

Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape

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Summary

1. We describe the pattern of colonization of suitable, but currently empty, habitat by a host butterfly and two specialist parasitoids living in a highly fragmented landscape.
2. Using survey data collected over 8 years, field sampling and small-scale experiments we show that the ability of the Glanville fritillary butterfly (*Melitaea cinxia*) to colonize new habitat is intermediate between that of its two larval primary parasitoids.
3. The butterfly forms a classic metapopulation, which the parasitoid *Hyposoter horticola* experiences as a single patchily distributed host population because of its high rate of dispersal and long colonization distances. In contrast, most of the local butterfly populations are presently inaccessible to the parasitoid *Cotesia melitaeorum*, which has a limited dispersal range and therefore persists only in tightly clustered networks of host populations.
4. At the regional scale, the butterfly may escape *C. melitaeorum* by colonizing empty habitat, but host dispersal does not limit parasitism by *H. horticola*, which consequently must be limited by local interaction.
5. The parasitoid *H. horticola* mostly avoids direct competition with *C. melitaeorum* because the majority of *H. horticola* populations are outside the range of dispersal by current *C. melitaeorum* populations. In contrast, all *C. melitaeorum* populations experience competition with *H. horticola*.

Key-words: competition, *Cotesia*, dispersal distance, *Melitaea cinxia*, metapopulation, parasitoid dispersal.

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Introduction

The relative dispersal abilities of interacting species can greatly influence their chances of persistence and the species composition of communities (MacArthur & Wilson 1967; Wilson 1992; Tilman 1994; Holt 1997; Hochberg & Ives 1999; Hassell 2000). An entire community of species may have rather similar dispersal behaviour; for example, where all of the species are adapted to living in an ephemeral or fragmented habitat (Southwood 1962; Hodge & Arthur 1997; Dubbert, Tschardt & Vidal 1998). In this case, coexistence of competitors and natural enemies and their prey is likely to be largely mediated by local interaction, though stochastic founder effects may also play a role. In other communities, interacting species may differ substantially in their rate and range of dis-

persal, such that they all experience a different spatial structure of the habitat in the same landscape (Levin 1992; Roland & Taylor 1997; van der Meijden, & van der Veen-van Wijk 1997; Roslin & Koivunen 2001). For example, a host plant species may disperse widely and persist as a single large patchily distributed population; the plant may have a herbivore that forms a classic metapopulation made up of local populations with relatively independent dynamics; and the herbivore may have several functionally important predators and parasites, each with their own relationship to the spatial structure of the populations with which they interact. While the spatial distribution of habitat will play some role in any species interaction, it is likely to be especially significant in those situations where the relative dispersal rates and distances of interacting species differ greatly.

There is an extensive theoretical literature on models of both competitive and host–parasitoid (predator–prey) interactions involving dispersal within a continuous habitat or among discrete habitat patches (reviews in Nee, May & Hassell 1997; Hassell 2000).

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The classic concept of competitive coexistence in a fragmented landscape involves a superior disperser that is an inferior competitor locally (Levins & Culver 1971; Hastings 1980; Münster-Swendsen 1982; Savill & Hogeweg 1999; Bengtsson 1991; Nee & May 1992; Nee *et al.* 1997). The few empirical studies that have addressed the importance of dispersal among arthropod competitors have reached dissimilar conclusions about the role of relative dispersal rates and ranges in influencing coexistence (Hanski & Ranta 1983; Hopper 1984; Lei & Hanski 1998; Amarasekare 2000).

In the classic model of host–parasitoid (prey–predator) interaction in a fragmented landscape, the host disperses better than the specific parasitoid, enabling the host to locate currently empty sites fast enough to compensate for the mortality caused by the locally efficient parasitoid (Comins, Hassell & May 1992; Holt 1997; Hassell 2000). Dispersal among habitat patches adds to the stability of the interaction, unless the rate of dispersal is very high, in which case the increased synchrony of local dynamics, due to dispersal, might be detrimental to persistence at the metapopulation level. However, asymmetric dispersal capacity is neither a necessary nor a sufficient condition for host–parasitoid coexistence in a fragmented landscape (Slatkin 1974; Taylor 1988; Harrison & Taylor 1997; Nee *et al.* 1997; Amarasekare 2000). Outbreaks of herbivorous insects may in fact be controlled by relatively mobile parasitoids, effectively blocking the spatial spread of the host (Roland & Taylor 1995; Brodmann, Wilcox & Harrison 1997; Maron & Harrison 1997). Unfortunately, relatively few empirical studies have addressed the assumptions and predictions of host–parasitoid models involving spatial structure and dispersal (Huffaker 1958; Murdock *et al.* 1984; Murdoch 1994; Comins & Hassell 1996; Holyoak & Lawler 1996; Jones, Godfray & Hassell 1996; Harrison & Taylor 1997; van der Meijden & van der Veen-van Wijk 1997).

In this paper, we use both long-term and large-scale observational data and the results of field experiments to quantify the colonization rate and distances in *Melitaea cinxia* (L.) (Lepidoptera: Nymphalidae) (the Glanville fritillary butterfly) and two primary parasitoids in the Åland Islands in SW Finland. The butterfly has a classic metapopulation structure with a high rate of population turnover (Hanski 1999). The two specialist parasitoids, *Cotesia melitaearum* (Wilkinson) (Braconidae: Microgastrinae) and *Hyposoter horticola* (Gravenhorst) (Ichneumonidae: Campopleginae), live in meadows occupied by the host butterfly and compete directly for hosts. The two wasps differ in their behaviour and phenology (Lei *et al.* 1997; Lei & Hanski 1998; van Nouhuys & Hanski 2002). We quantify the distances over which the butterfly and the parasitoids are able to successfully colonize suitable but currently unoccupied habitat and we discuss the impact of the observed spatial pattern of colonization on the

large-scale interactions between the parasitoids and their host as well as between the parasitoids themselves.

Material and methods

THE SPECIES AND THE LANDSCAPE

The geographical range of the Glanville fritillary butterfly in Finland is currently restricted to an area of 50 by 70 km² in the Åland Islands in the northern Baltic. Meadows that are suitable for the butterfly are small (typically < 1 ha) and they are distributed across the rural agricultural landscape. Our database currently contains about 4000 such meadows in Åland, but less than half of them were known in the years 1993–97. The several hundred butterfly populations inhabiting the meadows are also small and prone to local extinction (Hanski & Kuussaari 1995; Hanski 1999). The meadows have been divided into 127 habitat patch networks (Hanski *et al.* 1996), which are defined as clusters of patches (meadows) separated by at least 1.5 km from other patch networks. Given the dispersal range of the butterfly (Hanski *et al.* 1994; Kuussaari, Nieminen & Hanski 1996; this paper), there is little exchange of butterflies among patch networks and the respective metapopulations have relatively independent dynamics (Hanski *et al.* 1996; Hanski 1999).

The Glanville fritillary lays clutches of 150–200 eggs on the host plants in June. Upon hatching, the larvae live gregariously in silken webs until they disperse to pupate in the following May. Larval development is interrupted by winter diapause. The parasitoid *Cotesia melitaearum* is small, sedentary and gregarious, with two to three generations per year. In contrast, *Hyposoter horticola* is large, mobile and solitary, with one generation per year and per host generation. Both parasitoids are specialists of melitaeine butterflies in Europe, but use only the Glanville fritillary butterfly in the Åland Islands (Lei *et al.* 1997; Lei & Hanski 1998; van Nouhuys & Hanski 2002).

SURVEY DATA TO RECORD PATCH OCCUPANCY AND COLONIZATION BY *M. CINXIA* AND *C. MELITAEARUM*

Every autumn since 1993, each known habitat patch in Åland has been surveyed for the presence and size (number of larval groups) of local butterfly populations. These survey data provided information on the locations of butterfly populations and unoccupied habitat patches over time. Successful colonization by the butterfly was recorded when a habitat patch that had not been occupied during one autumn survey was found to be occupied in next autumn survey. Altogether, 906 such colonizations were recorded in 1993–2000.

The parasitoid *C. melitaearum* was censused in the spring, when immature parasitoids that had spent the winter within host larvae pupated in abandoned larval

webs. It is more difficult to reliably record the presence of *C. melitaearum* than it is to find its host, because the parasitoid populations are smaller and individual cocoons are less conspicuous than the host larval groups. We therefore used only those censuses that were carefully conducted by S.v.N. or were considered to be otherwise reliable. During 1998–2001, the careful parasitoid census included the host populations in all the habitat patch networks in which *C. melitaearum* had ever been found. We believe that the 26 colonizations that were recorded represent well the true pattern of colonizations. For 1993–97 we accumulated 38 colonizations from the parts of the study area that were most thoroughly studied. Many of these colonizations occurred in the densely populated habitat patch network studied intensively by Lei & Hanski (1997, 1998). Thus, altogether the material includes 64 colonizations of host populations by *C. melitaearum* between 1993 and 2001. Colonization by *C. melitaearum* was detected when a host population that was unoccupied by the wasp in one spring was found to be occupied in the following spring.

MEASUREMENT AND ANALYSIS OF CONNECTIVITY

A habitat patch that is located near possible source populations is more likely to become colonized than a habitat patch that is located far away from possible source populations. Furthermore, colonization is more likely if nearby source populations are large. We calculated an index of connectivity (S) for each habitat patch (meadow) for the butterfly and for each host population for *C. melitaearum*. For the butterfly, $S_i = \sum p_j \exp(-\alpha d_{ij}) A_j^b$, where d_{ij} is the Euclidean distance between patches j and i , and $\alpha = 1 \text{ km}^{-1}$ as estimated with mark-recapture data for the Glandville fritillary (Hanski *et al.* 1996). A_j^b is the scaled area of patch j with $b = 0.5$ (Hanski *et al.* 1996), which is used as a proxy for emigration rate from patch j (Hanski, Alho & Moilanen 2000). For meadows occupied by the butterfly $p_j = 1$, and for unoccupied meadows $p_j = 0$.

For *Cotesia melitaearum* we used the same formula to calculate connectivity of each butterfly population to wasp source populations. The host population size (number of larval groups) was used instead of patch area. $\alpha = 1 \text{ km}^{-1}$ was chosen, based on a limited amount of data on *C. melitaearum* movement distances (Lei & Hanski 1997; van Nouhuys & Hanski 1999). It is worth emphasizing that the analyses for which we use the connectivity measure in this paper are not very sensitive to α . In the formula for connectivity, $p_j = 1$ if the host population was occupied by the wasp, otherwise $p_j = 0$. In the case of *H. horticola* a different approach had to be used, as the presence of this parasitoid cannot be reliably scored in the field (below).

We used logistic regression to analyse the association between butterfly colonizations and habitat patch connectivity and, in a separate analysis, between

colonizations and the distance to the nearest possible source population. Year was included as another explanatory variable in both models. Logistic regression could not be used for the analysis of colonization by *C. melitaearum*, because very few of the available host populations were colonized in each year. Instead we used survival analysis with Cox regression (Cox 1972; Allison 1995) to measure the association between time until colonization (or lack of colonization) and the connectivity of each host population through time. In a separate analysis we modelled the association between time until colonization and the distance to the nearest possible source population. There were insufficient data to compare the connectivities of host populations colonized by the parasitoid in different years. Direct comparison between the patterns of colonization by the butterfly and the parasitoid was made using only patches in networks that had been occupied by the parasitoid (582 butterfly colonizations in 45 patch networks).

METAPOPULATION CAPACITY AND THE PRESENCE OF *M. CINXIA* AND *C. MELITAEARUM*

As explained in the section ‘The species and the landscape’, the large number of meadows in Åland that are suitable for occupancy by the Glandville fritillary has been divided into 127 habitat patch networks (Hanski *et al.* 1996). Each patch network is made up of a cluster of meadows that range in size, average isolation and quality. The metapopulation capacity (λ_M) is a measure of the capacity of a patch network to support a metapopulation of the focal species (Hanski & Ovaskainen 2000). This measure takes into account the total amount of habitat in the network but also the spatial configuration of the patches making up the network (Hanski & Ovaskainen 2000; Ovaskainen & Hanski 2001). We calculated the metapopulation capacity of each habitat patch network in the database, assuming $\alpha = 1$ as in the calculation of connectivity above. We then examined the occurrence of the butterfly and *C. melitaearum* in the networks as a function of metapopulation capacity.

INCIDENCE OF *HYPOSOTER HORTICOLA* IN NATURALLY OCCURRING BUTTERFLY POPULATIONS

In the spring of 1999, 5–50 larvae of the Glandville fritillary were sampled from each of 50 host populations. These populations included 20 newly established populations (colonization in 1998) and 30 older populations throughout the Åland Islands. In the spring of 2000, 3–5 larvae were sampled from each of 13 host populations colonized in 1999. For each of these 13 populations, a nearby butterfly population that was at least 3 years old was also sampled. We were constrained to taking small samples in order to avoid perturbing

the small newly established butterfly populations. The larvae were reared in the laboratory until they became butterfly pupae or produced parasitoid cocoons. Butterfly larvae that died were dissected to find out whether they were parasitized by *H. horticola*. Upon pupation, unparasitized hosts were returned into their original population. Associations between the age and the connectivity of host populations and the presence of *H. horticola* were analysed using multiple logistic regression. We used the connectivity values calculated for the butterfly (as described above) because *H. horticola* occupied most host populations. The fraction of the sample parasitized was analysed using analysis of variance. Year and sample size were included as covariates in each analysis.

PARASITOID COLONIZATION EXPERIMENT ALONG A TRANSECT

This experiment was designed to measure the colonization distances from source populations of *C. melitaearum* and *H. horticola* during one season. We created small host populations in suitable but unoccupied habitat patches at 5–6 distances ranging from 0 to 1400 m along a transect starting from a source population. The experiment was repeated at two locations in 1998 and at two other locations in 1999. The four specific source populations were chosen, based on the criteria that both parasitoids were present and that there were no butterfly populations within at least 3 km in the 180 degree sector around the transect of experimental host populations. These criteria limited the experiment to four replicates, but also allowed us to be certain of the source populations.

In the first year there were five experimental populations at distances of 50, 100, 200, 500 and 1000 m from the source population. Each host population was made up of five larval groups of 70–150 larvae of the Glanville fritillary. The larvae were placed in the field as 1st instars, which was too late for parasitism by *H. horticola* (we learned only in the summer 2000 that *H. horticola* parasitizes fully developed larvae inside the egg). Colonization by the summer and autumn generations of *C. melitaearum* was possible. In the second year, there were six experimental populations, including one within the source population itself. The experimental populations were made up of five larval groups, each starting out as 100 eggs. At one site the experimental populations were located at 0, 150, 300, 500, 800 and 1000 m from the source population; at the second site they were at 0, 150, 500, 750, 1050 and 1400 m. In this year there was an opportunity for colonization by both parasitoid species. The larval groups were checked weekly until the larvae had built the winter nest and entered diapause in early September. Larvae were reared until they became butterfly pupae or produced parasitoid cocoons. Individuals that died as larvae were dissected and examined for parasitism by *C. melitaearum* and *H. horticola*.

HYPOSOTER HORTICOLA COLONIZATION EXPERIMENT USING SENTINEL HOST POPULATIONS

In order to establish that there is indeed some limit to the dispersal range of *H. horticola*, we created small host populations in suitable habitat patches far away from any natural butterfly populations in the summer of 2000. Two populations were placed in habitat patches on the island of Föglö 8.5 km from the nearest known natural butterfly population. Two more populations were placed on the island of Simskåla 11.3 km by land and water from the nearest known butterfly population. A third pair of populations, used as a control, was placed in unoccupied habitat patches in a patch network populated by the Glanville fritillary, 0.2 km from the nearest host population. Four plants containing egg clusters of 100–150 were placed in each experimental population in the beginning of the *H. horticola* flight period. The larvae were brought back to the laboratory during their second instar and dissected to count the number of host larvae containing *H. horticola* larvae.

Results

HABITAT PATCH OCCUPANCY AND COLONIZATIONS BY THE GLANVILLE FRITILLARY

The fraction of meadows occupied by the butterfly varied between 16 and 37% in the years 1993–2000. The meadows typically occur in clusters, hence most habitat patches are not particularly isolated (Fig. 1a). As previously shown (Hanski *et al.* 1996; Hanski 1999), the fraction of habitat patches occupied by the butterfly increases with connectivity (Fig. 1b; mean $\ln S$ of occupied patches = 0.57 differs significantly from the overall mean $\ln S$ of -0.78, $P < 0.001$). Though most meadows are relatively well-connected to existing butterfly populations, it is noteworthy that there is a long tail of unoccupied meadows with connectivity $\ln S < -3$ (Fig. 1a). This level of connectivity would be obtained, for example, if there were a single occupied patch of 1 ha located 3 km away from the focal patch.

From autumn 1993 until autumn 2000 we recorded 906 colonizations of empty habitat patches. The average colonization distance from the nearest possible source population was 0.6 km, while the longest distance was 6.8 km. 95% of the colonizations occurred within 2.3 km of the nearest source. About 10% of the habitat patches available for colonization were outside the range of the longest colonization distances observed, and hence these habitat patches were temporarily out of reach by the butterfly. As previously shown (Hanski *et al.* 1996; Hanski 1999), the rate of colonization increased with connectivity (Fig. 1b; logistic regression $\chi^2_{\text{isolation};1,112502} = 393$,

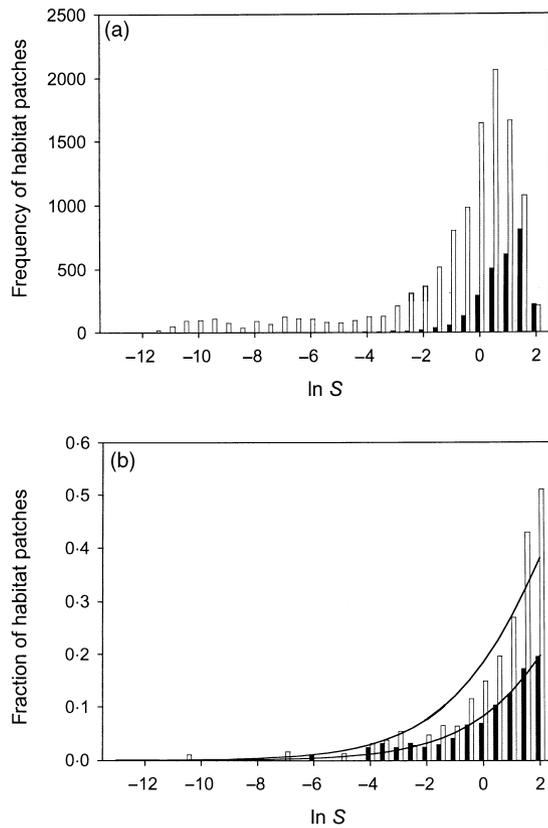


Fig. 1. Habitat patch occupancy and colonizations by the Glanville fritillary as a function of patch connectivity in 1993–2000. The horizontal axis gives the logarithm of S , the connectivity index. (a) Frequency distribution of unoccupied (\square) and occupied (\blacksquare) habitat patches. (b) Proportion of habitat patches occupied by the butterfly (\square) and the proportion of empty patches that became colonized in the following year by the butterfly (\blacksquare). The two lines show the fitted functions of yearly colonization probability ($C = 1/(1 + y/S^x)$) and long-term probability of occupancy ($p = 1/(1 + E y/S^x)$) based on the incidence function model. y and x are two model parameters, while E is the yearly extinction rate. The estimated value $E = 0.4$ is consistent with the observed level of population extinction, which is very high due to large number of very small populations with high extinction risk (Hanski 1999).

$P < 0.001$), such that up to 20% of the least isolated unoccupied habitat patches were colonized in one year (Fig. 1b). The frequency of colonizations differed among the years (Table 1; logistic regression $\chi^2_{\text{years}; 6, 11250} = 157$, $P < 0.001$), as did the distance from the nearest possible source population (Table 1; logistic regression $\chi^2_{\text{years} \times \text{distance}; 6, 11250} = 13.08$, $P = 0.04$). Variation in the level of connectivity of newly colonized meadows among years was not significant (Table 1; logistic regression $\chi^2_{\text{years} \times \ln S; 6, 11250} = 10.89$, $P = 0.09$).

The fraction of occupied patches increases more steeply with connectivity than the fraction of newly colonized patches (Fig. 1b). This is to be expected because populations accumulate in the better connected patches. The incidence function model (Hanski 1994, 1999) was used to calculate the probability of colonization (C) and the long-term probability of

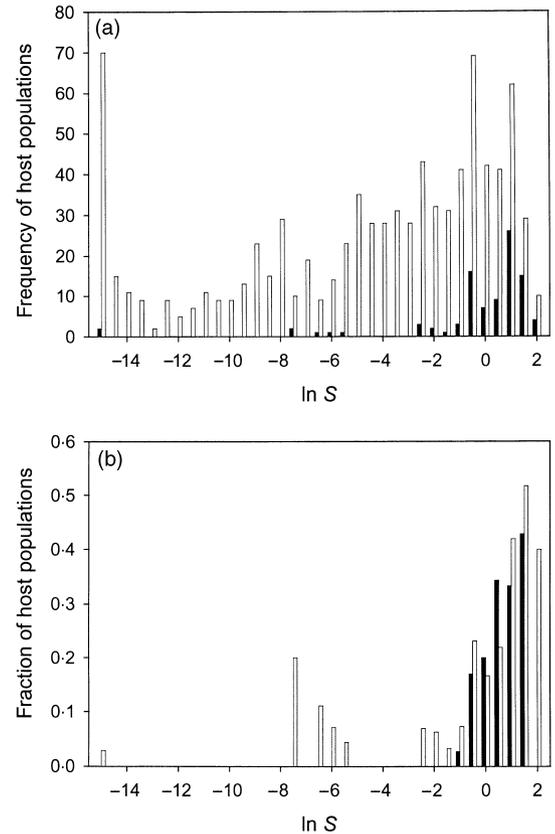


Fig. 2. Habitat patch occupancy and colonizations by *Cotesia melitaearum* as a function of patch connectivity in 1998–2000 (including material from selected areas in 1994–97 as explained in the Material and methods). The horizontal axis gives the logarithm of S , the connectivity index. (a) Frequency distribution of host populations unoccupied (\square) and occupied (\blacksquare) by the wasp. (b) Proportion of host populations occupied by the wasp (\square) and the proportion of empty host populations colonized in the following year by the wasp (\blacksquare).

occupancy (p) as functions of connectivity. The results are shown in Fig. 1b.

HABITAT PATCH OCCUPANCY AND COLONIZATIONS BY THE PARASITOID *COTESIA MELITAEARUM*

Cotesia melitaearum has occupied 5–19% of the host populations in different years (11% on average). Most of the occupied populations have occurred in tight clusters (Fig. 2a), and the fraction of host populations occupied by the wasp increases with connectivity (Fig. 2b; see also Lei & Hanski 1997; van Nouhuys & Hanski 1999). Note that though most parasitoid populations have occurred in the least isolated host populations, there are also some relatively isolated parasitoid populations, with $\ln S$ less than -5 in Fig. 2. We shall comment on these cases in the discussion.

Between spring 1994 and spring 2001, we recorded 64 colonizations by *C. melitaearum* for which we have sufficient information about the surrounding populations to include in the analysis. The colonizations

Table 1. Data on butterfly colonization events in each year

Year	Number of colonizations	Ratio of colonizations to populations*	Connectivity of newly established populations		Distance to the nearest possible source population (km)			
			Mean ln S	SD	Mean	SD	Max	95%†
93–94	110	0.22	0.296	1.000	0.73	0.89	4.0	2.81
94–95	106	0.29	0.351	1.014	0.52	0.71	4.5	1.67
95–96	97	0.26	0.108	0.840	0.54	0.60	3.49	1.76
96–97	145	0.47	0.099	0.972	0.65	0.77	4.41	2.03
97–98	140	0.41	0.374	1.052	0.61	0.89	6.79	2.21
98–99	97	0.22	0.407	1.310	0.67	0.92	4.36	3.31
99–00	211	0.56	0.449	0.869	0.55	0.66	3.48	2.28

*The number of empty habitat patches colonized in one year divided by the number of possible source populations in the previous year.

†Distance from possible source populations of all but the most extreme 5% of colonizations.

occurred in well-connected host populations (Fig. 2b), and the colonization probability increases significantly with connectivity (Cox regression Wald $\chi^2_{1,870} = 28.18$ $P < 0.0001$; Risk ratio = 2.163). The same pattern is apparent while using the distance to the nearest possible source population instead of connectivity (Cox regression Wald $\chi^2_{1,870} = 43.79$ $P < 0.0001$; Risk ratio = 0.323). By comparing the two risk ratios we see that colonization probability changes more with connectivity than with distance to the nearest neighbour. Because most colonizations by the parasitoid occurred within 0.5 km of the existing populations, and the longest observed colonization distance was 1.6 km, the vast majority of butterfly populations was not accessible to the parasitoid during this study. In 1998–2000, which are the years for which we have the most complete data, 82, 82 and 91% of the host populations were beyond the longest colonization distance observed for the wasp.

In contrast to the respective results for the butterfly, there is no great difference in the connectivity of occupied and newly colonized patches in *C. melitaearum* (Figs 1b and 2b). This result implies a high extinction rate of wasp populations which, in the context of the incidence function model, would make p similar to C (Hanski *et al.* 1996; Hanski 1999; see legend to Fig. 1). Indeed, the wasp populations must have a higher extinction rate than the butterfly populations, because the high rate of parasitoid extinction for various reasons (van Nouhuys & Tay 2001) is further elevated by the high rate of host extinctions, necessarily causing the extinction of the wasp.

COLONIZATION AND HABITAT PATCH OCCUPANCY BY THE BUTTERFLY VS. *C. MELITAEARUM*

Over the years, the butterfly has been found in 104 of the 127 habitat patch networks in the Åland Islands, and in any one year about 60% of the networks have been occupied. The habitat patch networks that have been occupied are characterized by high metapopulation

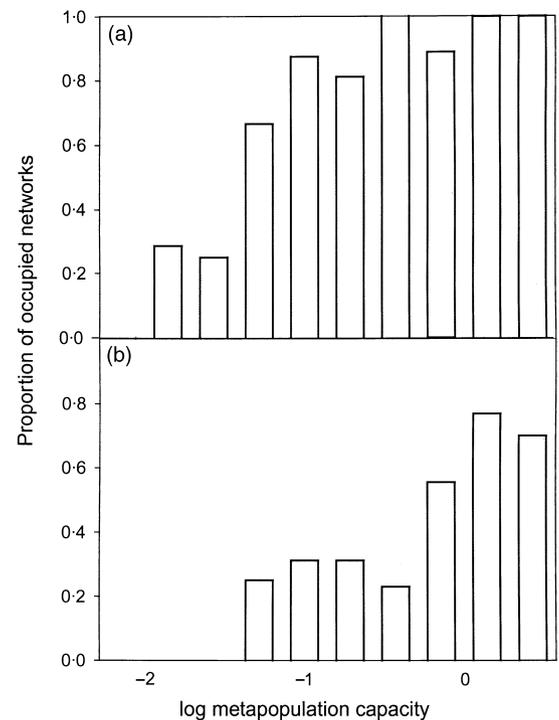


Fig. 3. The fraction of habitat patch networks occupied by (a) the Glanville fritillary and (b) *Cotesia melitaearum* as a function of the metapopulation capacity of the network (calculated with $\alpha = 1$).

capacity (Fig. 3a, see also Hanski & Ovaskainen 2000). The parasitoid *C. melitaearum* has been found in 46 of these patch networks, and these networks tend to be the ones with the highest butterfly metapopulation capacity (Fig. 3b). It is in these latter networks that we may directly compare the colonization ability of the butterfly with that of the wasp. There were 582 butterfly colonizations in the parasitoid-occupied networks, with the mean ln S of 0.52 (SD = 0.72). There were 64 parasitoid colonizations in the same networks, with mean ln S of 0.19 (SD = 0.67). The newly colonized parasitoid populations were thus significantly more isolated than the newly colonized butterfly populations (t -test with unequal n and variance, $t = 3.74$; P

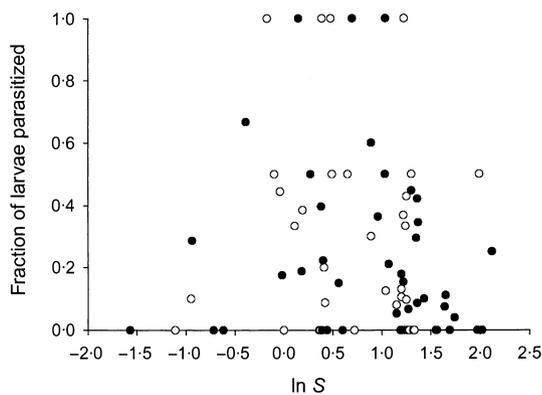


Fig. 4. Fraction of host larvae parasitized by *Hyposoter horticola* as a function of host population connectivity ($\ln S$) and age. S is parameterized for the butterfly. ●, butterfly populations that have persisted for at least 3 years; ○, newly colonized host populations.

< 0.001). We return to the interpretation of this result in the discussion.

PRESENCE OF THE PARASITOID *HYPOSOTER HORTICOLA* IN NATURALLY OCCURRING HOST POPULATIONS

Most butterfly populations sampled were occupied by *H. horticola*. Populations located far from other butterfly populations and newly established butterfly populations were as likely to be occupied by *H. horticola* as well-connected and old host populations (Fig. 4; logistic regression, no statistical association between the presence of *H. horticola* and the age or connectivity of the host population). Note, however, that *H. horticola* was absent from four of the six most isolated populations sampled ($\ln S < -0.5$; Fig. 4), which suggests a weak trend in the direction of reduced occupancy in the most isolated host populations. The distance of the least connected newly established host population occupied by *H. horticola* in Fig. 4 was 1.6 km from the nearest host population, while the two least connected host populations sampled, neither of which appear to have been occupied by *H. horticola*, were isolated by 2.9 and 1.7 km.

PARASITOID COLONIZATION EXPERIMENTS

The experimental populations in the transect experiment were available for colonization by the late spring and summer generations of *C. melitaearum*. The late spring generation can be large because 20–30 parasitoids develop in each parasitized late instar host caterpillar and there can be hundreds of them in a local population (Lei *et al.* 1997). In 1997, *C. melitaearum* parasitized larval groups at 50, 100, 200 and 500 m but not at 1000 m from the source population 565 (Table 2). In contrast, there was no colonization by *C. melitaearum* from the source population 273, most likely because the source itself became extinct during the summer of 1997 and therefore probably produced few if any dispersing adult wasps. In 1998 *C. melitaearum* parasitized host larvae at 0 and 800 m from the source population 877, and parasitized only larval groups at 0 m from the source population 21 (Table 2).

There were no colonizations of experimental host populations by *H. horticola* in 1997, because the host populations were placed in the field as first instar larvae, which are not parasitized by *H. horticola* (see Material and methods). In 1998, *H. horticola* parasitized larvae in all experimental populations available, up to 800 m from the source population 877 and up to 1050 m from the source population 21 (Table 2).

In the experiment in which small sentinel host populations were exposed to parasitism by *H. horticola* at distances of 8.5 and 11.3 km from the nearest natural butterfly population, none of the host larvae in the four very isolated populations were parasitized. In contrast, host larvae in each larval group in the two control populations surrounded by Glanville fritillary populations were parasitized.

Discussion

POPULATION DYNAMICS OF THE BUTTERFLY AND THE PARASITOID *C. MELITAEARUM*

The spatial population dynamics of a parasitoid are constrained by the wasps' own dispersal capacity and

Table 2. Results of transect experiments on parasitoid colonization

Source population ID	Year	Source population size*	Subsequent source pop. size*	Distance (m) of experimental populations from source population†	Most distant colonization (m) by <i>Cotesia melitaearum</i>	Most distant colonization (m) by <i>Hyposoter horticola</i> ‡
273	97	11	0	50, 100, 200, 500, 1000	None§	–
565	97	29	11	50, 100, 200, 500, 1000	500	–
877	98	28	12	0, 150, 300, 500, 800, 1000	800	800
21	98	37	10	0, 150, 500, 750, 1050, 1400	0	1050

Each experimental population was made up of five larval groups of 70–150 individuals.

*Number of *Cotesia* cocoons.

†Experimental populations in italics were consumed by egg predators and hence could not have been colonized by parasitoids.

‡The larvae in the experimental populations were unavailable to *Hyposoter horticola* because they were placed in the field too late to be parasitized (see text).

§Colonization was unlikely to occur by *C. melitaearum* because the source population itself went extinct.

Table 3. Approximate local population sizes of the host butterfly and the parasitoids and the maximum colonization distances

Species	Brood size	Adult population size (relative to 100 <i>M. cinxia</i>)	Maximum colonization distance
<i>M. cinxia</i>	150 eggs/batch	100	5 km
<i>H. horticola</i>	1 egg/host	30	Several km (but < 8 km)
<i>C. melitaearum</i>			1.5 km
1st generation (summer)	1.2 eggs/host	3	
2nd generation (autumn)	2.5 eggs/host	10–25	
3rd generation (spring)	18 eggs/host	20–1500	

Based on Lei *et al.* (1997), Kuussaari (1998), and S. van Nouhuys (unpublished data).

behaviour and by the spatial dynamics of the host. *Cotesia melitaearum* is a very efficient parasitoid at the local scale. The wasp has up to three generations per host generation, and it is gregarious, laying 1–30 eggs per host larva depending on their size (Lei *et al.* 1997; Lei & Camara 1999). The wasp thus has a very high intrinsic rate of population increase, potentially large local population size in comparison with the host population size (Table 3), and the wasp is efficient in finding the host larval groups (Stamp 1982; Lei & Hanski 1998; Lei & Camara 1999). It is therefore not surprising that the wasp may even cause the extinction of local butterfly populations (Lei & Hanski 1997; van Nouhuys & Hanski 1999). Nonetheless, at the regional scale *C. melitaearum* persists only at a low level within the host metapopulation in the Åland islands. This is both because it experiences an even more fragmented landscape than is experienced by the host, and because of its limited dispersal range.

In fragmented landscapes, both the host and the parasitoid are expected to be absent from those parts of the landscape in which the availability of suitable habitat patches is below a species-specific extinction threshold. In the context of classic metapopulation theory, the concept of metapopulation capacity (Hanski & Ovaskainen 2000; Ovaskainen & Hanski 2001) is helpful in allowing a quantitative assessment of the extinction threshold. Unfortunately, the quality of the data for *Cotesia melitaearum* does not allow us to fit the metapopulation model to the data in the manner that Hanski & Ovaskainen (2000) did for the Glanville fritillary. Here we did a more approximate analysis by comparing the metapopulation capacities of wasp-occupied and butterfly-occupied networks. The results (Fig. 3) illustrate that the metapopulation capacity of habitat patch networks that are able to support a wasp metapopulation is higher than the capacity of networks in which the butterfly may occur. In other words, the wasp is restricted to the parts of the landscape that are most favourable for occupancy by the host butterfly. Even if the parasitoid would have an equal colonization capacity to that of the host, it would nonetheless be unable to persist in a very fragmented landscape in which its host has a low incidence of patch occupancy.

In reality, the dispersal range of *C. melitaearum* is less than that of its host. There are very few studies of

dispersal distances by free-living parasitoids (Antolin & Strong 1987; Onillon 1990; reviewed by Godfray 1994; Brodman *et al.* 1997), and especially few studies in which population sizes are known or have been estimated. We found that in one season and during two parasitoid generations, *C. melitaearum* colonized experimentally placed host populations up to 0.5 and 0.8 km from the nearest possible source population, while in a third experiment there was no colonization beyond the source population itself (Table 2). Amongst the 64 natural colonizations in our 8-year data set, the mean colonization distance from the nearest source population was 0.46 km and the most distant colonization occurred at 1.57 km from the nearest source.

More is known about dispersal of butterflies in general and the movements of the Glanville fritillary in particular (Hanski *et al.* 1994; Kuussaari *et al.* 1996; Hanski 1999). In a study of 1737 marked Glanville fritillaries (Hanski *et al.* 1994), most transfers took place among habitat patches located less than 0.5 km apart, but the longest observed movement distance was 3.1 km. The results of two other mark–recapture experiments produced similar results (Kuussaari *et al.* 1996; I. Hanski unpublished). Among the 906 colonizations observed between 1994 and 2000 in the present study, the mean distance from the nearest population was 0.6 km and the longest recorded colonization distance was 6.8 km. These results are similar to those reported for another morphologically similar butterfly species, *Proclissiana eunomia*, while it was spreading into a previously unoccupied fragmented landscape in Morvan, central France (Nève *et al.* 1996).

Based on previous mark–recapture data for the Glanville fritillary (Hanski *et al.* 1994, 2000; Kuussaari *et al.* 1996), our experimental results on the colonization of host populations by the parasitoid, and natural colonizations over 8 years, we conclude that *C. melitaearum* has a higher yearly colonization rate than the host in well-connected habitat patches. However, the host is able to colonize unoccupied patches over longer distances than the parasitoid (though this difference between the species may be overestimated because of a difference in sample sizes). The higher colonization rate of well-connected patches by the parasitoid (0.2–0.4 per year) than by the host (0.1–0.2 per year) is probably to a large extent because *C. melitaearum* has

two or three generations per year while the butterfly has just one, and because many *C. melitaearum* can develop in each parasitized late instar host individual (Table 3).

Examining colonizations in the networks that were occupied both by the butterfly and the parasitoid produced the seemingly unexpected result that the parasitoid colonizations occurred at more isolated sites on average than the host colonizations. The explanation of this result is that sites available for colonization were more isolated for the wasp than for the host butterfly (Figs 1a and 2a), to some extent because of the higher colonization rate of the parasitoid in well-connected habitat patches. The average connectivity of empty habitat available for colonization by the butterfly in the networks occupied by the wasp was $\ln S = 0.39$, which is only slightly smaller than the mean connectivity of colonized patches (0.52; Fig. 2a). In contrast, the mean connectivity of butterfly populations available for colonization by the wasp was $\ln S = -5.42$, which corresponds to habitat patches much more isolated than sites ever colonized by the wasp (mean $\ln S$ of colonized patches was 0.19).

The generally small population sizes, high rate of local population extinction, and short colonization distances of *C. melitaearum* imply relatively high extinction risk from entire patch networks and low rate of colonization of empty networks afterwards. A case in point is the network studied by Lei & Hanski (1997, 1998). This network is made up of 45 habitat patches that were occupied by 28 well-connected host populations in 1993, some of which were very large. In this network, *C. melitaearum* had large populations and high colonization rate in 1993–95. Subsequently, and in part as a result of high rate of parasitism, the butterfly populations declined and many went locally extinct (Lei & Hanski 1997), causing the connectivity for the wasp to decrease. By 1997 there were 15 relatively small butterfly populations and no wasps. Since then the number of butterfly populations has increased and some of them are large, and hence the network could again support the parasitoid. However, recolonization of the network has not happened so far, and is unlikely to happen in the short term, because the nearest *C. melitaearum* population is 3 km away.

The interaction between the host butterfly and *Cotesia melitaearum* thus shows great spatial and temporal variation. If the parasitoid is present in a large butterfly metapopulation in a well-connected network, the interaction can be strong and may lead to elevated extinction rate of host populations due to parasitism (as demonstrated by Lei & Hanski 1997; see also Hanski 1999). On the other hand, a more typical situation in the Åland Islands is that *C. melitaearum* is completely absent from the host metapopulation, either because the regional patch network is too sparse to support a sufficiently large host metapopulation or because the host metapopulation has gone through a bottleneck in size causing a network-wide extinction of the parasitoid. The isolated *C. melitaearum* populations

in Fig. 2 are mostly remnants of population clusters in declining host metapopulations. Additionally, factors other than host spatial dynamics and parasitoid dispersal rate and range influence the spatial population dynamics of the parasitoid. For example, the rate of colonization of host populations by *C. melitaearum* and their subsequent persistence depends also on the food plant species used by the host butterfly (van Nouhuys & Hanski 1999).

POPULATION DYNAMICS OF THE BUTTERFLY AND THE PARASITOID *H. HORTICOLA*

The presence of *Hyposoter horticola* in most host populations, including those that are newly established and quite isolated, suggests that it disperses at least as well as the butterfly and probably even better. Note that the parasitoid achieves the high colonization rate and long colonization distances in spite of having a smaller overall population size than the host (Table 3). It is clear that the Glanville fritillary cannot escape parasitism by dispersal, and hence *H. horticola* population size is regulated by local mechanisms rather than by limited access to spatially isolated local host populations. What limits *H. horticola* is the extremely short window of opportunity available for parasitism (S. van Nouhuys, unpublished). While *H. horticola* moves freely among host populations and finds most egg clusters, it is only able to parasitize a fraction of the eggs in each cluster. This is because *H. horticola* parasitizes fully developed larvae that are still in the eggshell. The eggs in a cluster do not mature simultaneously, and the time interval during which they are vulnerable to parasitism is extremely short (a few hours). Additionally, eggs located in the centre of the egg cluster may be physically inaccessible to the ovipositing wasp. Finally, *H. horticola* females appear unwilling to visit eggs in previously parasitized clusters (S. van Nouhuys, pers. obs.). The population dynamic impact of *H. horticola* is to make host populations uniformly smaller, which may indirectly increase the probability of their extinction.

The presence of *H. horticola* in both newly colonized and in relatively isolated host populations might suggest that it has alternative hosts in our study area. However, in 6 years of study we have found no evidence for *H. horticola* using hosts other than the Glanville fritillary in Åland. The sentinel host larval groups placed in habitat patches in Föglö and Simskåla, two large islands isolated by 8.5–11.3 km from the nearest populations of the Glanville fritillary, were not parasitized even though the habitat patches were large, of high quality and located near to other suitable meadows with insects that typically occur with the Glanville fritillary. *Hyposoter horticola* has also failed to colonize very isolated Glanville fritillary populations established for other experiments (Nieminen *et al.* 2001), indicating that the parasitoid is not present where the butterfly is absent. Additionally, the foraging behaviour

of adult *H. horticola* seems to be extremely specialized to gregarious hosts on specific host plants, and the wasps do not parasitize the most likely alternative host in the Åland Islands, *Mellicta athalia* (S. van Nouhuys, pers. obs.).

COMPETITION AMONG THE PARASITOIDS

Coexistence of competing parasitoids in a fragmented landscape does not have to be facilitated by dispersal. For example, Amarasekare (2000) describes an interaction between competing parasitoids that disperse equally well but the inferior larval competitor uses lower quality host patches. In another study, Hopper (1984) argues that colonization ability of five parasitoids is not a function of their relative dispersal capacity but of their host-finding ability once they are in a host population.

Nonetheless, if dissimilar dispersal rates were to be important for coexistence of competing parasitoids, it would seem likely to happen in a system such as the one described here. *Hyposoter horticola* is so well dispersed in the host metapopulations that most individuals do not occur together with *C. melitaeorum*, whereas *C. melitaeorum* cannot avoid direct interspecific competition with *H. horticola*. *Hyposoter horticola* has a much larger and more stable regional population size than *C. melitaeorum*, because it is able to use virtually all host populations, and its dynamics at a large spatial scale would probably change little if *C. melitaeorum* were absent. However, at the local scale things may be different. Lei & Hanski (1998) found that the rate of parasitism of host larval groups by *H. horticola* was higher in the absence of *C. melitaeorum*, apparently because of direct competition between immature parasitoids developing in the host larvae (van Nouhuys & Tay 2001; E. Punju & S. van Nouhuys, unpublished). These results suggest that while *H. horticola* is the superior disperser it may be the inferior competitor at the local scale.

CONCLUSION

Our results demonstrate a striking difference in the spatial population structures and dynamics of two specialist parasitoids using the same host population in a highly fragmented landscape. The host butterfly (*Melitaea cinxia*) lives in networks of habitat patches as a classic metapopulation. One parasitoid (*Hyposoter horticola*) has such a high rate of dispersal and long colonization distances that it effectively experiences the host as a single patchily distributed population. The other parasitoid species (*Cotesia melitaeorum*) has a high dispersal rate but such limited colonization distances that most (> 80%) local host populations are out of reach of this parasitoid at any one time. Consequently, *C. melitaeorum* only persists in those parts of the landscape in which host populations are largest and best connected. In spite of the striking difference in

their spatial population structures, the two parasitoids have a strong impact on the host metapopulation. In the case of *C. melitaeorum*, whose density varies greatly in space and time, the parasitoid may increase the extinction rate of the host in those populations where it is present. In the case of *H. horticola*, whose density varies little in time or in space, the impact on host populations is more indirect, due to reduction of host population sizes by roughly 30%, which leaves the host vulnerable to other mechanisms of local extinction (Hanski 1998, 1999).

The two parasitoids interact with each other. The majority of *H. horticola* individuals escape direct interspecific competition because most host populations are, at any one time, too isolated to be reached by *C. melitaeorum*. On the other hand, *C. melitaeorum* cannot avoid competition with *H. horticola*. The direct interaction between the wasps in shared host populations is complex, and more research is needed to understand the actual mechanisms of their within-host competition. Nonetheless, regional coexistence of the two parasitoids may be facilitated by a trade-off between their colonization and competitive abilities.

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References

- Allison, P.D. (1995) *Survival Analysis Using the SAS System. A Practical Guide*. SAS Institute, Cary, North Carolina.
- Amarasekare, P. (2000) Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology*, **81**, 1286–1296.
- Antolin, M.F. & Strong, D.R. (1987) Long-distance dispersal by a parasitoid (*Anagrus delicatus*, Mymaridae) and its host. *Oecologia*, **73**, 288–292.
- Bengtsson, J. (1991) Interspecific competition in metapopulations. *Metapopulation Dynamics: Empirical and Theoretical Investigations* (eds M. E. Gilpin & I. Hanski), pp. 219–237. Academic Press, London.
- Brodmann, P.A., Wilcox, C.V. & Harrison, S. (1997) Mobile parasitoid may restrict the spatial spread of an insect outbreak. *Journal of Animal Ecology*, **66**, 65–72.
- Comins, H.N. & Hassell, M.P. (1996) Persistence of multispecies host–parasitoid interactions in spatially distributed models with local dispersal. *Journal of Theoretical Biology*, **183**, 19–28.
- Comins, H.N., Hassell, M.P. & May, R.M. (1992) The spatial dynamics of host–parasitoid systems. *Journal of Animal Ecology*, **61**, 735–748.
- Cox, D.R. (1972) Regression models and life tables. *Journal of the Royal Statistical Society, Series B*, **34**, 187–220.

- Dubbert, M., Tschamtkke, T. & Vidal, S. (1998) Stem-boring insects of fragmented *Calamagrostis* habitats: herbivore-parasitoid community structure and the unpredictability of grass shoot abundance. *Ecological Entomology*, **23**, 271–280.
- Godfray, H.C.J. (1994) *Parasitoids Behavioural and Evolutionary Ecology*. Princeton University Press, New Jersey.
- Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 51–63.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, London.
- Hanski, I., Alho, J. & Moilanen, A. (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239–251.
- Hanski, I. & Kuussaari, M. (1995) Butterfly metapopulation dynamics. *Population Dynamics: New Approaches and Synthesis* (eds N. Cappuccino & P. Price), pp. 149–171. Academic Press, San Diego.
- Hanski, I., Kuussaari, M. & Nieminen, M. (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology*, **75**, 747–762.
- Hanski, I., Moilanen, A., Pakkala, T. & Kuussaari, M. (1996) The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology*, **10**, 578–590.
- Hanski, I. & Ovaskainen, O. (2000) Metapopulation capacity of a fragmented landscape. *Nature*, **404**, 755–758.
- Hanski, I. & Ranta, E. (1983) Coexistence in a patchy environment: three species of *Daphnia* in rock pools. *Journal of Animal Ecology*, **52**, 263–279.
- Harrison, S. & Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds I. Hanski & M. E. Gilpin), pp. 27–42. Academic Press, San Diego.
- Hassell, M.P. (2000) *The Spatial and Temporal Dynamics of Host-Parasitoid Interactions*. Oxford University Press, London.
- Hastings, A. (1980) Disturbance, coexistence, history and the competition for space. *Theoretical Population Biology*, **18**, 363–373.
- Hochberg, M.E. & Ives, A.R. (1999) Can natural enemies enforce geographic range limits? *Ecography*, **22**, 268–276.
- Hodge, S. & Arthur, W. (1997) Asymmetric interactions between species of seaweed fly. *Journal of Animal Ecology*, **66**, 743–754.
- Holt, R.D. (1997) From metapopulation dynamics to community structure. *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds I. Hanski & M. E. Gilpin), pp. 149–165. Academic Press, San Diego.
- Holyoak, M. & Lawler, S.P. (1996) Persistence of an extinction prone predator-prey interaction through metapopulation dynamics. *Ecology*, **77**, 1867–1879.
- Hopper, K. (1984) The effects of host-finding and colonization rates on abundance of parasitoids of a gall midge. *Ecology*, **65**, 20–27.
- Huffaker, C.B. (1958) Experimental studies of predation: dispersal factors and predator-prey oscillations. *Hilgardia*, **27**, 343–383.
- Jones, T.H., Godfray, H.C.J. & Hassell, M.P. (1996) Relative movement patterns of a tephritid fly and its parasitoid wasps. *Oecologia*, **106**, 317–324.
- Kuussaari, M. (1998) *Biology of the Glanville fritillary butterfly* (*Melitaea cinxia*). PhD Thesis, University of Helsinki.
- Kuussaari, M., Nieminen, M. & Hanski, I. (1996) An experiment on migration in the butterfly *Melitaea cinxia*. *Journal of Animal Ecology*, **65**, 791–801.
- Lei, G.C. & Camara, M.D. (1999) Behaviour of a specialist parasitoid, *Cotesia melitaearum*: from individual Behaviour to metapopulation processes. *Ecological Entomology*, **24**, 59–72.
- Lei, G.C. & Hanski, I. (1997) Metapopulation structure of *Cotesia melitaearum*, a specialist parasitoid of the butterfly *Melitaea cinxia*. *Oikos*, **78**, 91–100.
- Lei, G.C. & Hanski, I. (1998) Spatial dynamics of two competing specialist parasitoids in a host metapopulation. *Journal of Animal Ecology*, **67**, 422–433.
- Lei, G.C., Vikberg, V., Nieminen, M. & Kuussaari, M. (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.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Levins, R. & Culver, D. (1971) Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences USA*, **68**, 1246–1248.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Maron, J.L. & Harrison, S. (1997) Spatial pattern formation in an insect host-parasitoid system. *Science*, **278**, 1619–1621.
- van der Meijden, E. & van der Veen-van Wijk, C.A.M. (1997) Tritrophic metapopulation dynamics: a case study of ragwort, the Cinnabar moth and the parasitoid *Cotesia popularis*. *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds I. Hanski & M. E. Gilpin), pp. 387–406. Academic Press, San Diego.
- Münster-Swendsen, M. (1982) Interactions within a one-host-two-parasitoids system, studied by simulations of spatial patterning. *Journal of Animal Ecology*, **51**, 97–110.
- Murdoch, W.W. (1994) Population regulation in theory and practice. *Ecology*, **75**, 271–287.
- Murdoch, W.W., Reeve, J.D., Huffaker, C.B. & Kennett, C.E. (1984) Biological control of olive scale and its relevance to ecological theory. *American Naturalist*, **123**, 371–392.
- Nee, S. & May, R.M. (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology*, **61**, 37–40.
- Nee, S., May, R.M. & Hassell, M.P. (1997) Two species metapopulation models. *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds I. Hanski & M. E. Gilpin), pp. 123–148. Academic Press, San Diego.
- Nève, G., Barascud, B., Hughes, R., Aubert, J., Descimon, H. & Lebrun, P. (1996) Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclissiana eunomia* (Lepidoptera: Nymphalidae). *Journal of Applied Ecology*, **33**, 14–22.
- Nieminen, M., Singer, M.C., Fortelius, W., Schöps, K. & Hanski, I. (2001) Experimental confirmation that inbreeding depression increases extinction risk in butterfly populations. *American Naturalist*, **157**, 237–244.
- van Nouhuys, S. & Hanski, I. (1999) Host diet affects extinctions and colonizations in a parasitoid metapopulation. *Journal of Animal Ecology*, **68**, 1248–1258.
- van Nouhuys, S. & Hanski, I. (2002) Multitrophic interactions in space: metacommunity dynamics in fragmented landscapes. *Multitrophic Level Interactions* (eds T. Tschamtkke & B. A. Hawkins), pp. 124–147. Cambridge University Press, Cambridge.
- van Nouhuys, S. & Tay, W.T. (2001) Causes and consequences of mortality in small population of a parasitoid wasp in a fragmented landscape. *Oecologia*, **128**, 126–133.
- Onillon, J.C. (1990) The use of natural enemies for the biological control of whiteflies. *Whiteflies: Their Bionomic, Pest Status and Management* (ed. D. Gelling), pp. 287–314. Intercept, Hampshire, UK.
- Ovaskainen, O. & Hanski, I. (2001) Spatially structured metapopulation models: global and local assessment of metapopulation capacity. *Theoretical Population Biology*, **60**, 281–302.

- Roland, J. & Taylor, P.D. (1995) Herbivore–natural enemy interactions in fragmented and continuous forests. *Population Dynamics: New Approaches and Synthesis* (eds N. Cappuccino & P. Price), pp. 195–208. Academic Press, San Diego.
- Roland, J. & Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, **386**, 710–713.
- Roslin, T. & Koivunen, A. (2001) Distribution and abundance of dung beetles in fragmented landscapes. *Oecologia*, **127**, 69–77.
- Savill, N.J. & Hogeweg, P. (1999) Competition and dispersal in predator–prey waves. *Theoretical Population Biology*, **56**, 243–263.
- Slatkin, M. (1974) Competition and regional coexistence. *Ecology*, **55**, 128–134.
- Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biological Reviews of the Cambridge Philosophical Society*, **37**, 171–214.
- Stamp, N.E. (1982) Searching behaviour of parasitoids for web-making caterpillars: a test of optimal searching theory. *Journal of Animal Ecology*, **52**, 387–395.
- Taylor, A.D. (1988) Large-scale spatial structure and population dynamics in arthropod predator–prey systems. *Annales Zoologici Fennici*, **25**, 63–74.
- Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.
- Wilson, D.S. (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, **73**, 1984–2000.

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