



Competition as a structuring force in leaf miner communities

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The role of competition in structuring communities of herbivorous insects is still debated. Despite this, few studies have simultaneously investigated the strength of various forms of competition and their effect on community composition. In this study, we examine the extent to which different types of competition will affect the presence and abundance of individual leaf miner species in local communities on oak trees *Quercus robur*. We first use a laboratory experiment to quantify the strength of intra- and interspecific competition. We then conduct a large-scale field experiment to determine whether competition occurring in one year extends to the next. Finally, we use observational field data to examine the extent to which mechanisms of competition uncovered in the two experiments actually reflect into patterns of co-occurrence in nature. In our experiment, we found direct competition at the leaf-level to be stronger among conspecific than among heterospecific individuals. Indirect competition among conspecifics lowered the survival and weight of larvae of *T. ekebladella*, both at the branch and the tree-level. In contrast, indirect competition among heterospecifics was only detected in one out of three species pairs examined. In the field experiment, the presence of a given moth species in one year affected the relative abundance of leaf miner species in the next year. Nevertheless, patterns of competition observed in these experiments did not translate into repulsion among free-ranging leaf miners: conspecific larvae of four leaf-mining species were aggregated on the same trees, shoots and leaves. In contrast, heterospecific larvae were only aggregated at the tree-level. We propose that despite the fact that leaf miners do compete and that such effects extend through time, the incidence and strength of competition is relatively small at realistic densities. Hence, competition will likely be of minor importance in shaping the distribution of leaf miners in a natural setting.

Whether competition is an important structuring force in communities of folivorous insects has been the subject of hot debate (Hairston et al. 1960, Murdoch 1966, Janzen 1973, Lawton and Strong 1981, Kaplan and Denno 2007). For decades, competition was assumed to be unimportant – largely because insect densities in the field are typically much lower than those needed to consume the complete host plant (Hairston et al. 1960, Lawton and Strong 1981, Strong et al. 1984). Such a pattern would seem unexpected in a world governed by fierce competition, in which we would expect herbivores to compete for consuming the very last host plant. Hence, direct interference competition will seem rare (but see Roslin and Roland 2005). Nevertheless, the role of intra- and interspecific competition has recently been resurrected as a factor to take account of (Denno et al. 1995, Ohgushi 2005, Kaplan and Denno 2007). This revival has partly been due to an increased focus on a less obvious form of competition. Even in a predominantly green world, indirect competition may be mediated by the host plant (Ohgushi 2005, Kaplan and Denno 2007), or by shared natural enemies (Holt 1977, Morris et al. 2005).

Leaf miners form interesting targets for studies of competition. Due to the sedentary feeding mode of their larval stage, spatial patterns in the behavior of ovipositing females will largely determine the potential for different

forms of competition. The larvae themselves will not be able to alleviate competition by dispersing. As a likely consequence, several studies have addressed patterns of distribution in leaf miners (Bultman and Faeth 1985, Sato 1991, Cornelissen and Stiling 2008), or the strength and prevalence of individual forms of competition among this type of insects (Faeth 1992, Fisher et al. 2000). Nevertheless, few studies have attempted to relate the inferred strength of competition to patterns of co-occurrence realized in nature (but see Bultman and Faeth 1986). Even less is known about the temporal scales on which competition acts: whether the effects only extend for a few days or whether they also act on individuals in the next growing season (cf. Karban and Baldwin 1997).

In this paper, we use leaf miners of the pedunculate oak *Quercus robur* as a model system to compare the role of different modes of competition in structuring herbivorous communities. We define direct competition as the performance of a focal individual being lowered by other individuals present on the same leaf, and indirect competition as performance being lowered by individuals present on other parts of the plant. In this context, we explicitly focus on indirect competition as mediated by the host plant, and exclude apparent competition through shared natural enemies (sensu Holt 1977) by excluding all parasitoids from

our experimental treatments. We then use a three-step approach to quantify the importance of such interactions at different temporal scales: we first use a laboratory experiment to quantify the strength of intra- and interspecific competition. We then conduct a large-scale field experiment to determine whether competition occurring in one year actually extends to the next. Finally, we use observational field data on the distribution of four species to examine the extent to which mechanisms of competition uncovered in the two experiments actually reflect into patterns of co-occurrence in nature. More specifically, we ask 1) at what hierarchical levels (trees, branches and/or leaves) we can detect competition; 2) how the strength of different modes of competition compare to each other; 3) whether competitive effects extend across years, as mediated by the host plant and 4) to what extent individual modes of competition are reflected in patterns of co-occurrence among leaf miners in nature.

Material and methods

Study system

In Finland, *Quercus robur* is the only representative of a large genus of trees. This species forms the host of a diverse insect community. Across Europe, more than 200 species of Lepidoptera alone feed on oak leaves – a figure higher than for any other European tree species (Southwood 1961). The number of leaf miners is particularly high, most of which are host specific (Hering 1957). Hence, from the

perspective of these species, the oak forms a taxonomically well defined host. In the landscape of Finland, *Q. robur* is a relatively rare tree species, hence offering a patchy resource with a distinct spatial structure. In addition, the trees themselves are structured into several hierarchical units: branches, shoots (i.e. twigs grown from a single bud in the current year) and leaves (see Fig. 1 in Roslin et al. 2006).

Among the more than twenty leaf miner species occurring in southern Finland on *Q. robur*, three families are quantitatively dominant in terms of individual abundances. In the family Tischeriidae, two species (*Tischeria ekebladella* and *T. dodonaea*) form shallow blotch mines on the upper surface of the leaves. In the family Gracillariidae, species *Phyllonorycter harrisella* and *P. quercifoliella* form tent-like mines on the lower surface of the leaf. These two congeneric species cannot be reliably distinguished on the basis of external leaf-mine morphology, and will therefore be treated as a compound group in the observational parts of our data. In the family Nepticulidae, species *Ectoedemia albifasciella*, *Stigmella ruficapitella*, *S. roborella*, *S. samiatella* and *S. svenssoni* form mines of varying morphology on the upper surface of the leaf. Of these, congeneric species of *Stigmella* cannot be reliably identified, and their larvae are hence treated as a group in observational data.

While mining slightly different parts of the leaf blade, all the above groups co-occur on leaves during major parts of the summer, and might therefore compete with each other. The univoltine tischeriids occur on mature leaves in the late summer, the bivoltine gracillarids occur both on fresh leaves in early summer and mature leaves in autumn. Of the nepticulids the species *E. albifasciella* and *S. svenssoni* are

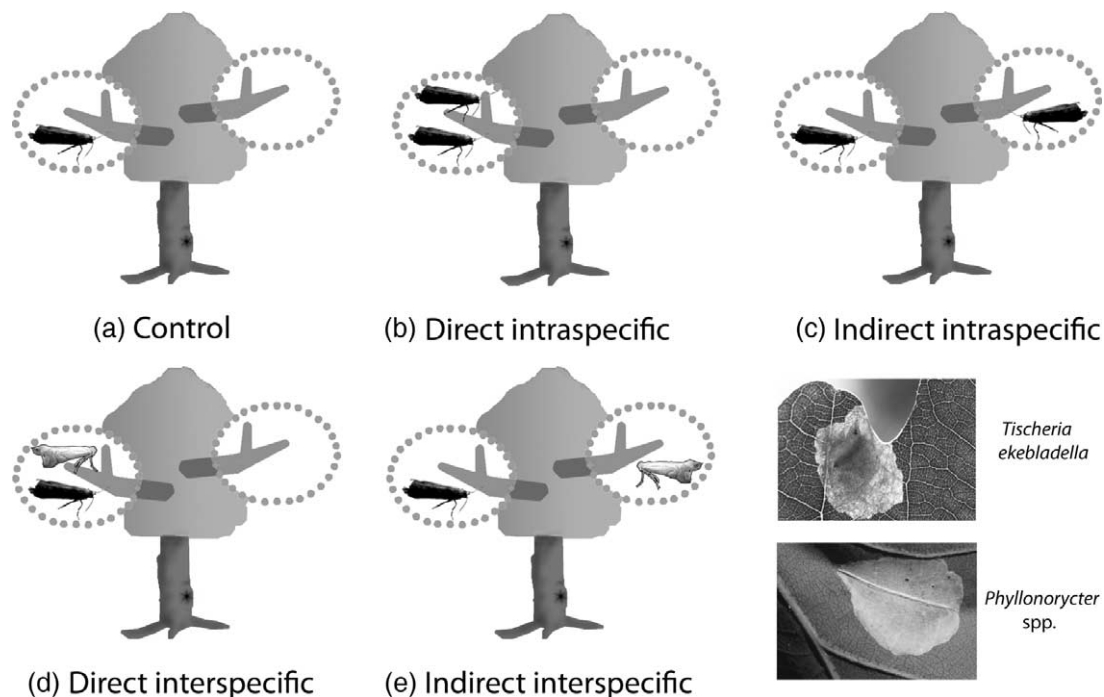


Figure 1. Treatment types applied in the laboratory experiment: (a) control treatment, in which one moth-pair was introduced on a single branch on the tree; (b) direct intraspecific, in which two pairs of the same moth species were introduced on the same branch, resulting in a higher density of leaf mines; (c) indirect intraspecific, in which two pairs of the same moth species were introduced on different branches on the same tree; (d) direct interspecific, in which two moth pairs of different species were introduced on the same branch; (e) indirect interspecific, in which two moth pairs of different species were introduced on different branches on the same tree. Shown in the bottom-right are the leaf mines of *Tischeria ekebladella* and of *Phyllonorycter* spp.

univoltine, whereas *S. ruficapitella*, *S. roborella* and *S. samiatella* are bivoltine. Tischeriids hibernate as larvae, while gracillarids and nepticulids pupate in autumn.

Direct versus indirect competition

To examine the strength of intra- and interspecific competition, we conducted an experiment at the Haapasensyrjä tree breeding station in Läyliäinen (60°37'N, 24°26'E), Finland. To exclude parasitoids and other folivores, 55 small oak trees were placed in a large (12.5 × 10 × 3 m) cage covered by muslin net. On these trees, three species of leaf-miners (*T. ekebladella*, *P. harrisella* and *P. quercifoliella*) were introduced in different combinations (Fig. 1). Five treatments were included, representing different modes of competition between both conspecific and heterospecific individuals: direct competition between individuals present on the same leaf, and indirect competition as mediated by the host plant among individuals present on different parts of the host plant. We focused on three species and obtained nine combinations of the following treatments (missing combinations dictated by lack of adequate material): 1–3) control treatments, in which one moth pair was introduced on a single branch (Fig. 1a), 4) direct intraspecific, in which two conspecific moth pairs were introduced on the same branch (Fig. 1b; for *T. ekebladella* only), 5) indirect intraspecific, in which two conspecific moth pairs were introduced on different branches within the same tree (Fig. 1c; for *T. ekebladella* only), 6–7) direct interspecific, in which two heterospecific moth pairs were introduced on the same branch (Fig. 1d; the combination *P. harrisella* and *P. quercifoliella* was not included, as the mines of these species cannot be distinguished) and 8–9) indirect interspecific, in which two heterospecific moth pairs were introduced on different branches on the same tree (Fig. 1e). Treatments differed in the number of replicates – again due to a lack of adult moths (see Fig. 2 for exact numbers of replicates per treatment).

Introductions were conducted by inserting pairs of adult moths (1 ♂ and 1 ♀) in muslin bags (50 × 60 cm), which were placed around individual branch tips during introduction. Adults of *Tischeria ekebladella* were removed when they had laid more than 20 eggs. When introductions failed (i.e. when the female died before ovipositing or failed to initiate ovipositing within five days from introduction), another pair was introduced into the bag. For introductions of *Phyllonorycter*, we used the second generation of this bivoltine species. *Phyllonorycter harrisella* and *P. quercifoliella* were left in the bag until the adults had died.

As our primary response variable, we used larval survival. For *T. ekebladella*, which hibernates as a full-grown larva in the leaf, we measured the dry weight of final instar larvae as an additional response variable. To establish survival rates, we first recorded the leaf-specific abundance of small mines. In the late autumn, before leaf-fall, the trees were revisited and the larvae of each species scored as being either alive or dead. At the same time, larvae of *T. ekebladella* were collected in eppendorf tubes and immediately frozen. To obtain dry weights, larvae were thawed and dried for 24 h at 80°C before weighing to the nearest microgram.

Competition over different time periods

To examine the extent to which effects of competition may extend over time, we conducted a field experiment. Here, we transplanted moths of *T. ekebladella* onto 50 oak trees on the island of Wattkast, southwestern Finland (for a map, see Gripenberg and Roslin 2005). We selected naturally growing oak trees varying in height between 1 and 3 m, so that every single leaf could be examined. On the 50 trees branch tips were bagged in early spring 2004 (close to budbreak) to prevent oviposition by wild females. One pair (♂♀) of *T. ekebladella* was later introduced in each muslin bag (50 × 60 cm), which was left on the trees until late autumn to prevent parasitism. The bags were filled in random order. To control for an effect of bagging per se, we added an additional, empty bag on a subset of 21 of the 50 trees.

To examine competition across years, we revisited the experimental trees in 2005 and scored species-specific abundances of the four most abundant leaf-mining species on the branches on which *T. ekebladella* had been introduced in the previous year. As a reference group for each tree, we used species-specific abundances on 20 control shoots within the same tree.

Natural patterns of co-occurrence

To analyze the patterns of co-occurrence of leaf miners at different hierarchical levels (tree, shoot and leaf) we used data collected in 2004 on 113 oak trees of similar size as the trees used in the previous experiment. From each tree, 20 randomly selected shoots were searched through and the abundance of four focal taxa (*E. albifasciella*, *Phyllonorycter* spp., *Stigmella* spp. and *T. ekebladella*) was recorded at the leaf-level.

Statistical models

We used generalized linear mixed models to quantify individual modes of competition. For data on the survival and presence/absence of species (both binary responses), we assumed a logit link function and binomially distributed errors. To adjust for an unbalanced design, we used Satterthwaite's approximation to derive relevant degrees of freedom. For weight data, we assumed an identity link and normally distributed errors. These models were fitted using Proc Glimmix in SAS 9.1 (Littell et al. 2006, SAS Institute 2001). For the abundance data, we assumed a multivariate Poisson model with a log link, which was fitted using a Bayesian MCMC approach.

Direct versus indirect competition

In order to assess whether larval survival in the laboratory experiment was affected by the number of conspecifics and heterospecifics on the same leaf, and whether there were any indirect effects as mediated by the host tree, we modeled survival as a function of the fixed variables species, treatment (control, direct, indirect; Fig. 1), the interaction species × treatment (representing the species-specific responses to the treatments), and the density at the leaf-level

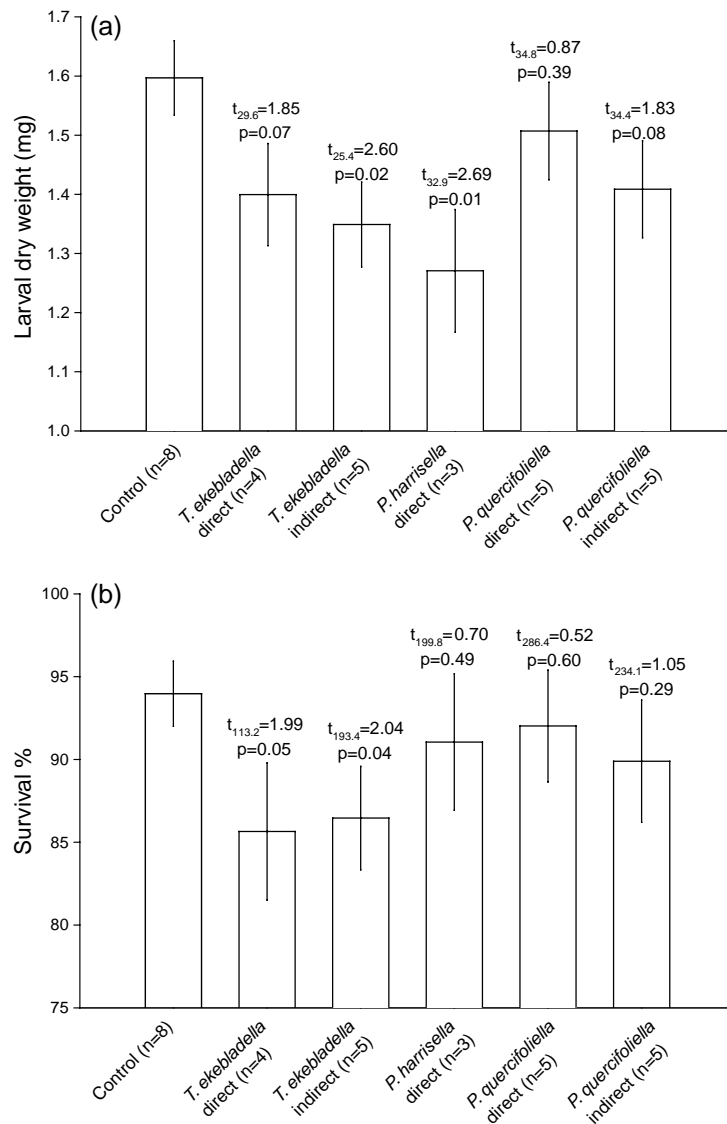


Figure 2. Estimated (a) larval survival and (b) larval weight of *T. ekebladella* offspring in different treatments, where “control treatment” refers to one pair of *T. ekebladella* introduced onto a single branch; “*T. ekebladella*, direct” to two pairs of this species introduced onto the same branch; “*T. ekebladella*, indirect” to two pairs introduced onto different branches on the same tree; “*P. harrisella*, direct” to one pair of *T. ekebladella* and one of *P. harrisella* introduced onto the same branch; “*P. quercifoliella*, direct” to one pair of *T. ekebladella* and one of *P. quercifoliella* introduced onto the same branch; “*P. quercifoliella*, indirect” to one pair of *T. ekebladella* and one of *P. quercifoliella* introduced onto different branches on the same tree. Shown are least-square means (with SE) for individuals alone on a leaf. t- and p-values refer to comparisons of survival in each treatment with the survival in the control treatment. Number of replicates per treatment is shown within brackets under the vertical bars.

of conspecifics and heterospecifics. Furthermore, to model species-specific differences in the strength of competition, we included an interaction between species identity and the density of conspecific individuals on the leaf (representing intraspecific competition), and an interaction between species identity and the density of heterospecific individuals on the leaf (representing interspecific competition). In order to capture variation in the strength of intra- and interspecific density in the different treatments, we included third-order interactions between treatment, species and densities at the leaf-level. To allow for variation in quality between trees and between branches (as nested within tree \times treatment), these variables were included as random factors. As including densities of conspecifics and hetero-

specifics at the shoot-level did not significantly improve the model ($F_{1,2119} = 0.003$, $p = 0.96$ and $F_{1,2506} = 0.53$, $p = 0.47$, respectively), these factors were excluded from subsequent models.

To test whether the weight of *T. ekebladella* was affected by the presence of conspecific and heterospecific larvae, we modeled this response as a function of the fixed variable treatment (control, direct or indirect; Fig. 1) and conspecific and heterospecific densities at the leaf-level (representing the strength of intra- and interspecific competition at the leaf-level). In order to account for differences in intra- and interspecific competition among the treatments, we included an interaction between treatment and densities at the leaf-level. Finally, to allow for

variation in quality between trees and between branches, we added the random factors tree and branch (nested under tree \times treatment).

Competition over different time periods

To assess whether responses induced by herbivores in one year affect the distribution of herbivores in the next, we compared the density of the different species in 2005 between branches where *T. ekebladella* was introduced in the previous year with control branches on the same tree. First, we compared shoot-specific densities of four species in 2005 between 20 randomly selected free shoots and shoots within control branches which had been bagged but empty in 2004. As this test revealed a significant effect of bagging per se in all four species ($F_{1,55.5} = 4.87$, $p = 0.03$), we focused the final analyses on the subset of trees that contained a control bag ($n = 21$). Here, we modeled presence at the leaf-level as a function of species (fixed effect) and treatment (fixed effect: whether *T. ekebladella* was introduced on the branch in the previous year or not). Furthermore, to quantify different responses in different species, we included the interaction species \times introduction. Tree identity and the interaction tree \times treatment were included as random effects to account for variation in tree quality and variation in treatment effects among trees of different quality, respectively.

Natural patterns of co-occurrence

For analyzing patterns in the natural distribution of leaf miner individuals, we quantified variation in the abundance of conspecific individuals, and correlations in the abundance of heterospecifics, for each of three hierarchical scales (tree, shoot and leaf). For this we modelled the abundance data with a multivariate hierarchical Poisson model with over- or underdispersed error structure. To do so, we extended the multivariate logistic regression model with an underlying normal structure (O'Brien and Dunson 2004, Holmes and Leonhard 2006) to the Poisson distributed case as described in Appendix 1. Model parameters were estimated using a Bayesian approach (Appendix 1). The key advantage of this method is that it allows us to estimate aggregation at each specific hierarchical level, while simultaneously adjusting for aggregation at higher hierarchical levels.

Results

Competition at different hierarchical levels

The competition experiment revealed that individuals of all three species compete strongly with conspecifics present on the same leaf, and that the presence of conspecifics and heterospecifics on the same tree may also affect the survival and weight of *T. ekebladella* (Fig. 2, 3).

Overall, survival rates differed among species ($F_{2,83.1} = 10.74$, $p < 0.001$; Fig. 3). In the two *Phyllonorycter* species, survival rates were not affected by the density of heterospecifics on the tree (all pair-wise comparisons among treatments $p > 0.10$). For *T. ekebladella*, survival was highest in the treatment where a single female was transplanted to a tree, and significantly lower in treatments

where the offspring of a conspecific female was present on the same branch, or on another branch within the same tree (Fig. 2a). A similar pattern emerged for larval weight: when offspring of another female of *T. ekebladella* was present on the same tree, larval weight was lower (Fig. 2b). In terms of interspecific competition, the weight of *T. ekebladella* larvae was significantly reduced by the presence of *P. harrisella* leaf-mines on the same branch (Fig. 2b), whereas the presence of *P. quercifoliella* had no effect on the larval weight of *T. ekebladella*. Hence, *T. ekebladella* was affected by both direct and indirect interactions with conspecifics and heterospecifics, whereas both *Phyllonorycter* species were unaffected by indirect interactions with either congeneric or heterogeneric individuals on the same tree.

At the leaf level, survival was significantly lower for each species when conspecifics were present on the same leaf ($F_{1,4284} = 84.90$, $p = 0.002$; Fig. 3a). The strength of intraspecific competition did not detectably differ between species ($F_{2,4284} = 2.21$, $p = 0.11$). As the strength of intraspecific competition was different in different treatments (interaction species \times treatment \times density at the leaf-level; $F_{10,4284} = 2.79$, $p < 0.002$), we assessed the effect of conspecific density on larval survival for the control treatment only (i.e. the treatment where a single moth pair was introduced on the tree). Heterospecific individuals at the same leaf did not detectably compete, though there was a trend for *T. ekebladella* lowering the survival of *P. harrisella* ($t_{4284} = 1.74$, $p = 0.08$; Fig. 3b). However, in contrast to the effect observed at the branch level (above), larvae of *T. ekebladella* grew significantly larger on leaves where *P. harrisella* was also present ($t_{1408} = 3.61$, $p < 0.001$). In contrast, the presence of *P. quercifoliella* had no effect on the weight of *T. ekebladella* ($t_{1403} = 0.30$, $p = 0.76$).

Competition over different time periods

The field experiment revealed signs of host-mediated indirect effects between years (Fig. 4): introductions of *T. ekebladella* in one year significantly affected the community composition in the next. Here, each species showed a different response to the introduction of *T. ekebladella* in the previous year (interaction species \times introduction: $F_{3,160} = 4.27$, $p = 0.006$), with some species actually being favored by the addition of *T. ekebladella*, whereas *T. ekebladella* itself was disfavored by the treatment (Fig. 4).

Natural patterns of co-occurrence

In the wild, conspecific leaf miners were more strongly aggregated at the tree level than at the shoot level. Furthermore, individuals of all species were aggregated at the leaf level, leading to overdispersion in the Poisson model (Fig. 5a). Heterospecific leafminers were highly aggregated on the tree level, while they were mainly randomly distributed within trees (Fig. 5b). The only deviations from a random distribution within trees were detected at the shoot level, where *E. albifasciella* and *Phyllonorycter* showed a tendency to avoid each other and *Stigmella* and *T. ekebladella* showed aggregation. However, these deviations at the shoot level were more variable in sign

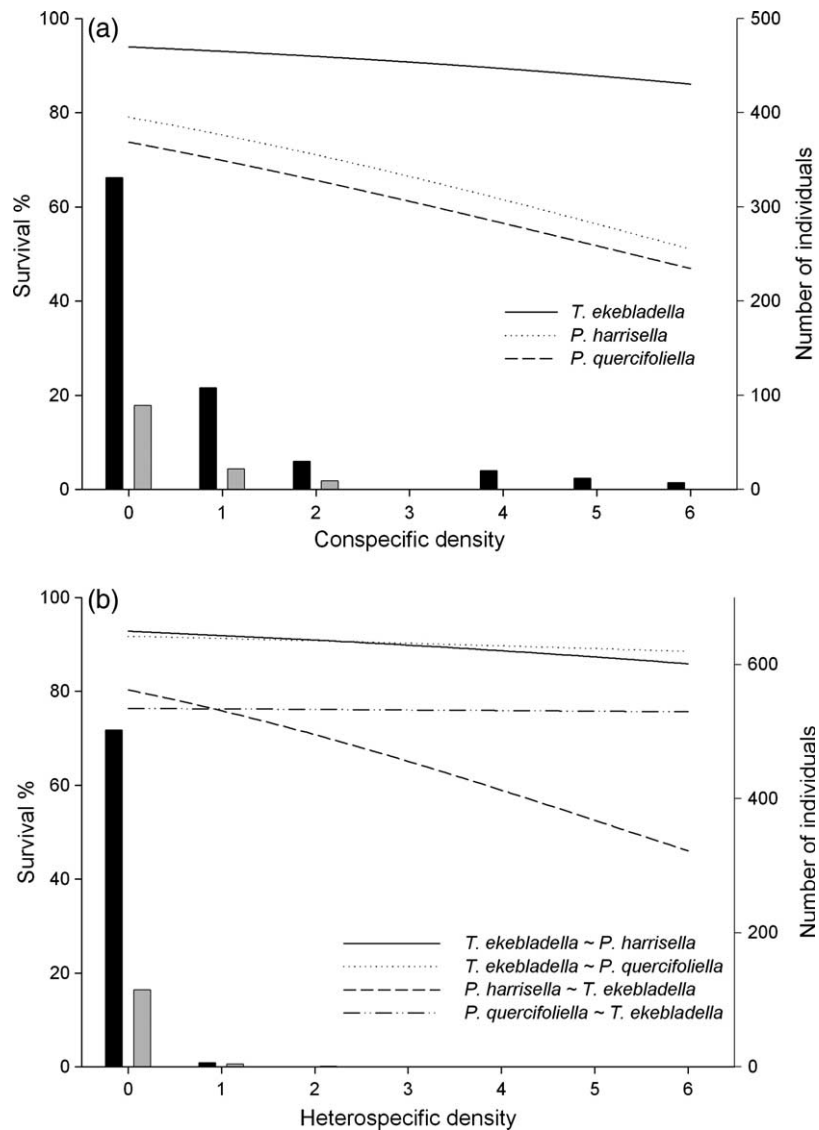


Figure 3. Density-dependence of competitive effects at the leaf-level as observed in the laboratory experiment (lines), and frequency of co-occurrence in nature (histograms). Shown are the estimated effects of (a) conspecific larval density at the leaf-level on survival for three species of leaf miners; (b) heterospecific larval density at the leaf-level on survival of the focal leaf miner species for four species-pairs. Survival of the focal species is depicted as a function (\sim) of the density of the second species on the same leaf. The histogram shows the number of individuals in the field that encounter (a) conspecifics and (b) heterospecifics on the very same leaf. Black bars show number of individuals of *T. ekebladella* and grey bars numbers of individuals of *Phyllonorycter* in each category.

and generally weaker than the consistent positive aggregation observed at the tree level (Fig. 5b).

Despite the strong aggregation of conspecifics and heterospecifics on the same trees, absolute densities of all species were still low. This implies that in nature only a small fraction of individuals will encounter conspecific or heterospecific individuals on the very same leaf (as shown for both *T. ekebladella* and *Phyllonorycter* species in Fig. 3a and 3b, respectively).

Discussion

Few previous studies have tried to disentangle the strength of competition at different hierarchical levels and through time, or to assess how these forms of competition are

reflected in the structure of natural communities of herbivorous insects. Our study reveals that competition occurs both directly at the leaf-level and indirectly, as mediated by the host plant, and that such effects extend both within and between years. Nevertheless, the effects uncovered are not reflected in patterns of co-occurrence among leaf-mining taxa in nature.

Mechanisms and strength of competition in space and in time

In our laboratory experiment, the imprint of competition was distinct but complex. Intraspecific competition at the leaf-level caused significant mortality in all three leaf-mining species, whereas interspecific competition at the leaf-level was only detected as a trend for one out of four

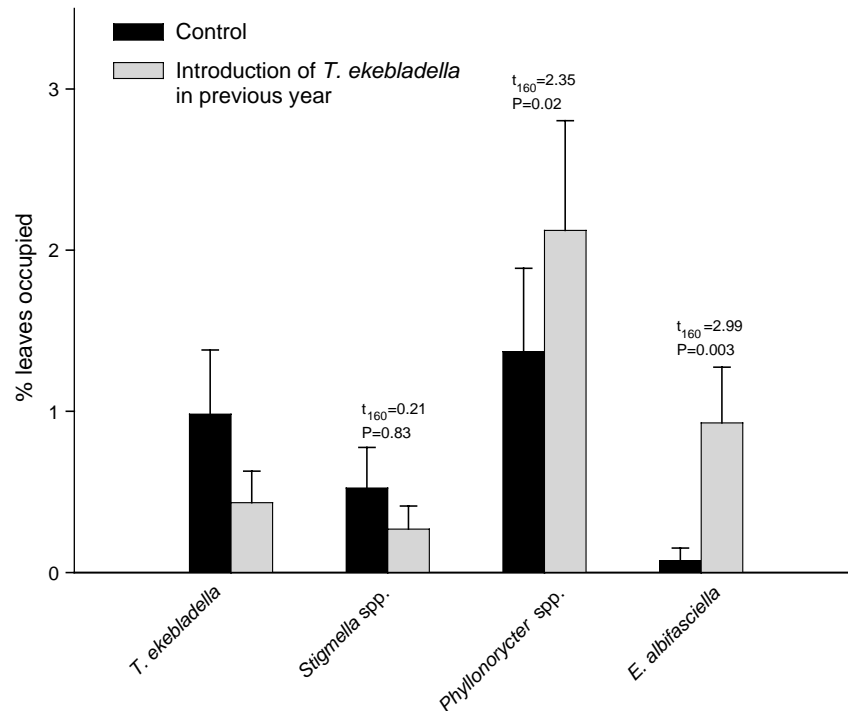


Figure 4. Density of the four most abundant species in 2005 on control branches and experimental branches (onto which *T. ekebladella* was introduced in 2004; n = 21). t- and p-values refer to pair-wise comparisons between the response of the species in question to the treatment compared to the response of *T. ekebladella*.

species combinations – *T. ekebladella* affecting the survival of *P. harrisella*. In this single case, the strength of the effect was comparable to that of intraspecific competition within either species (Fig. 3). Competition among conspecifics sharing the same leaf has been detected for various other leaf miners (Condrashoff 1964, Murai 1974, Tuomi et al. 1981, Quiring and McNeil 1984, Stiling et al. 1984, Bultman and Faeth 1986, Auerbach and Simberloff 1989), whereas direct competition among heterospecific leaf miners has not – to our knowledge – been investigated before. Taken together, the patterns observed in our study suggest that intraspecific competition at the leaf-level is stronger than interspecific competition, and that species affect each other asymmetrically.

At a higher hierarchical level, the tree, *T. ekebladella* was affected by indirect interactions between conspecifics and heterospecifics, whereas *Phyllonorycter* species appeared insensitive to competition by either congeneric or heterocongeneric individuals. For *T. ekebladella*, both survival and weight were negatively affected by conspecifics on the same tree. These effects seem more internally consistent than those observed in the only previous study examining indirect interactions among conspecific leaf miners. Working on *Eriocrania* leaf miners, Fisher et al. (2000) reported that survival decreased whereas the biomass of surviving individuals increased when a conspecific was present on an adjacent leaf. Regarding indirect interactions with heterospecifics, the only effect that we were able to detect was a decrease in the larval weight of *T. ekebladella* in interaction with *P. harrisella*. Decreased weight as induced by intra- and interspecific competition does come with a likely fitness cost, since female size is linked to fecundity in a wide range

of moths and insects (Haukioja and Neuvonen 1985, Honěk 1993, Tammaru et al. 1996).

Common to the effects of both direct and indirect competition was a general pattern of asymmetry: one species usually affected another more than vice versa. Just why species affect each other asymmetrically may be due to both interspecific differences in triggering host response, and in species-specific reactions to such induced effects (Stout et al. 1998). *Tischeria ekebladella* and the *Phyllonorycter* species feed on different tissues within the leaf (Hering 1951), and may thereby cause damage to leaf parts of very different functionality. Different layers of the leaf might also be differentially affected by the induced response. Indirect interactions may then be expected to occur most frequently among conspecific individuals, since they share the very same resource (Hutchinson 1959, Price 1984, Sato 1991). This is the exact pattern observed in the laboratory experiment – and also through time: when *T. ekebladella* was introduced to a branch in one year, this lowered the abundance of conspecifics in the next year, while two out of three other leaf miner species actually increased their relative abundance.

The finer, phytochemical mechanism behind the responses observed here are still to be resolved. While induced responses have previously been demonstrated in some sections of the oak genus (Faeth 1986, Rossiter et al. 1988, Wold and Marquis 1997), these studies do not identify the exact chemical mechanisms behind the observed pattern. Indeed, pinning down the processes involved is complicated by both the diversity of tannin compounds (Salminen et al. 2004) and species-specificity in the response to individual tannin compounds (Roslin and Salminen 2008). Hence, at this stage, we are faced with

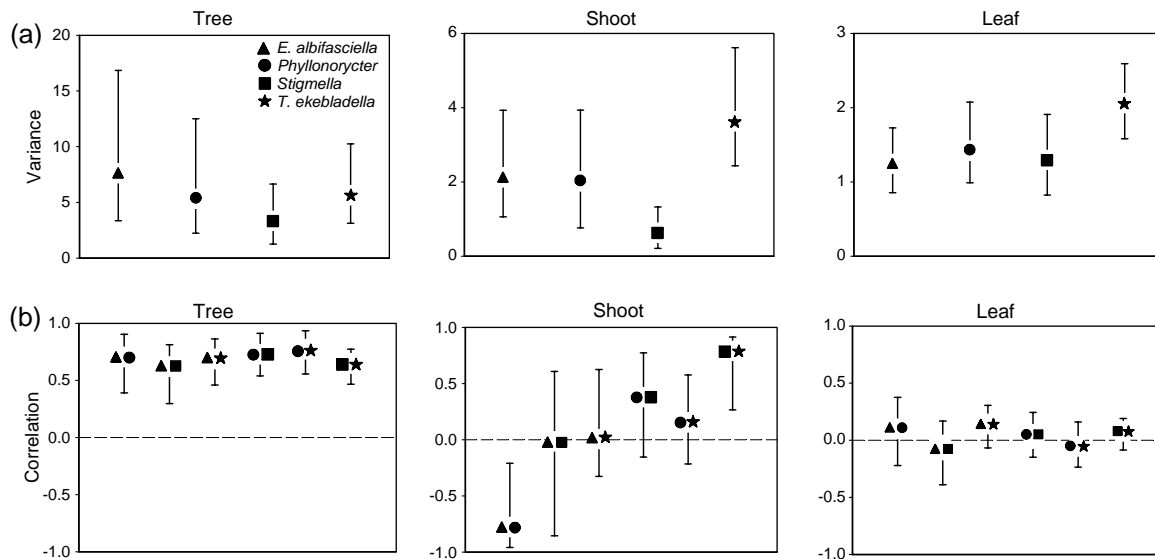


Figure 5. Patterns of co-occurrence of wild leaf miners at three hierarchical levels – trees, shoots and leaves: (a) variance in counts of conspecific individuals and (b) correlations in counts among heterospecific individuals attributed to respective level. In panel (a), a value > 1 at the leaf-level indicates overdispersion and a value < 1 indicates underdispersion (cf. Appendix 1). In panel (b), the identity of each species pair is identified by two symbols at the median value. In both panels, vertical bars show 95% CI.

a pattern but lacking an exact mechanistic explanation for it.

At a more general level, species-specific responses by host plants to damage induced by different insect species have been amply demonstrated – mostly with respect to free-feeding taxa (Stout et al. 1998, Traw and Dawson 2002, Van Zandt and Agrawal 2004, Viswanathan et al. 2005). While some studies have suggested that damage early in a season may differentially affect the performance and abundance of species later in the same year (Faeth 1986, Kaplan and Denno 2007), the current study indicates that such effects may also extend between years. This opens up intriguing avenues for future research.

But how frequent is competition?

Importantly, regardless of the competition observed in the experiments, competition was not reflected in the distribution of wild leaf miners. Instead, both conspecific and heterospecific individuals aggregated at the same trees in the landscape (Fig. 5). Moreover, conspecific individuals aggregated within these trees at the same shoots and leaves (Fig. 5a). Similar patterns of intraspecific and interspecific aggregation at various scales have been observed in leaf miner communities (Bultman and Faeth 1985, Sato 1991, Cornelissen and Stiling 2008, but see Heads and Lawton 1983). This is quite opposite to the pattern expected if leaf miner communities were strongly structured by competition. Hence, the pattern observed can be used to formulate two opposing hypotheses: either competition is extremely weak and has little effect on the distribution of leaf miners, or, alternatively, an aggregated distribution is caused by a tradeoff between competition and other factors (such as high variation in leaf quality; cf. Gripenberg and Roslin 2005, Roslin et al. 2006, Gripenberg et al. 2007), causing individuals to rather bear the cost of competition than renouncing the leaves already occupied by others.

To distinguish between these two theories, we may compare the distributional patterns as found in the field with the strength of various forms of competition as uncovered in the laboratory experiments. In nature, roughly every third leaf miner individual shares a leaf with at least a single conspecific or congeneric individual (Fig. 3a). Sharing a leaf with a heterospecific individual is even rarer: for example, only 4.2% of *Phyllonorycter* individuals will ever encounter a larva of *T. ekebladella* on the same leaf (Fig. 3b). While the few realized cases of co-occurrence will certainly cause some reduction in survival, the effects are likely to be small. Given the limited range of densities encountered in nature, realized reductions in survival attributable to intraspecific competition will only correspond to a change in survival from 94% to 86% between minimum and maximum densities for *T. ekebladella* and from 76% to 68% for *Phyllonorycter* species (Fig. 3a). Likewise, Stiling et al. (1984) report only a small decrease in survival due to intraspecific competition at natural field densities (80.2% and 68.8% on single and multiple mined leaves, respectively). Regarding interspecific competition, the impact of interactions between heterospecific individuals at the leaf-level are even more doubtful, since such effects were only detected as a trend for one out of four species pairs (reduction of survival of *P. harrisella* by *T. ekebladella*). Hence at natural densities, the total proportion of individuals dying due to competition with conspecifics at the leaf-level will only reach 0.8% for *T. ekebladella* and 1.7% for *Phyllonorycter*, whereas an estimated 0.2% of *Phyllonorycter* larvae will die because of competition with heterospecifics. In conclusion, at natural densities there is a relatively weak role for both intraspecific and interspecific competition at the leaf-level in affecting the mortality rate of leaf miners, despite their aggregated distributions.

As most leaf miners do occur singly on leaves, there is still substantial scope for indirect interactions as mediated by the host-tree. Yet, the laboratory experiment suggested

only small effect sizes, with the survival of *T. ekebladella* varying relatively little among treatments (ranging from 94% to 86%). Similar patterns emerged for interspecific competition: in the one instance where indirect interactions among heterospecifics was detected in the laboratory experiment, larval weight of *T. ekebladella* decreased from 1.60 to 1.27 mg – a change of only 21%. Hence, as densities used in the experiments were relatively high compared to densities in the field, indirect competition will cause only a minor reduction in survival and fecundity at natural densities.

In conclusion, competition does occur, but is very unlikely to structure insect communities at densities occurring in the field. Hence, other factors will have to be investigated to explain the mortality and distribution of leaf miners in the landscape. One promising future research direction is the study of dispersal of the different leaf miner species in the landscape (cf. Gripenberg et al. 2008). If species are not affected by trophic interactions but are limited by their dispersal, we would expect different species to aggregate in areas with a high density of the host plant. This could then account for intra- and interspecific aggregation observed on certain trees in the landscape.

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Appendix 1.

We quantified variation in the abundance of leaf-miner taxa at three hierarchical levels (tree, shoot and leaf), and correlations among species-specific abundances, by fitting a multivariate hierarchical Poisson model with the possibility of over- or underdispersion at the leaf-level. To this end, we extend the multivariate logistic regression model with an underlying normal structure (O'Brien and Dunson 2004, Holmes and Leonhard 2006) to the Poisson distributed case.

We start by constructing the univariate Poisson model from an underlying normal model. Let e be a random variable following the univariate normal distribution $N(0,1)$. Then the random variable y defined by

$$y = \min(n \in \mathbb{N} | F_{\mu}(n) \leq F(e))$$

follows a Poisson distribution with mean μ . Here \mathbb{N} denotes the set of non-negative integers, F_{μ} is the cumulative density of the Poisson distribution with mean μ , and F is the cumulative density function of the $N(0,1)$ distribution.

We then extend the model to a multivariate model of m species, and incorporated the hierarchical structure of trees, shoots and leaves. We let the m -dimensional vector y_{ijk} denote the abundances of the m species on leaf k on shoot j of tree i . We consider the model

$$\begin{aligned} y_{ijk} &= f(\mu_{ij}, e_{ijk}), \\ e_{ijk} &\sim N(0, V_{\text{leaf}}) \\ \log \mu_{ij} &= c + a_i + b_{j(i)}, \\ a_i &\sim N(0, V_{\text{tree}}), \\ b_{j(i)} &\sim N(0, V_{\text{shoot}}) \end{aligned}$$

Here V_{tree} , V_{shoot} and V_{leaf} represent the variance-covariance matrices at the tree, shoot and leaf levels. If the matrix V_{leaf} would be a correlation matrix (with diagonal elements equal to one), the marginal distributions would be Poisson distributed. Thus a greater than unity diagonal element in V_{leaf} corresponds to overdispersion (aggregation of conspecifics on given leaves), and a smaller than unity diagonal element corresponds to underdispersion (segregation of conspecifics among leaves).

We used inverse Wishart priors $W^{-1}(m+2, I)$ for the variance matrices, and the normal distribution $N(0,3)$ for the parameter c . We numerically integrated out the leaf-level random effects from the model. The remaining parameters were updated using the Metropolis-Hastings (MH) algorithm as follows.

For the random effects a_i and $b_{j(i)}$, we used multinormal proposals with variance covariance matrices $k_i \times V_{\text{tree}}$ and $k_{j(i)} \times V_{\text{shoot}}$, respectively. Here the constants k_i and $k_{j(i)}$ were adjusted to give an acceptance ratio of 0.44.

The matrices V_{tree} , V_{shoot} and V_{leaf} were transformed to a vector of standard deviations and unique correlation elements (Barnard et al. 2000). We log-transformed the variances and logit-transformed the correlations so that all variables ranged from minus infinity to infinity. We then used the componentwise adaptive algorithm (Haario et al. 2005) to update the transformed parameters.

Due to computational limitations associated with performing high-dimensional integrals, we estimated the interspecific correlations separately for each species-pair. The reported variance estimates are based on univariate analyses.