Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology 78:1898.

———. 1999. Local and regional diversity in a patchy landscape: Native, alien, and endemic herbs on serpentine. Ecology 80:70–80.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics: a critical review. Pages 27–42 *in* I. Hanski, and M. E. Gilpin, eds. *Metapopulation dynamics: Ecology, genetics and evolution.* Academic Press, San Diego, CA.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

Kitching, R. L. 2000, *Food webs and container habitats: The natural history and ecology of phytotelmata.* Cambridge University Press, New York, NY.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez, A.. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. Ecology Letters 6:673–679.

McPeek, M. A., and S. Kalisz. 1998. On the joint evolution of dispersal and dormancy in metapopulations. Advances in Limnology 52:33–51.

Mehranvar, L., and D. A. Jackson. 2001. History and taxonomy: Their roles in the core-satellite hypothesis. Oecologia 127:131–142.

Mouquet, N., J. L. Moore, and M. Loreau. 2002. Plant species richness and community productivity: Why the mechanism that promotes coexistence matters. Ecology Letters 5:56–65.

Taylor, A. D. 1990. Metapopulations, dispersal, and predator-prey dynamics: An overview. Ecology 71:429–433.

Worthen, W. B. 1989. Effects of resource density on mycophagous fly dispersal and community structure. Oikos 54:145–153.

In Metacommunities - spatial dynamics and ecological communities eds - M. Holyoak, M. A. Leibold, R. D. Holt. University of Chicago Press 2005 pp. 99-121

CHAPTER 4

Metacommunities of Butterflies, Their Host Plants, and Their Parasitoids

Saskya van Nouhuys and Ilkka Hanski

The great bulk of population biological research on butterflies is focused on single species, but in reality butterfly populations are dynamically coupled with other populations representing species at higher, lower, and equal trophic levels. Often these interactions take place in fragmented landscapes because the focal butterfly may use only one or a few larval host plant species, which may be habitat specialists with fragmented distributions. Butterfly eggs, caterpillars, and pupae are attacked by a range of more or less specialized parasitoids (Dempster 1983; Shaw and Fitton 1989; Van Nouhuys and Hanski 2004), which themselves host hyperparasitoids (parasitoids of the primary parasitoids). The behavior and population dynamics of the parasitoids are often influenced by the host plants of their host butterfly (Price et al. 1980; Vet and Dicke 1992; Hochberg and Ives 2000), so there are direct links between species on the first trophic level (plants) and species at the third trophic level (parasitoids). The patchy distribution of the host plants combined with the specificity of the butterflies and their natural enemies leads to metacommunity dynamics in the plant-butterfly-parasitoid assemblage, which often includes on the order of ten species. These species are typically interacting with yet other species, which may be less specific and whose populations are often less strongly spatially structured than the populations of the butterflies, their host plants and the specialist parasitoids. For instance, the host plants may support polyphagous herbivores in addition to the specialist butterflies, and all the insect species may be attacked by diseases, generalist arthropods, and vertebrate predators. Thus we view closely interacting species around the focal butterfly as embedded in a more comprehensive community made up of species that may have different spatial distributions than the focal plant-butterfly-parasitoid metacommunity. This may be a common situation in nature in general.

We present an overview of metacommunities associated with butterflies, with a particular focus on a well-studied species of checkerspot butterfly, the Glanville fritillary (Hanski 1999; Ehrlich and Hanski 2004). We illustrate several ecological processes taking place in metacommunities with examples drawn from the metacommunity of the Glanville fritillary and its host plants and parasitoids, including plant-butterfly interactions, the trade-off between competitive ability and dispersal rate / ability in competing species, tritrophic interactions involving the host

plants, butterflies and parasitoids, and apparent competition. We then address two aspects of metacommunity structure. First, the length of food chains in relation to the spatial extent of the landscape occupied by the metacommunity. Second, we discuss to what extent different coexisting checkerspot community modules (Holt and Hoopes, chapter 3) are linked together via shared host plants and parasitoids to form more comprehensive metacommunities. Here we examine coexisting community modules around two checkerspot species in Finland, five checkerspot species in the steppe region in Buryatia, Russia, and five checkerspot species in the Montseny mountains in northern Spain. This analysis reinforces the view that community modules are often relatively independent. Therefore, the primary task is to understand how interspecific interactions within the relatively small community modules are affected by the spatial structure and dynamics of the constituent species, and vice versa, which sets a manageable challenge for research on metacommunities.

An Overview of Plant-Butterfly-Parasitoid Metacommunities

Butterflies and moths have been the subject of much study in population, metapopulation, and community ecology, to a large extent because they are conspicuous and are frequently the targets of either conservation effort or pest control. Many butterfly species occur as metapopulations (Hanski and Kuussaari 1995; Thomas and Hanski 1997), and studies of butterflies have contributed greatly to the development of the concept (Harrison et al. 1988; Hanski et al. 1994; Hanski and Gaggiotti 2004) and theory (Hanski 1994; Hanski and Ovaskainen 2000) of metapopulations. Butterfly studies have yielded some of the most useful data to test the assumptions and predictions of metapopulation models (Boughton 2000; Thomas and Hanski 2004; Hanski et al. 2004), because butterflies possess characteristics that both facilitate their study and make them a good model group in which to study metapopulation biology (Murphy et al. 1990). Many habitats used by butterflies are naturally or anthropogenically fragmented, which leads to a fragmented structure of populations. Butterflies are small and therefore the number of individuals in even small habitat fragments may be large enough to constitute a local breeding population. Butterflies have a high rate of population growth, which means that following population establishment local populations may grow quickly to the local carrying capacity. Finally, butterflies have short generation times, and hence stochastic events are not buffered by great longevity of individuals, which would reduce the risk of population extinction.

Turning to community studies on butterflies and moths, they include, first of all, surveys of species diversity associated with different habitat types such as grassland and tropical forest; many recent studies demonstrate the impact of habitat fragmentation or degradation on butterfly diversity (Steffan-Dewenter and Tscharntke 2000; Kitahara and Sei 2001; Collinge et al. 2003; Horner-Devine et al. 2003). Other studies have examined the butterfly and moth communities associated with specific host plant species (Courtney and Chew 1987; Thomas et al. 1990; Harrison and Thomas 1991). Few if any of these large-scale butterfly community studies include the associated parasitoid communities, and in fact little is known about parasitoid communities associated with most butterflies (Shaw and Fitton 1989; Shaw 1994). There are however studies of insect communities that include Lepidoptera and parasitoids among other taxa (Memmott et al. 1994; Holyoak 2000; Kruess and Tscharntke 2000), such as the quantitative food web study by Lewis et al. (2002) describing the complex community of 93 leaf mining insect species (primarily moths, beetles, and flies) and their 84 parasitoid species in a 8500 m^2 area of tropical forest in Belize. There is also a handful of studies collating information for communities of Lepidoptera and their parasitoids across larger areas (Hawkins and Sheehan 1994; Hochberg and Ives 2000), such as the study of 60 tachinid parasitoids associated with 196 species of externally feeding Lepidoptera in a mesquite-oak savanna in Arizona (Stireman and Singer 2003), the parasitoids associated with tortricid moths (Mills 1993), and the rich invasive parasitoid community associated with forest moths in Hawaii (Henneman and Memmott 2001).

Literature-based host records have been used to generate hypotheses about parasitoid community structure and how it is affected by host characteristics such as feeding niche and abundance, affected by parasitoid characteristics such as host breadth and attributes of the host plants, and affected by habitat and the landscape (Askew and Shaw 1989; Hawkins et al. 1992; Hawkins 1994; Hawkins and Sheehan 1994; Sheehan 1994; Hawkins 2000; Holyoak 2000). These studies do not consider spatial population structure or dynamics in any detail, if at all, and the vast majority of studies are concerned with herbivores living in plant structures such as galls or leaf mines. In brief, though there is much knowledge about the spatial population structures and metapopulation dynamics of butterflies, and there is much information about community structure in Lepidoptera in terms of host plant and parasitoid associations, there is yet little knowledge of the combination of the two—that is, metacommunity structure and dynamics of butterflies and their associated species.

The Community Associated with the Glanville Fritillary Butterfly

The Glanville fritillary butterfly (*Melitaea cinxia*) is restricted, like many other checkerspot butterflies, to larval host plants that produce iridoid glycosides, supposedly in defense against generalist herbivores (Bernays and De Luca 1981; Bowers 1983; Wahlberg 2001). Throughout its range, *M. cinxia* feeds on plants in the genera *Plantago* and *Veronica*, in the family Plantaginaceae (Kuussaari et al. 2004). In the Åland Islands in southwestern Finland, the larval host plants are *Plantago lanceolata* and *Veronica spicata*, which grow in dry open meadows in a rural landscape (*P. lanceolata* is not limited to the meadows used by the butterfly,

and it is found throughout the islands in open and disturbed habitats). The adult butterflies emerge, mate, and lay eggs in June. Eggs are laid in clusters of 100 to 200 on the underside of host plant leaves. Upon hatching in early July the larvae live gregariously in silken nests until they disperse to pupate in the leaf litter in the following May. The larvae winter in dense silken nests on or near the host plants (Kuussaari et al. 2004).

There are altogether around 4000 small meadows that are suitable for *M. cinxia* in the Åland Islands within an area of 50 by 70 km. In any one year 400 to 500 of these meadows are occupied by typically small local butterfly populations (figure 4.1; Nieminen et al. 2004). There is much population turnover, and the butterfly persists as a classic metapopulation in the highly fragmented landscape (Hanski et al. 1994; Ehrlich and Hanski 2004). A local population of *M. cinxia* consists of individuals on a single meadow. A local community includes the species that interact directly or indirectly within the same meadow, whereas a metacommunity is a set of local communities connected by dispersal of the constituent species.

Melitaea cinxia experiences little direct interspecific competition because few other insect herbivores feed predominantly on *P. lanceolata* and *V. spicata*. However, there is probably more indirect competition, mediated by the host plants, with a powdery mildew, thrips, aphids, agromyzid flies, several moth species, and seed-head feeding weevils (Nieminen et al. 2004). Powdery mildew is present in only some of the *M. cinxia* populations, whereas thrips and aphids are abundant only during some years. We have observed no predation of *M. cinxia* by vertebrates, but eggs, larvae, and occasionally adults are consumed by generalist invertebrate predators such as lacewing, ladybird beetle larvae, and pentatomid bugs. The red ant *Myrmica rubra* consumes *M. cinxia* eggs, and spiders, and dragonflies have been observed to catch adult butterflies (Van Nouhuys and Hanski 2004).

The parasitoid community associated with *M. cinxia* in the Åland Islands is relatively simple (figure 4.2). The larvae are attacked by two parasitoid wasps, *Cotesia melitaearum* (Wilkinson; Braconidae: Microgastrinae), which is a gregarious endoparasitoid that has two to three generations during each host generation, and *Hyposoter horticola* (Gravenhorst; Ichneumonidae: Campoplaginae), a solitary endoparasitoid with one generation during each host generation (Lei et al. 1997; Van Nouhuys and Hanski 2004). Neither parasitoid has other hosts in Åland. Though restricted to the same host species, the two parasitoids differ greatly in natural history, behavior, spatial dynamics, and impact on host population dynamics (Lei and Hanski 1997, 1998; Lei and Camara 1999; Van Nouhuys and Hanski 2002a; Van Nouhuys and Ehrnsten 2004; Van Nouhuys and Lei 2004). Additionally, there are several generalist pupal parasitoids (Lei et al. 1997), but no egg parasitoids, larval-pupal parasitoids, nor tachinid fly parasitoids.

Each larval parasitoid has an abundant secondary parasitoid. *Cotesia melitaearum* is parasitized by the generalist pseudohyperparasitoid *Gelis agilis* (Fabricius) (Ichneumonidae: Cryptinae), which is a solitary ectoparasitoid that lays

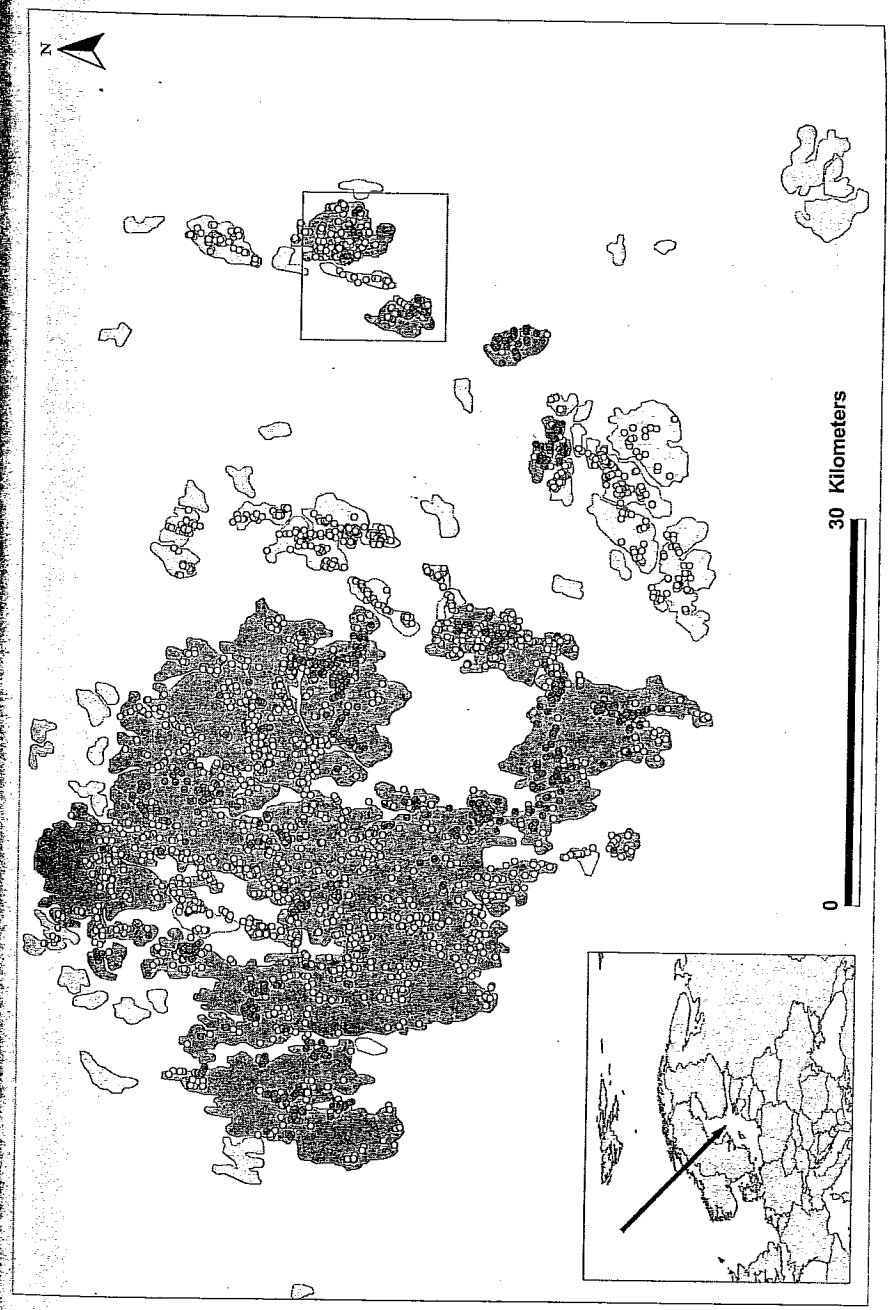


Figure 4.1 A map of the Åland Islands in Finland with empty but suitable habitat patches for *Melitaea cinxia* represented by open circles, and those occupied by the butterfly in 2002 by filled circles. The square indicates the habitat patch networks on the islands of Kumlinge and Seglinge. Dark background indicates regions occupied by the butterfly, and the light background areas not occupied.

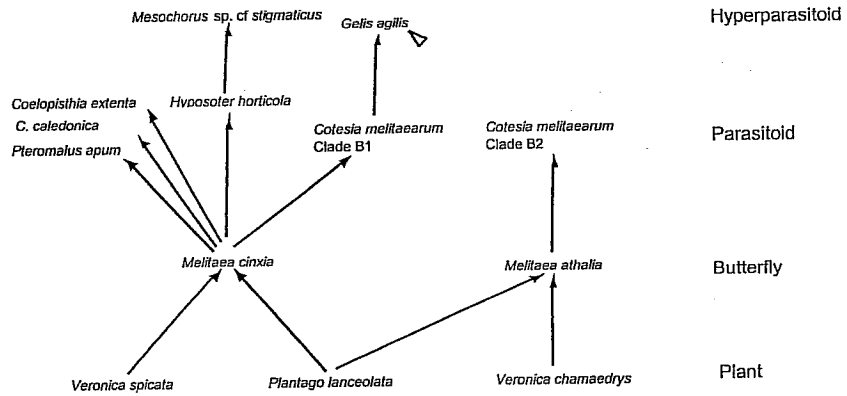


Figure 4.2 The food web of the checkerspot butterfly community in the Åland Islands. Alternate hosts of the generalist hyperparasitoid *Gelis agilis*, such as *Cotesia glomerata* (a parasitoid of Pierid butterflies), are present in surrounding habitats. Note: *Coelopisthia extenda, C. caledonica, and Pteromalus apum* may use other melitaeine and nonmelitaeine hosts. *Gelis agilis* may use other *Cotesia* and non-*Cotesia* hosts.

eggs on host parasitoid pupae in silken cocoons after they have left the butterfly larva (hence the term pseudohyperparasitoid). *Hyposoter horticola* is parasitized by the solitary hyperparasitoid *Mesochorus* sp. cf. *stigmaticus* (Brischke; Ichneumonidae: Mesochorinae), which lays eggs in *H. horticola* larvae within the butterfly host larvae. The taxonomy of the genus *Mesochorus* is not well worked out, but probably in Åland *M. stigmaticus* is restricted to parasitoids using *M. cinxia* larvae, and principally to *H. horticola* (Van Nouhuys and Hanski 2004).

The Glanville fritillary butterfly, its two host plant species, two specialist parasitoids, and two common hyperparasitoids comprise a group of seven species that interact closely with one another. These species represent a relatively independent module (Holt and Hoopes, chapter 3) in the large community of species found in open dry meadows with *V. spicata* and *P. lanceolata*. We have studied the metacommunity of the seven species over large spatial and temporal scales. Because we work with a relatively small number of species we do not address here conventional issues of (meta)community ecology, such as species diversity, community assembly, food web topology, species sorting, and so forth. Instead, we focus on the mechanisms, such as dispersal, extinction-colonization dynamics, host specialization and competition, which contribute to metacommunity structure and dynamics from local to regional scales in the assemblage of species around the Glanville fritillary.

Processes Operating in Butterfly-Parasitoid Metacommunities

In this section we review the key processes in the dynamics of the metacommunity associated with *M. cinxia* with reference to other butterfly-parasitoid metacommunities where relevant. To count as a metacommunity process in this context, we require that the interaction involves at least three species and that the interaction is critically influenced by the spatial structure of the (meta)populations of particular species. For comprehensive accounts of the biologies of the species involved see chapters in Ehrlich and Hanski (2004).

Host Plant–Butterfly Interactions

Many butterflies are specialized to use only one or a few host plant species in a particular region, though they may use a wider range of host species across their geographical range. This is a common situation in checkerspot butterflies including *M. cinxia*, and is especially well documented for the North American *Euphydryas editha* (Singer and Thomas 1987; Singer et al. 1992; Kuussaari et al. 2004; Singer 2004). In fragmented landscapes, it is likely that there is substantial variation in host plant composition from one habitat patch to another within butterfly metapopulations. Results for *M. cinxia* demonstrate that such variation may have profound consequences both for the ecological and the evolutionary dynamics of the host plant-butterfly interaction.

The two host plants used by *M. cinxia* in Åland are not distributed uniformly across the main island: *V. spicata* is absent from the east and is increasingly abundant toward the west, whereas *P. lanceolata* is present throughout the area but varies in density among habitat patches (Kuussaari et al. 2004). Genetically determined butterfly oviposition preference shows broadly matching geographic variation, shifting from preference for *P. lanceolata* in the east, where only *P. lanceolata* is available, to preference for *V. spicata* in the west, where both host plants are present (Kuussaari et al. 2000). Host plant use by larvae varies spatially because of spatial variation both in host plant occurrence and female oviposition preference. Unexpectedly, variation in adult oviposition preference appears to be unrelated to variation in larval performance or host plant suitability. Thus *P. lanceolata* and *V. spicata* are equally suitable for larval development where they are used by the butterfly and where one or the other is not used, and larvae are not locally adapted, as assessed by larval growth and survival, to the locally used host plant (Van Nouhuys et al. 2003).

Though butterfly oviposition preference does not appear to be correlated with larval survival, oviposition preference does affect regional population dynamics. Hanski and Singer (2001) found that the establishment of new populations by female butterflies was strongly influenced by the match between the host species composition of an empty habitat patch and the relative host use by larvae in the

surrounding patches during previous years. For instance, a patch with only or mostly *P. lanceolata* remained frequently uncolonized in a region where most eggs were laid on *V. spicata*. A comparable patch was significantly more likely to become colonized if located in a region where *P. lanceolata* is widely used. Hanski and Singer (2001) investigated several possible mechanisms that could lead to such biased colonizations. They concluded that the most likely mechanism is female movement behavior—emigration from and immigration to patches being influenced by the correspondence between their oviposition preference and the plant species composition in the habitat patches.

Hanski and Heino (2003) demonstrated that biased colonizations due to host plant preference (Hanski and Singer 2001) may influence the evolution of oviposition preference in fragmented landscapes. The idea is simple: assuming that butterflies evolve to prefer the more common host plant species, the realized commonness of the host plants is influenced by how frequently butterflies actually encounter them, which is influenced, among other things, by the colonization rate of habitat patches with dissimilar host plant composition. One challenge for empirical research is to understand why the butterflies tend to evolve to prefer the more common host plant species, given that there is no evidence for preference-performance correlation in this case (Van Nouhuys et al. 2003). One possibility is that specialization is selected for by decreased cost of host searching, which the females do using visual cues (host plant morphology).

We have described here how butterfly metapopulation structure is in part the result of the behavioral response of females to the spatial distribution of the two host plant species, and how metacommunity dynamics may be critically influenced by the behavioral responses of the constituent species (see Resetarits et al., chapter 16, "Interactive Habitat Selection"). This interaction between the butterfly and the host plants influences both directly and indirectly the dynamics of other community members as discussed below in the section on tritrophic interactions between the host plants, the butterfly, and its parasitoids.

Contrasting Spatial Dynamics and Competition among Parasitoids

If two or more species are specialized to use the same host species, our first expectation might be that their biologies are broadly similar due to similar shared selection pressures. In the Åland Islands, *C. melitaearum* and *H. horticola* parasitize only *M. cinxia*, which has a highly fragmented and dynamic metapopulation structure. We might expect that, for example, the movement behaviors of the two parasitoids are similar. But in reality, just the opposite is the case. *Hyposoter horticola* is very mobile, and can disperse up to at least 5 to 8 km in one generation, which is more than the host dispersal range of up to 3 to 4 km (Van Nouhuys and Hanski 2002a). In contrast, *C. melitaearum* has a clearly shorter dispersal range than the host, up to 1 km (Lei and Hanski 1998; Lei and Camara 1999; Van Nouhuys and Hanski 2002b). As a consequence, *C. melitaearum* has a classic

metapopulation structure in Åland, like the host butterfly, whereas *H. horticola* experiences the host metapopulation more like a single patchily distributed population. In other words, at any one time only 10% of the host populations can be reached by *C. melitaearum* (because of dispersal limitation), whereas practically all host populations are accessible to *H. horticola*.

Two species sharing the same resource must partition the resource to persist. The two parasitoids of *M. cinxia* compete directly for the same host individuals where they co-occur (Lei and Hanski 1998; Van Nouhuys and Hanski 2002a). One possible mechanism of coexistence in a fragmented landscape is based on a trade-off between competitive and dispersal abilities: the species that is an inferior competitor locally is a superior disperser (Levins and Culver 1971; Hastings 1980; Nee and May 1992; Nee et al. 1997). *Hyposoter horticola* is extremely dispersive while *C. melitaearum* is quite sedentary, sometimes attending individual larval groups in a host population for days. Therefore, the two might coexist if *C. melitaearum* is a stronger competitor locally, while *H. horticola* would largely avoid the adverse effects of competition by moving to host populations currently unoccupied by *C. melitaearum*. Lei and Hanski (1998) interpreted observational data in support of the competition-dispersal trade-off, but more recent research has shown that the competitive interaction between the two parasitoids is more complex. There are two and sometimes three generations of *C. melitaearum* during each host and *H. horticola* generation, hence there are two to three different stages in host development during which the two immature wasps compete. Surprisingly, it is only during the second (overwintering) generation that *C. melitaearum* has a competitive advantage. During the two other generations, *C. melitaearum* eggs or larvae in hosts previously parasitized by *H. horticola* die (Van Nouhuys and Hanski 2004; Punju 2002). These results provide little or no support for the notion that *C. melitaearum* is able to coexist with *H. horticola* because it is a superior competitor. Instead, it now appears that the persistence of *C. melitaearum* is enhanced by *H. horticola* typically leaving a fraction of the larvae in each host larval group unparasitized (for reasons discussed by Van Nouhuys and Ehrnsten 2004). The previous observation that parasitism by *H. horticola* is reduced in the presence of *C. melitaearum* (Lei and Hanski 1998) is probably explained by many of the doubly-parasitized host larvae dying (Punju 2002; Van Nouhuys and Tay 2001).

The idea that two competing species in a metacommunity coexist because one is a good local competitor and the other one is a good disperser is compelling, especially in situations like the present one where the two competing species differ greatly in host searching behavior and dispersal ability. However, our detailed studies of the mechanisms of host finding and parasitism behavior, and of the competitive interactions inside the host larvae, have shown that resource partitioning takes place primarily at the level of host larval groups rather than among populations. The few other studies critically testing the idea of competition-dispersal trade-off in parasitoids have similarly failed to support this mechanism

(Hopper 1984; Amarasekare 2000). The competition-dispersal trade-off has been suggested to operate in several nonparasitoid systems, but convincing examples are very few. Perhaps the best one is Pajunen's work on two species of corixid water bugs living in a network of rock pools (1979, 1982). In this case there is direct experimental evidence both for asymmetric competitive and dispersal abilities. Two other likely examples involve fungi in a laboratory system (Armstrong 1976) and mosses colonizing dung pats in the field (Marino 1991).

Tritrophic Interactions among Plants, Butterflies, and Parasitoids

Interactions between species at two trophic levels, such as between a parasitoid and its host butterfly, or the butterfly and its host plant, may be influenced directly and indirectly by other trophic levels (Price et al. 1980; Tscharntke 1992; Roininen et al. 1996; Abrahamson and Weis 1997; Sullivan and Völk 1999; Tscharntke and Hawkins 2002; Dyer and Letourneau 2003). Traditionally multitrophic interactions are studied within local communities or under laboratory conditions, but such studies can be profitably extended to include dispersal of the species among multiple local communities. The indirect effects of lower and higher trophic levels may increase the stability of populations by moderating the use of a potentially limiting resource, or decrease the stability of local populations by facilitating the consumption of the resource until it has gone locally extinct (Van Nouhuys and Hanski 2002b). The extent to which these local multitrophic interactions contribute to metacommunity dynamics then depends on the movement rate of the interacting species among local communities (see Holt and Hoopes, chapter 3). Conversely, movement among communities (species sorting, assembly or mass effects) can influence greatly which local interactions actually occur.

One much-studied tritrophic interaction involves a parasitoid using a host insect that feeds on two or more host plant species (Price et al. 1980; Vet and Dicke 1992; Hochberg and Ives 2000; Tscharntke and Hawkins 2002). The pattern of host plant use by the insect host may influence the rate and success of parasitism both directly through differential host performance and indirectly through host plant signaling and apparency. Spatial variation in the attributes of host plant individuals and species may then contribute to the dynamics of parasitoids and ultimately to the dynamics of the entire metacommunity. For example, we have found that local populations of *C. melitaearum* persist for a longer time, and that the probability of establishment of new populations is greater, where the host larvae use *V. spicata* rather than *P. lanceolata* as a host plant (Van Nouhuys and Hanski 1999). There are several possible mechanisms that could lead to these effects in natural populations. Adult parasitoids may be more attracted to caterpillar-infested *V. spicata* than *P. lanceolata;* caterpillars eating *V. spicata* may be more vulnerable to parasitism; or immature parasitoid development may be retarded in *P. lanceolata*-feeding larvae. In laboratory experiments *C. melitaearum* adults appear equally willing to parasitize larvae reared on the two host plant species, and

there is no difference in the number and sizes of progeny produced. However, female *C. melitaearum* are more attracted to hosts feeding on *V. spicata* than to those feeding on *P. lanceolata* (Anton 2001; Van Nouhuys and Hanski 2004). Therefore, *C. melitaearum* populations may perform better in host populations using *V. spicata* because foraging parasitoids find hosts more easily on *V. spicata* than on *P. lanceolata.*

Apparent Competition

The indirect interaction between two species that share a natural enemy is termed apparent competition, because the two species appear to have a negative impact on one another that is similar to the impact of direct competition (Holt 1977; Holt and Hoopes, chapter 3). Apparent competition may occur wherever herbivores share a pathogen, predator or parasitoid (Bonsall and Hassell 1997; Müller and Godfray 1997; Bonsall and Hassell 1998; Pope et al. 2002), and at higher trophic levels when predators or parasitoids share hyperparasitoids or their own predators. At the metacommunity level, (hyper)parasitoid-mediated apparent competition is likely to be stabilizing if host species occur in different patches and the (hyper)parasitoids aggregate, but destabilizing if host species co-occur (Hanski 1981; Bonsall and Hassell 1999; Holt and Hoopes, chapter 3).

We have used the species assemblage consisting of *M. cinxia,* the primary parasitoids *C. melitaearum* and *C. glomerata,* and the shared hyperparasitoid *G. agilis* to study apparent competition in the field (Van Nouhuys and Hanski 2000). The hyperparasitoid *G. agilis* is a very common, wingless generalist ectoparasitoid of many kinds of insects that build silken cocoons. *Gelis agilis* is found in virtually all *C. melitaearum* populations in Åland (Van Nouhuys and Tay 2001), and it aggregates locally where the host density is high (Lei and Camara 1999). *Cotesia glomerata* parasitizes *Pieris* butterflies in agricultural areas in Åland. Though it does not naturally occur in the meadows with *C. melitaearum,* the hyperparasitoid *G. agilis* uses *C. glomerata* as well as *C. melitaearum. Cotesia glomerata* is therefore a potential member of the food web if the movement of *G. agilis* spans both meadows and agricultural areas. We hypothesized that the addition of *C. glomerata* in *C. melitaearum* populations, close to the existing *C. melitaearum* aggregates and larval nests of *M. cinxia,* would reduce the population size of *C. melitaearum* by causing *G. agilis* to aggregate in response to high total host density, resulting in a high rate of hyperparasitism of *C. melitaearum* in the same and subsequent generations.

In the spring of the first season of the experiment cocoon clusters of *C. glomerata* were added to a randomly selected population in each of three pairs of *M. cinxia* populations occupied by *C. melitaearum.* Parasitism by *G. agilis* was later confirmed in each population by finding *G. agilis* exit holes in the cocoons of both *Cotesia* species. Following the one-time augmentation of hosts for *G. agilis* all three treatment populations of *C. melitaearum* declined, two of them to extinc-

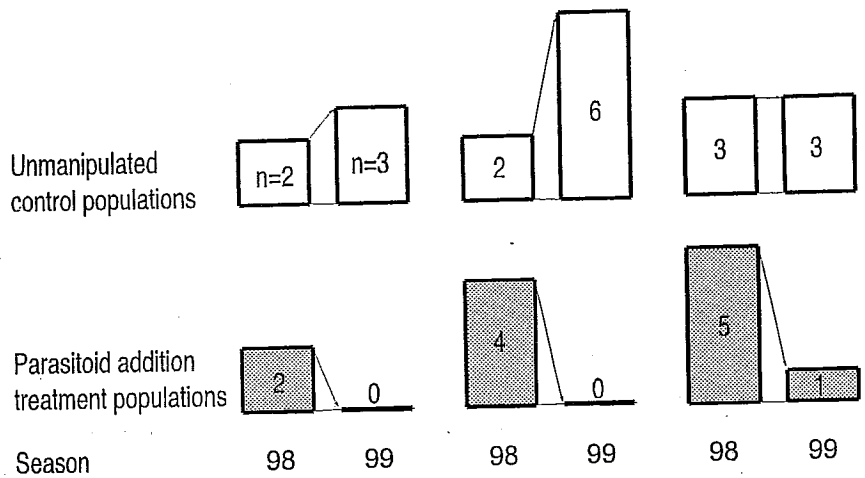


Figure 4.3 Change in *Cotesia melitaearum* population sizes, measured as the number of host larval groups parasitized in the spring between 1998, before the treated populations were augmented with *Cotesia glomerata* cocoons, and 1999, one butterfly generation and two to three parasitoid generations after the augmentation (redrawn with permission, Van Nouhuys and Hanski 2000).

tion, while the untreated control populations remained the same or increased in size (figure 4.3). We did not detect an increase in butterfly population size following the decline in parasitoid populations, but this is not surprising considering the many other factors that contribute to changes in *M. cinxia* population size (Nieminen et al. 2004).

In this experiment the cocoons of the second parasitoid were added to *C. melitaearum* populations next to the host butterfly larval groups, which likely caused the hyperparasitoid to aggregate in the patch close to the sites where *C. melitaearum* would be found subsequently. The dispersal behavior of the hyperparasitoid and the spatial distribution of potential shared host parasitoids, within and among host populations, are expected to influence the extent to which apparent competition links species within communities and metacommunities.

Metacommunity Structures

Food Chain Length and the Size of the Habitat Patch Network

As the amount of habitat available for a community decreases, the number of species decreases—this is the familiar species-area relationship (Rosenzweig 1995). Since species at higher trophic levels tend to have smaller and more extinction-prone populations than species at lower trophic levels, habitat loss and fragmentation should lead to disproportionate loss of species at higher trophic levels (Lawton and May 1995; Holt 1997, 2002). This tendency should increase with decreasing resource breadth or host range. Empirical examples include the insect community associated with bracket fungi in old-growth forests (Komonen et al. 2000) and the insect community associated with bush vetch (*Vicia sepium*) seed pods (Kruess and Tscharntke 2000).

In the case of a metacommunity living in a fragmented landscape, the expectation is that species at higher trophic levels would be absent from small, sparse, or low-quality host population networks, because the probability of a natural enemy persisting as a metapopulation in a host metapopulation decreases with decreasing size of the host metapopulation (Hanski 1999; Holt 2002; Van Nouhuys and Hanski 2002a, 2002b; Holt and Hoopes, chapter 3). The suitable habitat patches for *M. cinxia* in the Åland Islands are clustered into patch networks, between which butterfly movement is restricted by distance or barriers such as forest or sea. Therefore different networks have relatively independent butterfly metapopulations (Hanski et al. 1996; Hanski 1999). These networks, of which there are more than 100 in the Åland Islands, differ in terms of the number of patches (1 to 192, mean = 34), host plant species composition, and other attributes.

The presence of *M. cinxia* in the patch networks shows clear evidence for an extinction threshold, such that the least favorable networks as judged by their metapopulation capacities (Hanski and Ovaskainen 2000) do not have butterfly metapopulations (figure 4.4a; the metapopulation capacity is determined by the number of habitat patches in the network, and by their areas and spatial connectivities). Considering the occurrence of the parasitoid *C. melitaearum* in the same networks, only those butterfly metapopulations that occur in networks with the highest metapopulation capacities have been occupied by the parasitoid (Van Nouhuys and Hanski 2002a; figure 4.4b). On the other hand, the occurrence of the second primary parasitoid, *H. horticola*, is not similarly restricted by the properties of the patch networks or of the host butterfly metapopulations. The two parasitoids show contrasting patterns because *H. horticola* is more mobile than its host and hence little affected by habitat fragmentation, whereas *C. melitaearum* disperses shorter distances than the host and is consequently restricted to the subset of the most favorable patch networks (Van Nouhuys and Hanski 2002a).

Moving up to the fourth trophic level, the generalist hyperparasitoid *G. agilis* has a spatial population structure that is largely independent of the butterfly and the host parasitoid *C. melitaearum* at large spatial scales. However, because *G. agilis* aggregates locally in response to small-scale variation in host density, it is likely to have a great impact on *C. melitaearum* where the density of the latter is high (Lei and Camara 1999; Van Nouhuys and Tay 2001). The specialist hyperparasitoid *Mesochorus* sp. cf. *stigmaticus* parasitizes *H. horticola* larvae inside the host butterfly larvae. We expect that a fourth trophic level with a restricted host range should be absent from small isolated patch networks. Our rearing records support this prediction. The hyperparasitoid is present in most host populations in the main Åland Islands, and there is no evidence that it is limited by host population

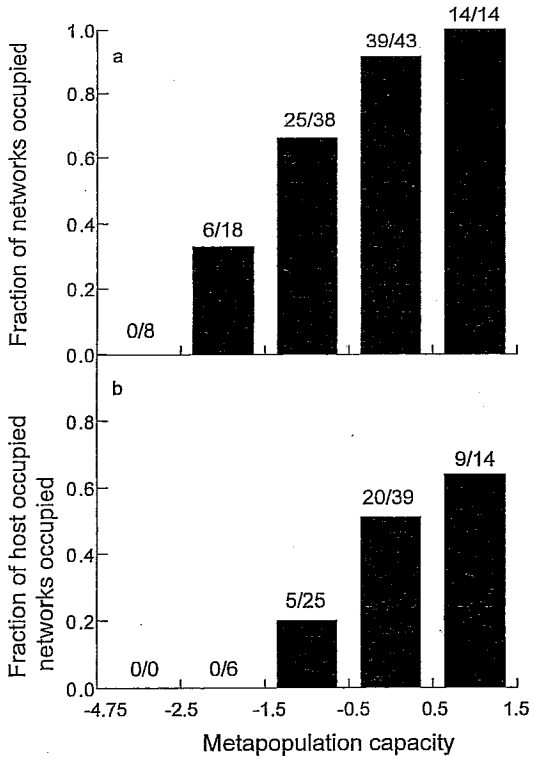


Figure 4.4 The fraction of habitat patch networks that have been occupied by *Melitaea cinxia* (a) and the butterfly-occupied networks that have been occupied by the parasitoid *Cotesia melitaearum* (b) as a function of the metapopulation capacity of the network (modified from Van Nouhuys and Hanski 2002a).

isolation at this spatial scale (Lei et al. 1997; Van Nouhuys and Hanski 2002a). On the other hand, the hyperparasitoid is absent from the butterfly metapopulations inhabiting relatively small and isolated patch networks on the islands of Kumlinge and Seglinge, at a distance of 30 km from the main islands (figure 4.1).

To summarize, the parasitoid community associated with *M. cinxia* in Åland illustrates the effects of network size, species' dispersal range, and host range on the spatial occurrence of the parasitoids. In particular, this system provides support for the notion that higher trophic levels are more limited by isolation and network size than species at lower trophic levels. Distributional patterns for two species, the primary parasitoid *C. melitaearum* and the hyperparasitoid *M.* sp. cf. *stigmaticus*, fit well the expectations based on network size. The other two species have less restricted spatial distributions, in one case (the hyperparasitoid *G. agilis*) because the species is a generalist and hence not solely dependent on the focal host

(*C. melitaearum*), and in the second case because the species (*H. horticola*) is extremely mobile and experiences the local host population (*M. cinxia*) as a single patchily distributed population rather than a fragmented metapopulation.

Linkages between Different Checkerspot Community Modules

The section on apparent competition above illustrates how population dynamics of two or more species may be dynamically linked via shared enemies. More broadly, butterfly species living in different habitat types, or even in overlapping habitats, may be linked by shared host plants and parasitoids. Considering the species assemblages around each butterfly species as a community module, these linkages potentially create more extensive metacommunities, in which direct and indirect interactions may be locally and regionally stabilizing or destabilizing, depending in part on the dispersal behavior of the species involved.

Many checkerspot species occupy overlapping habitat types, some of them even sharing the same host plant species (Wahlberg 2001; Ehrlich and Hanski 2004). They also share parasitoids, many of which parasitize only checkerspots (Van Nouhuys and Hanski 2004; Kankare and Shaw 2004; Kankare, Van Nouhuys, et al. 2005, Kankare, Stefanescu, et al. 2005). These features, along with what we have learned about the population and metapopulation ecology of the checkerspot butterflies and their host plant use (Ehrlich and Hanski 2004), make this group of butterflies an informative model system in which to address spatial aspects of food web ecology. Here we will discuss the situation in the Åland Islands in Finland with two butterfly species (Kankare, Van Nouhuys, et al. 2005), as well as in the Russian Republic of Buryatia in Siberia (Wahlberg et al. 2001) and in the Montseny mountains in Catalonia, Spain (Kankare, Stefanescu, et al. 2005), both with five butterfly species.

The Glanville fritillary *M. cinxia* and the heath fritillary *Melitaea athalia* are both relatively common in the Åland Islands. *Melitaea cinxia* is restricted to open dry meadows and it feeds on *P. lanceolata* and *V. spicata* (figure 4.2). *Melitaea athalia* uses a much more widespread habitat, forest edges, and it feeds primarily on *Veronica chamaedrys*. Both butterfly species are similar in their movement behavior and distances (Wahlberg et al. 2002), but because its habitat is more continuous, *M. athalia* has a widespread distribution in the Åland Islands whereas *M. cinxia* is restricted to the sparse network of dry meadows. The distributions of the two butterflies overlap in some *M. cinxia* habitat patches bordering forests, and occasionally larvae of the two species are even found together. Both butterflies are parasitized by *C. melitaearum*. However, phylogenetic analyses of the six recognized species of *Cotesia* parasitizing melitaeine butterflies using mitochondrial DNA (mtDNA) and microsatellite markers have revealed that each butterfly species is parasitized by a genetically distinct form of *C. melitaearum* (figure 4.2; Kankare and Shaw 2004). In behavioral experiments adult female parasitoids were only willing to parasitize the host species from which they had been reared

(Kankare, Van Nouhuys, et al. 2005). Therefore, and contrary to what traditional taxonomy would suggest, the dynamics of the two butterfly species are not linked by a shared *Cotesia* parasitoid. Much is known about the metapopulation structure of the *Cotesia* parasitizing *M. cinxia,* as we have described in the previous sections. This form is constrained by the distribution and dynamics of its host, and its occurrence is effectively limited to tightly clustered host population networks. If this wasp could use both host species it would experience a much less fragmented habitat, and could occupy a much larger faction of host populations, perhaps even influencing host metapopulation dynamics to a greater extent than it does at present. Unfortunately, nothing is known of the population structure of the *C. melitaearum* form using *M. athalia* in Åland, as this parasitoid is very difficult to sample. The two distinct forms of *C. melitaearum* must be linked by the hyperparasitoid *G. agilis* where the butterfly habitats overlap, but for the most part the respective habitats are separate, and because the wingless *G. agilis* likely disperses slowly, this coupling should be weak. There are several generalist pupal parasitoids of *M. cinxia* in Åland that are likely to also parasitize *M. athalia,* though there have been no studies of this.

In the steppe region of Buryatia in Russia, larvae of five species of checkerspot butterflies feeding on three different host plants in one habitat were collected and reared to adults by Wahlberg et al. (2001). Two species of *Cotesia* were collected from four of the butterfly species. Two butterfly species using different host plants in the same habitat were parasitized by the same genetic form of *C. melitaearum* (figure 4.5a); hence here the host butterflies are linked by a shared parasitoid. The two other butterfly species that were parasitized by *Cotesia* were each host to a distinct form or cryptic species of *Cotesia acuminata* (clades A2 and A4 in the phylogeny of Kankare and Shaw 2004; figure 4.5a). Interestingly, the three butterfly species that shared the same host plant (*Veronica incana*) did not share even closely related *Cotesia* (though not all the host-parasitoid combinations may have been sampled). Four non-*Cotesia* parasitoid species were collected from three of the butterfly species (Wahlberg et al. 2001; figure 4.5a), each of which may in fact use the other checkerspot butterflies as hosts (Van Nouhuys and Hanski 2004) but were not present in the sample.

The third metacommunity, at El Puig in the Montseny mountains in northern Spain, is similar in structure to the previous communities (figure 4.5b). There are five co-occurring species of checkerspot butterflies, three of which are parasitized by one recognized *Cotesia* species (*melitaearum*) and another one by another recognized species (*acuminata*). However, extensive sampling, genetic analyses and behavioral observations revealed again that the four host species were each parasitized by a member of different a clade in the *Cotesia* phylogeny (Kankare, Stefanescu, et al. 2005; Kankare and Shaw 2004), each possibly representing a cryptic species. In this case three of the butterfly species are linked by the shared host pant *P. lanceolata* (figure 4.5b).

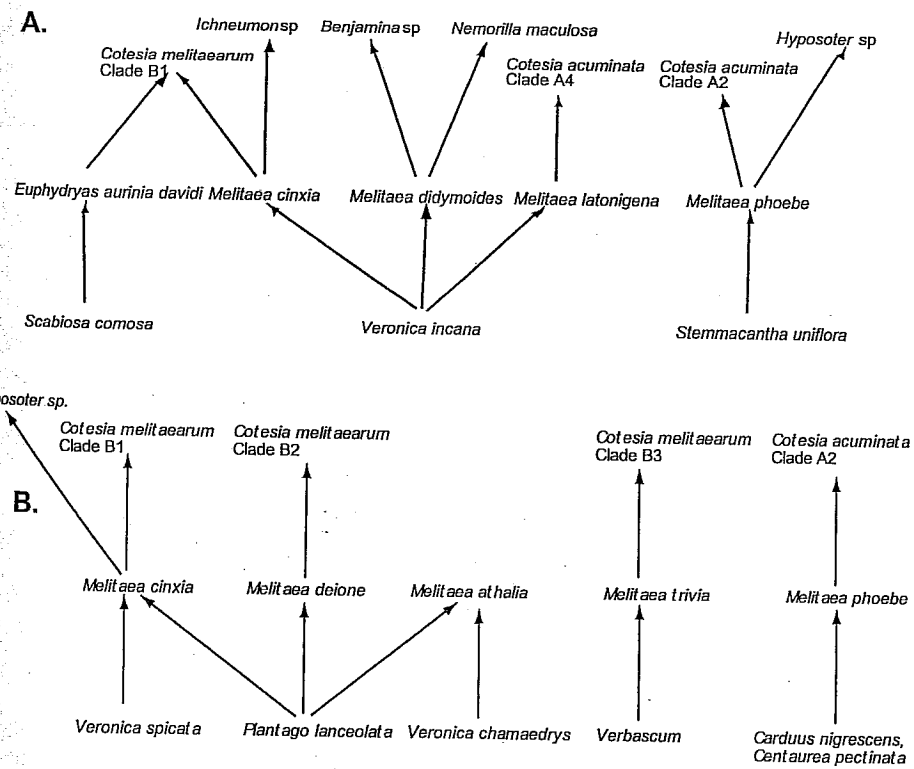


Figure 4.5 Food webs of checkerspot butterfly communities in (a) the steppe habitat in Buryatia, Russia (based on data from Wahlberg et al. 2001; Kankare and Shaw 2004), and (b) meadow habitats in El Puig in the Montseny mountains of northern Spain (based on data from Kankare and Shaw 2004; Kankare, Stefanescu, et al 2005). Note: In figure 4.5a, *Ichneumon* sp., *Benjamina* sp., and *Hyposoter* sp. may use other melitaeine hosts; *Nemorilla maculosa,* first on record on a melitaeine, may use non-melitaeine hosts; and for *Cotesia acuminata,* there is no molecular data for this parasitoid, but it most probably falls in clade A2, which includes *C. acuminata* collected from *M. phoebe* in Spain and France.

Surprisingly, *Cotesia* parasitoids appear to link species of host butterflies in only one of the three metacommunities. These checkerspot-associated *Cotesia* present a strikingly clear example of parasitoids evolving closely with their hosts, and leading to more compartmentalized ecological interactions than previously suspected. In this case evolution tends to isolate the dynamics of each community module, which have, however, remained to some extent coupled due to shared host plant species and other primary parasitoids, and between the different cryptic species of *Cotesia* and their hyperparasitoids (such as *Gelis*). Other parasitoids in these communities have genuinely broader host ranges, and they serve to link the population dynamics of their host species. For instance, the chalcid pupal parasitoids of *M. cinxia* in Åland (figure 4.2) parasitize many other host species

(Lei et al. 1997), as do tachinid flies in many checkerspot communities (Van Nouhuys and Hanski 2004). It is however noteworthy that the interaction between the host butterflies and *Cotesia* parasitoids is the potentially strongest host-parasitoid interaction in these communities, occasionally even driving local host populations to extinction (Lei and Hanski 1997).

Conclusions

We have described in this chapter the operation of several processes in butterfly metacommunities using *M. cinxia* and its host plants and parasitoids in Finland as an example. One important result to emerge from these studies is the coupling of behavioral, ecological, and evolutionary dynamics in the metacommunity context. A prime example is the contribution of variation in host plant species composition and female butterfly oviposition preference throughout the Åland Islands to metacommunity dynamics.

Another point that we have illustrated is that both local-scale processes operating within communities and large-scale processes operating among relatively independent communities may contribute to metacommunity structure and dynamics (as in Miller and Kneitel, chapter 5). Different scales may dominate in particular interactions. A case in point is the two parasitoids *C. melitaearum* and *H. horticola* sharing the same host in the same landscape. In this case the among-community processes appear to be immaterial for the interaction of the two competing parasitoids, though among-community processes explain the dissimilar distributions and dynamics of the host and the two parasitoids. The large-scale population dynamics of the butterfly, largely driven by the spatial configuration of the habitat and spatially correlated weather (Hanski 1999), affects the dynamics of the two primary parasitoids in a very different manner because of their contrasting dispersal behaviors.

We have compared the small food webs or community modules in the Åland Islands with similar modules in other checkerspot communities to explore the degree to which host species can be linked into larger metacommunities by shared resources and enemies. In all of the communities butterflies are linked by shared host plants and probably also by shared generalist enemies. Many of the butterflies appear superficially to be linked by shared parasitoids in the genus *Cotesia*. However, detailed molecular analyses and studies of host acceptance behavior indicate that most of these wasps are actually even more host specific than previously thought, and the recognized species appear to include several cryptic species, each specialized to use a single host species. Our current understanding of the structures of these butterfly-parasitoid metacommunities makes it clear that we cannot assume that identifying species by name is necessarily sufficient for understanding the ecological links among them.

A still largely open question is the population dynamic significance of the less

obvious indirect interactions in which the focal butterfly species are engaged. One example is the plant pathogenic fungus that shares the host plant *P. lanceolata* with *M. cinxia* and may interfere with larval feeding, and influences butterfly and plant metapopulation dynamics (Laine 2004a, 2004b). Another example is seed-feeding beetles, which may have a substantial impact on the recruitment of the host plant (Nieminen et al. 2004). Another area where more research is needed, and which is central to our interests in this volume, is the role of habitat fragmentation in molding the dynamics of entire metacommunities. Conducting empirical research on many species at a large spatial scale poses obvious problems; replicating such studies across landscapes with dissimilar structures means even more challenging work. Such research is however badly needed to answer some of the fundamental questions in the interface between the biology of metacommunities and changing landscapes structures.

Literature Cited

Abrahamson, W. G., and A. E. Weis. 1997. *Evolutionary ecology across three trophic levels goldenrods, gallmakers, and natural enemies.* Princeton University Press, Princeton, NJ.

Amarasekare, P. 2000. Coexistence of competing parasitoids on a patchily distributed host: Local vs. Spatial mechanisms. Ecology 81:1286–1296.

Anton, C. 2001. Host selection and performance of the parasitoid *Cotesia melitaearum* in tritrophic context. Diploma thesis. Institute for Ecology, Friedrich-Schiller University, Jena, Germany.

Armstrong, R. A. 1976. Fugitive species: Experiments with fungi and some theoretical considerations. Ecology 57:953–963.

Askew, R. R., and M. R. Shaw. 1989. Parasitoid communities: Their size, structure and development. Pages 225–26 *in* J. Waage and D. Greathead, eds. *Insect parasitoids.* Academic Press, Cambridge, UK.

Bernays, E. A., and C. De Luca. 1981. Insect anti-feedant properties of an iridoid glycoside: Ipolamiide. Experimentia 37:1289–1290.

Bonsall, M. B., and M. P. Hassell. 1997. Apparent competition structures ecological assemblages. Nature 388:371–378.

———. 1998. Population dynamics of apparent competition in a host-parasitoid assemblage. Journal of Animal Ecology 67:918–929.

———. 1999. Parasitoid-mediated effects: Apparent competition and the persistence of host-parasitoid assemblages. Researches in Population Ecology 41:59–68.

Boughton, D. A. 2000. The dispersal of a butterfly: A test of source-sink theory suggests the intermediate-scale hypothesis. American Naturalist 156:131–144.

Bowers, M. D. 1983. The role of iridoid glycosides in host-plant specificity of checkerspot butterflies. Journal of Chemical Ecology 9:475–493.

Collinge, S. K., K. I. Prudic and J. Oliver. 2003. Effect of local habitat characteristics and landscape context on grassland butterfly diversity. Conservation Biology 17:178–187.

Courtney, S. P., and F. S. Chew. 1987. Coexistence and host use by a large community of Pierid butterflies: Habitat is the template. Oecologia 71:210–220.

Dempster, J. P. 1983. The natural control of populations of butterflies and moths. Biological Review 58:461–481.

Dyer, L. A., and D. K. Letourneau. 2003. Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecology Letters 6:60–68.

Ehrlich, P. R., and I. Hanski. 2004. *On the wings of checkerspots: A model system for population biology.* Oxford University Press, Oxford, UK.

Hanski, I. 1981. Coexistence of competitors in patchy environment with and without predation. Oikos 37:306–312.

———. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

———. 1999. *Metapopulation ecology.* Oxford University Press, Oxford, UK.

Hanski, I. and Gaggiotti, O. E. 2004. *Ecology, genetics and evolution of metapopulations.* Elsevier Academic Press, London, UK.

Hanski, I. and M. Heino. 2003. Metapopulation-level adaptation of insect host plant preference and extinction-colonization dynamics in heterogeneous landscapes. Theoretical Population Biology 64:281–290

Hanski, I., J. J. Hellmann, C. L. Boggs, and J. F. McLaughlin. 2004. Checkerspots as a model system in population biology. Pages 245–263 *in* P. R. Ehrlich, and I. Hanski, eds. *On the wings of checkerspots: A model system for population biology.* Oxford University Press, Oxford, UK.

Hanski, I., and M. Kuussaari. 1995. Butterfly metapopulation dynamics. Pages 149–171 *in* P. Price and N. Cappuccino, eds. *Population dynamics: New approaches and synthesis.* Academic Press, San Diego, CA.

Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia.* Ecology 75:747–762.

Hanski, I., A. Moilanen, T. Pakkala and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10:578–590.

Hanski, I. and O. Ovaskainen. 2000. Metapopulation capacity of a fragmented landscape. Nature 404:755–758.

Hanski, I., and M. C. Singer. 2001. Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. American Naturalist 158:341–353.

Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis:* Evidence for a metapopulation model. American Naturalist 132:360–382.

Harrison, S. and C. D. Thomas. 1991. Patchiness and spatial pattern in the insect community on ragwort *Senecio jacobaea.* Oikos 62:5–12.

Hastings, A. 1980. Disturbance, coexistence, history and the competition for space. Theoretical Population Biology 18:363–373

Hawkins, B. A. 1994. *Pattern and process in host-parasitoid interactions.* Cambridge University Press, Cambridge, UK.

Hawkins, B. A. 2000. Species coexistence in parasitoid communities: Does competition matter? Pages 198–214 *in* M. E. Hochberg and A. R. Ives, eds. *Parasitoid population biology.* Princeton University Press, Princeton, NJ.

Hawkins, B. A., M. R. Shaw, and R. R. Askew. 1992. Relations among assemblage size, host specialization, and climatic variability in North American parasitoid communities. American Naturalist 139:58–79.

Hawkins, B. A., and W. Sheehan. 1994. Parasitoid community ecology. Oxford University Press, Oxford, UK.

Henneman, M. L., and J. Memmott. 2001. Infiltration of a Hawaiian community by introduced biological control agents. Science 293:1314–1316.

Hochberg, M. E., and A. R. Ives. 2000. *Parasitoid Population Biology.* Page 366. Princeton University Press, Princeton, NJ.

Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. Theoretical Population Ecology 12:197–229.

———. 1997. From Metapopulation dynamics to community structure. Pages 149–165 *in* I. Hanski and M. E. Gilpin, eds. Metapopulation biology. Academic Press, San Diego. CA.

———. 2002. Food webs in space: On the interplay of dynamic instability and spatial processes. Ecological Research 17:261–273.

Holyoak, M. 2000. Comparing parasitoid-dominated food webs with other food webs: Problems and future promises. Pages 184–197 *in* M. E. Hochberg and A. R. Ives, eds. *Parasitoid population biology.* Princeton University Press, Princeton, NJ.

Hopper, K. 1984. The effects of host-finding and colonization rates on abundance of parasitoids of a gall midge. Ecology 65:20–27.

Horner-Devine, C. M., G. C. Daily, P. R. Ehrlich, and C. L. Boggs. 2003. Countryside biogeography of tropical butterflies. Conservation Biology 17:168–177.

Kankare, M., and M. R. Shaw. 2004. Molecular phylogeny of *Cotesia* Cameron, 1891 (Insecta: Hymenoptera: Braconidae: Microgastrinae) parasitoids associated with Melitaeini butterflies (Insecta: Lepidoptera: Nymphalidae: Melitaeini). Molecular Phylogenetics and Evolution 32:207–220.

Kankare, M., C. Stefanescu, S. van Nouhuys, and M. R. Shaw. 2005. Host specialization by *Cotesia* wasps (Hymenoptera: Braconidae) parasitizing species rich Melitaen (Lepidoptera: Melitaeine) communities in northeastern Spain. Biological Journal of the Linnean Society, in press.

Kankare, M., S. van Nouhuys, I. Hanski. 2005. Genetic divergence among host specific cryptic species in Cotesia Melitaearum agg. a parasitoid of checkerspot butterflies. Annals of the Entomological Society of America, in press.

Kitahara, M., and K. Sei. 2001. A comparison of the diversity and structure of butterfly communities in semi-natural and human-modified habitats at the foot of Mt. Fuji, central Japan. Biodiversity and Conservation 10:331–351.

Komonen, A., R. Penttilä, M. Lindgren, and I. Hanski. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90:119–126.

Kruess, A., and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium.* Oecologia 122:129–137.

Kuussaari, M., M. C. Singer, and I. Hanski. 2000. Local specialization and landscape-level influence on host use in a herbivorous insect. Ecology 81:2177–2187.

Kuussaari, M., S. van Nouhuys, J. Hellmann, and M. C. Singer. 2004. Larval biology of checkerspot butterflies. Pages 138–160 *in* P. R. Ehrlich, and I. Hanski, eds. *On the wings of checkerspots: A model system for population biology.* Oxford University Press, Oxford, UK.

Laine, A.-L. 2004a. A powdery mildew infection on a shared host plant affects the dynamics of the Glanville fritillary butterfly populations. Oikos 107 (2):329–337.

———. 2004b. Resistance variation within and among host populations in a plant pathogen metapopulation—implications for regional pathogen dynamics. Journal of Ecology, in press.

Lawton, J. H., and R. M. May. 1995. *Extinction rates.* Oxford University Press, Oxford, UK.

Lei, G. C. and M. D. Camara. 1999. Behaviour of a specialist parasitoid, *Cotesia melitaearum:* From individual behavior to metapopulation processes. Ecological Entomology 24:59–72.

Lei, G. C., and I. Hanski. 1997. Metapopulation structure of *Cotesia melitaearum,* a specialist parasitoid of the butterfly *Melitaea cinxia.* Oikos 78:91–100.

———. 1998. Spatial dynamics of two competing specialist parasitoids in a host metapopulation. Journal of Animal Ecology 67:422–433.

Lei, G. C., V. Vikberg, M. Nieminen, and M. Kuussaari. 1997. The parasitoid complex attacking the Finnish populations of Glanville fritillary *Melitaea cinxia* (Lep: Nymphalidae), an endangered butterfly. Journal of Natural History 31:635–648.

Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. Proceedings of the National Academy of Sciences, U.S.A. 68:1246–1248.

Lewis, O. T., J. Memmott, J. Lasalle, C. H. C. Lyal, C. Whitefoord, and H. C. J. Godfray. 2002. Struc-

ture of a diverse tropical forest insect-parasitoid community. Journal of Animal Ecology 71:855–873.
Marino, P. C. 1991. Dispersal and coexistence of mosses (Splachnaceae) in patchy habitats. Journal of Ecology 79:1047–1060.
Memmott, J., H. C. J. Godfray, and I. D. Gauld. 1994. The structure of a tropical host-parasitoid community. Journal of Animal Ecology 63:521–540.
Mills, N. J. 1993. Species richness and structure in the parasitoid complexes of tortricid hosts. Journal of Animal Ecology 62:45–58.
Müller, C. B. and H. C. J. Godfray. 1997. Apparent competition between two aphid species. Journal of Animal Ecology 66:57–64.
Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. Conservation Biology 4:41–51.
Nee, S., and R. M. May. 1992. Dynamics of metapopulations: Habitat destruction and competitive coexistence. Journal of Animal Ecology 61:37–40.
Nee, S., R. M. May, and M. P. Hassell. 1997. Two Species Metapopulation Models. Pages 123–148 *in* I. Hanski and M. E. Gilpin, eds. *Metapopulation biology.* Academic Press, San Diego, CA.
Nieminen, M., M. Siljander, and I. Hanski. 2004. Structure and dynamics of *Melitaea cinxia* metapopulations. Pages 63–91 *in* P. R. Ehrlich, and I. Hanski, eds. *On the wings of checkerspots: A model system for population biology.* Oxford University Press, Oxford, UK.
Pajunen, V. I. 1979. Competition between rock pool corixids. Annales Zoologici Fennici 16:138–143.
———. 1982. Replacement analysis of non-equilibrium competition between rock pool Corixids (Hemiptera: Corixidae). Oecologia 52:153–155.
Pope, T., E. Croxson, J. K. Pell, and H. C. J. Godfray. 2002. Apparent competition between two species of aphid via the fungal pathogen *Erynia neoaphidis* and its interaction with the aphid parasitoid *Aphidious ervi.* Ecological Entomology 27:196–203.
Punju, E. 2002. Larval competition between two specialist parasitoids *Cotesia melitaearum* and *Hyposoter horticola* inside the hose larva. Diploma thesis. Department of Ecology and Systematics, University of Helsinki, Finland.
Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis. 1980. Interaction among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics 11:41–65.
Roininen, A., P. W. Price, and J. Tahvanainen. 1996. Bottom-up and top-down influences in the trophic system of a willow, a galling sawfly, parasitoids and inquilines. Oikos 77:44–50.
Rosenzweig, M. L. 1995. *Species Diversity in Space and Time.* Cambridge University Press, Cambridge, UK.
Shaw, M. R. 1994. Parasitoid host ranges. Pages 111–144 *in* B. A. Hawkins and W. Sheehan, eds. *Parasitoid community ecology.* Oxford University Press, Oxford, UK.
Shaw, M. R., and M. G. Fitton. 1989. Survey of parasitoids of British butterflies. Entomologist's Record 101:69–71.
Sheehan, W. 1994. Parasitoid community structure: Effects of host abundance, phylogeny, and ecology. Pages 90–110 *in* B. A. Hawkins and W. Sheehan, eds. *Parasitoid community ecology.* Oxford University Press, Oxford, UK.
Singer, M. C. and Hanski, I. 2004. Oviposition preference: Its measurement, its correlates and its importance in the life of checkerspots. Pages 181–198 *in* P. R. Ehrlich, and I. Hanski, eds. *On the wings of checkerspots: A model system for population biology.* Oxford University Press, Oxford, UK.
Singer, M. C., D. Ng, D. Vasco, and C. D. Thomas. 1992. Rapidly evolving associations among oviposition preferences fail to constrain evolution of insect diet. American Naturalist 139:9–20.
Singer, M. C., and C. D. Thomas. 1987. Variations in host preference affects movement patterns within a butterfly population. Ecology 68:1262–1267.
Steffan-Dewenter, I., and T. Tscharntke 2000. Butterfly community structure in fragmented habitats. Ecology Letters 3:449–456.

Stireman III, J. O., and M. S. Singer. 2003. Determinants of parasitoid-host associations: insights from a natural Tachinid-Lepidoptera community. Ecology 84:296–310.
Sullivan, D. J., and W. Völk. 1999. Hyperparasitism: Multitrophic ecology and behaviour. Annual Review of Entomology 44:291–315.
Thomas, C. D., and I. Hanski. 1997. Butterfly metapopulations. Pages 359–386 *in* I. Hanski and M. E. Gilpin, eds. Metapopulation biology. Academic Press, San Diego, CA.
———. 2004. Metapopulation dynamics in changing environments: Butterfly responses to habitat and climate change. Pages 489–514 *in* I. Hanski and O. Gaggiotti, eds. Ecology, genetics and evolution of metapopulations. Academic Press, San Diego.
Thomas, C. D., D. Vasco, M. C. Singer and D. Ng. 1990. Diet divergence in two sympatric congeneric butterflies: Community or species level phenomenon? Evolutionary Ecology 4:62–74.
Tscharntke, T. 1992. Coexistence, tritrophic interactions and density dependence in a species-rich parasitoid community. Journal of Animal Ecology 61:59–67.
Tscharntke, T., and B. A. Hawkins. 2002. Multitrophic Level Interactions. Cambridge University Press, Cambridge, UK.
Van Nouhuys, S., and J. Ehrnsten. 2004. Wasp behavior that leads to uniform parasitism of a host available only a few hours per year. Behavioral Ecology 15:661–665.
Van Nouhuys, S., and I. Hanski. 1999. Host diet affects extinctions and colonizations in a parasitoid metapopulation. Journal of Animal Ecology 68:1–12.
———. 2000. Apparent competition between parasitoids mediated by a shared hyperparasitoid. Ecology Letters 3:82–84.
———. 2002a. Colonisation rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. Journal of Animal Ecology 71:630–650.
———. 2002b. Multitrophic interactions in space: Metacommunity dynamics in fragmented landscapes. Pages 124–147 *in* T. Tscharntke, and B. A. Hawkins, eds. *Multitrophic level interactions.* Cambridge University Press, Cambridge, UK.
———. 2004. Natural enemies of checkerspot butterflies. Pages 161–180 *in* P. R. Ehrlich, and I. Hanski, eds. *On the wings of checkerspots: A model system for population biology.* Oxford University Press, Oxford, UK.
Van Nouhuys, S., and G. C. Lei. 2004. Parasitoid and host metapopulation dynamics: The influences of temperature mediated phenological asynchrony. Journal of Animal Ecology 73:526–535.
Van Nouhuys, S., M. C. Singer, and M. Nieminen. 2003. Spatial and temporal patterns of caterpillar performance and the suitability of two host plant species. Ecological Entomology 28:193–202.
Van Nouhuys, S., and W. T. Tay. 2001. Causes and consequences of mortality in small populations of a parasitoid wasp in a fragmented landscape. Oecologia 128:126–133.
Vet, L. E. M., and M. Dicke. 1992. Ecology of infochemicals used by natural enemies in a tritrophic context. Annual Review of Entomology 37:141–172.
Wahlberg, N. 2001. The phylogenetics and biochemistry of host plant specialization in melitaeine butterflies (Lepidoptera: Nymphalidae). Evolution 55:522–537.
Wahlberg, N., T. Klemetti, V. Selonen, and I. Hanski. 2002. Metapopulation structure and movements in five species of checkerspot butterflies. Oecologia 130:33–43.
Wahlberg, N., J. Kullberg, and I. Hanski. 2001. Natural history of some Siberian melitaeine butterfly species (Melitaeini: Nymphalidae) and their parasitoids. Entomologica Fennica 12:72–77.