

# **Spatial ecology of a specialist insect herbivore – the leaf-mining moth *Tischeria ekebladella* on the pedunculate oak *Quercus robur***

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Academic dissertation

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# Spatial ecology of a specialist insect herbivore – the leaf-mining moth *Tischeria ekebladella* on the pedunculate oak *Quercus robur*

Sofia Gripenberg

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I Gripenberg, S. & Roslin, T. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. – *Oikos* 116: 181-188.
- II Roslin, T., Gripenberg, S., Salminen, J-P., Karonen, M., O'Hara, R. B., Pihlaja, K. & Pulkkinen, P. 2006. Seeing the trees for the leaves – oaks as mosaics for a host-specific moth. – *Oikos* 113: 106-120.
- III Gripenberg, S., Salminen, J-P. & Roslin, T. 2007. A tree in the eyes of a moth – temporal variation in oak leaf quality and leaf-miner performance. – *Oikos* 116: 592-600.
- IV Gripenberg, S., Morriën, E., Cudmore, A., Salminen, J-P. & Roslin, T. 2007. Resource selection by female moths in a heterogeneous environment: What is a poor girl to do? – *Journal of Animal Ecology* 76: 854-865.
- V Gripenberg, S. & Roslin, T. 2005. Host plants as islands: Resource quality and spatial setting as determinants of insect distribution. – *Annales Zoologici Fennici* 42: 335-345.
- VI Gripenberg, S. & Roslin, T. 2007. Neither the devil nor the deep blue sea: larval mortality factors fail to explain the abundance and distribution of *Tischeria ekebladella*. – Submitted manuscript.
- VII Gripenberg, S., Ovaskainen, O., Morriën, E. & Roslin, T. 2007. Spatial population structure of a specialist leaf-mining moth. – Submitted manuscript.

# Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

	I	II	III	IV	V	VI	VII
<b>Design</b>	SG	TR, SG	SG, TR	SG, TR	TR, SG	SG	SG, TR, EM
<b>Material</b>	SG	TR, SG, JPS, MK, PP, KP	SG, JPS, TR	SG, EM, AC, JPS, TR	TR, SG	SG	SG, EM, TR
<b>Model</b>	--	--	--	--	--	--	OO
<b>Statistical analyses</b>	--	TR, BOH	SG, TR	SG, TR	TR, SG	SG, TR	SG
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## 0 Summary

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## 1 Introduction

Plants and herbivorous insects comprise a major part of terrestrial biodiversity: as much as 70% of all known species on Earth are either insects or plants (Wilson 1992), and current estimates of the total diversity of plant-feeding insects reach a staggering 4-10 million species (Ødegaard 2000, Novotny *et al.* 2002). These insects form important nodes in many food webs. For example, some plant populations are suppressed by their insect herbivores (Louda 1982, Crawley 1989, 1997, Maron & Gardner 2000, Maron & Crone 2006), and phytophagous insects are the food source for a high diversity of secondary consumers (Askew & Shaw 1986, Hawkins & Lawton 1986, Godfray 1994, Hawkins *et al.* 1997). From a human perspective, herbivorous insects cause a large amount of damage as pest species on crops and forest trees (Barbosa & Schultz 1987, Speight & Wainhouse 1989, Dent 2000, Harausz & Pimentel 2002). Not surprisingly, research on herbivorous insects has developed into major fields within both the biological and agricultural sciences. But while some insect populations reach very high densities, a fundamental question in ecology still is why most herbivorous insects do *not* reach pest status despite seemingly plentiful food resources, and why insects are often *absent* from potential host plant individuals. A wide range of mechanisms have been proposed to explain the patchy distribution and typically “low” abundances of insect herbivores:

Insect populations are sometimes considered to be strongly influenced by abiotic factors such as weather and climatic conditions (Andrewartha & Birch 1954, Milne 1957, DeBach 1958, Dempster 1983). In recent decades, the ecology of herbivorous insects has increasingly been examined from a trophic perspective. In this context, the distribution and dynamics of herbivorous insect populations is thought to match variation in plant quality and predation pressure (e.g. Hairston *et al.* 1960, Lawton & McNeill 1979, Denno & McClure 1983, Strong *et al.* 1984, Hunter *et al.* 1992, Hawkins 2001, Agrawal 2004, Schoonhoven *et al.* 2005). Nevertheless, many studies of herbivorous insects conducted within the realm of trophic interactions (notably the ones examining the effects of plant quality) adopt a highly non-spatial view on the world. This contrasts with another paradigm: that of spatial ecology.

During the past few decades, ecology has become increasingly permeated by the notion that everything takes place within a spatial context, and that the distribution of habitat may strongly influence the distribution, dynamics, and evolution of natural populations (e.g. Hanski & Gilpin 1997, Tilman & Kareiva 1997, Hanski & Gaggiotti 2004). Thus, even in a hypothetical world without local variation in plant defences, natural enemies and environmental

conditions, we would hardly find insects on all plant individuals. At small spatial scales (within the movement range of the herbivore), the distribution of plants might influence the likelihood that the insect individual will find the plants, and the foraging decisions made by the insect (Root 1973, Singer & Wee 2005). At larger scales, the dispersal ability of the insect may interact with landscape structure to cause local absences on isolated plants (e.g. Eber & Brandl 1996, Hanski 1999, Doak 2000, Menéndez & Thomas 2000). Thus, at the landscape level, the spatial distribution of host plants may blur the importance of abiotic conditions and trophic interactions, or decouple herbivore distribution and abundance from local habitat quality (cf. Pulliam 1988, Thomas *et al.* 1996).

Despite the potentially important roles of both local habitat quality and intra-specific spatial processes, little is known about how their relative importance compares in different situations and settings. This thesis uses the leaf-mining moth *Tischeria ekebladella* (Box 1), a specialist herbivore of the pedunculate oak, *Quercus robur*, as a case study to disentangle trophic interactions from spatial population dynamics. The overall objective has been to assess how local “habitat quality” (in the form of host quality and predation pressure) compares to “landscape structure” (the spatial distribution of oak trees) in influencing the local and regional distribution, dynamics, and evolution of this insect herbivore. The conceptual context of the thesis is described in Box 2.

## 2 Outline of the thesis

The thesis has seven chapters. The first chapter (I) sets the stage for the rest of the thesis by providing an overview of means and processes by which spatial variation in abiotic conditions, trophic interactions and landscape structure may influence herbivorous insects.

Chapters II-IV examine spatial and temporal variation in host quality and its potential implications for the evolution of herbivore host use. In chapter II we ask how similar individual oaks are as habitat for *T. ekebladella*, and how large the variation within trees

is compared to that between trees. In chapter III, we assess how static or dynamic the spatial patterns of habitat quality are in time: Is a tree, branch or shoot that is favourable at one point in time likely to be so later, or does the relative ranking of resource units shift through time? Chapter IV tests hypotheses spurred by results from the two preceding chapters. Based on the documented spatial and temporal patterns, we investigate whether female resource selection matches spatial patterns of local habitat quality, whether females adjust their oviposition behaviour in response to plant traits commonly assumed to signal “quality”, and whether females select the resources on which their offspring perform best.

Chapters V-VII examine how the patterns of host quality described in II-III combine with other trophic interactions and with patterns of host distribution to structure the regional population of *Tischeria ekebladella*. In chapters V and VI we explore large-scale patterns of habitat quality and assess the role of trophic interactions in creating regional patterns of insect distribution. More specifically, we ask whether patterns of leaf miner distribution and abundance at the landscape level reflect spatial patterns of larval mortality incurred by the host plant (V, VI) or by natural enemies (VI).

In the final chapter (VII), we compress all that we have learnt in chapters II-VI into a metapopulation model. Here, the aim is to achieve a comprehensive understanding of the system, to assess the relative importance of local and regional processes on the tree-specific moth dynamics, and to make predictions about the degree of interaction between moths originating from different trees.

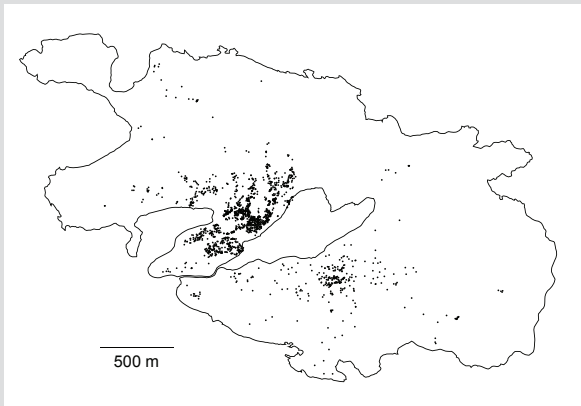
## 3 Methods

The thesis builds on data collected across several spatial and temporal scales. For details on sampling and experimental designs I refer to the “Material and Methods” sections of the individual chapters. Here I will briefly summarize the range of responses measured, and the spatial scales addressed.



### Box 1. The study system: *Tischeria ekebladella* on oak trees

Several features of both the plant and the insect render the oak-*Tischeria ekebladella* system ideal for studies of plant-insect interactions in a spatial context. In this system, the host has a long life span, and thereby offers a relatively stable landscape for many herbivore generations. The oak is also highly conspicuous. While mapping the distribution of potential habitat would be challenging for an insect species associated with, for example, an annual herb, it is easily achieved for a herbivore feeding on a single tree species. Moreover, as the oak has a scattered distribution throughout the Finnish landscape, it is possible to identify trees of varying degree of isolation (Fig. 1).



**Fig. 1.** To address some of the study questions of this thesis, I mapped the location of all oak trees on the island of Wattkast in south-western Finland. The fact that the system is closed (an island) makes it ideal for studies on metapopulation dynamics, as it will be minimally influenced by external processes.

The moth *Tischeria ekebladella* is highly host-specific, and in Finland it will only feed on oak trees. Hence, a map of oaks constitutes an adequate map of its landscape. The leaf-mining habit of *T. ekebladella* and the conspicuousness of the leaf mines (Fig. 2) also enable an accurate assessment of the distribution and abundance of the insect – a task that would hardly be feasible if the larvae were free-feeding. As a study species, *T. ekebladella* is highly cooperative and experimental manipulation of the system is possible. Moths can easily be reared from larvae collected in hibernating leaf mines. By enclosing adult moths into bags attached to the trees, it is possible to transfer the species to foliage of our choice (Fig. 3). Finally, the species can be experimentally removed from (small) trees by picking off all mined leaves.



**Fig. 2.** Oak leaf mined by *Tischeria ekebladella*.



**Fig. 3.** Bags used for experimental introductions. The success rate of introductions is generally high. For example, in the experiment described in chapter VI, eggs were found in 291 of the 329 bags into which we added adult moths.

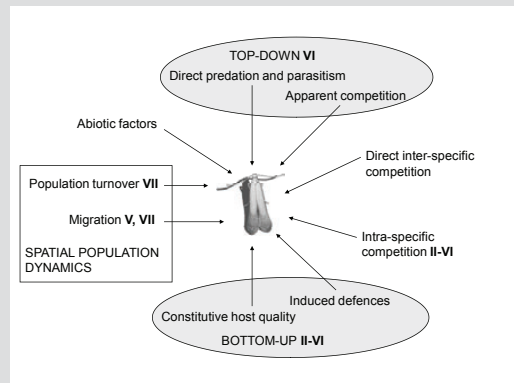
## Box 2. Conceptual context of the study

This thesis does clearly not address all factors affecting the abundance and distribution of *Tischeria ekebladella* – that is prevented by the complexity of nature. Herbivorous insects like *T. ekebladella* may form part of intricate food webs, where interactions with other species may influence both the ecology and evolution of the focal species. In addition to being directly affected by vertical forces acting bottom-up (properties of their host plants) and top-down (various types of natural enemies), herbivorous insects are also influenced horizontally through interactions with other herbivore species and plant pathogens (Faeth 1987). To complicate things further, some effects that appear to be vertical may in fact be indirect and mediated by species at the same trophic level (Ohgushi *et al.* 2007). Both vertical and horizontal, as well as direct and indirect effects have been recorded in leaf miners (e.g. Bultman & Faeth 1986, Sato & Higashi 1987, Masters & Brown 1992, Bylund & Tenow 1994, Fisher *et al.* 2000, Riihimäki *et al.* 2003, Morris *et al.* 2004). Chapter I provides an overview of these effects, and how they may vary in a spatial context.

The agents causing direct and indirect bottom-up and top-down effects on herbivores are many and diverse. Numerous host plant traits have been identified as important for leaf miners, such as leaf nutrition (De Bruyn *et al.* 2002, Cornelissen & Stiling 2006), host plant phenology (Mopper & Simberloff 1995, Eber 2004), early leaf abscission (Faeth *et al.* 1981, Preszler & Price 1993), and secondary chemistry (Hunter 1997). Similarly, the natural enemies causing top-down effects on leaf miners are highly diverse and represent several feeding guilds (e.g. Owen 1975, Sato & Higashi 1987, Lewis *et al.* 2002).

The general complexity of the target system calls for very explicit decisions in terms of what to address in the study and what to leave out. To disentangle trophic effects on *T. ekebladella* from the kind of effects which may arise from intra-specific spatial population processes, I have therefore made a conscious choice in terms of responses addressed. In selecting single components of a complex network, I explicitly assume that other factors left unaddressed do not introduce any systematic bias in the relations actually examined.

Another consequence of the complexity of matters is that not every detail of the mechanisms can be addressed. As an important corollary to the chosen level of resolution, this thesis examines trophic interactions without attempting to identify whether they are direct or indirect (Fig. 4; see also Fig. 1 in I). Since *T. ekebladella* shares its host with a large number of other herbivore species, it is indeed possible that some of the bottom-up and top-down effects might in part be mediated by other herbivores through processes like induced defences (Karban & Baldwin 1997) and apparent competition (van Veen *et al.* 2006). Only further studies dissecting individual components of the sketch drawn here will resolve these issues.



**Fig. 4.** Picture showing factors of potential importance for the ecology and evolution of *Tischeria ekebladella*. Among these trophic and non-trophic factors, I have focussed my studies on top-down and bottom-up factors, on intra-specific competition, and on intra-specific spatial population processes (population turnover and migration). In this schematic drawing, the direct and indirect effects of host quality and natural enemies are grouped to depict “realized” bottom-up and top-down effects (shaded areas). The box delineates factors influencing the spatial population dynamics of the species. Note that several of the factors may interact with each other.

### 3.1 Measuring local habitat quality

In previous studies of plant-insect interactions, the “quality” of plants has been assessed in many ways. While plant quality is sometimes considered as an “absolute” trait (such as the concentration of secondary compounds in the leaf tissue), it is becoming increasingly clear that “quality” is something more complex, and something specific to each insect-plant interaction (Haukioja 2003). Therefore, I have supplemented “absolute” traits of the host plant (chemical measures of oak leaf contents; **II-IV**, Box 3) with straight-forward measures of how the moth larvae grow (**II**) and survive (**II-VI**). Among many potentially important traits, the choice of these particular measures seems well justified: Leaf phenolics are considered key elements in the plant chemical defence system (e.g. Harborne 1994, Waterman & Mole 1994, Box 3), and larval growth and survival are central components of insect fitness (e.g. Reavey & Lawton 1991).

### 3.2 Assessing spatial patterns

Throughout the thesis, “space” is dealt with using several approaches: In chapters **II-IV**, the spatial context is implicit but mostly covers spatial scales that could be covered by an individual moth during its lifetime. To assess spatial patterns of variation in oak leaf chemistry and leaf miner performance, we used a hierarchical sampling protocol, which enabled us to partition the total variation into variation among, for example, trees, branches, shoots, and leaves (see Fig. 1 in chapter **II**). In the remaining chapters (**V-VII**), where the spatial scale is larger and the spatial context explicit, we build on georeferenced data.

To assess the effects of host tree distribution on the distribution and dynamics of *T. ekebladella*, and on the spatial structuring of the moth population, the location of all oak trees on the island of Wattkast in south-western Finland was mapped (Fig. 1 in Box 1). Data collected within this setting were analysed using multiple methods of spatial analysis. We used a structural connectivity measure to describe the degree of host tree isolation (**V**), K-function statistics to explore gradients in larval survival rates through the landscape (**VI**), and a spatially explicit metapopulation model to assess spatial structuring of the regional moth population on Wattkast (**VII**).

## 4 Main results and discussion

This thesis shows that both trophic interactions and metapopulation-level processes may form important facets of the ecology of *T. ekebladella*, but that their importance will vary with the scale examined. Below, I identify and discuss the most important findings.

### *At any given time, differences among trees are small*

When oak trees were compared at any one point in time, the average differences among tree individuals were minor compared to the large amount of variation within individual tree crowns (**II, III, V**). Although the exact patterns of hierarchical variation differed between the traits examined, the overall pattern is clear: From the perspective of *Tischeria ekebladella*, trees form units of extremely high internal heterogeneity. This finding has several important implications.

In the study of arboreal insects, the prevailing view has long been that the tree individual – the genet – is the relevant unit upon which the interplay between trees and insects takes place (e.g. Edmunds & Alstad 1978, Mopper *et al.* 1984, 1995, 2000, Weis & Campbell 1992, Hanks & Denno 1994, Memmott *et al.* 1995, Ruhnke *et al.* 2006). Nevertheless, our results suggest that we may need to shift our focus to smaller spatial scales. With most of the variation in larval performance found *within* individual tree crowns (**II**), insects might primarily respond not to host quality at the tree level, but rather to variation at smaller spatial scales, such as the shoot and leaf levels. With only minor variation at the tree level, ignoring variation in tree-specific “habitat quality” will also seem justified when examining insect population dynamics within a metapopulation framework (cf **VII**).

### *... and resource quality changes through time*

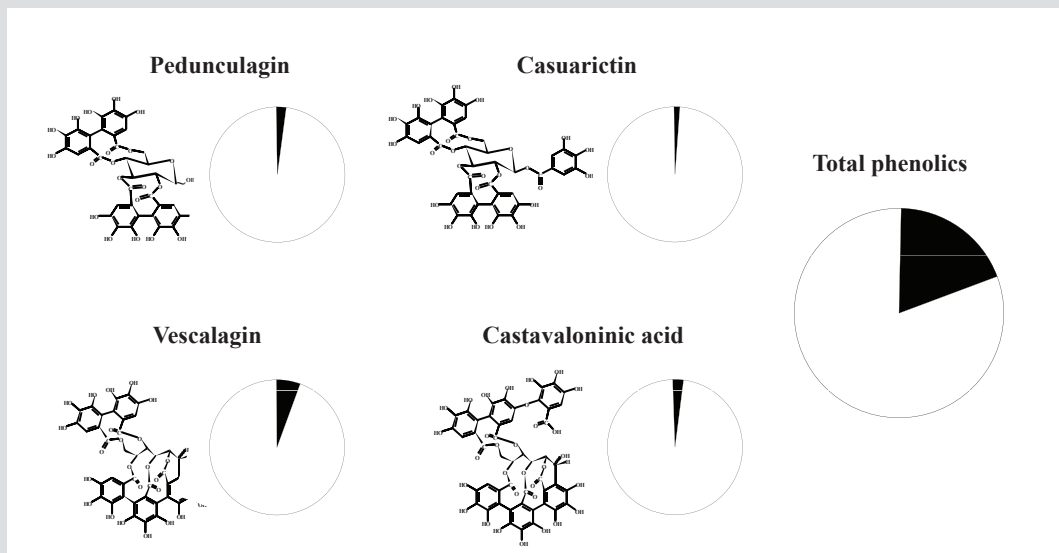
Our results show that any spatial patterns that occur at some point in time are only moderately stable through time (**III**). When examined within a season, trees were only partly consistent in their relative rankings in terms of phenolic chemistry and insect

### Box 3. Phenolic contents as a measure of host quality

Among the myriads of chemical compounds found in plant tissue, we have chosen leaf phenolics in general, and hydrolysable tannins and flavonoid glycosides in particular, as a measure of host quality. This choice was based on several considerations: Phenolics are both common and widely distributed among plant species (e.g. Harborne 1994, Waterman & Mole 1994), and especially in oaks, their concentration is extremely high (e.g. Fig. 5). Due to their influence on both the distribution, performance and community structure of insect herbivores, phenolics have often been considered an important part of the chemical defence system of oak trees (e.g. Feeny 1970, Rossiter *et al.* 1988, Abrahamson *et al.* 2003, Tikkanen & Julkunen-Tiitto 2003, Forkner *et al.* 2004). According to the paradigm prevailing at the outset of our study (Feeny 1970), the concentration of phenolics in general and tannins in particular would also increase during the course of the summer, and reach particularly high levels during the larval period of *T. ekebladella*.

While many ecologists have described phenolic contents by rough-and-ready summary measures, we opted to analyze them on a compound-specific basis (Fig. 5). This decision was motivated by two facts: different phenolic compounds have very different biological activities (Zucker 1983, Ayres *et al.* 1997, Kraus *et al.* 2003), and the total concentration of phenolics does not adequately reflect the concentration of individual compounds (Salminen *et al.* 2004).

During the course of my study, we realised that concentrations of most measured phenolic compounds actually peak in the early season (Fig. 1 in III), and decrease dramatically in late summer (cf. Salminen *et al.* 2004). This observation alters the prevailing view on seasonal variation in oak phenolics, and suggests that the measured compounds may be less likely to affect feeding by late-season leaf miners than we first thought. In hindsight, it might then have been equally motivated to focus our studies on some other aspects of leaf quality such as water content (Scriber 1984), nitrogen content (Mattson 1980, White 1993), or leaf toughness (Coley 1983, Howlett *et al.* 2001), which might still turn out to be more important determinants of foliage quality than mere phenolics. Nevertheless, I stress that different factors may interact in complex ways to determine plant quality (Kause *et al.* 1999), and that no single trait will suffice to explain insect performance.



**Fig. 5.** A selection of hydrolysable tannins found in oak leaves (sampling date 29 May). The pie charts show the proportion of leaf dry weight consisting of respective compound. The total content of hydrolysable tannins and flavonoid glycosides amounts to an impressive 19% of the total dry weight of an oak leaf.

survival. When insect abundances and survival rates were examined on the very same trees, branches and shoots in several consecutive years, the level of consistency was – at best – intermediate.

Temporal shifts in the rankings of tree individuals will make tree-to-tree differences even more subtle than if spatial patterns were stable in time. Within a season, the observed spatiotemporal variation might render it difficult for developing larvae to keep up with the changing conditions: a site that is optimal at one point in time might be unfavourable at a later stage of larval development (see Ruusila *et al.* 2005). If the within-crown mosaic is changing in time (which might also be the case within a season; cf. Yamasaki & Kikuzawa 2003), female moths may fail to select resources optimal for offspring development (IV).

#### *Spatiotemporal resource heterogeneity may hamper female choice*

Indeed, female preference does not match patterns of offspring performance: Larvae did not survive any better on shoots and trees particularly favoured by ovipositing females (IV). Nevertheless, patterns of female oviposition did not match our *a priori* expectation of low discrimination between individual trees (cf. II, V): despite little variation between trees compared to large variation within individual tree crowns (II, III, V), ovipositing females clearly discriminated between leaves from different trees (IV).

The reason for the lack of preference-performance coupling in this system can possibly be attributed to spatiotemporal resource heterogeneity (III). If resource units (e.g. trees, branches and shoots) commonly change their relative “quality rankings”, ovipositing females may fail to predict the fate of their developing offspring. Under such circumstances, the females might need to adopt a risk-spreading strategy to cover themselves against the risk of complete failure (den Boer 1968, Hopper 1999). Even if this is the case, the clear discrimination by females between different trees will still require an explanation. According to a tentative hypothesis outlined in chapter IV, the mismatch between the spatial scales of female choice and larval performance may be due to temporal shifts

in hierarchical patterns of variation. At the time of female choice, trees would then appear more different from each other than they are during the time of larval feeding. We do not know what traits females respond to when selecting foliage for offspring development. If leaf phenolics are important, that could explain female discrimination between trees (II; see also Salminen *et al.* 2004).

#### *Host plant quality fails to explain leaf miner distribution...*

When scaling up to the landscape level, there is again no detectable link between leaf miner distribution and performance. Experimentally introduced larvae sheltered from natural enemies survived just as well on trees from which the species was naturally absent as on trees that hosted wild leaf miners (V, VI). Thus, larval mortality incurred by the host tree does not suffice to explain the distribution and abundance of *Tischeria ekebladella* across the landscape.

Nevertheless, host-induced mortality seems low overall (III, V, VI), and hence this factor may be of secondary importance compared to other factors, such as mortality incurred by natural enemies.

#### *... and so do natural enemies...*

Mortality induced by natural enemies is very high: in one experiment, the survival rate of introduced larvae exposed to parasitoids and predators was below 10% (VI). Nevertheless, tree-specific differences in larval survival rates also fail to explain landscape-level patterns of distribution and abundance in *Tischeria ekebladella*. In the presence of natural enemies, the survival of transplanted larvae was unrelated to the abundance of wild mines on a tree, and the survival of introduced larvae was in fact *higher* on trees that were unoccupied by the species than on trees which sustained a population of wild individuals (VI).

Thus, although trophic influences (host quality and natural enemies) on larval survival rates may be locally important, they cannot be the prime determinants of leaf miner distribution and abundance across the landscape (V, VI).



... hence, the key is in spatial processes

While trophic interactions fail to account for patterns of leaf miner incidence across trees, the likelihood of a (small) tree being occupied by *Tischeria ekebladella* does depend on its spatial location in the landscape. On small oak individuals, leaf mines are more likely to be present on trees surrounded by other oak trees than on isolated oak individuals (V, VII). This is probably due to metapopulation processes (e.g. Hanski 1998, 1999). In this context, limited moth dispersal combined with the relative instability of small populations will cause the species to be absent from some of the small, isolated oaks (V, VII). The importance of regional processes on local leaf miner abundance has previously been demonstrated by Connor *et al.* (1983), who experimentally showed that the recruitment of leaf miners on individual oak trees – albeit much larger than the small trees in our study – is largely dependent on immigration from surrounding trees.

As a whole, our results also show that the regional population of *T. ekebladella* on Wattkast cannot be assigned to any strictly defined “metapopulation category” (cf. Harrison & Taylor 1997). The dispersal ability of the moth interacts with the spatial distribution of oak trees on Wattkast to create a continuum of tree-specific “population types”, ranging from populations where local processes dominate (isolated trees) to populations where regional processes override the local ones (well-connected trees and small trees; VII). Thus, it is only on the small trees that we will observe the extinction-colonization dynamics typical of “classical metapopulations” (Hanski 1998, 1999).

#### *Adaptive deme formation is context-dependent and unlikely*

As a consequence of the processes described above (and in chapter VII), the strength of gene flow between tree-specific moth populations will strongly depend on the spatial context (Slatkin 1987, Hastings & Harrison 1994, Harrison & Hastings 1996, Whitlock 2004). The likelihood of an insect population adapting evolutionarily to local conditions may thus be strongly influenced by the

spatial setting. On tree individuals surrounded by conspecifics, adaptive deme formation at the level of the tree individual (Edmunds & Alstad 1978, Mopper *et al.* 1995, 2000) seems highly unlikely. In contrast, local moth populations on isolated trees would have a greater potential of becoming adapted to the traits of their host (but see Morgan *et al.* 2005). Nevertheless, detecting local adaptations of moths even to very isolated trees seems rather unlikely in this particular system, since the differences in “local habitat quality” provided by different tree individuals are small (II, V) and temporally inconsistent (III).

## 5 Perspectives

All ecological communities contain species with different ecological characteristics, and what we observe in one system may not apply to another. Based on the results of this thesis, how much can we infer about patterns and processes in other systems?

Clearly, the documented spatial patterns of habitat quality may be restricted to the oak-*Tischeria ekebladella* system. In studies where substantial tree-to-tree differences in insect performance have been reported, phenological variation (such as variation in the timing of budburst) has commonly been advocated as an important causal factor (e.g. Crawley & Akhteruzzaman 1988, Mopper & Simberloff 1995, Tikkanen & Julkunen-Tiitto 2003, Mopper 2005). Thus, one potential explanation for the small differences in larval performance between trees in our study system might be the fact that larval *T. ekebladella* feed on mature oak leaves. At the time of larval feeding, the tree-to-tree differences in, for example, phenolic chemistry will be much smaller than at the early stage of leaf development (Salminen *et al.* 2004). Species feeding earlier – especially the ones that have to time their feeding with bud break – may then perceive larger among-tree differences than *T. ekebladella*. Before we can resolve whether the pattern found in our study system is common or not, we will need more studies – preferably on a range of insect species with different phenologies – describing hierarchical patterns of resource variation.

When it comes to the role of spatial processes in population dynamics, I expect processes similar to the ones described here to operate in many other systems: Many insect herbivores are host specific (Claridge & Wilson 1981, Bernays & Graham 1988, Schoonhoven *et al.* 2005), many tree species have a patchy distribution (e.g. Condit *et al.* 2000, Frost & Rydin 2000, Atkinson *et al.* 2007), and many insects have a limited dispersal ability (Tschamntke & Brandl 2004). Hence, I would expect to find similar spatial structuring at the landscape-level in many other insect populations. Nevertheless, the results from the oak-*T. ekebladella* system must not be uncritically applied to other systems. Specialist insect herbivores associated with trees form a large and diverse group of species, and in this respect no single study system will serve as an ideal “model system” for all tree-insect interactions. Among leaf miners of oaks, *T. ekebladella* is one of the species with the highest local abundances. This may render it an extreme among the types of spatial population structures encountered among insects on oaks. Studies have shown that even closely related species sharing the very same habitat network may respond very differently to its spatial structure (Gutierrez *et al.* 2001, Roslin & Koivunen 2001, van Nouhuys & Hanski 2002). In systems where tree-to-tree differences are larger, these might also impose some further structuring on the insect population (see above).

### 5.1 Applications

Research is often driven by the needs and interests of society (Ford 2000). While *T. ekebladella* is neither threatened nor a pest species (but see Jordan 1995), our results might have some applied value in other systems, primarily in the context of insect conservation. In particular, the current findings support one fundamental insight: that human impact on a landscape may affect a local population – even when the focal population itself is left undisturbed. This is likely to be true whenever the local presence and dynamics of a species are highly influenced by the surrounding landscape (I, V, VII). Yet, it is not sufficiently acknowledged in current conservation practises (which often focus on preserving local populations without considering their surroundings or internal relations).

### 5.2 Key priorities for future studies

While this thesis provides insights into the spatial ecology of a tree-insect interaction, it also leaves many questions open for future work. Some of these challenges are identified in the individual chapters, but I would here like to emphasize three topics where future research might prove particularly fruitful:

First, spatiotemporal variation in resource quality deserves closer examination. So far, rather few studies have assessed how spatial and temporal variation in resource quality interact, and how it affects herbivore host use and evolution. Results from the studies available so far (e.g. Yamasaki & Kikuzawa 2003, Riipi *et al.* 2004, Ruusila *et al.* 2005, III) suggest that spatiotemporal variation might indeed be a powerful mechanism preventing herbivores from utilizing their host plants efficiently. More studies covering a range of spatial and temporal scales will be needed before we can resolve how common the phenomenon is, and what consequences it has for the herbivores.

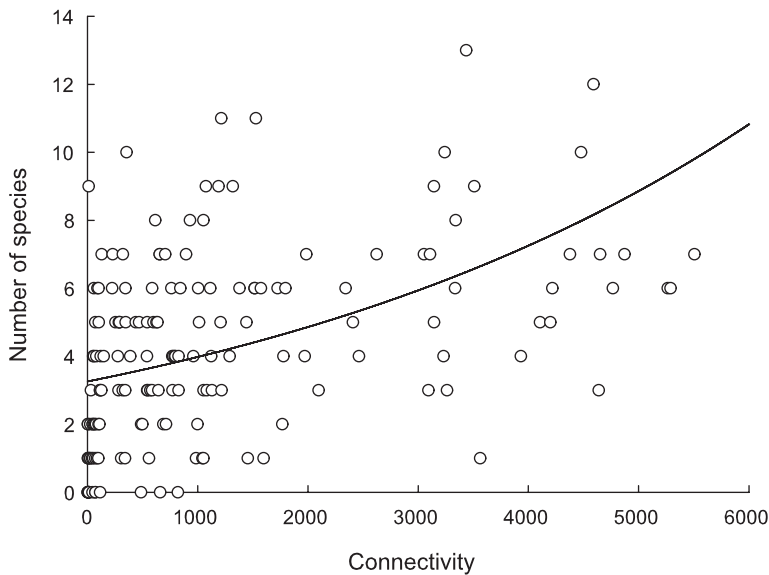
Second, given the great interest in the “adaptive deme formation hypothesis” (Edmunds & Alstad 1978), it seems rather surprising that adaptation of insect herbivores to their host trees has not yet been examined from an explicitly spatial perspective. While general theory addresses these issues (e.g. Slatkin 1987, Gandon & Michalakis 2002, Morgan *et al.* 2005), generalizations about the type of systems and situations facilitating local adaptations have so far focused exclusively on traits of the insects and the plants (van Zandt & Mopper 1998, Mopper 2005). The next step will be to examine how gene flow among local insect populations will affect the strength of local adaptation (VII).

Third, the effects of the spatial population dynamics of herbivores on other species in the community merits further study. Since herbivores interact with species at the same trophic level, and at both lower and higher trophic levels, the effects of landscape structure may extend well beyond those on the herbivore itself. The spatial dynamics of herbivores has already been shown to influence species at higher trophic levels (van Nouhuys 2005). To my knowledge, little is known about how the spatial population dynamics of herbivores feed back to affect the quality,

evolution and dynamics of the host. Moreover, while assemblages of insect herbivores on trees offer fascinating models for studies of metacommunity dynamics (Leibold *et al.* 2004, Holyoak *et al.* 2005), there are few field-based studies so far. A rough analysis reveals pervasive effects of the spatial context of an oak tree on local species richness (Fig. 6) and opens up many interesting possibilities for future research. I am therefore pleased to see that this kind of work is already being conducted in the context of

food webs sustained by oaks (R. Kaartinen and A.Tack, in preparation). There are plenty of hypotheses to be tested (I), and I look forward to seeing the field of spatial ecology firmly integrated into the study of plant-insect interactions.

*Tomas Roslin, Bob O'Hara, Julia Koricheva and Pekka Niemelä provided helpful comments on the summary chapter.*



**Fig. 6.** The number of oak-specific leaf-mining and galling insect species on each of 167 small oak trees (surveyed in 2004) in relation to the structural connectivity of the tree. The connectivity measure used is described in chapter V. The curve is based on results from a generalized linear model (log link, Poisson distributed errors) of the number of species as a function of host connectivity ( $\chi^2_1=57.5$ ,  $P<0.0001$ ).



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## References

- Abrahamson, W.G., Hunter, M.D., Melika, G., & Price, P.W. (2003) Cynipid gall-wasp communities correlate with oak chemistry. *Journal of Chemical Ecology*, **29**, 208-223.
- Agrawal, A.A. (2004) Plant defense and density dependence in the population growth of herbivores. *American Naturalist*, **164**, 113-120.
- Andrewartha, H.G. & Birch, L.C. (1954) *The distribution and abundance of animals* The University of Chicago Press, Chicago.
- Askew, R.R. & Shaw, M.R. (1986). Parasitoid communities: their size, structure and development. In *Insect parasitoids* (eds J. Waage & D. Greathead), pp. 225-264. Academic Press, London.
- Atkinson, P.M., Foody, G.M., Gething, P.W., Mathur, A., & Kelly, C.K. (2007) Investigating spatial structure in specific tree species in ancient semi-natural woodland using remote sensing and marked point pattern analysis. *Ecography*, **30**, 88-104.
- Ayres, M.P., Clausen, T.P., MacLean, S.F., Redman, A.M., & Reichardt, P.B. (1997) Diversity of structure and antiherbivore activity in condensed tannins. *Ecology*, **78**, 1696-1712.
- Barbosa, P. & Schultz, J.C., eds. (1987) *Insect outbreaks*. Academic Press, San Diego.
- Bernays, E. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology*, **69**, 886-892.
- Bultman, T.L. & Faeth, S.H. (1986) Leaf size selection by leaf-mining insects on *Quercus emoryi* (Fagaceae). *Oikos*, **46**, 311-316.
- Bylund, H. & Tenow, O. (1994) Long-term dynamics of leaf miners, *Eriocrania* spp., on mountain birch: alternate year fluctuations and interaction with *Epirrita autumnata*. *Ecological Entomology*, **19**, 310-318.
- Claridge, M.F. & Wilson, M.R. (1981) Host plant associations, diversity and species-area relationships of mesophyll-feeding leafhoppers of trees and shrubs in Britain. *Ecological Entomology*, **6**, 217-238.
- Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209-233.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R., & Yamakura, T. (2000) Spatial patterns in the distribution of tropical tree species. *Science*, **288**, 1414-1418.
- Connor, E.F., Faeth, S.H., & Simberloff, D. (1983) Leafminers on oak - the role of immigration and *in situ* reproductive recruitment. *Ecology*, **64**, 191-204.
- Cornelissen, T. & Stiling, A. (2006) Does low nutritional quality act as a plant defence? An experimental test of the slow-growth, high-mortality hypothesis. *Ecological Entomology*, **31**, 32-40.
- Crawley, M.J. (1989) Insect herbivores and plant-population dynamics. *Annual Review of Entomology*, **34**, 531-564.
- Crawley, M.J. (1997). Plant-herbivore dynamics. In *Plant ecology* (ed M.J. Crawley), pp. 401-474. Blackwell Science, Oxford.
- Crawley, M.J. & Akhteruzzaman, M. (1988) Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology*, **2**, 409-415.
- De Bruyn, L., Scheirs, J., & Verhagen, R. (2002) Nutrient stress, host plant quality and herbivore performance of a leaf-mining fly on grass. *Oecologia*, **130**, 594-599.
- DeBach, P. (1958) The role of weather and entomophagous species in the natural control of insect populations. *Journal of Economic Entomology*, **51**, 474-484.
- Dempster, J.P. (1983) The natural control of populations of butterflies and moths. *Biological Reviews of the Cambridge Philosophical Society*, **58**, 461-481.
- den Boer, P.J. (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica*, **18**, 165-194.
- Denno, R.F. & McClure, M.S. (1983) *Variable plants in natural and managed systems* Academic Press, New York.
- Dent, D. (2000) *Insect pest management. 2nd edition* CABI Publishing, Wallingford.
- Doak, P. (2000) Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. *Ecology*, **81**, 1828-1841.
- Eber, S. (2004) Bottom-up density regulation in the holly leaf-miner *Phytomyza ilicis*. *Journal of Animal Ecology*, **73**, 948-958.
- Eber, S. & Brandl, R. (1996) Metapopulation dynamics of the tephritid fly *Urophora cardui*: An evaluation of incidence-function model assumptions with field data. *Journal of Animal Ecology*, **65**, 621-630.

- Edmunds, G.F. & Alstad, D.N. (1978) Coevolution in insect herbivores and conifers. *Science*, **199**, 941-945.
- Faeth, S.H. (1987). Community structure and folivorous insect outbreaks: the roles of vertical and horizontal interactions. In *Insect Outbreaks* (eds P. Barbosa & J.C. Schultz), pp. 135-171. Academic Press, San Diego.
- Faeth, S.H., Connor, E.F., & Simberloff, D. (1981) Early leaf abscission - a neglected source of mortality for folivores. *American Naturalist*, **117**, 409-415.
- Feeny, P.P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**, 565-581.
- Fisher, A.E.I., Hartley, S.E., & Young, M. (2000) Direct and indirect competitive effects of foliage feeding guilds on the performance of the birch leaf-miner *Eriocrania*. *Journal of Animal Ecology*, **69**, 165-176.
- Ford, E.D. (2000) *Scientific method for ecological research* Cambridge University Press, Cambridge.
- Forkner, R.E., Marquis, R.J., & Lill, J.T. (2004) Feeny revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of *Quercus*. *Ecological Entomology*, **29**, 174-187.
- Frost, I. & Rydin, H. (2000) Spatial pattern and size distribution of the animal-dispersed tree *Quercus robur* in two spruce-dominated forests. *Ecoscience*, **7**, 38-44.
- Gandon, S. & Michalakis, Y. (2002) Local adaptation, evolutionary potential and host-parasite coevolution: interactions between migration, mutation, population size and generation time. *Journal of Evolutionary Biology*, **15**, 451-462.
- Godfray, H.C.J. (1994) *Parasitoids. Behavioral and evolutionary ecology* Princeton University Press, Princeton, New Jersey.
- Gutierrez, D., Leon-Cortes, J.L., Menendez, R., Wilson, R.J., Cowley, M.J.R., & Thomas, C.D. (2001) Metapopulations of four lepidopteran herbivores on a single host plant, *Lotus corniculatus*. *Ecology*, **82**, 1371-1386.
- Hairston, N.G., Smith, F.E., & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421-425.
- Hanks, L.M. & Denno, R.F. (1994) Local adaptation in the armored scale insect *Pseudaulacaspis pentagona* (Homoptera, Diaspididae). *Ecology*, **75**, 2301-2310.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.
- Hanski, I. (1999) *Metapopulation ecology* Oxford University Press, Oxford.
- Hanski, I. & Gaggiotti, O., eds. (2004) *Ecology, genetics, and evolution of metapopulations*. Elsevier, Amsterdam.
- Hanski, I. & Gilpin, M.E., eds. (1997) *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego.
- Haraus, E. & Pimentel, D. (2002). North American forest losses due to insects and plant pathogens. In *Encyclopedia of pest management* (ed D. Pimentel), pp. 539-541. Taylor & Francis Books.
- Harborne, J.B. (1994). Phenolics. In *Natural products. Their chemistry and biological significance* (eds J. Mann, R.S. Davidson, J.B. Hobbs, D.V. Banthorpe & J.B. Harborne), pp. 362-388. Longman, Harlow.
- Harrison, S. & Hastings, A. (1996) Genetic and evolutionary consequences of metapopulation structure. *Trends in Ecology & Evolution*, **11**, 180-183.
- Harrison, S. & Taylor, A.D. (1997). Empirical evidence for metapopulations. In *Metapopulation biology: ecology, genetics and evolution* (eds I. Hanski & M.E. Gilpin), pp. 27-42. Academic Press, San Diego.
- Hastings, A. & Harrison, S. (1994) Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics*, **25**, 167-188.
- Haukioja, E. (2003) Putting the insect into the birch-insect interaction. *Oecologia*, **136**, 161-168.
- Hawkins, B.A. (2001) Top-down and bottom-up forces in the population and community ecology of insects. *Basic and Applied Ecology*, **2**, 293-294.
- Hawkins, B.A. & Lawton, J.H. (1987) Species richness for parasitoids of British phytophagous insects. *Nature*, **326**, 788-790.
- Hawkins, B.A., Cornell, H.V., & Hochberg, M.E. (1997) Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology*, **78**, 2145-2152.
- Holyoak, M., Leibold, M.A., & Holt, R.D., eds. (2005) *Metacommunities. Spatial dynamics and ecological communities*, pp 513. The University of Chicago Press, Chicago.
- Hopper, K.R. (1999) Risk-spreading and bet-hedging in insect population biology. *Annual Review of Entomology*, **44**, 535-560.

- Howlett, B.G., Clarke, A.R., & Madden, J.L. (2001) The influence of leaf age on the oviposition preference of *Chrysophtharta bimaculata* (Olivier) and the establishment of neonates. *Agricultural and Forest Entomology*, **3**, 121-127.
- Hunter, M.D. (1997). Incorporating variation in plant chemistry into a spatially explicit ecology of phytophagous insects. In *Forests and insects* (eds A.D. Watt, N.E. Stork & M.D. Hunter), pp. 81-96. Chapman & Hall, London.
- Hunter, M.D., Ohgushi, T., & Price, P., eds. (1992) *The effects of resource distribution on animal-plant interactions*. Academic Press, San Diego.
- Jordan, T. (1995) Life-history and parasitoid community of the oak-leaf-mining moth *Tischeria ekebladella* (Bjerkander, 1795) (Lep, Tischeriidae) in Northern Germany. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, **119**, 447-454.
- Karban, R. & Baldwin, I.T. (1997) *Induced responses to herbivory* University of Chicago Press, Chicago.
- Kause, A., Ossipov, V., Haukioja, E., Lempa, K., Hanhimäki, S., & Ossipova, S. (1999) Multiplicity of biochemical factors determining quality of growing birch leaves. *Oecologia*, **120**, 102-112.
- Kraus, T.E.C., Yu, Z., Preston, C.M., Dahlgren, R.A., & Zasoski, R.J. (2003) Linking chemical reactivity and protein precipitation to structural characteristics of foliar tannins. *Journal of Chemical Ecology*, **29**, 703-730.
- Lawton, J.H. & McNeill, S. (1979) Between the devil and the deep blue sea: on the problem of being an herbivore. *Symp. Br. Ecol. Soc.*, **20**, 223-244.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, **7**, 601-613.
- Lewis, O.T., Memmott, J., Lasalle, J., Lyal, C.H.C., Whitefoord, C., & Godfray, H.C.J. (2002) Structure of a diverse tropical forest insect-parasitoid community. *Journal of Animal Ecology*, **71**, 855-873.
- Louda, S.M. (1982) Distribution ecology - variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs*, **52**, 25-41.
- Maron, J.L. & Crone, E. (2006) Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2575-2584.
- Maron, J.L. & Gardner, S.N. (2000) Consumer pressure, seed versus safe-site limitation, and plant population dynamics. *Oecologia*, **124**, 260-269.
- Masters, G.J. & Brown, V.K. (1992) Plant-mediated interactions between 2 spatially separated insects. *Functional Ecology*, **6**, 175-179.
- Mattson, W.J. (1980) Herbivory in relation to plant nitrogen-content. *Annual Review of Ecology and Systematics*, **11**, 119-161.
- Memmott, J., Day, R.K., & Godfray, H.C.J. (1995) Intraspecific variation in host plant quality - the aphid *Cinara cupressi* on the Mexican cypress, *Cupressus lusitanica*. *Ecological Entomology*, **20**, 153-158.
- Menéndez, R. & Thomas, C.D. (2000) Metapopulation structure depends on spatial scale in the host-specific moth *Wheeleria spilodactylus* (Lepidoptera : Pterophoridae). *Journal of Animal Ecology*, **69**, 935-951.
- Milne, A. (1957) Theories of natural control of insect populations. *Cold Spring Harbor Symposium on Quantitative Biology* **22**, 253-271.
- Mopper, S. (2005) Phenology - how time creates spatial structure in endophagous insect populations. *Annales Zoologici Fennici*, **42**, 327-333.
- Mopper, S. & Simberloff, D. (1995) Differential herbivory in an oak population - the role of plant phenology and insect performance. *Ecology*, **76**, 1233-1241.
- Mopper, S., Beck, M., Simberloff, D., & Stiling, P. (1995) Local adaptation and agents of selection in a mobile insect. *Evolution*, **49**, 810-815.
- Mopper, S., Faeth, S.H., Boecklen, W.J., & Simberloff, D.S. (1984) Host-specific variation in leaf miner population dynamics - effects on density, natural enemies and behavior of *Stilbosis quadricustatella* (Lepidoptera, Cosmopterigidae). *Ecological Entomology*, **9**, 169-177.
- Mopper, S., Stiling, P., Landau, K., Simberloff, D., & Van Zandt, P. (2000) Spatiotemporal variation in leafminer population structure and adaptation to individual oak trees. *Ecology*, **81**, 1577-1587.
- Morgan, A.D., Gandon, S., & Buckling, A. (2005) The effect of migration on local adaptation in a coevolving host-parasite system. *Nature*, **437**, 253-256



- Morris, R.J., Lewis, O.T., & Godfray, H.C.J. (2004) Experimental evidence for apparent competition in a tropical forest food web. *Nature*, **428**, 310-313.
- Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L., & Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841-844.
- Ohgushi, T., Craig, T.P., & Price, P.W., eds. (2007) *Indirect interaction webs: Nontrophic linkages through induced plant traits*. Cambridge University Press, Cambridge.
- Owen, D.F. (1975) Efficiency of blue tits *Parus caeruleus* preying on larvae of *Phytomyza Ilicis*. *Ibis*, **117**, 515-516.
- Preszler, R.W. & Price, P.W. (1993) The influence of *Salix* leaf abscission on leaf-miner survival and life-history. *Ecological Entomology*, **18**, 150-154.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.
- Reavey, D. & Lawton, J.H. (1991). Larval contribution to fitness in leaf-eating insects. In *Reproductive behaviour of insects* (eds W.J. Bailey & J. Ridsdill-Smith), pp. 293-329. Chapman & Hall, London.
- Riihimäki, J., Kaitaniemi, P., & Ruohomäki, K. (2003) Spatial responses of two herbivore groups to a geometrid larva on mountain birch. *Oecologia*, **134**, 203-209.
- Riipi, M., Haukioja, E., Lempa, K., Ossipov, V., Ossipova, S., & Pihlaja, K. (2004) Ranking of individual mountain birch trees in terms of leaf chemistry: seasonal and annual variation. *Chemoecology*, **14**, 31-43.
- Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats - fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95-120.
- Roslin, T. & Koivunen, A. (2001) Distribution and abundance of dung beetles in fragmented landscapes. *Oecologia*, **127**, 69-77.
- Rossiter, M., Schultz, J.C., & Baldwin, I.T. (1988) Relationships among defoliation, red oak phenolics, and gypsy-moth growth and reproduction. *Ecology*, **69**, 267-277.
- Ruhnke, H., Schadler, M., Matthies, D., Klotz, S., & Brandl, R. (2006) Are sawflies adapted to individual host trees? A test of the adaptive deme formation hypothesis. *Evolutionary Ecology Research*, **8**, 1039-1048.
- Ruusila, V., Morin, J.-P., van Ooik, T., Saloniemi, I., Ossipov, V., & Haukioja, E. (2005) A short-lived herbivore on a long-lived host: tree resistance to herbivory depends on leaf age. *Oikos*, **108**, 99-104.
- Salminen, J.P., Roslin, T., Karonen, M., Sinkkonen, J., Pihlaja, K., & Pulkkinen, P. (2004) Seasonal variation in the content of hydrolyzable tannins, flavonoid glycosides, and proanthocyanidins in oak leaves. *Journal of Chemical Ecology*, **30**, 1693-1711.
- Sato, H. & Higashi, S. (1987) Bionomics of *Phyllonorycter* (Lepidoptera, Gracillariidae) on *Quercus*. II. Effects of ants. *Ecological Research*, **2**, 53-60.
- Schoonhoven, L.M., van Loon, J.J.A., & Dicke, M. (2005) *Insect-plant biology* Oxford University Press, Oxford.
- Scriber, J.M. (1984). Host plant suitability. In *Chemical ecology of insects* (eds W.J. Bell & R.T. Cardé), pp. 159-202. Chapman & Hall, London.
- Singer, M.C. & Wee, B. (2005) Spatial pattern in checkerspot butterfly-host plant association at local, metapopulation and regional scales. *Annales Zoologici Fennici*, **42**, 347-361.
- Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science*, **236**, 787-792.
- Speight, M.R. & Wainhouse, D. (1989) *Ecology and management of forest insects* Oxford University Press, Oxford.
- Strong, D.R., Lawton, J.H., & Southwood, R. (1984) *Insects on plants. Community patterns and mechanisms* Blackwell Scientific Publications, Oxford.
- Thomas, C.D., Singer, M.C., & Boughton, D.A. (1996) Catastrophic extinction of population sources in a butterfly metapopulation. *American Naturalist*, **148**, 957-975.
- Tikkanen, O.P. & Julkunen-Tiitto, R. (2003) Phenological variation as protection against defoliating insects: the case of *Quercus robur* and *Operophtera brumata*. *Oecologia*, **136**, 244-251.
- Tilman, D. & Kareiva, P. (1997) *Spatial ecology: the role of space in population dynamics and interspecific interactions* Princeton University Press, Princeton.
- Tscharntke, T. & Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, **49**, 405-430.
- van Nouhuys, S. (2005) Effects of habitat fragmentation at different trophic levels in insect

- communities. *Annales Zoologici Fennici*, **42**, 433-447.
- van Nouhuys, S. & Hanski, I. (2002) Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. *Journal of Animal Ecology*, **71**, 639-650.
- van Veen, F.J., Morris, R.J., & Godfray, H.C.J. (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, **51**, 187-208.
- Van Zandt, P.A. & Mopper, S. (1998) A meta-analysis of adaptive deme formation in phytophagous insect populations. *American Naturalist*, **152**, 595-604.
- Waterman, P.G. & Mole, S. (1994) *Analysis of phenolic plant metabolites* Blackwell, Oxford.
- Weis, A.E. & Campbell, D.R. (1992). Plant genotype: a variable factor in insect-plant interactions. In *Effects of resource distribution on animal-plant interactions* (eds M.D. Hunter, T. Ohgushi & P.W. Price), pp. 75-111. Academic Press, San Diego.
- White, T.C.R. (1993) *The inadequate environment. Nitrogen and the abundance of animals*. Springer, Berlin.
- Whitlock, M.C. (2004). Selection and drift in metapopulations. In *Ecology, genetics, and evolution of metapopulations* (eds I. Hanski & O. Gaggiotti), pp. 153-173. Elsevier Academic Press, Amsterdam.
- Wilson, E.O. (1992) *The diversity of life* Belknap Press, Harvard University Press.
- Yamasaki, M. & Kikuzawa, K. (2003) Temporal and spatial variations in leaf herbivory within a canopy of *Fagus crenata*. *Oecologia*, **137**, 226-232.
- Zucker, W.V. (1983) Tannins: Does structure determine function? An ecological perspective. *American Naturalist*, **121**, 335-365.
- Ødegaard, F. (2000) How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society*, **71**, 583-597.