2

Population dynamics of the Macu model

2.1 Introduction

As a first step, it is essential to get a feeling for the system to be analysed. Hence, we give an overview on typical dynamics produced by the Maculinea model Macu. The frame of this presentation is given by the general aim of this thesis; analysing effects of spatial host distribution on persistence of Maculinea populations within a site.

Extinction of populations is often accompanied by typical patterns in time series of population sizes (Stephan & Wissel, 1999; Lande et al., 2003; Wichmann et al., 2003). This results from the fact that extinction is a stochastic event (Wissel & Stöcker, 1991; Wissel et al., 1994) and risk of extinction is increased for small populations (Matthies et al., 2004, and references therein). Therefore, we analyse time series on Maculinea population sizes, calculated by the Macu model.

In single species systems with density dependent population growth, two temporal phases can be distinguished for their different population dynamics: a short initial transient phase during which the population size approaches a quasi-stationary distribution, and a second phase, when this quasi-stationary distribution is established but decays slowly (Nisbet & Gurney, 1982; Stephan & Wissel, 1994b; Lande et al., 2003). Extinction risk can strongly vary between both phases (see ch. 3.2 and references therein). We expect a similar effect for the multi-species Maculinea system, among other reasons because such phases are observed in another Maculinea model (Hochberg et al., 1994). Hence, we analyse population sizes for initial and established phases separately.

To investigate the influence of the spatial distribution of hosts on the fate of Maculinea populations, we perform time series analysis on a large number of different scenarios. Each scenario consists of a fixed set of spatial host distributions and species traits, influencing dispersal of host ants (see ch. 1). Comparing results from different scenarios reveals dependency of Maculinea population dynamics on species traits and spatial host distribution.

Findings of this chapter motivate the methodology applied in the following parts of the thesis. Additionally, here these findings are used to compare dynamics of Macu and HCET model (Hochberg et al., 1994; Clarke et al., 1997, 1998) in respect to influences of spatial host distributions. This 'validation' of the Macu model by means of the more naturally realistic and partly validated model for the Maculinea rebeli system is expected to improve understanding of effects resulting from different processes in the models. Such an understanding is important, because it helps transferring results of the general Macu model to case studies of natural Maculinea systems.

2.2 Methods

We analyse time series of population sizes of Maculinea butterflies and Myrmica host ants, and numbers of Myrmica host ant nests.

Having in mind the main purpose of this thesis, the analysis of the influence of spatial host distributions on persistence of Maculinea, we mainly keep to the set of standard parameters 1.1. The idea is to only change parameters with direct spatial impact: that is dispersal, plant distribution and ant nest distribution. Further parameters (species traits) are only varied to get an impression of robustness of results.

The investigated parameter space contains all host plant and initial host ant distributions described in sec. 1.3.4.2. Budding range σ can assume one of three values $[4, 8, 12]$. For each of 17895 parameter combinations of these three spatially relevant parameters, we keep track of population sizes in each generation from three subsequent simulation runs. These data are graphically analysed to identify qualitatively different dynamics.

In a further step quantitative analyses are performed. Each simulation run, where populations survived for at least 1000 generations, is taken into account. This results in 18960 analysed runs. To avoid effects resulting from initial conditions, we skip data from the first 40 generations. We calculate two types of statistics. Summary statistics (mean, median, standard deviation) is calculated on the basis of data from three simulation runs of each simulation experiment. Time series analysis (Chatfield, 2000) is performed for each run separately. For this analysis, a run is taken into account, if it consists of at least 10 generations (after skipping the 40 initial generations). We assess autocorrelation, spectrum and phase-shift of the multivariate time-series on Maculinea population size, number of Myrmica host ants and number of Myrmica host ant nests.

Explicit spatiotemporal host ant dynamics are observed only exemplarily, because it is ineffective to search for patterns in such complex data in a coarse analysis.

Data analysis is calculated with statistical software R (R Development Core Team, 2005). Data is stored in a local MySQL database (MySQL, 2003; Lapsley & Ripley, 2005).

2.3 Results

2.3.1 Typical population dynamics

Fig. 2.1 shows a typical example of dynamics of Maculinea butterflies, Myrmica host ants and number of host ant nests. After an initial peak in population sizes of butterflies and ants, the data vary around a constant value. For ants and their nests, this value is close to the median (mean correlates with median). In contrast, butterfly data is biased to higher values (mean $\geq$ median; cor = 0.580), resulting from peaks with high maxima.

Figure 2.2a shows the relation between the number of host plants and the average number of Maculinea butterflies. For low numbers of plants, number of butterflies increases with increasing host plant number. For higher numbers of plants (more than about 500), mean numbers of butterflies reach a constant level. In contrast, for high numbers of host plants, median

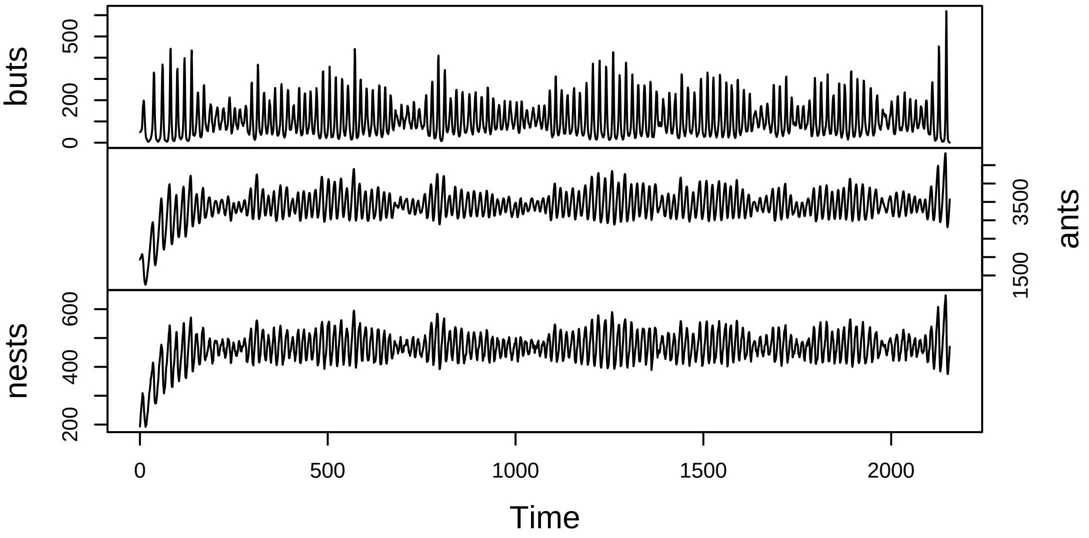


Figure 2.1: Typical population dynamical output from the Macu simulation model. Top: number of Maculinea butterflies; centre: number of Myrmica host ants; bottom: number of host ant nests.

numbers decline (not shown in the graph). For both measures, mean and median, variance increases.

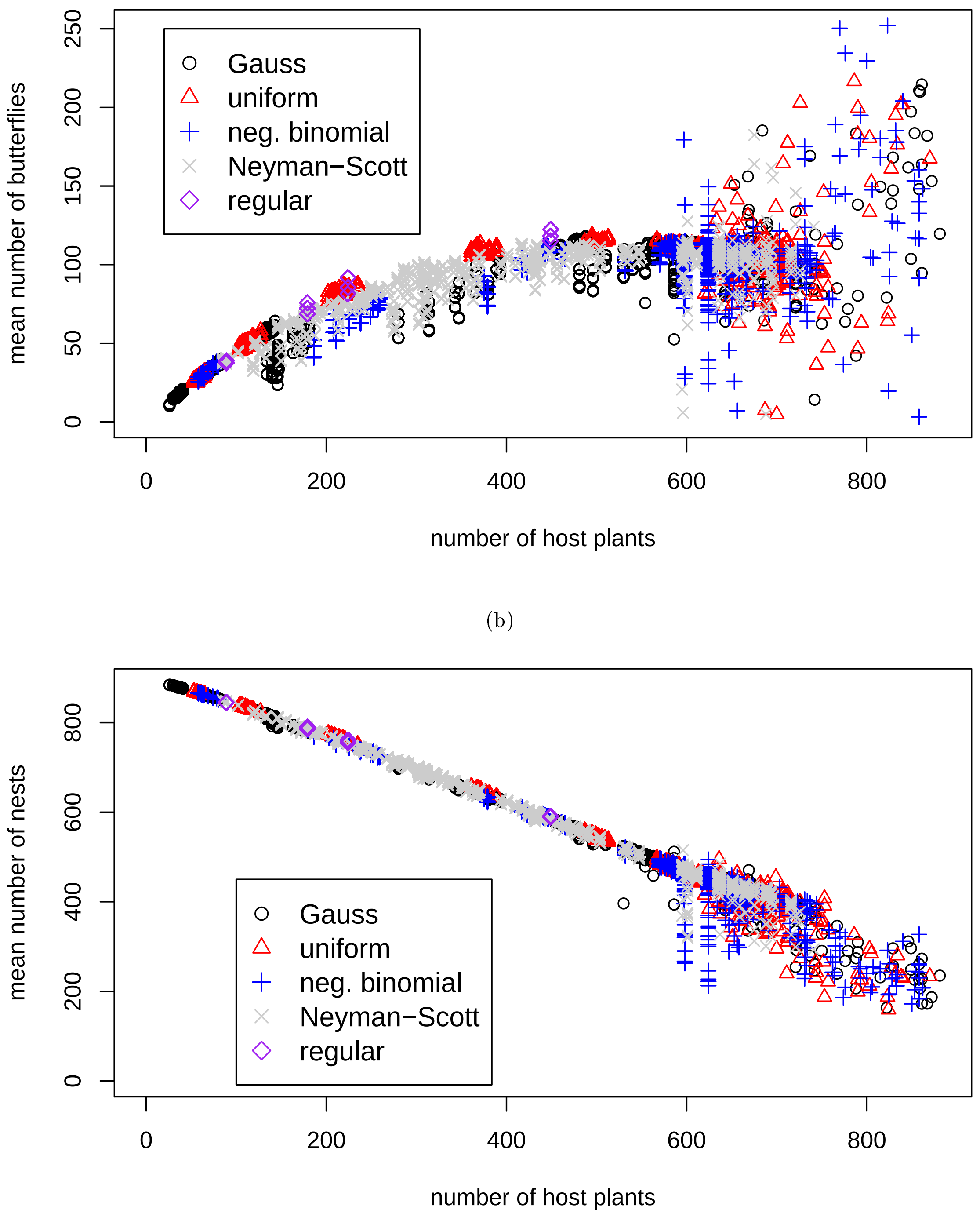
There is an interesting finding: for host plant numbers, higher than 600, median of butterfly numbers can be very small (below 10). That means, that in 50% of all generations, there are less than 10 individuals in a population. On the other hand, mean numbers of butterflies rarely drop below 80. Hence, there is an enormous variance in population size. High numbers of butterflies can be found in one moment, but at least half of time, population is very small and underlies a high risk of extinction due to demographic stochasticity.

In fig. 2.2b, dependency of the mean number of host ant nests on the number of host plants is depicted. With increasing number of plants, average number of host ants declines. This decline is linear for less than 600 host plants. For higher numbers of plants, decline in number of host ants becomes stronger. Variance in data increases, too.

In contrast to number of host plants, host ant budding range (σ) and number of initial ant nests do not show systematic influence on sizes of Maculinea and Myrmica populations.

We know concentrate on time series of single runs. Fluctuations in population size seems to change randomly within a run (see fig. 2.1). But the three time series are strongly correlated. This can be seen in the correlation diagrams of fig. 2.3. Significant correlation or anti-correlation between sizes of Maculinea populations (buts), Myrmica ant population (ants) and number of Myrmica nests (nsts) can be observed up to about 100 time steps. Such a long temporal correlation between population sizes of different species indicates strong relation of their dynamics.

In the following, the correlation diagrams will be closely inspected. In different graphs of fig. 2.1, cycles with declining amplitudes can be observed. The diagrams are not symmetric to the x-axis, indicating higher correlation than anti-correlation.



(a)

(b)

Figure 2.2: Mean number of butterflies (graph (a)) and host ant nests (graph (b)). Data from simulations on 17895 different scenarios. Different shapes of data points indicate different spatial random processes which are used to create spatial host plant distributions (ch. 1.3.4.2).

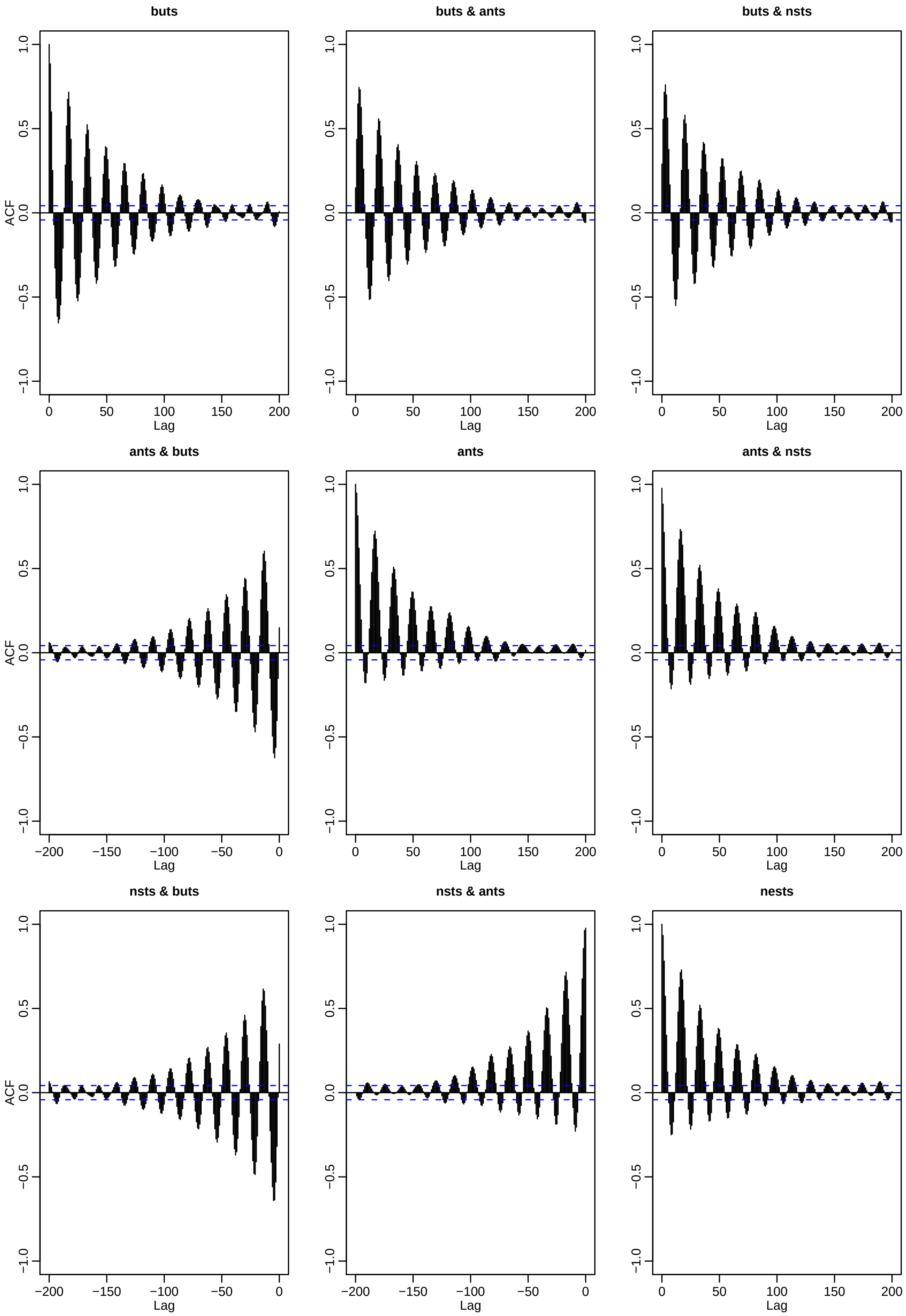


Figure 2.3: Auto- and cross-correlation functions (bar-plots) of number of Maculinea butterflies (buts), number of Myrmica host ants (ants) and number of Myrmica host ant nests (nsts). Same data as in fig. 2.1. Dashed lines indicate the 95% confidence-interval of uncorrelation.

Cyclic autocorrelation functions (graphs on diagonal from upper left to lower right corner in fig. 2.3) result from cycles in the original data with the same period (Chatfield, 2000). Hence, although there is high variation in the amplitudes of population sizes (fig. 2.1), on a short time scale of about $T_{\mathrm{P}} \approx 17$ (duration of one cycle in the autocorrelation diagrams fig. 2.3), population sizes vary periodically.

A decline of autocorrelation functions results from a loss of memory in the data with increasing time. When after about 100 generations, the autocorrelation looses significance in fig. 2.3, population sizes at time t are not dependent on population sizes at least 100 generations earlier. A decline of autocorrelation is related to chaotic dynamics or stochastic perturbations of a system.

Especially for the autocorrelation function of Myrmica ant dynamics, we find that the cyclic declining pattern is not symmetric to the x-axis. Instead, positive correlation is stronger than anti-correlation. Additionally it is found, that the phase of positive autocorrelation is longer than the phase of negative correlation, within one cycle. This pattern results from an unequal distribution of times, when population size is higher or lower than the average population size. Actually, within one cycle, population size of Myrmica ants increases slowly to its maximal size, but within a short time drops down to its minimum.

Cyclic autocorrelation functions with declining amplitudes are classified as phase-forgetting quasi-cycles (see Nisbet & Gurney, 1982, p. 250ff). Knowing the fact that in the simulation model no external oscillating driving force is included (see sec. 1.3), either the quasi-cycles are 'endogenous resonant' (a deterministically stable but underdamped system is perturbed by stochasticity) or 'perturbed limit cycles'. Endogeneous resonant means, that a deterministic system has a stable equilibrium. However, stochastic influence perturbs the stable state. Both processes, acting together, lead to cyclic behaviour. Hence, cyclic behaviour is induced by stochasticity. In contrast, limit cycles are intrinsic to the deterministic system. Stochastic influence only perturbs the periodic trajectories of population sizes. In both cases, the underlying deterministic system shows the tendency of returning to some kind of stability.

Autocorrelation functions which result from dynamics of only one species show the same pattern as cross-correlation functions which describe temporal correlation of dynamics of different species. Hence we conclude that the cycles in population size of Maculinea butterflies and Myrmica ants are strongly correlated. These quasi-cycles result from species interaction. Cycles are well-known from predator-prey, host-parasite or epidemic systems (Nisbet & Gurney, 1982; Wissel, 1989; Grenfell & Bjornstad, 2005). In the Macu model, coupled quasi-cycles of butterfly population size and ant population size are found. Coupling results from interaction of both species. Quasi-cycles can be explained by parasitism of Maculinea butterflies on Myrmica ants and stochastic effects (sec. 1.3.3).

Spectral analysis of population dynamics reveals almost no variation in period length of one cycle between time series of butterflies, ants and nests (see tab. 2.1). Fig. 2.4, as an example, shows a power spectrum of the population dynamics displayed in fig. 2.1. Clearly, a major peak can be seen at $T_{\mathrm{P}} = 16.74$ (top scale) simultaneously in all three spectra for butterflies, ants and nests. There is only very view variation in the period between time series of coupled Maculinea and Myrmica. Increasing number of host plants leads to slightly increasing period time. Increasing budding range σ leads to a small decline in period.

Phase shift $\phi_{\text{ants, butterflies}} \approx 1$ for all analysed population runs. This means, ant dynamics follows butterfly dynamics after one generation. In the presented example $\phi_{\text{ants,butterflies}} = 1.11$. Phase shift can be observed in fig. 2.3 graph 'ants & buts'. In this cross-correlation diagram, the initial peak is delayed by one generation (positive correlation at time lag 1).

Table 2.1: Distribution of period times T_P for Maculinea butterflies and Myrmica ants.

	1^{st} quantile	median	3^{rd} quantile
Maculinea	12.98	13.96	16.83
Myrmica	13.22	14.79	17.44
Myrmica nests	13.02	14.00	16.83

Values are derived from spectra of all simulation runs, where time series analysis is performed (see sec. 2.2)

Fig. 2.5 shows an example of spatial host ant and host plant distributions (bottom graphs) during one cycle of Maculinea butterfly number (top graph). Numbers in the top graph indicate times, when ant distribution is sampled. Circles show positions of host plants which are constant throughout the simulation (sec. 1.3.4.2). Different colours indicate the number of ants per nest. The lighter the colour, the higher is the number of host ants in a cell. Cells without ants do not contain an ant nest. In all graphs the upper left corner contains only few ants. In this area, plants are particularly clumped. Whereas in the lower right corner, which is almost free of host plants, there is a high density of ants (nest size reaches capacity $\epsilon = \frac{R-1}{\Theta}$ see eqn. 1.5 in sec. 1.3.2.5 or Hochberg et al. (1994, ϵ is referred to as 'equilibrium nest size in the absence of the butterfly')). $\epsilon_{\text{standard}} = 10.8$ for the standard parameter set (tab. 1.1). Starting with the snap shot number 1 in fig. 2.5 (minimum number of butterflies), the two areas are clearly distinguished. Cells without plants contain nests with high numbers of ants, whereas in many cells with plants no ant nest can be found. In step 2, although the number of parasitic butterflies increases, an increased number of cells with host plants contains ant nests. Hence butterfly larvae benefit from a large amount of suitable habitat. Butterfly population grows further. In step 3, the highest butterfly population size is reached. But the ant nest distribution does not show big difference to steps 1 or 2. The change occurs at step 4, when a high fraction of cells containing host plants is free of ants. Remaining nests in that area are highly threatened of extinction. Thus this next generation of Maculinea larvae is confronted with a very low number of suitable cells. Population decline is faster than the increase before the peak. In step 5, reduction of the Myrmica ant population seems to be even severe. During the following generations, butterfly population size stays low. But the ant population can recover. Refuges for Myrmica host ants can be identified in the graph: although in step 4 and 5, Maculinea butterflies damage their host ants severely, nests far away from plants are not affected (e.g. lower right corner).

2.3.2 Extinction

In the example run (fig. 2.1), Maculinea butterflies go extinct after 2156 generations (extinction: butterfly population size is 0). In our survey, we find three categories of survival times: First, a population survives very short time. It goes extinct after only few generations. Second, a population survives for several hundreds or thousands of generations before it goes extinct. Third, the population survives for the time of $T_H = 5000$. This is the maximal duration of a simulation run (see standard parameters in tab. 1.1). A detailed consideration of times to extinction in Maculinea systems is given in chapter 4. Here, we concentrate on population dynamical patterns, which correspond to different reasons of extinction.

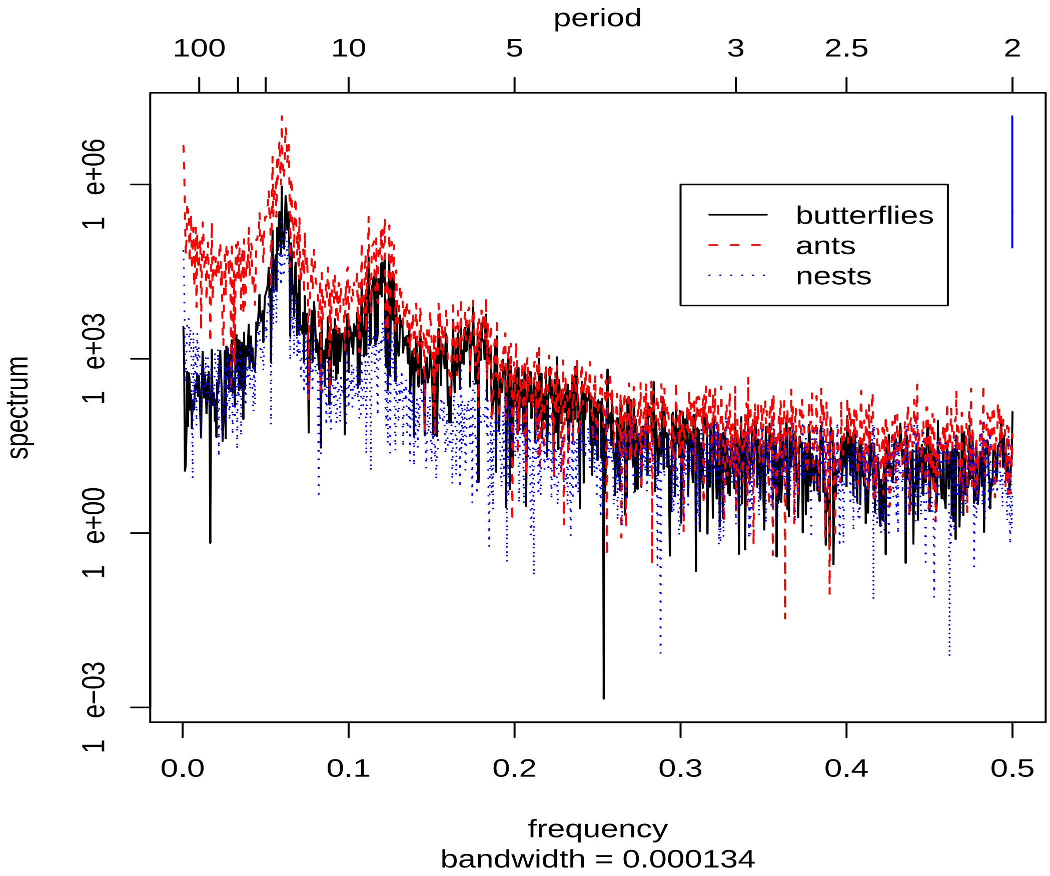


Figure 2.4: Power-spectrum of number of Maculinea butterflies (line), number of Myrmica ants (dashed line) and number of Myrmica ant nests (dotted line). Same data as in fig. 2.1

In all model experiments, extinction of Myrmica host ants is never observed. One reason can be seen in fig. 2.1. Comparing the minimum individual numbers of Myrmica ants and Maculinea butterflies reveals a strong difference. Myrmica ant numbers (except of the first few generations) do not drop below 2800 and nest number is always higher than 370, however butterfly numbers often reach very low values. Finally, the population size of butterflies drops to 0, which means extinction. In the model, small populations of Maculinea underly a risk of extinction due to demographic stochasticity. That is, fate of single individuals might strongly influence development of the whole population, because the population does only consist of few individuals (Nisbet & Gurney, 1982; Wissel, 1989). Another reason can be seen in fig. 2.5. Myrmica host ant nests are not affected by parasitic Maculinea butterflies, when there is no host plant in vicinity of the ant nest. These refuges (see sec. 2.3.1) guarantee a minimum number of surviving ants. Refuges for hosts are known as an important factor to stabilise parasitic or predator-prey systems (Huffaker, 1958; Ellner et al., 2001; Poggiale & Auger, 2004). One could argue, that an increase in host plant density will increase pressure on host ants in the system. Although occupying the whole area with plants (which is one of the standard

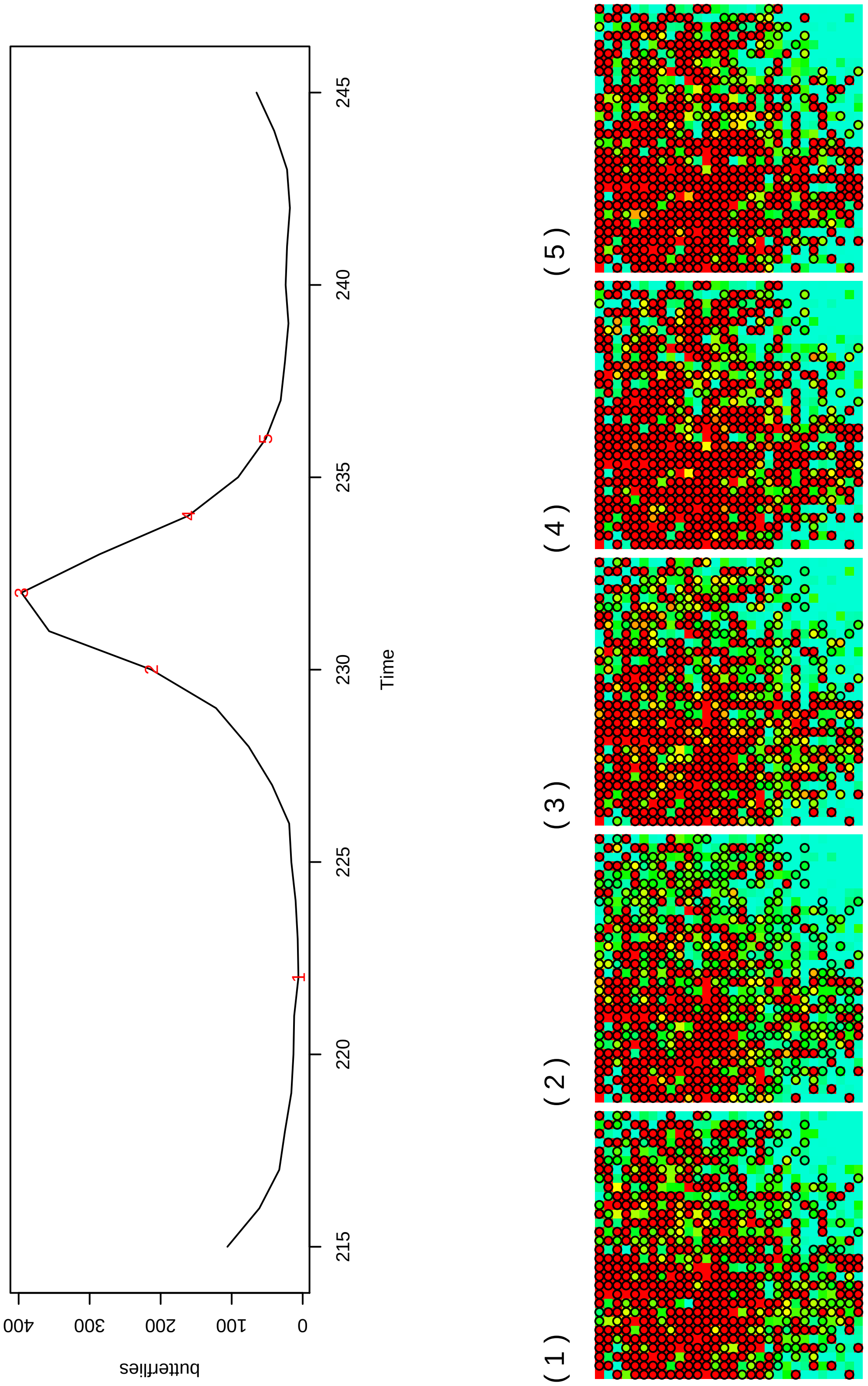


Figure 2.5: Spatial distribution of Myrmica host ant nests within one population cycle. Top figure displays Maculinea population size. Bottom graph shows explicit spatial distribution of Myrmica host ants. Different colours represent different ant nest size. Dark: small nests, Light: large nests. Circles represent host plants.

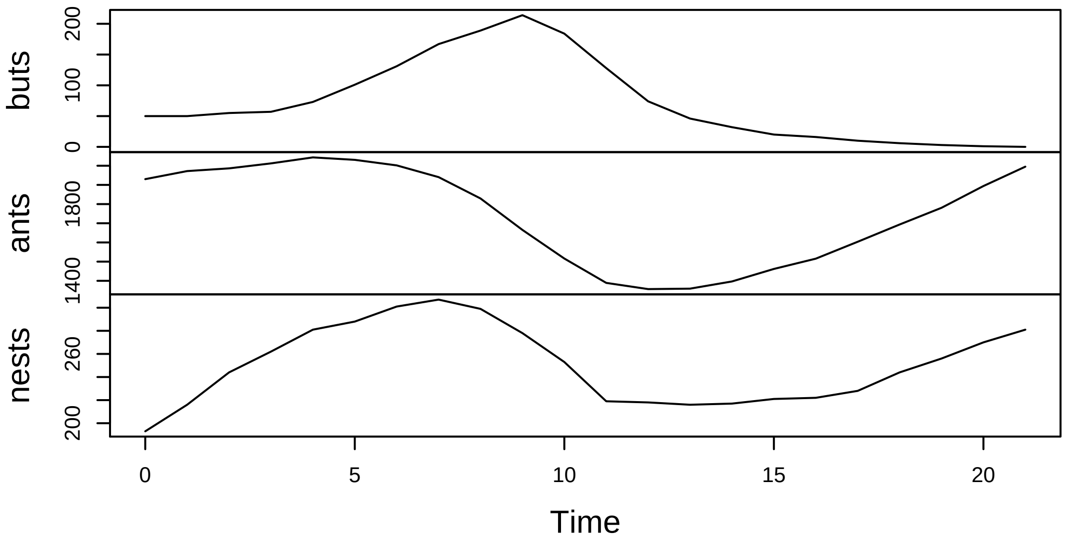


Figure 2.6: Population extinction within few generations. Ant population has not reached establishment. Same parameter set as in fig. 2.1.

plant distributions see. 1.3.4.2), we did not find extinction of host ants[1]. One reason, why the parasitic Maculinea population goes extinct earlier than its Myrmica host population, can be seen, referring to sec. 1.3.2.4. It is assumed, that small Maculinea caterpillars in autumn reduce host ant brood only slightly. Therefore a part of the ant larvae in the nest survive parasitism (parameter $m = 0.5$, see tab. 1.1). Hence, a large ant nest has a good chance to survive a strong attack of Maculinea butterflies. Although, if the Maculinea population is extremely high, it cannot deplete the Myrmica population. Another reason becomes relevant for situations of low population sizes of Maculinea and Myrmica. In this case, there are not enough Maculinea caterpillars to parasite all nests. Hence, some of the ant nests are not affected by the butterfly. They can recover.
Anyway, extinction of Myrmica ants would be followed immediately by extinction of Maculinea on the site, because the ants are obligatory hosts for the butterflies (see chapter 1.2).

2.3.3 Initial behaviour of the system

We consider effects of initial conditions on our simulations, because they might have a high impact on the performance of Maculinea butterflies. Fig. 2.6 shows another outcome of the example experiment, which produced the population dynamics in fig. 2.1. In this simulation run, extinction of Maculinea takes place after only few generations, although the parameter set is the same for both runs. Difference in survival of butterflies simply results from stochasticity in the model (see sec. 1.3.3).
In this type of initial behaviour of the model, butterfly numbers increase to high values, while

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[1] in 6 of 120977 simulation runs, ants are driven to extinction, in cases where all cells are occupied with host plants. Extinction of ants leads immediately to extinction of butterflies. Extinction events happen within the first 15 generations. These simulations are test simulations on a larger grid; They are performed assuming strong interaction of butterflies and ants $m = 0.9$.

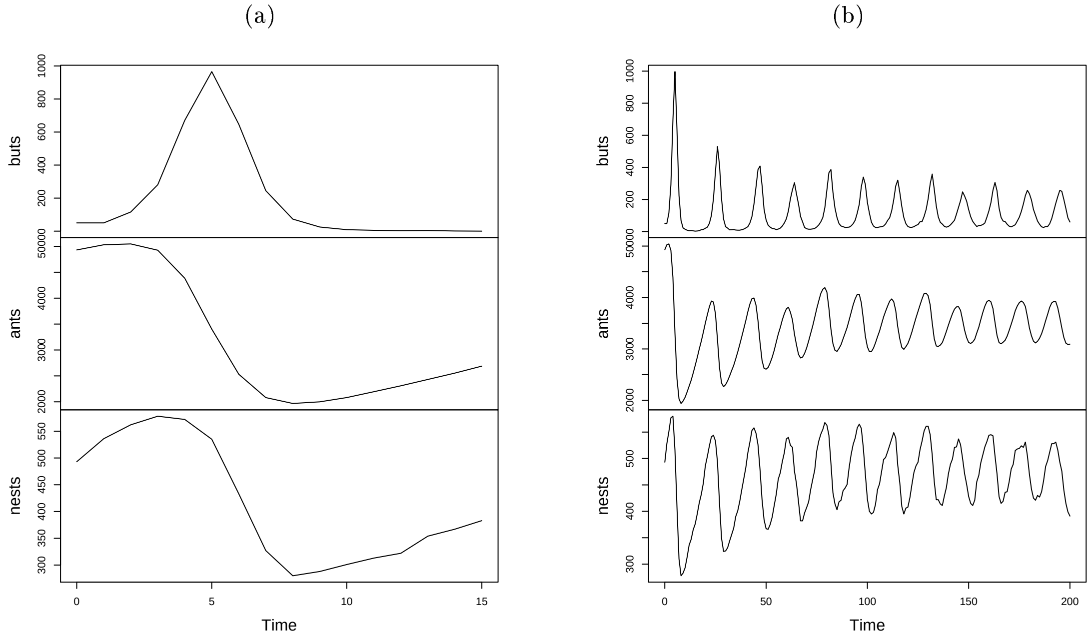

Figure 2.7: Census data of two runs with same model parameters. (a): Butterfly population goes extinct after running through an initial peak. (b): Within first 200 generations populations have not gone extinct.

the number of ants decreases. Comparing both, fig. 2.1 and fig. 2.6 regarding their initial population dynamics, it can be seen that the behaviour is similar. An initial peaking cycle of butterfly numbers is accompanied by a decline of ant and ant nest numbers. Only, by chance, in the second run, the Maculinea population goes extinct. When looking at dynamics following the initial 20 generations in fig. 2.1, one recognises that butterfly population seems to be in a stable situation. In contrast, ant and ant nest numbers have a clear trend of increase. Even maxima of cycles are below the long term mean in population size. It takes the ants about 100 generations to reach long term behaviour. Closely inspecting butterfly numbers reveals that during the transient phase of ants, the minima in butterfly numbers are only slightly above 0. Further on for long time, minima assume higher values, until – introduced by high peaks in butterfly numbers – the Maculinea population goes extinct. Our observations suggest that the system behaves differently during a long initial transient state compared to its steady state behaviour.

Another type of initial behaviour is shown in fig. 2.7. Again, two population runs with the same set of parameters are depicted. Butterfly population in fig. 2.7a goes extinct after 16 generations, whereas in fig. 2.7b no extinction occurs during the first 200 generations. Comparing population dynamics during initial and established state in fig. 2.7b shows, that Myrmica ant number starts on a higher level than is reached in further generations. This high number of food resource provides an outbreak of butterflies, twice as high as normal peaks reach. Overexploitation let the butterfly population collapse, but furthermore reduces ant population size. During the following 50 generations, the mean number of Myrmica ants increases. During this time, the variance of butterfly population size is increased in comparison to later generations.

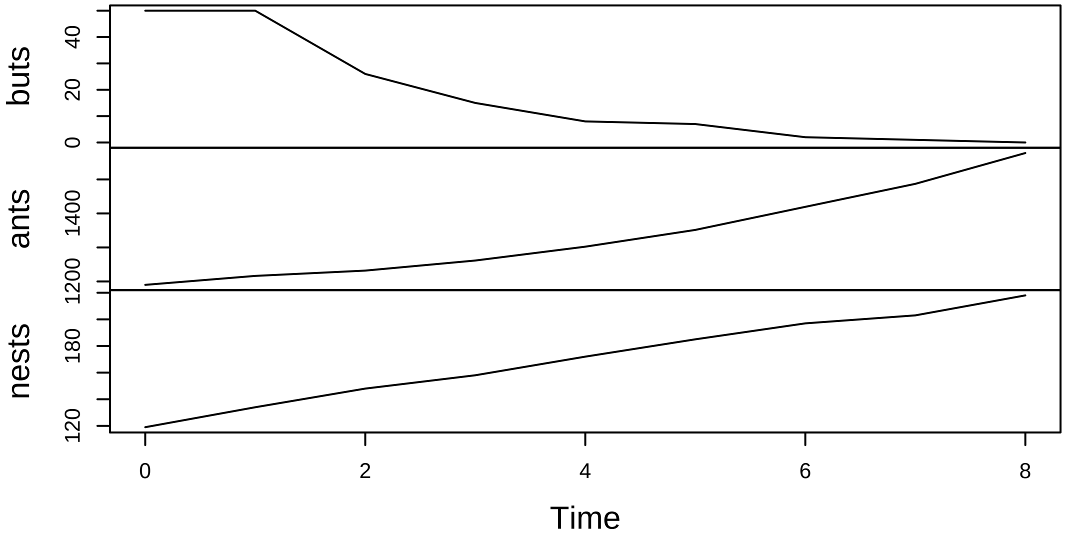

Figure 2.8: Butterfly population is declining, while number of ants and ant nests increases.

A third example (fig. 2.8) shows a declining population of butterflies which goes extinct after 8 generations. Meanwhile ant nest number and total population size of ants increase.

2.4 Discussion

2.4.1 Characterisation of dynamics of the Macu model

Quasi-cycles are found in most simulations of the Macu model. Dynamics of butterflies and ants are linked together by a phase shift of one generation. This coupling can be explained by parasitism of Maculinea butterflies on Myrmica host ants. Reason is the feedback of predacious Maculinea on its ant brood prey. Thus, the Maculinea model shows predator-prey cycles. Stochastic processes disturb this deterministic dynamics. Main effect of stochasticity expresses in a strong variance of amplitudes of the cycles. These random changes in population size lead to phase shifts during the course of the system. Both, beats and loss of coherence can be attributed to the interaction of stochastic and deterministic processes. It cannot be decided, whether observed fluctuations result from stochastically introduced fluctuations around a stable equilibrium point (endogenous resonant quasi cycles) or if they are 'perturbed limit cycles' (Nisbet & Gurney, 1982).

It must be remarked, that no long time trend on population sizes of butterflies or ants can be observed. Predator prey cycles stabilise the system in the sense, that fluctuations or perturbations are redirected by deterministic behaviour of the system and do not amplify. Such a behaviour is known from classical predator-prey models like Lotka-Volterra systems with density limitation in prey population (damped Lotka-Volterra) when stochastic influence is not too strong (e.g. Nisbet & Gurney, 1982; Dimentberg, 2002). Damping in the Macu model, results from density dependance of Myrmica host ants (eqn. 1.4). Phenomenologically, dynamics of Maculinea butterflies, like predator dynamics in principal can be described as oscillation with noise on the amplitude and with slight changes in phase. This is a relevant fact for the application of the PVA method, developed in ch. 3.

2.4.1.1 Initial behaviour of the system

We distinguish three different types of initial behaviour. In one of them (fig. 2.8) the butterfly population declines monotonously to extinction within a very short time span. Ant resource seems to be insufficient to support the predator. Compared to both other cases, the initial number of ants and nests is lower.

The examples depicted in fig. 2.6 and fig. 2.1 point out that the mean number of butterflies can be close to the stationary population size. However, mean ant population size is far away during the initial phase. Considering only census data of Maculinea butterflies, it cannot be recognised that the system undergoes a transient phase. Differentiation of population dynamics during the transient and established state is crucial for habitat management.

In fig. 2.7 both butterfly populations undergo an initial outbreak in population size, which provokes overexploitation of the host ant resource. For one of the populations, this self-generated habitat destruction leads to extinction. In the other example, it can be observed that host ants need some time to recover. Note that the second peak in butterfly population size is higher and sharper than following peaks, although ant number is low. Very low butterfly numbers preceding the peak, almost do not affect the recovering host ants. Suddenly, butterfly population size increases,because the population can profit from a well developed resource.

2.4.1.2 Equilibration of the system

For many ecological questions, initial conditions of a system cannot be ignored (e.g. system reaction after catastrophes or colonisation of new sites). As we can see above, the Maculinea model shows remarkably different behaviour during a few years after simulation start in comparison to long time behaviour. Even extinction is possible. Hence, this phase of population dynamics cannot be ignored in our analysis.

It is notoriously difficult to estimate the time, a system takes to adapt to new conditions (Fath et al., 2003; Labra et al., 2003). In fig. 2.7b it can be seen, that population dynamics of Maculinea seems to enter into a regular cyclic structure after about 2 cycles, whereas the number of Myrmica ants shows a trend until the fourth cycle. Can parasitic Maculinea butterflies been adapted although its prey still is not? How does the system show, that it is completely adapted?

Nisbet & Gurney (1982, ch. 6.2; p. 170) discuss a statistically quasi-stationary state of density dependent single isolated populations. The statistically quasi-stationary state of a population is determined by repeatedly simulating population dynamics, always starting with the same initial conditions. Distribution of population sizes at time t is determined from population sizes at time t of all simulation runs. Nisbet & Gurney (1982) show in fig. 6.1a that this distribution changes strongly during some initial time (transient behaviour) and then builds up an almost constant distribution, which decays slowly (quasi-stationary behaviour). The decay results from the fact that extinction of populations is an attracting boundary to closed populations. Leaving out all simulations in which populations have gone extinct before reaching time t, it can be shown that the resulting distribution of population sizes is stable for long time spans (see Nisbet & Gurney (1982) and fig. 1 in Stephan (1992)). Stephan (1992)

calculates colonisation times, which correspond to the duration of the transient behaviour.
When the concept of a quasi-stationary state should be applied to population dynamics resulting from the Macu model, it needs amplifications. Firstly, in the Maculinea model, we deal with three species instead of one. In such cases, usually a system state is defined multi-dimensional, comprising all state variables of the system (Wissel, 1989; Fath et al., 2003). Secondly, population dynamics shows quasi-cyclic behaviour. This cyclic behaviour, as well, will express in the quasi-stationary distribution of system states. Therefore, the shape of a cyclic quasi-stationary distribution changes periodically with time. Thirdly, the Macu model is phase-forgetting. Because stochasticity provokes a loss of information about initial conditions, population dynamics from different simulation runs are out of phase. Hence, although each simulation run shows periodical fluctuations, cycles are not found in the quasi-stationary distribution of system states. The distribution might resemble to fig. 1 in Stephan (1992), hiding the real structure of cyclic dynamics.
Determining a quasi-stationary distribution of system dynamics in the Maculinea model must be done carefully. However, the theoretical concept of a quasi-stationary state is helpful to derive a PVA method for interacting species in ch. 3.

2.4.2 Comparison of the Macu model with the HCET model

As mentioned already in ch. 1, the Macu model, we use for our analysis, is based on the HCET model for Maculinea rebeli. To detect differences in behaviour of both models, we compare results, which are important in respect to effects of different host plant or host ant distributions. This can be done only qualitatively, because of model differences. For example plants are modelled more detailed in the HCET model than in the model presented here. Hence absolute values of plant densities are not comparable between the models.

2.4.2.1 Influence of the initial ant distribution

As in the HCET model, in our model the initial ant nest distribution does not strongly influence long-term distributions of species (Hochberg et al., 1994, tab. 3). Hence, populations in both models reach one stable state from different initial situations. In our model, depending on the initial conditions and random effects, the stable state sometimes is not reached, because butterfly population goes extinct within only a few generations after simulation start. Such extinction events are not reported from the HCET model, maybe because in HCET simulations, ants are allowed to equilibrate for 50 generations before Maculinea is introduced.

2.4.2.2 Population sizes of Maculinea and Myrmica ants

In our model, total numbers of butterflies are smaller than in the HCET model, whereas numbers of host ant nests are higher. This result sounds contra-intuitive but can be attributed to differences of the models. Lower number of Myrmica ants in the HCET model should be expected, because of interspecific competition between Myrmica ants and because some area of the habitat is unfavourable for Myrmica schencki host ants (low quality; reproduction rate R is small). Fig. 1 in Clarke et al. (1998) shows the ratio of area occupied by Myrmica schencki ants, which is at most only one half of the total area.
Larger Maculinea populations observed with the HCET model might result from a higher number of butterfly caterpillars reaching ant nests (see sec. 1.3.4). Although, afterwards there

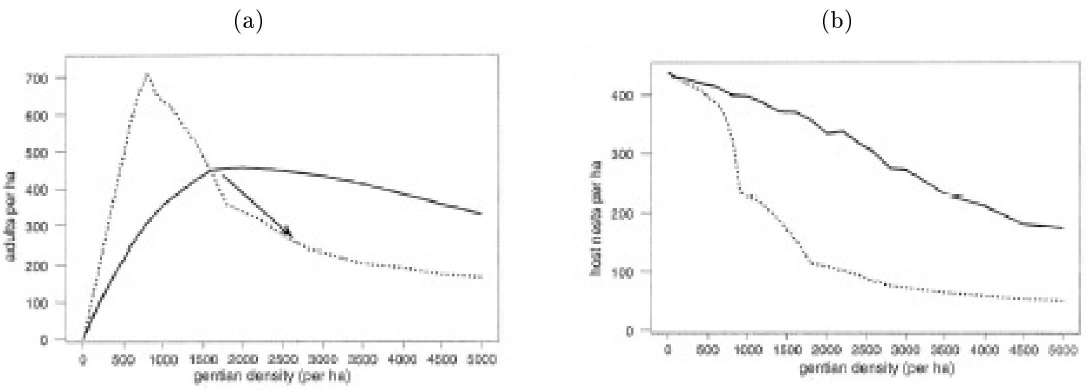
(a) (b)

Figure 2.9: Population size of Maculinea butterflies (a) and host nest density (b) for different densities of Gentiana cruciata. Solid line: host plants are clumped according to equation 2 from Clarke et al. (1998); Dotted line: host plants are uniformly distributed. (Clarke et al., 1998, From HCET model; figures according to fig. 2c and 2d in).

is high mortality due to adoption by non-host ants, resulting butterfly reproduction in the HCET model still might exceed that of the Macu model.

2.4.2.3 Temporally averaged population sizes - dependency on host plant distribution

We now compare fig. 2c and 2d from Clarke et al. (1998), which are shown in fig. 2.9, with results from the Macu model (fig. 2.2). Graphs show butterfly numbers and host ant nest numbers for different host plant distributions. Clarke et al. (1998) report an initial linear increase of mean Maculinea population size with increasing numbers of host plants, which after running through a maximum, changes to a slight decline. Our model reproduces this curve qualitatively (top graph). The optimum plant density to get highest mean numbers of Maculinea butterflies lies slightly below $\frac{1}{2}$ of the possible maximal plant number. In contrast to Clarke et al. (1998), who showed a strong difference between clumped and non-clumped host-plants, we did not find this effect, although using many host plant distributions with different degrees of clumping. Corresponding to Clarke et al. (1998), we find higher numbers of butterflies for plant numbers below optimum density, when plants are less clumped (uniformly or even regularly distributed). But, we do not see a peak or strong changes in the mean of butterfly numbers, when varying the degree of host plant clumping. Curves, resulting from our model, resemble to the curves that are observed for clumped Gentian distributions in the HCET model. As stated in Clarke et al. (1998), for plant densities above the optimum we observe a stronger decline of mean butterfly population size, if host plant distributions are less clumped. But, the effect we find is much lower and underlies high variation.

Both models show a decline in host ant nest numbers (graphs (b)) with increasing host plant density. Independent of the degree of host plant clumping, our results show a linear correlation of mean number of host ant nests and number of host plants. This again resembles to HCET model observations for clumped host plant distributions. However, a stated difference with changed degree of clumping (Clarke et al., 1998) is not reproduced by the Macu model.

Looking closer to differences in models helps to understand, why we cannot find the effects

provoked by host plant clumping, as stated in Clarke et al. (1998). The reason lies in different definitions of plants in the two models. In the Macu model, one host plant in a cell means that an unlimited number of Maculinea eggs can be supported by this plant. Instead, Clarke et al. (1998) model strong intra-specific competition of Maculinea caterpillars on host plants, but they allow several host plants per cell. With increasing number of host plants in a cell, the number of butterfly caterpillars supported by this cell increases. In both models, a density of $900\mathrm{ha}^{-1}$ evenly distributed plants mean that no host ant nest escapes parasitism (all cells are occupied by at least one plant). In the Macu model, in this case, every ant nest can be affected by an infinite number of caterpillars. In the HCET model, due to caterpillar mortality on a plant, this density leads to only low parasitation rates. In both models at a density of $900\mathrm{ha}^{-1}$ evenly distributed plants there are no ant refuges. However, clumping of host plants in the HCET model means that there are refuges for ant nests even for high plant densities. This corresponds to the way, how we model plant distribution. Our model reproduces HCET-evenly-distributed plants only for HCET densities below $900\mathrm{ha}^{-1}$ or in the case, when in the HCET model very high plant densities are used and in our model all cells are occupied with host plants (that is 900 host plants). Hence, it becomes clear that in general the Macu model reproduces curves which result from clumped host plant distributions in the HCET model.
Anyhow, in results of the Macu model for high host plant densities, mean population size of butterflies varies strongly. This variance might result from changes in system regimes. That is, when host plant density is high, there is space left for only few ant refuges. Depending on the arrangement of these refuges, the Macu model either might act as the HCET model with evenly distributed host plants or with clumped host plant distributions. As known from fig. 2.9, changes in the degree of clumping provoke strongly differing population sizes.

2.4.2.4 Temporal variation in population sizes

Hochberg et al. (1994) give a temporal coefficient of variation of 6.7% for Maculinea butterflies. Our simulation results range from 24% to 203%, which is almost 1 to 2 orders of magnitude higher. In contrast to observations of the HCET model, we find host-parasite cycles. Mainly these deterministic cycles contribute to variation in population sizes, whereas the part from demographic stochasticity is smaller.
The HCET model structurally incorporates feedback between Maculinea rebeli and Myrmica schencki populations. Why are oscillations suppressed in that model? To argue on this question, we can profit from keeping our model close to the HCET model. Because we know the difference of both models, we are able to assume reasons for damping in the HCET model. There are two additional forms of competition in the HCET model: interspecific competition between Myrmica ants and intraspecific competition of Maculinea caterpillars on their initial Gentiana host plants. We suppose the first mechanism to have lower influence. Observations of simulations from the HCET model Hochberg et al. (1994, figure 5b,d) suggest that rearing of Maculinea caterpillars is not strongly influenced by non-host ants, in the main range of the Myrmica schencki distribution. Instead we suspect intra-specific competition of young Maculinea caterpillars – during stages before they leave their host plants – to damp later interaction with Myrmica ant brood.

2.4.2.5 Influence of initial conditions

The HCET model for Maculinea rebeli always produced an initial peak in the number of butterflies with a width of about 4 generations (Hochberg et al., 1994). A new model by (Thomas et al., pers. comm.) for a predacious species of Maculinea arion does not show this peak. In our model we see both initial situations. The later mainly in cases when there are only few ants at the beginning of a simulation. Hence, we suppose that in the HCET model for Maculinea rebeli, the butterfly population always finds good conditions at the time of introduction. But it is not clear, if results of both models can be compared, because of different initial conditions of the host ants. In the HCET model, introduction of Maculinea is delayed for 50 generations in order to initially get an equilibrium distribution of host and non-host ants. In the Macu model, the butterfly is introduced immediately. Butterflies and host ants equilibrate at the same time.

2.4.2.6 Interpreting the results of our model in context of the HCET model

From model comparison ahead, we are now able to evaluate results of our more abstract and generic predator-prey model in the context of specific species of Maculinea. The reason is that both models qualitatively give similar results concerning our questions on importance of spatial host distributions. Degree of similarity is surprisingly high. Firstly, because spatial distribution of host ants is different in both models due to interspecific competition in the HCET model. Secondly, because in our model parasitism of Maculinea butterflies seems to drive population dynamics much stronger (missing intraspecific competition of young Maculinea caterpillars on host plants).

Correspondence of both models indicates that we grasped main processes for on the one hand analysing general problems of spatiotemporally interacting species, on the other hand inferring results to the specific Maculinea system. We assume that we made a step forward to discuss Maculinea systems in a broader more general context. This is an example to show how theory and practice can be linked closer via mediating models.

2.4.3 Conclusion

We present population dynamics simulated by the Maculinea model (ch. 1). Census data shows typical behaviour of a host-parasite system. Deterministic cyclic structure interacts with stochasticity, which leads to phase-forgetting quasi-cycles. Population data has a complex structure.

Two temporal phases can be distinguished. The initial state is transient and often shows a trend in census data. However, the trend is not necessarily obvious in all populations, although they interact. This initial phase is followed by a stationary oscillating state. Stationary in the sense that no trend can be observed. Population cycles vary in shape and size.

Extinctions are observed only for the butterfly population.

Chapter 3

Foundation of a PVA approach for interacting species

3.1 Introduction

Population viability analysis (PVA) focusing on extinction risk of single species is a well established technique in conservation biology. Different problems which might drive populations to extinction have been addressed by PVA methods. Studies have been made on habitat destruction, fragmentation of landscapes, metapopulations, disturbance or even catastrophes. Although reliability of PVA models was criticised because of their caricatured picture of natural processes, difficulty to parameterise them, and complication of validation, the models might help to understand processes and influence of internal and external factors of the ecological system under consideration. Comparative PVA on different management options has been used in decision making (e.g. Akcakaya & Sjögren-Gulve, 2000; Beissinger & McCullough, 2002; Frank et al., 2002).

In spite of their success in single species systems, only few PVA studies on interacting species systems can be found in literature (Ives et al., 2000, 2003; Sabo, 2005). One reason might be the high level of complexity in such systems, which makes them difficult to evaluate (Akcakaya & Sjögren-Gulve, 2000). Especially for the distribution of extinction times, which is the general measure for length of persistence of a system, Holyoak et al. (2000) formulated the problem as follows: 'Density cycles cause predator and prey populations to regularly reach low abundances where extinction through demographic stochasticity may be more likely. With cyclical dynamics, the timing and likelihood of extinction may be a function of the density cycles [...]'.

Attempts to analytically derive a formula for the mean time to extinction were made by Renshaw (1991, ch. 6) for a Volterra model following an approach of Nisbet & Gurney (1982) for single species and assumed that both species might be treated separately. Hitchcock (1986) derived approximated formulae for two predator-prey systems formulated as stochastic differential equations. Nisbet & Gurney (1982, ch. 10) used a patch occupancy model to calculate extinction times for Huffaker's experiment of a predator-prey system of mites (Huffaker, 1958). They could show, in accordance to the experiments, that at least one of the species should go extinct after a few predator-prey cycles.

In a case study on a predator-prey system by means of an individual based simulation model, Holyoak et al. (2000) tried to cope with the problem of handling the distribution of extinction times by considering the mean and 95% confidence interval for both, predator and prey. They found reasonable agreement with experimental results. In a theoretical study of spatial effects on survival probability of predator and prey species Donalson & Nisbet (1999) found differences in the tail of the distribution of extinction times. They therefore based their analysis on a visual examination of the frequency distribution of extinction times.

Analysing population dynamics of the Maculinea model (ch. 1), we found eventual extinction of the butterfly population (sec. 2.3.2). Assessing viability of Maculinea would be helpful to analyse habitat suitability, as it is standard for single species systems. However, the studies of Holyoak (2000) and Donalson & Nisbet (1999) show, that species interaction might introduce patterns to the distribution of times to extinction, which are not known from simpler single species systems. Hence, PVA methods for single species systems cannot be applied directly to the host-parasite Maculinea system.

In this chapter, we aim to develop a suitable PVA method for interacting species systems by enhancing a recently suggested unifying PVA-approach for single species systems. For this purpose, we initially briefly review this so called $\ln(1-P_0)$-method for estimation of risk to extinction from single species models (Wissel & Stöcker, 1991; Stephan, 1992; Stephan & Wissel, 1994b; Wissel et al., 1994; Stelter et al., 1997; Frank et al., 2002; Grimm & Wissel, 2004). Then, we analytically enhance this method to a PVA approach for interacting species systems. Finally we present two example studies: typical effects of interacting species systems like strong cyclic fluctuations or mixing of stochastic and deterministic influences are analysed by the PVA method.

3.2 PVA in single species systems

We first provide a brief introduction to evaluation of extinction processes in single species systems. This will be the background for assessing population viability in interacting-species systems, because many concepts can be transferred to the new situation. In our brief presentation, we mainly summarise a recently published paper from Grimm & Wissel (2004), who suggest a 'unifying approach to analysing persistence and viability of populations' (see also Stelter & Grimm, 1994; Frank et al., 2002).

3.2.1 Theory

From a simple Markov model[1], a formula for the probability that a population is extinct at time t can be derived

$$P_0(t) = 1 - c_1 e^{-\frac{t}{t_m}} \tag{3.1}$$

t_m is interpreted as intrinsic mean time to extinction of the population, c_1 is related to the probability that the population does survive an initial transient phase (Keilson, 1979; Wissel & Stöcker, 1991). An exact interpretation of both parameters follows below.

Stelter et al. (1997); Frank et al. (2002); Grimm & Wissel (2004) argue, that for most population dynamical simulation models the negative exponential decline of distributions of times to extinction (eq. 3.1) holds. That is, these models fulfill Markov condition: they are processes

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[1] Grimm & Wissel (2004) work with a Master equation of birth and death type for populations with overlapping generations (see also Leigh, 1981; Nisbet & Gurney, 1982). Stephan (1992) developed a corresponding approach for non-overlapping generations (see also Ludwig, 1996)

without memory. It is assumed, that a Markovian state can comprise many state variables of the model like individual age, weight and size. To test this assumption, they give a protocol.

3.2.2 Protocol for PVA analysis

1. Perform many simulation runs with an appropriate population model without changing initial conditions up to a maximum number of iterations (time horizon T_H). From each run, determine the number of iterations (generations) the population persists.

2. Count these times in a histogram (see fig. 3.1a). This is the frequency distribution of times, when the population went extinct in the simulation experiment. Simulation runs without extinction event are skipped. They can be seen in the final bar in the histogram of fig. 3.1a.

3. Estimate the probability that a population goes extinct at time t. These are relative frequencies of the histogram.

4. Build the cumulative probability distribution $P_0(t)$ by summing up the estimated probabilities (see fig. 3.1b). $P_0(t)$ is the probability, that a population is extinct at time t.

5. Transform the probability distribution $P_0(t)$ according to

$$-\ln(1 - P_0(t)) = -\ln(c_1) + \frac{t}{t_m} \tag{3.2}$$

   which is the logarithmic form of eq. 3.1. It allows a linear fit of distributions of extinction times $P_0(t)$ calculated from simulation runs against time of extinction t (see fig. 3.1c).

6. Determine measures of persistence t_m and c_1 from the fit. (In the example $t_m = 1308$gen and $c_1 = 1.033$ – for interpretation see caption of fig. 3.1.)

The estimated persistence measures describe probability distribution $P_0(t)$, if the fit is accurate. In this case, the simulation model follows the assumption of Markov conditions and can be estimated with the approach. Correlation coefficient r^2 can be used as a quantitative measure for fit quality (Frank et al., 2002).

Grimm & Wissel (2004) cite several studies for different ecological applications, where the $\ln(1 - P_0(t))$ showed linear dependency on time. The approach is tested widely and is suggested to be used for PVA in models, which are density regulated.

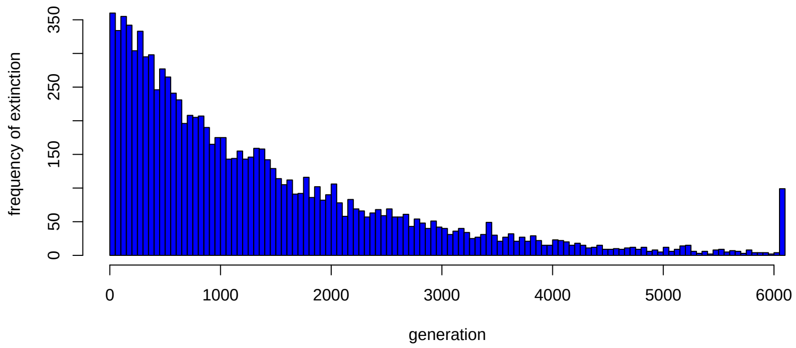
3.2.3 Description of measures of persistence

Here, measures of persistence t_m and c_1 are explained in greater detail. It is shown, how they correspond to other measures for assessment of viability and persistence discussed in literature.

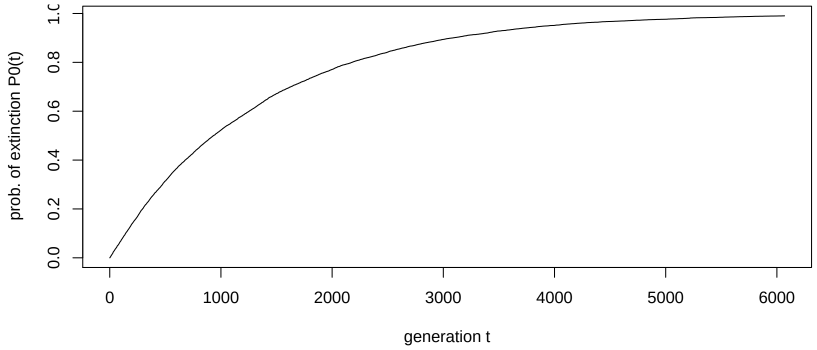
3.2.3.1 Intrinsic mean time to extinction t_m

Density-regulated single species systems have an established state. This is a quasi-stationary probability distribution of population sizes (Darroch & Seneta, 1965; Nisbet & Gurney, 1982;

(a) Histogram of extinction events at each generation



(b) Cumulative probability of extinction $P_0(t)$



(c) $-\ln(1-P_0(t))$-plot

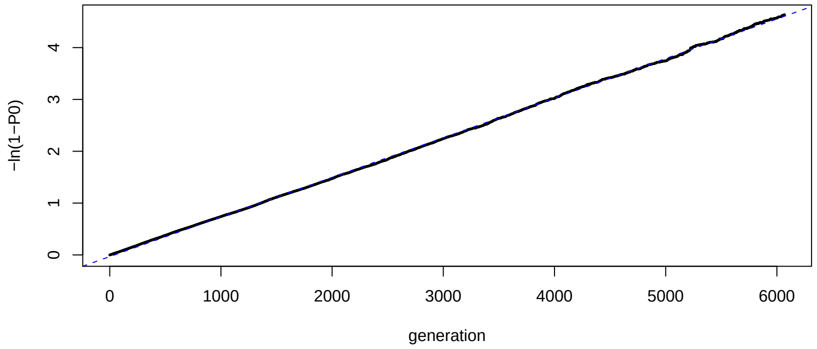


Figure 3.1: Protocol of $\ln(1-P_0)$-PVA method for an example metapopulation study of one artificial type of species. Calculations are performed with a commercial software for metapopulation viability analysis MetaX (Frank et al., 2002; Grimm et al., 2004). Graphs show sequence of data transformations to calculate measures of persistence t_m and c_1. In this example, $t_m = 1308\text{gen}$, $c_1 = 1.03$. Persistence measure $c_1 \approx 1$ indicates that the metapopulation system initially was in the established state. From the intrinsic mean time to extinction t_m the probability that the population goes extinct within 100 generations can be estimated to $P_0(t = 100\text{gen}) \approx 0.08$. In graph. (b) this estimation is confirmed.
The PVA example is taken from tests on the software tool MetaX (unpublished data).

Stephan, 1992; Wissel et al., 1994; Pollett, 1996). In a time-series of population sizes of a single type of species, at each point of time,population size is realised according to this distribution. Population sizes stochastically fluctuate around the most likely positive population size (see e.g. Nisbet & Gurney, 1982, fig. 1.4). There is no trend of a deterministic long-term change in population size.

However, the probability distribution of population sizes is not completely stationary in time. This is due to the fact that an extinct population cannot recover without external help from immigrating individuals. Extinction (that is a population size of 0) is an absorbing state for closed populations.

It is shown that density-regulated populations have a non-zero probability to go extinct (Nisbet & Gurney, 1982; Wissel et al., 1994, e.g.). However, in many cases, extinction is a rare event. For this reason, the probability that a population is extinct $P_0(t)$ increases slowly in time (see fig. 3.1b).

In the following, the probability that a population goes extinct at time t is called extinction rate $p(t)$. If a population is in the established state, extinction occurs with a constant probability per time (i.e. $p(t) = p = \text{const}$). In this case, the intrinsic mean time to extinction $t_m = \frac{1}{p}$. Therefore, t_m is related to risk of extinction of a population in the established state (Grimm & Wissel, 2004, and references therein). High values of intrinsic mean time to extinction t_m indicate low risk of extinction of a population in the established state.

3.2.3.2 Estimation of the probability to reach the established state - Persistence measure c_1

For different reasons a population might not be established (e.g. after a severe decline of population sizes due to a catastrophe or after colonisation of a new site Wissel et al. (1994)). During the following time, the population tends towards establishment or extinction. During this transient phase, distribution of population sizes changes quickly (Nisbet & Gurney, 1982, fig. 6.1a).

The question is, if the population reaches the established state before going extinct. The probability for a population to reach the established state can be calculated as $c_1 \cdot e^{-\frac{T_{ini}}{t_m}}$, where T_{ini} is the time a population takes to reach establishment (Grimm & Wissel, 2004). Time T_{ini} is difficult to be obtained from simulation data. But assuming $T_{ini} \ll t_m$, which should be the normal case for an application of the approach, the probability[2] can be approximated by c_1.

Values for c_1 are positive. A value close to 0 indicates that a population has a low chance to reach the established state. The risk of extinction during the initial transient state is high. If $c_1 \approx 1$, the population is already established in its initial state. Therefore, there is no change in extinction rate. c_1 assumes values higher than 1 when the extinction risk during the initial transient phase is lower than during the established phase.

3.2.4 Assessment of viability

The general measure for PVA analysis is to determine the probability that a population has gone extinct after a certain time horizon $P_0(t = t_h)$. Length of this time horizon t_h as well as critical levels for the probability of extinction are discussed in literature (see Grimm &

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[2] c_1 can take values above 1. In this case, the probability should be approximated by 1

Wissel, 2004, and references therein). The intrinsic mean time to extinction t_m is related to $P_0(t)$ according to equation 3.1. Under conditions of $c_1 \approx 1$ and $P_0(t_h) \ll 1$, which normally is the interesting case, $P_0(t_h) = \frac{t_h}{t_m}$. Grimm & Wissel (2004) suggest the intrinsic mean time to extinction t_m as a general currency to measure viability.

3.2.5 Summary of the $\ln(1 - P_0(t))$-method

The method has several advantages to other PVA measures. Because of exploiting a general mathematical relation, parameters can be estimated highly accurately from simulation data. The linear fit allows assessment to what extent the approach can be used with the model. Deviations from the linear fit can be analysed to gain insight in the reasons for the unexpected pattern in the distribution of times to extinction. Very helpful is that the complete distribution of times to extinction can be described by only two parameters c_1 and t_m. These parameters give access to two crucial but different processes of extinction in single species systems: extinction during the initial transient phase and during the established phase.

3.3 Development of the multi-species PVA method

To develop a PVA method for multi-species systems, we enhance the single species approach presented in sec. 3.2. The reason, why this approach is powerful to analyse single species, lies in the Markov structure of the system (sec. 3.2.1 and the resulting slow decay of the quasi-stationary distribution of population sizes (sec. 3.2.3.1). It is already mentioned that distributions of population sizes do not show quasi-stationary states for the Macu model. Instead, the distribution of population sizes oscillates (sec. 2.4.1.2).

In the following, in a short review on literature, we show that the behaviour of the Macu model is typical for predator-prey systems. We summarise characteristics of the phenomenology of predator-prey systems in three observations. From these observations the most general model is build that describes the cyclic properties of interacting species systems. Based on this model we analytically derive the distribution of times to extinction of populations with an oscillating number of individuals. This distribution of extinction times is analysed according to the protocol for PVA on single species in sec. 3.2.2.

3.3.1 Overview on behaviour of oscillating populations

It is difficult to observe population cycles in the field, because long time series of observations during decades are necessary. However, from analysing observations on three sites during 13 years Hondo (2003) assumes to have found predator-prey cycles in the system of mulberry tiger moth (Thanatarctia imparilis) and its carabid predator Parena perforata. He shows that on two of the three sites both species are closely related.

In experimental studies on predator-prey systems quasi-cyclic structure of population dynamics is observed. Begon et al. (1996) find that introducing a third interacting species into a two species system changes periodicity of the cycles. However, cycles still are observed. Bjornstad et al. (2001) show that differences in time series of a single type of species reflect strength of coupling to other species. Kendall et al. (1999) review several time series of cycling populations. They suggest a synthesis of statistical and mechanistic models, to reveal reasons for cyclic behaviour. In all of these studies time series of population sizes are presented, in which cycles can be observed. These cycles seem to be disturbed by stochastic processes. The

studies show that system traits can be revealed from the information of single time series.
Holyoak et al. (2000) compare results of an experimental study with predictions from an individual-based population model. They find good coincidence, especially when adding stochasticity to the model. Stochastic effects noticeably reduce persistence of prey and predator.
Much insight on oscillating population dynamics is gained from theoretical studies. Nisbet & Gurney (1982, ch. 7.2) give an example for statistical properties of a birth and death process with an externally oscillating factor. They indicate that these oscillations can be observed when averaging time series of population sizes calculated from many simulation runs as well as in the temporal course of a single simulation run. Stephan & Wissel (1994a, 1999) analyse a stochastic resource-consumer system, where birth and death processes of the resource undergo random fluctuations. The underlying deterministic population model shows limit cycles. Resulting, they find gross fluctuations of population sizes due to deterministic variation and small stochastically induced fluctuations (Stephan & Wissel, 1994a, fig. 4). Studying a model with time-delay in density-dependence, Kaitala et al. (1996) show that random disturbance might induce sustained oscillations, which can be observed directly in population size as well as in autocorrelation diagrams (Kaitala et al., 1996, fig. 1). They argue that observed oscillations coincide surprisingly well with observed long-term dynamics of Finnish grouse populations (Kaitala et al., 1996, and references therein). Wilson & Hassell (1997) investigate a stochastic predator-prey metapopulation model and find that stochastic fluctuations at small levels of population sizes are amplified by the dynamics. They observe an initial transient state in their model, but do not closer analyse it. Hastings (2001) outlines that transient dynamics in a deterministic coupled species system can enhance persistence of the species. Therefore importance of initial transient dynamics should not be underestimated. Ives et al. (2000) analyse the effect of periodic mortality events in predator-prey systems. In the deterministic model several stable cycles and transient dynamics are found for predator and prey population sizes. When stochasticity is introduced, these phenomena influence variance of population sizes, because random effects might induce switching between stable cycles or alter the transient dynamics. Spagnolo et al. (2003) investigated effects of increasing sinusoidally modulated external noise intensity to dynamics of a Lotka-Volterra system. For low intensity of noise both species coexist. Increasing noise, quasi-deterministic oscillations occur. For high noise intensity, they detect stochastic resonance (but in this state, one of the two species goes extinct immediately Spagnolo et al. (2003, fig. 2b)).
For the Maculinea system, Hochberg et al. (1994) with the HCET model find an initial outbreak of the butterfly population, which afterwards quickly stabilises due to damping of fluctuations (see sec. 2.4.2). However, with the Macu model (see ch. 1), several types of initial behaviour and afterwards an oscillating Maculinea population is observed (see ch. 2). Population dynamics of the Macu model comprises most of the behaviour which is described in literature.
Summarising the literature survey, population dynamics show periodic oscillations, which are stochastically disturbed. Effects of stochasticity are not strong enough to destroy the cyclic pattern (but see Spagnolo et al., 2003). However, demographic stochasticity is mentioned to be the reason for extinction in this systems (Nisbet & Gurney, 1982; Stephan & Wissel, 1994a, 1999; Holyoak et al., 2000; Hastings, 2001). Stephan & Wissel (1994a); Holyoak et al. (2000) point out that risk of extinction is enhanced, when – due to the population cycle – population size is small. The phenomenona observed in cyclic population dynamics can be condensed by the following statements:

(O1) After an initial time T_{ini}, stochastic distribution of population sizes for several simulations shows almost stable periodical oscillations[3] in time (e.g. see ch. 2). These might for a predator-prey-system result from intrinsic population dynamical cycles or can be driven by an external factor like seasonality. The observation (O1) transfers the concept of a quasi-stationary distribution of population sizes for single species systems 3.2.3 to interacting species systems. Note, that here the probability distribution of population sizes is not quasi-stationary, but changes periodically.

(O2) Reason for extinction of populations in such systems is stochasticity, because deterministically driven extinction events would not allow to build up the cycling population dynamics.

(O3) Probability $p(t)$ that a population which survived for time $t-1$ goes extinct at time t (actual rate of extinction) does only implicitly depend on time t. Explicitly it is determined by the distribution of population sizes of the population $N(t)$ at time t. Therefore $p(t) = p(N(t))$.

3.3.2 Analytical development of the PVA method

According to observations (O1) and (O2) we formulate the general model for population dynamics showing cyclic behaviour.

$$N(t) = \begin{cases} N(t) & ; t \leq T_{ini} \\ N(T_{ini} + ((t - T_{ini}) \bmod T_P)) & ; t > T_{ini} \end{cases} \tag{3.3}$$

$N(t)$ denotes the stochastic distribution of population sizes. The upper line in eqn. 3.3 describes the initial transient state of the system before establishment (ch. 3.2). For the initial state, we do not have information about the temporal development of the distribution of population sizes. Hence, we use the most general distribution.

It is assumed that after time T_{ini} the system reaches its established state (O1). This state is described by the lower line in eqn. 3.3 - a deterministically oscillating distribution of population sizes. T_P is periodic time of cycles. mod denominates the modulo-division. For the model, we assume separate generations as often occur in e.g. insect populations. Anyhow, with slight modifications our approach is applicable to systems with mixed generations, too (Nisbet & Gurney, 1982, p. 234).

According to observations (O2) and (O3), we determine the rate of extinction $p(t)$ (i.e. probability that a population, which has survived for the time $t-1$, goes extinct at time t) from equation 3.3. Periodic structure of $N(t)$ is transmitted to probability $p(t)$. This is due to observation (O3), which couples $p(t)$ to the distribution of population sizes $N(t)$.

$$p(t) = p(N(t)) = \begin{cases} p(t) & ; t \leq T_{ini} \\ p(T_{ini} + ((t - T_{ini}) \bmod T_P)) & ; t > T_{ini} \end{cases} \tag{3.4}$$

Now we are able to calculate distribution of times to extinction for the general model in eqn. 3.3. The probability, that a population goes extinct exactly at time t, is the probability,

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[3] Fath et al. (2003) point out, that a stationary distribution of population sizes can be considered as a degraded cycling distribution

that it has survived until time $t-1$ and goes extinct at time t: $p(t) \cdot \prod\limits_{i=1}^{t-1}(1-p(i))$, where $\prod$ denotes a product. Hence, by summing up these values for all times t, we receive the probability $P_0(t)$ that a population is extinct at time t.

$$\begin{aligned} P_0(t) &= \sum_{j=1}^{t}\Big[p(t) \cdot \prod_{i=1}^{j-1}(1-p(i))\Big] \\ &= 1 - \prod_{j=1}^{t}(1-p(j)) \end{aligned} \tag{3.5}$$

For single species systems, when a population is in the established state, $p(t)$ is assumed to be constant[4]. Formalism for Markov processes can be applied. A linear relation between transformation $-\ln(1-P_0(t))$ and time t (sec. 3.2) can easily be shown (Stephan & Wissel, 1994b; Wissel et al., 1994).

In the case regarded here, periodic structure in $p(t)$ (eqn. 3.4) leads to a more complex mathematical form. But, it can be shown that for long time scales the $-\ln(1-P_0(t))$ transformation leads to a linear dependency, too. For the calculation, a separation of time scales is introduced according to natural scales T_{ini} and T_P in model eqn. 3.3:

$$t = T_{ini} + l \cdot T_P + i \tag{3.6}$$

where like before T_{ini} is the time, the system takes to reach the established state and T_P denotes duration of one cycle. l is the number of cycles, the system has completed until time t. i indicates the remaining time steps after the last completed cycle. Applying separation of time scales (eqn. 3.6) leads to

$$\begin{aligned} P_0(t) &= 1 - \left\{\prod_{j=1}^{Tini}(1-p(j)) \cdot \prod_{j=T_{ini}+1}^{t}(1-p(j))\right\} \\ &= 1 - \left\{\prod_{j=1}^{Tini} \cdot \underbrace{\prod_{j=T_{ini}+1}^{T_{ini}+T_P} \cdot \prod_{j=T_{ini}+T_P+1}^{T_{ini}+2T_P} \cdot\cdot\cdot\cdot\cdot \prod_{j=T_{ini}+(l-1)T_P+1}^{T_{ini}+lT_P}}_{\text{all products are equal because of periodicity}} \cdot \prod_{j=T_{ini}+lT_P+1}^{t}\right\} \end{aligned} \tag{3.7}$$

$$= 1 - \left\{\prod_{j=1}^{Tini}(1-p(j)) \cdot \Big[\prod_{j=T_{ini}+1}^{T_{ini}+T_P}(1-p(j))\Big]^l \cdot \prod_{j=T_{ini}+lT_P+1}^{t}(1-p(j))\right\}$$

To save space and present the equation more clearly, some products are only symbolised by $\prod$ and their limits (that is $\prod\limits_{j=a}^{b} \equiv \prod\limits_{j=a}^{b}(1-p(j))$).

Performing transformation, $-\ln(1-P_0)$ we receive

$$\begin{aligned} -\ln(1-P_0(t)) &= -\ln\left(\prod_{j=1}^{Tini} \cdot \Big[\prod_{j=T_{ini}+1}^{T_{ini}+T_P}\Big]^l \cdot \prod_{j=T_{ini}+lT_P+1}^{t}\right) \\ &= -l \cdot \ln\left(\prod_{j=T_{ini}+1}^{T_{ini}+T_P}\right) - \ln\left(\prod_{j=1}^{Tini} \cdot \prod_{j=T_{ini}+lT_P+1}^{t}\right) \end{aligned} \tag{3.8}$$

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[4] This is the discrete form of eqn. 3.1 for non-overlapping generations. It describes a binomial instead of a negative exponential distribution of times to extinction.

The last line of eqn. 3.8 separates into two terms. The first part is linear in l. The product in this term represents the probability, that the population survives one cycle. It is equal for each cycle, thus independent of time on a long time scale. Hence, this part of eqn. 3.8 is linear in time on the long run. Contributions of the nonlinear second term are under general conditions of $t \gg T_{ini}$ and $t \gg T_P$ small in comparison to the linear part. These conditions are fulfilled, when we ask for long time survival of populations.

This explains, why the standard $\ln(1 - P_0(t))$-PVA method suggested by Grimm & Wissel (2004, and references therein) can be applied to more complex stochastic systems with a cyclic fluctuating probability distribution of population sizes. On a short time scale ($t < T_P$), extinction of a population is driven by deterministic cycles of the system. But on the long run, these short time fluctuations accumulate to a total value for a cycle. This value is constant in time (see Nisbet & Gurney, 1982, who perform analysis for a periodically disturbed single species system).

In our analysis, although we aim to describe systems of interacting species, we have restricted to the distribution of population sizes $N(t)$ of one single species. This would be one focused species of a system of interacting species. We now argue, that this result is valid also for the entire system. Without further assumptions, we can interpret $N(t)$ as the distribution of states of the interacting species systems (which of course might be very complex multi-dimensional objects). These states then cyclically oscillate with a period time of T_P. On the time scale of completed cycles (T_P is the naturally shortest time scale), the stochastic process fulfills Markov condition. Time of memory in the process is shorter than T_P. Hence, the distribution of extinction times on long time scales follows a Markov process, as it is well known from single species systems (Goel & Richter-Dyn, 1974; Grimm & Wissel, 2004; Lande et al., 2003).

The PVA protocol in ch. 3.2.2 can be applied to very general interacting species systems. To analytically derive measures of persistence t_m and c_1 under conditions of deterministic cycles in a distribution of population sizes, the Gaussian mean square fit for eqn. 3.8 is calculated in the limit of an infinite time horizon T_H (see appendix A.1). The formulae for the measures of persistence are

$$\begin{aligned} t_m &= -\frac{T_P}{\ln\Big\{\prod\limits_{i=T_{ini}+1}^{T_{ini}+T_P}(1-p(i))\Big\}} \\ c_1 &= \Big[\prod_{i=1}^{T_{ini}}(1-p(i))\Big]\cdot\Big[\prod_{i=T_{ini}+1}^{T_{ini}+T_P}(1-p(i))\Big]^{\frac{1+T_P}{2T_P}}\cdot\Big[\prod_{i=T_{ini}+1}^{T_{ini}+T_P}(1-p(i))^{-\frac{i}{T_P}}\Big] \\ &= \Big[\prod_{i=1}^{T_{ini}}(1-p(i))\Big]\cdot\Big[\prod_{i=T_{ini}+1}^{T_{ini}+T_P}(1-p(i))^{\frac{T_P-2i+1}{2T_P}}\Big] \end{aligned} \tag{3.9}$$

The intrinsic mean time to extinction t_m is the negative reciprocal arithmetic mean over one cycle of the natural logarithm of the probability that the population survives at time t. This is an averaged measure for the probability, that populations in the system survive during one cycle. From a corresponding result for a single species system with periodic perturbations Nisbet & Gurney (1982) argued that mean time to extinction can be calculated already from one cycle. This statement holds for the calculation of the intrinsic mean time to extinction t_m in systems of interacting species.

The formula for the persistence measure c_1 is composed of two parts. The first describes survival probability during the initial phase, the second is a weighted geometrical mean of the survival probability during the first cycle. Due to weighting, high extinction risk at the

Table 3.1: Limit approximations for PVA-parameters t_m and c_1 for extremes in risk of extinction

	established state persistence $(\prod^{T_P} \to 1)$	established state extinction $(\prod^{T_P} \to 0)$
transient state persistence $(\prod^{T_{ini}} \to 1)$	$t_m \to \infty$, $c_1 \to 1$	$t_m \to 0$, $c_1 \to 0 \vee c_1 \to \infty$
transient state extinction $(\prod^{T_{ini}} \to 0)$	$t_m \to \infty$, $c_1 \to 0$	$t_m \to 0$, $c_1 \to \pm\infty$

$\prod^{T_P} \to 0$: infinitely high risk of extinction during the established phase
$\prod^{T_P} \to 1$: no risk of extinction during the established phase
$\prod^{T_{ini}} \to 0$: infinitely high risk of extinction during the initial phase
$\prod^{T_P} \to 1$: no risk of extinction during the initial phase.

beginning of the cycle decreases c_1 stronger than at the end. Grimm & Wissel (2004) interpreted c_1 as an index for the probability that a population reaches its established state, provided $T_{ini} \ll t_m$ (see sec. 3.2.3.2). In context of interacting species, initial transient phase is extended to the first cycle. This is not surprising, as cyclic behaviour is of course transient. Only on the long run (that is taking into account many cycles), stationarity of periodicity can be perceived.

3.3.3 Extrapolation for the $\ln(1 - P_0)$-PVA-method

In this section we analyse behaviour of PVA-parameters for extremes in risk of extinction. Extremes mean that either the risk of extinction is extremely high (probability of survival $\prod^{t} \to 0$) or extremely low (probability of survival $\prod^{T_P} \to 1$). Extremes in risk of extinction are analysed for the initial and the established state. Table 3.1 shows results from extrapolations of persistence measures t_m and c_1 for all four combinations of extremes in risk of extinction. The upper left entry refers to the case of a persisting population. In this case, $c_1 \to 1$ and $t_m \to \infty$. These approximations are in accordance with the expectation we have for the persisting populations. Going to the lower left entry of tab. 3.1, extinction risk during the initial transient phase is extremely high. In the approximation $c_1 \to 0$. In such cases, populations have a very small chance to survive longer than the initial phase. But a population, which overcomes the high risk of extinction during the initial phase, will persist on the long run. Hence, in this case populations undergo an initial bottleneck (for single species see e.g. Ludwig, 1996). For the Maculinea model, this effect is found frequently (see ch. 4.5.2.2).

Right entries of tab. 3.1 refer to habitat conditions which are insufficient to sustain a population during the established phase. Correctly $t_m \to 0$ indicates that a population cannot survive any time during the established phase. In such cases, immediate habitat management must

be established in order to save endangered populations. Here, a change of initial conditions does not reduce the substantial problem, hence we ignore them. Qualitatively values of c_1 can be interpreted taking into account eqn. 3.13 which is discussed in sec. 3.4.1.
This analysis of extreme values for risk of extinction reveals an important result. Although mathematical conditions of the $\ln(1-P_0)$-approach are violated and actual extinction rate $p(t)$ does not follow a binomial distribution on a long time scale, the behaviour of persistence measures t_m and c_1 qualitatively follows our expectation. Behaviour of t_m and c_1 is robust approaching borders of applicability of the $\ln(1-P_0)$-method. Hence for simulation studies we hypothesise: extremely high values of t_m should correctly indicate persistence and extremely low values of c_1 can be interpreted as high risk of extinction during the initial phase. In ch. 4 these assumptions are tested for the Maculinea model.

3.4 Application of $\ln(1-P_0)$ to different systems

It is analytically shown in eqn. 3.7 that $\ln(1-P_0(t))$ is proportional to the time t, for the general model of oscillating population sizes (eqn. 3.3). By applying eqn. 3.2, Measures of persistence c_1 and t_m are estimated, according to the PVA protocol for single species systems in sec. 3.2.2. Hence, it is demonstrated that the PVA protocol suggested by Stelter et al. (1997); Frank et al. (2002); Grimm & Wissel (2004) can be applied to the general description of species systems with oscillating population sizes.
In this section, we show applicability of the protocol for models of different complexity in population dynamics. We analyse general behaviour of PVA parameters intrinsic mean time to extinction t_m and c_1 in context of multi-species systems, check for enhancements and fathom robustness of the approach.

3.4.1 Influences of system characteristics on measures of persistence – a sinus model

3.4.1.1 Description of the sinus model

We construct a model for the phenomenological description of a population with a sinusoidally fluctuating distribution of population sizes. Mean level of population size follows the deterministic equation

$$\overline{N}(t) = \begin{cases} N_{ini} & ; t \leq T_{ini} \\ a \cdot \sin(\frac{2\pi}{T_p} t - \varphi) + n_0 & ; t > T_{ini} \end{cases} \tag{3.10}$$

The six parameters are interpreted in the following way: N_{ini} is a constant population size for the initial phase, T_{ini} is duration of the initial phase. In the established phase, a is amplitude, T_P is period length, φ is phase shift and n_0 is an all time average population size. Amplitude a is stochastically disturbed according to

$$a = a_{max} + 2a_r(p(t) - 1) \tag{3.11}$$

where a_{max} describes the deterministic part of the amplitude and a_r denotes the strength of noise. Random numbers p(t) are uniformly distributed ($p(t) \in [0;1)$). The population goes extinct, when its number of individuals drops to zero or below.
We have chosen this extremely oversimplified model for two reasons. First, it is easy to handle, because parameters in the sinus model and their effects are well-known. Hence, their influence

on the measures of persistence t_m and c_1 can be interpreted easily. Parameter variation in the sinus model gives an impression, how different cyclic population dynamics express in different values of the persistence measures. Second, actual rate of extinction $p(t)$ can be calculated explicitly by solving inequation $N(t) \leq 0$.

$$p(t) = \begin{cases} p_{ini} & ; t \leq T_{ini} \\ \min\Big\{1, \max\Big[0, 1 - \frac{1}{2a_r}\Big(a_{max} + \frac{n_0}{\sin(\frac{2\pi}{T_P}t - \varphi)}\Big)\Big]\Big\} & ; (t > T_{ini}) \wedge (\sin(\frac{2\pi}{T_P}t - \varphi) > 0) \\ \min\Big\{1, \max\Big[0, \frac{1}{2a_r}\Big(a_{max} + \frac{n_0}{\sin(\frac{2\pi}{T_P}t - \varphi)}\Big)\Big]\Big\} & ; (t > T_{ini}) \wedge (\sin(\frac{2\pi}{T_P}t - \varphi) < 0) \\ 0 & ; (t > T_{ini}) \wedge (\sin(\frac{2\pi}{T_P}t - \varphi) = 0) \end{cases} \tag{3.12}$$

Hence, measures of persistence can be calculated numerically from eqn. 3.9. By comparison of analytical and simulation results, accuracy of the parameter estimation from the protocol (described in sec. 3.2.2) can be assessed.

3.4.1.2 Population and extinction dynamics of the sinus model

For simulations we used a standard parameter set presented in table 3.2. The maximum amplitude a_{max} is bigger than the deterministic mean population size n_0. Hence, the deterministic model always goes extinct. In contrast, the stochastic model only goes extinct with a certain probability $p(t)$ (see eqn. 3.12). The parameter p_{ini} is chosen to be constant: $p_{ini} = p(N_{ini}) = 0.005$.

Fig. 3.2 shows three realisations calculated with the stochastic simulation model for the set of standard parameters. The resulting histogram of times to extinction and the corresponding $\ln(1 - P_0)$-plot for 50000 runs can be seen in fig. 3.3. Looking at the time series of population sizes, deterministic and stochastic fluctuations can be clearly distinguished. They reproduce in sharp peaks of extinction events (fig. 3.3a) and in a stair-structure around the fit line (fig. 3.3b). From the fit, we deduce mean time to extinction $t_m = 349$gen and $c_1 = 1.0437$. The fit has an accuracy of $r^2 = 0.9975$, which means perfect applicability of the PVA-approach.

On the one hand, we find that the fit method suggested in the protocol (sec. 3.2.2) can be applied and results in high accuracy. On the other hand, an unexpected pattern is observed. In contrast to the single species case (fig. 3.1c), where data points in the $\ln(1 - P_0)$-plot arrange in a straight line, we find a stair-structure in the case of the sinus model. As well, histograms of extinction events are different in the single species and the sinus model cases. Instead of a stochastically disturbed decline in the frequency of extinction events with time (see fig. 3.1a), we find regularly ordered single peaks with high frequency of extinction events (fig. 3.3a).

Table 3.2: Standard parameter set for sinus model with stochastic variation of amplitude.

Established phase		Transient phase	
a_{max}	30	T_{ini}	0
a_r	10	p_{ini}	0.005
T_P	80		
φ	0		
c	29		

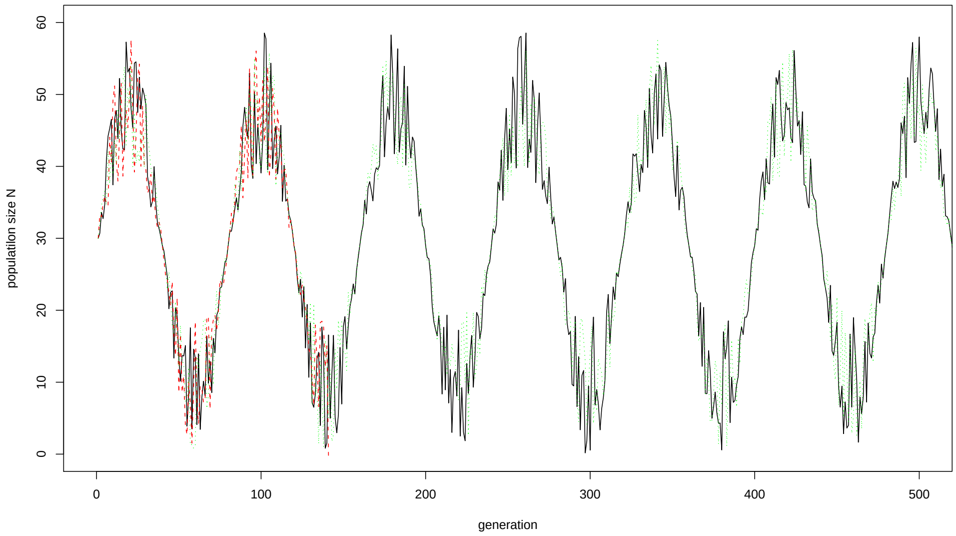

Figure 3.2: Sinus model: population sizes of three independent example simulation runs (solid, dotted and dashed lines). Simulations are performed with parameters in tab. 3.2

Between two extinction peaks, surprisingly populations do not go extinct. Amplitude of the peaks however declines in the same form as in the single species case.

With help of eqn. 3.7 for the probability $P_0(t)$ of a population to be extinct at time t, the observed pattern can be explained. The last line of eqn. 3.7 contains three terms. The first term accounts for effects during the initial phase of population dynamics. It can be ignored, because $T_{ini} = 0$ (see tab. 3.2). The second term contains an aggregated probability that the population survives during l full cycles. This term transforms to the linear relationship between $\ln(1 - P_0)$ and l in eqn. 3.8. As remarked in sec. 3.3.2, the linear relation is an approximation for long times. It is only valid, when the third factor in eqn. 3.7 on the long run becomes small in comparison to the second factor. For this reason, we find the linear fit in fig. 3.3b to be highly accurate. It is valid for long time scales.

However, to explain the stairs (fig. 3.3b) and peaks (fig. 3.3a), we must turn to a shorter time scale – to a time scale shorter than the period T_P of one cycle. The last product in the equation $\prod_{j=T_{ini}+l\cdot T_P+1}^{t} (1 - p(j))$ aggregates the rate of extinct during the last uncompleted cycle. If up to time t in the last cycle, actual rate of extinction $p(t) \approx 0$, the product evaluates to 1. $P_0(t)$ does not change from one time step to the next. So, while population sizes are high, no extinction event occurs. The $\ln(1 - P_0)$-plot produces a straight line. Only during times when extinction is possible, the values of $\ln(1 - P_0)$ change. t_m averages over the duration of one cycle. Therefore, the fit line intersects steps in fig. 3.3b.

Hence, the observed short-term patterns in extinction dynamics of the sinus model result from cyclic variation of population size. Only, when population size is small, the risk of extinction is high. This corresponds to observation (O3) in sec. 3.3.1 and to findings in systems of interacting species (Stephan & Wissel, 1994a; Holyoak et al., 2000) or systems with seasonally driven population dynamics (Stephan (1992); Stelter and Grimm, pers. comm.). When analysing the

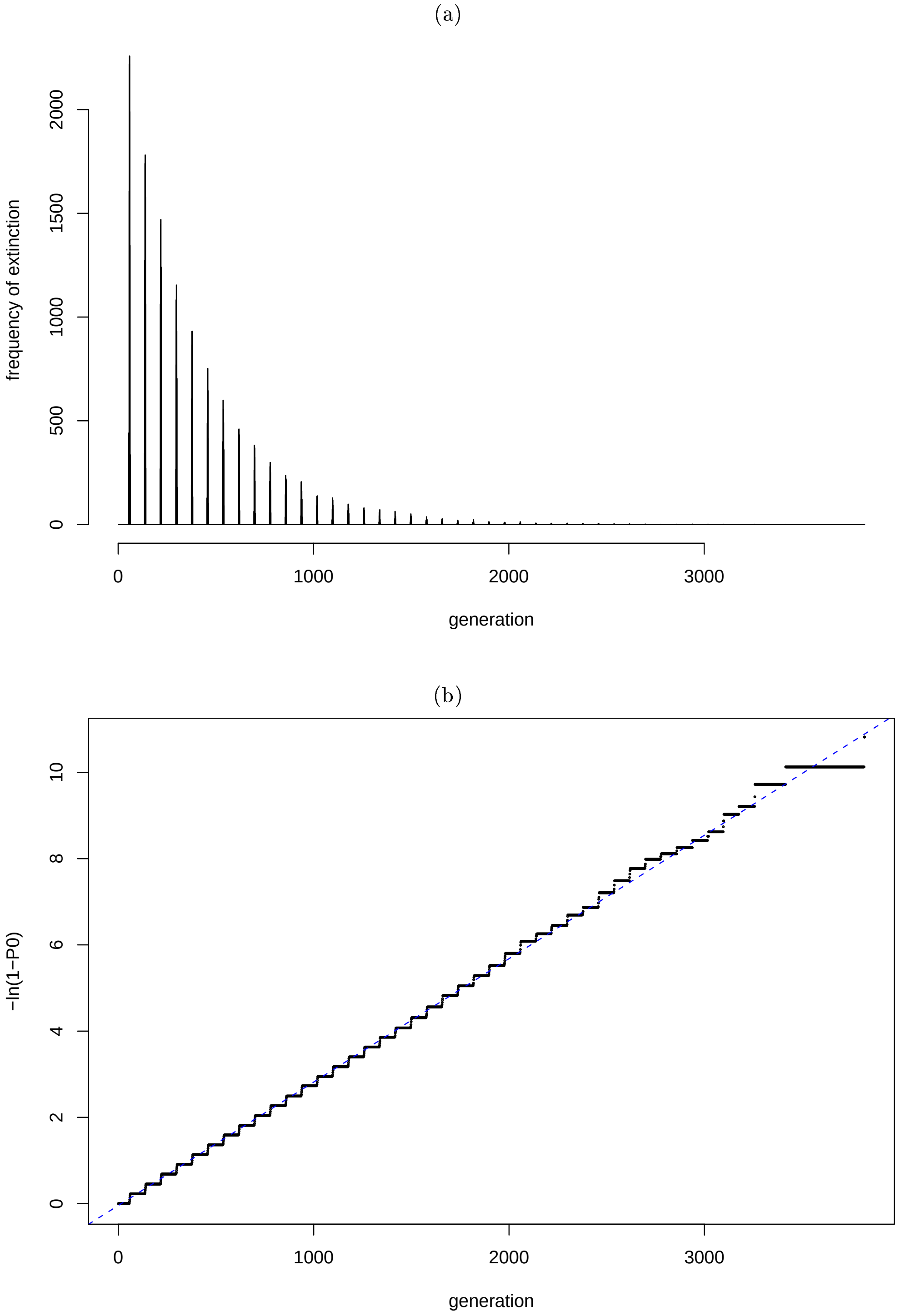

Figure 3.3: Sinus model: Distribution of times to extinction and $\ln(1-P_0)$-PVA-plot. In graph (a) spikes are found at times of increased risk of extinction. In graph (b) these spikes transform to a step structure around the fit line. Inaccuracies for large generation numbers result from the low number of extinction events (compare graph (a)). Simulation is performed with parameters in tab. 3.2

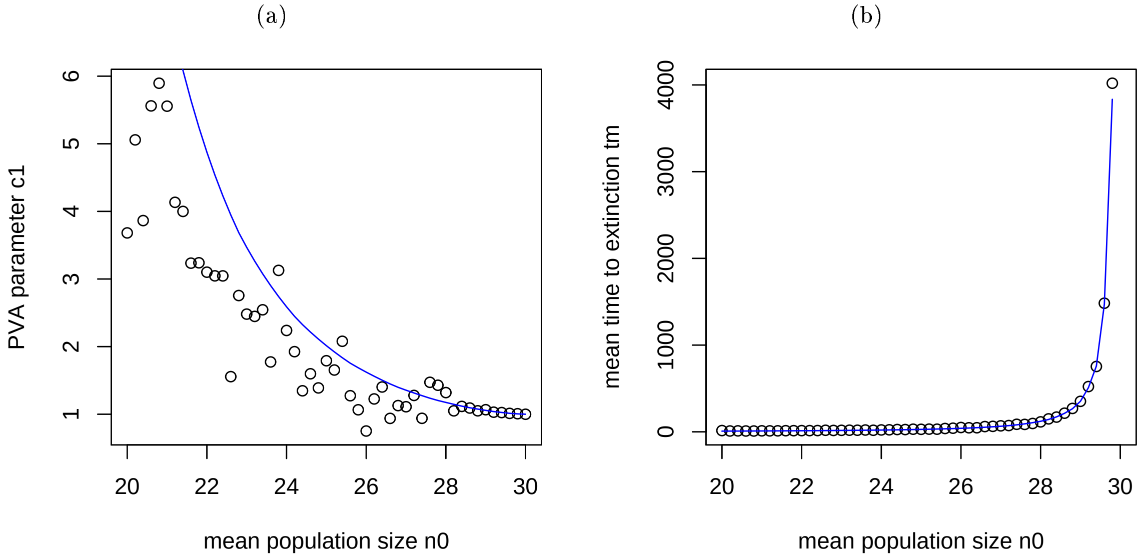

Figure 3.4: Sinus model: Measures of persistence c_1 (graph (a)) and t_m (graph(b)) for different values of mean population size n_0. Dots indicate simulated values, lines numeric calculation.

Macu model, the histogram of times to extinction shows peaks. However, they are broadened (see ch. 4).

3.4.1.3 Parameter variation experiments

Parameter variation of the sinus-model is calculated both analytically and in simulations with software Mathematica (Wolfram, 1988). We expect small differences in results, because in contrast to the analytical formulas (eqn. 3.9), which are developed for an infinite time horizon T_H (appendix A.1), simulation studies only can be performed for a finite time horizon T_H (maximal simulation time within one run). Surprisingly, in all experiments, we find good agreement of results (see e.g. fig. 3.4). This shows that a time horizon of $T_H = 1000$ generations for a simulation run, is enough to calculate the parameters in the sinus model with sufficient accuracy. This is an important information for studies of systems, where an analytical solution is not accessible. Our general experience is that simulation models for a reasonable time horizon T_H provide measures of persistence with reasonable accuracy (see ch. 4 for qualitative reasons; ch. 5 and ch. 6 for an estimation of accuracy for persistence measures calculated from the Maculinea model).

In the following, results of the parameter variation are summarised. There are only two parameters n_0 and a_r, which show a strong influence on mean time to extinction t_m. Results of variation of mean population size n_0 can be seen in fig. 3.4b. There is a threshold behaviour in t_m. Below $n_0 = 28$, populations die out almost immediately. A population is endangered severely during a long time in each cycle. For very small values of n_0, a population almost surely dies within the first cycle. But, when $n_0 > 28$, mean time to extinction t_m increases extremely. The model is very sensitive to mean population size n_0. n_0 must be seen as the crucial factor in the PVA. This is not surprising as n_0 influences the probability to survive in a double sense. First, it regulates the actual rate of extinction $p(t)$. Second, it has an influence on the period of time during which the population size is low and the population is prone to extinction (a result of the nonlinear min function in eqn. 3.12). As we know from eqn. 3.9, the intrinsic mean time to extinction t_m is determined by a mean value of extinction risk for the whole cycle. Hence extinction risk at all times during the cycle accumulates. Decreasing n_0 affects this accumulated value extremely.

Model parameter a_r describes the amount of stochastic temporal variance in population sizes (variance $\sigma^2(a(t)) = \frac{1}{3}a_r$). In a first experiment, maximum amplitude is fixed to 30. With increasing a_r, the mean amplitude is decreasing ($\overline{a}(t) = a_{max}(t) - a_r(t)$; see eqn. 3.11). Hence, frequency of large amplitudes in the stochastic process is decreased with increasing a_r. Only these extreme values lead to extinction at times, when the sinus function is in vicinity of its minimum. This explains the increase of mean time to extinction t_m with increasing parameter a_r. But, there is one exception: for $a_r = a_{max} = 30$, t_m drops to only half the value as for $a_r = 29$. This jump is surprising, but for such high variance, even when the sinus function reaches its maximum, extinction is possible. Here, this result seems to be an artefact. However, increasing variance in population size, while keeping the maximum constant, also in natural systems might lead to a sudden drop in times to extinction. In the second experiment, we keep the mean value of amplitude a constant ($\overline{a} = 29$), while only the stochastic variance is changed. In that case t_m is decreasing with increasing variance. Extinction risk of a population is higher, because small population sizes can be reached. Our finding corresponds to observations for single species systems; an increase in environmental stochasticity increases extinction risk (e.g. Ludwig, 1996). Stephan & Wissel (1999) show that in a resource-consumer system, environmental stochasticity increases extinction risk but the effect of internal cycles is different. Dimentberg (2002) shows that the number of consumers in damped Lotka-Volterra systems stays at low levels for long times, when environmental stochasticity is high.

For the other parameters, only small influences on t_m can be detected. These result from the discrete model structure and can be considered as artefacts. For period length T_P, this finding is surprising. It means for long term behaviour of the sinus-model that duration of phases with low numbers of individuals (high risk of extinction) is perfectly balanced by phases with sufficient numbers of individuals[5]. Wichmann et al. (2003) analyse influence of periodically oscillating environmental conditions on persistence of the tawny eagle in South Africa. In this more realistic model they find strong dependency of persistence on the duration of a period.

In contrast to the few parameters, which influence intrinsic mean time to extinction t_m, persistence measure c_1 is affected by all model parameters. As mentioned in ch. 3.3, extinction risk during an initial phase of the population dynamics should influence c_1. Hence, we first focus on parameters connected directly to this initial transient phase. T_{ini} and p_{ini} describe the transient state. If risk of extinction during the initial phase p_{ini} is higher than risk during the established state then $c_1 < 1$ and vice versa. Longer T_{ini} enhances the effect. This corresponds to eqn. 3.9 where initial extinction risk enters as a product over duration of initial phase T_{ini}.

An increase of parameter φ shortens initial time of no extinction risk within the first cycle. This leads to a decrease in c_1. According to the interpretation of formula 3.9 in sec. 3.3, c_1 accounts for temporal distribution of extinction risk within a cycle. Low extinction risk at the

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[5] (Singer, unpublished) analysed a model consisting of only two mean levels of population sizes. For this model, intrinsic mean time to extinction t_m depends on the ratio of time, the system stays in one of the two levels.

beginning of a cycle increases c_1.
When increasing duration of a period T_P in the sinus model, an increase in c_1 is observed. This can be explained by the extension of the time with low risk of extinction during the early stage of the first cycle.
Anyhow, it must be taken into account that in each experiment, a single parameter was varied. According to eqn. 3.9 for c_1 and eqn. 3.12 interactions between parameters can be expected. Having in mind the interpretation of c_1 from single species systems (sec. 3.2.3), it can be assumed that a total risk of extinction prior to first extinction in the established phase can be seen as risk of extinction during the transient phase. c_1 is determined by the ratio of this initial extinction risk and the risk of extinction during the established state.
A strong influence on c_1 is found for variation of n_0 or a_r In fig. 3.4a exemplarily variation of n_0 is depicted. Results from simulation as well as results from the analytic calculations show a strong decline of c_1 from values far greater than 1 down to 1 with increasing value of n_0. Note, both parameters n_0 or a_r determine population dynamics during the established state of the system. However, intuitively, they are not supposed to affect the initial transient phase. Can c_1 be used as an indicator for extinction risk during the transient state anyhow? The answer is yes. Effects of n_0 and r_a can be explained, when the formula for c_1 in eqn. 3.9 is transformed slightly, by inserting the formula for t_m

$$c_1 = [\prod_{i=1}^{T_{ini}} (1 - p(i))] \cdot [\prod_{i=T_{ini}+1}^{T_{ini}+T_P} (1 - p(i))^{-\frac{i}{T_P}}] \cdot e^{-\frac{T_P+1}{2t_m}} \tag{3.13}$$

Here, the first product in eqn. 3.13 describes the influence of the initial phase. To the second product mainly the phase shift φ contributes. But, via the exponential function in the last term, changes of parameters determining risk of extinction during the established state influence c_1 exponentially, too.
Now, notice that for $T_P \ll t_m$ the exponent approaches almost unity. Hence, in ecologically reasonable situations, when intrinsic mean time to extinction t_m is sufficiently long, transient state and established state are evaluated independently by c_1 and t_m. This can be observed in fig. 3.4. For $n_0 > 29$, t_m increases tremendously meanwhile c_1 is almost not influenced.
In contrast, for low values of n_0, $t_m \approx 0$. In this case, the $\ln(1 - P_0)$-approach is used beyond its range of applicability. Correlation coefficient $r^2 \ll 1$, which indicates difficulties with the method. Anyhow, as explained in sec. 3.3.3, measures of persistence t_m and c_1 qualitatively tend to the right direction. Indeed, c_1 should assume values above 1, because the risk of extinction during the initial phase is much lower than afterwards, when populations immediately go extinct.
In fig. 3.4a simulation results (circles) deviate from analytic calculations (line) for low values of n_0. Simulation results are evaluated inaccurately, because the data is not appropriate for the $\ln(1 - P_0)$-approach. The exponent in eqn. 3.13 assumes large values because of an estimated value of $t_m \approx 0$. Small errors in calculations of t_m provoke high variation in c_1. Hence, inaccuracy in values of c_1 has to be expected, when estimated values of t_m are low.
It is possible to explain errors in the c_1 estimation, because initial phase and established phase are separated artificially in the simple sinus model. Hence, parameters n_0 and r_a can be attributed to the established phase. Observing influence on c_1 for example in fig. 3.4a motivates a thorough analysis and reveales technical reasons for c_1 variation and inaccuracy. It becomes clear that inaccuracy has to be expected, when extrapolating PVA parameters for high risk of extinction. In complex simulation models, the impact of parameters is not previously clear.

A parameter affecting both t_m and c_1 must be seen as acting on initial and established state. It would be much more difficult to reveal an artefact. In ch. 4 PVA analysis of the Maculinea model in certain cases results in low values of t_m and high values of c_1. Referring to findings with the simple sinus model, we immediately conclude that c_1 values might be incorrect. In this case, the simple model helps to understand results of the complex one. It protects from misinterpretation.

3.4.2 Stochastic variations influence deterministic periodicity – a predator-prey model

We use a mathematical predator-prey model (eqn. 3.14), which is similar to a Lotka-Volterra system but includes density dependence for the prey. Interaction between species is formulated as laissez-faire-predation (see e.g. Wissel, 1989). The discretised equations for non-overlapping generations of the deterministic model are

$$\begin{aligned} N_{t+1} &= N_t \cdot \left[1 + r\left(\tfrac{1-N_t}{K}\right)\right] - V(N_t)P_t \\ P_{t+1} &= P_t \cdot \left[wV(N_t)\right] \\ V(N_t) &= \begin{cases} aN_t & ; aN_t < V_{max} \\ V_{max} & ; else \end{cases} \end{aligned} \tag{3.14}$$

N_t and P_t represent the size of prey and predator population respectively. Values of N_t and P_t are continuous; we do not account for demographic effects of single individuals. In the model a population goes extinct, when population size is 0. A simulation run ends, when the first population is extinct. This simple mathematical model includes only 5 parameters. r describes growth rate of the prey population, K is its capacity, w regulates predator reproduction, coupling is determined by a and V_{max}, where a is the coupling strength ($0 \leq a < 1$) and V_{max} defines the maximal impact of the predator species on its prey. Parameter values are given in tab. 3.3.

In contrast to the sinus model (sec. 3.4.1) which only describes phenomenologically the deterministically induced oscillations in the system, the predator-prey model can be used to study interaction between species. Parameter variation of the model shows many kinds of qualitatively different behaviour, reaching from stable equilibrium states via limit cycles toward chaos (data not shown here). Hence, this model is an appropriate example to check, if the PVA method can be applied to stochastic models of interacting species.

We introduce stochasticity to coupling parameter a via

$$a \rightarrow a - a_r + 2a_r p(t)$$

where the new stochastically influenced parameter a varies by $\pm a_r$ around its original value. $p(t)$ are uniformly distributed random numbers between 0 and 1. Stochasticity in a can be

Table 3.3: Standard parameter set of the deterministic predator-prey model

r	0.5	a	0.02
K	120	V_{max}	3
w	1		

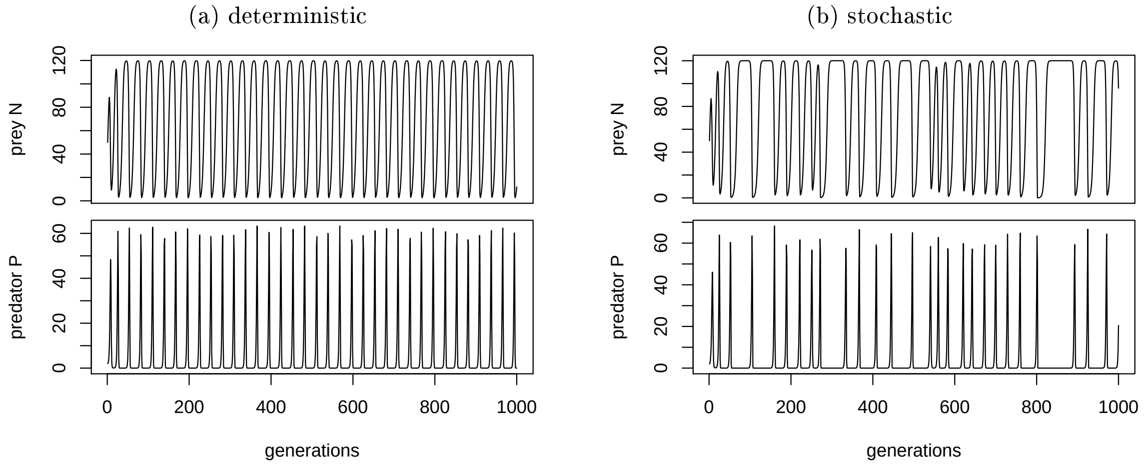

Figure 3.5: Predator-prey model: population size of predator P and prey N for example simulation runs with standard parameter set (tab. 3.3). Graph (a): without stochastic influence ($a_r = 0$), graph (b): with stochastic influence ($a_r = 0.002$)

interpreted as random chance of finding prey by the consumer species. This corresponds to randomly distribute butterfly eggs on food plants in the Maculinea model (ch. 1). Hence, this study might give insight, if the $\ln(1 - P_0)$-approach can be applied to the complex Maculinea model.

Fig. 3.5 shows two example runs. Fig 3.5a is from the deterministic model ($a_r = 0$). For the run in fig. 3.5b, stochastic variation was implemented via coupling parameter a ($a_r = 0.002$ which corresponds to ±10% variation). The deterministic model shows periodic cycles, where amplitude in peaks of population size of predator species is slightly varying. In fig. 3.5b, it can be seen that stochasticity increases these fluctuations in the amplitude. But, it influences the period length of cycles, too. In some cases it even seems that cycles are lost. Strict periodicity of the deterministic system is disturbed.

Stochastic effects, which influence periodic structure of cycling populations, are not taken into account in the analytical calculations of sec. 3.3.2. Formulae 3.9 for the measures of persistence do not hold in these situations, because they are derived assuming deterministically oscillating population sizes with fixed periodicity. However, in this example for a simple predator-prey model, population dynamics show quasi-cycles with disturbed periodicity.

Nevertheless, we apply the protocol for PVA (sec. 3.2.2), having in mind that accuracy of the $\ln(1 - P_0)$-fit is a measure for applicability of the approach. Hence, when the fit does not demonstrate the linear relation in our data, we simply conclude that the PVA method suggested by Grimm & Wissel (2004) is not appropriate to study this type of interacting species systems.

But, application of the PVA method returns even better linear fits than in the periodic case of the sinus model (sec. 3.4.1), as can be seen in fig. 3.6. Correlation coefficient for the fit is $r^2 = 0.999$. In the following, we will discuss reasons for this result: Earlier calculation (sec. 3.3) revealed that the stochastic process, which leads to extinction, is a Markov-process, if probability of survival is aggregated for single cycles. This result is only a convenient special case. Generally, the Markov condition is fulfilled, when a system has the same risk of

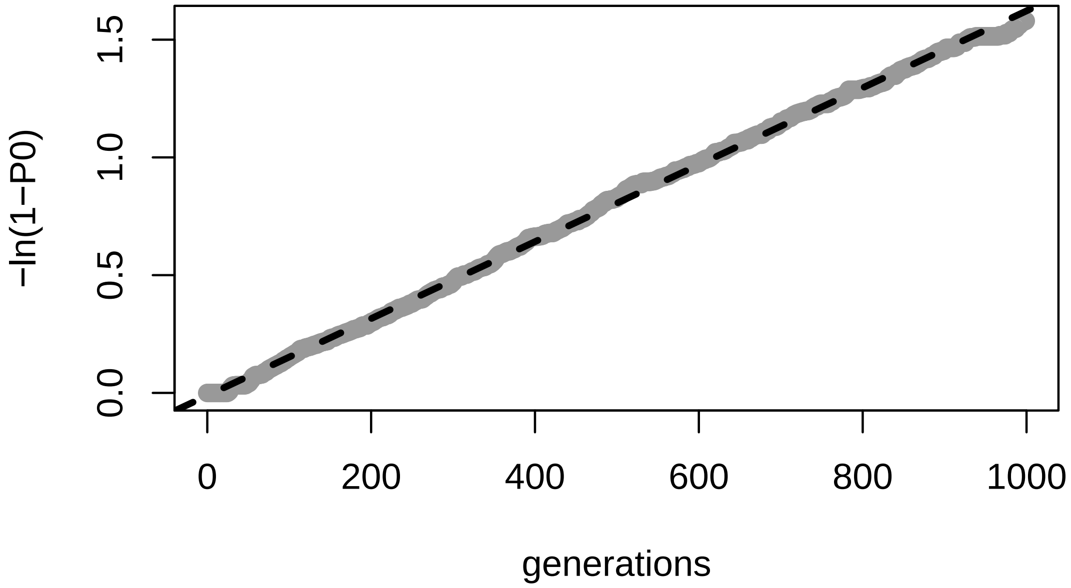

Figure 3.6: Predator prey model: ln(1 − P_0)-plot for an example simulation with standard parameter set (tab. 3.3). Stochasticity is introduced via coupling strength a ($a_r = 0.002$). Grey circles indicate simulation data, the dashed line represents the fit line. PVA results: $t_m = 612$, $c_1 = 1.01$, $r^2 = 0.999$, in 206 simulation runs, both populations survived.

extinction any time it assumes the same state. This is

$$N(t_1) = N(t_2) \Rightarrow p(t_1) = p(t_2)$$

at any times t_1, t_2 before the population goes extinct. Observation (O3) in ch. 3.3 assures this condition independently of the type of periodicity in the fluctuations of the distribution of population sizes. Hence, instead of using eqn. 3.7 to describe probability $P_0(t)$ of a population to be extinct at time t, dynamics of $P_0(t)$ also can be written in a more general form

$$P_0(t) = 1 - \prod_{k=1}^{N} \left[(1 - p_k)^{l_k(t)} \right] \tag{3.15}$$

Here, k is a system state. Without loosing generality we assume the simple case, where k can be interpreted as population size ($k \in \{1, \ldots, N\}$). $l_k(t)$ counts, how often a population at time t already has passed through state k (that is, how often there have been k individuals in the population,before time t is reached). The actual rate of extinction $p(t)$ can be transformed to a rate p_k to go extinct from state k within the next time step (that is the risk that a population consisting of k individuals goes extinct within the next time step). This extinction rate p_k is independent of time. From transformation $-\ln(1 - P_0)$ follows

$$\begin{aligned} -\ln(1 - P_0(t)) &= -\ln\Big(\prod_{k=1}^{N} \Big[(1 - p_k)^{l_k(t)} \Big] \Big) \\ &= -\sum_{k=1}^{N} \left[l_k(t) \cdot \ln(1 - p_k) \right] \end{aligned} \tag{3.16}$$

We now analyse, in which case $-\ln(1-P_0(t))$ is proportional to time t. Because if this condition is fulfilled, a $\ln(1-P_0(t))$-plot will lead to a straight line and the PVA-approach can be applied. The only time-dependent term in eqn. 3.16 is $l_k(t)$. $l_k(t)$ is a time-dependent distribution of frequencies to realise state k. That is, at time t it is determined, how often each state k has been realised (or how often the population has consisted of k individuals). Determining $l_k(t)$ from many simulation runs and normalising the result leads to the relative frequency

$$\frac{l_k(t)}{\sum\limits_{i=0}^{N} l_i(t)}$$

This can be interpreted as the probability that at time t a population of k individuals can be found. If this probability distribution is quasi-stationary on a long time scale, the Markov condition is fulfilled. The PVA procedure can be applied. In this general Markov description, intrinsic mean time to extinction t_m is a weighted mean of the logarithmic probability to survive in states k. l_k are weights.

In the special case of periodic deterministic oscillations of the distribution of population sizes (sec. 3.3), all l_k are equal for a full cycle. Within a cycle, these l_k vary depending on the phase in the cycle. Therefore, in $\ln(1-P_0)$-plots for the sinus model, a stair like pattern appears.

In general, if

$$\frac{l_k(t)}{\sum\limits_{i=0}^{N} l_i(t)}$$

varies in time only on a short time scale, compared to the intrinsic mean time to extinction t_m, the method can be applied. Hence, the method is valid for cycles and quasi-cycles. In contrast, if there are long trends in the distribution (no quasi-stationary state is reached), the Markov condition is violated. The transformed distribution of extinction times cannot be fitted linearly. Therefore this method is not useful for declining populations until they reach an established state. Recently, occurrence of supertransients and mesotransients (sudden changes of system dynamics after time scales of hundreds or thousands of generations, respectively) have been reported for spatial population models (Saravia et al., 2000; Labra et al., 2003). We assume that these sudden changes destroy quasi-stationarity and therefore cannot be analysed by this PVA-approach.

In contrast to fig. 3.4, fig. 3.6 does not express cyclic structure of population dynamics. The cyclic structure is lost by statistically aggregating phase-forgetting population dynamics. Therefore we see a straight line in the $\ln(1-P_0)$-plot (fig. 3.6). This graph looks structurally the same as a plot for a single species system (fig. 3.1c). Hence, restricting on interpretation of the distribution of times to extinction can lead to misinterpretation of short term ecological processes.

3.5 Discussion

3.5.1 Dynamics of the extinction process in interacting species systems

Although population viability analysis is an important and established tool in conservation of single species, to our knowledge for the first time a PVA method for systems of interacting species is suggested. Reason for this lack in methodology might have been the great variety and complexity of dynamics in these systems.

In our study, we revise literature in order to identify common reasons for extinction of populations in interacting species systems. We end up with a surprisingly small list of important phenomena (see observations in sec. 3.3.1): Population sizes are periodically oscillating, however cycles are disturbed by stochasticity (O1). Extinction of a population is a random event (O2). Risk of extinction depends on population size (O3); small populations are more endangered than large populations (see e.g. Nisbet & Gurney, 1982; Stephan, 1992; Stephan & Wissel, 1994a, 1999; Holyoak et al., 2000).

This is an interesting set of observations. Observation (O1) describes dynamic of population sizes, which is mainly deterministic. Observation (O2) determines an extinction event as stochastically driven. Observation (O3) finally links together deterministic population dynamics and stochastic extinction. Hence, the observations indicate that stochastic and deterministic processes hardly interact. The only way, deterministic processes can influence extinction is by varying population sizes (O3). Therefore, it is sufficient to describe deterministic processes phenomenologically by their effects on population size in order to analyse persistence of a population.

With the most general model fulfilling the observations it is shown that deterministic and stochastic processes affect persistence on different timescales. Deterministic processes act below the natural timescale of period T_P. They influence persistence of a population within one oscillation. In contrast, stochasticity acts on longer timescales of many population cycles.

On this long scale, deterministic effects within a cycle can be aggregated. They cause the risk that a population goes extinct within one cycle. Due to periodicity of the deterministic process, this risk is equal for each cycle.

Consequently, details of deterministic effects on persistence are not detectable on the long run. Hence, different deterministic processes which provoke the same risk of extinction during one population cycle cannot be distinguished. Particularities of interacting species systems result in a characteristic risk of extinction. But, the stochastic extinction process is equal for all of the many different systems. Although variety and complexity of population dynamics is high in systems of interacting species, there is only one type of extinction process.

The derived dynamics of the stochastic extinction process in interacting species systems is the same as the well known dynamics in systems of single species with non-overlapping generations (Stephan, 1992; Wissel et al., 1994). Within each generation (in the interacting species system, within each complete cycle) the population has the same risk to go extinct. In single species systems, the probability that a population at time t already has gone extinct $P_0(t)$ is geometrically distributed. In systems of oscillating populations, $P_0(t)$ is geometrically distributed on the time scale of one cycle.

This general finding comprises and helps to explain earlier results on special cases for example from Nisbet & Gurney (1982, sec. 7.2), Stephan (1992, sec. 3.1), Stephan & Wissel (1994a, 1999) and Bonsall & Hastings (2004).

3.5.2 PVA for interacting species systems

Stephan (1992) suggests an effective way to calculate intrinsic mean time to extinction of single species from simulation data. With this so called $\ln(1 - P_0(t))$-method the general pattern of extinction dynamics in single species is evaluated. The method is widely and successfully used (Grimm & Wissel, 2004, and references therein). On this background Stelter & Grimm (1994); Frank et al. (2002); Grimm & Wissel (2004) give a protocol for a general PVA analysis on single species systems. They outline the power of the intrinsic mean time to extinction t_m as a unifying currency to assess and compare persistence in single species systems.

We find the long term extinction process in interacting species systems to be equal to that in single species systems. Hence, it is natural to test the applicability of the PVA protocol for more complex systems of interacting species. Grimm & Wissel (2004) indicate that the PVA protocol contains an internal mechanism to check whether it is suitable to analyse a certain system. Because of this security mechanism, we can apply the protocol to any system of interacting species and afterwards, according to the internal test, decide if the PVA protocol is successful.

The PVA protocol consists of several steps (see sec. 3.2.2). Initially from many repeated simulation runs determine the distribution of times to extinction of species in the system. Afterwards calculate the cumulative probability $P_0(t)$ that at time t species are already extinct. The function $-\ln(1 - P_0(t))$ is fitted linearly. Measures of persistence are $c_1 = \exp(-\text{intersection})$ and $t_m = 1/\text{slope}$. If the linear fit is not accurate (correlation coefficient $r^2 \ll 1$), the PVA protocol cannot be applied (test for applicability). Persistence measure c_1 is an indicator for the probability that populations establish and do not go extinct during the initial transient phase. Intrinsic mean time to extinction t_m is a measure for long term persistence of the populations.

Our results suggest, that the PVA protocol is suitable and useful for PVA on interacting species systems. However, due to different dynamics in systems of single or interacting systems, we find differences in results of PVA on short timescales.

- Oscillations of population size provoked by interaction of species result in short term modulation of risk of extinction. Therefore extinction risk varies on a short timescale. Stephan & Wissel (1994a, 1999) indicate that the internal noise from species interactions has a different effect on persistence than stochastic environmental noise. For this reason, depending on the type of noise, different management methods have to be applied. Wichmann et al. (2003) find that even short term patterns of periodical environmental variation influence persistence of populations. Johst & Wissel (1997) add different types of correlated noise to population dynamics and estimate the risk of extinction. They find that correlation in environmental stochasticity increases risk of extinction of a population. We think that correlated random effects tend to act as a mixture of deterministic dynamics and stochasticity. Correlations seem to enhance the time during which the population is small. Hence populations have a higher risk of extinction.

- In contrast to oscillations with fixed periodicity, quasi-cycles sometimes cannot be identified from short term patterns in risk of extinction. Quasi-cycles result from interaction of deterministic and stochastic processes. Stochastic influence wipes out the clear deterministic patterns.

- Measure of persistence c_1, as an indicator for risk of extinction during the initial phase of an interacting species systems, is evaluated in a slightly different way to single species systems. Grimm & Wissel (2004) argue that $c_1 \leq 1$ can be directly interpreted as the probability that a population reaches the established state. In the case of interacting species systems, Persistence measure c_1 additionally depends on the pattern of extinction risk within the first population cycle, which means the initial phase effectively lasts longer.

Short term patterns in the distribution of times to extinction result from characteristic properties of the system like for example species traits, species interaction, or habitat condition. But, the short term patterns do not explicitly reflect in the value of intrinsic mean time to extinction t_m. They express as the aggregated risk of extinction during one cycle. This aggregated risk is perceived by the persistence measure t_m. The big advantage from a point of measurement is that intrinsic mean time to extinction t_m is a single scalar value, which evaluates persistence of species in a system, accounting for all conditions and processes that affect species performance.

Therefore, intrinsic mean time to extinction t_m is a comparable measure for many different types of species systems. It is a unifying currency for PVA on either single species or community systems.

Chapter 4

Distributions of times to extinction of Maculinea populations

4.1 Introduction

Assessing viability of populations is essential for species conservation. Shaffer (1981) suggested to use stochastic population models to evaluate the fate of species in their environment. Probability of extinction of a population within a certain time horizon is estimated from repeated simulation runs. Since then population viability analysis (PVA) has developed to a standard tool in conservation biology (Beissinger & McCullough, 2002; Frank et al., 2002; Grimm et al., 2004). It is included as one of the criteria to assess threat of species extinction in the IUCN Red List (IUCN, 2004; Lande et al., 2003).

The aim to preserve species diversity in whole regions (e.g. Soule et al., 2005) has invoked a new application for PVA. It is expected that a range of rare species can be preserved by managing only few indicator species. Lande et al. (2003, p. 104) point out that 'PVA for selected species of certain interest should be an integral part of large-scale conservation efforts'. Indicator species are selected, because they are 'typical' in the planning area; that is, the environment meets their special needs. Hence, they are closely linked to both, habitat conditions and community. But it must be taken into consideration that interaction between different species provokes qualitatively different population dynamics and therefore viability than it is shown by single species (Berger, 1999; Amezcua & Holyoak, 2000; Arditi et al., 2001). Hence viability of populations should not be assessed separately from their community.

For single species systems, the $\ln(1-P_0)$-approach constitutes a framework to asses population viability. Strength of this approach is that it measures risk of population extinction for the transient and the established phase of population dynamics separately; therefore taking into account the different dynamics of a population when it is either colonising or established (see sec. 3.2 and references therein). However, it becomes obvious in ch. 3 that the more complex population dynamics of interacting species systems influence their risk of extinction. This finding leads to a modification of the single species framework.

In this chapter, we apply this modified framework. We perform population viability analysis for Maculinea butterfly species, which are supposed to act as indicators for special types of habitats (Settele et al., 2002, 2005), especially because of their close interactions with their obligate host ants of genus Myrmica and host plants (see ch. 1.2). With the generic but quite realistic Macu model (see ch. 1 and 2), we calculate distributions of times to extinction for a variety of spatially structured habitat sites. From these, we estimate persistence measures t_m and c_1.

Our objectives are twofold. We want to get a systematic overview of extinction dynamics occurring in the Macu model. Additionally we want to assess, if these extinction dynamics fulfill assumptions of the $\ln(1 - P_0(t))$-approach and thus can be analysed with the method.

4.2 Methods

In this chapter, we aim to analyse population persistence of Maculinea in a large number of different scenarios. In fact, we use the same scenarios as in ch.2, i.e. all scenarios with variations in spatially relevant parameters spatial host plant distribution, initial spatial host ant distribution, and budding range σ. Other parameters are set to standard values (tab. 1.1). To analyse persistence of Maculinea for all these scenarios, a high number of simulation runs is required. Thus the analysis is time consuming even on powerful computers. To cope with this problem, we use a two step adaptive approach towards analysing distributions of times to extinction. For a broad overview we calculate distributions of times to extinction from only 300 simulation runs of the Macu model. This first step enables us to scan the large parameter space. However, we have to accept that the resulting histograms of times to extinction are only sparsely occupied. In mean, there are $\frac{300}{5000} = 0.06$ measurements of extinction events per generation, provided populations in all simulation runs went extinct before reaching time horizon $T_H = 5000$ generations. To overcome this drawback we apply a second type of analysis, where we repeat the simulations for selected scenarios, performing 50000 simulation runs. In the following it is described, how these analysis stick together.

For the initial overview analysis, inspecting all histograms by eye would fail because of the amount of different scenarios. But even more severely, because most of these sparsely occupied histograms look very similar. Fortunately, the $\ln(1 - P_0(t))$-method presented in ch. 3 is able to extract intrinsic mean time to extinction t_m from small amounts of data.

We define three viability classes: persistence ($t_m > 10^6$gen) [1], medium risk of extinction (10^2gen $< t_m \leq 10^6$gen) and not persistent ($t_m < 10^2$gen). These categories correspond to qualitative observations of different shapes of distributions of times to extinction[2] and are ecologically reasonable for assessment of species performance (ch. 3). The distributions of times to extinction are analysed within these viability classes.

The variety of extinction dynamics, which is found in the initial overview analysis for the Maculinea model, is broader than the variety detected in less complex models analysed in ch. 3. Therefore, in the second step of the analysis, we select typical representatives of the viability-categories defined above and repeat simulations with the increased number of 50000 simulation runs. The few but highly detailed results are accurately analysed. We calculate histograms of times to extinction and perform PVA according to the protocol discussed in

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[1] For practical reasons t_m is given a maximum value of $t_m^{max} = 10^7$gen in coarse analysis.

[2] At this stage, we effectively use two descriptions of viability. On the one hand the risk of being extinct $P_0(t)$ at time t is assessed directly from the distribution of extinction times. On the other hand we aggregate those applying the $\ln(1 - P_0(t))$-method with resulting measures of persistence c_1 and t_m. In sec. 3.2.4 it is shown that persistence can be defined equally in the frame of both descriptions. To define persistence for an established population in a single species system, a threshold has to be laid down for either the maximum probability that a population goes extinct within a given time horizon or for the minimum intrinsic mean time to extinction t_m. According to eqn. 3.9, this procedure is also suitable for interacting species systems, if the intrinsic mean time to extinction t_m is much longer than duration of cycles in population sizes T_P.

ch. 3. We analyse results qualitatively, inspecting histograms of times to extinction and $\ln(1 - P_0(t))$-plots. We then study the relation between extinction dynamics and measures of persistence.
Finally, we assess the ability of the $\ln(1-P_0(t))$-method to cope with the patterns of extinction dynamics, which are found for the Macu model. For this purpose, the accuracy of $\ln(1-P_0(t))$-fits is studied by analysing the resulting correlation coefficient r^2. Reasons for inaccuracies are assessed taking into account the knowledge, which is gained in the second analysis step.
Jumping between broad and detailed analysis, we improve the understanding of patterns occurring in distributions of times to extinction of our model.

4.3 Results

In the coarse parameter variation analysis, we find a broad range of resulting intrinsic mean times to extinction t_m (t_m ranges from 6.21gen to 10^7gen). This means that, depending on the parameter settings, Maculinea populations might persist or go extinct. In ch. 6 influence of the factors is analysed in detail. Here, we concentrate on classifying patterns in distributions of times to extinction.

4.3.1 Long term persistence of a population

Distributions of times to extinction can be categorised into three different idealised classes (see sec. 4.2), which afterwards are subdivided due to different patterns for the initial transient phase. Ranges of t_m defined in ch. 4.2 are chosen reasonably, anyhow arbitrarily. Hence, an observed histogram may share properties from several classes. The categories serve to distinguish different underlying behaviours for extinction, which allows to only investigate typical representatives of each class.

4.3.1.1 Type I: Long-term persistence

In stochastic population models, there is no absolute persistence. Because of random effects, populations have to go extinct in the limit of infinite time. However, we define populations to be persistent, when they do not go extinct in all (or almost all) runs of a simulation. Quantitatively a population is defined as persisting when $t_m > 10^6$gen (see sec. 4.2). When $t_m = 10^6$gen, the risk that an established population goes extinct before reaching time horizon $T_H = 5000$gen is $P_0(T_H = 5000\text{gen}) \approx \frac{T_H}{t_m} = \frac{5000}{10^6} = 0.005$ (see ch. 3). This low risk of extinction justifies the assumption of persistence. A typical histogram of times to extinction for a persisting population looks like fig. 4.1a, where populations in all simulation runs reach time horizon $T_H = 5000$ generations. The $\ln(1-P_0(t))$-plot (fig. 4.1b) is a horizontal line. This leads persistence measures of $t_m = \infty$ and $c_1 = 1$, in accordance with theoretical estimation of PVA measures for persisting species in sec. 3.3.3. Although the distribution of times to extinction in fig. 4.1a does not resemble to the expected decline (see ch. 3), estimated measures of persistence are reasonable.
Fortunately long survival is a frequent result for the simulated Maculinea system.

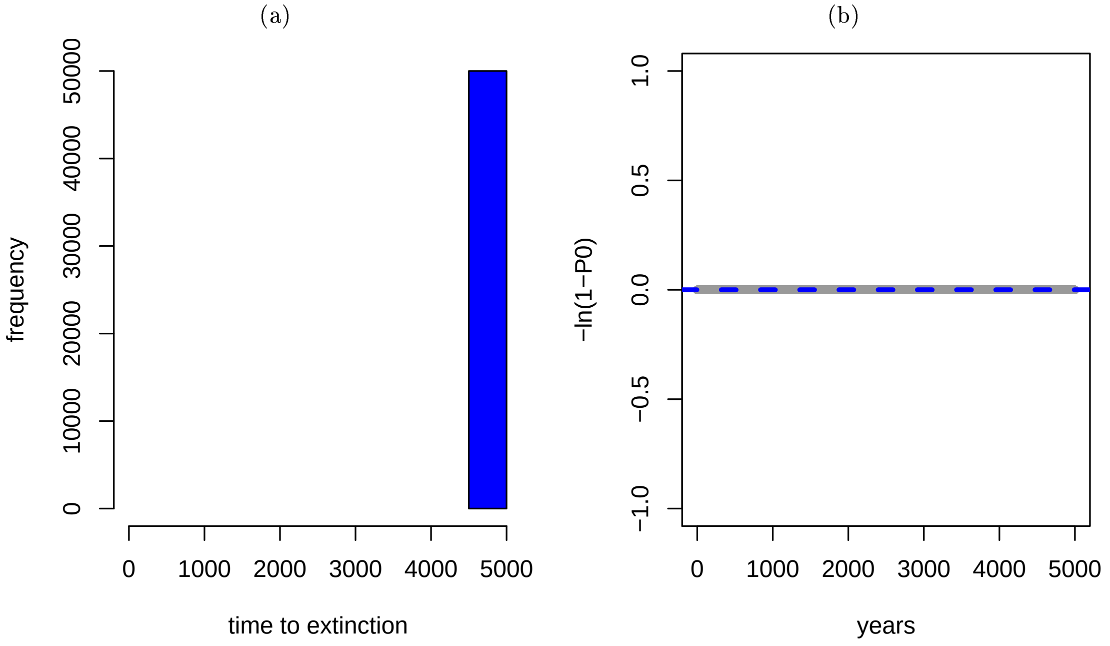

Figure 4.1: Histogram of times to extinction (a) and $\ln(1 - P_0(t))$-plot (b) for Experiment 115_3. Within 50000 simulation runs, extinction events are not observed.

4.3.1.2 Type II: Medium risk of extinction

Fig. 4.2a depicts the histogram of times to extinction of a population with noticeable risk of extinction. On the long run, a decline in number of extinction events can be observed. In sec. 3 it is predicted that the longtime shape of the distribution should decline following a power law, well-known from single species systems (Stephan, 1992; Stephan & Wissel, 1994b; Wissel et al., 1994). The plot in fig. 4.2b confirms this prediction with impressive accuracy. Data is fitted exactly. Resulting measures of persistence are $t_m = 457$gen and $c_1 = 0.886$. The value of $r^2 = 0.998$ ensures that the $\ln(1 - P_0(t))$-PVA-method can be applied to analyse Maculinea model results on a long time scale. The fit becomes inaccurate for high numbers of generations, because only few populations survive long enough. Therefore, there are only few extinction events if times to extinction are long (sparsely occupied slots for high numbers of generations in the corresponding histogram 4.2a). The limited number of 50000 simulations is not sufficient to realise exactly the theoretically predicted distribution. Data differs from the fit curve in 4.2b for the first generations, too. This effect of a transient phase in population dynamics will be discussed in sec. 4.3.2.

Fig. 4.2c and 4.2d show the same simulation data as fig. 4.2a and 4.2b, but only the first 350 generations are displayed. This higher resolution graph has a completely different aspect. In the histogram (fig. 4.2c), humps can be observed, which become smaller and broader with increasing time. Humps are separated by lags of several years, especially for low numbers of generations. Obviously, there are generations, when populations do not go extinct or only go extinct with a very low probability. Durations of these 'save periods' decline with increasing time.

The histogram in fig. 4.2c shows exactly what one expects from cyclic population dynamics

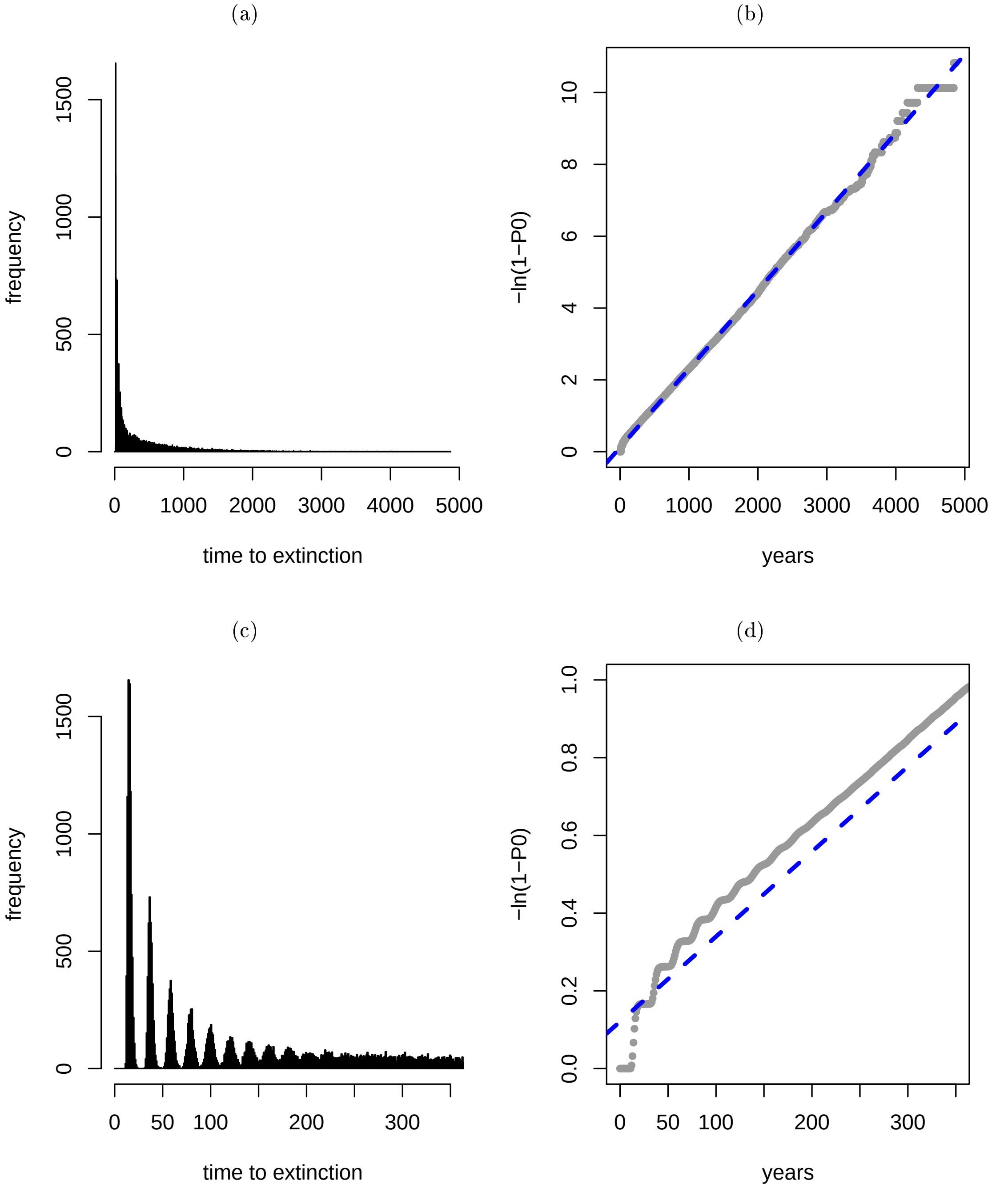

Figure 4.2: Histogram of times to extinction and $\ln(1 - P_0(t))$-plot for Experiment 133_16. Graphs (a) and (b) show extinction dynamics over 5000 years. The distribution of times to extinction (a) declines exponentially, which expresses in linearity of the $\ln(1 - P_0(t))$-plot (b). Non-linear behaviour for times above 3000 years is due to statistical errors resulting from small numbers of data (compare the sparsely occupation in the histogram of times to extinction above 3000 years). Graphs (c) and (d) depict only the first 350 years. Humps can be seen in the histogram of times to extinction (c). These express in steps in the $\ln(1 - P_0(t))$-plot (d). The fit in the $\ln(1 - P_0(t))$-plot underestimates, due to the influence of initial conditions.

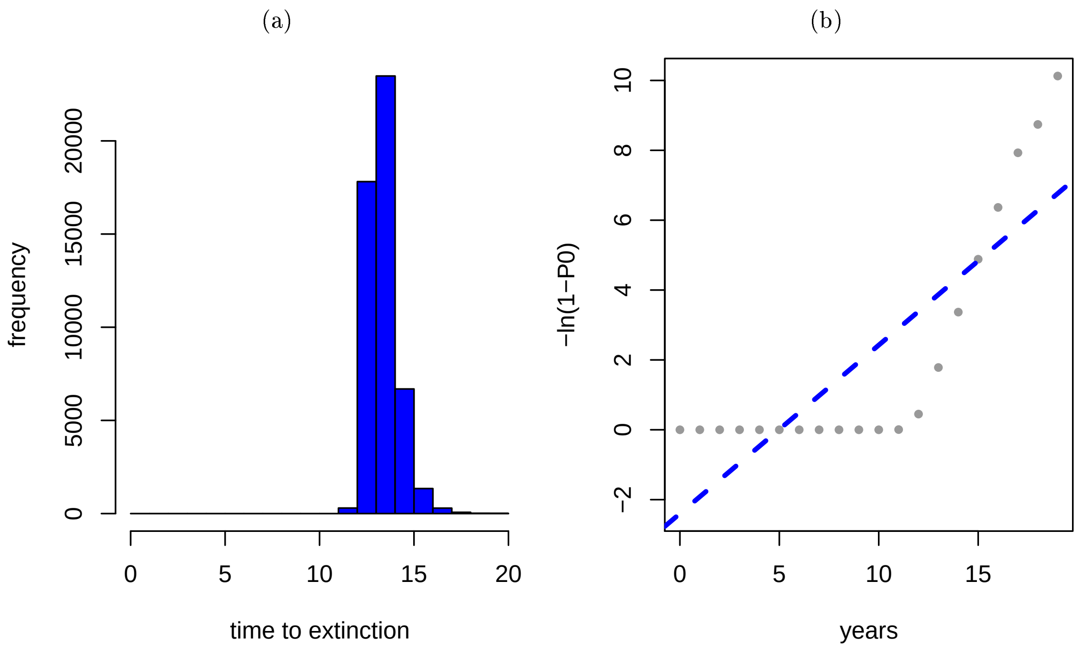

Figure 4.3: Histogram of times to extinction (a) and $\ln(1 - P_0(t))$-plot (b) for Experiment 116_1. Populations in all simulations go extinct during first 20 generations.

(see ch. 3). As already mentioned in ch. 2 (see fig. 2.1), numbers of butterflies can drop to very low values. When the butterfly population size undergoes a minimum, there is an increased risk of extinction due to demographic stochasticity. Meanwhile, when population sizes are high, this risk is reduced and populations do not go extinct.
The $\ln(1 - P_0(t))$-plot in fig. 4.2d shows a step structure in the data, which is already known from fig. 3.3b. Hence, as predicted in ch. 3, host-parasite cycles of the Maculinea system express themselves in periodical variation of extinction risk. Periodic fluctuation in risk of extinction can be observed only for some early generations, because of losing coherency. As mentioned in ch. 2, the system shows phase-forgetting quasi-cycles.
There is clear deviation of data from the predicted line. As mentioned before, the system behaves different during transient and established state, which leads to inaccuracy of the fit for the first generations. From ch. 3 it is known that deviation of transient and established behaviour expresses in a shift of the intercept, which is observed in fig. 4.2d graphically as a parallel shift of the fitting line in comparison to the data points. Slope of the line and therefore t_m stays almost uninfluenced. Importance of initial conditions is discussed explicitly in sec. 4.3.2.

4.3.1.3 Type III: Non-Persistence

Populations of this type cannot persist. Fig. 4.3a shows that in all simulation runs populations go extinct within only a few generations. In general, no single run can be observed, which survives for longer times. The reason is that either populations go extinct deterministically or have a tremendous risk of extinction. Note the fact that during the first 10 generations in fig. 4.3a no extinction event is counted. This results from favourable conditions for the

populations during this short period.
The $\ln(1 - P_0(t))$-plot in fig. 4.3b does not show linear behaviour of the transformed $P_0(t)$ with increasing time. The fit is bad ($r^2 = 0.686$), which is not surprising, as the PVA method is valid for long time scales (see ch. 3). But, in the process, long time scales are not realised. Anyhow, low $t_m = 2.073$gen points to the right direction: no persistence of populations[3]. This result corresponds to the theoretical estimation (ch. 3.3.3), that $t_m \to 0$ for populations, which cannot persist (which is far beyond conditions of applicability of the approach). Hence, t_m can be used as a qualitative indicator for non-persisting populations.

4.3.2 Extinction during an initial transient phase

Population dynamics of Maculinea systems during an initial phase differ from longtime behaviour (see ch. 2.3.3). These short-time effects express in the distribution of times to extinction for the first few generations. Note, in a single species system, initial dynamic of the system depends only on the initial conditions (e.g. Ludwig, 1996). Due to the complex interactions in multi-species systems, the initial transient phase might last longer and dynamics can be different from dynamics during the established state (ch. 2.3.3 or Hastings (2001); Neubert et al. (2004)). For this reason, we have a close look on risk of extinction for the initial transient phase of the Maculinea system. We distinguish between

reduced extinction: Few populations go extinct during the transient phase because of good initial conditions. The adaptation process of the system deteriorates these conditions. Measure of persistence $c_1 > 1$.

increased extinction (bad conditions): Conditions at beginning of the simulation are bad but improve with system adaptation. This case is known from single species systems with a constant resource (e.g. Ludwig, 1996), when the initial number of individuals in the population is low. Measure of persistence $c_1 < 1$.

increased extinction (overexploitation): Initial conditions provoke the consumer population to grow immensely, which leads to overexploitation of resources. Afterwards, the consumer population declines to very low numbers of individuals, which increases the risk of extinction. Such a scenario can last for several cycles. This case results from species interactions. Measure of persistence $c_1 < 1$.[4]

For the Maculinea system we find all of these transient phase behaviours. In principal, they co-occur with all three types of longtime persistence, which might effectively change distributions of times to extinction. Consequences are different for persistence types. Hence, we present them for each type separately.

4.3.2.1 Type I: Persistence

Fig. 4.4a shows the tremendous effect of bad initial conditions to a longtime persistent population. 56% of the populations go extinct during the first 61 generations. All other populations

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[3] Note, t_m is smaller than time of first extinction event in fig. 4.3. t_m cannot be interpreted as intrinsic mean time to extinction, in cases where the PVA approach of ch. 3 is not applicable.

[4] Whether extinction risk is increased due to initially bad conditions or due to overexploitation cannot be distinguished easily and doubtless from distributions of times to extinction. It is better to check population dynamics to securely determine the reason of extinction (see e.g. ch. 2.3.3)

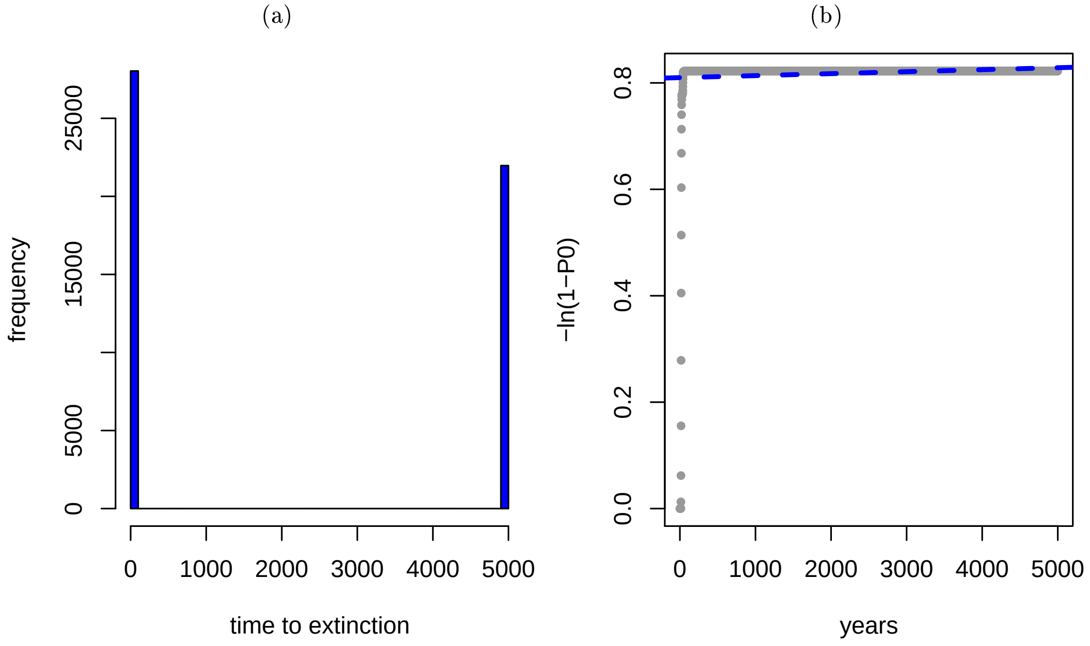

Figure 4.4: Histogram of times to extinction (a) and $\ln(1-P_0(t))$-plot (b) for Experiment 168_2. Either populations go extinct within 61 generations or they survive.

survive; during the established state no further extinction events are observed. In other words, although conditions are good for a population, when it has established, the chance of colonisation of a new site is small. Hence, we find a bottleneck to Maculinea populations. The butterfly population has problems to establish, because it needs some time to change habitat conditions. Self-regulation mechanisms of the system increase quality of habitat during the transient phase. To our knowledge this is the first observation, in a PVA study, that a colonising species changes habitat condition and hence increases its own probability of persistence. Furthermore, colonising Maculinea individuals can turn habitat conditions of a site from unsuitable to suitable.

This does not mean that population sizes of butterfly or ant species need to decrease during the initial phase. In fact, in both scenarios of slow adaption or overexploitation, which means an increase or decline in numbers of butterflies respectively, high extinction risk during the initial phase can be found (see ch. 6.4.2.3). The decisive measure for persistence is the risk of extinction.

$\ln(1-P_0(t))$-analysis of this simulation can be seen in fig. 4.4b. Obviously, the approach is not suitable to fit the non-linear shape of the $\ln(1-P_0(t))$-plot ($r^2 = 0.013$). We are not astonished, when we consider the bimodal distribution of fig. 4.4a. Theoretical estimation, how the approach reacts in this extreme case, shows that $c_1 \to 0$, $t_m \to \infty$ (see 3.3.3). In simulations, $c_1 \ll 1$ and t_m assumes very large values. The approach extrapolates correctly and can be taken as an index for these situations.

4.3.2.2 Type II: Medium risk of extinction

Depending on the ratio of risk to extinction during the initial and the established state, all three cases of transient behaviour are realised for type II persistence. Return to fig. 4.2. This is an example of increased risk of extinction during the initial phase. The histogram in fig. 4.2c shows higher counts of extinction events for the first generations than expected, if the population had been initially established. The $\ln(1 - P_0(t))$-plot in fig. 4.2d initially starts with a strong increase, diverging from the linear fit. As argued above, the arising error to t_m is negligible. In contrast, the value of $c_1 = 0.886$ indicates an about 10% higher risk of extinction during the initial transient phase than during the established phase.

4.3.2.3 Type III: Non-Persistence

Non-persistence might have two reasons. First, long term conditions of the habitat do not support the species community. Second, initial conditions avoid establishment of populations, although habitat conditions would support them on the long run. Distributions of times to extinction resemble each other in both cases. The reason for extinction only can be deduced, if either initial conditions or longtime conditions of the habitat can be varied.

If the intrinsic mean time to extinction t_m is very low, parameter c_1 is not a secure measure, because the population does not establish (see sec. 3.4.1). For this reason, we do ignore c_1 in PVA analyses of non-persisting populations.

4.4 Applicability of the PVA protocol and the coarse analysis method

The Maculinea model (ch. 1) shall be used to test the applicability of the $\ln(1 - P_0)$-PVA method for complex spatially explicit individual-based population-dynamical simulations of interacting species. We are especially interested in its applicability in coarse analysis, where a wide range of scenarios is characterised by measures of persistence t_m and c_1. Such coarse analyses of population viability can be enormously powerful. For the first time, they allow comparative studies on the influence of a huge amounts of parameter settings and processes on the performance of species in communities. However, coarse analysis are limited by time and computational power. For this reason, in coarse analysis, simulations are restricted to a short time horizon T_H or to a low number of simulation runs. We assume some inaccuracy when estimating measures of persistence in coarse analysis. In the following, we asses these inaccuracies and analyse, why they occur.

4.4.1 Using the PVA-approach to analyse different types of extinction dynamics

The PVA protocol based on the $\ln(1-P_0(t))$-approach for single species incorporates a natural test for its applicability: A population can be analysed with the approach, when the resulting $\ln(1 - P_0)$-plot of data is linear (see Grimm & Wissel (2004) or sec. 3.2). Accuracy of the plot is estimated qualitatively by graphical inspection or numerically by the correlation coefficient r^2 of the linear fit. This test possibility allows to naively apply the method and either accept or reject results according to their accuracy. The $\ln(1 - P_0)$-method for interacting species changes this type of model test by accepting slightly higher inaccuracy due to fluctuations in population size and therefore resulting short term patterns in distributions of times to extinction (ch. 3).

Applicability of the $\ln(1-P_0)$-approach means that the examined system obeys to a certain rule: Deterministic temporal fluctuations of quasi-stationary distributions must act on a much shorter time-scale than stochastic extinction provides. This means, for single species systems that the quasi-stationary distribution is constant, for interacting species systems it may be short-time cyclic or constant according to loss of coherency in quasi-cycles.

It is by no means clear for an ecological system that its population dynamics follow the predicted law, although many example studies for single species systems support the assumption (Grimm & Wissel, 2004, and references therein). However, a general protocol for PVA should be applicable to an as large as possible set of species systems. If we can show, that the protocol delivers sufficiently accurate measures of persistence for the relevant types of occurring extinction dynamics, the method can be applied without necessity to check applicability in every special case.

Three types of behaviour are distinguished from our analysis. Only type II (medium extinction) shows good agreement with a theoretically predicted long-time linear behaviour of the $\ln(1-P_0)$-plot. The other two classes behave structurally different. Populations of type I do not go extinct within the predefined time horizon T_H. Of course, in this case, a method based on the assumption of certain extinction is not applicable. Type III population dynamics do not allow longtime survival. The $\ln(1-P_0)$-method must fail, because it requires the probability of long term survival before extinction.

Surprisingly, analytically and from simulation studies it can be shown that the $\ln(1-P_0(t))$-approach extrapolates values for t_m qualitatively correct for both, type I and type III behaviours. Therein lies a strong power of the method, because it can be applied to the whole range of system behaviour, when one is interested in only qualitative or comparative results. Comparative studies are a usual use of PVA (Beissinger & McCullough, 2002; Grimm et al., 2004). We will see that the method developed in ch. 5 and applied in ch. 6 is successful, because of this nice property of the $\ln(1-P_0)$-approach. But we have to keep in mind that the method is applied inadmissibly to type I and type III behaviour. Hence, if there are doubts about the type of extinction dynamics, the save way should be taken, which means checking the $\ln(1-P_0)$-plot graphically or numerically via r^2.

4.4.2 Statistical error of the approach

In the following, we restrict to type II behaviour, which can be assessed in accordance with the assumptions made for the development of the $\ln(1-P_0(t))$-approach. In coarse analyses, we find 10101 type-II-simulations. Correlation coefficient r^2 of these experiments ranges from 0.01 to 1.00. Fig. 4.5 depicts the dependency of the correlation coefficient r^2 on the intrinsic mean time to extinction t_m. It is striking that data varies extremely for high and low values of t_m. In a small range, from $t_m \approx [10^{3.5}\text{gen}, 10^{4.5}\text{gen}]$, fit quality is high for all PVA experiments. We now discuss several causes for errors in the linear fit.

Low number of simulation runs: In coarse analysis, only 300 simulation runs are included to determine measures of persistence. In sec. 4.2 it is argued that on average less than one observation is counted per slot. From theoretical considerations, we assume times to extinction to decline according to a power law. Hence, as can be seen in fig. 4.2a, there is a high concentration of data points in histogram slots for low values of t, whereas others are almost not occupied. Even in this graph, which shows results of a PVA

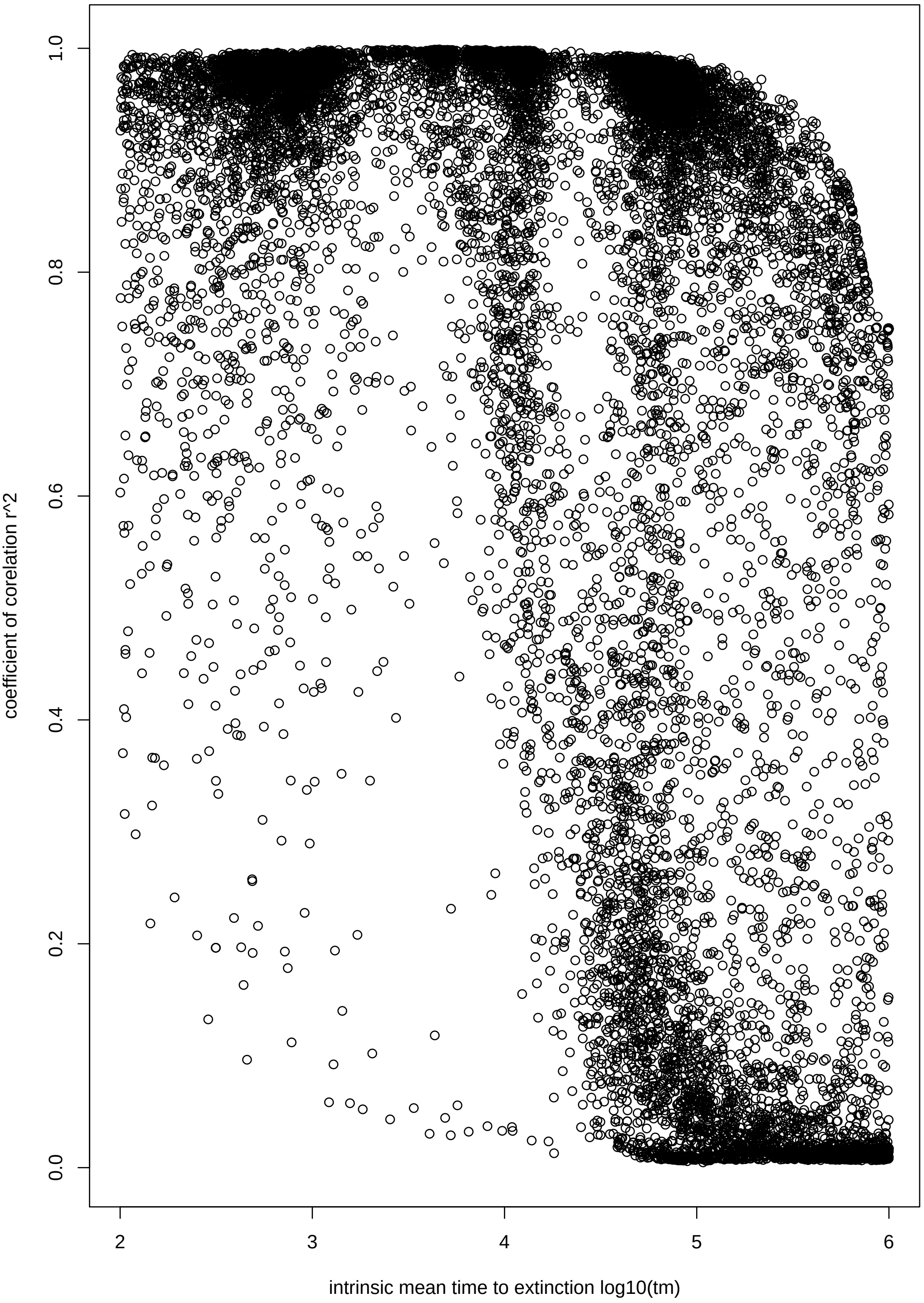

Figure 4.5: Dependency of fit quality r^2 on intrinsic mean time to extinction t_m for all coarse type II PVA analysis. The x-axis is $\log_{10}$-scaled. Number of simulation runs is 300.

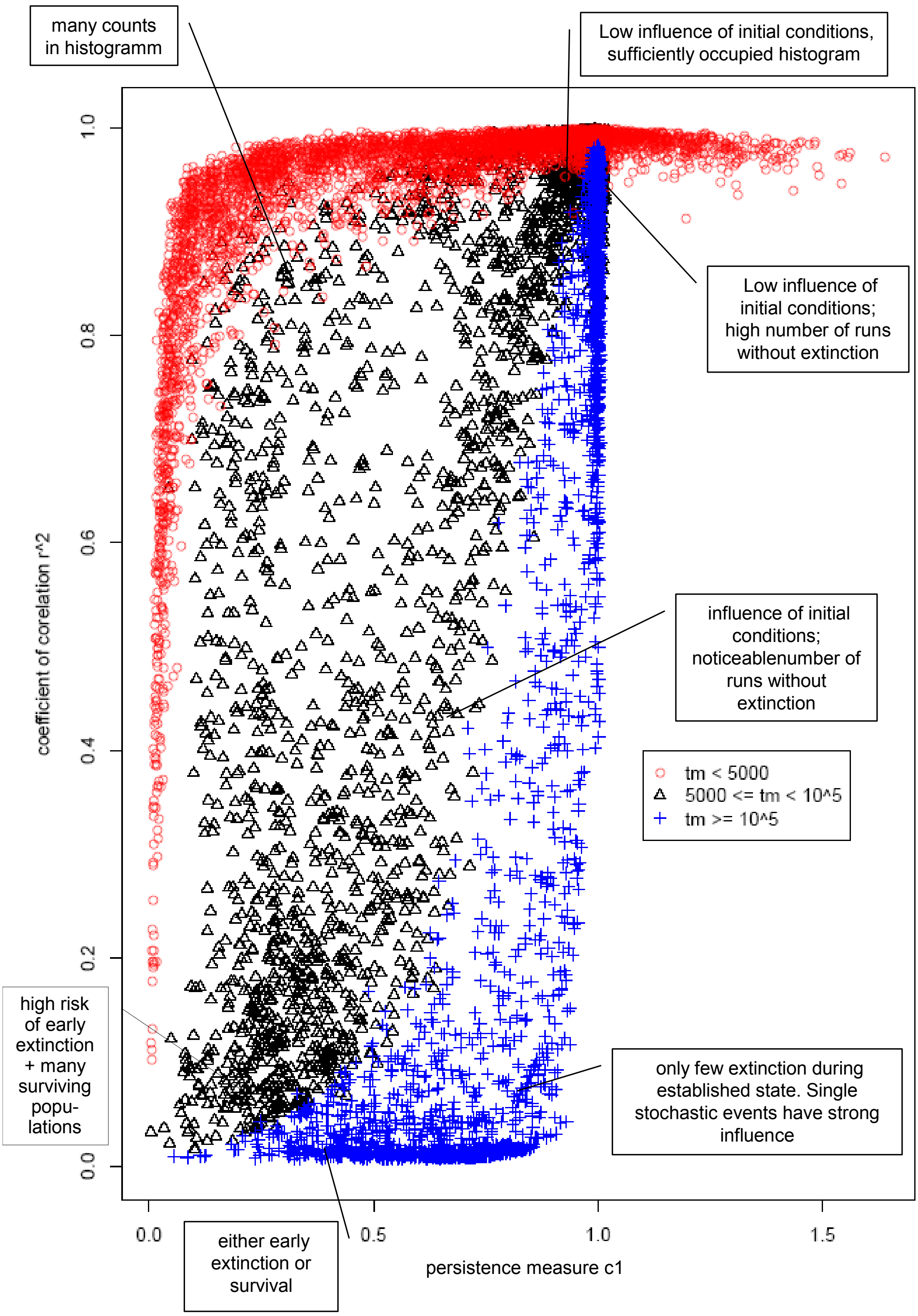

Figure 4.6: Dependency of fit quality r^2 on persistence measure c_1 for all coarse type II PVA analysis. Number of simulation runs is 300.

study including 50000 simulation runs, data deviates from the fit for late generations ($t > 4000$gen). This error is attributed to the stochastically imperfect realisation of the theoretically predicted distribution (see ch. 4.3). The $\ln(1 - P_0(t))$-fits of coarse analysis base on sparser occupied histograms, hence stochastic errors influence the estimation already for earlier generations.

Decreased fit quality for high t_m (survival): Intrinsic mean time to extinction t_m ranges from 100gen to 10^6gen. For the example study in ch. 4.3.1.2 $t_m = 457$gen. Nonetheless, in several of the simulations, populations survive for $T_H = 5000$gen (no extinction), as can be seen in fig. 4.2. With increasing intrinsic mean time to extinction t_m, the number of simulation runs without extinction events increases. For systems with high values of t_m, we find survival in 90% and more of the runs. These simulation runs are counted in the last slot of a histogram of times to extinction. These runs, which would in reality go extinct after final time horizon T_H of the experiment, due to practicability of the approach are accumulated at T_H. They enter into the PVA analysis indirectly (theoretically without provoking a mistake, as described in ch. 3), because many simulation runs with surviving populations increase the value of t_m. But, in real PVA experiments, because the rate of extinction is low, there are only few extinction events counted for $t < T_H$. As mentioned before, the sparsely occupied histogram provokes statistical errors.

Influence of initial conditions: Accuracy of persistence measure c_1 is difficult to be estimated. For different risks of extinction during the established state, r^2 describes accuracy of c_1 differently. Hence, in fig. 4.6 points are marked differently, according to ranges of intrinsic mean time to extinction t_m. Corresponding shapes of typical distributions of times to extinction are described with legends. We can summarise results as follows:

Low values of t_m (circles): Fit quality is bad only for very small values of c_1. In other cases, histograms show the theoretically predicted decline. When extinction due to initial conditions is extremely high, slots corresponding to the established state are sparsely occupied, which results in low fit quality.

High values of t_m (crosses): Low risk of extinction during the established state results in high numbers of simulation runs without extinction. Bad initial conditions (c_1 is small) lead to bimodal distributions of times to extinction as shown in fig. 4.4, which cannot be analysed with the $\ln(1 - P_0)$-approach (see ch. 4.3.2). Hence, $r^2 \approx 0$. With increasing c_1, the variance in r^2 increases. In corresponding histograms, single extinction events can be found during the established state. The linear fit strongly reacts on these points, as can be observed in graphical fit analysis (here not shown). Hence, both t_m and r^2 strongly vary with single stochastic events.

According to our classification, these cases should be mapped as type I. Here, extrapolation of the $\ln(1 - P_0)$-approach cannot estimate t_m appropriately. Effects of initial conditions, sparsely occupied histograms and high numbers of runs with surviving populations are mixed. Surprisingly, c_1 still indicates correctly, if populations are endangered due to the initial conditions.

Medium values of t_m (triangles): The intermediate case is effected by the same factors as both cases before. Values of t_m indicate, if either one or the other case is more important. Hence, r^2 varies strongly. This is exemplary discussed for $c_1 \approx 0.2$. Points with high values of t_m have very poor fit quality. In contrast, correlation coefficient of $r^2 \approx 0.9$ is realised for points, which correspond to low values in t_m.

We show, that for type II systems, in the coarse analysis, low fit quality arises from different reasons. Results from exemplary analysis with 50000 simulation runs show, that fit quality can be improved by increasing the number of runs in most cases (sec. 4.3). But, increasing sample size is not helpful, when the $\ln(1-P_0)$-approach is not applicable for principle reasons. Especially high variance of r^2 in fig. 4.6 results from systems, which do not have extinction events in many PVA simulation runs.

We conclude from our analysis of fig. 4.6 that only the small part of experiments, which results in $100\text{gen} < t_m < 5000\text{gen}$ (cycles in the graph), fulfils required conditions of the $\ln(1-P_0)$-approach. In fact, time horizon $T_H = 5000$ is too short to appropriately evaluate simulations of the Maculinea model. If we chose a higher value for T_H, we would grasp more simulation runs into the histogram to asses the distribution of times to extinction more accurately. Anyhow, we argue that a time horizon $T_H = 5000\text{gen}$ is sufficient for this work. First, because from an ecological point of view, $t_m = 5000\text{gen}$ corresponds approximately to a probability of extinction within 100 years of $P_0(t = 100) \approx 0.02$. Second, because the approach extrapolates values for t_m to the right direction, when populations do not go extinct in many population runs. Third, because assessment of spatial patterns can be done sufficiently accurate with the selected time horizon T_H (see ch. 6). Hence, for economic reasons of saving time and computer power, we accept the level of accuracy, which can be achieved with a time horizon of $T_H = 5000\text{gen}$. It's a moot point, why persistence measures t_m and c_1 are estimated with sufficient accuracy, meanwhile fit quality r^2 varies extremely. There are different reasons for the behaviour of each of the three measures:

Intrinsic mean time to extinction t_m: The $\ln(1 - P_0)$-approach is designed to evaluate population dynamics according to a theoretical model (see ch. 3 and below). When simulated dynamics obey that theory, the method is very powerful to perform good estimations even from very few data points. This is, because data from runs with surviving populations is not completely ignored. It at least contains information about the number of runs surviving $T_H - 1$ generations.

On the other hand, high accuracy in t_m values is not necessary. t_m is a qualitative indicator on vulnerability of populations under certain conditions. Model inaccuracy might have a much stronger influence on t_m than uncertainty in the outcome of the PVA method. Hence, it is sufficient to consider orders of magnitude of t_m. This rough measure is robust against small changes in t_m.

Measure of persistence c_1: c_1 measures differences between extinction behaviour during the transient and the established state. It is mainly influenced by population extinction during the first generations of simulation runs. Behaviour during the established state is perceived aggregately. Detailed information on exact times of extinction during the established state is not necessary to estimate c_1. Hence, already from very few simulation runs, sufficient data can be gained to fit the value of c_1.

Coefficient of correlation r^2: It is explained above that variance in values of correlation coefficient r^2 results from a low probability that a population can go extinct during the established state. Single extinction events have a strong influence in the sparsely occupied histograms of times to extinction. Hence, r^2 from two similar PVAs are probably

different.
The problem is that statistics r^2 does not account for the number of extinction events, which have actually occurred in the $\ln(1-P_0)$-PVA-method. The number of data points to estimate r^2 in the approach is always $T_H - 1$. If number of extinction events during the established state is sufficiently high, fit quality parameter r^2 can and should be used to determine accuracy of the approach (cycles in fig. 4.6). In other cases, a possible lag of accuracy can be evaluated by counting the number of extinction events during the established state. If this number is low, one should be careful in interpreting PVA results.

In ch. 5, a bootstrap method is described, which allows to estimate the deviation in persistence measures t_m and c_1. This method can be applied in critical cases.

4.4.2.1 Influence of population cycles on the accuracy of the approach

For the Maculinea model, periodicity cannot be found to strongly influence results of PVA. This might be on the one hand, because quasi-cycles wipe out phase information and humps in distribution of times to extinction. On the other hand, variation of period length estimated in ch. 2 is small in comparison to time scales of extinction. Hence, the Maculinea model cannot be used to test effects of large changes in period length to the $\ln(1-P_0)$-PVA-method (but see Wichmann et al., 2003).

4.4.3 Is the approach appropriate to analyse complex interacting species systems?

In this chapter, the PVA protocol is applied in two different kinds of analysis. For single scenarios, we evaluate viability with high accuracy. This effort cannot be made for comparative studies of many scenarios. Hence, in this type of analysis, lower accuracy has to be accepted (however, accuracy has to be sufficient to distinguish extinction dynamics by the persistence measures). Therefore, we apply different criteria for a successful PVA in the both types of analysis.

4.4.3.1 Detailed highly accurate PVA

In detailed analysis we want to estimate measures of persistence t_m and c_1 highly accurate. For the Maculinea model, it is found that the $\ln(1-P_0(t))$-approach gives very good results, when population dynamics is cyclic or quasi-cyclic and time horizon T_H as well as the number of simulation runs is high. Hence, spending sufficiently large effort to improve statistical accuracy, persistence of oscillating populations can be assessed with high accuracy by the method.
An important feature of the applied PVA-protocol is that risk of extinction can be estimated independently for an initial transient and the established state. In our assessments, we find good accuracy for both persistence measures c_1 and t_m. Therefore, this method is powerful enough to be applied to spatially explicit or interacting species systems, where the importance of a transient phase has been pointed out recently (Hastings, 2001; With, 2002; Snyder, 2003; Gardner & Gustafson, 2004; Grez et al., 2004; Frank, 2005a, and ch. 6 in this thesis).

4.4.3.2 Coarse comparative PVA analysis for a wide range of scenarios

In a coarse PVA analysis, high accuracy is renounced in favour to the possibility to assess persistence of species or communities in a broad range of scenarios. In this type of analysis special difficulties occur due to variety of extinction dynamics and inaccuracy in statistics.

For the Macu model, we assessed uncertainty in persistence measures t_m and c_1. In spite of the wide range of extinction dynamics and the small number of only 300 simulation runs, the two measures of persistence characterise different types of extinction dynamics astonishingly well. Although, in many experiments, correlation coefficient $r^2 \ll 1$ indicates that the persistence measures are uncertain, accuracy is high enough to estimate the order of magnitude of the intrinsic mean time to extinction t_m and to assess the risk of early extinction by persistence measure c_1.

This result confirms impressively, what is indicated by the theoretical studies in ch. 3: The PVA protocol is applicable to a wide range of dynamics of population extinction. Hence, analytical and numerical results suggest that the PVA protocol can be used in coarse analysis to assess persistence of species in many different scenarios. In ch. 5, we present an example, how spatial habitat structures can be assessed for their effects on persistence of Maculinea butterflies. Generally, coarse PVA allows to install broad mechanistic analysis on the conditions of survival for species and communities of species. From this new type of analysis, we expect a deeper mechanistic understanding of ecological patterns (see e.g. ch. 6 and ch. 7).

4.5 Discussion

4.5.1 Methodology of the analysis

In this study, we present a structured overview on extinction risk of Maculinea butterflies. Challenge of such an analysis is twofold. On the one hand, a wide parameter space has to be scanned to record most of possible extinction behaviour. On the other hand, detailed analysis is necessary to understand the occurring behaviours. Time and computer power limit broadness and specificity of investigations.

This constraint determines structure of our analysis. In two complementary investigations, we adjust the level of accuracy to either survey patterns of extinctions or inspect their structures.

- Coarse PVA on a wide range of parameter sets evaluates extinction risk in Maculinea systems. The two numerical persistence measures t_m and c_1 aggregate complex data on stochastic distributions of times to extinction and even more complex census and spatial data on population dynamics. Behaviour of these measures can be overlooked easily. Gained overview allows us to distinguish time scales on which extinction risk becomes important. According to these scales, we define types of extinction.

- Detailed analysis of extinction in simulations of the Maculinea system cannot be done for a high number of parameter sets. Hence, we concentrate on only few examples. These are selected to effectively cover the range of possible patterns of extinction. That is, we choose single representatives for each of the types of extinction, we found in the coarse PVA.

Using both investigations complementarily, we receive a fairly exhaustive understanding of possible reasons for extinction in Maculinea systems in the range of reasonable parameter settings. Hereby, coarse PVA serves to find as many characterising patterns as possible. Detailed analysis helps to find characteristics of filtered types and mechanistic explanations for different behaviour of the types. Hence, one feels secure about completeness of the observed extinction behaviours, because of the high number of samples and because of an intellectual review of their behaviour.

Another important outcome of the twofold analysis is that the theoretically motivated $\ln(1-P_0)$ method has shown to be useful for qualitative surveys in a wide range of extinction types, occurring in the Maculinea model. Persistence measures t_m and c_1 are good indicators for persistence during established and transient state, respectively. This makes the PVA-method especially helpful in comparative landscape analysis of ch. 5 and ch. 6. As good applicability of the $\ln(1-P_0)$ method is generally indicated by analytical calculations (see ch. 3), and we can confirm this finding in a concrete example for the complex simulation model of Maculinea butterflies, we strongly recommend the application of the method.

4.5.2 Patterns of population extinction in parasitic systems

Maculinea butterflies are known for obligate parasitism on their host ants of genus Myrmica. Population dynamics of our model shows typical host-parasite characteristics like for example cycles (see ch. 2). Hence, results of this study can be interpreted in a broader framework of resource-consumer theory.

4.5.2.1 Persistence time

For different settings of parameters, the system realises the whole range from immediate extinction on one end to factual persistence on the other. Therefore fate of butterflies and ants depends on the varied parameters: host plant distribution, initial host ant distribution and dispersal range. The influence of each of them is discussed in ch. 6.

Longtime persistence of the Maculinea system is the outcome for pleasingly many parameter sets. This result is in accordance to a rather new impression gained from work of the MacMan-Project that undisturbed populations of Maculinea butterflies persist relatively well (Settele; personal communication). The effects of different parameters on persistence of Maculinea populations is analysed in ch. 6.

If populations do not persist for more than a few generations, it cannot be distinguished from our analysis, whether they go extinct due to habitat unsuitability or due to only initial problems. Further investigations might help in this case (see e.g. ch. 6). In systems of interacting species, it might be much more difficult to separate initial short-term from long-term reasons of extinction than in single species systems, as will be discussed below.

For intermediate risk of extinction, distributions of times to extinctions can be fitted astonishingly well with the $\ln(1-P_0)$-method for interacting species systems. From a point of view of the approach, longtime model behaviour can be characterised by a stochastically disturbed oscillating population size (see ch. 3). Extinction on a long time-scale can be described by a Markov process. Hence, on a certain time scale[5], the rate of extinction is constant. This time scale is the length of one period - for the Maculinea model approximately 10 - 20 generations (see ch. 2). In contrast, within one period, risk of extinction is strongly varying. In fig. 4.2c one cycle expresses as a hump and its following lag. Only during a fraction of the period, the risk of extinction is high. During this time, the population is endangered. It is the time,

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[5] The time scale needs to be much shorter than the scale for extinction (see. ch. 3)

when cycles in population size take low values and therefore can be affected by demographic stochasticity. Note that with increasing time, no more humps can be observed in the histogram of times to extinction. As mentioned earlier, this is because the quasi-cycles in the butterfly population forget about their initial phase. Within one simulation run, a population goes through a minimum of population size to a slightly different time, than another one. The histogram looks as if there was an equal risk of extinction during a cycle (effectively cyclic structure is lost). But, only the minima in different simulation runs are shifted. Population sizes are still cyclic. It is therefore necessary to determine cyclic structure of a population directly from time-series analysis of census data. Distribution of times to extinction might suppress the cycles. This might lead to mistakes in the interpretation of the data: distribution of times to extinction and resulting $\ln(1 - P_0(t))$-plots look the same in parasitic Maculinea systems as in single species systems (see Grimm & Wissel (2004), Stephan (1992)).

When quasi-cycles in population dynamics and humps in histograms of times to extinction are correctly determined, one should think about possible management actions. Clearly, highest risk of extinction is acute, when the population size is small. Hence, it could be assumed to support the endangered population especially at these points of time. This would be correct, if population cycles result from an extrinsic force, like seasonality (see Nisbet & Gurney, 1982; Stephan, 1992; Wichmann et al., 2003). Yet, Maculinea is a parasitic butterfly. Cycles are intrinsic to the resource-consumer-system. An increase of numbers of butterflies could lead to additional exploitation of its Myrmica host ant during a phase of host recovery. At least, this mechanism would slow down population growth of host ants and extend the critical time span of low Maculinea numbers. In an extreme case, overexploitation of the already weak host ant population could lead to extinction of even both host and parasite. From theory of harvesting, it is known, that pasture needs breaks of grazing and time to recover after stocking was high (Müller; personal communication). This system is comparable, in the way that Maculinea butterflies feed on their host ants.

In our opinion, it would be better to avoid strong variance in population sizes. This procedure would reduce times with low numbers of individuals. In many respects, deterministic variation in our model can be compared to environmental stochasticity. Variation on population level might produce situations of low numbers of individuals with an increased risk of extinction due to demographic stochasticity (Johst & Wissel, 1997; Wichmann et al., 2003).

4.5.2.2 The danger of initial extinction

If populations in general go extinct immediately after the start of a simulation, substantial improvement of habitat conditions will be necessary. In systems of single species with an unchanging resource, the type of management action is the same for long time or short time objectives. In contrast, interacting species might have substantially different needs during the process of establishment than in the established state. This is impressively demonstrated in fig. 4.4a. In this distribution of times to extinction, it is revealed that Maculinea populations might have an extremely high risk of extinction for a time of at least three population cycles[6], although the general habitat condition is perfect for established populations. The initial transient phase of establishment of populations can be an important factor for the conservation of endangered species. During this time span, colonising species have to build up their links in the community. This phase of self-regulation in interacting species systems can be an additional bottleneck for colonising species in addition to others like the Allee effect or genetic

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[6] Period length during established state is 11gen

Table 4.1: Comparison of different PVA methods

class	experiment	$P_0(t = 200\text{gen})$	median	mean	t_m	c_1
type I	E168	0.56	21	2207	268496	0.445
type II	E133	0.47	229	391	457	0.886

PVA analysis for Experiment 168_2 (see fig. 4.4) and Experiment 133_16 (see fig. 4.2). $P_0(t = 200\text{gen})$ is almost equal for both experiments. Different reasons for extinction are only resolved by the $\ln(1 - P_0(t))$- approach.

effects from inbreeding. In our analysis, parasites and hosts are introduced at the same time to the site, which means that they undergo the transient phase at the same time. Anyhow, it can be assumed that when a single species enters a community, the adaptation phase is crucial, too.

The bottleneck effect cannot be safely detected when measuring the risk of a population to be extinct after a given time span. We calculate statistics $P_0(t = 200\text{gen})$, median and mean of times to extinction of data presented in fig. 4.2a (exp 133) which is type II behaviour and fig. 4.4a (exp 168) of type I with extinction due to initial conditions. These results are compared to estimations from $\ln(1 - P_0)$-plots (tab. 4.1). Probability that a population has gone extinct after 200 years $P_0(t = 200\text{gen})$ is almost the same in both cases. But from histograms of times to extinction, it is clear that the reason of going extinct is different. Even worse: $P_0(t = 200\text{gen})$ does not indicate, that in experiment 168, the main risk of extinction has been overcome after 200 generations and that during more than 100 generations before, no extinction event has been counted. Often, it is suggested to use the median of times to extinction of a population as PVA measure (Lande et al. (2003); Drake & Lodge (2004); Saether & Engen (2004), but see Grimm & Wissel (2004)). In this case of a bottleneck, the 'median' would be misleading. Both distributions of times to extinction are evaluated to have very high risk of extinction. Oddly enough, the in reality long term persisting population in exp 168 is assessed even more endangered than the population in the really vulnerable case (exp 133). The measure of mean time to extinction $\bar{t}_{ext}$ distinguishes both experiments, indicating that experiment 133 has a high risk of extinction. But, problems during initial phase in experiment 168 are ignored. Instead, $\ln(1 - P_0)$ correctly distinguishes longterm and shortterm risk of extinction of both experiments. Although, the data displayed in fig. 4.4 can be estimated only extrapolated, resulting persistence measures perceive the different structures of distributions of times to extinction in both experiments.

The $\ln(1 - P_0)$-analysis indicates that experiments 168 and 133 need different management to improve persistence of Maculinea butterflies. In experiment 133 longterm habitat improvement is required (t_m is low). Only small effort is necessary, to support colonising populations ($c_1 < 1$). In contrast, for experiment 168 assistance to invading populations is important ($c_1 \ll 1$), whereas conditions for established populations are good (t_m high).

4.5.3 Conclusion

We conclude from reviewing dynamics of extinction of spatially explicit, individual-based simulations for parasitic Maculinea butterflies that extinction in interacting species systems might take place at different time scales and for different reasons. Rate of extinction might vary deterministically due to short term population dynamics. But the actual extinction event is triggered by demographic stochasticity. Therefore, longtime distribution of times to extinction can be described with a Markov process, known from single species systems. This structural similarity allows the comparison of PVA for systems with different communities and numbers of species. Hence, it is possible to test the effect of different species compositions on the system. We suppose this as a method to determine indicator species for a community or a region. As demanded in (e.g. Soule et al., 2005), PVA is an essential part to build up regional species biodiversity.

Increased importance must be given to the transient phase of species colonisation. In our investigations, we find that populations might need rather long time to adapt to conditions on a site. Species interactions strongly drive population dynamics and influence colonisation success. We interpret this effect of species interaction as a new bottleneck mechanism for colonising populations.

We used the theoretically based $\ln(1-P_0)$-PVA-method suggested by Grimm & Wissel (2004) for single species systems and enhanced it in ch. 3 for interacting species systems. It revealed to be highly potential to estimate persistence measures for established and colonising phases of population systems for all types of extinction dynamics occurring in the system of parasitic Maculinea butterflies.

Part IV

The influence of spatial structure

Chapter 5

Methodology for assessing landscape structures from population viability

5.1 Introduction

Effects of habitat loss or fragmentation on biodiversity are intensively studied in conservation biology (e.g. Fahrig, 2003). It is empirically shown that reduction of the total amount of habitat decreases biodiversity. However, changes in spatial structure (keeping the amount of habitat constant) can have both, positive and negative effects on biodiversity (see review in Fahrig, 2003).

In landscape ecology, a common way to assess influence of landscape structure on biodiversity is, to relate landscape characteristics to biodiversity measures (e.g. Turner, 1989). Outcome of this type of analysis strongly depends on the choice of predictor variables (landscape indices) and response variables (biodiversity measures). Accepting these variables means defining a view on the system. This view does not necessarily correspond to species perception of the landscape structure. Therefore when choosing wrong indices, detected effects are difficult to be interpreted or can be misleading (Tischendorf, 2001). Especially because spatial measures tend to be correlated (Schumaker, 1996; Gustafson, 1998; Dale et al., 2002; Fahrig, 2003), wrong predictors might hide the real reason of an observed effect. This problem goes together with another shortcomings of this statistical approach. The step from neutral spatial measures to biodiversity indicators is usually too far to learn about processes of species-landscape interaction. Hence, this method poorly supports understanding, why species perform different in certain landscapes.

On the other end of the spectrum, studies on species behaviour, theoretically supported by process or rule-based models, aim to understand small scale interaction of individuals or populations with the spatially structured landscape in which they are embedded (Kramer-Schadt et al., 2004; Revilla et al., 2004; Wiegand et al., 2005; Heinz et al., 2005; Peer et al., 2006). However, these detailed studies are usually restricted to single species and few landscape structures to reduce system complexity.

Yet landscape structure is of special interest in systems of interacting species (refuges in predator prey systems, wave propagation of epidemics or natural and agricultural areas in biological pest control (Amezcua & Holyoak, 2000; Schneider, 2001; Bonsall et al., 2002; Tscharntke et al., 2002; Hansen et al., 2003; Orrock et al., 2003). Because of variety in processes and effects, influence of spatial heterogeneity to multi-species systems is either studied theoretically on a highly abstract level (De Roos et al., 1998; Gurney et al., 1998; Donalson & Nisbet, 1999; Grenfell et al., 2001; Lima, 2002; Pascual et al., 2002b; Briggs & Hoopes, 2004, and references therein) or in case studies (Hochberg et al., 1994; Arditi et al., 2001; Winder et al., 2001; Wootton, 2001). Results of different studies are difficult to be compared and hence only contribute in small parts to a more general understanding.

The missing link could be a framework to evaluate influence of spatial landscape structures to population dynamics in species communities. Such an approach has to be flexible to allow incorporation of detailed population dynamical processes and a variety of spatial structures. However, assessment of resulting dynamics has to be comparable and therefore needs to be fixed by the methodology.

The PVA-protocol presented in sec. 3 and sec. 4 provides the power for such a framework. Flexibly a variety of species traits and landscape characteristics can be included into simulation models. Resulting extinction dynamics can be uniformly evaluated by the two simple measures of persistence c_1 for initial risk of extinction and intrinsic mean time to extinction t_m for extinction risk during the established state of a community.

In this section, we describe a framework to assess many highly complex landscape structures by their ability to sustain species communities. A spatially explicit model is used to simulate species and their interaction with landscapes. According to ranking order of species persistence, suitability of landscapes can be estimated. Hence, simulated species themselves evaluate their ability to cope with particular spatial structures.

In our opinion, by this method, species perception of landscape structures can be revealed. This landscape assessment can be seen as a filter: Suitable and unsuitable landscapes are distinguished. Hence, further investigations by neutral spatial indices can be directed to evaluate differences between landscapes of different suitability.

We illustrate usage of the framework by applying it to the host-parasite Maculinea system. By means of the spatially explicit Macu model (ch. 1), we analyse influence of host plant density on persistence of the butterfly. In this section, we restrict to a consideration of methodological aspects, whereas in sec. 6 we extensively analyse effects of spatial host distribution to Maculinea performance.

5.2 Framework for assessing spatial habitat patterns from PVA analysis

Extensive studies require a conceptual hierarchical approach. Figure 5.1 displays, how the suggested analysis of ecologically relevant spatial structures takes its course.

To start, we choose a variety of spatial configurations of habitat, which could potentially occur for the species system under consideration. Following standard methods from landscape ecology, we calculate spatial indices as characteristics for the habitat structures. Instead of correlating these measures to population data from field investigations (like abundance or occurrence of individuals), we evaluate spatial structures by PVA. For this purpose, we construct a spatially explicit simulation model for the ecological system. It might incorporate species behaviour or other important species traits. The previously selected habitat structures are applied to the model in form of a 'parameter variation'. That is, for each spatial structure, we perform a PVA on results of the simulation model. Hence, the ability of the ecological system to cope with offered different landscapes is calculated. In the next step, knowledge is gained on importance of spatial properties of habitat for species persistence by comparing

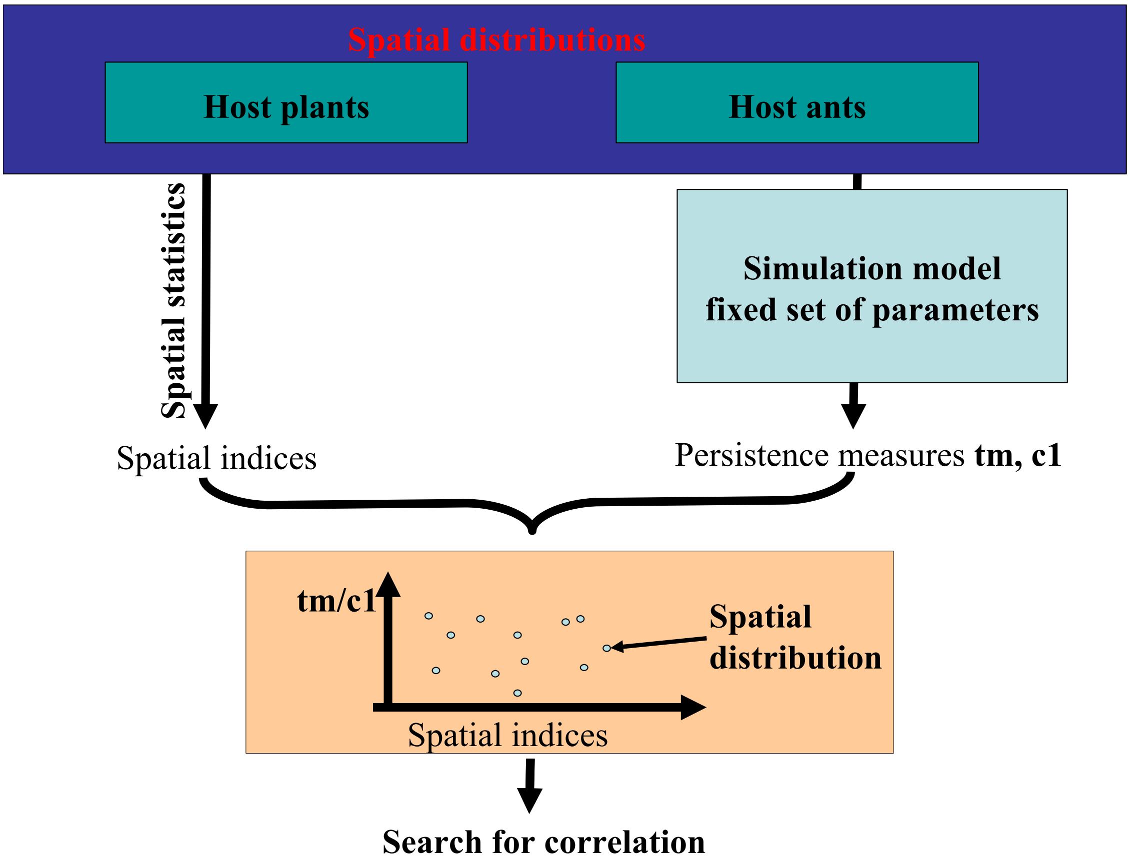

Figure 5.1: Conceptual overview how to analyse the influence of spatial patterns on population dynamics

PVA evaluation with standard spatial indices. This information helps to understand, how species perceive different spatial structures, concerning survival in a certain area.
We suggest to apply PVA instead of directly analysing simulated population sizes because of four reasons. First, PVA is a standard method, which is successfully used to asses conservation management options (Shaffer, 1981; Grimm et al., 2004; Beissinger, 2002; Lacy & Miller, 2002). Hence, landscape structures can be assessed in a well known framework. Second, PVA, as it is a form of statistical aggregation, delivers robust results for minor model inaccuracy, especially when used as a ranking order method (see ch. 4 and Grimm et al. (2004); Frank et al. (2002)). This means for the presented method that, although model abstraction or uncertainty in parameters reduce reliability of the simulation model, qualitative ranking of habitat structures is stable. Third, in ch. 3, a PVA method was presented, which is applicable to a large variety of species systems. This PVA characterises species' extinction risk by only two numerical parameters: Mean time to extinction t_m evaluates viability during the established state (that is viability of species in the system). Persistence measure c_1 contains information about the risk of extinction during an initial transient phase (Grimm & Wissel, 2004). These two persistence measures allow to evaluate long term suitability of a spatial habitat structure (t_m) and initial suitability of the habitat configuration (c_1), e.g. in a reintroduction scenario. Fourth, species persistence is the relevant measure for habitat suitability. It explicitly contains information about how species cope with their environment in critical situations of small population sizes

Table 5.1: Standard PVA parameter set for habitat suitability analysis

parameter description	name	value
time horizon: maximum number of generations calculated within one simulation run	T_H	5000
number of simulation runs from which times to extinction are calculated	*NumRuns*	300
number of runs for which population dynamics was saved (always the first runs in a PVA experiment)	*savedRuns*	3
maximum value of t_m *	t_m^{max}	10^7

* t_m^{max} was adaptively defined from observed PVA results to avoid $t_m \rightarrow \infty$ in the database and in further statistical calculations. $t_m \rightarrow \infty$ is calculated by the numerical PVA method, when all simulation runs reach T_H (populations survive in all simulation runs).

(ch. 3). It can be said: if a species cannot persist with a spatial habitat configuration, the configuration is unsuitable.

5.3 An exemplary application

We illustrate this framework, applying it to the host-parasite system of Maculinea (ch. 1). We want to answer the question, if explicit spatial plant structures are important for survival of Maculinea butterflies on a site or if plant density is a sufficient predictor for persistence of the butterfly. For this purpose, we estimate suitability of 687 host plant distributions (see ch. 1.3.4.2). Each of these host plant distributions represents one landscape in our case study.

5.3.1 Methods

Following the protocol, we parameterise the simulation model with the set of standard parameter and a standard spatial host ant distribution (see tab. 1.1). PVA is performed for all different plant distributions. Standard simulation parameters for the PVA calculations can be seen in tab. 5.1. *NumRuns* $= 300$ is a very low value (see ch. 4), but it is a trade off between simulation time ($687 \cdot 300 \cdot 5000$gen $\approx 10^9$gen need to be simulated for the full analysis) and accuracy of PVA results.

To estimate accuracy, we select different host plant patterns and repeat the PVA procedure with each of these spatial patterns for 166 times. Hence, for each host plant pattern we receive 166 estimates of persistence measures t_m and c_1. Resulting distributions[1] of persistence measures can be evaluated by their range of 90%-quantiles. This is a 'rough analysis of deviation'.

Finally, we calculate density of host plants in each of the spatial host plant patterns. The predictor variable 'plant density' is related to the response variable 'intrinsic mean time to extinction t_m' (see bottom of fig. 5.1).

---

[1] In different simulations, we observe that the distributions of persistence measures are usually concentrated around the maximum likelihood but are not normally distributed

5.3.2 Results

5.3.2.1 Relevance of plant density

In fig. 5.2, the result of the example study is presented. For plant densities up to about 50%, values of intrinsic mean time to extinction t_m range from 10^4 to 10^7 generations. These high t_m-values indicate long viability of populations. However, there is variance in the data. Increasing plant density decreases values of t_m. Hence we conclude that not too high density of host plants on a site is good for persistence of Maculinea butterflies. Finally, for very high plant densities we find $t_m < 10$ generations. Thus, very high plant densities are unsuitable for Maculinea persistence. Transition between both extremes happens on a small range of plant density.

Distinguishing three types of system reactions for different ranges of plant densities, we already implicitly assume that spatial index 'density of plants' is a proper predictor for system viability. Why can we draw this assumption? Because points in fig. 5.2 arrange themselves in a functional pattern according to plant density and not totally random. This means that viability of the system is related to plant density.

5.3.2.2 Relevance of explicit spatial patterns

But remember, each point in fig. 5.2 represents a full spatial host plant distribution. This is more information than the numerical value of 'plant density' contains. We find that points in the graph do not string on a narrow line. There are some deviations. These can arise from two causes. Either persistence measures are measured inaccurately, resulting from errors in statistical analysis of the stochastic simulation model (ch. 4.4.2). Or, the analysis results in differences in viability because the explicit spatial distribution of host plants is different. In this case, an effect of spatial structure on species persistence is found.

To distinguish between both alternatives at points, where an explicit spatial effect is suspected, the 'rough analysis of deviation' (sec. 5.3.1) should be applied. Exemplarily, we show results for two plant patterns with the same number of 146 host plants (corresponding, plant density = 0.162). The upper row of fig. 5.3 displays boxplots of the distributions of t_m-values from 166 repeated PVA-analysis for each pattern. Pattern 1 has unique $t_m = t_m^{max} = 10^7$gen. The histogram in the middle row of fig. 5.3 confirms this observation. All 50000 simulation runs reach time horizon $T_H = 5000$ generations. In contrast, pattern 2 shows a narrow distribution of t_m around $10^{4.8}$. All of the 166 values are far below 10^7. The corresponding histogram shows that Maculinea populations can go extinct during the first 5000gen. Comparing boxplots and histograms for both patterns, it is obvious that there must be a substantial difference in population dynamics for both patterns, although they consist of the same amount of host plants. Looking at the plant distributions at bottom row of fig. 5.3, it is not surprising that they have a clearly different aspect. In pattern 1, plants are much more arbitrarily distributed than in pattern 2, which consists of only one patch. Hence, explicit distribution of host plants is important for the system.

5.3.3 Conclusion of the example study

In the example study, results of the suggested approach are manifold. First, plant density can be seen as a good predictor for persistence of Maculinea butterflies. Second, it is deduced that, in certain cases, the explicit spatial patterns of plant distributions have strong influence

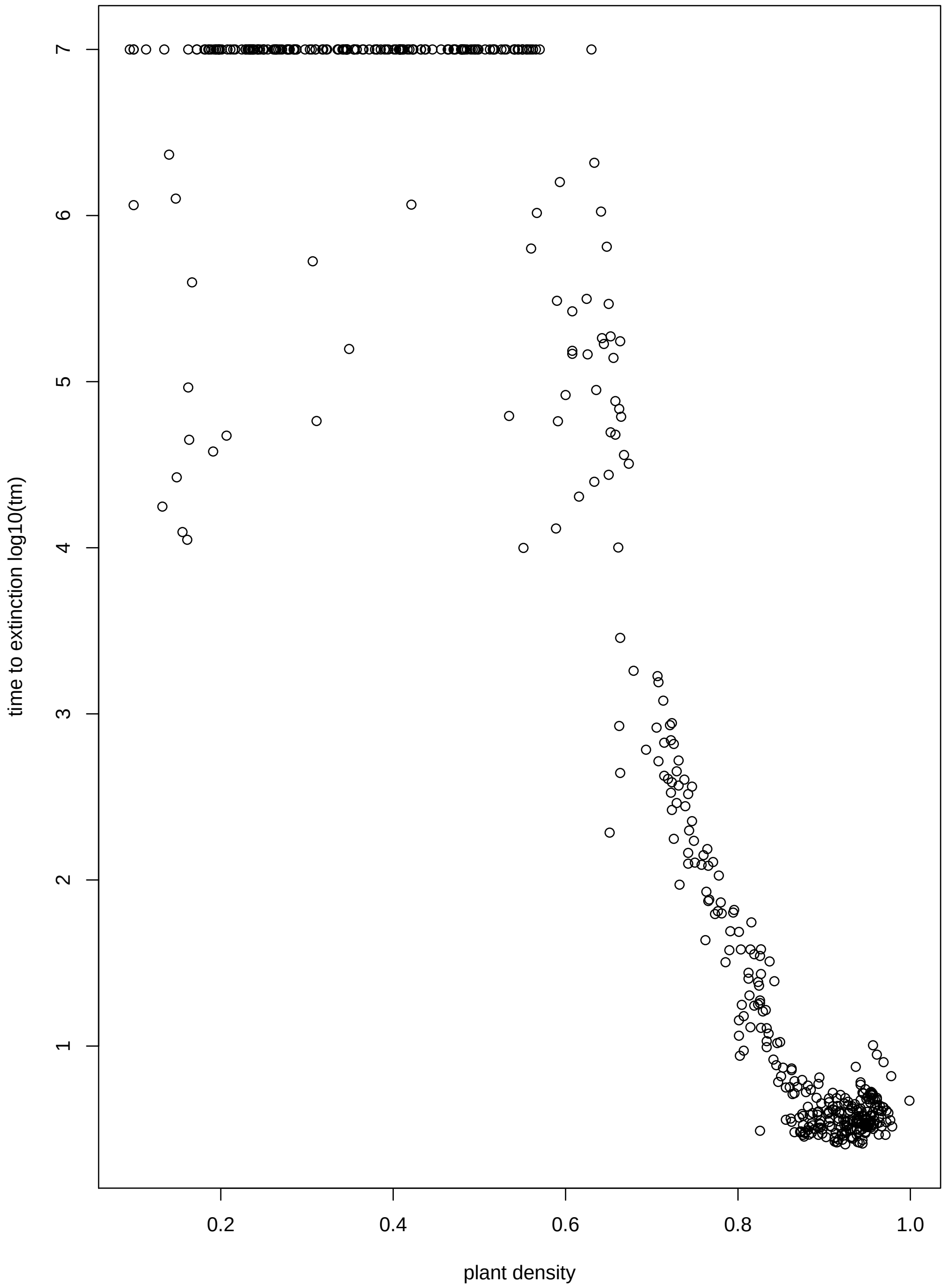

Figure 5.2: Times to extinction $log_{10}(t_m)$ for different host plant distributions of Maculinea. Parameter to characterise the spatial plant distribution is 'density of plants'. Although showing a functional relation between plant density and t_m, there is a high variance at least for low plant densities. This variance results from different effects of plant distributions, which are equally dense.
Note, for simplicity, least plant density is about 10%. In analysis of ch. 6, lower host plant densities are considered.

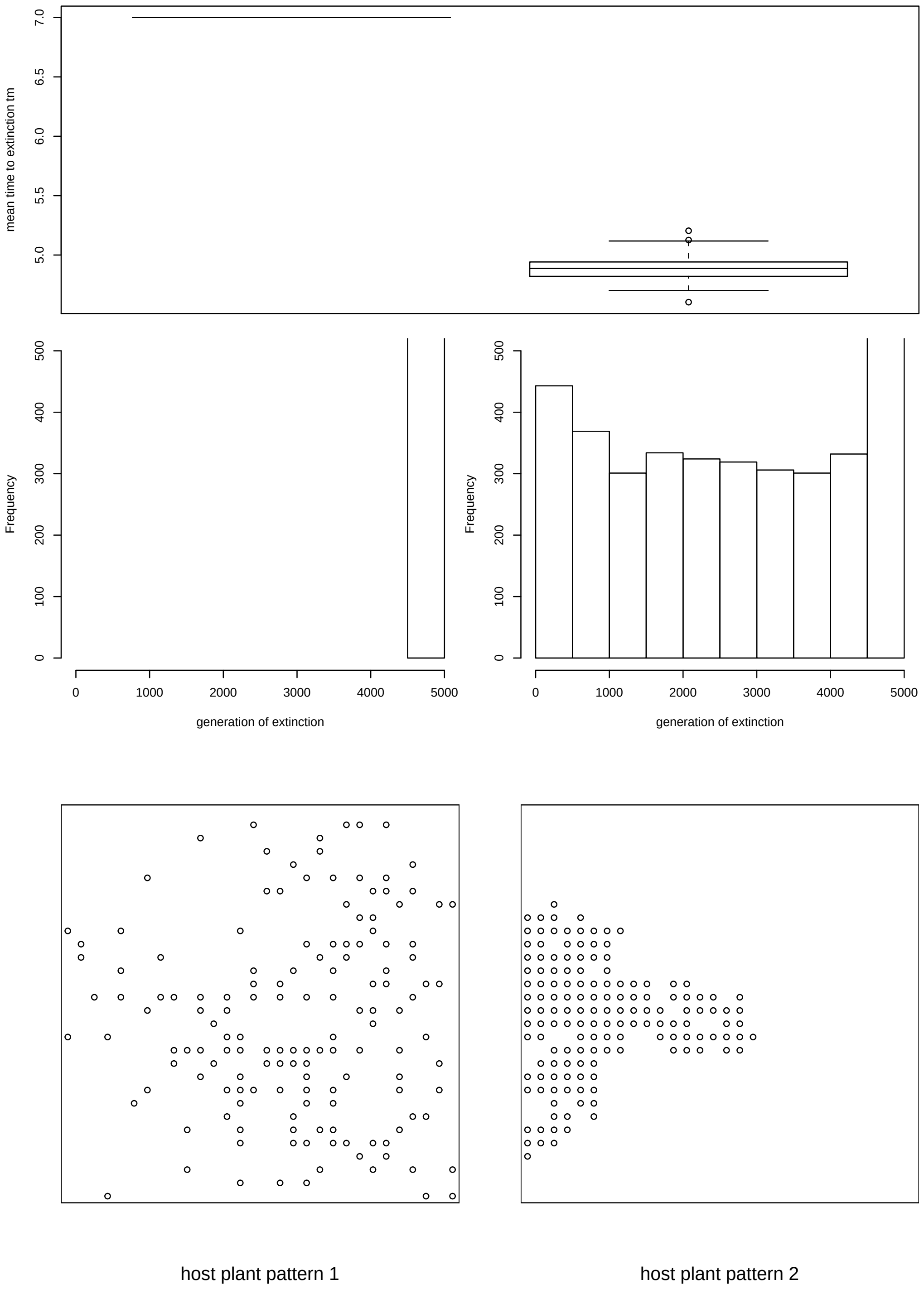

Figure 5.3: Analysis of spatial host plant distribution with the help of mean time to extinction t_m. Each column represents results of one plant distribution pattern. Both patterns comprise 146 host plants. Upper row: distribution of mean time to extinction from 166 t_m-calculations. Middle row: Histograms of times to extinction from 50000 simulation runs (y-axis break at 500). Bottom row: spatial host plant distributions. Note that for pattern 1, no extinction event could be found, whereas for pattern 2 extinction of Maculinea butterflies was not unusual.

on persistence. Third, the framework filters out, in a comfortable way, the critical patterns (those with strong variances in t_m-plant density correlations). And fourth, it indicates that, for different patterns, population dynamics might result from different processes.

5.4 Discussion

5.4.1 The meaning of population persistence for the assessment of landscapes

In the approach, population viability is used to assess spatial habitat configurations. What is the meaning of population persistence for the landscape analysis?

PVA measures persistence of a population under fixed environmental conditions. It is a common methodology to vary external environmental factors in order to evaluate their effects on the viability of a population (see different authors in Beissinger & McCullough, 2002). In the suggested framework, spatial configurations are varied and evaluated. High viability of a population indicates that this type of species performs good with the tested spatial arrangement. Hence, the arrangement is suitable.

Neutral landscape indices consist of purely spatial measures which ignore any ecological attributes. Habitat suitability or population viability, however, always summarise both, the landscape setting and the species' specific response to it.

In the example study, the spatial configuration is a spatial distribution of host plants. This arrangement is evaluated by the persistence of a Maculinea population. Assume that persistence is high, hence we conclude that the plant distribution is suitable. However, another species acts in this system: host ants of genus Myrmica. For these Myrmica ants, suitability of the host plant distribution could be assessed to be completely different. The ants have other demands on suitable habitat (Elmes et al., 1998). Hence, suitability of a spatial habitat configuration normally is different for different species. But, it can be different for the same species as well, when other environmental factors change: On a site without host ants, Maculinea butterflies cannot persist, although the host plant distribution would be suitable, if Myrmica ants were present.

It is obvious that the suggested method does not only assess spatial properties of a habitat structure, but as well includes influencing environmental conditions. This approach of landscape evaluation is useful, because the same landscape can have different suitabilities for different species and under different environmental conditions.

5.4.2 Suitability of landscape structure for colonising and established species

The method presented in this section automatically assesses suitability for two different situations: for an initial colonisation by a species and for a time, when the species is established. Usually we are interested in suitability of a spatial habitat arrangement on the long run that is for an established population. In this case, habitat suitability is assessed by the intrinsic mean time to extinction t_m. High values of t_m indicate high suitability of the spatial configuration. However, some species might have different needs to a spatial habitat structure during colonisation than during the established phase (see ch. 4). For such species, it is important to assess, if spatial habitat structures are suitable for colonisation. Because, if colonisation of a site is never possible, we won't find an established population on the site, although it would be suitable.

Table 5.2: Assessment of habitat suitability for a site

	$c_1 < 1$	$c_1 \approx 1$	$c_1 > 1$
t_m high	suitable habitat, but less suitable during adaptation phase	suitable habitat	suitability of habitat is even higher during adaptation phase
t_m low	habitat less suitable and even worse during adaptation phase	habitat less suitable	habitat less suitable, but the system adapts well
$t_m < 1000$	habitat unsuitable		

Suitability for colonisation can be evaluated by persistence measure c_1. A value of $c_1 < 1$ indicates that, under the given conditions, a spatial habitat configuration is less suitable for colonisation than for being established.

Table 5.2 helps to assess habitat suitability from persistence measures.

5.4.3 Analysing spatial structures and spatial interactions

PVA tells us, which spatial habitat configuration is suitable. However, it is important to know, why it is different to an unsuitable one. To answer this question, the framework supports a variety of methods.

5.4.3.1 Testing a spatial index for habitat suitability and population viability

In the example study, we used a neutral spatial measure (host plant density) to characterise geometry-statistical properties of landscapes. This approach, inspired by methods from landscape ecology, relates geometric landscape characteristics to habitat suitability. A good spatial statistical descriptor for suitability reveals, which spatial structures in the landscape are relevant for the performance of species.

The important spatial structures are revealed by the help of the population dynamical process. Their relevance is approved by the species system. However, these spatial patterns are geometrical properties of the landscape, independent of the population dynamical process. Hence, we can attach suitability of a landscape to its spatial properties, ignoring the spatiotemporal population dynamics of the system.

This means, a good spatial descriptor for suitability of a habitat configuration, on the one hand is a simple spatial statistic. On the other hand, it is approved to describe the relevant properties of a landscape to sustain species. Hence, it is a spatial index which takes into account species demands on the spatial habitat configuration. Such indices are required for species conservation (Frank, 2005b).

5.4.3.2 Learning from variance in data

In our example study of the Maculinea model, we find that host plant density is a good predictor for habitat suitability. However, several host plant distributions are less suitable than indicated by their density (sec. 5.3.2.2; data points which lie below the general trend in fig. 5.2). We argue that, for these types of host plant patterns, density is not sufficient to predict suitability. Hence, further spatial properties, which are not assessed by density, affect suitability.

Structurally, our reasoning follows the way of statistical modelling (e.g. in an analysis of deviation). Sadly, these established statistical methods cannot be applied in our case, because we do not know the distribution of data or errors. However, in sec. 5.2 an alternative method is suggested, which can be used to assess significance of variance in data (which is a type of Monte-Carlo method).

Here, we want to discuss what we can learn, if a spatial index does not sufficiently reflects suitability. A spatial index is the quantification of the assumption, that a spatial property of a landscape relevantly influences suitability. By this assumption, other spatial properties are ignored explicitly. Hence, if the spatial index is insufficient, we learn that excluded spatial properties are relevant for suitability.

In particular, if two spatial patterns are equally evaluated by the spatial index, but their suitability is highly different, the effect of excluded spatial properties is strong. There has to be a reason, why the same population dynamical system performs different in two spatial habitat configurations. Therefore it is promising to compare such spatial patterns, in order to reveal, which of their properties are the reason for the variance in suitability. Probably their spatial configurations clearly differ (like shown in fig. 5.3). This clear difference can be used to generate hypothesis about the relevant spatial properties.

In practice, learning from variance can have large impact. It is easy to overview a graph, which relates a spatial index to habitat suitability (such as fig. 5.2). Variance in data points is obvious. Hence, we quickly know, where to search for unrevealed patterns. In detailed analysis, we can restrict to few spatial habitat configurations for which we already know that their structures have strong different effects on suitability. This allows to limit the effort of complicate and demanding spatial or spatiotemporal analysis, because it has to be done for only few examples. The alternative would be, to investigate all spatial habitat configurations by maximum effort and to deal with high amounts of redundant information.

In ch. 7, using knowledge on variance, a spatiotemporal analysis of population dynamics of the Maculinea system of about 2000 scenarios can be restricted to only 18. A spatial index to assess suitability, developed from detailed investigations on the 18 scenarios, approved to be effective as well in all the other scenarios.

5.4.3.3 Comparing between spatial statistics

The framework suggested in this chapter has another important advantage: predictive power of different statistics for spatial habitat structure can be compared, because they are assessed against standardised measures t_m and c_1. Here, we show two ways, why this is useful. Firstly, spatial statistics can be compared to identify, which of them is the best indicator for population persistence, hence the best spatial index. Secondly, knowing about their characteristics, the spatial statistics can be applied to generate hypothesis. For example, if measures for spatial clumping are better predictors for t_m than those ignoring clumping, spatial structure probably has an influence on population persistence[2].

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[2] Within the work of this thesis, five different types of spatial statistics were compared for their predictive power of persistence measures t_m and c_1. Although not explicitly showing this comparison here, the results strongly improved understanding of the system and motivated analysis of ch. 7

5.4.4 Understanding certifies models of habitat suitability and landscape indices

We see an important advantage of the framework in its guiding structure. The scientist is taken through several steps which all give a different point of view on habitat characteristics. In each step, the scientist refines and approves thinking about the species' habitat use.

First step is that PVA provides a view on habitat suitability through the eyes of the modelled species. Populations react with high or low viability to the given environment. Second, the method works as a filter. It characterises different patterns according to their spatial properties and to their ability of supporting populations. A spatial index, which describes suitability well, seizes spatial properties, which are relevant for species persistence. Additional variance, which cannot be explained by the spatial index, can be attributed to unconsidered spatial properties. Third, to explain variance, the scientist can concentrate on few spatial patterns, where unexplained effects are large. Detailed analysis of population dynamics on only these patterns provides understanding of spatiotemporal processes and spatial patterns. Fourth, knowledge from these few scenarios can be reformulated as hypothesis and tested on the other scenarios.

In our opinion, the framework can improve investigations on spatiotemporal population systems, because it allows to quickly assess a broad range of different spatial habitat configurations. Results can be presented in few graphs that provide overview on the effects of different spatial patterns. Weaknesses in understanding patterns are easily revealed. Improving understanding is supported by the framework, as following analysis can be concentrated to spatial patterns which provoke unexplained effects on species viability.

5.5 Conclusion

The presented framework allows assessment of suitability of spatial habitat configuration for species and species communities by means of a generally applicable population viability analysis. In comparative investigations of many different spatial habitat structures, it can be revealed, which spatial characteristics are relevant for suitability.

In the framework, advantages of detailed analysis of localised spatiotemporal process are combined with large scale approaches from landscape ecology. Suitability incorporates species interaction with a habitat and environmental conditions. Therefore the framework allows to switch between analyses of ecological processes and of geometrical properties of spatial habitat distributions.

The framework can be used to develop spatial indices. These indices are approved to seize properties of a habitat configuration, which are relevant for species persistence.

As well, the framework facilitates detailed analysis of spatiotemporal population dynamics resulting from different spatial habitat structures. Hence, understanding the influence of spatial heterogeneity on populations can be improved.

The framework supports investigation on reasons for extinction that result from habitat change and fragmentation, because it allows insight on species perception of spatial habitat structure.

Chapter 6

Effects of spatial host distributions on viability of Maculinea butterflies

6.1 Introduction

Some of the previous chapters, are concerned with developing methodology. In others, dynamics of the Macu model is analysed to get a general understanding of the behaviour of the Maculinea model. With this background we are now in the position to tackle the main topic of this thesis – to study how persistence of Maculinea populations is affected by the spatial distribution of hosts.

Host plants form the fixed part of the spatial habitat distribution for the Maculinea population. Their spatial configuration can be considered as a landscape for oviposition of Maculinea (sec. 1.3.2.1). Adult Maculinea butterflies are supposed to be able to reach every host plant on a site. That is, they disperse globally (sec. 1.3.2.6). In contrast, Myrmica host ants are the dynamical part of the spatial habitat configuration. Spatial host ant distribution is affected by ant population dynamics (sec. 1.3.2.5) as well as by parasitism of Maculinea caterpillars (sec. 1.3.2.4). Thereby we want to remind that several processes of the system are confined to different spatial patterns and scales.

In ch. 2, it is found that global parasite distribution leads to synchronisation in nest dynamics of host ants. However, host ant movement and parasitism take place locally. These processes are spatially related to the spatial habitat structure caused by the host plant distribution. As population dynamics are strongly influenced by spatial distributions of hosts (plants and ants), these spatial configurations are supposed to affect persistence of Maculinea butterflies, too (Bonsall et al., 2002; Briggs & Hoopes, 2004; Hosseini, 2003).

From model definitions in ch. 1 and results in ch. 2, it can be concluded that strength of spatially acting processes changes temporarily. Hence, spatial effects are observed differently at different time scales. In the following, we summarise spatiotemporal effects, which can be expected:

Long time scale - established state: Spatial host plant distribution is fix during a simulation run. It imprints long term spatial fragmentation of Maculinea habitat on a site. In contrast, host ants dynamically adapt to spatially distributed parasitism of Maculinea caterpillars. During the established phase, a fluctuating quasi-stationary distribution of host ants is observed. This distribution is found to be independent of the initial host ant distribution (see ch. 2). We hypothesise that host plant distribution and budding range σ influence persistence in the established state, whereas initial Myrmica host ant distribution does not have any effects. (H1)

Short time scale - initial transient state: The degree of spatial correlation between the plant distribution and the ant nest distribution during the transient phase should affect persistence of Maculinea butterflies. Imagine an initial situation, where host ants and host plants are spatially separated. In such a case, the Maculinea butterfly population cannot colonise a site. At least few cells, containing plants and ants, are necessary. On the other hand, a contrasting situation, where all ant nests are situated in cells with host plants, is possibly not suitable, because ant nests might be overexploited and cannot sufficiently recover (Singer & Merelo, 2004, unpublished work). We hypothesise that the initial host distributions and adaption processes have an influence on persistence during the initial phase. Interaction is expected to be complex, depending on explicit spatial distributions and ability of ants to build new nests. (H2)

The method for analysing the spatial habitat structure in terms of its effect on population viability presented in ch. 5 can differentiate habitat conditions according to their effects during initial transient state and during the established state of the system. Hence, it gives a chance to test our hypotheses. Further, if persistence during establishment is actually not influenced by initial host ant distribution, investigation can be simplified by ignoring this parameter.

In this and the following chapter, we restrict investigation to three 'parameters', which are supposed to drive spatial influence on population dynamics of Maculinea systems: host plant distribution, initial Myrmica host ant distribution and budding range of Myrmica host ant nests σ. We perform 'parameter variation' experiments on σ and both explicit spatial distributions of host plants and host ants.

6.2 Methods

We investigate the influence of spatial distributions of host plants and host ants using the methodology described in ch. 5. For designing our experiments we follow fig. 5.1. To analyse effects of spatial patterns, we use the pool of spatial host distributions described in ch. 1. We characterise host distributions by numbers of host plants and numbers of initial host ant nests. Absolute host numbers correspond directly to densities

$$\text{density} = \frac{\text{total number of respective hosts}}{\text{maximum number of cells}} = \frac{\text{total number of respective hosts}}{900}$$

as each cell can be occupied at most by one nest and one plant.

In all experiments, the Maculinea model is parameterised with the set of standard parameters (tab. 1.1). For PVA we use the parameter set from tab. 5.1. Keeping these parameters constant makes results of PVA comparable (see protocol in ch. 5). Hence, measures of persistence t_m and c_1 can be used to assess persistence under different conditions of host plant density, initial Myrmica host ant nest density and Myrmica budding range σ.

In the following sections, parameter variation experiments for each of the three spatially relevant parameters are described precisely.

6.2.1 Variation of host plant distribution

In our first experiment, host plant distribution is varied. We run the Maculinea model with all 645 plant distributions described in ch. 1.3.4.2. To test the dependence on either initial

Table 6.1: Scenario groups and representative host plant distributions

SG	Scenario group description	Range of # host plant[+]	Persistence type	Host plant pattern[!]	# plants	fig.[*]
SG1	Lowest host plant coverage	< 100	Type II	plantsSG1	39	6.3
SG2	Highly suitable host plant coverage (intermediate coverage)	100 – 500	Type I	plantsSG2a	146	6.4
				plantsSG2b	478	6.5
SG3	Declining persistence (high plant coverage)	500 – 700	Type II	plantsSG3	598	6.6
SG4	Highest host plant coverage	> 700	Type III	plantsSG4	858	6.7
SG5	Intermediate plant density with decreased persistence	119 – 186	Type II	plantsSG5	146	6.8

[+] see fig. 6.2

[!] names of host plant configurations indicate the functional group, which they represent. Note, the two plant patterns for SG2 are distinguished by letters 'a' and 'b'

[*] Column 'fig.' refers to graphs depicting variation of initial ant distribution.

host ant distribution or on budding range of Myrmica ants σ, this study is repeated for different combinations of these additional parameters. Noticing that effects are small we restrict further analysis to three initial ant nest distributions ants1 (#nests: 217), ants2 (#nests: 483), ants3 (#nests: 716) with nest sizes of 10 caterpillar equivalents and budding range $\sigma = 4\text{m}, 8\text{m}$ or 12m. These parameters are chosen to cover a reasonable range of nest numbers and movement scales.

6.2.2 Distinguishing scenario groups

Dependence of intrinsic mean time to extinction t_m on plant density allows to define different groups of scenarios. These groups sort scenarios together, for which certain functional relations of intrinsic mean time to extinction and host plant density can be assumed. The scenario groups are discriminated by eye from the plot and in doubting cases confirmed by the analysis of variance method described in ch. 5.3.1 (see e.g. fig. 5.3). From these scenario groups, randomly one or two representative plant patterns are chosen for further analysis. Representative plant patterns are listed in tab. 6.1.

6.2.3 Variation of initial Myrmica host ant distribution

Host ant distribution is varied for each representative of a scenario group and each of the values $\sigma = 4\text{m}, 8\text{m}$ or 12m. We apply 605 different initial host ant nest distributions, where each nest is occupied with 10 caterpillar equivalents (see ch. 1.3.4.2). This nest size corresponds to nest capacity, when parasitic Maculinea butterflies are absent. Results are analysed in context of their scenario group.

6.2.4 Variation of Myrmica host ant budding range σ

We further restricted parameter variation of σ to scenario groups, where an influence of budding range on long term persistence has been found. Parameter σ is varied between 1m and 18m. We used spatial host plant distributions from scenario groups 1, 3 and 5 (see tab. 6.1) and the same three initial host ant distributions as in sec. 6.2.1.

6.3 Results

We find that the parameter variations have a strong and complex, often interacting influence on persistence of Maculinea. To cope with interactions, we carefully describe analyse and interpret effects in context of their occurrence. Results are linked to earlier mentioned properties of PVA (ch. 3 and ch. 4) and of the spatial analysis framework (ch. 5) in order to extract characteristics of the Maculinea system.

6.3.1 Influence of host plant distribution

In fig. 6.1 the measures of persistence t_m and c_1 are displayed for varying host plant distribution. Spatial distributions of host plants are characterised by the total number of host plants on the site. Note, there are several host plant distributions with equal number of plants but different spatial arrangements. Different symbols in graphs represent simulations with different initial Myrmica host ant distributions. Budding range is not varied ($\sigma = 8$m).

In the following, we concentrate on fig. 6.1a[1]. Evidently, range of intrinsic mean time to extinction t_m is broad, when host plant density is varied. According to their effect on persistence of Maculinea populations, four categories of host plant densities can be distinguished. There is a critical density d_c^{low} ($d_c^{low} \approx 10\%$) below which the intrinsic mean time to extinction t_m of a Maculinea population strongly declines with declining host plant density. For host plant densities higher than d_c^{low} but below an upper limit $d_c^{high} \approx 60\%$, t_m assumes highest values. For host plant densities above d_c^{high} intrinsic mean time to extinction t_m declines sharply. For highest host plant densities, values of t_m are lowest.

The strong difference in long term persistence of Maculinea populations for different plant distributions motivates to divide plant distributions into several different scenario groups (see ch. 6.2.2). Results for each scenario group are presented separately. In the following, scenario groups (SG) are defined and analysed according to dependence on host plant distribution. Criteria to distinguish groups are determined qualitatively from observations in graph 6.1a. Definitions of scenario groups are chosen pragmatically to make analysis easier. Scenario groups should not be considered as absolutely fixed and exact categories. Description of each group ends with a short assessment of consequences for the persistence of Maculinea populations. In sec. 6.3.2, representative host plant distributions for each scenario group are selected to investigate effects of the initial host ant distribution.

6.3.1.1 SG1 - Lowest host plant coverage

Sites with less than $d_c^{\text{low}} \approx 10\%$ host plant coverage provide high variance in viability of Maculinea butterflies. With increasing plant density, intrinsic mean time to extinction t_m

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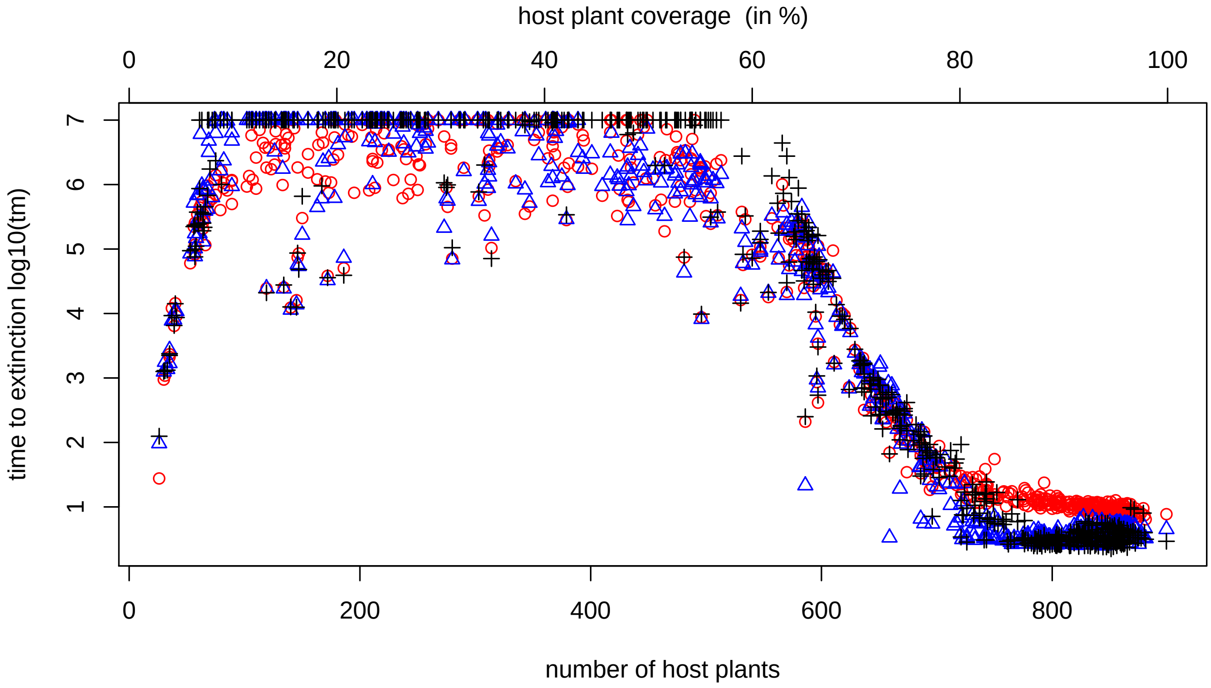
[1] In fig. 5.2 a similar analysis is depicted, but with a different initial ant nest distribution. General shape of graphs is similar, hence revealing that initial ant nest distribution is of minor importance for intrinsic mean time to extinction t_m

(a)



(b)

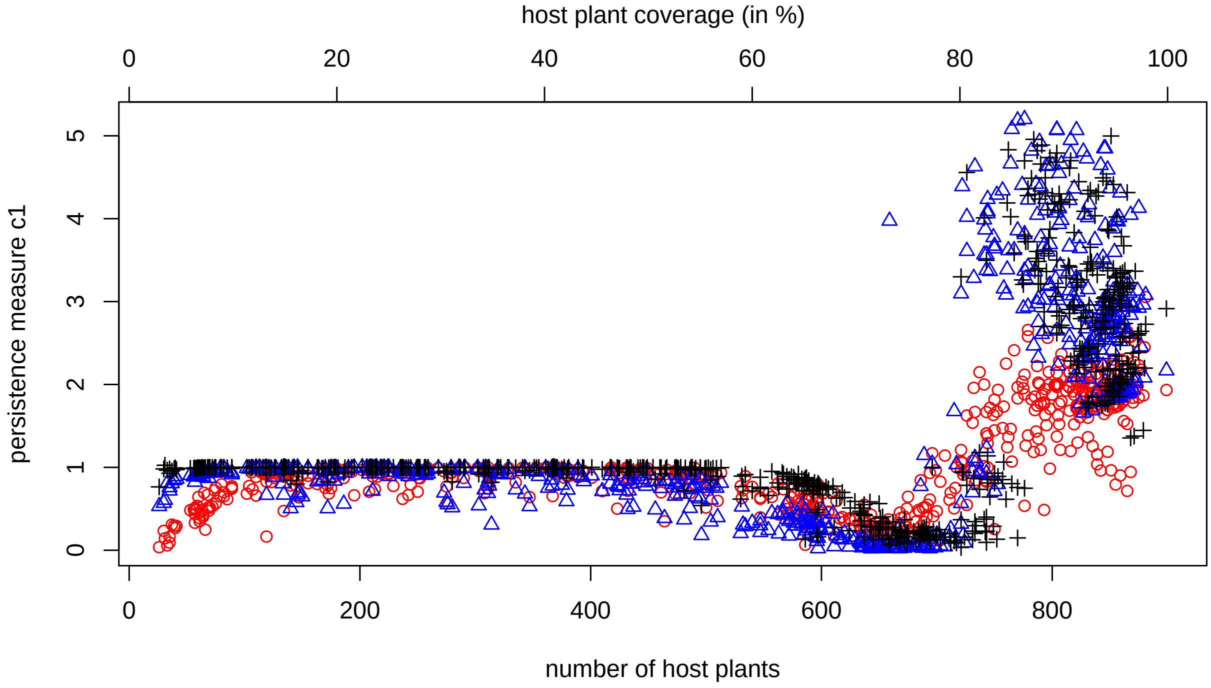


Figure 6.1: Measures of persistence t_m and c_1 for variation of plant patterns. Budding range σ = 8m. Different symbols correspond to different initial ant distributions (nest size is 10); circle: ants1, triangle: ants2, cross: ants3.

increases strongly. Values range from a few decades in one case with 26 plants up to the maximally allowed value $t_m^{max} = 10^7$gen. Influence of initial host ant distribution on t_m is not found (except for one case with lowest ant nest density[2]). Now, we turn to fig. 6.1b, where persistence measure c_1 is displayed for varying host plant density. c_1 indicates extinction risk during initial phase (see ch. 3). It responses strongly to the variation of host plant numbers and initial host ant distributions. For the smallest initial Myrmica host occupancy (circles), c_1 increases from 0 to 1 with increasing host plant numbers. Increasing numbers of initial host ant nests provoke an increased onset and a reduced number of host plants, which are necessary to reach saturation $c_1 \approx 1$.

When we summarise, it can be said that in scenario group 1 (very low host plant coverage), persistence of Maculinea populations during initial and established state increases with increasing host plant density. Hence, in the case of low host plant coverage, the more host plants are on a site, the more suitable it is for a Maculinea population. In contrast, the initial ant nest distribution effects persistence of a Maculinea population only during the initial transient phase. Thus, initial host ant distribution influences performance of Maculinea, while it colonises the site.

6.3.1.2 SG2 - Highly suitable host plant coverage (intermediate plant density)

Host plant distributions with densities between $d_c^{low} \approx 10\%$ and $d_c^{high} \approx 60\%$ are favourable for Maculinea butterflies. For many simulations maximum value $t_m^{max} = 10^7$gen is reached. In most simulation runs of a PVA study, populations survive to time horizon T_H. However, there is variance in t_m. On the one hand, initial ant nest distributions influence t_m. On the other hand, different plant distributions can lead to noticeable lower values in t_m and to different properties in extinction dynamics (see sec. 5.3.2.2). Hence, these plant distributions and resulting persistence measures are collected in an extra class (SG5 - Intermediate plant density with decreased long term persistence) and are described in sec. 6.3.1.5.

The reason, why initial ant nest distribution can decrease t_m for up to 1.5 orders of magnitude, is discussed in sec. 4.4 and is known to be an artifact. As hints we find: First, quality of the $\ln(1 - P_0)$-fit is low ($r^2 \approx 0$). Second, number of simulation runs with populations surviving until time horizon $T_H = 5000$ is high. Third, c_1 strongly varies between about 0.5 and 1. Hence, we refer to crosses at the lower border of fig. 4.6 or even type I - persistence (ch. 4.3.1.1 and ch. 4.3.2.1). That is, populations either persist on long term or go extinct early during the initial phase. Measured variation in t_m can be contributed to inaccuracy of the PVA method when applied beyond its applicability (sec. 4.4).

Summarising, intermediate host plant coverage provides highly suitable habitat conditions for Maculinea butterflies. However, during the initial phase, there is a potential risk that Maculinea cannot establish. Depending on initial host ant and host plant distributions, population dynamics during the initial transient phase influences colonisation and hence can be decisive for occupancy of the site (see ch. 4.5.2.2).

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[2] In this case, risk of extinction during the initial transient phase is extremely high ($c_1 \approx 0$) for ant nest distribution ants1. Hence, the PVA-method cannot distinguish properly between initial and established state (see sec. 4.4). t_m is strongly influenced from both, initial and established extinction.

6.3.1.3 SG3 - Declining persistence due to high plant density

For denser host plant coverage up to about 80%, a sharp decline of intrinsic mean time to extinction t_m is observed. Shape of the decline seems to be exponential. Most data points lie on a line in the logarithmic plot (fig. 6.1a). But, for some plant distributions t_m is reduced by several orders of magnitude in comparison to plant distributions with similar density. Hence, explicit spatial host plant distribution can change survival ability of Maculinea populations in this scenario group (see ch. 7 for detailed analysis). No cases are found, in which plant patterns enhance viability of butterflies compared to the average density dependence.

An influence of initial host ant distribution on intrinsic mean time to extinction t_m is not observed. But there is an effect on persistence measure c_1. c_1 declines with increasing host plant density. Onset of the decline is shifted for different ant nest distributions and values of c_1 rank with ant nest distribution. Mean of persistence measure c_1 calculated from Myrmica distribution ants2 (triangles in fig. 6.1) is significantly smaller than c_1 of both other distributions (Paired two sample t-test (Zar, 1998) on persistence measure c_1 [3]; $P_{ants3;ants1} < 2.2 \cdot 10^{-6}$; $P_{ants3;ants2} < 2.2 \cdot 10^{-6}$; df = 132). Surprisingly, suitability of ant nest distributions for surviving the initial state is ranked differently in comparison to SG1 (sec. 6.3.1.1). A reason can be found in an overexploitation effect, explained in sec. 6.3.2.2.

Summarising, increase of host plant coverage for values between 60% and 80% leads to a strong decline of persistence of Maculinea populations during initial and established phase. Influence of explicit spatial host plant patterns on long term persistence is observed but effects are low in comparison to density effects.

6.3.1.4 SG4 - Highest host plant coverage

A site, which is for more than 80% covered by host plants, is unsuitable for Maculinea populations. Intrinsic mean time to extinction $t_m \ll 100$gen. Variance of about 30 generations is found, which is provoked by the initial ant nest distribution. Distribution ants1 (circles) provides highest values of t_m. An explanation is given in sec. 6.3.2.4.

It has to be mentioned that the PVA approach is inappropriate for this scenario group. Initial and established state of population dynamics are not sufficiently separated (type III persistence, see ch. 4.3.1.3). Accuracy of the persistence measure c_1 is heavily affected. High values of $c_1 \gg 1$ are shown to be artifacts of the PVA-approach (see sec. 3.4.1). Hence, they are ignored.

We conclude that Maculinea butterfly populations cannot persist on meadows with too high density of host plants. Estimations of intrinsic mean time to extinction t_m indicate that appropriate initial host ant distributions might delay population extinction for few generations. However, general unsuitability of sites with too high plant density is demonstrated.

6.3.1.5 SG5 - Intermediate plant density with decreased long term persistence

As mentioned in description of SG2 (sec. 6.3.1.2), explicit spatial host plant distribution can lead to qualitatively different extinction dynamics. In fig. 6.1a, for some host plant distributions, with numbers of plants ranging from about 100 to 200, intrinsic mean time to extinction $t_m < 10^5$gen. These values of t_m are clearly below the values for the majority of PVA analysis with plant distribution of that density (see variance estimation for t_m for two different

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[3] Five samples are removed from the data set, because $c_1 > 1$. These values are supposed to be wrong, because of an artificial effect on c_1 for PVA studies which result in very low values of t_m (sec. 3.4.1)

host plant distributions of equal density: sec. 5.3.1 and fig. 5.3). Difference in viability of Maculinea butterflies for SG2 and this scenario group results from the influence of explicit spatial patterns in the host plant distributions (see fig. 5.3 bottom and ch. 7). Extinction dynamics are different for both scenario groups (see sec. 5.3.2.2). For this scenario group type II extinction is determined, whereas PVA of SG2 results in type I (sec. 6.3.1.2).

Persistence measure c_1 varies unsystematically with host plant density. But, the initial Myrmica host ant distribution has an influence. The mean values of persistence measure c_1 for the distribution ants3 is significantly higher than for the other two initial ant distributions. (Paired two sample t-test Zar (1998); $P_{ants3;ants1} = 0.050$; $P_{ants3;ants2} = 1.731 \cdot 10^{-6}$; df $=$ 7). Mean c_1 of distribution ants2 is not significantly lower than mean c_1 of distribution ants1. Persistence measure c_1 does not rank according to ant nest density. This result is attributed to overexploitation (sec. 6.3.2.2).

We summarise that long term persistence of Maculinea butterflies is sufficiently high, however lower than in SG2 (sec. 6.3.1.2). As host plant densities of this group are similar to the densities of scenarios in SG2, we conclude that explicit spatial host plant distribution influences persistence of Maculinea butterflies. This effect is analysed in ch. 7. Short time persistence for initial ant nest distribution ants2 is slightly lower compared to other PVA analysis of the same plant densities.

6.3.2 Influence of initial host ant distribution

Five different scenario groups are distinguished according to host plant coverage and distribution. They are graphically indicated in fig. 6.2. From each group one or two plant patterns are chosen to investigate the dependence of Maculinea persistence on initial ant nest distribution and on ant nest dispersal σ. The patterns are listed in tab. 6.1.

From variation of initial host ant distribution and host ant dispersal parameter σ, it becomes obvious that selection of scenario groups is reasonable. Extinction dynamics vary remarkably between groups, not only according to host plants (see sec. 6.3.1) but also according to host ants. We find it necessary that the reader gets an overview on possible effects of Myrmica host ants on extinction dynamics of Maculinea butterflies. Hence, for each scenario group, host ant influence is described separately. Displayed graphs are all of the same type. Measures of persistence t_m and c_1 are presented for the variation of initial host ant distributions, which is characterised by number of host ant nests. Symbols correspond to different values of σ (circles: $\sigma = 4$m shortest dispersal range; triangles: $\sigma = 8$m intermediate dispersal range; crosses: $\sigma = 12$m furthest dispersal range).

6.3.2.1 SG1 - Lowest host plant coverage

Initial Myrmica variation depicted in fig. 6.3 is calculated for plant distribution pattern plantsSG1. For very few numbers of host ant nests, intrinsic mean time to extinction t_m is very small (values below 10 generations). Increasing the initial number of Myrmica nests, t_m jumps for 3 to 4 orders of magnitude. Further increase of ant nest number does not affect t_m anymore. Intrinsic mean time to extinction t_m is not influenced by almost all initial Myrmica distribution. In contrast, budding range σ (different symbols in fig. 6.3) affects t_m. In an additional parameter variation it is found that increasing σ from $1m$ to $18m$ reduces t_m for almost one order of magnitude.

Measure of persistence c_1 for low numbers of host ant nests is highly varying with values above

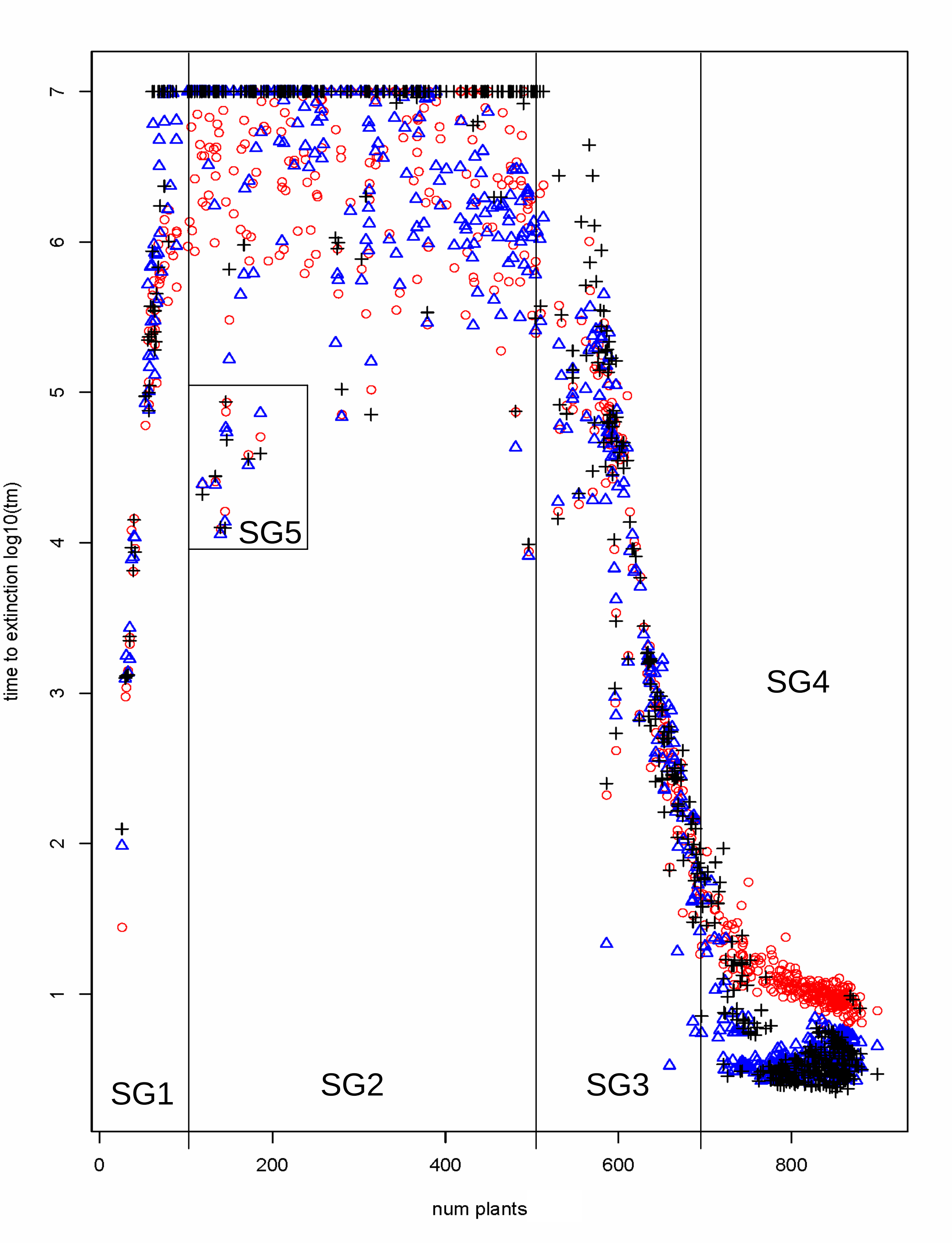

Figure 6.2: Identified scenario groups. The scenario groups distinguish qualitatively different extinction dynamics resulting from the variation in number of host plants. This schematic graph is based on fig. 6.1a.

1 , which is according to the known artifact of the PVA method for non-persisting populations (t_m very low) described in sec. 3.4.1 and is therefore ignored. With increasing initial number of host ant nests, c_1 grows up to a saturation value of $c_1 \approx 1$. Saturation is reached for about 600 initial host ant nests.

A small number of initial host ant patterns is evaluated to be unsuitable (t_m very low). In sec. 4.3.2.3 it is argued, that non-persistence of a population might occur because of long term unsuitable conditions or because extinction risk during the initial transient phase is extremely high. Without further information, it cannot be determined from extinction dynamics, for which of the two reasons a population is not persistent. Here, information is provided to ensure that, in fact, Maculinea butterfly populations cannot overcome the initial conditions. This can be seen for two reasons. First, for slightly higher numbers of initial Myrmica host ant nests, $c_1 \approx 0$ indicates that almost no population survives the initial phase, but $t_m \approx 10^4$ means high long term persistence. Second, in all but these few cases, initial Myrmica distribution does only influence c_1 but not intrinsic mean time to extinction t_m. Therefore, no long term effect of initial host ant distribution can be detected. Hence, for very low numbers of host ants, Maculinea butterflies do not persist for long term, because populations already go extinct during the initial transient phase. In other scenario groups, non-persistence because of extinction during the initial phase is found for low numbers of initial host ant nests, too (see below).

6.3.2.2 SG2 - Highly suitable host plant coverage (intermediate plant density)

Two examples of parameter variation for intermediate plant coverage can be seen in fig. 6.4 and fig. 6.5. Fig. 6.4 results from an experiment with host plant distribution plantsSG2a (146 host plants). Fig. 6.5 is calculated for host plant distribution plantsSG2b (478 host plants). Except for very few numbers of host ants (see sec. 6.3.2.1), intrinsic mean time to extinction $t_m > 10^5$gen. For high numbers of host ant nests (coverage > 60%), $t_m = t_m^{max} = 10^7$gen. This saturation is reached on different ways in both examples. In fig. 6.4 with increasing number of Myrmica nests, values of t_m grow. Contrasting in fig. 6.5, after an early increase, t_m undergoes a minimum at ≈ 350 ant nests, before it augments to saturation. Note, in this case t_m values depend on budding range of Myrmica host ants. Lower dispersal range leads to higher intrinsic mean time to extinction t_m.

For persistence measure c_1, the shape of the curve is qualitatively the same as for t_m. For high numbers of Myrmica nests, saturation value $c_1 = 1$ is reached. In fig. 6.4 for ant nest numbers below 400 a trend of increasing values of c_1 can be observed with augmenting abundance of host ant nests (but there is high variance on the data). Instead, in fig. 6.5, the minimum observed in the t_m values is repeated for c_1, again with dependency on σ.

Analysing histograms of times to extinction more thoroughly, type I persistence (see ch. 4.3.2.1) is found. Maculinea populations on sites with intermediate host plant density either go extinct during the initial transient phase or persist for long time. Extinction risk during the established phase is very low. Hence, according to analysis in sec. 4.4.2, values of $t_m < 10^7$ result from accuracy problems of the PVA-approach, where early extinction influences t_m. Effects on risk of extinction during the established phase cannot be detected, because no extinction events occur during the established phase until time horizon T_H is reached. Here, the $\ln(1 - P_0)$-PVA-approach is used beyond its applicability. But it delivers the qualitatively correct result that the butterfly population is persistent in the established state (see ch. 3.3.3, ch. 4.3.2.1 and ch. 4.5.2.2). Hence, patterns in both measures of persistence t_m and c_1 are provoked by the risk of extinction during the initial phase, which is explained in the following. Two different patterns of reaching saturation in measures of persistence are found. They result from different population dynamics during the transient phase. Be reminiscent of section 2.4.1.1, where three types of behaviours are distinguished for the transient phase of Maculinea butterflies and Myrmica ants. Here, we find that the $\ln(1 - P_0(t))$-PVA method is sensitive enough to detect these behaviours. In fig. 6.5, initial increase of c_1 for low numbers of host ants can be attributed to population dynamics, where numbers of Myrmica ants start at low levels and slowly increase until saturating at levels of the established state. Depending on the initial number of Maculinea, population size of butterflies might drop within few generations due to low resource availability, then grows with Myrmica ant number again. Such population dynamics is depicted in fig. 2.6 or in fig. 2.8. Decline of persistence measure c_1 begins, when resource availability is high enough to be initially overexploited by Maculinea butterflies. Because of initially sufficient Myrmica ant nests (high resource), the predacious Maculinea population can grow to a high population size. Exploitation depresses the host ant population. In following generations, number of butterflies declines to very low values until the host ant population recovers. During this phase, butterfly population is prone to go extinct (see e.g. fig. 2.7). For initial numbers of host ants higher than about 400 (minimum in c_1), the reservoir of host ants in cells without host plants is high enough to quickly recolonise overexploited cells. Hence, decline of number of butterflies is weaker and extinction risk lower; c_1 increases. For high numbers of initial ant nests, there are enough unparasitised nests, which quickly recolonise emptied cells. Initial overexploitation can be absorbed in almost all simulation runs. $c_1 \approx 1$. In fig. 6.5, it can be observed, that a wider spatial range of ant nest budding (σ is high) results in lower values for persistence measure c_1. Two different processes provoke this effect. First, large budding range allows Myrmica ants to quickly colonise the whole site. Hence, butterflies profit from a big resource. Higher numbers of butterflies are detected in the initial peak, when σ is high. These abundant butterflies very effectively exploit host ant nests, leaving a poor situation for following generations. Not parasitised host ant nests from cells without host plants quickly recolonise and produce suitable habitat, but on cost of their own nest size. This recolonisation might be too slow for the remaining butterflies. Or, it leads to a further explosion of butterfly numbers. The following phase of recolonisation is based on already weakened ant resources. Second, with large budding range σ, in the model, the probability is high, that host ants try to colonise area outside the site. In such a case, the colonisation attempt is unsuccessful and the ants return to their original nest (ch. 1). But the possibility is lost that the nest colonises an empty cell within the study site, in that year. Hence, this edge effect reduces colonisation efficiency of the Myrmica population, and therefore the number of suitable cells for the Maculinea population after an overexploitation event. The different types of initial population dynamics are found in the next scenario group, too. Summarising, long term persistence of populations is found for intermediate plant coverage. Initial ant nest distribution has to be monitored, because it can lead to early population extinction. This scenario group especially is affected by the bottleneck effect described in ch. 4.5.2.2. Large budding range of Myrmica host ants increases extinction risk during the initial transient phase.

6.3.2.3 SG3 - Declining persistence due to high plant density

For this scenario group, representative host plant distribution plantsSG3 is analysed exemplarily. In fig. 6.6 for very low nest numbers, t_m is low and c_1 is high, which indicates that

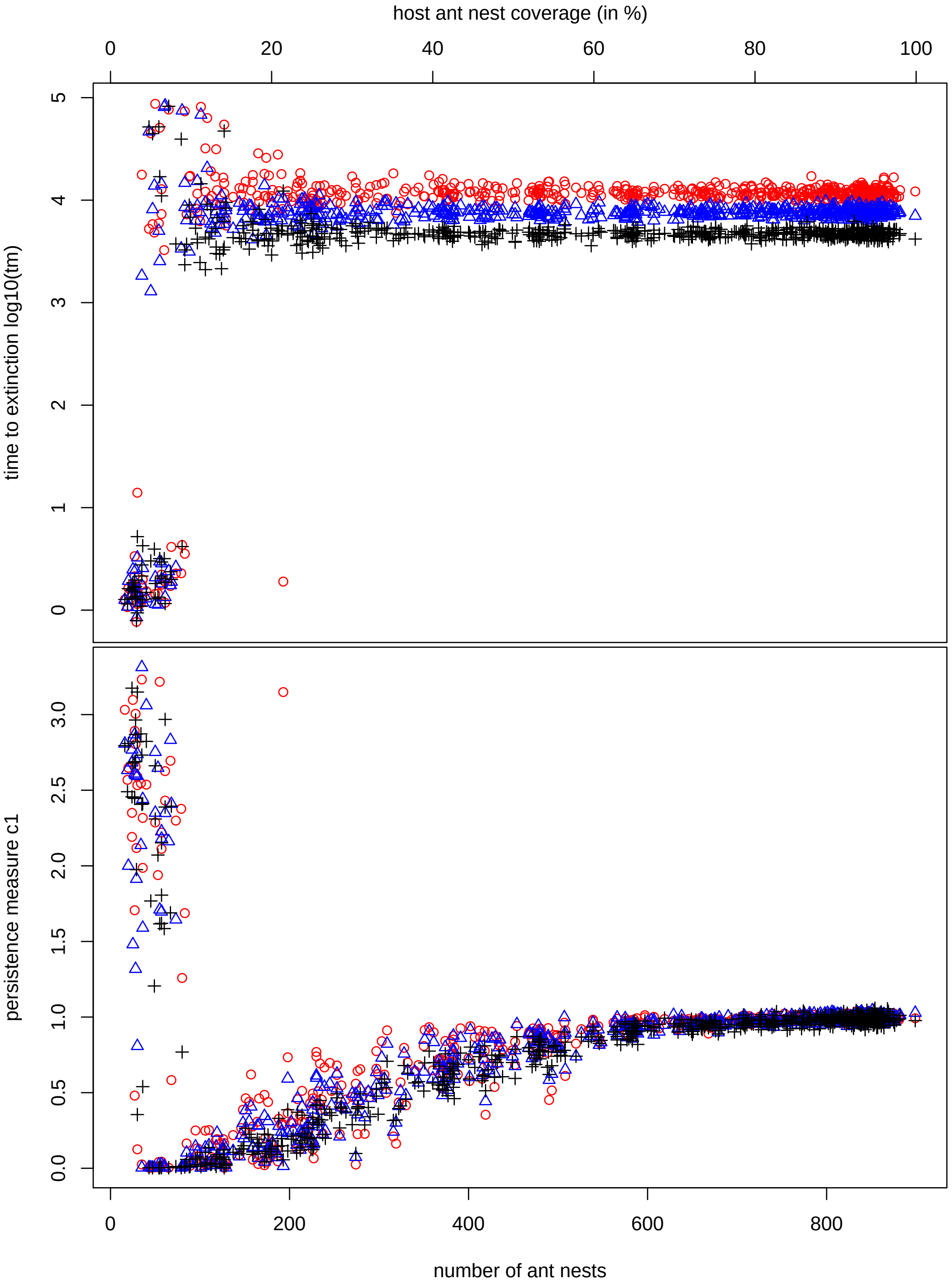

Figure 6.3: Variation of initial host ant distribution for scenario group 1 (plants: PlantsSG1; number of plants: 39, σ- Variation; circle: $\sigma = 4$, triangular: $\sigma = 8$, cross: $\sigma = 12$)

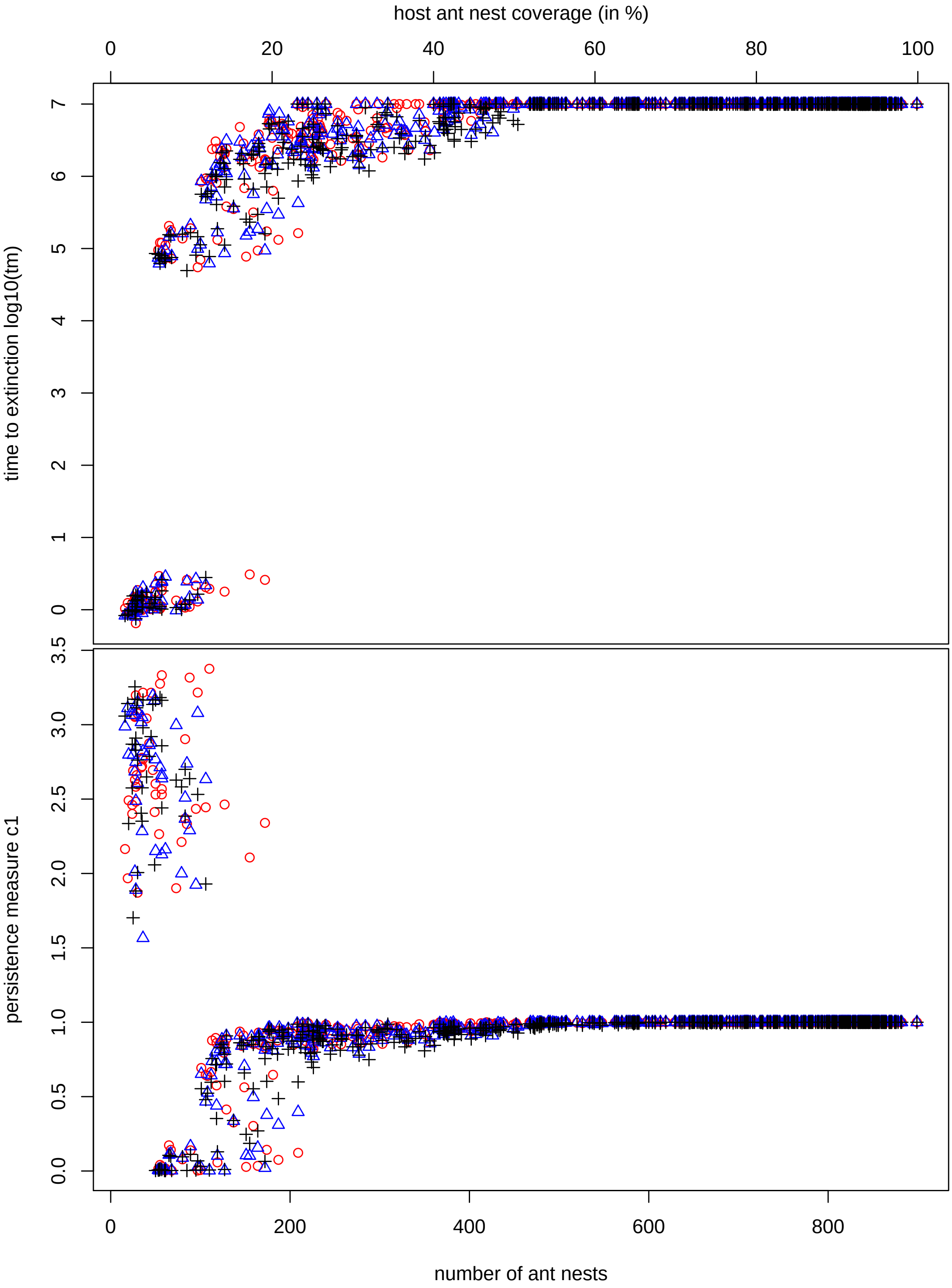

Figure 6.4: Variation of initial host ant distribution scenario group 2 (plants: plantsSG2a; number of plants: 146, σ- Variation; circle: $\sigma = 4$, triangular: $\sigma = 8$, cross: $\sigma = 12$)

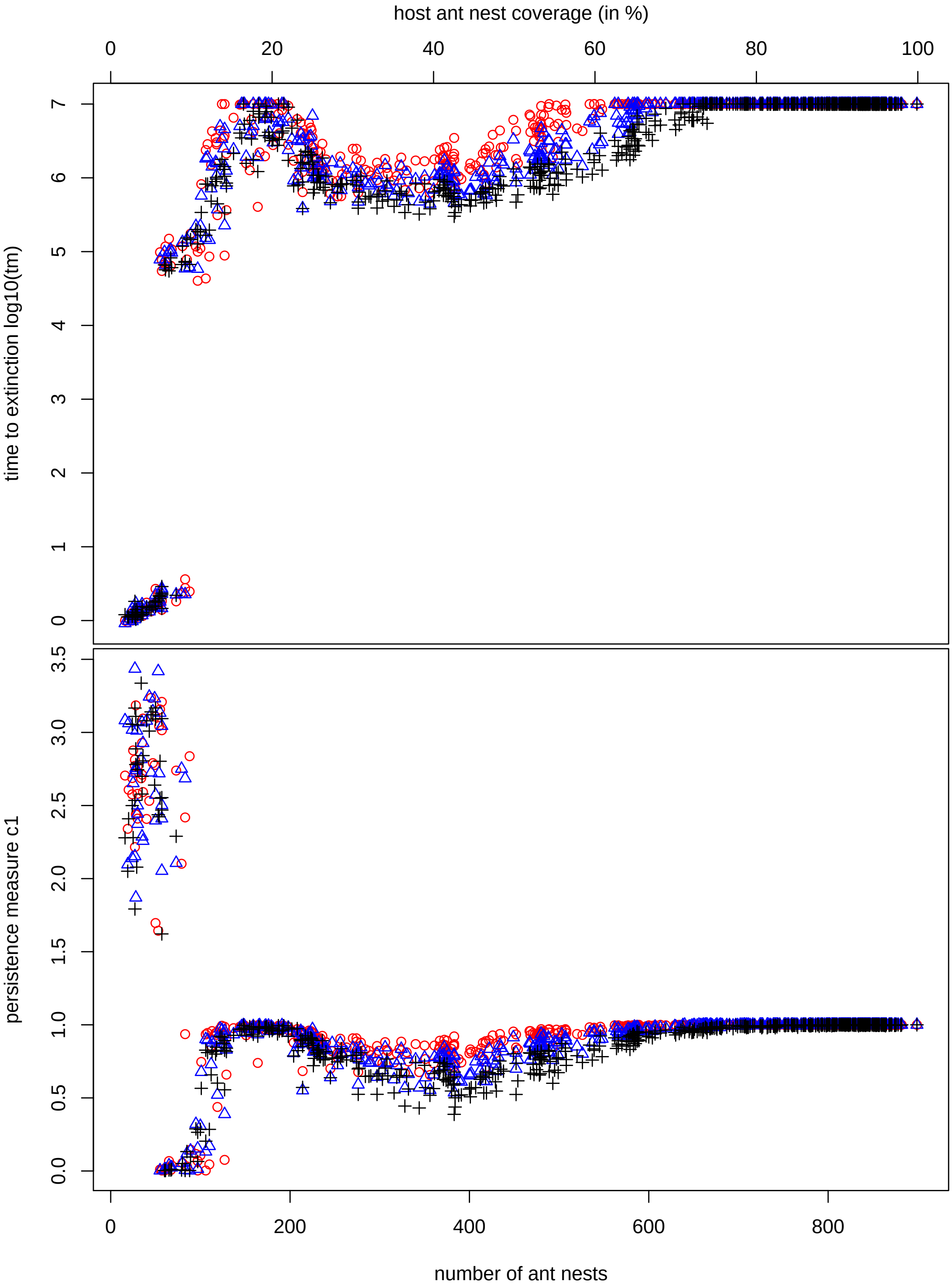

Figure 6.5: Variation of initial host ant distribution scenario group 2 (plants: PlantsSG2b; number of plants: 478, σ- Variation; circle: $\sigma = 4$, triangular: $\sigma = 8$, cross: $\sigma = 12$)

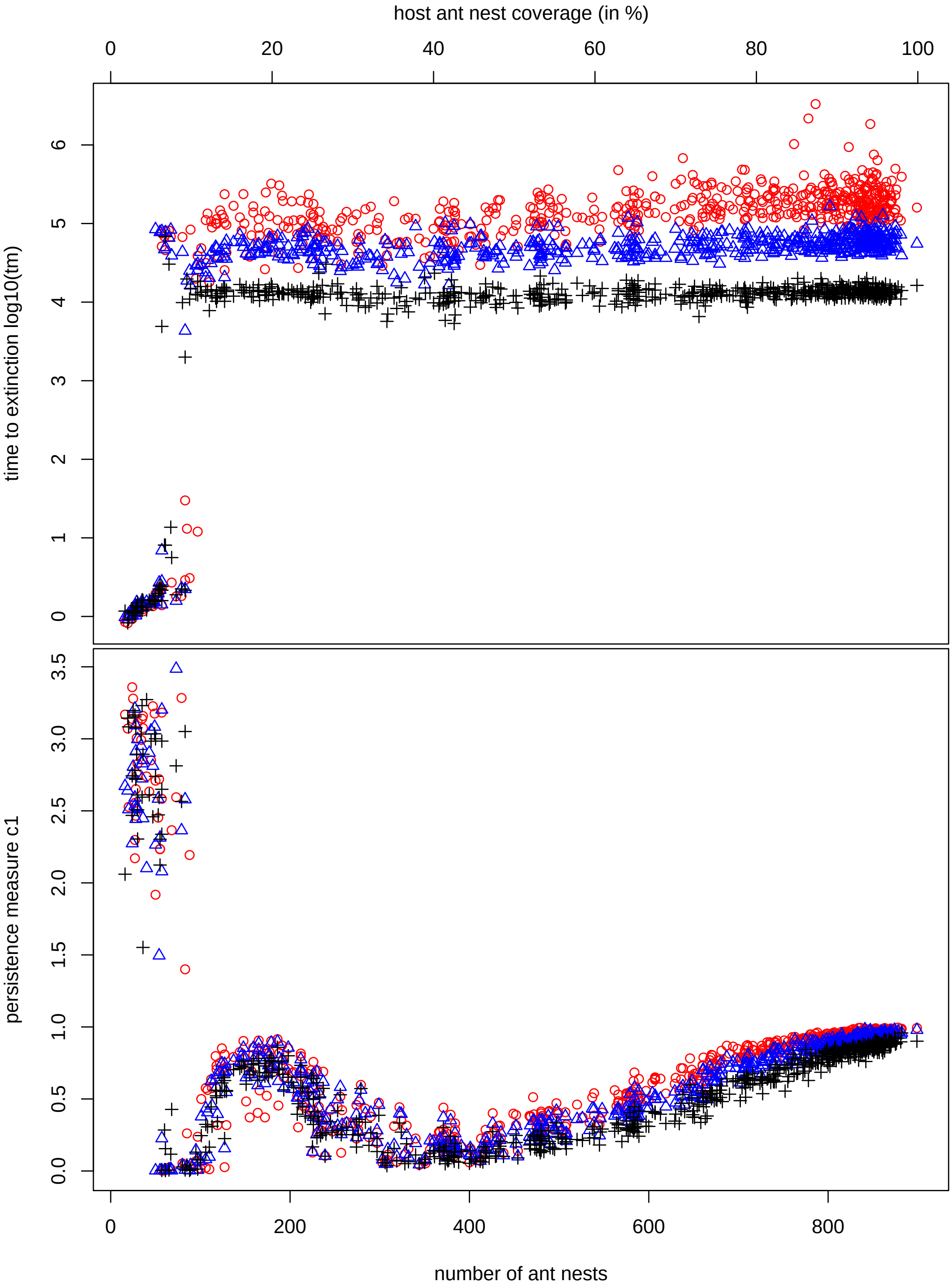

Figure 6.6: Variation of initial host ant distribution scenario group 3 (plants: plantsSG3; number of plants: 598, σ- Variation; circle: $\sigma = 4$, triangular: $\sigma = 8$, cross: $\sigma = 12$)

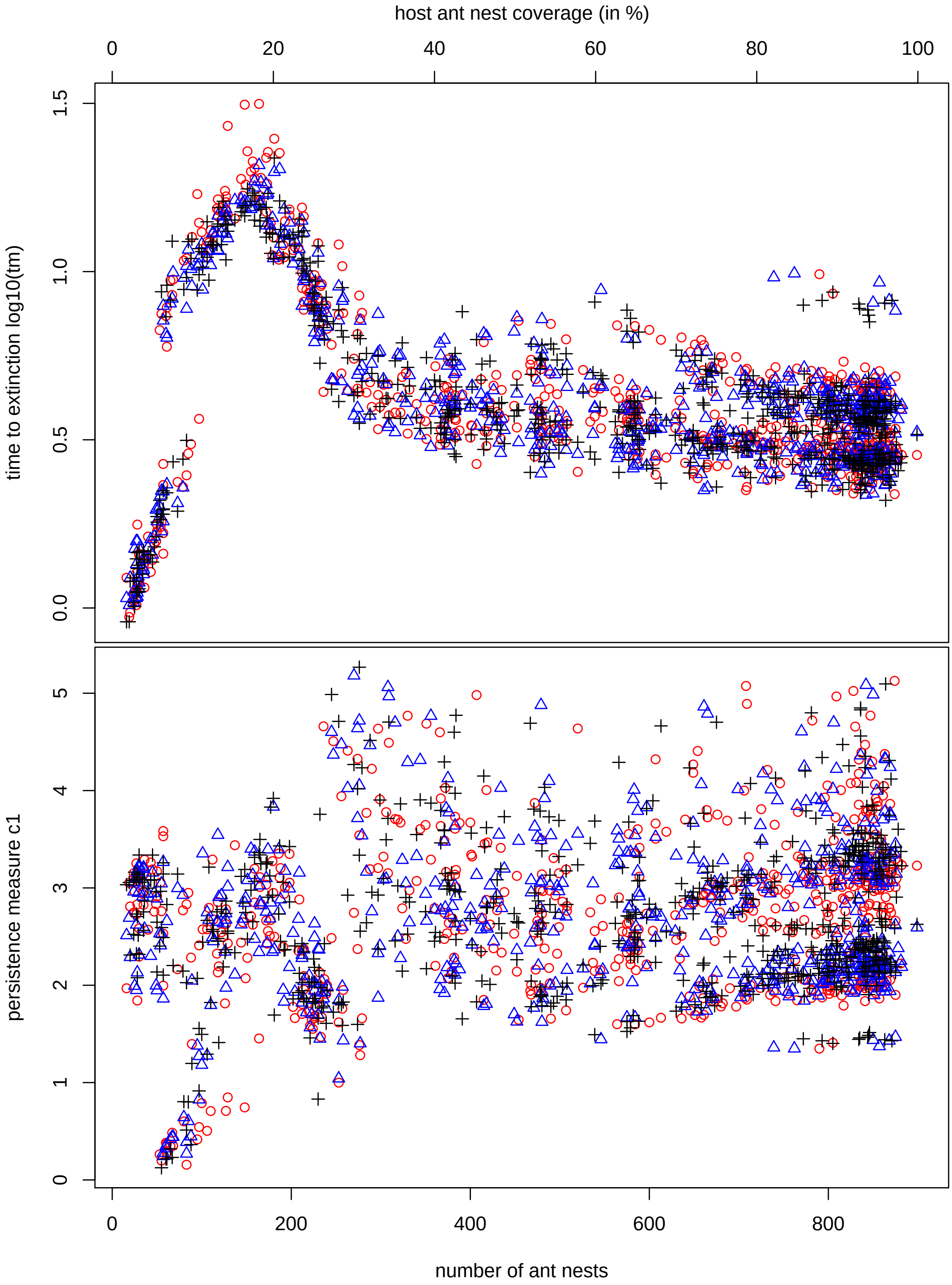

Figure 6.7: Variation of initial host ant distribution scenario group 4 (plants: plantsSG4; number of plants: 858, σ- Variation; circle: $\sigma = 4$, triangular: $\sigma = 8$, cross: $\sigma = 12$)

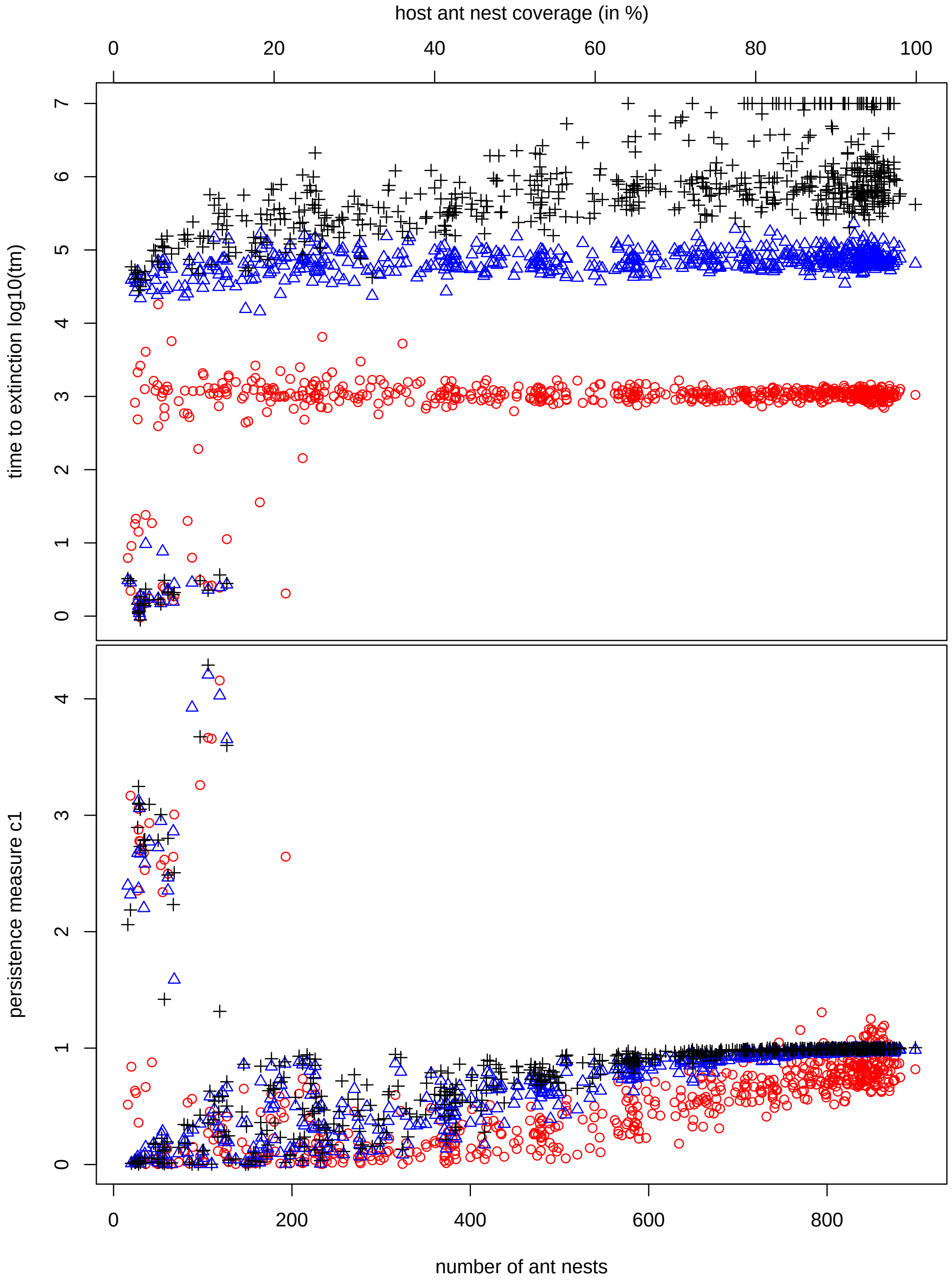

Figure 6.8: Variation of initial host ant distribution scenario group 5 (plants: plantsSG5; number of plants: 146, σ- Variation; circle: $\sigma = 4$, triangular: $\sigma = 8$, cross: $\sigma = 12$)

populations do not survive the initial transient phase (see sec. 6.3.2.1). For higher numbers of initial host ant nests, $t_m \approx \text{const}$ [4]. Most data variation can be explained from different budding ranges of host ants. Smaller dispersal ranges (σ small) result in higher intrinsic mean time to extinction t_m. It must be noticed that, with increasing σ, variation of t_m around a mean level declines.

Persistence measure c_1 reaches very high values for very low numbers of host ant nests (effect explained in sec. 6.3.2.1). For slightly higher numbers of initial Myrmica ant nests, c_1 sharply increases from $c_1 = 0$ to $c_1 = 1$. Afterwards, it drops, reaching a minimum at about 400 initial Myrmica nests and then increases up to values of almost $c_1 \approx 1$. For host ant nest numbers above 400 (after minimum in c_1), it can be seen that the higher the budding range parameter σ, the lower the persistence measure c_1. Shape of the curve in the lower graph of fig. 6.6 follows the described overexploitation-effect in sec. 6.3.2.2. But minimal values of c_1 are noticeably lower than in fig. 6.5. A strong artificial effect of initial extinction dynamics to t_m, like described in sec. 6.3.2.2, is not found for the scenario group of higher numbers of host plants[4].

Long-term persistence in this example is sufficiently high. But, it must be kept in mind that persistence of this scenario group depends extremely on host plant coverage and ranges from high chance of population persistence to high chance of population extinction (sec. 6.3.1.3). Initial Myrmica ant distribution affects vulnerability of populations during the initial phase. Because of different initial population dynamics, increasing initial ant nest number can lead to both augmentation and decline of early extinction risk. An important finding is that colonisation probability (surviving the initial phase) of Maculinea is sensitive to initial host ant nest numbers on the whole range. Budding range of host ants influences persistence during the initial and the established phase.

6.3.2.4 SG4 - Highest host plant coverage

Simulations with host plant distribution plantsSG4 (number of host plants: 858) are investigated representatively for this scenario group. Results are presented in fig. 6.7. t_m ranges from 0 to 1.5 for all ant nest distributions. c_1 varies from 0 to 5 (usually higher than 1). Such persistence measure values are restricted to situations with very low numbers of ant nests in other scenario groups (see sec. 6.3.2.1). Here, for this almost entire plant coverage, non-persistence (type III) is found for all host ant distributions. Hence, it can be deduced, that sites with high host plant coverage are unsuitable for Maculinea butterflies.

For about 100 ant nests, a maximum of t_m can be observed in fig. 6.7. It results from a delay of population extinction, because of favourable ant nest distributions. Contrasting to lower initial numbers of host ant nests, these favourable distributions ensure sufficient numbers of cells with ants and plants. But, their limited number of nests additionally avoids an immediately peaking butterfly population, which occurs for higher numbers of initial host ant nests. In sec. 6.3.1.4 it is described that the initial host ant distribution ants1 provides higher values of t_m than the other ant distributions: This can be explained from the fact that number of Myrmica nests for ants1 (#nests 217) is in the range of the observed peak in fig. 6.7.

An effect of budding range of Myrmica ants is not detected. This corresponds to the expecta-

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[4] t_m very slightly follows the shape of the curve of c_1, in particular for low values of σ. This results from inaccuracies in the PVA-procedure (see fig. 4.6 crosses). The linear fit to estimate measures of persistence is affected by single extinction events during the established state, because many populations might go extinct during the initial phase (c_1 is low) or survive until time horizon T_H

tion that dispersal on different scales should not change persistence strongly on homogeneously covered sites. Hence a globally dispersing parasite should not percept whether its host disperses further or shorter.
Concluding, it can be said that very high host plant density is unsuitable for Maculinea butterflies. Populations cannot persist. Favourable density of host ant nests can delay extinction of the Maculinea population for some generations.

6.3.2.5 SG5 - Intermediate plant density with decreased long term persistence

For data depicted in fig. 6.8, host plant distribution plantsSG5 is chosen as a representative. It consists of 146 plants, the same number as in plant distribution plantsSG2a (sec. 6.3.2.2), but has a different spatial pattern. Host plants in pattern plantsSG5 are much more clumped (see bottom of fig. 5.3).
For very low numbers of host ants, the effect of extinction during the initial phase is found, which is already described in sec. 6.3.2.1. In contrast to other scenario groups the effect can also occur for nest numbers up to 200 nests. In general, t_m does not depend on initial Myrmica nest density. This constance begins for lower nest numbers than in other scenario groups. But, dependence of intrinsic mean time to extinction t_m on Myrmica dispersal range is observed. For $\sigma = 4$m, $t_m \approx 1000$gen, whereas for $\sigma = 12$m, t_m is almost about 2 orders of magnitude higher. In a separate study (not shown here), we find that for $\sigma > 15$m, $t_m = t_{max} = 10^7$gen can be reached, depending on initial host ant distribution and the strength of the numerical artifact (see sec. 4.4.2) they provoke[4]. Note, the effect of varying budding range σ is reversed compared to effects observed in other scenario groups.
Measure of persistence c_1 tends to augment with increasing number of host ant nests up to saturation value $c_1 \approx 1$. Budding range of Myrmica ants influences c_1 positively up to a saturation. However, height of the saturation depends on the distribution of Myrmica ant nests. Although σ influences c_1 positively, the effect is not strong enough to compensate for bad initial conditions (data not shown here). Variance of c_1 is very high, especially for $\sigma = 4$ (circles).
For scenarios with few clumped host plants, it is not surprising that explicit initial host ant distribution and dispersal ability of ants have an impact on the initial performance of a Maculinea population. If, initially, ants and plants are mainly located in separate spatial areas, it takes some time until host ants will have dispersed towards host plants. During this phase, the butterfly population is vulnerable. In contrast, if initially ants and plants are situated more favourable, Maculinea butterflies do not suffer during the initial phase.
Long term persistence of Maculinea butterflies in scenarios of this group depend on budding range of host ants. We find in this example that, for high and intermediate values of σ, Maculinea populations persist, whereas for $\sigma = 4$ the population is vulnerable. An additional effect on probability of extinction during the initial phase is found. Especially, when Myrmica ants have a locally restricted budding range, early extinction is a considerable factor up to 600 initial host nests. This finding demonstrates that host ant dispersal can be crucially important for colonisation success of Maculinea, e.g. after catastrophes like an inundation, during which an ant population has been destroyed.
Strong dependence of persistence on dispersal abilities of host ants indicates that spatial structures of host distributions can strongly influence Maculinea fate.

6.4 Discussion

6.4.1 Spatial analysis on the Maculinea system

Analysing effects of spatial patterns on population dynamics is a difficult task for several reasons. First, previously, it is not clear at all, which kind of patterns might be relevant for the ecological process (Grimm et al., 2005). Second, spatial scale of ecological processes determines on which scale spatial objects are important (Perry et al., 2002; Wiegand & Moloney, 2004, and references therein). Third, there are many spatial indices, which quantify particular characteristics of point patterns. But, most indices are correlated with intensity and many are correlated among each other (Gustafson, 1998; Dale et al., 2002; Fahrig, 2003). Hence, it is difficult to reveal, which of the slight differences of measures are important. Fourth, the parameter space is large.

For these reasons, spatial analysis has to fulfill several requirements to be successful. It has to incorporate ecological processes. It flexibly has to incorporate different spatial scales. It has to measure differences between correlated patterns accurately. And finally many different spatial patterns have to be processed, for which results of the analysis need to be comparable (see ch. 5). In the following it is discussed how the spatial analysis of host distributions in the Maculinea system fulfills these requirements.

6.4.1.1 Incorporating ecological processes into the analysis

The assessment of spatial host distributions is based on their suitability for persistence of Maculinea populations. This is achieved by applying PVA on a rule based population model for Maculinea systems (ch. 1), which incorporates dynamics and processes of the system. The model, although generic, is related to a model for a case study (Hochberg et al., 1994; Clarke et al., 1997, 1998) and is therefore quite realistic. Using the generic model in this study we take advantage of its special design to emphasise effects of spatial host distributions and dynamics (sec. 1.3). With this model, we are able to incorporate all relevant ecological processes into the analysis.

6.4.1.2 Spatial scales of the system

Species in the system act on different scales. Myrmica host ant foraging range is restricted to a small scale, however, their dispersal range (budding process) is larger. Maculinea butterflies are not restricted in reaching host plants on the site. Additionally, host plant distribution introduces a further scale of spatial organisation. These different scales are considered and implemented in the Macu simulation model and thus can be assessed in the analysis.

6.4.1.3 Resolution in the evaluation of spatial patterns

In our analysis, the resolution, to which spatial patterns can be assessed, is limited by the accuracy of PVA estimations. In sec. 4.4 it is found that measures of persistence can be reliably estimated only for a small range of intrinsic mean times to extinction ($t_m \in [10^{3.5}\text{gen}; 10^{4.5}\text{gen}]$ [5]. For other values of t_m, both persistence measures can be inaccurate. However, it is argued in sec. 4.4 that we can trust the trend of a PVA, although exact values for the measures of persistence cannot be determined.

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[5] The range depends on the setting of PVA parameters. For PVA parameters in this study, see tab. 5.1.

From the knowledge on inaccuracy of the PVA results, there are two possibilities how to proceed with the analysis of effects of spatial host patterns. Either, accuracy is increased by performing more simulation runs with a longer time horizon, or inaccuracy is taken into account for further analysis. Assessing increased accuracy by applying the first possibility for several scenarios, we decided that this way is not practicable for reason of computer and time resources.

However, the second way is successful. To deal with the accepted inaccuracy, we transform the data. We categorise the continuous measures of persistence and host plant coverage by only five so called scenario groups. Data of each group can be characterised by unique properties. The suggested categorisation is rougher than numerical estimates of measures of persistence. For this reason, inaccuracy does not matter. In a similar way, we describe results from variation of initial distribution of host ants.

Obviously, the PVA method is too inaccurate to allow distinction of small effects of spatial patterns. But, general trends are revealed. The method is accurate enough to distinguish strong effects of spatial distributions (for e.g. it is shown, that clumping of host plants influences persistence of Maculinea). This accuracy is sufficient for analysing effects of spatial patterns on performance of species, because in general, for conservation neither data nor management methods are more accurate.

6.4.1.4 Completeness of spatial patterns and processes

In this analysis, suitability of 645 host plant distributions and 605 initial host ant distributions is assessed. The distributions are generated by different random processes and are clumped on different spatial scales (ch. 1). This set of scenarios is assumed to be large enough to represent the major part of possible distributions.

Many different reasons for vulnerability of Maculinea populations are found (sec. 6.4.2). We assume that spatial effects provoking extinction during the established phase are completely detected. On the one hand, strong influence of host plant density, on the other hand, no influence of initial host ant distribution, allow to separate effects of the three different parameters. Hence, the parameter space is strongly reduced and mostly scanned by our investigations.

In contrast, it is much more difficult to find reasons for extinction during the transient phase. Influence of all three parameters is strong. Hence parameter interaction can provoke qualitatively new effects. Anyhow, main processes should be grasped by our method. All effects mentioned in sec. 6.4.2 are found at least in variations of two parameters or for different scenario groups. Hence, these effects are double checked. It is unlikely that a probable further mechanism is not seen in one of these parameter variation experiments.

In our analysis, observed effects of explicit spatial structures of hosts on the risk of extinction during the initial phase are much smaller than for the risk during the established phase. Hence categorisation of data might hide further effects. However, the effort to achieve higher accuracy in data cannot be taken in this thesis. To our opinion, further effects would not relevantly (that is for purpose of species conservation) influence persistence of Maculinea.

6.4.1.5 What can be achieved with the spatial analysis?

From the sections above, it can be concluded, that the method of spatial analysis presented in ch. 5 can be successfully applied to analyse effects of spatial host distributions on persistence of Maculinea populations. The results give a broad and comprehensive overview on how different host plant coverage and host ant nest numbers affect Maculinea. In particular, we can deduce three kinds of results:

1. We find, whether the spatially implicit measure 'host plant coverage' is sufficient to predict persistence of the butterfly population. It is sufficient, if variance in measures of persistence is small for different host plant distributions of the same coverage.

2. The circumstances are determined, under which initial host ant distribution is an important factor for persistence of Maculinea.

3. Results of the analysis are derived separately for two different time scales - for an initial period of butterfly colonisation and for the phase, when a population has established.

These types of results are essential to analyse how the spatial host distributions affect dynamics of the Maculinea system (following sections) and to deduce recommendations for management of Maculinea sites (sec. 6.4.5).

6.4.2 Summary of effects

Our analysis was guided by the objective to collect spatial factors and processes, which affect persistence of Maculinea populations. Parameter interactions forced us to perform investigations for different scenario groups separately. Analysing one group at a time, we have tried to compile all important effects. Findings are explained in context of scenario groups.
Necessarily, this type of piecewise analysis is troublesome, when trying to get a broad overview. Therefore, to complete our investigations, we now change the emphasis and turn from scenario groups to effects. This change allows to elaborate circumstances for population extinction in terms of parameter constellations. In other words, we answer the question, how the parameters affect the processes and how they influence persistence of Maculinea.

6.4.2.1 Effects of spatial distributions during different temporal periods of system dynamics

Spatial parameters and processes are found to affect persistence differently during initial transient phase or established phase. Due to parasitism, Maculinea influences spatial distribution of its host ant and again affects its own dynamics. A similar result is found by Tobin & Bjornstad (2003) who have observed that the spatial distribution of a prey fly changed after introducing a predatory beetle.
For the Maculinea population we state that on one hand it depends on the parameters (host ant distribution) at each moment, on the other hand it changes these parameters continuously. Subject to system state, effects of parameters and processes change. This is an important finding, which implies that conditions of a site are differently suitable for colonising Maculinea butterflies or for an established population (sec. 4.5.2.2, sec. 6.4.5). For this reason, in the following we consider initial and established phase separately.

6.4.2.2 Effects of spatially induced processes on risk of extinction during the established state

Three main reasons can provoke high risk of extinction during the established state.

Few host plants: On a site with only few host plants (below ≈ 30), Maculinea populations are endangered. Slightly increasing number of host plants, improves conditions for the butterflies strongly.
A small number of host plants provides only few oviposition places for adult Maculinea butterflies. Their effective amount of suitable habitat on the site is small. It is widely observed that small habitats can only support small populations because capacity is small. In field observations on 13 sites and modelling studies, Elmes et al. (1996) find a linear dependence of numbers of observed Maculinea rebeli eggs and number of Gentians, when food plant density is below 1200-1600 gentians per ha (see comparison of HCET and Macu model in ch. 2). Equally for Maculinea rebeli, Kery et al. (2001) show, a positive relation of host plants (Gentiana cruciata) and population size as well as persistence of Maculinea rebeli populations on sites with low densities of Gentiana cruciata.

High plant density: When plant density is high on a site, Maculinea eggs are distributed widespread. Many host ant nests can be affected by parasitism. Only few nests are save in areas without host plants.
Assume a large population of Myrmica ants. Maculinea caterpillars will exploit this large resource almost entirely. Therefore, nests in vicinity of host plants will go extinct. Suddenly, the butterfly population must cope with a shortage of resource. It will decline until extinct nests are replaced by budding from nests, which are not in vicinity of host plants. The process is explained in more detail in ch. 7 and 8.
This overexploitation effect provokes extinction in scenarios of group 3 and 4. (sec. 4.5.2.1).

Unfavourable host plant configuration and small host ant budding range: SG5 comprises host plant patterns with high clumping. It is found that small dispersal range leads to high risk of extinction in this scenario group (sec. 6.3.2.5). Similarly, Clarke et al. (1998) find an effect of host plant clumping on Maculinea rebeli population size. For a detailed discussion refer to sec. 2.4.2. In ch. 7, effects of spatial host plant patterns on Maculinea butterflies are investigated in detail.

Spatial parameters are ranked according to the strength of their influence on Maculinea persistence. Host plant density mainly drives persistence of Maculinea butterflies. But, to a certain extent, explicit spatial host plant patterns vary viability of Maculinea. Especially on habitats with inhomogeneous plant distributions, Myrmica budding range is an important factor. In contrast, longterm viability is insensitive to changes in the initial Myrmica distribution.
As mentioned already in ch. 4, variation of spatial factors can drive Maculinea viability from extinction (type III) to persistence (type I). Resuming results for different scenario groups, it is found that intuitive classification corresponds to these persistence types (see tab. 6.1). Hence, it is clear that although plant densities are similar, distinction of persistence types requires separation of SG2 and SG5.

6.4.2.3 Effects of spatially induced processes on risk of extinction during the transient phase

Risk of extinction during the transient phase of population dynamics is determined by different processes. Effects of these processes are common to several scenario groups. This is not surprising. Groups are classified according to the influence of host plant distributions on longterm persistence. Effects provoked during the initial phase can be independent of those found

during the established phase.
High initial risk of extinction for Maculinea populations is provoked from the following factors:

Too few Myrmica host ants: On sites with a very small number of initially distributed host ant nests, risk of extinction is extremely high for Maculinea butterflies. Initial vulnerability might even totally imped establishment of populations. This effect is independent of host plant distribution or Myrmica budding range.
High extinction risk of Maculinea populations reflects two search problems. First, assume few host plants on the site. Hence, Myrmica nests are located in vicinity of host plants with only a small probability. But, the constellation of neighbouring nests and plants is essential for Maculinea to reproduce. The amount of suitable habitat is too low. In the second case, host plant density is high. The few Myrmica nests are located close to host plants with high probability. But, chance is low that adult Maculinea select plants with nests, from the large host plant pool. Host eggs are lost after oviposition.

Few host plants and few Myrmica host ant nests: As explained before, the probability is low that both spatial distributions of host plants and host ants fit to each other. Hence, the amount of suitable habitat is low.
In contrast to the case before, few numbers of host plants do not endanger Maculinea populations, when abundance of Myrmica ants is high enough (lower graph in fig. 6.3). The reason is found in the way, adult Maculinea butterflies perceive a site. Butterflies restrict oviposition to host plants. Myrmica abundance is high. Thus, ant nests are situated in vicinity of plants and can adopt caterpillars. Hence, when ant nest number is high enough, Maculinea finds only suitable habitat.

Intermediate to high host plant density and intermediate host ant number: This constellation provokes overexploitation of Myrmica ants by Maculinea butterflies and is an important reason for extinction during the initial phase. The process is explained in sec. 6.3.2.2. Overexploitation is a reason for extinction of Maculinea butterflies for established populations, too (sec. 6.4.2.2). But, there is an important difference between both processes. If the system is established, spatial distribution of Myrmica host ants is adapted to the spatial pattern of parasitism (see ch. 7). In particular, host ant nests occupy most area, which is far away from host plants and therefore is not affected by parasitism. Hence, destroyed host ant nests can be effectively substituted from save Myrmica host nests.
If Maculinea butterflies overexploit Myrmica during the initial phase, nest distribution is not yet adapted. Hence, efficiency to recover parasitised ant nests is reduced. For high numbers of initial host ant nests, this efficiency is augmented, because more ant nests are available. Highest risk of extinction due to the overexploitation effect occurs for intermediate Myrmica host ant density.
In fig. 6.1b, increased initial risk of extinction because of overexploitation can be observed for host plant numbers above 450 specimen. Strongest effect is found for the initial Myrmica distribution ants2 with an intermediate number of 483 nests.

Unfavourable host ant distribution, short-range budding: Unfavourable host ant distribution in combination with host ant budding on a short range, increase risk of extinction for Maculinea butterflies during the initial phase. High numbers of host ant nests are required to compensate the negative effect.

During the initial phase, initial Myrmica host ant nest density plays a crucial role. It determines suitability of host plants. Plants with a neighbouring host ant nest provide resource for Maculinea reproduction. Without Myrmica host ant nests, host plants are sinks. Our result is influenced by the assumption that adult Maculinea butterflies perceive their habitat only via host plants. Hence, they cannot adapt to host ant distribution (see Hochberg et al. (1994), but vanDyck et al. (2000); Wynhoff et al. (2001)). Host ant budding range σ is of minor relevance.

6.4.3 Hypothesis

We are now able to evaluate the hypothesis raised in the introduction of this chapter (sec. 6.1). It was hypothesised that the initial Myrmica host ant distribution is not relevant for persistence of Maculinea butterflies during the established state (H1). Results confirm this statement. Only in the case, when initial conditions imped the system to survive the transient state, initial host ant distribution affects long-term persistence.

Influence of host plants and Myrmica dispersal range on survival of Maculinea during the established phase is found, according to hypothesis H1. Additionally, it can be stated that host plant density is the most important factor. Dispersal range of host ants has strong effects, when host plant distribution is inhomogeneous.

Persistence of Maculinea populations during the initial phase depends on all three factors, as predicted by hypothesis H2. Occurrence of spatially induced effects is influenced by interactions of parameters.

6.4.4 Population dynamical processes provoking high risk of extinction

Fig. 6.9 shows population sizes and their relation to long-term persistence of Maculinea populations. The population sizes are compiled from the same experiments as measures of persistence in fig. 6.1a. Statistics on the population sizes is calculated according to the protocol described in sec. 2.2. Data from experiments with different initial host ant distributions is clumped together, because long-term behaviour is not influenced by this factor. Fig. 6.9a depicts dependency of mean Maculinea population size on the number of host plants. Different symbols indicate scenario groups. As expected, the shape of the curve corresponds to the shape in fig. 2.2a.

Comparing graph 6.9a and fig. 6.1a, it is learned that for small numbers of butterflies, both mean population size and intrinsic mean time to extinction increase. A threshold in population size ($\approx$ 50 individuals) indicates transition to SG2 (triangles), that is persistence. Hence, persistence of Maculinea butterflies depends on a critical population size, when number of host plants is low. In contrast, for numbers of plants above 500, although mean Maculinea population size is high, the intrinsic mean time to extinction t_m declines (SG3). High variance in mean population size, can be explained partly from the influence of long transient phases (a dependency on initial conditions is found). But stronger effect results from large amplitudes in population cycles (see ch. 2.3.1).

Therefore, in the following, effects of temporal population fluctuations are discussed. Fig. 6.9b, shows correlation between the intrinsic mean time to extinction t_m and the coefficient of variation of population sizes (CV). $\mathrm{CV}(x) = \frac{\mathrm{s}(x)}{\overline{x}}$, where $\mathrm{s}(x)$ denotes the standard deviation and

$\overline{x}$ is the mean value of x [6]. CV is a measure for fluctuation originating either from stochastic or from deterministic variation. In fig. 6.9b it is found for SG3 (crosses +), that increase of t_m means declining CV. That is, strong variation in data leads to high risk of extinction. Fluctuations mainly result from deterministic predator-prey cycles (see ch. 2). Hence, although mean number of butterflies is high, temporal cycles strongly increase and decline population size. Demographic stochasticity affects the population for low numbers of individuals and might lead to extinction (see ch. 3 and ch. 4). Mean number of butterflies is misleading when assessing persistence. The concept of minimum viable populations (MVP; Shaffer (1981)) cannot be applied to the Maculinea system, as the butterfly population only temporarily drops below a critical threshold. This is typical for systems with overexploitation (Abrams, 2002).

Returning to SG1 (circles). As before, increasing mean time to extinction goes together with a decline in variance. But, although extinction risk is comparably high, CV values of SG1 are smaller than those for SG3. Low risk of extinction is even possible, for values of CV below those of SG2 (persistent populations). Why are systems of SG1 vulnerable? The reason is easily seen in fig. 6.9a: census data indicates a low mean number of butterflies of only few individuals. Hence demographic extinction is not necessarily restricted only to minima in temporal variation. Generally, population size is low and therefore affected by demographic stochasticity.

Hence, fig. 6.9 illustrates that extinction of Maculinea butterflies is driven by two different processes: small mean population size due to low numbers of host plants or overexploitation of Myrmica ants due to high numbers of host plants.

Remarkably, SG5 (diamonds) cannot be attributed to one of both processes. CV values lie in between. Mean numbers of butterflies although slightly below the values of persistent group SG2, are higher than values of SG1. In ch. 7 it is argued, that clumping of host plants on sites with low numbers of host plants invokes Maculinea butterflies to be affected by both reasons.

6.4.5 Conservation aspects

Results presented in this section show that host plant distribution has a strong impact on persistence of Maculinea butterflies, especially during the established phase. In ch. 5, it is argued that with the applied method, suitability of habitat can be measured in terms of t_m. For these reasons, host plant distribution should be taken into account as an important factor for habitat quality. From a point of view of adult butterfly behaviour, these plants represent suitable habitat, at least for oviposition and early larval stages. In contrast, initial Myrmica host ant distribution does not affect suitability, provided that a least number of host ants is present.

6.4.5.1 Critical densities of host plants to support Maculinea populations

Discussing host plant distribution in terms of habitat quality, allows to check which are least conditions that Maculinea populations can persist. Critical are scenarios with either low or high numbers of host plants. Additionally, extinction during colonisation of a new site must be considered. It is an important factor for landscape management.

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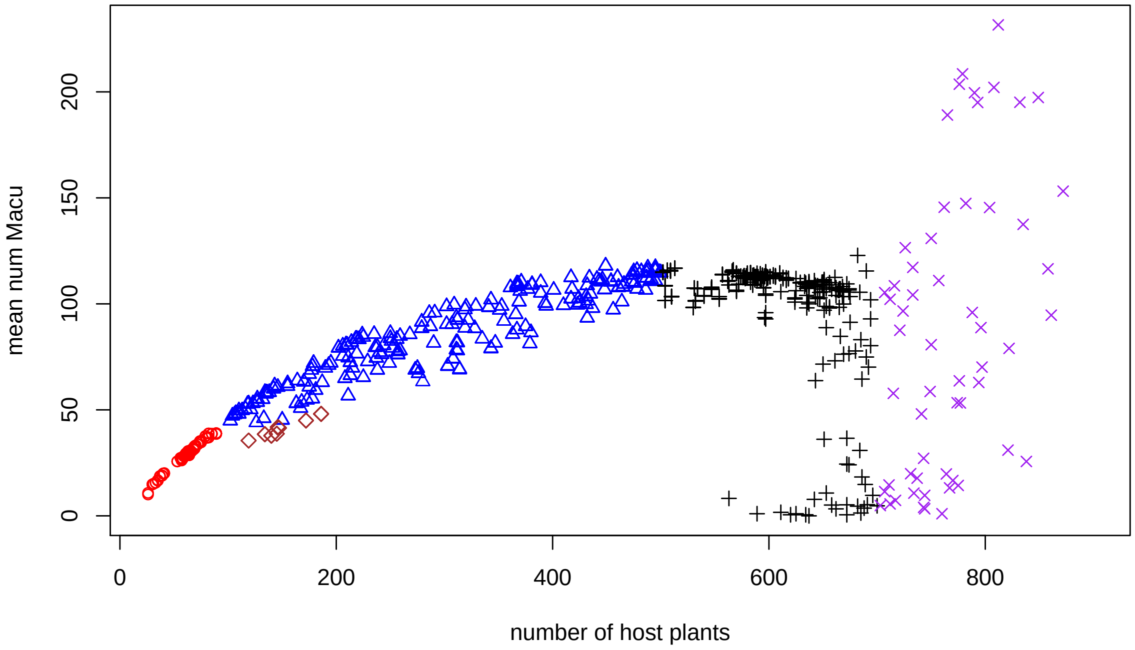
[6] In this context, usage of CV is critical because census data is far from being normally distributed. Hence, distribution of data points cannot be modelled correctly. However, as CV is a non-robust measure, CV is influenced by strong amplitudes, which are essential for persistence. Therefore, CV is suitable to analyse risk of extinction due to high data variation

(a)



(b)

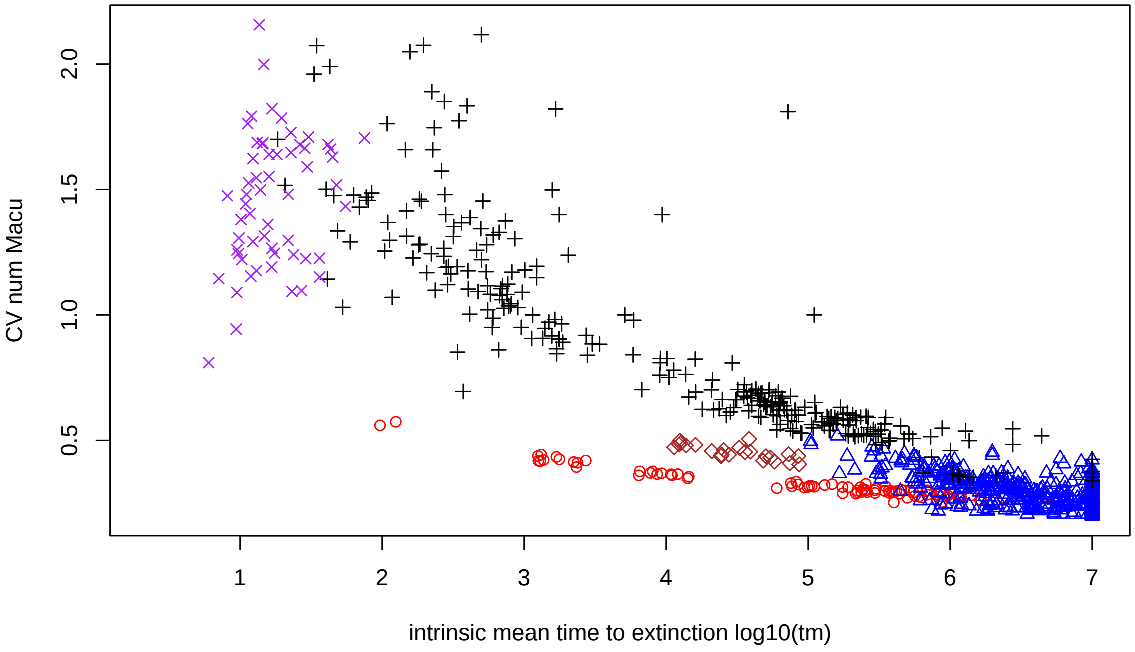


Figure 6.9: Number of Maculinea butterflies is compared to persistence of Maculinea populations. In graph. (a) dependency of mean Maculinea population size on number of host plants is depicted. Fig. (b) compares the coefficient of variation of Maculinea population size with intrinsic mean time to extinction. Different symbols correspond to scenario groups: SG1 - circles, SG2 - triangles, SG3 - crosses (+), SG4 - crosses (x), SG5 - diamonds. Statistics on census data is calculated following the protocol in sec. 2.2

Minimum host plant density to support Maculinea butterflies Too few host plants are risky for Maculinea populations, because they restrict the amount of suitable habitat. Surprisingly, for long-term persistence, this restriction is not critical. Very low numbers of plants can support Maculinea butterflies. See for example fig. 6.3 (top), which results from a scenario with only 39 plants. Intrinsic mean time to extinction is in the order of $t_m \approx 10^4$, which corresponds to an extinction risk of approximately 1% within 100 years. A comprehensive study on sites in the natural reserve Moerputten (the Netherlands) was performed by Wynhoff (2001). She found Maculinea nausithous populations on sites with not more than 30 host plants (Sanguisorba officinalis) with about 50 flowerheads per plant. Results of a model for Maculinea arion, based on field observations, indicate that low densities of host plants are sufficient to support the Large Blue Butterfly (Griebeler & Seitz, 2002). Glinka et al. (2004) mention the existence of small populations of Maculinea nausithous and teleius along streets or ditches.

In fig. 6.3 (bottom) is demonstrated that extinction during the initial transient phase after colonisation of a site, can be the crucial factor to imped population persistence. Establishment is only save for high numbers of initial host ant nests.

Maximum host plant density to support Maculinea butterflies Overexploitation of Myrmica host ants endangers Maculinea populations in case of too many host plants. First, a bottleneck effect during the colonisation period can extinct butterfly populations. This effect depends on the joint initial distribution of host plants, host ants and their budding range. Wynhoff (2001) suspected overexploitation after reintroduction as one reason for a strong decline in population size of a population of Maculinea teleius: The site was highly occupied by host plant Sanguisorba officinalis (15 plants per m^2 with on average 30 flowerheads). Cooccurring with low number of butterflies, Myrmica host ant density was comparatively high (0.4 - 1.3 nests/m^2) in contrast to all other sites in the natural reserve (0 - 0.6 nests/m^2).

Second, long-term persistence strongly declines with increasing host plant density. Too high densities make a site completely unsuitable. There are several anecdotal reports that Maculinea butterflies are not found in the middle of meadows with high density of host plants. They prefer to occupy boarder range of such meadows or sites with only few plants (Tagfalter-Workshop Leipzig 2003, pers. comm.). Clarke et al. (1998) find that the number of Maculinea rebeli declines, when 1000 host plants are added to a 1 ha site containing 1700 Gentiana cruciata plants (see fig. 2.9).

6.4.5.2 Rules of thumb

The Maculinea model presented in ch. 1 and used in this investigation is not close enough to natural conditions to predict exact threshold densities for host plants. Exemplary variation of model parameters describing species traits, immediately shows that quantitative results are not robust. However qualitatively, findings should be relevant for Maculinea systems. Therefore it is useful to restrict on qualitative results. We formulate them as rules of thumb:

- Maculinea habitat sites should not contain too less host plants, although low numbers of host plants can support small Maculinea populations surprisingly well.

- For introduction of Maculinea to sites with low host plant density, high density of Myrmica host ants is necessary.

- Sites with dense host plant coverage are unsuitable for Maculinea butterflies.

6.5 Summary

This chapter is the central part of the thesis. Different threads are brought together in order to investigate, how spatial host distributions influence persistence of Maculinea butterflies. The complete methodological framework developed throughout the thesis is applied. That is, simulation model (ch. 1), $\ln(1-P_0)$-PVA-approach (ch. 3) and assessment of spatial host distributions by means of viability of Maculinea populations (ch. 5). This hierarchical approach leads to highly aggregated information on Maculinea population dynamics. On the one hand, results give complete overview on the influence of spatial host distributions to Maculina persistence. On the other hand, the aggregated data incorporate methodological inaccuracy, different population dynamical processes and complex parameter interaction of up to 900 dimensional spatial objects. Hence, interpretation of data requires a manifold of background information. This is provided by comprehensive analysis of methodological difficulties (ch. 1, ch. 3, ch. 4, ch. 5) and non-spatial investigations on Maculinea population dynamics (ch. 2) as well as extinction dynamics (ch. 4).
Main results are compiled in a short list:

- Host plant distribution is an important factor of habitat quality for Maculinea sites.
- Both scenarios of too many or too few host plants provide high risk of extinction to Maculinea populations. Few host plants are negative, because the amount of suitable habitat is reduced. Dense host plant coverage provokes Maculinea to overexploit its host ant resource. Host-parasite cycles have large amplitudes.
- Too low initial density of Myrica host ants impedes Maculinea populations to establish on a new site.
- During the established state of the system, Myrmica host ant distribution is spatiotemporally adapted to parasitism. Initial host ant distribution is irrelevant.

Chapter 7

Analysis of spatiotemporal population dynamics of the Maculinea system to derive a spatial index

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7.1 Introduction

In the last chapters, it was investigated, how host plant distribution affects persistence of Maculinea populations. It has been found that the aggregated measure 'coverage of host plants' is an important factor for survival of Maculinea populations. However, in certain cases, it could be shown that patterns of host plant distribution and budding range σ of Myrmica host ants have a remarkable effect on persistence of Maculinea populations. Factors like host plant distribution or budding range affect interaction of parasitic Maculinea butterflies and Myrmica host ants only locally, not globally on the complete site. Hence, if these locally acting factors influence persistence of the whole system, it must be assumed that local processes play an important role for the behaviour of the complete system. Local processes need to be taken into account when trying to understand Maculinea systems.

For this reason, in this chapter, we analyse spatiotemporal population dynamics of the Maculinea system on highest resolution - that is, we observe local processes of species movement and species interaction (see ch. 1.3.5.5). Here, we need to cope with a problem, which was avoided in analysis of earlier chapters, because we used highly aggregated measures like e.g. intrinsic mean time to extinction t_m to quantify population dynamics. Now, we are forced to consider full spatiotemporal population dynamics, which are represented by time series on multi-dimensional spatial distributions of host ants. Each time series is a realisation of the stochastic spatial host-parasite process of the Maculinea system.

In fig. 2.5, only a short part of such a time series is displayed. Anyhow, already the few maps in this figure contain large amounts of information. Processing and categorising this data is a demanding task for the researcher. Extensive, specially designed methods for the analysis of stochastic spatiotemporal population dynamics have to be developed. In the literature, there are few examples, where analysis of spatiotemporal dynamics of an ecological process are performed successfully (e.g. Donalson & Nisbet, 1999; Pascual et al., 2001)

These examples restrict to analyse only few scenarios of different landscapes. However, in our study, we aim to compare Maculinea systems on many different sites with different spatial arrangements. Like in chapters 2, 4 and 6 we want to analyse dynamics, which result from different host plant distribution and different host ant behaviour.

Such an investigation can only be performed, when one restricts to a concrete problem. Here, restriction is given by the general question of this thesis: How do spatial distributions of host plants and host ants influence persistence of Maculinea populations in the established state[1]? Focusing on the question, we can profit from results in earlier chapters, to simplify the investigations.

- In sec. 6.3.2 it is found that intrinsic mean time to extinction t_m in principle is not affected by an initial Myrmica host ant distribution, provided there is a least number of host ant nests (sec. 6.4.2.3). For this reason, we ignore initial distribution of host ants as an influencing factor for population dynamics during the established state.
- We restrict detailed spatiotemporal studies to representative examples (according to suggestions in sec. 5.4.3). As examples, we select scenarios, for which we can assume that persistence is strongly influenced by local dynamics. In concrete, we select host plant distributions, which contain an equal number of host plants. However, persistence of Maculinea varies depending on the selected host plant distribution.

Restricting the problem provides another important advantage. According to the general question, persistence is the decisive measure. We can use this measure to check findings of properties of local processes. If a property shows to be a relevant factor in the representative examples, it can be tested on other scenarios, whether it affects long term persistence in the suspected way (see sec. 6.4.2.3).

Final aim of the study is to develop a spatial index, which allows to measure properties of spatial host distributions, which relevantly influence persistence of Maculinea populations. Such an index can be used to assess suitability of spatial host distributions for Maculinea persistence on a habitat site and therefore is an important management tool for conservation of the species.

7.2 Analysis

Our aim is to investigate, how localised processes in the population dynamics of Maculinea butterflies and their Myrmica host ants influence persistence of the parasitic butterfly population. Analysing stochastic spatiotemporal dynamics on the level of single local processes is difficult due to the complex information of the data sets. It is in particular an unresolved problem, how to compare different realisations of the same or even of different stochastic processes (which are in our case dynamics resulting from simulations on different scenarios).

We try to cope with this task by concentrating analysis on extreme scenarios. For these example scenarios we know from earlier studies in ch. 6 that local dynamics strongly affect persistence of Maculinea butterflies. We think that it is easier to detect microscopic local processes when they provoke strong effects.

Once understanding dynamics of these extreme examples, we develop ideas about how dynamics of the system generally work. These ideas are tested on other scenarios.

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[1] Here, we restrict our analysis to the established state of the system. In principle, the methodology suggested in this chapter could be used to analyse transient dynamics of the system, too. For this case, we would expect further interesting results. However such an investigation is beyond the frame of this thesis

Table 7.1: Host plant patterns used in analysis of spatiotemporal dynamics.

Host plant pattern	# plants	t_m in gen$^+$		
		$\sigma = 4m$	$\sigma = 8m$	$\sigma = 12m$
plantsSG5	146	1276	86576	927310
plantsSG2a	146	10^7	10^7	10^7
plantsSG1	39	12285	6519	4342
plantsSG3a	597	294782	161848	26869
plantsSG3b	597	2177	3018	1548
plantsSG3c	597	366	540	555

Patterns with identical plant density are grouped together.
$^+$ Intrinsic mean time to extinction t_m is calculated for initial host ant distribution ants3.

Organisation of the analysis needs to go stepwise. We take this natural coarse into account by describing steps sequentially. In this way, methods, results and interpretation of each step can be explained in the context of earlier results.

7.2.1 Selection of scenarios

We select scenarios, for which we have found that local dynamics strongly influence persistence of Maculinea butterfly populations. We follow the idea of sec. 5.4.3. In fig. 5.3 it is demonstrated that simulations with two different host plant distributions can result in strongly varying extinction dynamics of the butterfly population, although host plant coverage in the two distributions is equal. It is argued that the explicit spatial structure of the host plant distributions influences dynamics of the system. Hence, local interactions and processes play an important role. From results in ch. 6 we especially select these scenarios (defined by host plant distribution and budding range σ), for which PVA results in strongly varying intrinsic mean time to extinction t_m, although host plant coverage is equal. Selected scenarios comprise a wide range of plant coverage and mean time to extinction. The scenarios are listed in tab. 7.1. It can be seen that, for some scenarios, intrinsic mean time to extinction t_m is varying, although number of host plants is equal. We take this set of scenarios as basis for the following analysis of spatiotemporal dynamics.

7.2.2 Simulations

For each scenario, we simulate population dynamics of the Maculinea system. We track number of host ants per cell and the total number of butterflies in each simulation step (Compiler option *ant* see sec. 1.3.5.5). We use the standard parameter set (tab. 1.1). Initial host ant distribution is ants4. This host ant distribution contains 899 nests (only one corner cell initially does not contain an ant nest). We choose this high initial host ant coverage, because results from sec. 6.3.2 indicate that Maculinea populations reach the established state with highest probability, if initial number of host ants is highest. We analyse only one realisation of the stochastic process for each scenario. The simulation procedure is repeated until butterfly population at least survives for 350 generations. Maximum number of generations in a run is limited to 5000.

7.2.3 Time series of numbers of Myrmica ants within cells

We analyse the number of Myrmica host ants within the individual cells for each time step. Fig. 7.1 shows four typical time series. Upper two graphs belong to cells with host plants, lower two graphs result from cells without host plants.

In the upper two graphs (cells with host plants), the number of host ants varies between 0 and 8 caterpillar equivalents. 0 ants mean that there is no ant nest. In lower graphs (cells without host plants), host ant number ranges from 4 to 10.8 caterpillar equivalents. Hence, these cells are always occupied by host ants. Nests are likely to reach maximum size of 10.8 caterpillar equivalents, which is the capacity of ants per nest in absence of Maculinea (see eqn. 1.5). The observation corresponds to our expectation that Maculinea butterflies have a stronger negative influence on their host ants in cells, where the butterfly caterpillars are adopted by worker ants to the nest and can exploit - direct parasitism only takes place in cells with host ants and host plants.

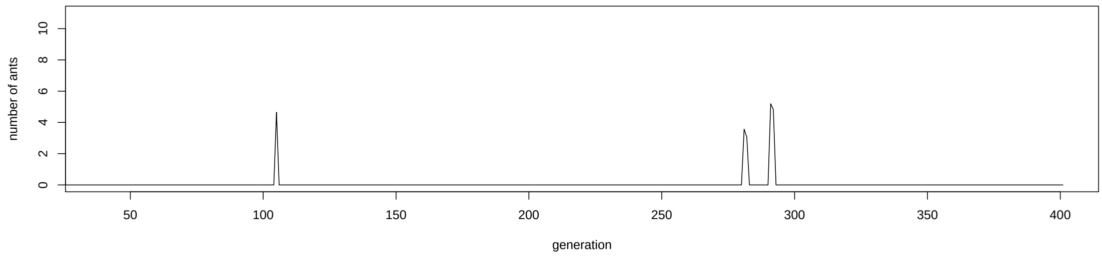
Number of ants displayed in fig. 7.1a shows that the cell is seldom occupied by host ants. Once a nest can establish (number of host ants > 0), it vanishes shortly afterwards. It must be remarked, that established nests have at least a nest size of 4 caterpillar equivalents. Time series in fig. 7.1b shows that the cell is frequently occupied by host ants. However, although peaks are broader than in fig. 7.1a, it seems that ant nests cannot establish for long time in the cell. They vanish after several generations. Host ant number in fig. 7.1c frequently drops steeply, but afterwards it recovers. Hence, nests do not go extinct. Finally, ant nest number in fig. 7.1d does not change and stays equal to nest capacity.

Although for total number of butterflies or total number of host ants, periodic behaviour is observed (see sec. 2.3), periodic cycles are not found for number of ants in single cells. Variation seems to be driven by stochastic events. This is an effect of global synchronisation (e.g. Bjornstad et al., 1999; Bonsall & Hastings, 2004, and references therein) provoked by Maculinea predation, which is affected by dynamics of Myrmica ants on a smaller scale. Pascual et al. (2001) stated a dependence on the spatial scale for predator-prey dynamics.

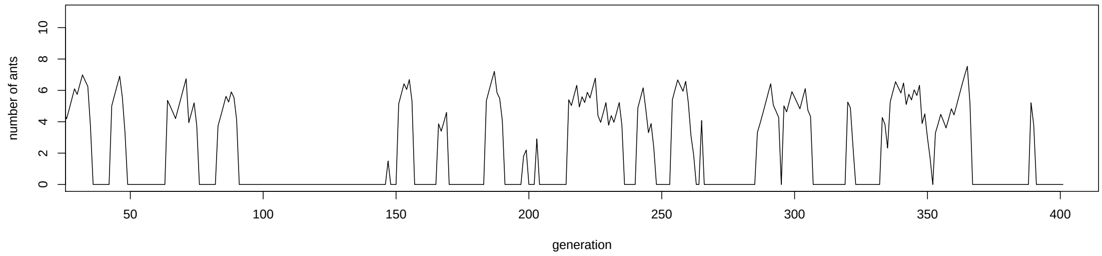
We now have a closer look to the shape of curves in fig. 7.1. It is striking that peaks in graph 7.1b steeply build up or drop down within only one generation. However, in between, number of ants only slightly varies. Hence, we can conclude that creation or destruction of an ant nest have stronger effects to number of ants than other processes, which affect an existing ant nest. The strong increase in number of ants at the beginning of a peak is provoked by colonisation of an empty cell. Colonisation via budding is the only process, which leads to creation of a new nest (see sec. 1.3). The sharp decline of ant number at the end of a peak is due to the loss of ants, when a nest goes extinct (see sec. 1.3.2.5). Hence small peaks in graph 7.1a indicate that an ant nest after being established immediately goes extinct. Shape of the curve in fig. 7.1c is different from the shape in graphs above. It steeply declines to recover afterwards. From model description in sec. 1.3 it is clear that the budding process provokes the decline in numbers of ants. It is the only process, which can reduce host ant number of large nests in cells without host plants. The steepness of drops in time series graph 7.1c to about one half of the original nest size verifies this assumption (compare sec. 1.3.2.5). Recovery of the ant nest after a budding event is driven by logistic growth (e.q. 1.4). In contrast, constancy of number of host ants in fig. 7.1d indicates that the ant nest does not bud any empty cells.

Local processes of the simulation model result in typical shapes of time series on host ant

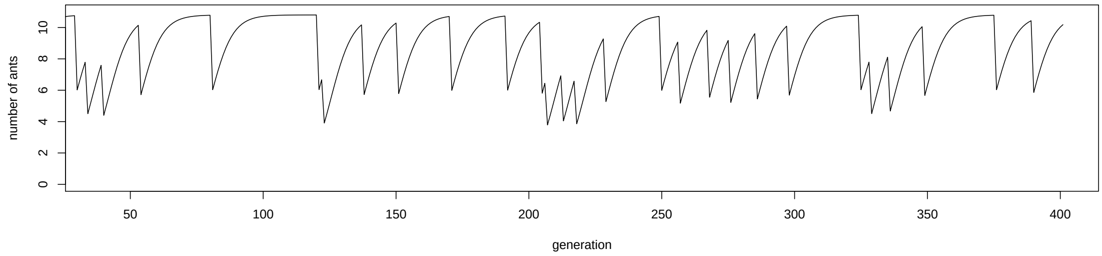
(a) sink cell



(b) reproductive cell



(c) buffer cell



(d) non-contributing cell

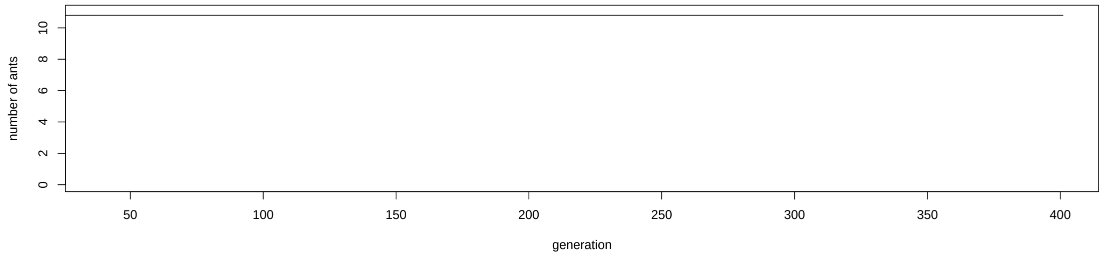


Figure 7.1: Temporal development of host ant numbers within one cell. A typical example is shown for each of the four cell effectiveness classes. In reproductive cells (graph (b)) and buffer cells (graph (c)), host ant number is strongly varying, whereas, in sink cells (graph (a)) and in non-contributing cells (graph (d)), number of host ants is constant, except for single short events. Ant number is measured in caterpillar equivalents.

number within a cell. Vice versa, if a time series of ant numbers in a cell has a certain shape, we can argue, which processes mainly drive ant dynamics in the cell. For this reason, it is worth to analyse the type of time series (respectively the type of ant dynamics) we find for different cells.

7.2.4 Quantification of properties of time series

Time series in fig. 7.1 show four types of qualitatively different behaviours. Other time series share to a certain extent characteristics of these four types. It is useful to measure the type of a time series quantitatively.

The two top graphs in fig. 7.2 show, how quantitative characteristics of time series on ant number in a cell are determined. First, we skip 100 simulation steps at the beginning of each run to avoid effects of initial conditions. Second, data points from the time series are aggregated temporarily. The histogram in the middle graph of fig. 7.2 displays the relative frequency of finding a certain number of ants in the cell. Width of each class in the histogram is 1 caterpillar equivalent. This corresponds to the butterfly rearing mechanism in host ant nests (eq. 1.1). Third, from the histogram, two values are determined:

relative frequency of main mode f_{ant}: The main mode of the distribution is the number of ants, which most frequently occurs. In the middle graph of fig. 7.2, most often, there are no ants in the cell. As measure f_{ant}, we use the relative frequency of this main mode ($f_{ant} = 0.6$ in the example). This value indicates how often the number of ants can be found in its most probable value. In the example, during 60% of the time, the number of host ants is equal. Hence, the described value measures constancy of host ant number in a cell. We denote this measure by f_{ant}.

The relative frequency of the main mode[2] f_{ant} accounts for the occurrence of peaks or drops. A time series with only few peaks like in graph 7.1a frequently assumes the same value. Hence, f_{ant} assumes values close to 1. In contrast, a frequently changing time series (like that in graph 7.1b) will be evaluated by lower values of f_{ant} [3].

In section 7.2.3 strong changes of host ant number in a cell are shown to be provoked by either budding or nest destruction. In cells with frequent changes of host ant number, these processes often occur (time series like in graphs 7.1b or 7.1c). Hence, we can detect occurrence of nest colonisation and destruction by measuring f_{ant}. $f_{ant} \approx 1$ indicates that these processes hardly happen. f_{ant} decreases with increasing number of colonisation or extinction processes.

mean number of host ants: We calculate the average number of host ants over time. Time series 7.1c and 7.1d will result in a higher mean number of host ants, than the two other time series of fig. 7.1. Highest mean values are usually measured in cells without host plants.

The temporal mean of number of host ants in a cell indicates the mean potential power

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[2] f_{ant} is related to the information contained in a time series, as it measures the probability to predict a certain value (Fath et al., 2003).

[3] Why don't we use a standard measure such as variance? The reason is that we aim to quantify constance of the number of ants in a cell. Variance determines deviation of values from the mean. In this sense, small variance would indicate that the mean value is frequently assumed. However, to asses constance of the distribution in graph 7.1b, variance is obviously not the right measure. In this case, we are neither interested in the concentration of values around the mean, nor how data deviates.

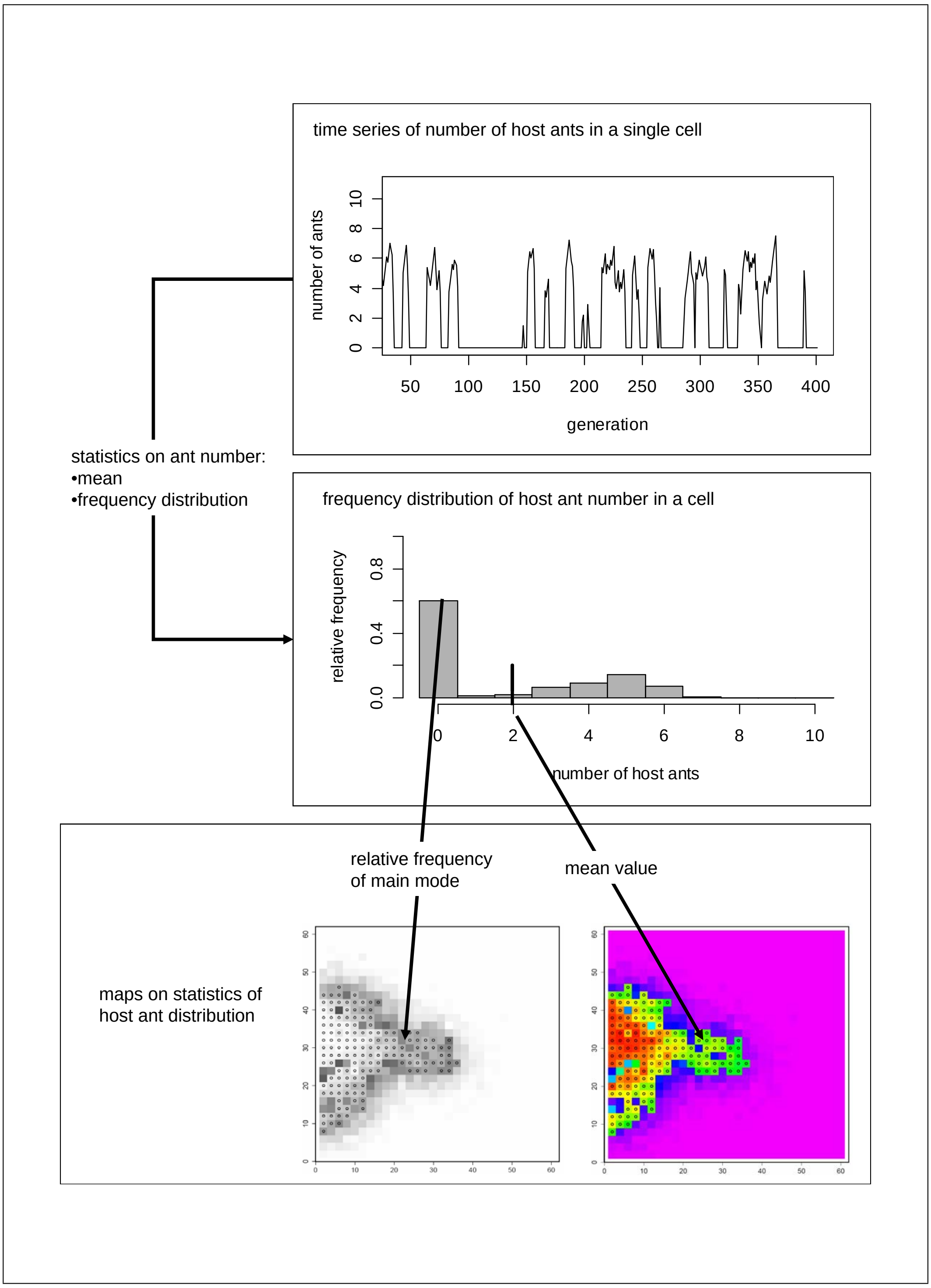

Figure 7.2: Protocol to create maps on host ant distribution. Calculate statistics on temporal host ant variation in a cell. The mean value is a measure for the effective power of the cell to reproduce Maculinea. Relative frequency of the main mode determines whether host ant number is almost constant. Strongly varying ant number indicates that the cell contributes to the process of Maculinea reproduction. Ant number is measured in caterpillar equivalents.

> of the ants to support butterfly reproduction. Cells with host plants and a high mean number of host ants have a high capacity to rear Maculinea larvae.

The two measures sufficiently distinguish between the four types of histograms from fig. 7.1. Time series in graphs 7.1a and 7.1b can be distinguished from the other two because mean number of ants is clearly lower. Within the two groups, the time series can be distinguished by their tendency to stay at the same value. This is measured by the relative frequency of the main mode f_{ant}.

Following the methodology depicted in fig. 7.2, in the last step, maps are plotted, which display characteristics of the time series of each cell. That means, for each cell, the two quantities 'mean number of host ants' and 'relative frequency of main mode' are determined from the time series on host ant number and depicted in maps by different colours. Additionally, in the maps, circles indicate the position of host plants.

Creating these maps, we subsume time series information of each cell in temporally aggregated measures. Spatiotemporal dynamics is reduced to a spatial representation.

7.2.5 Maps of spatial distribution of host ant dynamics

7.2.5.1 Mean number of host ants per cell

Maps of mean number of host ants per cell are calculated from all simulations of representative scenarios summarised in tab. 7.1. They are displayed in fig. 7.3. In a row in fig. 7.3, budding range σ increases from left to right by values 4m, 8m to 12m. Different rows contain simulation results for different host plant patterns.

It can be seen that spatial host plant distribution (small circles) influences the distribution of mean numbers of host ants per cell (different colours). Cells with host plants on average contain less host ants than cells without plants. The negative effect of host plants to host ant nest size is stronger, if the cells are surrounded by other cells with host plants. We now have a look at the left map of graph 7.3a (first row). Cells at the edge of the plant patch on average contain about 2 to 4 caterpillar equivalents (green). Deeper inside the host plant patch, cells are not occupied by ants (red). Cells without host plants are the less occupied, the closer they are located to the plant patch. Cells in direct vicinity of host plants contain about 8 caterpillar equivalents. Farer away from the host plants, nests contain more than 10 caterpillar equivalents.

This spatial structure of mean numbers of host ants is found in all maps of fig. 7.3. It is more pronounced for a short budding range $\sigma = 4m$. Increasing σ, the spatial pattern wipes out.

7.2.5.2 Constancy of host ant occupation - Relative frequency of main mode of host ant number f_{ant}

Influence of spatial host plant distribution is reflected in maps of f_{ant} (fig. 7.4), too[4]. It can be observed that in areas containing both, cells with and without host plants, host ant occupation is highly fluctuating (grey; $f_{ant} < 1$). In contrast, in areas, which either are homogeneously occupied or homogeneously unoccupied by host plants, number of Myrmica host ants is quite constant (white; $f_{ant} \approx 1$).

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[4] Maps of relative frequency of main mode of host ant number f_{ant} in fig. 7.4 are created from the same simulation results as maps of mean number of ants in fig. 7.3.

Similar to description in sec. 7.2.5.1, spatial patterns of host ant activity wipe out with increasing budding range σ.

7.2.5.3 Spatial distribution of host ant dynamics

The spatial distributions of temporal mean number of host ants and relative frequency of main mode of host ant number f_{ant} give an overview on the spatial distribution of host ant dynamics. We can distinguish spatial areas with high turnover of host ants from areas, where host ants do not show any dynamics.

No host ant dynamics is observed in areas, where host plants are homogeneously distributed. Areas, which are homogeneously occupied by host plants, on average contain almost no host ants. Hence, the absence of ants avoids host ant dynamics. These red cells in fig. 7.3 correspond to time series in graph 7.1a. In contrast, areas which are homogeneously unoccupied by host plants contain highest numbers of host ants. Obviously, although large ant nests are present, these show no dynamics (violet cells in fig. 7.3 and time series 7.1d).

From patterns in f_{ant}-maps (fig. 7.4) we conclude that dynamics of Myrmica host ant population is restricted to areas with a heterogeneous distribution of host plants. Following argumentation in sec. 7.2.3, in this area, ant nests in cells with host plants frequently go extinct and afterwards cells become recolonised (graph 7.1b). Whereas ants in cells without host plants often bud empty cells (graph 7.1c).

It is obvious that spatial distribution of host ant dynamics arranges according to spatial distribution of host plants. Additionally, the spatial pattern is influenced by budding range σ. In contrast to the spatial distribution of host ants, which temporarily changes as can be seen in fig. 2.5, spatial distribution of ant dynamics is fix in time.

7.2.6 'Cell effectiveness' - Effective dynamic contribution of cells

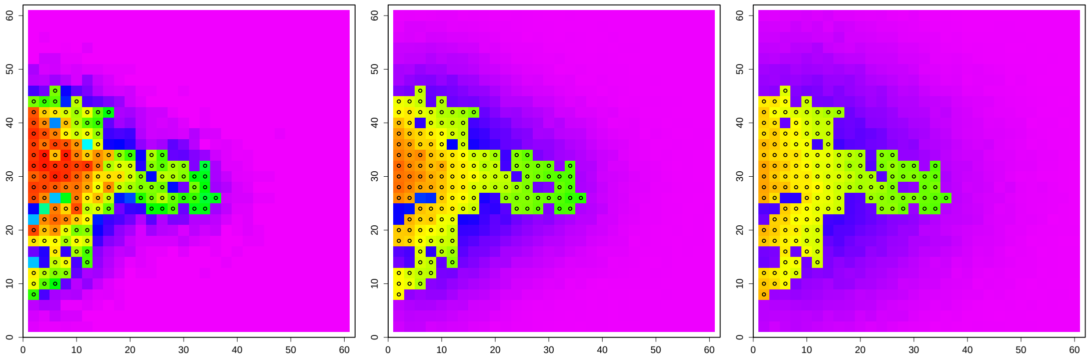
We now discuss the combined dynamics of host ants and Maculinea butterflies within a cell. We concentrate on the question, how hosts affect performance of Maculinea population within a cell. From maps in figures 7.3 and 7.4 it is verified that, to a high extent, host ant dynamics within cells follows one of the four types of temporal dynamics represented in time series of fig. 7.1. Hence, host ant dynamics within most cells can be described by one of these four types. Therefore, in the following, we restrict to these types. According to the four identified types of host ant dynamics and presence or absence of a host plant, we categorise the grid cells. For each of the four cell classes, we describe butterfly caterpillar development and host ant dynamics. From these considerations, we evaluate the contribution of a cell to the performance of the Maculinea population. The cell categorisation is called 'cell effectiveness'.

Cells with host plants (suitable for Maculinea oviposition)

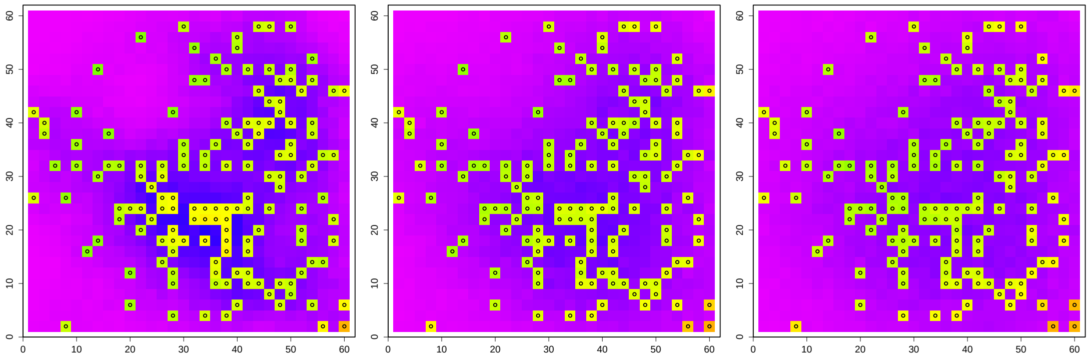
Sink cells: Cells containing almost no Myrmica ants. Maculinea butterflies can oviposit on these cells, but larvae will not be adopted. Hence, eggs are lost. The cells are sinks for Maculinea.
Time series: 7.1a; cell colour: red or yellow in fig. 7.3 and white in fig. 7.4

Reproductive cells: Cells which often contain Myrmica ants. These cells reproduce Maculinea butterflies. Rearing of butterfly larvae reduces Myrmica nest size and can lead to extinction of ant nests. However, they become recolonised. These cells

(a) host plant distribution plantsSG5



(b) host plant distribution plantsSG2a



(c) host plant distribution plantsSG1

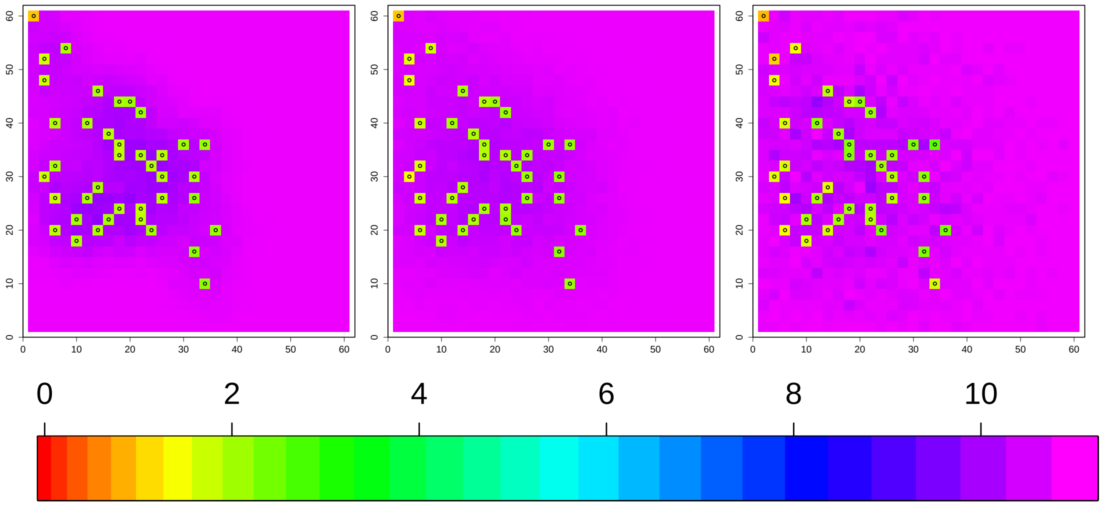
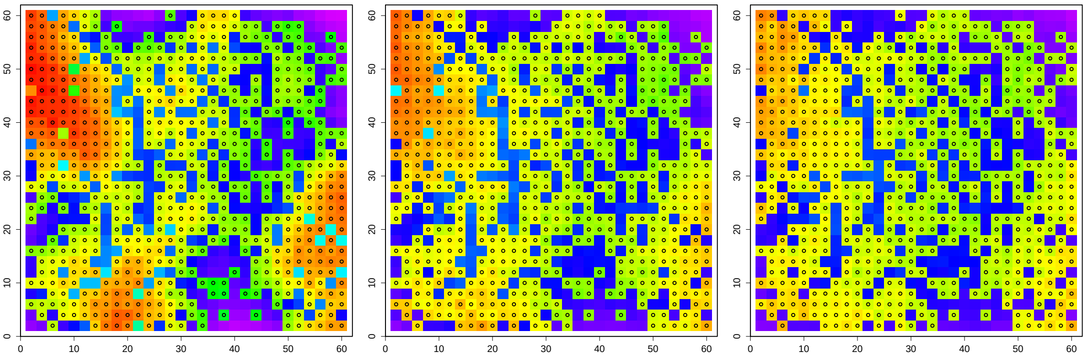
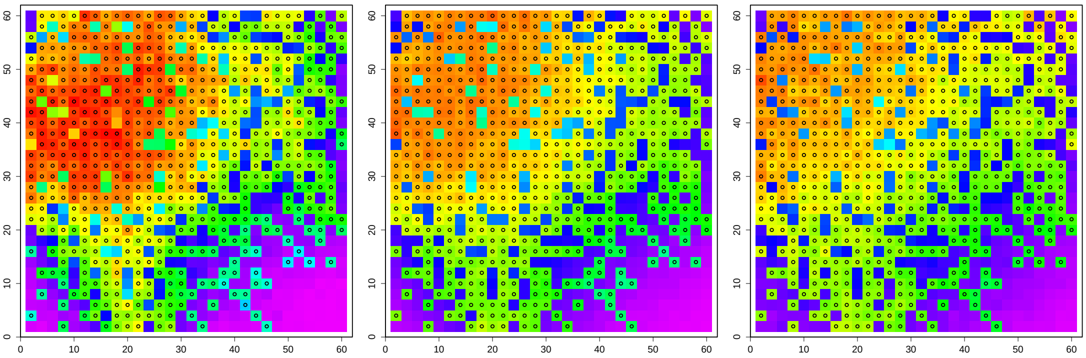


Figure 7.3: Temporal averaged number of Myrmica ants per cell, in the established state. Circles indicate position of host plants. Different colours represent mean number of Myrmica host ants. Red is 0, Purple is 11 (see scale bar).
Each row displays data from simulations with equal host plant distribution but different Myrmica budding range. From left to right, budding range increases ($\sigma = 4, 8, 12$).

(d) host plant distribution plantsSG3a



(e) host plant distribution plantsSG3b



(f) host plant distribution plantsSG3c

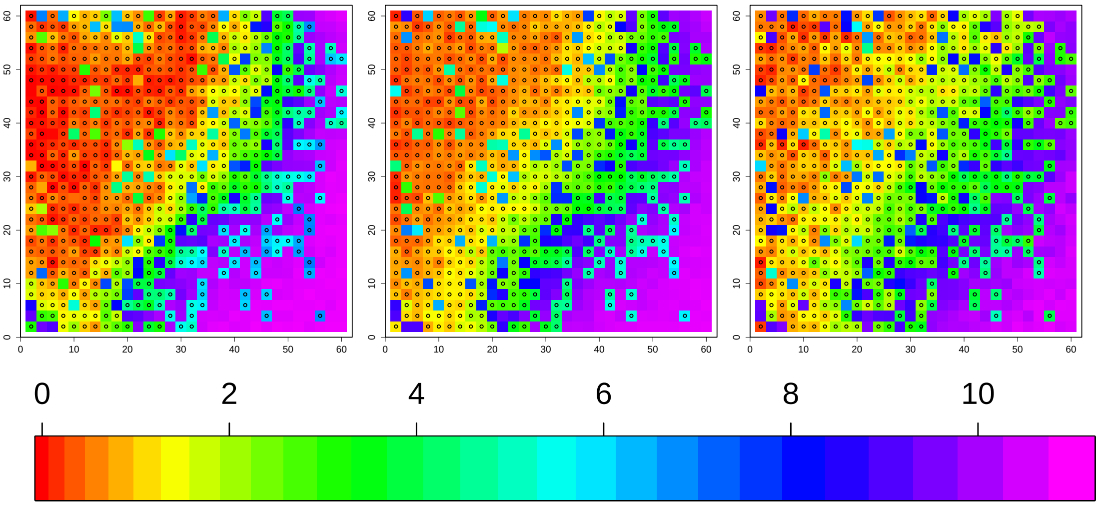
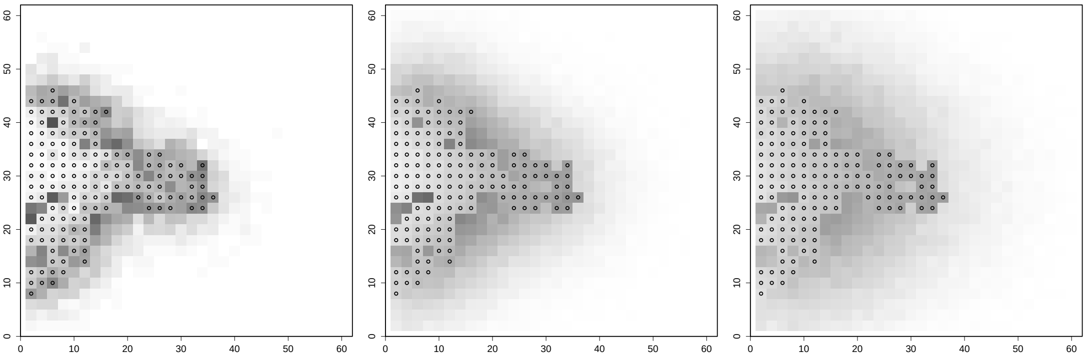


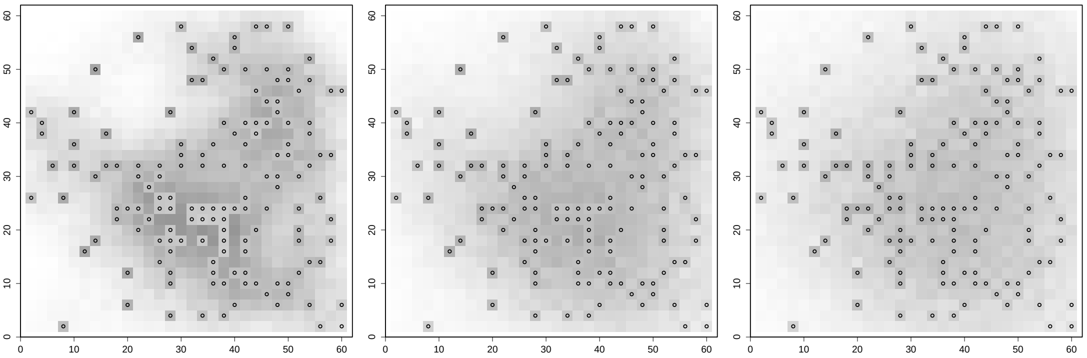
Figure 7.3: Temporal averaged number of Myrmica ants per cell, in the established state. Circles indicate position of host plants. Different colours represent mean number of Myrmica host ants. Red is 0, Purple is 11 (see scale bar).

Each row displays data from simulations with equal host plant distribution but different Myrmica budding range. From left to right, budding range increases ($\sigma = \{4, 8, 12\}$).

(a) host plant distribution plantsSG5



(b) host plant distribution plantsSG2a



(c) host plant distribution plantsSG1

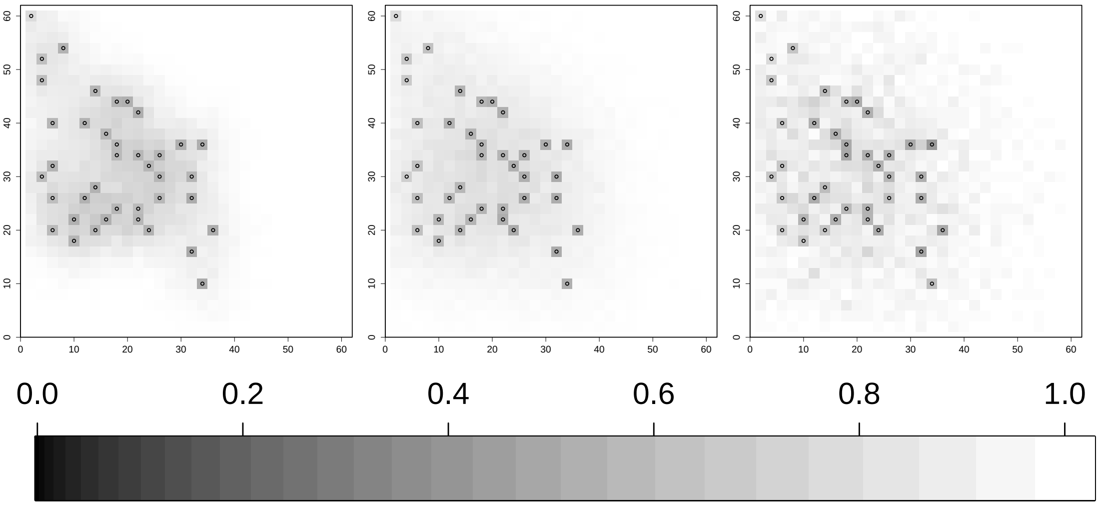
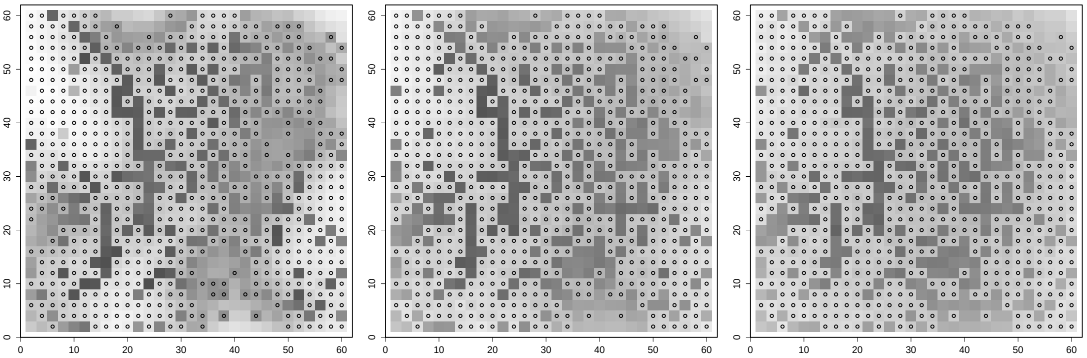
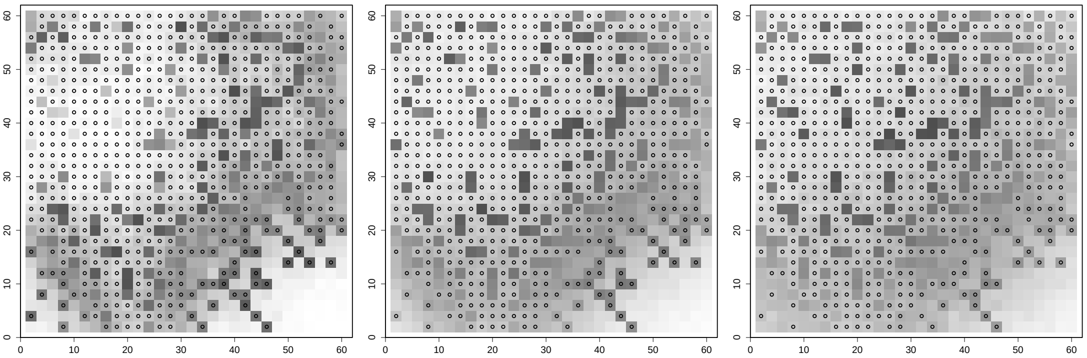


Figure 7.4: Relative frequency f_{ant} of most frequent number of Myrmica ants per cell, in the established state. Circles indicate position of host plants. Different grey levels represent relative frequencies. Black is 0, White is 1 (see scale bar).
Each row displays data from simulations with equal host plant distribution but different Myrmica budding range. From left to right, budding range increases ($\sigma = 4, 8, 12$).


(d) host plant distribution plantsSG3a


(e) host plant distribution plantsSG3b

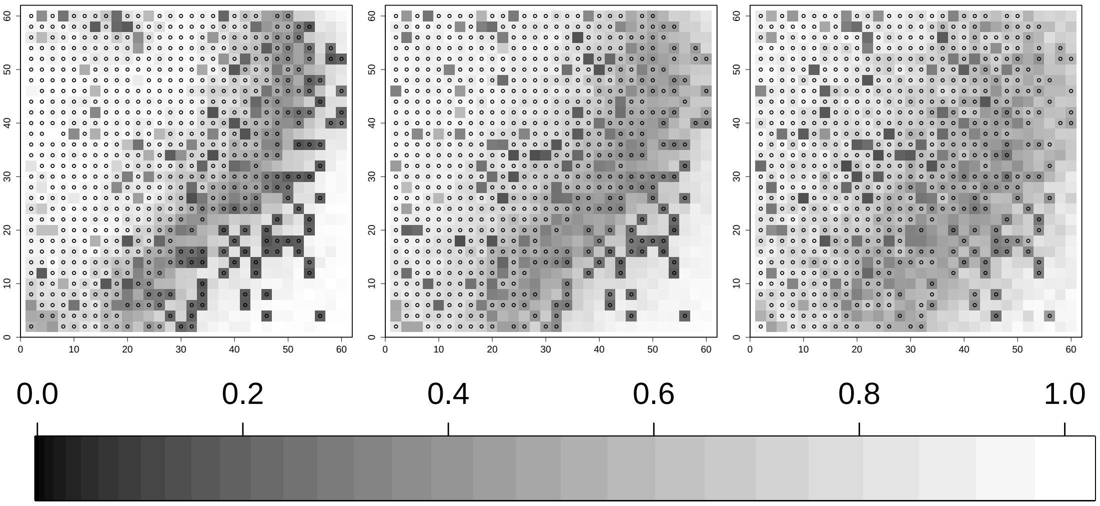

(f) host plant distribution plantsSG3c

Figure 7.4: Relative frequency f_{ant} of most frequent number of Myrmica ants per cell, in the established state. Circles indicate position of host plants. Different grey levels represent relative frequencies. Black is 0, White is 1 (see scale bar).

Each row displays data from simulation with equal host plant distribution but different Myrmica budding range. From left to right, budding range increases ($\sigma = 4, 8, 12$).

are called 'reproductive cells'.
Time series: 7.1b; cell colour: green in fig. 7.3 and grey in fig. 7.4

Cells without host plants (unsuitable for Maculinea oviposition)

Buffer cells: Cells with host ant nests which often bud empty cells. Although nests in these cells are not directly parasitised, because host plants are missing, they are affected by the Maculinea population. Ants from these cells bud empty cells in the parasitised area. They recolonise the reproduction area. Host ants from these cells work as buffer for the parasitised cells, in the sense that they refill resources for Maculinea in the area with host plants. These cells are called buffer cells.
Time series: 7.1c; cell colour: blue in fig. 7.3 and grey in fig. 7.4

Non-contributing cells: Cells with large ant nests which do not show ant dynamics. Host ants in these cells are almost not affected by parasitism of Maculinea. In contrast to buffer cells, ants from here almost do not colonise empty cells. If they colonised empty cells, ant dynamics would be much more active. Because these cells do not contribute to butterfly reproduction, they are denoted 'non-contributing cells'.
Time series: 7.1d; cell colour: violet in fig. 7.3 and white in fig. 7.4

7.2.7 Quantifying cell effectiveness

Up to now, cell effectiveness is a qualitative concept to summarise and explain the influence of microscopic processes on performance of a Maculinea population. For statistical analysis, it would be useful to find a quantification of the qualitative concept. That is, we search for quantitative criteria to decide, whether a cell belongs to one or the other effectiveness class.

Let's think, what we try to do. Formally speaking, cell effectiveness is a categorisation (hence a statistical model) of in-cell population dynamics (input parameter) according to their effect on butterfly performance (explanatory variable). Using language of statistics, there is a clear frame, how to find a correct quantitative categorisation for cell effectiveness. It is a satisfactory model, which allows description of explanatory variables by the input parameter[5].

Hence, doubtless it is allowed to take an arbitrary model for cell effectiveness e.g. based on our qualitative reasoning in sec. 7.2.6 and test, whether it reveals a relation of cell effectiveness and macroscopic measures. If the model is satisfactory, resolution of the categorisation is sufficient to relate microscopic processes with macroscopic observables. That is, cell effectiveness correctly represents effects of local dynamics on butterfly performance.

But note, if such a model is successful, we implicitly demonstrate another statistical assumption: we show that variance of elements within a class is irrelevant for explaining the effect. In concrete, all cells of one effectiveness class contribute equally to performance of the Maculinea population. This means, cell effectiveness aggregates the system on a spatially implicit level.

For the quantitative categorisation, we orientate on the qualitative description of cell effectiveness in sec. 7.2.6. The categorisation consist of four classes. These classes are firstly separated by presence or absence of a host plant. Secondly, presence or absence of host ant dynamics is taken as an indicator.

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[5] In a strict statistical sense, the best model should be found, comparing different variants by a formal criteria (e.g. Akaike index for model evaluation). In our context, we can restrict to a 'satisfactory' definition of cell effectiveness, which shows dependency of mean time to extinction t_m on cell effectiveness.

It is known from sec. 7.2.3 that in sink cells sometimes host ants can be found. Host ant dynamics is not completely absent. For this reason, a threshold needs to be introduced, which allows to distinguish strong host ant dynamics from low host ant dynamics. It showed up that relative frequency of main mode $f_{ant} \geq 0.7$ is a suitable criteria to distinguish sink cells from reproductive cells and non-reproductive from buffer cells.
From simulations of all scenarios listed in tab. 7.1, effectiveness is determined for each grid cell. We count the number of cells corresponding to each of the four effectiveness classes.
For example, the number of sink cells of a scenario can be determined by

$$\#(sinks) = \sum_{c=\text{ grid cells}} \mathbb{1}[(c \text{ contains plant}) \wedge (f_{ant}(c) \geq 0.7)]$$

where $\mathbb{1}$ symbolises an indicator function

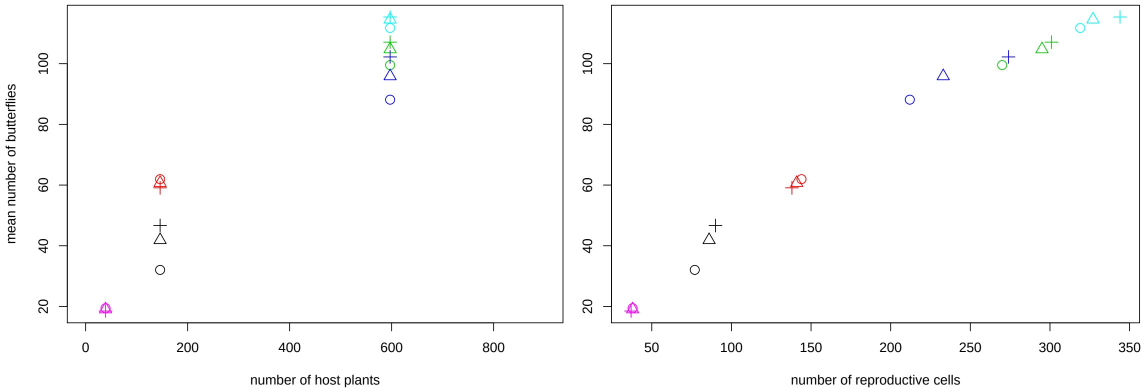
$$\mathbb{1}(x) = \begin{cases} 1 & ; x \in \{true\} \\ 0 & ; x \in \{false\} \end{cases}$$

Resulting numbers of cells for each effectiveness are correlated. Correlation is caused geometrically, because total area of the habitat site and number of host plant cells is limited. For example we find relation $\#(sinks) = \#(plants) - \#(reproductive)$. But, population dynamics is another reason for correlation. For example, an increased number of buffer cells allows a higher number of reproductive cells.

7.2.8 Comparison of cell effectiveness and macroscopic population data

For each of the scenarios described in tab. 7.1, we determine the number of cells per cell effectiveness class. These values are compared to macroscopic measures 'mean number of butterflies' and 'intrinsic mean time to extinction' t_m gained in simulations of ch. 2 and ch. 6.
In the left column of fig. 7.5 we show the relation of host plant numbers to macroscopic observables on butterfly performance as a reference. The right column depicts dependence of these macroscopic measures on the number of reproductive cells. Data points are marked by colours and symbols. Colours account for different host plant distributions. Symbols indicate different budding ranges σ. Hence, each scenario of tab. 7.1 is marked by one coloured symbol.
In the left column of fig. 7.5, it is seen that the number of host plants influences the macroscopic measures. However, scenarios, which contain equal number of host plants, can lead to different macroscopic effects and therefore different mean numbers of butterflies or intrinsic mean times to extinction. Hence, we verify earlier results from ch. 6 that in some cases, the number of host plants insufficiently evaluates host plant patterns to predict intrinsic mean time to extinction t_m or other macroscopic measures.
Number of reproductive cells overcomes this weakness. In the right graph of fig. 7.5a we find a clear increase of mean number of Maculinea butterflies with increasing number of reproductive cells. In the right graph of 7.5b dependency is not that clear. However, the resolution is better than in the left graph. As reproductive cells have clearer effects on population dynamics of Maculinea butterflies than plant cells, it is worth to inspect dependencies of macroscopic observables on effectiveness of cells in more detail.
First, we call attention to a difference between right graphs of fig. 7.5a and fig. 7.5b. Mean number of butterflies is related to the total number of reproductive cells. In contrast, intrinsic mean time to extinction has closer dependency on the quotient of number of reproductive cells

(a) Mean size of Maculinea population



(b) Intrinsic mean time to extinction t_m of Maculinea population

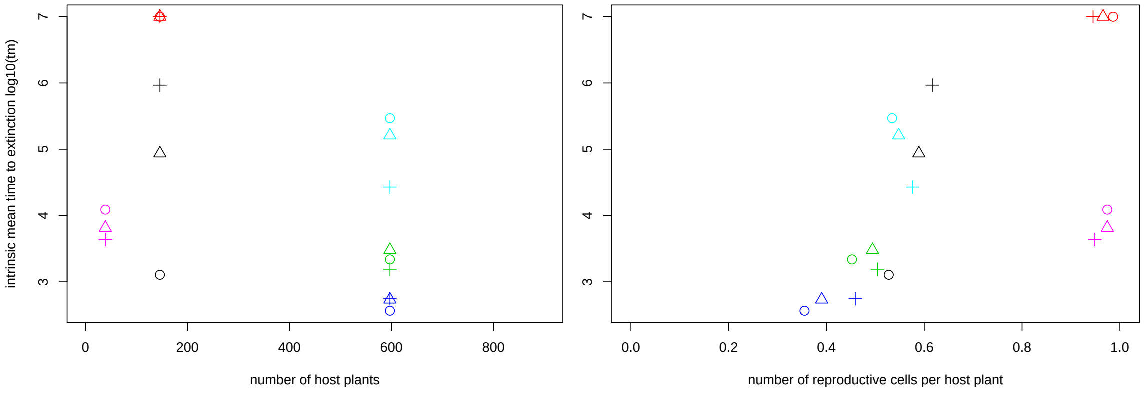


Figure 7.5: Dependency of macroscopic measures on cell effectiveness is measured for the different scenarios (tab. 7.1). Scenarios are distinguished by point marks (budding range; circles: $\sigma = 4$, triangles: $\sigma = 8$, plus: $\sigma = 12$) and colours (host plant distribution; black: plantsSG5, red: plantsSG2a, purple: plantsSG1, turquoise: plantsSG3a, green: plantsSG3b, blue: plantsSG3c). Number of reproductive cells is calculated, based on host plant presence and constancy of host ant number (see fig. 7.4). Number of ants in a cell is considered as constant, when its integer value is equal in at least 70% of all simulation steps (relative frequency of highest mode ≥ 0.7).
Graph (a) displays dependency of mean number of Maculinea butterflies in a population on number of host plants (left) and number of reproductive cells (right). Graph (b) depicts dependency of intrinsic mean time to extinction t_m on number of host plants (left) and number of reproductive cells per host plant (right). Note that in graph (a), total numbers of cells are given, whereas in graph (b) number of reproductive cells is measured relative to host plant number. Exchanging these measures weakens correlation in the graphs.

and number of host plants. Two different aggregated measures are decisive for two different macroscopic effects.

At this point, we learn about the process. Reproductive cells are the only area, where Maculinea individuals successfully develop. Hence, we find the well-known effect that increasing suitable habitat can support an increasing population. However, persistence of Maculinea in most cases does not depend on the average number, but on low numbers of butterflies. The population undergoes a high risk of extinction, when temporarily population size is low, that is when the cyclic population dynamics goes through a minimum. When number of butterflies is low, their number of eggs is low, too. Hence there is a critical situation whether there are enough of these few eggs laid in cells with plants and ants. Such cells can only be reproductive cells. The probability to either lay an egg into a reproductive or a sink cell is expressed in the ratio how many of the plant cells are reproductive. The number of reproductive cells must be normalised by the number of plant cells to predict persistence of Maculinea.

There is a quite clear increase of intrinsic mean time to extinction with the increasing quotient of number of reproductive and number of plant cells in fig. 7.5b. But, a group of three purple data points does not fit into the observed pattern. Although, for these points it is indicated that all plant cells are reproductive, which should lead to high intrinsic mean time to extinction (red points), persistence of Maculinea butterflies for the purple points is very low. These points result from simulations with host plant pattern plantsSG1. This pattern consists of 39 plants (see tab. 7.1), which is a very low number. As can be seen in the right graph of fig. 7.5a, mean butterfly population is very low (purple data points). This low number of butterflies underlies risk of extinction by demographic stochasticity. Instead of the number of reproductive cells, the number of host plants is limiting, in this case. For scenarios of very low numbers of host plants, the quotient of number of reproductive cells and number of host plants is a bad predictor for the assessment of Maculinea persistence. The absolute number of reproductive cells is decisive.

Number of reproductive cells is closely related to macroscopic observables of the system. For measures, based on other effectiveness classes, we find relations, too. These mainly can be explained by correlation between the different aggregated measures and the number of reproductive cells (see sec. 7.2.7). If detailed questions are to be answered, it can be useful to take into account measures based on cell effectiveness classes other than the reproductive cells.

Our analysis reveals that indeed aggregated measures based on cell effectiveness well explain macroscopic properties of the Maculinea system. Hence, we can follow the argumentation in sec. 7.2.7. We deduce that cell effectiveness is an aggregation level, where local dynamics is aggregated spatially implicitly. For this reason, cell effectiveness is an important concept, when trying to understand the effects of local dynamics on the behaviour of the Maculinea system.

7.2.9 Revision of analysis and results

Before turning to an application of our findings, we want to briefly recapitulate the last sections, to be aware of some important points. By the analysis, knowledge is won for different topics: methodology, aggregation of microscopic dynamics on the level of cell effectiveness, and understanding of dynamics of the Maculinea system. In the following, each of these themes will be discussed in an own section.

7.2.9.1 Methodology

We want to explain, in a short and general way, how we achieve to analyse spatiotemporal dynamics. The methodology is typical for science, but to our knowledge seldom applied to this extent.

To explain the approach, take the development of cell effectiveness as an example. It is mentioned in sec. 7.2.7 that cell effectiveness is a model to describe the effect of microscopic dynamics on macroscopic observables of the system. Hence, the only task to do is find that model.

This complete section deals with describing that model. Initially, input parameters, that are local dynamics, are presented. In the following, characterisation of input parameters is intended. This characterisation already is the actual modelling work. We search for a suitable model to evaluate the effect of observed local dynamics on performance of Maculinea: that is effectiveness. In the final step, we test, if the model is suitable for our purpose.

Now to some details. Finding the model of course is intuitive work. And, it might be surprising to inspect in-cell host ant dynamics, when one wants to explain persistence of butterflies. However, it is the natural way in the Maculinea system. Host ant dynamics is the only spatiotemporal dynamics of the Macu model – and, it is grid based. If spatiotemporal dynamics is too complex, it should be aggregated on lowest level. There are two convenient ways of aggregation. Either, aggregation over time or space. If spatial aggregation is performed, the object to observe is a time series of the total number of butterflies in the habitat. We choose to aggregate over time. Hence, we observe host ant dynamic within a cell and describe the in-cell time series aggregatedly.

The following step, finding a characterisation of the time series, here in fact is solved intuitively from knowledge of the model. However, there are different methods to support categorisation or model building (statistical methods like e.g. cluster analysis or stochastic methods like e.g. simulated annealing, genetic algorithms or neural networks). Hence, if one does not have any idea about the system, such methods might be helpful. Important at this step, it has to be clarified, which kind of effect shall be analysed. The effect is the purpose of the model.

In the final step, the model needs to be tested. In the model test, it is answered, if the description of macroscopic effects is good enough. The assessment is essential, because it defines accuracy. In this thesis, we consider a model as accurate, if effects of unexplained variance are small enough, not to disturb explanatory power of the model. In other words, can we assume two members of one class to be equal in respect to the effect? For example, we reject host plant density as a model for persistence of butterflies, because host plant patterns with the same density might provoke strong difference in intrinsic mean time to extinction. As well, we reject the quotient of number of reproductive cells and number of host plants as a model for patterns with small numbers of host plants. Indeed, we suggested to use total number of reproductive cells or total number of host plants instead.

The way of model testing, performed in this thesis, might be accused as subjectively depending on our opinion. In fact, we dispense with quantitative criteria. However, defining these strict objective criteria as well is a subjective decision of the researcher. We instead prefer a practically orientated model testing, which is evaluated, according to the power it provides to our mechanistic understanding of the system. For example, variance of data points in a graph makes us understand that the selected model has some weakness. In a further step, we analyse the reason for the error.

One point, which to our opinion is not clear in many studies, is applied often in this thesis: if a model is accepted to be sufficiently accurate, it implies that, in the following, the model can be used instead of the input data. This means, all unexplained variance of the input parameters can be ignored. Hence, all elements of a class defined by the model can be considered as equal in respect to the effect, they provoke. The total effect of a class is n times the effect of one element, when n denotes the number of elements in the class. Therefore, an accepted model defines an aggregation level, on which aggregated elements can be considered implicitly.

7.2.9.2 Properties of cell effectiveness

Cell effectiveness is derived from characteristics of system dynamics. Hence, several properties of population dynamics of Maculinea and Myrmica enter into cell-effectiveness. Some of these are necessary in further argumentation. For this reason, properties are listed and collectively explained here.

1. Cell effectiveness is a property of a cell.
   Host ants in a cell can interact with other components of the system from outside the cell (e.g. parasitic Maculinea butterflies). These interactions express in in-cell host ant dynamics. Hence, the way we observe host ant dynamics by time-series, already includes these interactions. In particular without interactions host ants in a cell cannot contribute to system dynamics (e.g. non-contributing cells). Cell effectiveness evaluates the contribution of host ants in a cell to Maculinea reproduction on the site. This effect of localised host ants certainly is a local property of a cell.

2. Cell effectiveness is constant in time.
   Cell effectiveness is derived from host ant dynamics in a cell, not from host ant number directly. Number of ants temporally varies, however this variation can be described by one of the four types of host ant dynamics presented in fig. 7.1. It is argued that, in the established state, the type of host ant dynamics is fix (7.2.5.3). Hence, cell effectiveness as well is constant in time.

3. Cell effectiveness is spatially localised.
   Overall spatiotemporal dynamics induce a spatial pattern to the distribution of cell effectiveness types. This pattern can be represented in spatial maps of effectiveness type distributions.

4. Spatial distribution of cell effectiveness types depends on host plant distribution and budding range σ of Myrmica host ants.
   In sec. 7.2.5.3 it is argued that spatial distribution of host ant dynamics depends on spatial host plant distribution and on budding range σ. This arrangement transfers to cell-effectiveness. Maps on distribution of host ant dynamics (fig. 7.3 and fig. 7.4) give a visual impression of the distribution of cell effectiveness, too. According to these maps, sink cells are cells with host plants, which are far away from cells without plants (that is in the centre of plant patches). Reproductive cells contain plants, too. But they are localised close to cells without host plants (that is e.g. at the boarder of plant patches). Buffer cells do not contain host plants, but are in vicinity of cells with plants. They surround cells with host plants. Non-contributing cells do not contain host plants and are far away from cells with host plants.

5. Contribution of host ants in a cell is equal in cells of the same cell effectiveness type. It is found that in-cell host ant dynamics qualitatively can be categorised by only four different types. This simple categorisation is sufficient to explain dependency of macroscopic observables on local processes. Hence, variance of dynamics in different cells of the same effectiveness class has minor effect on butterfly performance. For this reason, cells of the same effectiveness class contribute equally to population development of Maculinea. This finding means that system dynamics can be described spatially implicit on the level of cell effectiveness.

7.2.9.3 Why defining cell effectiveness?

Cell effectiveness is a model to describe microscopic population dynamics of the system with regard to its effect on performance of the Maculinea population. It aggregates microscopic processes spatially and temporarily. Hence, we are no longer forced to deal with numbers of host ants which vary in space and time.

In contrast to macroscopic measures like 'mean population size' or 'intrinsic mean time to extinction' used in chapters before, for cell effectiveness, we know the underlying model of aggregation. We have a mechanistic understanding, how 'cell effectiveness' depends on microscopic dynamics.

Thus, cell effectiveness can be seen as a link between full complexity of microscopic dynamics and ad hoc statistical measures on macroscopic effects.

7.2.9.4 Understanding spatiotemporal dynamics of the Maculinea model

Basing on cell effectiveness, we are now able to explain upward macroscopic effects and downward, why they are provoked by microscopic effects.

We find in sec. 7.2.8 that aggregations of reproductive cells can be used to describe persistence and mean size of the Maculinea population. This is not surprising, as Maculinea can reproduce successfully only in these cells. Hence, the reproductive area can be considered as the 'habitat' for Maculinea.

However, it must be kept in mind that this habitat is temporarily variable (see sec. 7.2.3). Whether a reproductive cell is suitable at a time, depends on the momentary number of host ants present. Hence, reproductive cells are the only cells, where Maculinea can reproduce, but they are not always suitable.

Complexity of the system enters, when taking into account that temporal suitability of a cell depends on earlier stages of the butterfly population. Hence, the butterfly population regulates its habitat. Butterfly population size as well as host ant distribution are self regulated by the system.

The resulting cyclic population dynamics of Maculinea butterflies is the reason, why mean size and persistence of the population depend on different aggregations of cell-effectiveness. Mean population size depends on the total amount of reproductive cells. It follows the rule that large total habitat allows high population size. In contrast, persistence of the butterfly population depends on the quotient of number of reproductive cells and number of host plants. This is, because the Maculinea population is only endangered by demographic stochasticity, when it is small. That is, when population cycles go through the minimum. At these times, the decisive process is, whether there are enough butterfly eggs laid on host plants in cells with ants. Because these cells are the only reproductive ones. Hence, with the aggregated quotient, we describe the probability for an egg to be laid into a reproductive cell.

It is found that for low numbers of host plants, persistence depends on total number of reproductive cells (or, what in this case is the same, total number of host plants). This is because, in such scenarios, population size of Maculinea is limited to low numbers by the few plants. Hence, we can explain macroscopic effects by numbers of reproductive cells. In the following, we discuss, how the amount of reproductive cells is limited by local processes.

Reproductive cells contain host plants and a fluctuating host ant population. Both components can be limiting to the amount of reproductive cells.

Low number of host plants: When number of host plants is low, all cells containing plants in general are reproductive. However, due to the low number of plants, there are only few reproductive cells.

Host ant dynamics: Host ant dynamics in cells with plants depends on how the cell can be reached. There are two factors which determine budding of a plant cell.

> **Large patches of host plants and limited budding range:** Host plants in the centre of large plant patches cannot be reached by host ants, because budding range is limited. These cells act as sinks. Reproductive range is limited to the boarder of a patch.
>
> **Few buffer cells:** On sites with many host plants, few space is left, which cannot be exploited by Maculinea caterpillars. This restricted amount of buffer cannot sufficiently support cells with host plants. Hence, although an empty cell with a host plant can be easily reached, there are no budding ants available to colonise the site. Number of reproductive cells is limited, because there are too few buffer cells.

There are three different causes, why number of reproductive cells is low. In many scenarios several reasons are limiting. That's why it is very difficult to determine these reasons for the Maculinea system.

But, having them identified, it is easy to explain dependency of intrinsic mean time to extinction t_m on the number of host plants (fig. 6.1a). For low numbers of host plants, persistence is reduced, because butterfly population is always low. For high numbers of host plants, few buffer cells are available to recolonise empty host plant cells. And large patches of host plants provoke a decline in t_m, although the number of host plants would suggest higher persistence. Hence, in fig. 6.1a, the general trend is given by sites with unclumped host plants.

7.3 A spatial index for the assessment of suitability of host plant distributions for the Maculinea system

In sec. 7.2.8 it is shown that aggregated measures based on cell effectiveness describe macroscopic measures of Maculinea dynamics in a better way than host plant coverage does. In particular, effects of explicit spatial patterns on Maculinea performance can be resolved.

However, in contrast to plant coverage, cell effectiveness is immanent of the system. In order to determine cell effectiveness, simulation results have to be analysed. Hence, cell effectiveness cannot be used to assess suitability of a habitat patch.

To overcome this disadvantage, we search for an index, which detects habitat suitability directly from external factors like for example host plant distribution. Because measures based

on cell effectiveness proved their ability to model performance of Maculinea populations, it is a good idea to orientate the new index on cell effectiveness.
According to ch. 5, suitability of habitat is best measured by the persistence of a species on the site. Therefore, we try to find an index, which predicts intrinsic mean time to extinction t_m.

7.3.1 Development of the index

We develop the spatial index in three steps. In the following these are developed from ecological understanding of the processes gained in previous sections.

1. It is stated in sec. 7.2.9.2 that spatial distribution of cell effectiveness is closely linked to distribution of host plants. Especially, reproductive cells and buffer cells are restricted to areas with spatially heterogeneous occupation by host plants.
   For these distributions it is known that they are constant (sec. 1.3.2 and sec. 7.2.9.2). They can be represented in maps (fig. 7.3 and fig. 7.4).
   Comparing these maps makes us aware of a pattern. Reproductive cells are situated on cells with host plants, but there have to be buffer cells without host plants in the surrounding (sec. 7.2.9.2). Hence, the index has to detect this pattern.

2. The reason for this pattern is explained in sec. 7.2.6. Cells with host plants can only have a positive effect to Maculinea reproduction, when they contain an ant nest. Overexploited and therefore extinct ant nests have to be replaced, before Maculinea caterpillars can grow up in that cell. Therefore, only cells that can be reached by budding ants from cells, which are not affected by Maculinea, can be reproductive.
   Additionally, if a plant cell can be reached by budding host ants from different cells, its probability to be recolonised is increased (sec. 1.3.2.5).
   Hence, the host ant budding process (sec. 1.3.4.4) introduces a scale to the spatial distribution of reproductive and buffer cells. For developing the index, this scale has to be taken into account.

3. Now, we develop a statistical measure, which detects reproductive cells depending on budding range and spatial host plant distribution.
   We take advantage from the fact that the system is spatially implicit on the level of cell effectiveness (sec. 7.2.9.2). Therefore, it is not necessary to take into account the exact spatial position of a host plant. An aggregated measure for the host plant distribution is sufficient.
   It is clear from steps 1 and 2 that this measure should account for the number of non-parasitised ant nests, by which a cell with a host plant can be budded. That is the number of cells without host plants within budding distance of cells with host plants. The budding process is a characteristic of the modelled host ant species (sec. 1.3.4.4) and not a property of the spatial arrangement of host plants on a site. This is considered by allowing variation of the spatial scale of the index.
   Finally, in sec. 7.2.8, it is found that persistence measure intrinsic mean time to extinction t_m and therefore habitat suitability is related to the ratio of number of reproductive cells and the number of host plants. For this reason, we assume a relative measure (normalised by number of host plants) to be adequate as index for habitat suitability.

Following this reasoning, we develop the spatial index $d_{empty}(r)$. It is defined as

$$d_{empty}(r) = \frac{1}{\#(\text{plants})} \sum_{n=\text{cells with plants}} \sum_{k=\text{cells without plants}} \mathbb{1}[\mathrm{d}(n,k) \leq r] \qquad (7.1)$$

$\mathbb{1}$ is an indicator function which is set to 1, if the condition $d(n,k) \leq r$ is fulfilled, else it is set to 0. $\mathrm{d}(n,k)$ denotes the Euclidean distance between the centres of cell n and k. The index is normalised by the number of plants $\#$(plants).

The spatial index $d_{empty}(r)$ is a simple measure. It measures the mean number of cells without plants around a cell with plants inside a neighbourhood of fixed radius r. It is closely related to Ripley's K function (ch. 4.4 in Stoyan & Stoyan, 1992). In fact, it is the discrete form of the bivariate quantity $\lambda_1 * K_{1,2}(r)$, where λ_1 is the intensity of cells with host plants and $K_{1,2}$ indicates bivariate Ripley's K of cells without plants around cells with plants without edge correction. How to discretise Ripley's K function on a grid is described for example in Wiegand & Moloney (2004).

The index $d_{empty}(r)$ depends on radius r. This radius defines the spatial scale of perceptivity of the measure. Only empty cells are counted, which lie within a distance of r from a host plant. Radius r is an important parameter of the index.

Looking at maps of distribution of host ant dynamics (fig. 7.4), we find that ant dynamics is highest in areas of heterogeneously distributed host plants (areas containing cells with plants and without plants). These areas are stated to contain reproductive and buffer cells (sec. 7.2.9.2). However, width of these areas depends on budding range σ. Comparing graphs from left to right columns in fig. 7.4, it can be seen that the area with strong host ant dynamics broadens with increasing σ (sec. 7.2.5.3).

Changing radius r of the spatial index $d_{empty}(r)$ allows to adjust spatial perception width of the index to the width of the area of strong host ant dynamics. If radius r is chosen too small for a spatial distribution of host ant dynamics, the index does not measure the complete area of ant dynamics. In contrast, if r is chosen too large, area is included in the measurement, which does not relevantly contribute to dynamics of the system. In this case, resolution of the index is decreased.

Thus, varying radius r provides information about the spatial scale of host ant dynamics. This is similar to studies, which use Ripley's L function (ch. 4.4 in Stoyan & Stoyan, 1992) or ring statistics (Wiegand et al., 1999; Wiegand & Moloney, 2004). The spatial scale depends on budding range σ. For this reason, dependence of $d_{empty}(r)$ on radius r for given scenarios can reveal further insight on the relation between system scale and σ.

7.3.2 Testing the index

It is found that the index $d_{empty}(r)$ is a predictor for the ratio of number of reproductive cells and number of host plants. In the following, we test that it is a predictor for suitability of habitat for Maculinea persistence, too.

According to the method for assessing spatial landscape structures by population viability (introduced in ch. 5), intrinsic mean time to extinction t_m is compared to the spatial index $d_{empty}(r)$. As discussed in sec. 7.3.1, radius r is varied to detect the relevant spatial scale of system dynamics. We perform simulations with standard parameter set (tab. 1.1), but budding range is set to $\sigma = 4m$ and initial host ant distribution is ants3. Host plant distributions are varied.

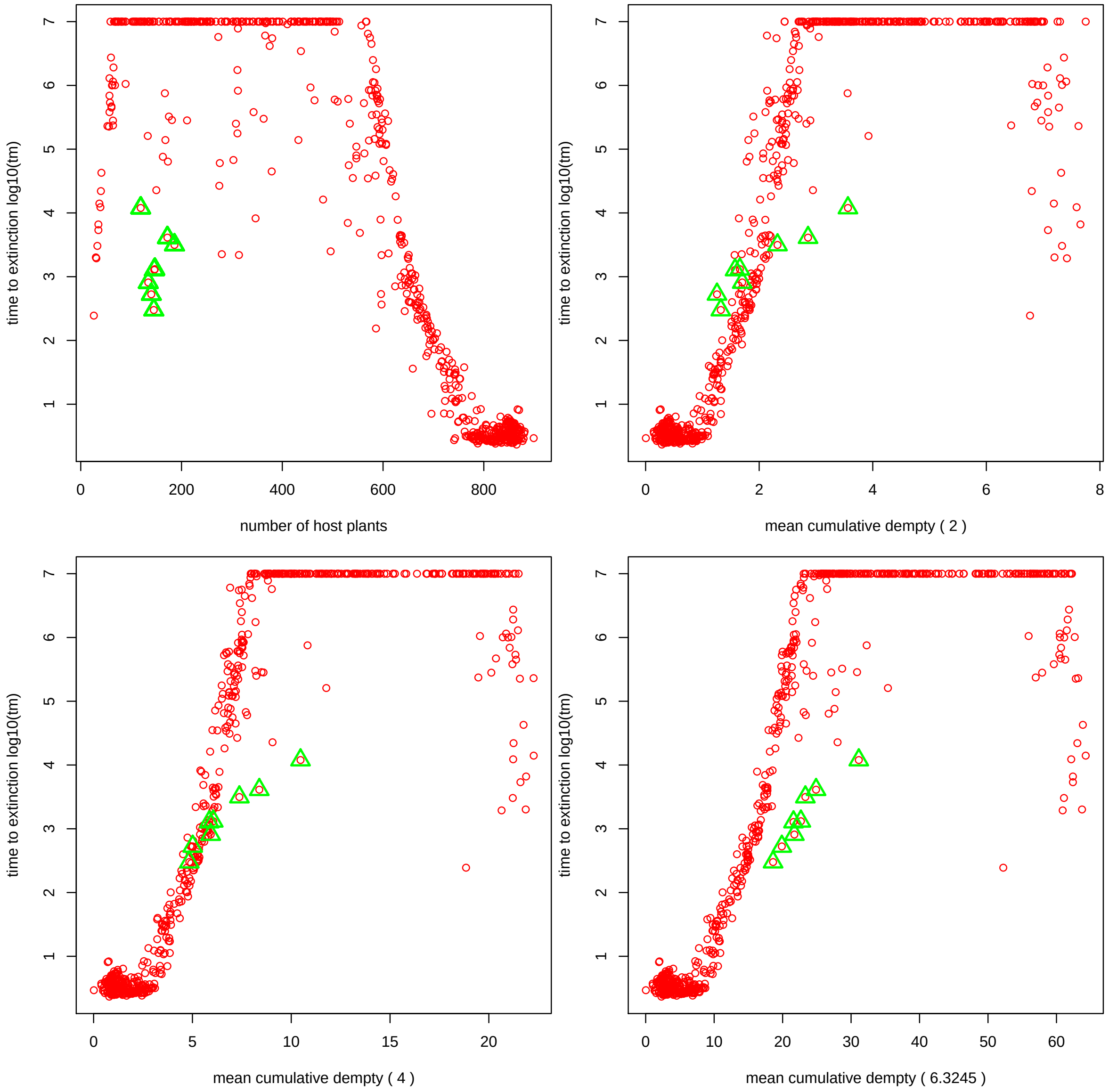


Figure 7.6: The four graphs show dependence of intrinsic mean time to extinction t_m on spatial host plant distribution (ant distribution: ants3; budding range $\sigma = 4m$). In each graph, spatial host plant distribution is characterised by a different spatial index. Left: number of host plants; the others: $d_{empty}(r)$ with scaling range $r \approx 2\text{m}, 4\text{m}, 6.3\text{m}$, respectively.
Data points designated to FG5 are marked by triangles. Note that these points are mapped towards points of FG3 depending on the range of perception of the spatial index $d_{empty}(r)$.

Fig. 7.6 shows results for different values of radius r. For comparison, the top left graph depicts relation of number of host plants and intrinsic mean time to extinction t_m. The typical shape is already known from graph 6.1a in ch. 6. The following three graphs show dependency of t_m on landscape index $d_{empty}(r)$ for increasing values of radius $r = \{2m, 4m, 6.3m\}$. In all three graphs, intrinsic mean time to extinction t_m increases with increasing index $d_{empty}(r)$ in form of a threshold. For very high values of the index, it can be observed that intrinsic mean time to extinction t_m drops to lower values. This pattern can be explained as follows.

Obviously, if number of empty cells around plant cells is too low (very low index values in the three graphs), Maculinea cannot persist. But, the more empty cells in mean are around a plant cell (increasing $d_{empty}(r)$), the higher is the probability that Maculinea populations persist. This finding is in accordance to the idea that $d_{empty}(r)$ is measuring heterogeneity[6] of host plant distribution on a spatial scale r. Regions with heterogenous host plant distribution are those with high numbers of reproductive cells (sec. 7.2.9.2). Hence, a high index value represents a high number of reproductive cells and thus high persistence of Maculinea populations.

However, if index values are too high, persistence of Maculinea populations decreases. To explain this effect, we look at the number of host plants in plant distributions, which lead to high values of $d_{empty}(r)$. It is found that these host plant distributions consist of less than 100 host plants. In sec. 6.4.2.2 and sec. 7.2.9.4, it is shown that in the case of low host plant coverage, the total number of host plants is the important parameter for the performance of Maculinea populations. The number of host plants limits the size of the Maculinea population. Resulting small Maculinea populations are endangered by demographic risk of extinction.

Comparing the top left graph with the others in fig. 7.6, it appears that the shape of the curve is reversed (i.e. intrinsic mean time to extinction t_m for scenarios with high host plant numbers can be mapped to values for low numbers of $d_{empty}(r)$ and vice versa). This pattern can be explained by the fact that for randomly distributed host plants, the index decreases with increasing number of host plants.

There is another important difference between the top left and the other three graphs. In the top left graph, many randomly distributed points are observed, which differ from the main shape of the curve. In contrast, in the other graphs, these points arrange much closer to the main shape. Variance in the top left graph indicates that, for some scenarios, the number of host plants is not sufficiently related to the intrinsic mean time to extinction t_m. The measure 'number of host plants' cannot account for differences in the spatial distribution of plants, when their number is not varied. In ch. 6, it is pointed out that the spatial arrangement of host plants influences persistence of Maculinea populations. Comparing graphs in fig. 7.6 it is obvious that there is a rather sharp functional relationship between intrinsic mean time to extinction t_m and landscape index $d_{empty}(r)$. This indicates that $d_{empty}(r)$ appropriately evaluates the effect of the spatial configuration on t_m.

Anyhow, for different values of radius r the sharpness of the relationship varies. To clarify this effect, some of the data points are marked by triangles. In the top left graph, these data points are evaluated by host plant number as a group of outliers (actually these points belong to scenario group SG5 in sec. 6.3.1.5). Evaluated by $d_{empty}(r)$ these points move towards the threshold-like main shape of the curve. On a spatial scale of r = 2m to 4m, the points marked by triangles integrate in the functional relationship. For the larger radius r = 6.3m,

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[6] A distribution of cells with host plants and without host plants is heterogeneous on a spatial scale r, if there are many cells of both types randomly distributed.

the triangles are separated from the main shape of the curve.

The radius r, for which the relation of index $d_{empty}(r)$ and intrinsic mean time to extinction t_m is closest, depends on budding range σ. This is observed in additional simulations, where the budding range is varied.

Hence, as required, the spatial index $d_{empty}(r)$ can be used to assess persistence of Maculinea populations by simply assessing spatial arrangement of host plants. It is sensitive to the spatial arrangement of the plants and can be adjusted to the spatial scale of host ant budding, hence to different Myrmica species.

7.3.3 Properties and applications of the index

Spatial index $d_{empty}(r)$ could be developed purely from geometric and statistical reasoning on the correlation of two spatial distributions. One of them, distribution of host plants, is an external factor, a landscape structure. The other, distribution of reproductive cells, indicates where Maculinea butterflies successfully reproduce offspring. Such an approach of matching spatial distributions of different habitat characteristics is widely used in landscape ecology. There, landscape structure is statistically related to species distribution. From this relation, attributes of suitable habitat are identified.

In contrast, the way the index is develop here, includes knowledge on processes and dynamics of the system. This additional ecological information improves our understanding of the index. Input parameters of the index, like radius r as well as the mechanism of aggregation, are deduced from knowledge about the ecological system. For this reason, we know how results of the index have to be interpreted in the ecological context (as for example requested by Tischendorf & Fahrig, 2000).

Taking into account ecological processes when developing a spatial index is essential (Tischendorf, 2001; Vos et al., 2001); especially in situations of complex habitat, when species can influence and change conditions like in the Maculinea system. Looking at spatial host ant or host plant distributions alone, would not allow to correctly assess habitat conditions for Maculinea butterflies. The important step is, to understand how these distributions contribute to the performance of a Maculinea population. This step enables us to derive the level of spatial aggregation, at which the effective contribution of host ants and host plants can be described spatially implicit and constant in time. Only from this point on, development of the spatial index is sound and straightforward.

To test power of the spatial index d_{empty}, we applied the methodological framework to assess landscape structures by their effect on population viability (sec. 5). This method is the final check for the spatial index. It ensures that d_{empty} is an appropriate statistic, which predicts persistence of Maculinea from measuring spatial host plant distribution.

Additionally, the method provides the link between spatial landscape structure and population viability (sec. 5.4.3). Our study showed that the explicit spatial host plant distribution is a component of Maculinea habitat, which has to be considered, when assessing suitability of a site for Maculinea persistence.

This can be done by calculating the index $d_{empty}(r)$ for the host plant distribution on a site. For this purpose, host plant coverage has to be assessed with a spatial resolution of foraging range of Myrmica host ants (2m to 3m; see caption of table 1.1) on the site. Practically, a grid with cells of size 2m x 2m is drawn on a map of the assessed host plant distribution. If there are host plants in a grid cell, the cell is evaluated as plant cell. Finally, $d_{empty}(r)$ is the average number of non-plant cells around plant cells within radius r (based on cell centres).

Hence, the spatial index $d_{empty}(r)$ is a handy measure to assess the suitability of the host plant distribution for Maculinea persistence on a habitat site. Although a simple measure, it is powerful. It originates from and thus incorporates dynamics and processes of the complex spatially explicit Maculinea model.

Deriving the index from a model has a major drawback. The spatial index is restricted to model assumptions. Does this mean, the index is only applicable in very special situations? No, if the definition of $d_{empty}(r)$ is not taken as absolutely fix but adaptable. In the following, we explain in one example, how the index can be flexibly adapted for different applications. This is possible for two reasons: First, because development of the Macu model is based on the HCET model (Hochberg et al., 1994; Clarke et al., 1997, 1998). Thus, we know how to link results from the Macu model to the case study of the Maculinea rebeli system (ch. 1). Second, the way, the index $d_{empty}(r)$ is derived from the Macu model, lets us understand its mechanism.

In the example, we assume a habitat site with Myrmica host ants and Myrmica non-host ants (see Hochberg et al., 1994). Non-host ants can adopt Maculinea caterpillars, however do not rear them sufficiently. Thus, the caterpillars do not survive. Myrmica non-host and host ants compete for suitable nest sites (i.e. areas where quality of host ant habitat is suitable for host and non-host species) (Elmes, 1991; Elmes et al., 1998; Hochberg et al., 1994). In this scenario, host plant distribution is not sufficient to predict persistence of a Maculinea population. Spatial distribution of host and non-host ants has to be taken into account (Clarke et al., 1997, 1998; Thomas et al., 1998a). However, the spatial index can be adapted to these new circumstances. When comparing results from the HCET and the Macu model, the main effect of non-host ants on host ant dynamics can be seen. Non-host ants might bud areas, where host ant nests have gone extinct due to parasitism of Maculinea caterpillars. For this reason, spatial distribution of host ants is restricted to areas which cannot be easily colonised by non-host ants, be it because nest sites are unsuitable for non-host species, the areas cannot be reached by budding or host ant nests do not go extinct because they are not in vicinity of host plants. The effect of non-host ants on Maculinea performance can be understood in terms of cell-effectiveness. By pushing away host ants, non-host ants will increase non-contributing and sink area. Simultaneously, they will decrease buffer and reproductive area. Therefore, number of butterflies should be decreased. Further, decrease of ratio of reproductive to sink area should decrease viability of Maculinea populations. Understanding these processes, a new index can be developed, taking into account effects of non-host ants. Following this approach, we expect that an index for the described scenario can be derived easily. Tischendorf (2001) found that correlation of landscape indices with measures of ecological processes can be inconsistent between different scenarios. Our reasoning shows that the index $d_{empty}(r)$ cannot be applied directly, when circumstances are different from those assumed for the model. Nonetheless, knowledge about the processes of the system allows to adapt the index to different scenarios in an educated way. Inconsistencies can be explained and avoided. In this thesis, we do not go further, however, adapting and testing the index to a variety of different Maculinea scenarios will be an interesting task for further investigations. Comparing the different modifications of $d_{empty}(r)$ should provide deeper understanding of differences of Maculinea systems.

The previous reasoning shows that understanding the mechanisms makes the index much more powerful. Now, we use our insight to interpret the results of an application of the index. It is common knowledge, often reported in anecdotal data (e.g. Discussion at Tagfalter workshop, Leipzig 2003) that Maculinea cannot be found within large meadows, which are densely occupied by the host plant. Applying the index to such a site would result in low values for all spatial scales of radius r, which reflects that the close host plant coverage does not support a buffer area. This corresponds to a recent finding: (Nowitzcki et al. at the MacMan conference Budapest) showed that activity patterns of Maculinea nausithous are concentrated around bushes, where coverage of host plant Sanguisorba officinalis is lower than in other parts of the habitat site.

7.4 Discussion

In this chapter, our earlier investigations are extensively enhanced. In chapters before, we restrict analysis to macroscopic effects of the Maculinea system. Most analysis are concentrated on persistence of the butterfly as a central measure to determine, whether habitat conditions are suitable for Maculinea populations. Macroscopic measures like intrinsic mean time to extinction t_m give answers to relevant questions for conservation. However, they do not allow mechanistic understanding of the reasons for persistence. Here, we turn to the microscopic level of the system dynamics. Our aim is to explain, how local processes contribute to persistence of a Maculinea population on a site.

The microscopic level in this system consists of spatiotemporal interacting Myrmica host ants and parasitic Maculinea butterflies. Resulting dynamics is multidimensional and highly complex. It is extremely difficult to find patterns in this large amount of data. Analysis is even more complicated, as different stochastic processes (resulting from simulations of different scenarios) need to be observed.

We cope with complexity by applying a contrasting method of model building. That is, we aggregate dynamical data as far as possible by simple parameters, with the purpose of accurately describing observed effects. Further on, we test accuracy of the aggregation. If variance of aggregated data does not noticeably influence the observations, the model is accepted. In following steps, variance of the dynamical data is ignored (or considered as implicit); hence further analyses are based on the model consisting of the approved simpler parameters. If variance in the data has an influence, we concentrate investigations on understanding that variance.

By means of this contrasting method, we for example select scenarios, which are sensitive for butterfly persistence, but insensitive to host plant coverage, or we build a model of cell effectiveness.

Cell effectiveness accounts for the contribution of host ants in a cell to performance of the Maculinea population. Cell effectiveness is an important concept. It defines a level of aggregation, where the spatiotemporal dynamics are described spatially and temporally implicit. It links macroscopic effects to the microscopic level of local processes. Cell effectiveness can be seen as the intermediate level of aggregation (Pascual & Levin, 1999).

The spatial distribution of cell effectiveness classes on a site reveals the reasons, why performance of a Maculinea population depends on the selected scenario. Population size and persistence are related to the amount of reproductive area. However, an area is reproductive only, if there are host plants, which can be reached by unparasitised budding host ants. If this condition is fulfilled, oviposition and rearing of Maculinea are supported. Additionally, the condition provides us with a spatial criterium, which defines a reproductive area: host plant distribution and dispersal ability of host ants must allow frequent budding of ant nest sites near host plants.

From this criterium we find limiting conditions for the persistence of Maculinea populations on a habitat site, which are all realised in the model:

- For low numbers of host plants, viability of Maculinea populations is low, because reproductive area is limited by the number of plants. This leads to a low number of butterflies. This small population is endangered from stochastic extinction.
- For large host plant patches, the reproductive area is restricted to the edge of the patch. The width of the reproductive area is limited by host ant budding range. A resulting small reproductive area leads to low numbers of butterflies and therefore to vulnerable Maculinea populations.
- For high host plant coverage, the area where host ants are not parasitised by Maculinea larvae (buffer zone) is small. Under these circumstances, a large part of the host ant population on the habitat site is exploited by Maculinea. For this reason, the reproductive area is limited by the size of the buffer zone (the number of unparasitised host ants). Persistence of the butterfly population depends on the ability of the ants in the buffer zone to recover and provide new ants for the parasitised area.

Conditions for the influence of host plant coverage on persistence of Maculinea populations can be derived form purely macroscopic analysis (e.g. sec. 6.4.2.2, sec. 6.4.5, Hochberg et al. (1994); Clarke et al. (1997, 1998); Thomas et al. (1998a); Griebeler & Seitz (2002); Mouquet et al. (2005). However, explanations for the conditions have to be guessed, because it is unknown, how microscopic processes build up macroscopic effects. In this chapter, we analysed the link of microscopic and macroscopic levels in Maculinea system. Result of this study is the microscopic explanation of macroscopic effects. We find the same conditions for persistence of Maculinea as in earlier studies. But, because they now can be explained mechanistically from microscopic processes, they are much more reliable. In this chapter, we 'proofed' the assumptions and guesses underlying earlier studies.

The listed conditions depend on host plant distribution on a site and on budding range. Therefore, based on these 'parameters' we construct the spatial index $d_{empty}(r)$. The index evaluates the mean number of cells without host plants around cells with host plants within a spatial scale. It is approved by two different ways: it is based on mechanistic understanding of local processes and its power is shown by PVA. Population viability analysis ensures that the index is linked to persistence of the Maculinea population.

We developed the index by means of a simulation model for a general type of Maculinea systems. But, we argue that the index can be adapted to different types of Maculinea systems and can be used to assess suitability of host plant coverage for persistence of Maculinea populations in the field.

Hence, the suggested spatial index $d_{empty}(r)$ is easily and flexibly applicable. It is meaningful and even mechanistically understood. Payne et al. (2005) ask for these properties for spatial indices used in conservation and management. We therefore suggest application of the index, when assessing habitat suitability of Maculinea sites.

Findings in this chapter should motivate detailed analysis of spatiotemporal systems. Methods used here can probably be applied effectively and successfully to investigate other systems.

Chapter 8

Prospects of developing a spatially implicit version of the Macu model

8.1 Introduction

Spatiotemporal models incorporating small-scale interactions are highly suitable to represent knowledge on individual behaviour from case studies. These models are typically high-dimensional, including large numbers of variables, distributed ecological interactions and stochasticity. Therefore, their macroscopic behaviour is complex, difficult to understand, and often restricted to special cases.
For this reason, deriving generic results from these models requires sophisticated analysis tools (e.g. ch. 7, Grimm et al. (2005) and Grimm & Railsback (2005, ch. 9)). Nonetheless, finding general principles for ecological systems requires generic results. These principles are important for building general theory (e.g. Turchin, 2001; Kitano, 2002), but as well for concrete problems in conservation biology (e.g. With, 2002; Norris, 2004; Huggett, 2005).
Generic, spatially implicit, typically analytical models provide a straight forward approach to generic theoretical results. But, to be easily treatable, these models are often kept at an abstract level. Results are difficult to be interpreted in concrete realistic ecological problems, as probably important processes are omitted and mechanisms of the system cannot be analysed in detail.
There is large theoretical interest in combining both approaches to gain insight in the links between complex, individual-based, spatially explicit models and abstract, spatially implicit models on the basis of aggregated measures. Much effort has been invested in finding the spatial scale, which allows aggregation (up-scaling) of pattern-forming small-scale interactions in predator-prey models (De Roos et al., 1998; Donalson & Nisbet, 1999; Pascual & Levin, 1999; Pascual et al., 2001, 2002a,b; Petrovskii & Malchow, 2001; Wootton, 2001; Keeling et al., 2002). In most of these studies, analytical models are enhanced to incorporate individuals and an explicit representation of space. Comparing results of these models at different spatial scales allows to assess the intermediate scale, below which explicit individual small-scale interactions can be ignored.
However, this approach does not allow to analyse population dynamical systems acting on heterogeneous landscapes. In ch. 7 of this thesis, we took a different approach: Instead of starting from an analytical model, we analysed and aggregated dynamics of the complex spatially explicit Macu model, until we derived a spatially implicit description of the dynamics:

cell effectiveness (sec. 7.2.9.2). Knowing that dynamics in the Macu model can be described spatially implicit, we are now in the position to derive a spatially implicit version of the model. Comparing results from spatially explicit and spatially implicit versions can provide further theoretical insight in the Maculinea system, in the same way as it is done in the earlier studies mentioned above. But, as the Macu model is based on a case study model, results can be interpreted in a concrete ecological context (ch. 1).

The spatially implicit version of the Macu model is only one of several spatially implicit Maculinea models, which were developed during the last years (Hochberg et al. (1992); Mouquet et al. (2005); Clarke et al. (2005) and (Thomas, pers. comm.)). Although simple, these models give realistic results. However, they are based on strong assumptions about dynamics of the Maculinea system. Here, we can derive a spatially implicit model from a spatially explicit mechanistic version. This background should enable us to test some of the assumptions.

Finally, there is the need for simple realistic Maculinea models for single habitat sites in the MacMan project (Settele et al., 2002), to develop a model on landscape scale.

In the following, we give some rules, how to derive a spatially implicit version of the Macu model. We then develop a simplified deterministic version. Results are briefly compared to outcome of the spatially explicit model. We only provide first results, which shall serve as an outlook on potential further studies.

8.2 Description of a mean field version of the Macu model

The results of the analysis in sec. 7.2 encourage us to develop a mean field model for the spatially explicit processes of the system. For this purpose, the Macu model of ch. 1 is simplified by aggregating system variables on the level of cell effectiveness.

8.2.1 Spatially implicit system variables

Variables for a mean field description of the Maculinea system are created by accumulating values from all cells of one effectiveness class[1]. They are listed here:

C_P: number of cells with host plants. This value is given by the host plant distribution and is constant in time.

$N(t)$: number of Maculinea eggs at time t. The number of adult butterflies is determined by $\frac{N(t)}{e}$, where e is the number of eggs per butterfly (see below).

$Z(t)$: number of Myrmica ants in cells with host plants at time t. This value contains ants from two effectiveness classes: reproductive cells and sink cells. However, sink cells are almost free of host ants. Number of reproductive ants Z approximately is the number of ants in reproductive cells.

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[1] Several of the presented mean field measures are build by accumulating values of cells from two effectiveness classes. This is done for a technical reason. It allows to accumulate over cells which either contain or do not contain host plants. Host plant cells are known in advance, as these cells are determined by the external factor host plant distribution. In contrast, the effectiveness class of a cell depends on system dynamics. It therefore can be determined only after the simulation.
Clearly, the two criteria of cell effectiveness and host plant occupancy are different. Especially cell effectiveness cannot be ignored, when it is important to measure e.g. the spatial area of a reproductive zone. However, the mean field measures we suggest to analyse population dynamics are almost equal for both criteria. Differences using either one or the other of these criteria can be ignored.

$C_{AP}(t)$: number of cells with host plants and Myrmica nests. This value, in good approximation, is similar to the number of nests in reproductive cells.

$B(t)$: number of host ants in buffer cells.

C_B: number of buffer cells. This value accumulates all cells without host plants, which are close enough to cells with plants, to allow budding of empty cells. According to results in ch. 7.2, cells which are not directly parasitised, do not go extinct. Hence, C_B is constant in time.
In the following mean field approach, we assume unlimited budding range for the host ants. Therefore, by definition, $C_B = 900 - C_P$. That is, C_B is equal to the number of cells without host plants.

The variables, defined in this section, allow a spatially implicit description of the Maculinea system.
Additionally, for simplicity, we set

$$\begin{aligned} e &= \omega \cdot \lambda_f \\ \beta &= ratio\_of\_budders \end{aligned}$$

where ω, λ_f and $ratio\_of\_budders$ are parameters of the spatially explicit Macu model (see tab. 1.1)

8.2.2 Rules to transform the spatially explicit model into a spatially implicit version

We simplify the spatially explicit model described in ch. 1 according to following rules:

1. Host ant dynamics is tracked only in cells which contribute to the process – in reproductive cells ($Z(t)$) and in buffer cells ($B(t)$).
2. To calculate the number of host ants, a mean field approximation is applied for different effectiveness classes separately. That is, numbers of host ants in all cells of one effectiveness class are assumed to be equal. The number of ants per reproductive cell is determined by $\frac{Z(t)}{C_{AP}(t)}$; the number of ants per buffer cell is $\frac{B(t)}{C_B}$.
3. In sec. 7.2 it is argued that the dynamical processes are spatially restricted to certain areas. In the mean field approach, we follow these findings. Hence, processes are limited to cells of the appropriate effectiveness class:
   - Reproduction of Maculinea butterflies takes place in reproductive cells.
   - Extinction of host ant nests only takes place in reproductive cells.
   - Successful budding events are always directed from buffer cells to reproductive cells.
4. The mean field approach requires a non-spatial version of the budding process. It is realised in the way that ants from all buffer cells are assumed to undertake one attempt to bud an empty cell in the reproductive area. The probability to find an empty reproductive cell is $\frac{C_P - C_{AP}(t)}{C_P}$. If an empty reproductive cell is found, the budding attempt is successful with probability ρ, otherwise ants do not bud in this time step. Budding parameter ρ is used to account for reduced reachability of the spatially explicit models in different scenarios.

Rule 1 is a strict condition, which assumes that sink cells and non-contributing cells do never take part in host ant dynamics. However, in sec. 7.2 we show that number of host ants in these cells is not strictly constant. We account for this weak definition of cell effectiveness classes, by using the number of cells with plants C_P instead of the number of reproductive cells in the mean field model. The exact number of cells occupied at time t by host ants and host plants $C_{AP}(t)$ corrects this simplification. Using C_P instead of the number of reproductive cells has another advantage. C_P is an external parameter given for a scenario, whereas the number of reproductive cells is determined internally from system dynamics.

Budding parameter ρ is the only free parameter in the mean field model in comparison to the spatially explicit version. All other relevant parameters (see tab. 1.1) are directly taken from the explicit model and are therefore fixed. Hence, parameters as reproduction rate of a host ant nest R have the same value in both versions of the Maculinea model. Aggregated parameters as number of host plants C_P are exactly determined from the host plant distribution.

Parameter ρ is used to adjust the mean field model to the explicit model. Such an adjustment is necessary, because spatially induced effects cannot be simulated with the implicit model. As known from sec. 7.2, budding is a process, which is acting on a small spatial scale. Nature of the mean field approach does not allow to include small scale processes. Budding parameter ρ accounts for the aggregated effects of local budding processes on the scale of a site. ρ therefore depends on local spatial structures of host distributions and on budding range σ.

A value of $\rho = 1$ assumes that in a scenario which realises budding as described in rule 4, every empty cell which is found by a group of budding ants will be colonised. Smaller values of ρ reduce the probability that a budding process is successful.

8.2.3 Approximation for the expected population sizes

In the sections above, we presented a generic way to create a spatially implicit version of the Macu model. However, to give a prospect on further research, in this chapter, we only want to show that it is possible to create a simplified spatially implicit version of the Macu model and derive some first results. Therefore, we undertake a further simplification: the stochastic model is approximated by a deterministic version. In the following, instead of keeping track of the complete stochastic distribution of the system variables, we approximate them by their expectation values.

8.2.4 Model equations

We give model description in the temporal course of one simulation step.

8.2.4.1 Distribution of Maculinea eggs

In the spatially explicit model, eggs are randomly distributed to cells with host plants. This process results in a Poisson distribution with mean $N(t)/C_P$. Proceeding to the distribution of eggs, it is decided, if the eggs are found by Myrmica host ants. This corresponds to a binomial process with probability $p = \frac{C_{AP}(t)}{C_P}$. Finally, each ant nest invests, at most, the fraction m of its size for caterpillar reproduction (see sec. 1.3.2.4). Hence, we must ignore all Maculinea eggs, which exceed fraction m times the nest size.

We now turn to the mean field approach. The Poisson distribution[2] of the egg distribution on plants is denoted by $P(x = j; \lambda = \frac{N(t)}{C_P})$, where j indicates the number of eggs per host plant. In the mean field approach, all nests in vicinity of host plants are assumed to contain the same amount of host ants $\frac{Z(t)}{C_{AP}(t)}$. Therefore, $j_{max}(t) = m \cdot \frac{Z(t)}{C_{AP}(t)}$ is the highest number of caterpillars which can be reared in the nest. Hence, the probability to find a cell with host plant and j potentially reared caterpillars can be calculated as

$$d_{eggs}^{pot}(j,t) = \begin{cases} P(x = j; \lambda = \frac{N(t)}{C_P}) & j \leq j_{max}(t) \\ 1 - \sum\limits_{k=0}^{j_{max}(t)} P(X = k; \lambda = \frac{N(t)}{C_P}) & \text{else} \end{cases} \tag{8.1}$$

However, caterpillars are only reared in a cell, when the cell additionally contains an ant nest. Hence, the probability to find k nests with j reared butterflies in a cell is

$$d_{eggs}(j,t) = B(x = j; n = \text{trunc}(C_P \cdot d_{eggs}^{pot}(j,t)); p = \frac{C_{AP}}{C_P}) \tag{8.2}$$

where B(x,n,p) denotes a binomial distribution[3]. We have to truncate[4] the value of n to avoid non-integer numbers of cells.

We now calculate the expected number of reared butterflies within generation t. The formula strongly simplifies, because expectation value of a binomial distribution is calculated as $n \cdot p$. Hence, we receive

$$N^{reared}(t) = \frac{C_{AP}(t)}{C_P} \sum_{j=0}^{j_{max}} [j \cdot \text{trunc}(C_P \cdot d_{eggs}^{pot}(j,t))] \tag{8.3}$$

According to model description in sec. 1.3, the number of butterfly eggs in the next generation is

$$N(t+1) = e \cdot N^{reared}(t)$$

The number of host ants (caterpillar equivalents) in cells with an ant nest and a host plant is reduced to

$$\hat{Z}(t) = Z(t) - N^{reared}(t)$$

8.2.4.2 Inner nest dynamics

Within nest dynamics is modelled in the same way as in sec. 1.3.2.5. But, all nests contain the same amount of ants (mean field approach). Extinction process takes place only in cells, where parasitism is possible (sec. 8.2.2). It can be calculated by the following rule:

If mean size of nests is below threshold Z_T, a nest can go extinct with probability $p^{ext} = 1 - \frac{\hat{Z}(t)}{Z_T}$ (compare sec. 1.3.2.5). For expectation values, we receive

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[2] Poisson probability distribution function $P(x, \lambda) = \frac{\lambda^x}{x!} \cdot e^{-\lambda}$ where λ equals mean and variance (McLaughlin & McLean, 1999)

[3] Probability distribution function of the binomial distribution: $B(x, n, p) = \binom{n}{x} \cdot p^x (1-p)^{(n-x)}$ with mean is $n \cdot p$ (McLaughlin & McLean, 1999)

[4] trunc(x) returns the next smaller integer value of the real number x.

if $(\frac{\hat{Z}(t)}{C_{AP}(t)} < Z_T)$

$$\begin{aligned}\tilde{C}_{AP}(t) &= \tfrac{\hat{Z}(t)}{Z_T}\\ \tilde{Z}(t) &= \tfrac{(\hat{Z}(t))^2}{Z_T C_{AP}(t)}\end{aligned}$$

else, nothing changes:

$$\begin{aligned}\tilde{C}_{AP}(t) &= C_{AP}(t)\\ \tilde{Z}(t) &= \tfrac{\hat{Z}(t)}{\tilde{C}_{AP}(t)}\end{aligned}$$

Reproduction of host ants takes place in all cells, independent of presence of host plants. Corresponding to eq. 1.4, we receive

$$\begin{aligned}\bar{Z}(t) &= R\frac{\tilde{Z}(t)}{1+\Theta\frac{\tilde{Z}(t)}{\tilde{C}_{AP}(t)}}\\ \bar{B}(t) &= R\frac{B(t)}{1+\Theta\frac{B(t)}{C_B}}\end{aligned}$$

8.2.4.3 Budding

The budding process, in the mean field model, is strongly simplified in contrast to the original spatially explicit model. First, according to rule 3 in sec. 8.2.2, only Myrmica ants from cells without plants can colonise cells with plants. Second, budding is no longer restricted to a local area. Instead, each budding cell can bud with probability $p_{bud}^{pot}(t) = \rho\Gamma\bar{B}(t)/C_B$ one of all cells on the site, where Γ controls the probability that ants start to bud (tab. 1.1) and parameter ρ accounts for effective budding range and spatial structures (see sec. 8.2.2). The budding process is successful, when the cell, to be budded, does not contain an ant nest, else, nothing happens. Probability of reaching an empty cell is $p_{\text{empty cell}}(i,t) = \frac{C_P - \tilde{C}_{AP}(t+1) - i}{C_{all}}$ where i is the number of cells which are already budded by host ants within generation t. C_{all} is the total number of cells. It is $C_{all} = field\_x \cdot field\_y = 30 \cdot 30 = 900$ in this model version (standard parameters in tab. 1.1). Probability $p_{\text{empty cell}}$ accounts for the change in probability, after a budding event was successful, because with each newly occupied cell, the probability to reach an empty cell is reduced for further budders.

Budding can be seen as a series of Bernoulli trials with changing probability of success, when a budding event was successful. When the number of already budded cells is i (see above), the probability of budding success is

$$\begin{aligned}p_{bud}(i,t) &= p_{\text{empty cell}}(i,t) \cdot p_{bud}^{pot}(t)\\ &= \frac{C_P - \tilde{C}_{AP}(t) - i}{900}\Gamma\rho\frac{\bar{B}(t)}{C_B}\end{aligned}$$

To calculate the expected number of newly budded cells, we estimate the mean number of budding attempts until budding was successful in the binomial process. Afterwards, probability of budding success is reduced and the next Bernoulli trials start with remaining buffer cells. The number of attempts, which are needed to successfully bud an empty cell, follows a Geometric distribution[5]. $G(x, p = p_{bud})$. The expected number of events, to bud the i-th cell

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[5] Probability distribution function of a geometric distribution $G(x,p) = p \cdot (1-p)^{x-1}$, with mean value $\frac{1}{p}$ (McLaughlin & McLean, 1999)

successfully, is $k = \frac{1}{p_{bud}(i,t)}$. The expected number of successful budding events achieved by C_B budding cells is

$$C_P^{bud}(t) = \min\left(\{x \in [0; C_B] \mid \sum_{i=0}^{x} \frac{1}{p_{bud}(i,t)} \geq C_B\}, (C_P - \tilde{C}_{AP}(t))\right) \tag{8.4}$$

Eq. 8.4 ensures, that maximally all cells with host plants can be occupied by host ants. The budding process changes population sizes as follows

$$\begin{array}{rcl} Z(t+1) & = & \bar{Z}(t) + \beta \cdot C_P^{bud}(t)\frac{B(t)}{C_B} \\ B(t+1) & = & \bar{B}(t) - \beta \cdot C_P^{bud}(t)\frac{B(t)}{C_B} \\ C_{AP}(t+1) & = & \tilde{C}_{AP}(t) + C_P^{bud}(t) \end{array} \tag{8.5}$$

where β denotes the ratio of ants, which are leaving an ant nest (sec. 8.2.1).

8.2.4.4 Model output

It is useful, for model output at the end of the procedure, to divide the number of Maculinea eggs $N(t+1)$ by parameter e, to receive the number of adult butterflies.
Interestingly, in the frame of this deterministic model, the mean probability of Maculinea population extinction per time step $p_{ext}(t)$ can be estimated from eq. 8.2. The population goes extinct in time step t, if we find all nests to contain no butterfly caterpillars. That is: $j = 0$.

$$\begin{array}{rcl} p_{ext}(t) & = & d_{eggs}(j = 0; t) \\ & = & (1 - \frac{C_{AP}(t)}{C_P})^{C_P(1-\exp(-\frac{N(t)}{C_P}))} \end{array} \tag{8.6}$$

From $p_{ext}(t)$, the intrinsic mean time to extinction t_m can be calculated according to equation 3.9.

8.3 Comparison of the spatially implicit model version with the spatially explicit Macu model

In the following, we verify that the spatially implicit mean field model reproduces results from the explicit model in high accuracy. Budding parameter ρ is used to adjust the mean field model to the spatially explicit model (sec. 8.2.2). Objective of the adjustment is to minimise the sum of mean square error of median number of butterflies and mean number of butterflies. The adjustment is done for all host plant distributions used in ch. 6 at the same time. Hence, in this overview study, we do not explicitly account for different local spatial plant distributions.
Fig. 8.1 shows a comparison between results of the spatially explicit Maculinea model (circles) and of the approximated mean field model (line). Simulation results of the spatially explicit model are gained by methods described in ch. 2. We choose budding range $\sigma = 12m$ to achieve long distance dispersal of host ants. With the initial host ant distribution ants3 (high number of initially distributed host ants, refer to sec. 6.2.1), the risk of unwanted extinction due to initial conditions is reduced (ch. 6). Host plant distributions are varied in the same way as in ch. 6.
The mean field model is adjusted to simulation results of the explicit model (mean number of butterflies: $R^2 = 0.94$, median number of butterflies: $R^2 = 0.95$). With this fit, budding

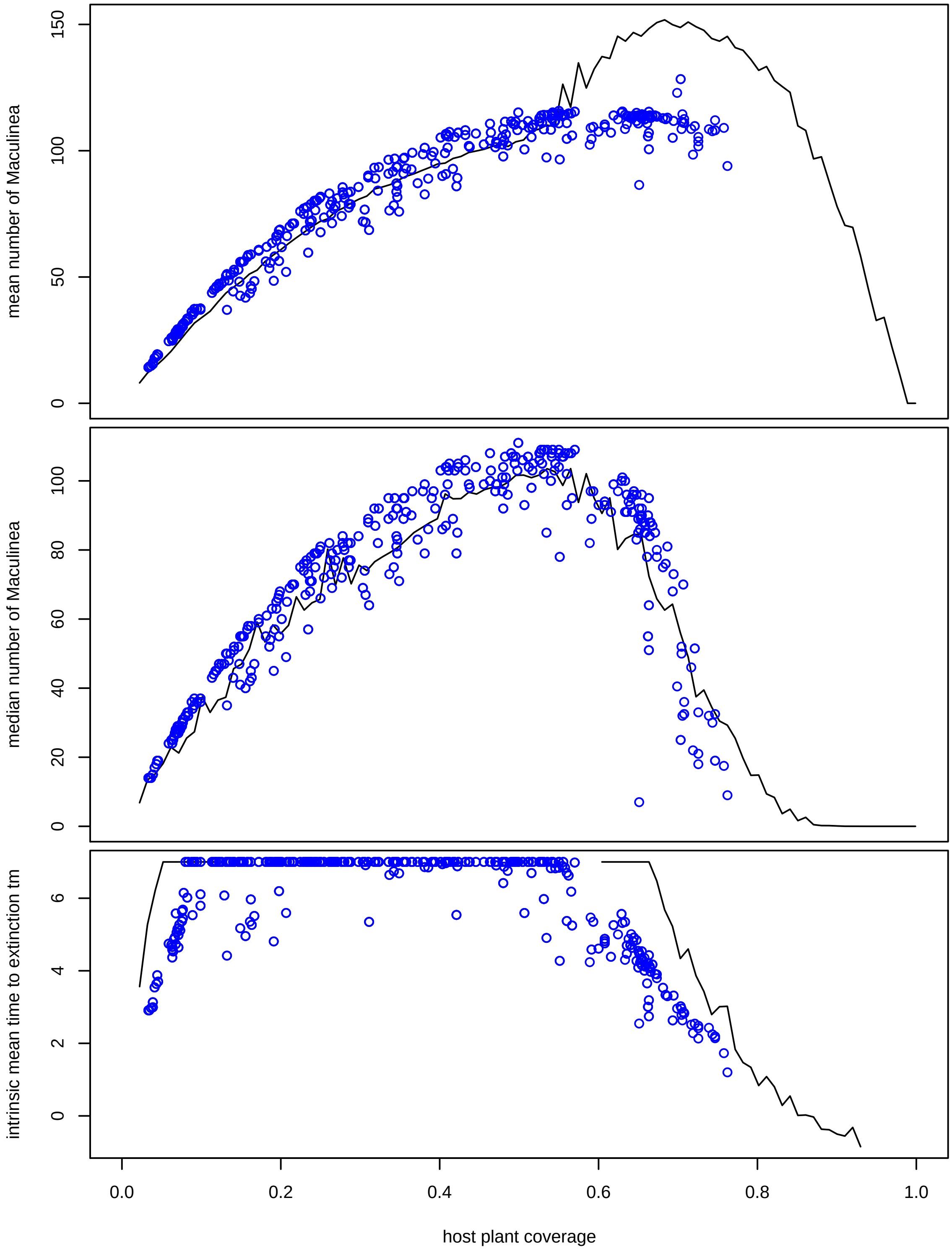

Figure 8.1: Results from the mean field model (lines) and the spatially explicit model 'Macu' (circles) are compared. Both models are parameterised with the standard parameter set in tab. 1.1. For the spatially explicit Macu model we used host ant scenario: budding range $\sigma = 12$, initial host ant distribution: ants3. The mean field model was run with colonisation parameter $\rho = 0.7$. Correlation of mean number of butterflies: 94%; correlation of median number of butterflies: 95%

parameter $\rho = 0.7$. The value of ρ is reasonable. On the one hand, with a budding range $\sigma = 12m$, host ant budding approximately fulfills the condition of unlimited dispersal, which would result in $\rho \approx 1$. On the other hand, the probability of successfully finding an empty nest is reduced in the explicit model, because of border effects. Budding parameter $\rho = 0.7$ indicates that about 30% of budding attempts fail because cells are searched outside of the habitat site.

Correspondence of results from spatially explicit and mean field model is close, as can be seen in fig. 8.1. The best reproduction of shape of a curve is accomplished for the median number of Maculinea butterflies (central graph). Both, the initial increase of median number of butterflies at low levels of host plant number as well as subsequent decline due to higher number of host plants is modelled well. In contrast, in the lower graph, intrinsic mean time to extinction t_m is overestimated for very small and intermediate number of butterflies. Anyhow, qualitative shape of the curve is correctly indicated by the mean field model.

A wrong shape of the curve is found for the mean number of Maculinea butterflies (top graph). For intermediate numbers of plants, the spatially explicit model (circles) indicates a slight decline, whereas the mean field model calculates an increase and a further strong decline. A possible reason for this discrepancy is the deterministic approximation of the mean field model. It is known that approximations, which only take into account expectation values of stochastic population models, might overestimate results from the stochastic model (Lande et al., 2003). For example in the Maculinea system, deviation of the expectation value in low numbers of Maculinea butterflies can be amplified during a cycle. It can be assumed that variance might damp the system. However, to test the influence of variance to the mean-field model, simulation experiments are required, which are beyond the scope of this preliminary study.

As well, it is interesting to analyse the shape of the curve calculated by the deterministic approximation of the mean field model (solid line in fig. 8.1). It is striking that dependence of population data on number of host plants is not smooth. Instead, the line is jagged, which indicates a non-linear relation. In stochastic simulations, such small deterministic fluctuations can hardly be distinguished from stochastic variance. However, they could be the reason for some concentrations or absences of data points (circles) in fig. 8.1.

Another interesting observation is that we do not find predator-prey cycles in the deterministic approximation of the mean-field model, if the number of host plants is below 500. With less than 500 host plants, either the system is in its equilibrium state or it switches between two states. This is in contrast to dynamics of the spatially explicit model, where cycles can be observed at all numbers of host plants. At about 500 host plants, the period of cycles increases in the spatially implicit deterministic version as well as in the spatially explicit version of the Macu model. Then duration of periods are almost the same in both model versions.

The reason, why the deterministic version is cyclic, when the number of host plants is above 500 plants, can be found in a retardation of Maculinea reproduction. This can be seen in eq. 8.2 for small numbers of butterfly eggs. When $N(t)$ is small, the probability distribution function in eq. 8.2, which describes spatial Maculinea egg distribution on host plants, can be approximated by a binomial distribution. This is, because it can be assumed that the few Maculinea eggs are solitarily distributed to the many host plants (the probability to find two eggs on the same plant is small). The approximated binomial distribution $B(p = \frac{C_{AP(t)}}{C_P}; n = N(t))$ determines the amount of eggs, placed in cells with host plants and Myrmica host ants. Thus, the expected reproduction rate of Maculinea butterflies for low numbers of eggs is

$$e\frac{C_{AP}(t)}{C_P}$$

where e is the number of offspring per adult butterfly, when all eggs are placed in suitable cells (sec. 8.2.1). Only for a reproduction rate greater than 1, the Maculinea population can grow. Hence, there is a condition for the least number of cells, which needs to be occupied by both, host plants and host ants, to allow growth of the Maculinea population:

$$C_{AP}(t) > \frac{C_P}{e} \tag{8.7}$$

The condition in ineqn. 8.7 is independent of the actual size of ant nests. Although, nests might be large, Maculinea larvae cannot exploit them, because there is not more than one caterpillar in a nest.

The negative effect of single caterpillars to host ant nests is small. Hence, growth of the ant population is only slightly hindered by Maculinea butterflies. As long as the number of ant nests is too small to support growth of the Maculinea population, these few nests can grow up to large sizes.

In contrast, when the threshold of a growth rate equal to 1 has been overcome, the growing butterfly population can profit from large host ant nests. Consumption on the large resource leads to high numbers of butterflies and to strong overexploitation effects.

Because reproduction of Maculinea can depend on different mechanisms at different times during a population cycle, the system is destabled.

There is an interesting point: The time, how long it takes for a small population of butterflies to fulfill the condition in ineqn. 8.7, depends on the amount of buffer cells in the system. It is stated in the model description of the mean field model (sec. 8.2.2) that empty cells can be colonised only from ants, which are coming from nests in buffer cells. For this reason, budding from buffer to reproductive cells triggers, at which moment in a cycle the Maculinea population starts to grow.

In this study, parameter $e = \omega \cdot \lambda_f = 4$ (see sec. 8.2.1 and standard parameter set tab. 1.1). Fig. 8.2 shows the percentage of time steps, in which condition 8.7 is not fulfilled. There is a clear threshold at approximately 500 host plants. Below this threshold condition 8.7 is almost always fulfilled. Fig. 8.2 demonstrates that overexploitation in the Maculinea system becomes severe, when the butterfly population destroys too many host ant nests. If that happens, colonisation from the buffer area is essential to recover the reproductive area. Budding from the buffer area takes time and provokes population cycles and further overexploitation.

8.4 Discussion

With the mean field model, we present a further step towards simplification of the Maculinea model. In contrast to ch. 1, where simplifications are introduced ad hoc by discussion of plausibility, in this chapter, simplifications are based on extensive analysis of system and processes. Before developing the mean field model, mean field properties of the spatially explicit model have been known, already. The mean field model is a reformulation of the spatial version. Similarity of both models is shown with surprising accuracy, even by using a first order deterministic approximation of the mean field model.

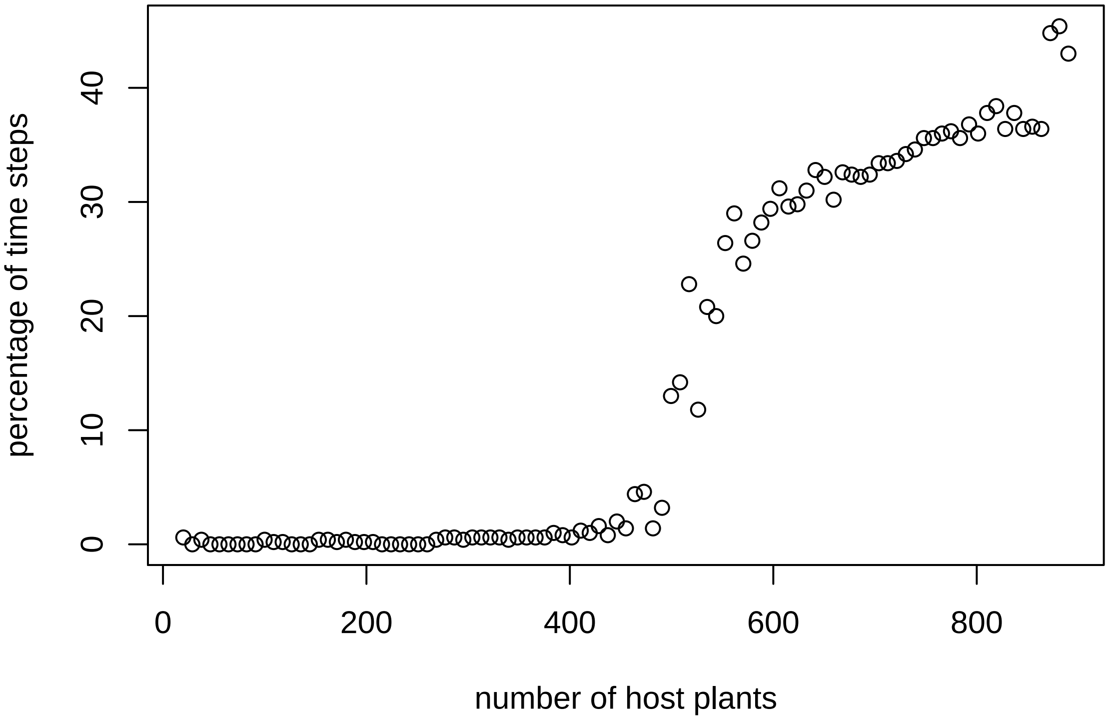

Figure 8.2: Percentage of time steps, when $C_{AP}(t) \leq \frac{C_P}{e}$ versus the number of cells with host plants C_P. If number of host plants is below 500, condition 8.7 is usually fulfilled.
Results from the deterministic mean field model; parameters as in fig. 8.1. $C_P = 900$ is excluded, because there is no buffer area left.

Hence, in many cases, the complex spatially explicit model can be substituted by the mean field model. Advantages will arise from simpler model structure, which can be understood easier and from quicker simulation routines. Different applications of the mean field model can be imagined. For example in the frame of EU-project MacMan. In this project, additional to analysis of local populations of Maculinea butterflies within a patch, population dynamics shall be investigated on landscape scale. That means, different local populations or subpopulations are observed for their interactions. In this context, the fast Maculinea mean field model could be used as a module. It could be integrated to simulate nearly realistic behaviour of local populations.

The simple mean field model can be applied as well, to better understand the Maculinea system. The deterministic model version, developed in this chapter, is used to generate new hypothesis on reasons for overexploitation. Depending on the size of the butterfly population, different processes are relevant. For low numbers of butterflies, number of host ant nests is decisive for reproduction rate. Instead, for large numbers of Maculinea individuals, size of the ant nests is relevant. Change in process types retards population development and provokes cyclic behaviour. In the deterministic approximation to the mean field model, cycles occur only for high numbers of host plants, because, for low numbers of host plants, deterministic mean butterfly numbers are high and allow only for the latter mechanism. In contrast, in the spatially explicit model, quasi-cycles can be found independently of the number of host plants. Tests reveal that, due to stochastic variance in spatially explicit simulations, Maculinea population size can drop to low values even for low numbers of host plants. For this reason, switching of reproduction types occurs and leads to a time delay. It can be observed that the resulting cycles have larger amplitudes (higher maxima) than in cases, where the time delay does not occur.

In sec. 2.3.1, it is discussed if observed quasi-cycles in the Maculinea system are 'endogenous resonant' or 'perturbed limit cycles'. Findings of the deterministically approximated mean field model indicate that both forms of quasi-cycles can occur in the system. For low numbers of host plants, the deterministic model calculates a stable population size (or switching between two close values). Hence, quasi-cycles in the stochastic spatially explicit model are probably provoked by perturbation of the underdamped system ('endogenous resonant'). Instead, for high numbers of host plants, the deterministic approximation shows limit cycles. Therefore, it can be assumed that in the spatially explicit model, these limit cycles transform to stochastically perturbed limit cycles.

In recent publications, Mouquet et al. (2005) suggest a spatially implicit analytical model for the support of management actions in a Maculinea arion system. Some of their results are similar to findings in ch. 6 and in this chapter. However, the study of Mouquet et al. (2005) is based on strong assumptions of spatial implicity, which are not explained in the publication. Our results in the last two chapters can firstly prove that the Maculinea system indeed can be described spatially implicit. Secondly, we show that there is a threshold-like change in exploitation regimes with increasing number of host plants. This change is emulated by Mouquet et al. (2005), when they argue that cycles in their Hassell-type single species model indicate increased risk of extinction for Maculinea. However, as they use a Hassell model, they find periodicity of one simulation step, which does not reflect duration of population cycles measured in the field. In contrast, our range of periodicity could explain them. For this reason, care has to be taken, when following their arguments on mechanisms for cyclic Maculinea populations.

In this chapter, we presented the development of a spatially implicit version of the Macu model. This model version is an application of results derived in the comprehensive analysis of the spatiotemporal dynamics of Maculinea systems, performed in this thesis. Aim of this chapter was, to give an example for the potential of the analyses in this thesis and to give an outlook on further investigations. For this reason, analysis in this chapter have a preliminary character.

Part V

Synopsis

Summary

Analysis of spatiotemporal population dynamics of interacting species is difficult because of the multitude of spatially distributed processes. However, understanding these systems is crucial for the development of methods to protect endangered species communities.

In this work, we develop a concept to analyse complex multi-species systems. It is adjusted to an important tasks of nature protection: conservation of species in their habitat. The hierarchical approach allows to detect scenarios, which might endanger a community of species on an aggregated level. Stepwise reducing aggregation, mechanisms can be identified, which negatively influence species of the community.

Following this concept, we analyse effects of species-interaction and spatiotemporal host distribution on persistence of Maculinea populations at isolated habitat sites. During their life cycle, parasitic Maculinea butterflies change their hosts. Young Maculinea caterpillars feed on the host plant, at which they have emerged from the egg, without impacting the plant seriously. However, after reaching 4th instar, a caterpillars leave their plants and wait in their vicinity for adoption by ants of genus Myrmica. Once accepted, the caterpillars parasite the ant colony. Depending on the kind of Maculinea species, they might directly feed on the ant brood or become fed by worker ants. In both cases, a sufficiently high number of adopted caterpillars can damage an ant nest to the extent that it will be abandoned by the ants. Surviving caterpillars pupate and emerge as adult butterflies from the nest in summer.

Spatial distribution of initial host plants (oviposition plants), implies a spatial distribution of 4th instar larvae. Therefore, parasitism of Maculinea caterpillars on Myrmica host nests is spatially distributed. This leads to pattern formation in the spatial distribution of host ant nests.

Self-organised pattern formation depends on the dispersal of the interacting species. In general, host plants change their spatial distribution only on a long time scale. For the Maculinea system, this distribution can be considered as stationary. It is assumed that adult Maculinea butterflies can reach every host plant of the habitat site for oviposition. Host ants have a small foraging area (radius about 2-3 metres) around their nest. Within this area, they can find Maculinea caterpillars for adoption. The process of colonising empty nest sites (budding process) happens on a larger scale than foraging, but on a smaller scale than movement of Maculinea butterflies.

Methodology

We develop a generic spatially-explicit rule-based simulation model for a Maculinea system (Macu-model). To achieve natural realism, the Macu-model is based on an existing realistic and mostly validated model for Maculinea rebeli (Hochberg et al., 1992, 1994; Elmes et al.,

1996; Clarke et al., 1997, 1998; Thomas et al., 1998a). However, as we aim to analyse the effects of spatially distributed parasitic interactions on persistence of Maculinea populations, we emphasise these interactions. This means that we consider only one Myrmica species and ignore inner-specific competition of young Maculinea caterpillars on their initial host plants, which would disturb spatial patterns resulting form Maculinea-Myrmica interactions. But, we enhance flexibility of the budding process, allowing Myrmica ants to colonise empty nest sites in larger distances (variable dispersal speed of host ants).

To analyse the influence of different spatially relevant parameters on the performance of a Maculinea population, scenarios are created that form the input parameters of the Macu-model. Each scenario consists of a spatial host plant distribution, an initial spatial host ant distribution and a parameter σ (budding-range), which defines the probability distribution of colonising distances of ants. The scenarios represent spatial distributions (density and clumping varied) of hosts in a Maculinea habitat. The scenarios allow to analyse, how different spatial host distributions affect population dynamics of the Maculinea system. In the next step, we are interested, how they influence persistence of the butterfly population.

Population viability analysis (PVA) is a standard method for single species systems. However, the Maculinea system consists of interacting species with more complex dynamics than it is known from single species systems. There is still no standardised methodology for PVA of multi-species systems. By means of literature research and investigations on simple examples and the complex Macu model, we derive a phenomenological description of distributions of extinction times for populations in a large class of systems of interacting species. We find in analytical calculations that the long term behaviour of distributions of times to extinction in multi-species systems can be analysed with the $\ln(1 - P_0)$-method suggested for single species systems (Wissel & Stöcker, 1991; Stephan, 1992; Stelter et al., 1997; Frank et al., 2002; Grimm & Wissel, 2004). The resulting measures of persistence are the intrinsic mean time to extinction t_m and a coefficient c_1. t_m indicates viability of an established population. c_1 is an indicator for the probability that a population reaches the established state before going extinct. It can be used to assess risk of extinction during an initial transient phase of system dynamics (e.g. after recent colonisation of a habitat site). Applicability of the method is assessed by means of analytical calculations and numerical simulations. The method shows robust and reliable results. To our knowledge, this is the first PVA-method, which can be applied to a large range of species communities.

Robustness of the method enables us to perform a new type of PVA analysis, which allows to efficiently assess viability of populations under many different conditions. This achievement is essential in the context of spatial analysis, where high-dimensional parameter spaces have to be scanned through. With comparably low effort, the method provides an overview on how different parameters influence population persistence. Aim of this screening study is, to grasp all major effects.

Going a step further, we develop a landscape analysis method for multi-species systems. For that purpose, suitability of different landscapes is assessed for their ability to sustain particular populations. Suitability is measured by population persistence. Therefore, dynamics of the system and requirements of the populations are taken into account when assessing suitability. However, it is not yet clear, which spatial properties of a landscape are relevant for its suitability. Here, methodology of landscape ecology can be applied to characterise landscapes geometrically and calculate spatial statistical indices. If there is a relation between an index and suitability, the index almost certainly characterises features of the landscape, which are important for population viability.

Therefore, such a spatial index is an important tool for nature conservation. It can be easily calculated for a given landscape by means of spatial statistics. However, it comprises knowledge about the importance of landscape features on population viability – it is automatically an indicator for habitat suitability for species of the system.
There is another situation, where the methodology provides important insight in the effect of landscape features on the species systems. This is the case, when the spatial statistical index evaluates landscapes equally, although population persistence in these landscapes strongly differs. This means that the index does not cover all relevant landscape elements adequately. However, we learn from the analysis, for which landscapes there might occur unexpected population dynamical processes. These special landscapes are worth a more detailed investigation. Hence, expensive and difficult landscapes analysis can be concentrated on few examples.
In this work, analysis follows two principles:

- It is hierarchically structured. That means, system dynamics are investigated on different levels of aggregation. Studies on the basis of highly aggregated measures (e.g. population persistence) aim on a comprehensive overview of effects, but details of the dynamics are perceived only implicitly. Stepwise reduction of levels of aggregation allow insight in the underlying details down to the complete complexity of the spatiotemporal dynamics.

- The analysis is effect driven. In this way, it can be decided, whether it is worth to decrease the level of aggregation. If the influence of a factor on the system is obvious on a high level of aggregation, there is no need for detailed studies on lower aggregation levels. Directing the analysis at effects allows to efficiently concentrate on critical factors.

To study the effects of spatiotemporal species interaction on persistence of Maculinea butterflies, we perform landscape analysis on the basis of multi-species PVA. 'Landscapes' consist of stationary host plant distribution and initial host ant distribution. In detailed studies of spatiotemporal dynamics of the system, we analyse, how small-scale interaction of Maculinea and its hosts influence performance of the butterfly population.

Results

Population dynamics

For the Macu model, we find quasi-cyclic population sizes of Maculinea butterflies and Myrmica host ants, resulting from their host-parasite interactions. Small-scale interactions are synchronised throughout areas with host plants, because adult butterflies can reach all host plants of a site for oviposition.
In simulation runs, it can be seen that the spatial distribution of host ants adapts to the spatially distributed parasitism from Maculinea caterpillars. Areas without host plants (unexploited areas) are completely inhabited by host ants. In areas with host plants (exploited areas) mean density of host ants is lower. Ant nests show dynamics. They are abandoned or nest sites are recolonised.
Because of spatial segregation of exploitable and non-exploitable areas and by small scale dispersal of host ants (budding), areas of different effectiveness for Maculinea population performance can be distinguished on a Maculinea habitat site:

Sinks: In areas of homogeneous dense host plant coverage, there are very few host ants.

These areas are sinks for the Maculinea population. Maculinea eggs are lost, because the developed 4th instar larvae are not adopted by their second host, the ants.

Reproductive area: In areas with heterogeneous host plant distribution, Maculinea can reproduce successfully. The reproductive area restricts to close vicinity of host plants. Under condition that there is at least one host plant within the foraging area of a host ant nest, Maculinea caterpillars can complete their development. If the ant nest becomes abandoned because of parasitic pressure from Maculinea caterpillars, surrounding unexploited ant nests can recolonise the area close to the plant.

Buffer: Non-exploitable ant nests in an area of heterogeneous host plant distribution can be considered as buffer of the ant resource for butterfly caterpillars. Ants in this area cannot reach a host plant, when foraging. They, therefore, do not adopt Maculinea caterpillars. However, the nests are close enough to colonise vacant nest sites in the vicinity of host plants.
Colonising ants from the buffer area build new nests in the reproductive zone. This process results in a lack of worker ants in the original nests of the buffer area. However, nest size hardly drops to such low numbers that a nest would be abandoned. For this reason, the buffer area is densely covered with ant nests.

Non-contributing area: Host ant nests, which are far away from host plants (further than the usual dispersal distance), do not contribute to the performance of Maculinea populations. In the Macu model, these nests cannot colonise vacant nest sites, because all sites are occupied in their surrounding. Size of these nests is around their capacity.

Consequently, number of host plants is not the only decisive factor for performance of a Maculinea population. As well it is important how well empty nest sites in the vicinity of host plants can be colonised by host ants.
Dynamic of the system during one cycle is as follows: a large butterfly population overexploits its ant resource in the reproductive area. This leads to a decline of both populations, butterflies and ants. Then, the small butterfly population has to survive a phase with only few host ants in the reproductive area, until host ant population in this area has recovered sufficiently.
We find two different mechanisms, which limit re-growth of the Maculinea butterfly population:

1. There is a sufficiently large number of host ant nests in the reproductive area. But these nests are too small to rear a large amount of butterfly caterpillars.

2. There are too few ant nests in the reproductive area. Hence, too many Maculinea eggs are lost on host plants, where there are no ant nests in the neighbourhood.

The two mechanisms lead to different types of system dynamics. In the first case, it is possible that host ant nests in the reproductive area recover on their own, because they grow with only low parasitic pressure from the few butterflies. Colonising ants from the buffer area support system recovery. In contrast, in the second case, contribution of the buffer is essential. Host ant nests in the reproductive zone in general are too small for colonisation. Therefore, they cannot compensate the lack of ant nests. Colonisation of vacant nests sites in the reproductive area by host ants from the buffer area is necessary.
In the second case, host parasite cycles have longer periods and larger amplitudes than in the first case. We show that the time delay, provoked by the time it takes to compensate the

lack of host ant nests in the reproductive area, leads to limit cycles. In the first case, cycles result from stochastic disturbance of the systems equilibrium state. The second case dynamic occurs, if host ant density in the area of host plants declines below a critical threshold. The probability for this event increases with increasing host plant density. Hence, interaction of deterministic dynamics and stochastic events decide on the momentary type of dynamics of the system. To our knowledge, this is a newly described phenomenon for population systems.

Extinction dynamics in multi-species systems

Risk of extinction is high, when populations consist of only few individuals, because of demographic effects. This general law is found in a phenomenological study of extinction risk for a general class of interacting species systems, too. Having a look on the distributions of times to extinction[6] of interacting species systems, we find similarities and differences to the single species case. Similarities are the different momentary extinction risks (rates of extinction) between an initial transient and an established phase of the system. In the established phase, long term extinction dynamics can be described as a Markov process. For this reason, we can show analytically that the single-species PVA method (see above) can be applied to analyse multi-species systems.

However, differences between single and multi-species systems can result in important differences of persistence of populations. For example, it is found that deterministic cycles in population sizes can affect momentary extinction risk. It is possible that, when the cycle is in its maximum, populations effectively never go extinct, meanwhile in the minimum, momentary extinction risk is drastically high. If this is the case, estimates of population size, counted only over a short period, can lead to incorrect assessment of the risk of extinction of a population.

In systems of interacting species, an initial transient phase (e.g. after colonisation of a new habitat site) can have a strong influence on persistence of the population. In simulations of the Macu model, we observe that it takes up to 50 generations until the system reaches its established state.

In this context, a new type of bottleneck effect is found. It expresses as a bimodal distribution of times to extinctions: either the population goes extinct during the first 20 generations (with high risk of extinction) or it survives for the maximum of 5000 generations (in the simulation). The bottleneck effect arises from interaction of Maculinea with its hosts. If this effect occurs, in principle, conditions are good to support long-term persistence of the butterfly population (survival for 5000 generations in the simulation). However, the populations undergo an initial phase of adaptation. During this phase, the spatial distribution of host ants is changed. Before this change, the butterfly population is highly endangered of going extinct. Afterwards, the risk has become extremely low. Effectively, the Maculinea population is able to improve its 'habitat conditions' during the initial phase.

Influence of host distribution on survival of Maculinea populations

For the Maculinea system, all these types of extinction behaviour are realised, depending on the selected scenario. In the following, we describe how these scenarios (that are spatial host distributions) influence persistence of Maculinea.

Analysing population dynamics, it is found that the spatial distribution of host ants adapts

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[6] Times to extinction of one of the populations of the interacting species system

to the spatially distributed parasitic pressure from Maculinea butterflies. For this reason, in the established state of the system, no effects of initial host ant distribution on persistence of Maculinea populations can be found. In contrast, spatial distribution of host plants has a main effect. Thus, the host plant distribution can be considered as landscape structure of the Maculinea system on the site.

Understanding the effects of host plant distribution on performance of the butterfly population, we can derive rules of thumb for the structure of suitable host plant distributions. In general heterogeneous host plant distributions of intermediate density are a good option. Problematic are:

Very low host plant densities: Low host plant densities limit the size of Maculinea populations and they become vulnerable to demographic effects. However, it is found that established Maculinea populations cope surprisingly well with small numbers of host plants.

But, colonisation of such sites is only possible, if Myrmica host ant density is high.

Very high host plant densities: If host plant density is too high, Maculinea caterpillars exploit Myrmica ants throughout the entire habitat site. There is only few space left for the host ant population to develop undisturbed from parasitism (Buffer area is too small). This situation leads to temporary overexploitation of the resource and to strongly fluctuating population sizes.

Overexploitation can be strong enough that too few host ants (as resource for Maculinea caterpillars) are left for following Maculinea generations to survive. The population goes extinct. For that reason, sites with an extremely dense host plant coverage are unsuitable for Maculinea populations.

Clumped host plants: If host plants are clumped, only the border of a plant patch can be used as reproductive area by Maculinea. Because of limited dispersal distance (budding range σ) ants from the buffer zone cannot reach further into the patch. Therefore, the inner area of a plant patch is a sink for Maculinea (host plants for oviposition, but no host ants for further rearing 4th instar larvae).

For this reason, suitable habitat is effectively restricted to only a part of the site. This leads to smaller Maculinea populations than on sites with a comparable amount of heterogeneously distributed host plants. Strength of the clumping-effect depends on dispersal distance of host ants. In general, dispersal distance is short. Therefore clumping of host plants can have a noticeable negative effect on persistence of Maculinea populations.

To make assessment of suitability of host plant distributions easier, we develop a spatial index. This landscape index evaluates whether host plants belong to the reproductive or the sink area. Included into the calculation of the index is an assessment, how good a host plant can be reached by colonising host ants.

We test power of the index with the Macumodel for a large amount of scenarios. The PVA based test includes population dynamical processes and therefore requirements of the system on the host plant distribution. Except for very low host plant densities, for which the absolute number of host plants is the most important factor, results of the index are good. High index values are a clear indication for suitable host plant distributions.

Main results of the thesis in short

- A method for population viability analysis (PVA) of interacting-species systems is developed.
- A method for landscape analysis is developed, which includes species behaviour (i.e. population ecological processes) into the assessment of spatial structures.
- In the Maculinea system, two different types of host parasite cycles occur. Behaviour of the system depends on momentary population sizes.
- In multi-species systems a bottleneck-effect can occur, because the colonising population and habitat conditions need time to adapt to each other. The colonising species influences its new environment.
- Rules of thumb and a spatial index for suitability of spatial host plant distributions, to support Maculinea populations, are derived.

Zusammenfassung

Die Analyse raumzeitlicher Populationsdynamiken interagierender Arten ist auf Grund der Vielzahl verteilt auftretender Prozesse schwierig. Dennoch hängt die Entwicklung von Maßnahmen zum Schutz von Artengemeinschaften vom Verständnis der Dynamiken ab.

In dieser Arbeit wird ein Konzept zur Untersuchung komplexer Mehrartensysteme entworfen. Es orientiert sich an einer zentralen Aufgabe des Naturschutzes: der Erhaltung vorhandener Arten in einem Lebensraum. Ein hierarchisches Vorgehen erlaubt auf grober Aggregationsstufe Szenarien zu erkennen, die einer Artengemeinschaft gefährlich werden können. Durch schrittweise Verringerung der Aggregation wird untersucht, welche Mechanismen die Gefährdung hervorrufen.

Diesem Konzept folgend analysieren wir Effekte raumzeitlicher Wirtsverteilung und Artinteraktion auf die Überlebenschance von Maculineapopulationen auf isolierten Habitatflächen.

Parasitische Schmetterlinge der Gattung Maculinea (Ameisenbläulinge) haben einen interessanten Lebenszyklus. Im Sommer legen die adulten (erwachsenen) Weibchen nach der Paarung Eier auf artspezifische Eiablagepflanzen. Die sich entwickelnden jungen Raupen bleiben während der ersten Häutungsstadien exklusiv auf diesem ersten Wirt (im folgenden Wirtspflanze), den sie aber nicht wesentlich beeinträchtigen. Zu Beginn des vierten Häutungsstadiums werden die Pflanzen verlassen. Am Boden angekommen, verharren die Larven in der Nähe ihrer Wirtspflanze. Sie warten darauf, von Wirtsameisen der Gattung Myrmica gefunden, adoptiert und mit ins Ameisennest genommen zu werden. Nicht adoptierte Larven sterben. Im Nest, leben die Larven als Parasiten der Ameisen. Es gibt zwei typische Lebensweisen: so genannte Kuckucksarten lassen sich von Arbeiterameisen füttern, wovon zwar die Schmetterlingslarven profitieren, die Ameisenbrut im Nest wird aber vernachlässigt und in ihrer Entwicklung beeinträchtigt. So genannte räuberische Maculineaarten fressen direkt an der vorhandenen Ameisenbrut. Der Parasitismus kann so stark sein, dass Ameisen ihre parasitierten Nester aufgegeben. Die Maculinealarven überwintern, verpuppen sich und verlassen erst als entwickelte adulte Schmetterlinge das Ameisennest.

Auf Grund der räumlichen Verteilung der Wirtspflanzen ist eine räumliche Verteilung der Maculineaeier vorgegeben. Diese führt zu räumlich verteiltem Parasitismus an Wirtsameisen. Daher kann eine selbstorganisierte Strukturierung der Wirtsameisennester auf einer Maculineafläche erwartet werden.

Die Strukturbildung hängt vom Dispersal (Ausbreitung) der interagierenden Arten ab. Es wird gemeinhin angenommen, dass adulte Maculinea Schmetterlinge jede Wirtspflanze auf einer Habitatfläche erreichen können. Von den Wirtspflanzen ist bekannt, dass sich ihre räumliche Verteilung nur sehr langsam über viele Generationen hinweg ändert. Sie wirken für das Maculinea-System ortsfest. Die Wirtsameisen haben einen kleinen Fouragierradius von etwa 2-3m um das Nest, in dem sie Nahrung suchen und auch Maculinea Larven finden können. Auf einer größeren, dennoch lokal begrenzten Skala verläuft der Prozess der Nestneugründung.

Dabei verlässt ein Teil der Arbeiterameisen sein Nest und besiedelt einen geeigneten leeren Nistplatz. Dieser Vorgang wird budding (engl. Sprossung) genannt.

Methodik

Um unsere Analyse durchzuführen konstruieren wir ein räumlich-explizites regelbasiertes Simulationsmodell für ein generelles Maculineasystem. Im Modell werden Effekte räumlich verteilter Artinteraktionen betont, um deren Einfluss auf die Persistenz einer Maculineapopulation möglichst deutlich beobachten zu können. Obschon stark abstrahiert, bleibt das entstandene so genannte Macu-Modell naturnah. Denn unser Modellaufbau basiert auf dem bereits existierenden HCET-Modell für die Art Maculinea rebeli, dessen Ergebnisse mehrfach an Feldbeobachtungen getestet wurden (Hochberg et al., 1992, 1994; Elmes et al., 1996; Clarke et al., 1997, 1998; Thomas et al., 1998a). Im Unterschied zum HCET-Modell berücksichtigt das Macu-Modell keine Konkurrenz zwischen verschiedenen Wirtsameisen, und die innerspezifische Konkurrenz von Maculinealarven auf Wirtspflanzen is unterdrückt. Im Gegenzug ist der Ausbreitungsmechanismus für Wirtsameisen flexibilisiert worden. Dadurch werden Nestgründungen in größerer Entfernung vom Ursprungsnest als im HCET-Modell möglich. Mit diesen Änderungen wurde das Modell auf die Untersuchung von Effekten räumlicher Wirtsverteilung und parasitischer Interaktion zugeschnitten. Durch Modellvergleich mit dem HCET-Modell ist es möglich, die Ergebnisse des Macu-Modells für ein natürliches System einzuschätzen.

Um den Einfluss verschiedener raumrelevanter Parameter auf die Entwicklung einer Maculinea-Population zu testen, werden Szenarien erzeugt, die dem Macu-Modell als Parametersatz übergeben werden können. Ein Szenarium besteht aus einer räumlichen Wirtspflanzenverteilung, einer räumlichen Anfangsameisenverteilung und einem Parameter budding-range σ, der die Wahrscheinlichkeitsverteilung der Entfernungen zwischen einem Ursprungsnest und einem neu zu gründenden Nest charakterisiert. Jedes Szenarium stellt eine Konfiguration von Wirten in einem Maculinea-Habitat dar. Die räumlichen Verteilungen werden durch verschiedene unterschiedlich stochastische Punktprozesse erzeugt. Klumpungen der Wirte auf verschiedenen Skalen sind realisiert.

Die Szenarien ermöglichen die Untersuchung der Effekte verschiedener räumlicher Wirtsverteilungen auf die Populationsdynamik einer Maculineapopulation. Uns interessiert, wie die Szenarien die Persistenz (Überlebenschance) einer Maculinea Population beeinflussen.

Vergleichende Populations-Überlebens-Analysen (PVA) sind eine Standardmethode für Ein-Art-Systeme. Das Maculinea-System ist aber ein Mehr-Arten-System. Für diese von ihren Dynamiken her deutlich komplexeren Systeme gibt es bisher keine standardisierte Vorgehensweise.

Mit Hilfe von Literaturrecherche und Beobachtungen an einfachen Modellen und am komplexen Macu-Modell gelingt eine phänomenologische Beschreibung der zeitlichen Verteilung von Aussterbeereignissen von Populationen in einer breiten Klasse von Systemen interagierender Arten. Diese Verteilungen lassen sich in ihrem Langzeitverhalten mit einer von Wissel & Stöcker (1991); Stephan (1992); Stelter et al. (1997); Frank et al. (2002); Grimm & Wissel (2004) für Ein-Art-Systeme vorgeschlagenen Methode analysieren. Die dabei auftretenden Persistenzmaße sind die intrinsische mittlere Lebensdauer t_m, die die Chancen für Persistenz einer etablierten Population anzeigt und Koeffizient c_1, der die Chance für das Erreichen des etablierten Zustands charakterisiert. Alternativ kann c_1 als ein Indikator für unterschiedliches Aussterberisiko während einer transienten Anfangsphase (z.B. nach Neubesiedelung einer Habitatfläche) und der etablierten Phase interpretiert werden. Die Persistenzmaße t_m und c_1 können in ihrer Bedeutung vom Ein-Art-System auf interagierende Arten übertragen werden. Damit wird nach unserem Wissen zum ersten Mal eine PVA-Methode vorgeschlagen, die für verschiedene Artengemeinschaften eingesetzt werden kann. Analytisch und in numerischen Simulationen wird gezeigt, dass diese Methode, selbst unter kritischen statistischen Bedingungen, qualitativ richtige Ergebnisse liefert (Robustheit).

Diese letzte Eigenschaft erlaubt eine neuartige breitangelegte PVA-Analyse, um effizient die Effekte vieler Szenarien testen zu können. Sie ist insbesondere essentiell, wenn der Effekt räumlicher Strukturen analysiert werden soll, denn die Methode ermöglicht es, hochdimensionale Parameterräume zumindest ausschnittsweise zu scannen. Dadurch kann man sich mit vergleichsweise geringem Aufwand einen Überblick verschaffen, wie die Persistenz durch unterschiedliche Parameter beeinflusst wird. Man zielt auf die möglichst vollständige Erfassung aller auftretender Effekte ab.

Mit Hilfe dieser breitangelegten PVA entwickeln wir eine Methode zur Landschaftsanalyse in Mehrartensystemen. Dabei werden unterschiedliche mögliche Landschaftsstrukturen auf deren Eignung zum Erhalt von Artengemeinschaften geprüft. Die Habitateignung wird durch die Persistenz der Arten gemessen. Folglich wird die Dynamik des Artensystems in die Bewertung der Landschaften mit einbezogen. Habitateignung ist ein Maß, das die Ansprüche der Artengemeinschaft an die Landschaft einbezieht.

Es bleibt die Frage, warum eine komplexe Landschaftsstruktur die Bedürfnisse einer Artengemeinschaft besser befriedigt als eine andere. Zur Klärung greift man auf Methodik der Landschaftsökologie zurück: man bestimmt geometrische (raumstatistische) Eigenschaften der Landschaften – gemessen als Landschaftsindizes. Zeigt sich, dass ein Index Landschaftsstrukturen ähnlich bewertet wie die Habitateignung, kann man erwarten, dass der Index gerade die Eigenschaften der Landschaft erfasst, die für das Überleben einer Artengemeinschaft relevant sind. Ein solcher Index fördert unser Verständnis des ökologischen Systems und seiner Interaktion mit Landschaftsstrukturen. Er kann genutzt werden, um Pflegemaßnahmen für den Naturschutz zu entwickeln.

Interessant können aber auch einzelne Landschaften sein, die, obwohl vom Index gleich bewertet, sich in ihrer Habitateignung unterscheiden. In einem solchen Fall erfasst der Index nicht alle relevanten räumlichen Strukturen der Landschaft. Hier ist es sinnvoll, die inkonsistent bewerteten Landschaften einer genaueren Analyse zu unterziehen. Dadurch lassen sich Gründe finden, warum die Population mit den verschiedenen Landschaftsmustern unterschiedlich zurecht kommt. Diese Vorgehensweise erlaubt es, aufwändige Raumanalysen auf Landschaften zu beschränken, welche die Populationsdynamik unterschiedlich beeinflussen – bei denen man also Unterschiede in der räumlichen Struktur erwarten kann.

Der Analyse in dieser Arbeit unterliegen zwei Prinzipien:

- Sie ist hierarchisch strukturiert. Das bedeutet, man untersucht Dynamiken des System auf unterschiedlichen Aggregationsstufen. Eine hohe Aggregation (wie zum Beispiel Persistenz) ermöglicht Überblicksstudien. Details werden implizit wahrgenommen. Schrittweise Reduktion der Aggregation gibt den Blick frei auf Details, bis hin zur vollen Komplexität der raumzeitlichen Dynamik.

- Die Analyse ist effektorientiert. Auf diese Weise entscheidet man, ob es sich lohnt, die Aggregationsstufe zu verringern. Erkennt man bereits in einer hohen Aggregationsstufe, wie ein Faktor das System beeinflusst, ist eine detaillierte Untersuchung nicht mehr nötig. Sich bei der Analyse an den Effekten zu orientieren hilft, den Analyseaufwand zu beschränken, indem man sich auf die wesentlichen Faktoren konzentriert.

Zur Bestimmung des Einflusses raumzeitlicher Artinteraktionen auf die Persistenz von Maculinea führen wir eine PVA-gestützte Landschaftsanalyse durch. Ortsfeste Wirtspflanzenverteilung und Anfangsameisenverteilung auf einer Fläche werden dabei als Landschaft betrachtet. In Detailuntersuchungen der raumzeitlichen Dynamik wird analysiert, wie lokale Interaktionen von Maculinea mit seinen Wirten die Entwicklung der Schmetterlingspopulation beeinflussen.

Resultate

Populationsdynamik

Das Macu-Modell zeigt quasi-zyklisch schwankende Populationsgrößen von Maculinea Schmetterlingen und Myrmica-Ameisen, hervorgerufen durch die Wirts-Parasit-Interaktion der beiden Spezies. Lokale Interaktionen sind in allen Gebieten mit Wirtspflanzen synchronisiert, da adulte Schmetterlinge ohne Einschränkung die gesamte Fläche überfliegen und jede Wirtspflanze zur Eiablage nutzen können.
Man beobachtet in Simulationsläufen, dass sich die räumliche Verteilung der Wirtsameisen der Parasitierung durch Maculinea Schmetterlinge anpasst. Gebiete ohne Wirtspflanzen, das sind nicht parasitierbare Gebiete, sind komplett von Wirtsameisen besiedelt. In Gebieten mit Wirtspflanzen (parasitierbare Gebiete) ist die mittlere Ameisendichte geringer. Ameisennester zeigen Dynamik, werden aufgegeben und frei gewordene Nistplätze werden wiederbesiedelt. Durch die räumliche Trennung parasitierbarer und nicht-parasitierbarer Bereiche und durch die lokale Ausbreitung von Wirtsameisen (budding range σ), teilt sich eine Maculineafläche in Bereiche unterschiedlicher Funktion für die Entwicklung der Schmetterlingspopulation ein:

Senken: In Bereichen mit homogener Wirtspflanzenbedeckung halten sich Wirtsameisen kaum auf. Diese Bereiche bilden Senken für Maculinea. Abgelegte Eier sind verloren, da die sich entwickelnden Larven nicht von Wirtsameisen adoptiert werden.

reproduktiver Bereich: In Bereichen mit heterogener Pflanzenverteilung kann Maculinea erfolgreich reproduzieren. Der reproduktive Bereich beschränkt sich auf die direkte Nachbarschaft von Wirtspflanzen (mindestens eine Pflanze im Fouragierradius der Ameisen). Dort können adulte Schmetterlinge Eier ablegen. Die Larven wachsen in den vorhanden Ameisennestern auf. Werden Wirtsnester durch intensive Parasitierung zerstört, können umliegende nicht parasitierbare Nester die parasitierbaren Gebiete wiederbesiedeln.

Puffer: Die nicht parasitierbaren Gebiete im Bereich heterogener Pflanzenverteilung kann man als Speicher der Ameisenresource des Schmetterlings ansehen. Die Nester in diesem Bereich haben keine Wirtspflanzen im Fouragierbereich. Doch gibt es Wirtspflanzen innerhalb des Ausbreitungsgebiets. Kolonisierende Ameisen aus Nestern des Pufferbereichs bilden neue Nester im reproduktiven Bereich. Die kolonisierenden Ameisen fehlen in den Puffernestern. Die Nester werden jedoch selten so klein, dass sie aufgegeben werden. Daher ist der Pufferbereich immer dicht mit Ameisennestern besiedelt.

nicht beitragender Bereich: Ameisennester, die nicht einmal im Ausbreitungsgebiet Wirtspflanzen haben, tragen nicht zur Maculineaentwicklung bei. Nestgrößen liegen im Bereich der Kapazität. Im Macu-Modell können diese Nester keine neuen Nistplätze kolonisieren, da keine leeren Plätze im Ausbreitungsgebiet vorhanden sind.

Folglich entscheidet nicht alleine die Anzahl vorhandener Wirtspflanzen über die Entwicklung von Maculineapopulationen, sondern auch wie gut die Bereiche der Wirtspflanzen durch Wirtsameisen besiedelt werden können.
Innerhalb eines Zyklus des parasitären Systems sieht die Dynamik folgendermaßen aus: viele Maculinea Schmetterlinge überweiden die vorhandene Ameisenresource im reproduktiven Bereich. Dadurch sinken beide, Schmetterlingspopulation und Ameisenpopulation. In der Folge muss die kleine Maculineapopulation eine Phase überstehen, in der nur wenige kleine Ameisennester im reproduktiven Bereich vorhanden sind, bevor die Ameisenpopulation im reproduktiven Bereich wieder ausreichend angewachsen ist.
Wir finden zwei verschiedene Mechanismen, die das Anwachsen der Maculineapopulation bei kleiner Populationsgröße limitiern:

1. Es gibt genügend Ameisennester im reproduktiven Bereich, aber diese sind zu klein, um eine ausreichende Menge adulter Schmetterlinge hervorzubringen.
2. Es gibt zu wenige Ameisennester, so dass schon zu viele Maculinea Eier verloren gehen, weil sie auf Wirtspflanzen abgelegt werden, bei denen sich kein Ameisennest im Fouragierradius befindet.

Die beiden Mechanismen führen zu unterschiedlicher Dynamik des Systems. Im ersten Fall ist eine Selbsterholung der Ameisen im reproduktiven Bereich durch Nestwachstum möglich. Kolonisierende Ameisen aus dem Pufferbereich wirken unterstützend. Hingegen ist im zweiten Fall der Puffer essentiell. Die Ameisennester im reproduktiven Bereich sind für gewöhnlich zu klein um zu kolonisieren. Daher können sie den Mangel an Nestern im reproduktiven Bereich nicht selbst ausgleichen. Dies geschieht erst durch den Puffer.
Man findet im zweiten Fall längere Wirts-Parasit-Zyklen mit größeren Amplituden als im ersten Fall. Es wird gezeigt, dass die Zeitverzögerung die durch den Mangel an Nestern entsteht zu Grenzzyklen führt, während die Zyklen im anderen Fall als Störungen des Gleichgewichts stochastisch angeregt werden. Die Dynamik des zweiten Falls tritt ein, wenn eine kritische Schwelle der Ameisendichte im Bereich der Wirtspflanzen unterschritten wird. Die Wahrscheinlichkeit dafür nimmt mit der Wirtspflanzendichte zu. Die Interaktion der deterministischen Dynamik und einzelne Zufallsereignisse entscheiden, welchem der beiden Dynamiktypen das System gerade unterliegt. Uns ist solches Verhalten von Populationssystemen bisher nicht bekannt.

Aussterbeverhalten in Mehrartensystemen

Das Aussterberisiko einer Population ist auf Grund demographischer Effekte erhöht, wenn die Population nur aus wenigen Individuen besteht. Dieser generelle Satz bewahrheitet sich auch bei der phänomenologischen Untersuchung des Aussterbeverhaltens einer Klasse generischer Systeme interagierender Arten.
Betrachtet man die Verteilung der Aussterbezeiten[7] von interagierenden Populationen findet man, verglichen mit Aussterbezeitenverteilungen von Ein-Art-Systemen, Gemeinsamkeiten und Unterschiede. Zunächst die Gemeinsamkeiten: man erkennt in beiden Verteilungen, dass

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[7] Verteilung der Zeiten, nach denen die eine der interagierenden Populationen ausstirbt.

sich das Aussterberisiko zwischen einer anfänglichen transienten und einer späteren etablierten Phase unterscheiden kann. In der späteren Phase des etablierten Zustands kann Aussterben, auf großer Zeitskala, als Markov-Prozess beschrieben werden. Auf Grund dieser Gemeinsamkeit im Aussterbeverhalten wird analytisch gezeigt, dass die oben erwähnte PVA-Methode auch zur Analyse der bisher nicht berücksichtigten Mehr-Arten-Systeme eingesetzt werden kann.

Die Unterschiede zwischen den beiden Systemen können dennoch gravierende Auswirkungen auf die Persistenz von Populationen haben. Man findet zum Beispiel, dass sich deterministische Zyklen in der Individuenzahl einer Population auf deren momentanes Aussterberisiko auswirken können. Es ist möglich, dass beim Durchlaufen des Maximums der Populationsgröße praktisch kein Aussterberisiko besteht, während beim Durchlaufen des Minimums, nur wenige Generationen später, das Risiko drastische Ausmaße annimmt. In einem solchen Fall können momentane Populationsgrößenschätzungen zu einer falschen Bewertung des Aussterberisikos einer Population führen.

In Systemen interagierender Arten kann das Aussterberisiko während der transienten Anfangsphase (z.B. nach Besiedlung einer Fläche durch eine neue Art) eine kritische Rolle spielen. In Simulationen des Macu-Modells wird beobachtet, dass sich das System erst nach etlichen (bis zu 50) Generationen im etablierten Zustand befindet.

In diesem Zusammenhang wird auch eine neue Art des Bottleneck-Effekts[8] gefunden. Dieser drückt sich in PVA als eine bimodale Verteilung der Aussterbezeiten aus. Entweder die Population stirbt mit erheblichem Risiko während der ersten 20 Generationen aus, oder sie überlebt bis zur maximalen Simulationsdauer von 5000 Generationen. Der Bottleneck-Effekt entsteht durch Interaktion des Schmetterlings mit seinen Wirten. Prinzipiell sind alle wesentlichen äußeren Komponenten für eine Langzeitpersistenz des Schmetterlings gegeben (erkennbar am Überleben während 5000 Generationen). Jedoch durchlaufen die Populationen einen anfänglichen Anpassungsprozess. Dieser verändert die räumliche Verteilung der Wirtsameisen. Erst danach ist Persistenz des Schmetterlings ermöglicht. Effektiv könnte man sagen, dass Maculinea während der transienten Phase in der Lage ist, äußere Bedingungen (die räumliche Verteilung seiner Wirte) an seine Bedürfnisse anzupassen.

Einfluss der Wirtsverteilung auf das Überleben von Maculinea Populationen

Im Maculinea-System findet man alle eben genannten möglichen Aussterbeverhalten abhängig von der Wahl des Szenariums. Im folgenden wird der Einfluss der Szenarien (also der räumlichen Verteilung der Wirte) auf die Persistenz von Maculinea beschrieben.

Bei der Untersuchung der Populationsdynamik stellt man fest, dass sich Myrmica Wirtsameisen in ihrer räumlichen Verteilung an die parasitierenden Schmetterlinge anpassen. Dies hat zur Folge, dass in etablierten Maculineasystemen kein Einfluss der Anfangswirtsameisenverteilung[9] auf die Persistenz einer Maculineapopulation gefunden wird. Die Verteilung der Wirtspflanzen hingegen zeigt einen wesentlichen Effekt. Diese ortsfeste Wirtspflanzenverteilung gliedert die Habitatfläche räumlich. Man kann die Wirtspflanzenverteilung als Landschaftsstruktur des lokalen Maculineasystems betrachten.

In diesem Sinne lassen sich Faustregeln für geeignete Pflanzenverteilungen formulieren. In der Regel ist eine heterogene Wirtspflanzenverteilung mittlerer Dichte gut für das Überleben von

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[8] Bottleneck-Effekt: Populationen durchlaufen nach Besiedlung einer Fläche eine Phase akuter Aussterbegefahr, obwohl die äußeren Bedingungen prinzipiell für die Art geeignet wären

[9] z.B. der Ameisenverteilung vor einer Besiedlung der Fläche durch Maculinea

Maculineapopulationen geeignet. Problematisch für den Erhalt von Maculinea sind:

Sehr geringe Pflanzendichten: Geringe Pflanzendichten limitieren die Größe einer Maculineapopulation und machen sie anfällig für demographische Effekte. Dennoch findet man, dass etablierte Maculineapopulationen überraschend gut auch mit wenigen Wirtspflanzen zurecht kommen.
Zur Neubesiedlung sind solche Flächen aber nur geeignet, wenn Myrmica Ameisen in hoher Dichte vorkommen.

Sehr hohe Pflanzendichten: Ist die Wirtspflanzendichte auf einer Fläche zu hoch, können Myrmica Ameisen flächendeckend von Maculinea parasitiert werden. Der Ameisenpopulation bleibt nur wenig Raum, um sich ungestört vom Parasitismus entwickeln zu können (der Pufferbereich des Systems ist zu klein). Dies führt zu zeitweiliger Überweidung der Resource und damit zu stark schwankenden Populationsgrößen. Maculinea kann die Ameisenpopulation derartig zerstören, dass folgenden Maculineagenerationen nicht ausreichend Resource zur Verfügung steht. Die Population stirbt aus. Daher sind Flächen mit extrem dichter Wirtspflanzenbedeckung für Maculinea völlig ungeeignet.

Lokal dicht stehende Wirtspflanzen (Klumpung): Sind die Pflanzen lokal dicht geklumpt, wird nur der Rand eines Pflanzenpatches zur erfolgreichen Reproduktion von Maculinea genutzt. Auf Grund limitierter Ausbreitungsdistanz (budding range σ) kann nur dieser äußere so genannte reproduktive Bereich durch nichtparasitierte kolonisierende Myrmica Ameisen aus dem Puffergebiet erreicht werden. Im reproduktiven Bereich können Ameisennester, die wegen zu starker Parasitierung zerstört wurden, durch Nestneugründung von Ameisen aus dem Pufferbereich ersetzt werden. Im Zentrum eines Pflanzenpatches, dem sogenannten Senkenbereich sind hingegen keine Wirtsameisennester vorhanden.
Dies führt zu einer effektiven Verkleinerung des nutzbaren Habitats und daher zu kleineren Populationen als auf Flächen, auf denen die Pflanzen heterogen verteilt stehen. Die Stärke des Effekts hängt von der Ausbreitungsdistanz der Wirtsameisenart ab. Diese ist im allgemeinen klein. Daher kann Klumpung von Wirtspflanzen einen deutlichen negativen Effekt auf die Persistenz von Maculineapopulationen haben.

Zur Beurteilung der Eignung einer Pflanzenverteilung für die Persistenz einer Maculineapopulation auf einer Fläche, wird ein räumlicher Index entwickelt. Dieser Landschaftsindex bewertet, wie viele Pflanzen im reproduktiven Bereich oder im Senkenbereich liegen. In die Berechnung wird einbezogen, wie gut eine Pflanze von kolonisierenden Wirtsameisen erreicht werden kann.
Die Aussagekraft des Index wurde mit dem Macu-Modell für eine große Zahl von Szenarien getestet. Der PVA gestützte Indextest bezieht populationsdynamische Prozesse und daher die Bedürfnisse des Systems in die Bewertung des statistischen Raummaßes mit ein.
Außer für sehr geringe Wirtspflanzendichten, bei denen die Absolutzahl der Pflanzen die wesentliche Bewertungsgröße darstellt, zeigt der Index für alle anderen Szenarien sehr gute Ergebnisse. Hohe Indexwerte sind ein sicheres Zeichen für eine geeignete Wirtspflanzenverteilung.

Kurz gefasst die wichtigsten Ergebnisse der Arbeit

- Eine Methode zur Populations-Überlebens-Analyse (PVA) von Mehrartensystemen wird bereitgestellt.

- Eine Methode zur Landschaftsanalyse wird entwickelt, mit der Artverhalten (d.h. populationsökologische Prozesse) in die Bewertung von Raumstrukturen einbezogen werden können.
- Im Maculinea-System werden zwei dynamisch verschiedene Wirts-Parasit-Zyklen beobachtet, die je nach momentanen Populationsgrößen das Systemverhalten bestimmen.
- In Mehrartensystemen kann ein Bottleneck-Effekt auftreten, weil sich kolonisierende Population und äußere Umgebung erst an einander anpassen müssen – die kolonisierende Art nimmt Einfluss auf die neue Umgebung.
- Faustregeln und ein Index zur Bewertung der Eignung räumlicher Wirtspflanzenverteilungen für die Erhaltung von Maculinea Populationen auf Habitatflächen werden entwickelt.

Part VI

Appendix

Appendix A

Population viability analysis

A.1 Analytical calculation of the measures of persistence for stochastic systems with a cyclic fluctuating probability distribution of population sizes

A.1.1 Calculation of the regression line parameters

This lengthy calculation is necessary to show that the limit of the fit parameters for high time horizons T_H (maximum time taken into account for calculation of the persistence measures t_m and c_1) lead to constant values. As a byproduct the exact values for c_1 and t_m can be presented. The formulas for the regression line parameters slope a and intersection b are

$$\begin{aligned} a &= \frac{\sum\limits_{i=1}^{N}(x_i - \bar{x})(y_i - \bar{y})}{\sum\limits_{i=1}^{N}(x_i - \bar{x})^2} \\ b &= \bar{y} - a\bar{x} \end{aligned}$$

where (x_i, y_i) denotes data point i, $\bar{x}$ and $\bar{y}$ denote respective mean values and N is the number of data points in the analysis (Zeidler et al., 1996). We set $N = T_H$ the time horizon for the calculation, $x = t$ and $y = -\ln(1 - P_0(t))$. Due to the mathematical structure of x, simplifications can be done:

$$
\begin{aligned}
\bar{t} &= \frac{1}{T_H}\sum_{t=1}^{T_H} t = \frac{1}{2}(T_H+1) \\
\sum_{i=1}^{T_H}(t_i-\bar{t})^2 &= \frac{1}{12}(T_H-1)T_H(T_H+1) \\
\sum_{i=1}^{N}(x_i-\bar{x})(y_i-\bar{y}) &= \sum_{i=1}^{T_H} x_iy_i + x_i\bar{y} - \bar{x}y_i - \bar{x}\bar{y} \\
&= \sum_{i=1}^{T_H} x_iy_i + \bar{y}\sum_{i=1}^{T_H} x_i - \bar{x}\sum_{i=1}^{T_H} y_i - \bar{x}\bar{y}\sum_{i=1}^{T_H} 1 \\
&= \sum_{i=1}^{T_H} x_iy_i - \bar{x}\sum_{i=1}^{T_H} y_i + T_H\bar{x}\bar{y} - T_H\bar{x}\bar{y} \\
&= \sum_{i=1}^{T_H} x_iy_i - T_H\bar{x}\bar{y}
\end{aligned}
$$

The values for $\bar{y}$ and $\sum_{i=1}^{T_H} x_iy_i$ can be calculated applying the separation of time scales eqn. 3.6, where an integer division is symbolised by $\div$ in front of a quotient:

$$
\begin{aligned}
\bar{y} &= \frac{1}{T_H}\sum_{i=1}^{T_H}(-\ln(1-P_0(i))) \\
&= \frac{1}{T_H}\{\sum_{i=1}^{T_{ini}} -\ln\prod_{j=1}^{i} \\
&+ \sum_{i=T_{ini}+1}^{T_H} -\ln\prod_{j=1}^{T_{ini}} - \div\frac{i-T_{ini}}{T_P}\cdot\ln\prod_{j=T_{ini}+1}^{T_{ini}+T_P} -\ln\prod_{j=T_{ini}+\div\frac{i-T_{ini}}{T_P}T_P+1}^{T_H} \quad \} \\
&= -\frac{1}{T_H}\sum_{i=1}^{T_{ini}}\ln\prod_{j=1}^{i} \\
&- \frac{T_H-T_{ini}}{T_H}\cdot\ln\prod_{j=1}^{T_{ini}} \\
&- \frac{1}{T_H}\ln\prod_{j=T_{ini}+1}^{T_{ini}+T_P}\cdot\{\sum_{l=0}^{\div\frac{T_H-T_{ini}}{T_P}-1}\sum_{i=0}^{T_P-1}\div\frac{i+lT_P}{T_P} + \sum_{i=0}^{(T_H-T_{ini}) \bmod T_P}\div\frac{i+\div\frac{T_H-T_{ini}}{T_P}T_P}{T_P}\} \\
&- \frac{1}{T_H}\{\sum_{l=0}^{\div\frac{T_H-T_{ini}}{T_P}-1}\sum_{i=0}^{T_P-1}\ln(\prod_{j=1}^{(i+l*T_P) \bmod T_P}) + \sum_{i=0}^{(T_H-T_{ini}) \bmod T_P}\ln(\prod_{j=T_{ini}+1}^{T_{ini}+(i+\div\frac{T_H-T_{ini}}{T_P}T_P) \bmod T_P})\} \\
&= -\frac{1}{T_H}\sum_{i=1}^{T_{ini}}\ln\prod_{j=1}^{i} \\
&- \frac{T_H-T_{ini}}{T_H}\cdot\ln\prod_{j=1}^{T_{ini}} \\
&- \frac{1}{T_H}\ln\prod_{j=T_{ini}+1}^{T_{ini}+T_P}\cdot\{\frac{1}{2}T_P\div\frac{T_H-T_{ini}}{T_P}(\div\frac{T_H-T_{ini}}{T_P}-1)+\div\frac{T_H-T_{ini}}{T_P}((T_H-T_{ini}) \bmod T_P+1)\} \\
&- \frac{1}{T_H}\div\frac{T_H-T_{ini}}{T_P}\sum_{i=0}^{T_P-1}\ln(\prod_{j=T_{ini}+1}^{i}) - \frac{1}{T_H}\sum_{i=0}^{\div\frac{T_H-T_{ini}}{T_P}}\ln(\prod_{j=T_{ini}+1}^{i})
\end{aligned}
$$

We use the same technique of splitting sums for the calculation of $\sum_{i=1}^{T_H} x_i y_i$. The result is

$$
\begin{array}{rcl}
\sum_{i=1}^{T_H} x_i y_i & = & \sum_{t=1}^{T_H} t \cdot (-\ln(1 - P_0(t))) \\
 & = & \sum_{i=1}^{T_{ini}} t \cdot \ln \prod_{j=1}^{i} \\
 & - & \frac{1}{2}(T_H^2 + T_H - T_{ini}^2 - T_{ini}) \ln \prod_{j=1}^{T_{ini}} \\
-\ln \prod_{j=T_{ini}+1}^{T_{ini}+T_P} \cdot \{ & & \frac{1}{2} T_{ini} \cdot T_P \div \frac{T_H - T_{ini}}{T_P} (\div \frac{T_H - T_{ini}}{T_P} - 1) \\
 & & + \frac{1}{6} T_P^2 \div \frac{T_H - T_{ini}}{T_P} (\div \frac{T_H - T_{ini}}{T_P} - 1)(2 \div \frac{T_H - T_{ini}}{T_P} - 1) \\
 & & + \frac{1}{4} T_P (T_P - 1)(\div \frac{T_H - T_{ini}}{T_P})(\div \frac{T_H - T_{ini}}{T_P} - 1) \\
 & & + \div \frac{T_H - T_{ini}}{T_P} T_{ini}((T_H - T_{ini}) \bmod T_P + 1) \\
 & & + (\div \frac{T_H - T_{ini}}{T_P})^2 ((T_H - T_{ini}) \bmod T_P + 1) T_P \\
 & & + \frac{1}{2}((T_H - T_{ini}) \bmod T_P)((T_H - T_{ini}) \bmod T_P + 1) \div \frac{T_H - T_{ini}}{T_P} \} \\
 & - & T_{ini} \div \frac{T_H - T_{ini}}{T_P} \sum_{i=0}^{T_P - 1} \ln(\prod_{j=T_{ini}+1}^{i}) \\
 & - & \frac{1}{2} T_P \div \frac{T_H - T_{ini}}{T_P} (\div \frac{T_H - T_{ini}}{T_P} - 1) \sum_{i=0}^{T_P - 1} \ln(\prod_{j=T_{ini}+1}^{i}) \\
 & - & \div \frac{T_H - T_{ini}}{T_P} \sum_{i=0}^{T_P - 1} i \cdot \ln(\prod_{j=T_{ini}+1}^{i}) \\
 & - & (T_{ini} + \div \frac{T_H - T_{ini}}{T_P} T_P) \sum_{i=0}^{(T_H - T_{ini}) \bmod T_P} \ln(\prod_{j=T_{ini}+1}^{i}) \\
 & - & \sum_{i=0}^{(T_H - T_{ini}) \bmod T_P} i \cdot \ln(\prod_{j=T_{ini}+1}^{i})
\end{array}
$$

All results are derived and tested with software Mathematica (Wolfram, 1988) for two different population dynamic functions $N(t)$ and for different parameters. We could not find any inconsistencies

A.1.2 Regression line parameters for infinite time horizon ($T_H \to \infty$)

An evaluation of the fit parameters a and b for $T_H \to \infty$ is possible. We get

$$\begin{aligned}
\lim_{T_H \to \infty} a &= -\frac{1}{T_P} \ln(\prod_{i=T_{ini}+1}^{T_{ini}+T_P}) \\
\lim_{T_H \to \infty} b &= -\frac{1}{T_P} \{ (\sum_{i=0}^{T_P-1} \ln \prod_{j=T_{ini}+1}^{T_{ini}+i}) + T_P \ln(\prod_{j=1}^{T_{ini}}) \} \\
&+ \frac{2T_{ini} + T_P - 1}{2T_P} \ln(\prod_{j=T_{ini}+1}^{T_{ini}+T_P})
\end{aligned}$$

which are both independent of T_H. This means that with increasing time horizon T_H, parameters a and b approach constant values. Hence, these parameters are well defined for all types of models described by eqn. 3.3.

The result for $\lim_{T_H \to \infty} b$ can be simplified using identity

$$\sum_{i=0}^{T_P-1} \ln \prod_{j=T_{ini}+1}^{T_{ini}+i} = (T_P + T_{ini}) \cdot \ln(\prod_{i=T_{ini}+1}^{T_{ini}+T_P}) + \ln(\prod_{i=T_{ini}+1}^{T_{ini}+T_P} (1 - p(i))^{-i})$$

which can be shown as follows

$$\begin{aligned}
\sum_{i=0}^{T_P-1} \ln \prod_{j=T_{ini}+1}^{T_{ini}+i} (1 - p(j)) &= \\
&= \sum_{i=0}^{T_P-1} (\sum_{j=T_{ini}+1}^{T_{ini}+i} (\ln(1 - p(j))) \\
&= \sum_{i=1}^{T_P} \{ (T_P - i) \cdot \ln(1 - p(T_{ini} + i)) \} \\
&= \ln\{ \prod_{i=1}^{T_P} [(1 - p(T_{ini} + i))^{T_P - i}] \} \\
&= \ln\{ \prod_{i=T_{ini}+1}^{T_{ini}+T_P} [(1 - p(i))^{T_P + T_{ini} - i}] \} \\
&= (T_P + T_{ini}) \cdot \ln(\prod_{i=T_{ini}+1}^{T_{ini}+T_P} (1 - p(i)) + \ln(\prod_{i=T_{ini}+1}^{T_{ini}+T_P} (1 - p(i))^{-i})
\end{aligned}$$

We receive a description of $\lim_{T_H \to \infty} b$, which does not include summations over time

$$\lim_{T_H \to \infty} b = -\frac{1}{T_P} \{ \ln(\prod_{i=T_{ini}+1}^{T_{ini}+T_P} (1 - p(i))^{-i}) + T_P \ln(\prod_{j=1}^{T_{ini}} (1 - p(j))) + \frac{1 + T_P}{2} \ln(\prod_{j=T_{ini}+1}^{T_{ini}+T_P} (1 - p(j))) \} \tag{A.1}$$

A.1.3 Measures of persistence t_m and c_1

We use definitions for the persistence measures, which are given in Grimm & Wissel (2004)

$$\begin{aligned} t_m &= \frac{1}{a} \\ c_1 &= e^{-b} \end{aligned}$$

to calculate them from fit parameters slope a and intersection b of the regression line. In analytical calculations, in contrast to numerical simulations, we can calculate exact values for the persistence measures for an infinite time horizon. An example that persistence measures evaluated from simulation studies with limit time horizon T_H are sufficiently exact, is shown in ch. 3.4.1. Formula for t_m is given in eqn. 3.9 without further calculations. The result for c_1 in eqn. 3.9 is received from inserting the sum free form eqn. A.1 and performing some algebraic transformations.

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