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Effects of habitat fragmentation at different trophic levels in insect communities

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Species experience landscapes differently depending on their needs and behaviors, and on their trophic level. We expect species at high trophic levels in a community to be more sensitive to habitat fragmentation than species at lower trophic levels. But this depends on attributes such as resource breadth, dispersiveness, reproductive rate, and longevity, which may not be related to trophic level. I address the association of fragmentation with trophic level using a literature review of 31 studies of herbivores and their natural enemies, and a case study of the parasitoids associated with the Glanville fritillary butterfly. Measures of species richness or total parasitism in an entire insect community provide the strongest support for the idea that negative effects of fragmentation amplify at higher trophic levels. Generally though, there is great variation among studies, due to variation among species, as well as in designs of both experimental and observational studies.

Introduction

As a landscape becomes fragmented, changes occur in the insect (meta)community inhabiting it. Understanding the mechanisms behind these changes is a task for contemporary community ecology. We expect different ecological and evolutionary responses to landscape change among species based on the breadth of their resource needs and their behavior. At one extreme individuals may be dispersive and long-lived, moving at such a large scale that they do not perceive the landscape as patchy. Similarly, a species that uses a broad range of resources may also experience the landscape as continuous. At the other extreme are sedentary species made up of individuals that usually spend their entire life within a single habitat patch. Correspondingly, if the resource requirements of a species are extremely narrow, it will perceive the landscape as highly fragmented because only a small fraction of the total area is useful (MacArthur & Levins 1964).

We also expect different responses to habitat fragmentation depending on the trophic level of a species. This is because food/prey/host species are limited to a subset of the suitable locations in the landscape, and because local population dynamics of species at the lower trophic level make them an unstable resource for the dependent species (Holt 2002, van Nouhuys & Hanski 2005). In some ways a fragmented habitat is simply a type of low quality habitat (summarized by Morin 1999) in which food chain length decreases with habitat quality. Within a single fragment species persistence decreases with fragment size. At the landscape scale, small total fragment area and long distance between fragments can decrease regional persistence. Where primary productivity is low there is not reliable food to support persistence of high trophic level species. In this context the prediction, and general observation, is that high trophic level species are absent from fragmented habitats (*see* summaries in Pimm 1982, Mikkelson 1993, Didham *et al*. 1996, Tscharntke & Kruess 1999, Holt 2002, Henle *et al*. 2004). While this is probably true, it is certainly not always the case.

As long as habitat fragmentation is not too extreme, fragmentation can promote regional coexistence of predators and prey (Hassell 2000, Holt 2002), and its effect can differ greatly among species. Attributes of species that affect their sensitivity to habitat fragmentation, such as dispersal behavior, rarity, reproductive potential, habitat specificity, competitive ability, and biogeography (Henle *et al*. 2004), do not necessarily correspond to trophic level. In fact, it may be that qualities that are advantageous at high trophic levels are also advantageous in fragmented landscapes. For example hyperparasitoids (4th trophic level or higher) tend to be ectoparasitic rather than endoparasitic (Brodeur 2000). While we know too little about the host ranges of hyperparasitoids to say how host specific they actually are, we do know that ectoparasitoids generally have much broader host ranges than endoparasitoids (Shaw 1994). Additionally many hyperparasitoids are facultative primary parasitoids. Both of these characteristics, broad host range and multitrophic level feeding, would decrease the negative effects of fragmentation by allowing the hyperparasitoid to make do with what is available in a given habitat fragment.

Because higher trophic levels experience a more fragmented habitat we expect them to suffer more from fragmentation than the species below them. On the other hand, the effects of fragmentation depend on attributes of the insect that may be unrelated to trophic level, or even predispose higher trophic level species to perform well in fragmented landscapes. With no clear conceptual resolution I will now approach this question using empirical studies from the literature, and a case study from my own work on the parasitoid community associated with the Glanville fritillary butterfly in Finland.

Literature review

This is a literature survey of empirical research papers that contain data about the impact of habitat fragmentation on herbivores and their parasitoids or predators. The papers surveyed were collected, in part, by searching ecological, conservation, and agricultural electronic databases using the key word "parasitoid" in combination with "fragmentation," "landscape," or "dispersal." In all there are 31 papers about 23 different research systems (Table 1). There are three types of studies. The first are 11 observational studies of naturally fragmented landscapes. An example of such a study is the work by Antolin and Strong (1987) showing that both the leaf hopper *Prokelesia marginata* and its egg parasitoid *Anagrus delicatus* routinely disperse up to one km to offshore islands in their fragmented salt marsh habitat. A contrasting study is that of Eber (2001), in which the agromyzid leaf miner *Phytomyza ilicis* and its parasitoids move very little among patchily distributed holly trees. The second category of data is from eight observational studies of anthropogenically fragmented landscapes. These studies include the effects of old growth forest fragmentation on the insects associated with bracket fungus (Komonen *et al*. 2000), and the insect communities associated with isolated nettle stands in an agricultural landscape (Zabel & Tscharntke 1998). Finally there are 11 manipulated fragmentation experiments, such as the study by Kruess and Tscharntke (2000b) of bush vetch (*Vicia sepium*) colonization by seed pod feeding insects and their parasitoids between 100 and 500 m from established vetch patches.

This distinction between natural and anthropogenic fragmentation is often subjective. For example, I categorized the holly bush study by Eber (2001) as naturally fragmented even though the distribution of trees is likely influenced by humans, and the study of *Silene latifolia* (J. A. Elzinga *et al*. unpubl. data) as anthropogenically fragmented because it grows in agriculturally

Table 1. Summary of studies used in literature review of the effects of habitat fragmentation on insects and their parasitoids and predators.

Cit. no.[1]	Authors	Type of community	Spatial and temporal scale and type[2] of study	Effects of fragmentation[3]
1	Amarasekare 2000a, 2000b	Sage scrub, *Isomeris*	Experiment: replicate clusters of patches separated by 20 and 40 m. 1.5 years (= 5 H generations & 14–16 P generations).	Isolation: no effect on 1 H; – effect on 2 P colonization.
2	Antolin & Strong 1987	Cod grass, *Spartina alternifolia*	Natural: Sticky traps on islets and mainland (about 1 km apart). 1 season.	Isolation: no effect on abundance of 1 H, + effect on 1 P.
3	Braschler *et al.* 2003	Calcareous grassland	Experiment: replicated patches (0.5 to 4.5 m^2) each 5 m apart, and unfragmented control plots. 3 years.	Patch size: + for H (multiple aphid species) density, no effect on H species richness or diversity, no effect on P.
4	Cappuccino *et al.* 1998	Balsam fir, *Abies balsamea* forest	Anthropogenic: unfragmented forest, “habitat islands” (0.25 to 2.0 ha) and “true islands”. 2 growing seasons.	Isolation: no effect for 1 H (spruce budworm); – for 1 parasitoid; + for 4 parasitoids on habitat islands but not true islands.
5	Cronin & Haynes 2004	Cod grass, *Spartina alternifolia*	Experiment: replicate patches (0.7 × 0.9 m), in clusters (5 m spacing) 30 m apart, in brome or mudflat matrix. 1 season.	Isolation (*per se*): no effect for 1 P or 1 H. Matrix: H & P move more in brome. Local extinction of H higher in brome (stronger for P).
6	Cronin 2003	Cod grass, *Spartina alternifolia*	Natural: 25 to147 patches (0.1 to 126.7 m^2; 1 to 46 m apart) in 65 ha. 3.5 years (7 H generations). Extinction and colonization dynamics.	Isolation: – for 1 H and 1 P (stronger for P). Patch size and density: – for 1 H and 1 P. Matrix: mudflat – for 1 H and + 1 P.
7	Cronin *et al.* 2000	Pine forest *Pinus taeda*, *P. echinata*	Mark recapture experiment: traps placed 0.1 to 5 km from origin. 1 sampling period.	Distance moved: H less than Pr (95% of H moved less than 2.3 km, 95% of Pr moved less than 5.1 km).
8	Cronin *et al.* 2004, Cronin 2003	Cod grass, *Spartina alternifolia* (spiders & insects)	Natural: 147 patches (0.1 to 126.7 m^2; 1 to 46 m apart) in 65 ha. 1.5 years (3 H generations).	Isolation: – for 1 H; no effect on Pr. Patch size: – for 1 H; + for Pr. Matrix: mudflat – for 1 H; no effect on Pr.
9	Dubbert *et al.* 1998	Grass, *Calamagrostis epigeios*	Natural: 25 patches (16 to 5000 m^2; 0 to 130 m apart; 0.5 to 95 shoots per m^2). 1–2 seasons.	Isolation: no effect on 4H; – effect on rare 2H; – effect 1 out of 18 P. Patch size: no effect on 4H or 18 P. Plant density: – effect on 4H; – effect some P (through effect on H).

continued

Table 1. Continued.

Cit. no.[1]	Authors	Type of community	Spatial and temporal scale and type[2] of study	Effects of fragmentation[3]
10a	Eber 2001	Meadow, creeping thistle, *Crisium arvense*	Natural: 35 km^2. Long term study.	Isolation: no effect on 1 H and several P. Patch size: – effect on 1 H and several P.
10b	Eber 2001	Holly, *Ilex aquifolium*	Natural: 15 patches in a 1.5 km^2 area. Long term study.	Isolation: no effect on 1 H and several P. Patch size: no effect on 1 H and several P.
11a	J. A. Elzinga *et al.* unpubl. data	White campion, *Silene bicruris*	Natural: 85 patches (1 to 13000 plants; at least 100 m part), 100 km along river. 3 seasons.	Isolation: no effect on H; – effect on 1 of 3 P. Patch size: no effect on H; – effect on all P.
11b	J. A. Elzinga *et al.* unpubl. data	White campion, *Silene bicruris*	Experiment: replicated patches 125 to 2000 m apart. 2 seasons.	Isolation: no effect on H; – effect on 1 of 3 P.
12	Faeth & Simberloff 1981	Oaklands, *Quercus* sp.	Experiment: 3 isolated trees transplanted 165 m from forest. 2 seasons.	Isolation: – for colonization by 2H, + for 1H, no effect on 3 H abundance; – for rate of parasitism, no effect for rate of Predation.
13	Ferrari *et al.* 1997	Wild roses, *Rosa canina*, *R. corymbifera*	Natural: 31 patches. 1 season.	Isolation: no effect 2 H; – 9 P (total parasitism). Patch size: – 2 H; no effect 9 P (total parasitism).
14	Golden & Crist 1999	Goldenrod, *Salidago canadensis*	Experimental: replicate plots made of replicated patches (1, 2 & 3 m^2). 1 season.	Fragmentation: No effect on H, P or Pr abundance (multiple species); small – effect on H diversity; + effect on 2H species; – rare species.
15	Harrison & Thomas 1991	Meadow, ragwort, *Senecio jacobaea*	Natural: 60 patches (12 to 10^4 m^2; 10–100 m apart) in a 1.3 km^2 area. 1 season.	Isolation: no effect on 10 H and 1 P. Disturbance: + and – effects on H, but not P.
16	Kareiva 1987	Meadow, goldenrod, *Solidago* sp.	Experimental: continuous *vs.* 1-m^2 blocks 1 m apart. 4 seasons.	Fragmentation: + for 1 H and 1 Pr abundance but not colonization.
17	Komonen *et al.* 2000	Forest bracket fungus	Anthropogenic: 8 unfragmented forests, 4 young isolated fragments, and 8 old isolated fragments. 1 sampling period.	Isolation: – for F and P; P absent from old fragment.
18	Kruess & Tscharntke 1994	Meadow, red clover, *Trifolium pratense*	Experimental: 18 patches (1.2 m^2; separated by 100 to 500 m). 1 season.	Isolation: – for abundance & diversity of 8 H (stronger for rare species); – for 12 P diversity and % parasitism (stronger for P than for H).

19a	Kruess & Tscharntke 2000a, 2000b	Meadow, bush vetch, *Vicia sepium*	Anthropogenic: 18 meadows (300 m to 70 ha). 1 season.	Patch area: – species diversity of 4 H and 10 P (stronger for P than H); – abundance of 1 H; – rate of parasitism; – rare species.
19b	Kruess & Tscharntke 2000b	Meadow, bush vetch, *Vicia sepium*	Experimental: 16 patches (12 plants each) isolated by 100 to 500 m, each paired with unisolated plants. 1 season.	Isolation: – species diversity 4 H and 2 P; – abundance of 2 out of 4 H and 2 out of 2 P. No effect on total parasitism, but – for 1 P; – rare species.
20	Kruess & Tscharntke 2000a	Meadow, red clover, *Trifolium pratense*	Anthropogenic: 18 meadows (300 m to 70 ha), isolated by 0 to 500 meters. 1 season.	Isolation: no effect. Patch size: – for diversity of 8 H and 15 P (stronger for P); – % parasitism.
21	Kruess 2003	Meadow, creeping thistle, *Crisium arvense*	Anthropogenic: 15 patches (at least 24 m apart), in crop, margin and fallow habitat types. 1 season.	Isolation: – for some H, – 9 P. Richness and abundance and % parasitism. Matrix: no effect on 9 H; effect on 6P richness and abundance % parasitism.
22	Roland & Taylor 1997	Aspen forest, *Populus temuloides*	Anthropogenic: Degree of forest fragmentation estimated around points on a 420 m^2 grid. 1 season.	Fragmentation: – for 1 H and 3 P, + for 1 P (measured as % parasitism).
23	Segarra-Carmona & Barbosa 1992	Tropical legume, *Crotalaria pallida*	Natural: 62 patches (20 to 200 plants, at least 1000 m apart), each sampled at least once over 4 years.	Isolation: not measured. Patch size: – effect for 1 H and 1 P (stronger for P than H).
24	Tscharntke & Kruess 1999; Athen & Tscharntke 1999	Reed, *Phragmites australis*	Anthropogenic: 28 habitat fragments (range from about 100 to 1500 m^2; 3 to 10 years old). 1 sampling period.	Patch size: – for presence of 2 H and 8 P. Patch age: – % parasitism of 2 H.
25	Tscharntke *et al.* 1998	Meadow, trap nesting bees and their parasitoids	Experimental: 42 patches (each made of 8 pots of plants and a bee trap) 0 to 1200 m from sources. 1 season.	Isolation: – diversity of B but not total abundance; – diversity of P and Pr, and % parasitism and predation.
26	van der Meijden & van der Veen-van Wijk 1997	Dune, ragwort, *Senecio jacobaea*	Natural: several 100 patches separated by about 100 to 500 m. Long term study.	Isolation and patch size: – for 1 H and 1 P (stronger for P).
27	van Nouhuys & Hanski 1999, 2002	Meadow, *Veronica spicata* & *Plantago lanceolata*	Anthropogenic: 4000 meadows (300–500 occupied by H) (100 m^2 to 10 ha; 100 to about 5000 m apart). Long term study.	Isolation and patch size: – for 1 H colonization and persistence; – for 1 P colonization and persistence (stronger for H); no effect on 1 P.

continued

Table 1. Continued.

Cit. no.[1]	Authors	Type of community	Spatial and temporal scale and type[2] of study	Effects of fragmentation[3]
28	Zabel & Tscharntke 1998	Meadow, stinging nettle, *Urtica dioica*	Anthropogenic: 32 patches (2 to 1000 m^2), 21 isolated by 75 to 300 m and 11 not isolated. 1 sampling period.	Patch size: – abundance and richness of H; no effect on richness of Pr. Isolation: no effect on abundance and richness of H; – effect on richness of Pr.

[1] The citation numbers correspond to the superscript numbers in Tables 2, 3, and 4.

[2] Observational studies are called natural (*see* Table 2) if the host plant distribution is generally undisturbed by people, or anthropogenic (*see* Table 3) if the plant distribution has been fundamentally changed by humans (*see* Table 3). In the experimental studies (*see* Table 4) the conditions have been manipulated by the researcher(s).

[3] Insects are identified as herbivores (H); fungivores (F); trap nesting bees (B); parasitoids (P); or predators (Pr). Criteria evaluated are decrease in patch size measured as area or number of plants (patch size); increase in isolation measured as distance or connectivity (isolation or fragmentation); decreasing years since fragmentation (patch age); history of disturbance (disturbance); distance moved by insects (distance moved); Type of matrix surrounding patches (matrix). The effects of fragmentation are designated as negative (–) or positive (+).

disturbed areas, even though it may have a naturally fragmented distribution as well. I attempt to distinguish between the two types of studies in order to separate insect communities that have a long evolutionary history in a habitat that we consider fragmented from those that have had a relatively short evolutionary history in a landscape, and whose continued persistence in that environment is uncertain.

The data for these studies were generally gathered in three ways. Most were surveys of individual species pairs or communities of interacting species. Some of these surveys were conducted over several years in the same locations (van der Meijden & van der Veen-van Wijk 1997, van Nouhuys & Hanski 1999, 2002, Eber 2001), over multiple insect generations (Amarasekare 2000b, Cronin 2004), or during one visit or over a season (Antolin & Strong 1987, Zabel & Tscharntke 1998, Kruess 2003). Herbivores were sampled or counted in place. Parasitoids were generally evaluated by the rate of parasitism of a sample of the host species collected from the research site (a sometimes misleading method of evaluation of parasitoids, *see* Askew & Shaw 1989). Several studies of the effects of fragmentation on specific taxa were conducted by trapping target species (Antolin & Strong 1987), and by mark-release-recapture (Cronin & Haynes 2004).

Fragmentation was evaluated in several different ways as well. These include the size of fragments, connectivity among them, and their age and quality. Fragment size varied from 0.1 m^2 tufts of grass (Cronin 2003, Cronin *et al.* 2004) to 70 ha fields (Kruess & Tscharntke 2000a, 2000b). The distances between fragments varied from one meter in the study of aphids and coccinelid beetles on goldenrod (*Salidago* sp.) (Kareiva 1987) up to several km in the study of the parasitoids of the Glanville fritillary (van Nouhuys & Hanski 1999, 2002). Connectivity was presented as the simple distance between patches or as a measure that one way or another took into account differing contributions of patches based on size and distance (for a review and discussion of measures of connectivity *see* Moilanen & Nieminen 2004). Alternatively, a landscape was simply characterized as fragmented or continuous without calculating connectivity among individual patches (such as Roland & Taylor 1997, Cappuccino *et al*. 1998, Komonen *et al*. 2000). Quality was generally density of host plant, but in some cases included plant size or the number of leaves or inflorescences. Several studies, such as Cronin and Haynes (2004) and Roland and Taylor (1997) also included aspects of the surroundings or the matrix. Once the data were collected they were presented as species occupancy or abundance, or species richness and diversity. When entire communities were involved, taxonomic groups were identified to species or lumped into functional groups or guilds.

Results

In all three types of studies of naturally (Table 2), anthropogenically (Table 3) and experimentally (Table 4) fragmented habitats, there were examples of positive, neutral and negative effects of fragmentation. The negative effects on parasitoids and predators were classified as "more negative" than for the herbivores if they declined with fragmentation but their hosts did not. Additionally, in some cases the authors explicitly demonstrated that the negative effects for the higher trophic level were greater than would be expected simply due to decline in host/prey density that went along with fragmentation.

In the 11 studies of naturally fragmented systems (Table 2), there was little negative effect of habitat patch connectivity on herbivores. This is not particularly surprising, because the insects in these systems are already known to persist in the fragmented landscape, though presumably there could still be effects of connectivity on patch occupancy. In five studies parasitoid abundance decreased with increasing patch isolation suggesting that at least some parasitoids in "naturally" fragmented habitats may be constrained by the spatial distribution of their hosts, but in seven studies there was no negative effect of connectivity. The effect of patch size and quality also varied among studies, but at least for herbivores, it had more of a negative effect than patch connectivity. The surrounding habitat or matrix was shown to be related to the distribution of parasitoid in two very different ways. In one, Cappuccino *et al*. (1998) suggest that mixed deciduous forest surrounding isolated Balsam fir patches may enhance the presence of some Spruce budworm (*Choristoneura fumiferana)* parasitoids by providing alternate prey or adult food sources. Such spillover between habitats is discussed by Tscharntke *et al*. (2005). In contrast, Cronin and Haynes (2004) suggest that in tall grass prairie local extinction of both a herbivore and its parasitoid is promoted by emigration from patches embedded in a smooth brome *Bromus inermis* matrix rather than in bare mudflats.

The negative effects of fragmentation on herbivores, in terms of both reduced patch size and to a lesser extent connectivity, are perhaps more apparent in the eight studies of anthropogenically fragmented systems (Table 3). The reduc-

Table 2. The effects of habitat fragmentation on herbivores and parasitoids in observational studies of naturally fragmented habitats.

Fragment	Herbivores[a]			Parasitoids/predators[a]		
	positive	none	negative	none/positive	negative	more negative
Size (decrease)		4[9], 1[10b, 11a]	1[6, 8, 10a, 23, 26], 2[13]	1+[8], 18[9], y[10b],9[13]	1[6, 26], y[10a], 3[11a]	1[23]
Connectivity (decrease)		1[2, 10a, b, 11a], 4[9], 2[13],10[15]	1[6, 8, 26], 2[9]	1+[2], 1[8, 15],17[9], y[10a,b], 2[11a]	1[9, 11a], 9[13]	1[6, 26]
Age (–)/disturbance(+)	y[15]		y[15]	1[15]		
Quality			4[9]		y[9]	
Matrix[b]			1[6, 8]	1+[6], 1[8]		

[a] Number of insect species or, if number is large but unspecified, then "y" indicates group effect. Superscript numbers correspond to citation numbers in Table 1. A positive effect on parasitoids/predators is indicated by "+".
[b] *See* citation for explanations of matrix types. A single matrix type can be negative for some insects and positive for others.

tion of patch size had a larger effect on parasitoids than on their hosts in three out of six cases, but the effect of connectivity on parasitoids was equivocal. There was little effect of the type of matrix on the herbivores. The matrix appeared to have a negative effect on several parasitoids, but a positive effect on one. Roland and Taylor (1997) attribute this to species-specific effects of surrounding forest (matrix) on connectivity.

The pattern is least clear in the collection of 11 experiments explicitly designed to test the effects of habitat fragmentation on herbivores and their predators or parasitoids (Table 4). There is no consensus on the effects of patch size or connectivity. This result is similar to the review of 20 fragmentation experiments by Debinski and Holt (2000).

There are three possible explanations for the variation of the effects of fragmentation in these studies. One is that the spatial scales differ greatly. At one extreme are the two studies of the insect communities on goldenrod (Kareiva 1987, Golden & Crist 1999) in which patches and distance between patches are on the scale of less than one to several meters. In these cases fragmentation is on a small scale relative to the movement of individual predators and parasitoids and some herbivores. Hence, the mechanisms behind the effects of fragmentation relate to local foraging decisions and efficiency. In the case of Kareiva (1987), the herbivorous hosts are aphids that do not in fact move among patches during the experiment, but the predators do. At the other extreme is the study by J. A. Elzinga *et al.* (unpubl. data) in which patches were distributed over 2 km. In these cases, the effects of hab-

Table 3. The effects of habitat fragmentation on herbivores and parasitoids in observational studies of anthropogenically fragmented habitats.

Fragment	Herbivores[a]			Parasitoids/predators[a]		
	positive	none	negative	none/positive	negative	more negative
Size (decrease)			4^{19a}, 8^{20}, $y^{21, 28}$, 2^{24}	y^{28}	3^{22}, 8^{24}	10^{19a}, 15^{20},9^{21}
Connectivity (decrease)		1^{4}, 8^{20}, y^{28}	$1^{17, 22}$	$4+^{4}$, 15^{20},$1+^{22}$	1^{4}, 3^{22},$y^{17, 28}$	
Age (–)/disturbance(+)		2^{24}			2^{24}	y^{17}
Quality						
Matrix[b]		9^{21}		$1+^{22}$	6^{21} , 2^{22}	

[a] Number of insects or, if number is large but unspecified, then "y" indicates group effect. Superscript numbers correspond to citation numbers in Table 1. A positive effect on parasitoids/predators is indicated by "+".
[b] *See* citation for explanations of matrix types.

Table 4. The effects of habitat fragmentation on herbivores and parasitoids in fragmentation experiments.

Fragment	Herbivores[a]			Parasitoids/predators[a]		
	positive	none	negative	none/positive	negative	more negative
Size (decrease)	y^{3}	$1^{5, 11b}$		y^{3}, 1^{5},		
Connectivity (decrease)	2^{14}, 1^{16}	1^{1}, 3^{12},y^{14}	1^{7}, 2^{12}, $y^{14, 25}$, 8^{18}, 4^{19b}	1^{7}, 2^{11b}, $1+^{12, 16}$, $y^{12, 14}$	2^{1}, 1^{11b}, $y^{12, 25}$, 4^{19b}	12^{18}
Age (–)/disturbance(+)						
Quality			1^{11b}			1^{11b}
Matrix[b]			1^{5}			1^{5}

[a] Number of insect species or, if number is large but unspecified, then "y" indicates group effect. Superscript numbers correspond to citation numbers in Table 1. A positive effect on parasitoids/predators is indicated by "+".
[b] *See* citation for explanations of matrix types. A single matrix type can be negative for some insects and positive for others.

itat fragmentation may be explained by migration rather than within-patch foraging behavior. These two scales are profoundly different, to a large extent because one is primarily explained by local interactions and the other is explained by landscape level spatial processes. Yet, the same language (fragmentation, patch, isolation …) is used to describe both. Presumably habitat fragmentation at all scales might influence species interactions in some way. What is important is for researchers to specify the scale they are working on relative to the landscape inhabited by the species, and ideally, the scale of movement of the species. Similarly, the temporal scale should be presented in terms of the generation times of the species involved (for a good example *see* Amarasekare 2000a, 2000b).

The second explanation for a lack of resolution is that some of these studies (such as Kareiva 1987, Amarasekare 2000b) are about particular pre-chosen individual species, whereas many of the other studies are of entire communities (such as Golden & Crist 1999, Kruess & Tscharntke 2000b). The parasitoids and predators that are known well enough to be singled out *a priori* are unlikely to be a random subset of the species involved. Specifically, they may be more abundant and larger. Some of the strongest support for the idea that habitat fragmentation has a large effect on high trophic levels is in the form of species richness data or total parasitism, and several studies made the important point that habitat fragmentation had the largest effect on species that were rare in the first place (Golden & Crist 1999, Kruess & Tscharntke 2000b). In contrast, some of the most convincing demonstrations of a lack of fragmentation effects emerge from studies of individual species — even when they were studied on a relatively large spatial scale (such as van Nouhuys & Hanski 2002, discussed below).

A third reason that the fragmentation experiments may present different results than the observational studies of naturally or anthropongenically fragmented settings is that the specific aspect being tested is the dispersal ability of the target species. The distance moved by individuals, and their propensity to move, is probably the main factor explaining their pattern of habitat use in the fragmentation experiments. This is because the experiments lasted only a short time. This short time frame may predispose the parasitoids to be more affected than their prey, because in order for the parasitoids to colonize a fragment, the host must have already colonized it. In fact, none of the fragmentation experiments explored the effects of fragmentation over time. Experimental studies that address both dispersal and persistence may be quite fruitful. Several observational studies that measured colonization (such as Cappuccino *et al*. 1998, van Nouhuys & Hanski 2000) got around the bias against colonizations by parasitoids relative to herbivores by assessing the effects of fragmentation separately for the herbivore and the parasitoid.

Case study

We gain further insight into the complexity of the relationship of trophic level with habitat fragmentation by looking in detail at one research system. The parasitoid community associated with the Glanville fritillary *Melitaea cinxia* (Lepidoptera: Nymphalidae) lends itself well to this task because there are only a few species involved, and these species cover four trophic levels and a range of different life histories. In addition, a long term study of this group of interacting species at both small and large spatial scales has resulted in the development of mechanistic explanations for the observed patterns of habitat use. I will briefly introduce the species involved, and then explain how I think habitat fragmentation affects each species separately, and the interactions among them.

The landscape, the host plants and the butterfly

The Glanville fritillary butterfly inhabits steppe and open meadow habitats in Europe and Asia (Wahlberg *et al*. 2004). In Finland, *M. cinxia* is restricted to the Åland Islands in the Baltic Sea, where it feeds on *Plantago lanceolata* and *Veronica spicata*. The Åland Islands are separated from other *M. cinxia* populations in Sweden and Estonia by several hundred km. The butterfly persists as a classical metapopulation comprised of 300 to 500 local populations with a

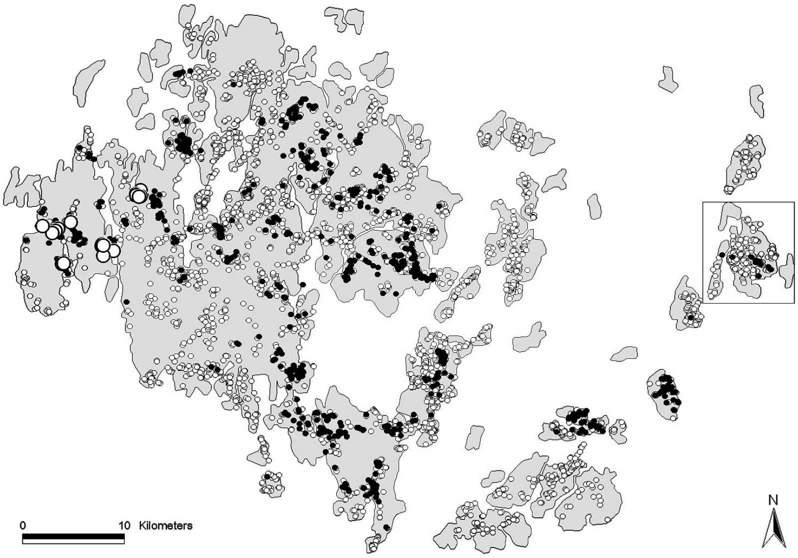

Fig. 1. Map of the Åland Islands showing locations of habitat patches unoccupied by the host butterfly, *Melitaea cinxia* (small white circles), patches occupied by *M. cinxia* and the parasitoid *Hyposoter horticola* (small black circles), and by the parasitoid *Cotesia melitaearum* (large white circles in the west) in 2004. The hyperparasitoid *Mesochorus* sp. cf. *stigmaticus* is absent from the islands enclosed by the square in the east.

high rate of turnover (local extinctions and colonizations) (Hanski *et al.* 1995, Ehrlich & Hanski 2004, Hanski & Meyke 2005). There are nearly 4000 suitable habitat patches for local populations in an area of 50 × 70 km (Fig. 1). Habitat patches range in size from less than 100 m^2 to 10 hectares (average less than 0.5 hectare). Most butterflies stay within their natal patch to breed. Local butterfly populations range in size from one to tens of gregarious larval nests, and are ephemeral, most persisting only a few years. About 25% have persisted the entire time they have been surveyed (14 years). The regional landscape is structured so that patches are clustered into 130 semi-independent patch networks separated by small-scale agriculture, water and forest. Mark-release-recapture studies and survey data show that there is very little movement of butterflies between patch networks, but significant movement among local populations within them (Nieminen *et al.* 2004).

The parasitoids

The natural enemy community associated with *M. cinxia* in Åland is relatively simple. There are two primary larval parasitoids that use only *M. cinxia* as a host, and each of these parasitoids has a closely associated hyperparasitoid. Less integral species in the community are several generalist pupal parasitoids (Lei *et al.* 1997), coccinelid beetle and lacewing (chrysopid) larvae that feed opportunistically on eggs and small larvae, predatory Hemiptera sometimes feeding on larvae, and spiders that occasionally capture adult butterflies (van Nouhuys & Hanski 2004).

One of the primary larval parasitoids is *Cotesia melitaearum* (Wilkinson) (Ichneumonoidae: Braconidae). This wasp is a parasitoid of several species of checkerspot butterflies in Europe and Asia. *Cotesia melitaearum* is a gregarious endoparasitoid, laying one to about 40 eggs inside a host larva, depending on the size of the host. There are two or sometimes three generations per year and host generation, and *C. melitaearum* spends the winter as a larva inside the host larva (van Nouhuys & Lei 2004). In the Åland Islands *C. melitaearum* has a metapopulation structure, and is extremely sensitive to habitat fragmentation and the turnover (extinctions and colonizations) of local host (*M. cinxia*) populations. Currently there are few small local populations (Fig. 1) (Lei & Hanski 1997, van Nouhuys & Hanski 2002).

Cotesia melitaearum is parasitized by *Gelis agilis* (Fabricius) (Ichneumonidae: Cryptinae). Female wasps in the genus *Gelis* are wingless generalist ectoparasitoids, and males are rare or unknown. In the Åland Islands *Gelis agilis* and several related species are hyperparasitoids of *C. melitaearum* pupae. *Gelis* have other hosts in Åland (though the species are not known), and can be extremely abundant, aggregating where there is a high density of *C. melitaearum* cocoons, and having a dramatic density dependent effect on *C. melitaearum*, even causing local extinctions (Lei & Hanski 1998, van Nouhuys & Hanski 2000, van Nouhuys & Tay 2001).

The second primary parasitoid of the butterfly *M. cinxia* is *Hyposoter horticola* (Gravenhorst) (Ichneumonidae: Campoplaginae). This wasp is also a parasitoid of checkerspot butterflies in Europe and Asia, but its only confirmed host is *M. cinxia* (van Nouhuys & Hanski 2004). It is a solitary endoparasitoid, laying eggs in first instar host larvae just before the larvae hatch from the egg (van Nouhuys & Ehrnsten 2004). In the Åland Islands there is one generation per year. *Hyposoter horticola* parasitizes about a third of the larvae in virtually all of the local host populations of *M. cinxia* in Åland (Fig. 1). The wasp maintains this remarkably uniform rate of parasitism because it is more dispersive than the host, and because it forages efficiently by learning the locations of multiple host egg clusters before the hosts are ready to be parasitized (van Nouhuys & Ehrnsten 2004, van Nouhuys & Hanski 2002).

The secondary parasitoid of *H. horticola* is *Mesochorus* sp. cf. *stigmaticus* (Brischke) (Ichneumonidae: Mesochorinae). Wasps in the genus *Mesochorus* are generally endoparasitic hyperparasitoids. The taxonomy in the genus is not well worked out, but it appears that *Mesochorus* sp. cf. *stigmaticus* is associated only with parasitoids of checkerspot butterflies (Lei *et al*. 1997). In the Åland Islands it is associated with *M. cinxia*, hyperparasitizing about a quarter of the *H. horticola*, and occasionally *C. melitaearum* as well.

Fragmentation and the second and third trophic levels

More than a decade of survey data, modeling and several large-scale mark-release-recapture studies show that the distribution of the butterfly, *M. cinxia*, is constrained by the fragmentation of habitat available in Åland (Nieminen *et al*. 2004, Hanski & Meyke 2005). One demonstration of this is the pattern of occupancy of habitat patch networks of differing configuration. Each of the 130 semi-independent patch networks in Åland differ in size, number and connectivity of suitable habitat patches. The "metapopulation capacity" is an index of the ability of a patch network to support a metapopulation of the butterfly, based on habitat area and connectivity (Hanski & Ovaskainen 2000). Only those networks with a high metapopulation capacity are occupied by butterflies.

The two primary parasitoids use the same resource (host) in the same habitat, but differ greatly in their abundance, distribution (Fig. 1) and dynamics. A large part of this difference is explained by their differing abilities to use a host in a fragmented habitat. *Hyposoter horticola* is not affected by the present fragmentation of the habitat. It experiences a single, perhaps patchily distributed, host population. The abundance and rate of parasitism is not affected by the size or isolation of local host populations and the wasp is able to colonize new host populations the same year as they are themselves initiated. *Cotesia melitaearum*, on the other hand, has a metapopulation structure. Based on annual survey and dispersal experiments it is evident that the wasp is more constrained by habitat fragmentation than the host is. This is probably due to the range (distance traveled) rather than rate of dispersal (propensity to move) of *C. melitaearum* (van Nouhuys & Hanski 2002).

Movement within the landscape is not the only difference between the two wasps that is related to their sensitivity to habitat fragmentation. *Cotesia melitaearum* is gregarious and has several generations per year. This means that it has a much higher potential rate of increase than the host, or *H. horticola*, which is solitary and has only one generation per year. Increased population size does help mitigate the effects of fragmentation for *C. melitaearum*, but large population size is rarely realized, and is dampened by density dependent hyperparasitism (van Nouhuys & Tay 2001, van Nouhuys & Lei 2004).

One might presume that because the two parasitoids differ in dispersal behavior their coexistence would be facilitated by a trade off between dispersal ability and local competitive ability (Lei & Hanski 1998, Holt 2002). However, it

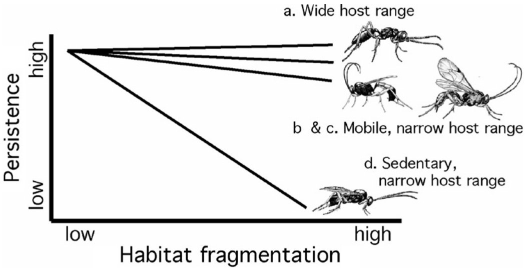

Fig. 2. Schematic drawing of the relationship between habitat fragmentation and the persistence of populations for the four parasitoids in the Glanville fritillary butterfly system. (**a**) The hyperparasitoid *Gelis agilis*, (**b**) the hyperparasitoid *Mesochorus* sp. cf. *stigmaticus*, (**c**) the parasitoid *Hyposoter horticola*, and (**d**) the parasitoid *Cotesia melitaearum*.

turns out that *H. horticola* is superior both as a disperser and as a local competitor. Hence, in this case, the inferior disperser *C. melitaearum* persists by using host left unused by *H. horticola*, and because of its high rate of reproduction (van Nouhuys & Hanski 2004).

Fragmentation and the fourth trophic level

Fragmentation of the habitat suitable for the butterfly probably has little impact on the hyperparasitoid *Gelis agilis*. This is because it has host species other than *C. melitaearum* (Schwarz & Shaw 1999), that presumably occupy other surrounding habitats. Indirect evidence of this is the fast rate that individuals are recruited, on foot (because they are wingless), to concentrations of *C. melitaearum* cocoons. *Mesochorus* sp. cf. *stigmaticus*, on the other hand, is restricted to the parasitoids of *M. cinxia*, and to *H. horticola* in particular. One would expect that a fourth trophic level specialist parasitoid would be constrained by habitat fragmentation. However, *M. stigmaticus* appears to be quite abundant throughout most of Åland. This is probably because *H. horticola* is a reliable resource even though it is at the third trophic level, and because *M. stigmaticus* is dispersive, like *H. horticola*. The one part of Åland where *M. stigmaticus* is absent is two small patch networks on isolated islands in the east (Fig. 1). Perhaps the absence of *M. stigmaticus* from these isolated poor quality networks can be attributed to them being too small to support four trophic levels (Holt 2002).

Conclusion

The case study of the parasitoids associated with the Glanville fritillary butterfly provides a clear illustration of the roles of dispersal behavior and host range in defining the range of effects of fragmentation for third and fourth trophic level species (Fig. 2). Other characteristics of species, such as their longevity and reproductive capacity, must also contribute to their sensitivity to fragmentation (Henle *et al*. 2004). Unfortunately, the natural history of higher trophic level insect species are rarely known well enough for specific predictions to be made for individual parasitoids or predators.

The results of individual fragmentation studies differed greatly. Some of this variation can be attributed to variation in definitions of fragmentation, durations of studies, and types of data collected. However, some is also due to interspecific differences in the effects of fragmentation, independent of trophic level, as was illustrated in the case study. With this much variation among species, the effect of fragmentation on different trophic levels may be detected most easily by gathering data about an entire community and recording species richness and diversity, and the distribution of rare *vs*. abundant species. These studies of entire communities show the strongest effects. However, detailed studies of individual species are necessary to understand many of the characteristics that make species sensitive to fragmentation. It may well be that on average, fragmentation affects the third trophic level (parasitoids and predators) more than the second trophic level (herbivorous insects), but this is not supported by Tables 2, 3 and 4.

An important implication for conservation from the case study is that fragmentation leads toward the loss of sedentary and specialized species at higher trophic levels. In fact, the parasitoid *C. melitaearum* (Figs. 1 and 2) is likely to become extinct in the Åland Islands (van Nouhuys & Hanski 2002). Based on several of the studies in the literature review, rarity should be on the list of attributes of fragile species, in addition to sedentariness and specialization. That is, parasitoids or predators that are initially rare in the landscape rapidly become increasingly rare with fragmentation (Dubbert *et al*. 1998, Golden & Crist 1999, Komonen *et al*. 2000, Kruess & Tscharntke 2000a, 2000b). The next important question is what happens to communities with the loss of sedentary, specialized, and rare higher trophic level species (for related discussion *see* Morris *et al*. 2005). If sedentary specialized parasitoids generally have strong effects on local host dynamics, as *C. melitaearum* once had in Åland (Lei & Hanski 1997), then community structure may change greatly. Thus, while the overall effects of habitat fragmentation may not be stronger for higher trophic levels than for the species upon which they depend, specific key high level community members may be affected in ways that disrupt community structure.

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References

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

Amarasekare, P. 2000b: Spatial dynamics in a host-multiparasitoid community. — *J. Anim. Ecol*. 81: 201–213.

Antolin, M. F. & Strong, D. R. 1987: Long distance dispersal by a parasitoid (*Anagrus delicatus*, Mymaridae) and its host. — *Oecologia* 73: 288–292.

Askew, R. R. & Shaw, M. R. 1989: Parasitoid communities: their size, structure and development. — In: Waage, J. & Greathead, D. (eds.), *Insect parasitoids*: 225–264. Academic Press, San Diego.

Athen, O. & Tscharntke, T. 1999: Insect communities of *Phragmites* habitats used for sewage purification: effects of age and area of habitats on species richness and herbivore–parasitoid interactions. — *Limnologica* 29: 71–74.

Braschler, B., Lampel, G. & Baur, B. 2003: Experimental small-scale grassland fragmentation alters aphid population dynamics. — *Oikos* 100: 581–591.

Brodeur, J. 2000: Host specificity and trophic relationships of hyperparasitoids. — In: Hochberg, M. E. & Ives, A. R. (eds.), *Parasitoid population biology*: 163–183. Princeton University Press, San Diego.

Cappuccino, N., Lavertu, D., Bergeron, Y. & Regniere, J. 1998: Spruce budworm impact, abundance and parasitism rate in a patchy landscape. — *Oecologia* 114: 236–242.

Cronin, J. T. 2003: Patch structure, oviposition behavior, and the distribution of parasitism risk. — *Ecol. Monogr*. 73: 283–300.

Cronin, J. T. 2004: Host–parasitoid extinction and colonization in a fragmented prairie landscape. — *Oecologia* 139: 503–514.

Cronin, J. T. & Haynes, K. J. 2004: An invasive plant promotes unstable host–parasitoid patch dynamics. — *Ecology* 85: 2772–2782.

Cronin, J. T., Haynes, K. J. & Dillemuth, F. 2004: Spider effects on planthopper mortality, dispersal, and spatial population dynamics. — *Ecology* 85: 2134–2143.

Cronin, J. T., Reeve, D. J., Wilkens, R. & Turchin, P. 2000: The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. — *Oikos* 90: 127–138.

Debinski, D. M. & Holt, R. D. 2000: A survey and overview of habitat fragmentation experiments. — *Conserv. Biol*. 14: 1–13.

Didham, R. K., Ghazoul, J., Stork, N. E. & Davis, A. J. 1996: Insects in fragmented forests: a functional approach. — *Trends Ecol. Evol*. 11: 255–260.

Dubbert, M., Tscharntke, T. & Vidal, S. 1998: Stem-boring insects of fragmented *Calamagrostis* habitats: herbivore–parasitoid community structure and the unpredictability of grass shoot abundance. — *Ecol. Entomol*. 23: 271–280.

Eber, S. 2001: Multitrophic interactions: The population dynamics of spatially structured plant–herbivore–parasitoid systems. — *Basic Appl. Ecol*. 2: 27–33.

Ehrlich, P. R. & Hanski, I. (eds.) 2004: *On the wings of checkerspots: A model system for population biology*. — Oxford University Press, Oxford.

Faeth, S. H. & Simberloff, D. 1981. Experimental isolation of oak host plants: effects on mortality, survivorship, and abundances of leaf-mining insects. — *Ecology* 63: 625–635.

Ferrari, J., Kruess, A. & Tscharntke, T. 1997: Effects of fragmentation of wild roses on their insect communities. — *Mitteilungen der Deutschen Gesellschaft fur Allgemeine und Angewandte Entomologie* 11: 89–90.

Golden, D. M. & Crist, T. O. 1999: Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. — *Oecologia* 118: 371–380.

Hanski, I. & Meyke, E. 2005: Large-scale dynamics of the Glanville fritillary butterfly: landscape structure, population processes, and weather. — *Ann. Zool. Fennici* 42: 379–395.

Hanski, I. & Ovaskainen, O. 2000: The metapopulation capacity of a fragmented landscape. — *Nature* 404: 755–758.

Hanski, I., Pakkala, T., Kuussaari, M. & Lei, G. C. 1995:

Metapopulation persistence of an endangered butterfly in a fragmented landscape. — *Oikos* 72: 21–28.

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

Hassell, M. P. 2000: *The spatial and temporal dynamics of host-parasitoid interactions*. — Oxford University Press, London.

Henle, K., Davies, K., Kleyer, M., Margules, C. & Settele, J. 2004: Predictors of species sensitivity to fragmentation. — *Biodivers. Conserv.* 13: 207–251.

Holt, R. D. 2002: Food webs in space: On the interplay of dynamic instability and spatial processes. — *Ecol. Res.* 17: 261–273.

Kareiva, P. 1987: Habitat fragmentation and the stability of predator-prey interactions. — *Nature* 326: 388–390.

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

Kruess, A. 2003: Effects of landscape structure and habitat type on a plant–herbivore–parasitoid community. — *Ecography* 26: 283–290.

Kruess, A. & Tscharntke, T. 1994: Habitat fragmentation, species loss and biological control. — *Science* 264: 1581–1584.

Kruess, A. & Tscharntke, T. 2000a: Effects of habitat fragmentation on plant-insect communities. — In: Ekbom, B., Irwin, M. E. & Roberts, Y. (eds.), *Interchanges of insects between agricultural and surrounding landscapes*: 53–70. Kluwer, London.

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

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. — *J. Anim. Ecol.* 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. — *J. Nat. Hist.* 31: 635–648.

MacArthur, R. H. & Levins, R. 1964: Competition, habitat selection, and character displacement in a patchy environment. — *Proc. Natl. Acad. Sci. U.S.A.* 51: 1207–1210.

Mikkelson, G. M. 1993: How do food webs fall apart? A study of changes in trophic structure during relaxation on habitat fragments. — *Oikos* 67: 539–547.

Moilanen, A. & Nieminen, M. 2002: Simple connectivity measures for spatial ecology. — *Ecology* 84: 1131–1145.

Morin, P. J. 1999: *Community ecology*. — Blackwell Science Inc., Malden.

Morris, R. J., Lewis, O. T. & Godfray, H. C. J. 2005: Apparent competition and insect community structure: towards a spatial perspective. — *Ann. Zool. Fennici* 42: 449–462.

Nieminen, M., Siljander, M. & Hanski, I. 2004: Structure and dynamics of *Melitaea cinxia* metapopulations. — In: Ehrlich, P. R. & Hanski, I. (eds.), *On the wings of checkerspots: a model system for population biology*: 63–91. Oxford University Press, Oxford.

Pimm, S. L. 1982: *Food webs*. — Chapman and Hall, London.

Roland, J. & Taylor, P. D. 1997: Insect parasitoid species respond to forest structure at different spatial scales. — *Nature* 386: 710–713.

Schwarz, M. & Shaw, M. R. 1999: Western Palaearctic Cryptinae (Hymenoptera: Ichneumonidae) in the National Museums of Scotland, with nomenclatural changes, taxonomic notes, rearing records and special reference to the British check list. Part 2. Genus *Gelis* Thunberg (Phygadeuontini: Gelina). — *Entomologist's Gaz.* 50: 117–125.

Segarra-Carmona, A. E. & Barbosa, P. 1992: Host-plant patches as islands: effects of patch size, patch extinction and seasonality of a herbaceous tropical legume (*Crotalaria pallida* Ait.) on a pod borer (*Etiella zinckenella* (Treit.) and its parasitoids. — *Insect Sci. Appl.* 13: 709–718.

Shaw, M. R. 1994: Parasitoid host ranges. — In: Hawkins, B. A. & Sheehan, W. (eds.), *Parasitoid community ecology*: 111–144. Oxford University Press, Oxford.

Tscharntke, T. & Kruess, A. 1999: Habitat fragmentation and biological control. — In: Hawkins, B. A. & Cornell, H. V. (eds.), *Theoretical approaches to biological control*: 190–205. Cambridge University Press, Cambridge.

Tscharntke, T., Gathmann, A. & Steffandewenter, I. 1998: Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. — *J. Anim. Ecol.* 35: 708–719.

Tscharntke, T., Rand, T. A. & Bianchi, F. J. J. A. 2005: The landscape context of trophic interactions: insect spillover across the crop–noncrop interface. — *Ann. Zool. Fennici* 42: 421–432.

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*. — In: Hanski, I. & Gilpin, M. E. (eds.), *Metapopulation biology: ecology, genetics, and evolution*: 387–406. Academic Press, San Diego.

van Nouhuys, S. & Ehrnsten, J. 2004: Wasp behavior that leads to uniform parasitism of a host available only a few hours per year. — *Behav. Ecol.* 15: 661–665.

van Nouhuys, S. & Hanski, I. 1999: Host diet affects extinctions and colonizations in a parasitoid metapopulation. — *J. Anim. Ecol.* 68: 1248–1258.

van Nouhuys, S. & Hanski, I. 2000: Apparent competition between parasitoids mediated by a shared hyperparasitoid. — *Ecol. Lett.* 3: 82–84.

van Nouhuys, S. & Hanski, I. 2002: Colonisation rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. — *J. Anim. Ecol.* 71: 638–650.

van Nouhuys, S. & Hanski, I. 2004: Natural enemies of checkerspot butterflies. — In: Ehrlich, P. R. & Hanski, I. (eds.), *On the wings of checkerspots: a model system for* *population biology*: 161–180. Oxford University Press, Oxford.

van Nouhuys, S. & Hanski, I. 2005: Metacommunities of butterflies, their host plants and their parasitoids. — In: Holyoak, M., Leibold, M. A. & Holt, R. D. (eds.), *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago. [In press].

van Nouhuys, S. & Lei, G. C. 2004: Parasitoid and host metapopulation dynamics: The influences of temperature mediated phenological asynchrony. — *J. Anim. Ecol.* 73: 526–535.

van Nouhuys, S. & Tay, W. T. 2001: Causes and consequences of mortality in small populations of a parasitoid wasp in a fragmented landscape. — *Oecologia* 128: 126–133.

Wahlberg, N., Ehrlich, P. R., Boggs, C. L. & Hanski, I. 2004: Bay checkerspot and Glanville fritillary compared with other species. — In: Ehrlich, P. R. & Hanski, I. (eds.), *On the wings of checkerspots: a model system for population biology*: 219–244. Oxford University Press, Oxford.

Zabel, J. & Tscharntke, T. 1998: Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differently? — *Oecologia* 116: 419–425.