Competitive effects of the forest tent caterpillar on the gallers and leaf-miners of trembling aspen

Tomas ROSLIN2, Metapopulation Research Group, Department of Biological and Environmental Sciences, P.O. Box 65 (Viikinkaari 1), FI-00014 University of Helsinki, Finland, and Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada, e-mail: tomas.roslin@helsinki.fi
Jens ROLAND, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

Abstract: Interspecific competition has been identified as a major structuring force in phytophagous arthropod communities. We would expect to find particularly strong competitive effects in communities with outbreaking components, where the joint food resource is depleted by a single super-abundant species. To assess how arthropod assemblages of the trembling aspen (Populus tremuloides, Salicaceae) respond to outbreaks by the forest tent caterpillar (Malacosoma disstria, Lepidoptera: Lasiocampidae), we sampled galls and leaf-mines in central Alberta, western Canada. Both the incidence and rank order of sympatric taxa varied with the abundance of M. disstria. While most species were “susceptible” to defoliation by M. disstria, declining in abundance with increasing densities of forest tent caterpillars, two species showed no response and one “resistant” species even increased. These patterns at the landscape scale appear to reflect competitive mechanisms acting at a local scale. In a laboratory choice experiment, M. disstria larvae were found to damage a higher proportion of “susceptible” galls than “resistant” galls. Patterns at the landscape scale were also indicative of large-scale movement of gallers and leaf-miners. Following a year of severe defoliation, population densities within an outbreak area declined with increasing distance from the outbreak edge. This finding identifies regional processes as important in the population dynamics of the target taxa. Our study suggests a major structuring role for M. disstria in local arthropod communities. As outbreaks regularly affect a large proportion of temperate forests, they create ample opportunity for competitive interactions among phytophagous arthropods.

Keywords: community structure, defoliation, gall, insect outbreaks, leaf-miner, regional dynamics.

Résumé : La compétition interspécifique a été identifiée comme une force structurante majeure des communautés d’arthropodes phytophages. On devrait donc s’attendre à trouver des effets compétitifs particulièrement importants chez les communautés sujettes aux épidémies, dans lesquelles les ressources alimentaires communes sont épuisées par une seule espèce extrêmement abondante. Afin de vérifier comment les assemblages d’arthropodes du peuplier faux-tremble (Populus tremuloides, Salicaceae) réagissent face aux épidémies de livrée des forêts (Malacosoma disstria, Lepidoptera : Lasiocampidae), nous avons échantillonné les arthropodes des cécidies et des trous creusés dans les feuilles des peupliers du centre de l’Alberta, dans l’ouest du Canada. La fréquence de même que l’ordre des taxons sympatriques varient en fonction de l’abondance de M. disstria. Alors que la plupart des espèces sont susceptibles d’être affectées par la présence de M. disstria, puisque leur abondance diminue lorsque les densités de livrées des forêts augmentent, deux espèces ne sont pour leur part pas affectées; au contraire l’abondance d’une de ces espèces s’accroît. À l’échelle du paysage, ces patrons semblent refléter les mécanismes compétitifs qui agissent à une échelle locale. En laboratoire, les larves de M. disstria endommagent une plus grande proportion de cécidies avec arthropodes peu résistants aux larves que de cécidies des espèces qui résistent mieux. À l’échelle du paysage, les patrons indiquent également un mouvement de grande échelle chez les insectes foreurs et ceux qui produisent des cécidies. Après une année de défoliation sévère, les densités de populations d’arthropodes diminuent à l’intérieur d’une région ravagée par les épidémies, à mesure qu’on s’éloigne des marges de la zone touchée. En somme, les processus régionaux ont une influence certaine sur la dynamique des populations des arthropodes touchés par une épidémie. La livrée des forêts joue un rôle structurant non négligeable chez les communautés locales d’arthropodes. Puisque les épidémies affectent de façon régulière une grande partie des forêts tempérées, elles contribuent à créer des interactions compétitives chez les arthropodes phytophages.

Mots-clés : cécidies, défoliation, dynamique régionale, épidémies d’insectes, insecte foreur, structure de la communauté.

Nomenclature: Moss & Packer, 1983; Poole, 1996.

Introduction

Whether or not interspecific interaction plays a key part in regulating phytophagous arthropod populations has been the subject of a heated debate. While many authors (notably Hairston, Smith & Slobodkin, 1960; Lawton & Strong, 1981; Strong, 1983; Price, 1983; Strong, Lawton & Southwood, 1984) earlier regarded competition as a negligible factor, the last few decades have seen the resurrection of competition as a force to contend with (Faeth, 1986; 1987; Auerbach, Connor & Mopper, 1995). In an influential review, Denno, McClure, and Ott (1995) found evidence of competitive interaction in 76% of the 193 species pairs examined and concluded that there is far more justification for retaining competition as a potentially important factor than for dismissing it.

Competition among arthropod herbivores may take several different forms and be broadly defined as either...
exploitation or interference competition (Denno, McClure & Ott, 1995). Interference competition occurs when one organism physically excludes the other from a portion of habitat and its resources, whereas in exploitation competition the adverse effects are caused by a reduction in resource level (Begon, Harper & Townsend, 1996). In its simplest form, interference competition is the result of individuals directly killing each other, whereas exploitation competition is often mediated by the host plant (Denno, McClure & Ott, 1995). The feeding damage caused by one species of herbivore may, for instance, cause short- or long-term changes in host plant quality (Karban & Baldwin, 1997), thereby changing the resource levels available to subsequent herbivores. As the response of both plants and herbivores is often species-specific, such induced responses may cause differences in the structure of arthropod communities on damaged and undamaged plants (Van Zandt & Agrawal, 2004). Leaf damage caused by a given species of herbivore can also cause premature leaf abscission, thereby increasing the mortality of sessile species inhabiting affected leaves (Askew & Shaw, 1978; Faeth, Connor & Simberloff, 1981).

If different forms of interspecific competition are indeed moulding the structure of arthropod communities on plants, we would expect the imprint of such competition to be particularly distinct on communities with outbreaking components. In such systems, single species become sufficiently abundant to defoliate the host plant, thereby depleting the resource base of the full community or modifying its chemical contents (Barbosa & Schultz, 1987).

In this study, we assess how communities of gallers and leaf-miners on the trembling aspen (Populus tremuloides) are affected by competition with the outbreaking forest tent caterpillar (Malacosoma disstria, Lepidoptera: Lasiocampidae; henceforth FTC). More specifically, we first examine to what extent the local density of FTC is reflected in the abundance and distribution of sympatric arthropods. Second, we attempt to identify some of the mechanisms through which the FTC affects other arthropods. Finally, we try to establish the roles of local and regional processes (i.e., local population growth versus immigration from other sites) in the recovery of local arthropod communities following an outbreak.

Methods

Study System

In the aspen-dominated forests of North America, insect outbreaks are a common phenomenon. Like several other defoliating insects native to the region, the FTC displays cyclic outbreak dynamics (Ives & Wong, 1988). During outbreak years, the FTC may cause more or less complete defoliation of its primary host tree species, the trembling aspen (Populus tremuloides). The outbreaks may extend over areas greater than 500 x 300 km (Emond & Cerezke, 1989; see also Figure 1) and occur with a periodicity of 6 to 16 y (Hildahl & Reeks, 1960).

The FTC shares its primary host plant with a large range of species. As no single sampling method will sample the full community, we explicitly focused on the gall-inducing and leaf-mining guilds. We chose these target groups for four reasons: 1) They are highly host-specific (Hering, 1951; Meyer, 1987; Gagné, 1989) and hence form a well-defined community confined to the host plant. 2) Being both highly abundant and species rich, they form an integral part of the total arthropod assemblage of aspen. Gall midges in the family Cecidomyiidae are particularly speciose: in areas with a well-described fauna, it is not unusual to find tens of sympatric species (Coulianos & Holmásen, 1991). 3) As the larvae develop on highly visible structures attached to the leaves proper, they are easy to sample under any weather conditions. 4) Since the larvae are sessile, they cannot escape feeding FTC larvae. Hence, we can expect them a priori to be vulnerable to FTC outbreaks.

Data Collection

Our study builds on both observational and experimental data. First, we inferred competition by the FTC from patterns observed across two types of sampling units: forest patches sampled simultaneously across a landscape with variable FTC densities (Spatial data) and single trees sampled repeatedly over time during progressing defoliation by the FTC (Temporal data). Second, we conducted a laboratory choice experiment, to assess whether the patterns observed in time and space could be causally linked to interference competition among FTC larvae, gallers, and leaf-miners (Experimental data).

Spatial Data

To assess the relationship between recent FTC outbreaks and the abundance and distribution of sympatric leaf-miners and gallers in space, we sampled 27 sites within the aspen forests between Calmar, Drayton Valley, and Rocky Mountain House in central Alberta, Canada, in 2002 (Figure 1). To eliminate systematic biases emanating from forest fragmentation, we defined forest struc-

Figure 1. Map of the study area. The inset shows the location of the area within Canada, while the main map shows the specific location of 27 sites sampled in 2002 (black circles). At two of the sites (marked with white dots) we monitored ten trees throughout the summer of 2002. On both maps, irregular-shaped patches correspond to areas defoliated by insects in the previous year (2001; aerial survey data provided by and reproduced with the permission of Alberta Sustainable Resource Development, Government of Alberta, all rights reserved). Areas outside the stippled regions are partly forests, partly pastures and fields.
ture according to Roland and Taylor (1997) and sampled our sites from the full range of fragmentation scenarios. We also sampled the range of FTC densities occurring in the previous year and the range of distances from the edge of a large defoliated area that occurred in that year, as determined by aerial surveys (Alberta Sustainable Resource Development, 2003, and Daniel Lux, pers. comm.). Maps sketched during repeated flights over defoliated areas are admittedly of low resolution (for data standards, see Alberta Sustainable Resource Development, 2002), but our field survey of FTC densities in 2001 confirmed the location of defoliated patch boundaries (cf. Figure 1) and identified the FTC as the principal defoliating agent (not other sympatric defoliators; cf. Alberta Sustainable Resource Development, 2003).

For each sampled site, the previous-year density of FTC had been quantified following methods described by Roland and Taylor (1997). In brief, the density estimates were based on fixed-time counts of FTC cocoons in the understory, as conducted in 2001. This method was selected as it provides a sensitive measure of the disturbance most relevant to gallers and leaf-miners, i.e., defoliation: the FTC will move down “en masse” after consuming all the foliage of higher forest strata (cf. Batzer et al., 1995; Jens Roland, unpubl. data). Of all life stages, cocoon counts are also associated with the smallest sampling errors (Batzer et al., 1995).

All sites were visited within a timeframe as short as possible (between June 25 and 27, 2002), when the morphology of most galls and leaf-mines was fully developed but defoliation by the FTC was still in its early stage. Hence, our sampling design was specifically aimed at providing a phenologically controlled snapshot of which species occurred where and in what abundance following defoliation by the FTC in the previous year and migration of adult gallers and leaf-miners in the spring and early summer.

At each sampled site, we selected five trees within approximately 10 m of each other. To minimize potential edge effects, trees within 10 m of the exposed forest margin were always avoided. We also deliberately focused on trees in the understory (2.5-11 m in height, < 6 cm in diameter). As defoliation in the understory takes place after the canopy layer has been fully defoliated (Batzer et al., 1995), any competitive effects observed in the understory are likely accentuated in the tree crowns: defoliation in the canopy stratum is always more severe than in the lower forest strata.

On each tree, we sampled 10 random branch tips 50 cm in length and counted the number of galls and mines present on the leaves of each tip. Galls induced by the mite Phyllocopetes didelphis were too abundant to be counted individually; instead, we scored the number of branch tips (out of the 10 examined) occupied and unoccupied by the species.

All galls and leaf-mines were collected in polyethylene bags, labelled with a site-, tree-, and branch-specific code and placed in a cooler with ice. Upon return to the laboratory, they were sorted according to morphology and identified as precisely as possible. Identifications were based on the following written sources: Coulianos and Holmåsen (1991; gallers in general); Davis and Deschka (2001; Lepidoptera: Gracillariidae); Gagné (1989; Diptera: Cecidomyiidae); Hering (1957; leaf miner families); Hiratsuka, Langor, and Crane (1995; all taxa); Ives and Wong (1988; all taxa); Jeppson, Keifer, and Baker (1975; Acari: Eriophyoidae); Keifer et al. (1982; Acari: Eriophyoidae); Lindquist, Sabelis, and Bruins (1996; Acari: Eriophyoidae); Wong, Melvin, and Harper (1977; gallers in general).

For the abundant galls in the family Cecidomyiidae (gall midges), the North American fauna on Populus is poorly known (cf. Gagné, 1989). Here, laboratory rearings of all species were established following the guidelines given by Gagné (1989). Voucher specimens of the larvae were stored in 70% ethanol and identified to genera by Dr. Ray Gagné at the USDA Systematic Entomology Laboratory in Beltsville, Maryland. Within genera, the analysis was conducted at the morphospecies level, based on clear-cut differences in gall morphology. A complete and illustrated key to all species and morphospecies encountered can be found in Roslin (2003).

During the main sampling event in late June, we found a total of 679 galls and leaf-mines caused by 20 different taxa (Table I). In addition, galls induced by the mite Phyllocopetes didelphis were found in high numbers (hundreds to thousands) on 922 of 1,350 sampled twigs and on 117 of the 135 sampled trees. Most of the galls and leaf-mines could unambiguously be assigned to a named species or morphospecies (Table I). For four taxa, we had no way of telling whether we were dealing with one or several species, and they were therefore excluded from our analyses of local species numbers (cf. Table I). Galls of Ectoedemia sp. (Lepidoptera: Nepticulidae) were also omitted, as the timing of the sampling did not match the phenology of the species (T. Roslin, unpubl. data). Analyses of species numbers were hence based on a source material of 643 galls and leaf-mines of 15 different species, plus a vast number of galls of the mite Phyllocopetes didelphis. From the analyses of the local abundance and regional distribution of species, we excluded five additional species that did not meet the quantitative criteria defined below (cf. Statistical models). These analyses were based on a source material of 624 galls and leaf-mines of 10 different species, while data on Phyllocopetes didelphis were analyzed separately.

**Temporal Data**

To assess the relationship between progressing feeding damage by the FTC and the abundance of sympatric arthropods in time, we followed 10 trees (five trees at each of two high-density sites; Figure 1) over the course of the summer. We made our first observations in mid-June, when the majority of galls and leaf-mines were already visible but FTC damage was still light. During this first visit, we individually marked 10 branch tips (ca 50 cm) per tree and counted the number of galls present per branch (there were no leaf-miners on these trees). Galls induced by the mite Phyllocopetes didelphis were scored as above (cf. Spatial data). The same branch tips were re-inspected in late June and July, and the galls recounted. During the last visit, we also estimated the proportion of the total leaf area consumed by FTC on each tree, the
extent of new leaf production, and the extent to which fresh foliage was invaded by galls or leaf-mines.

**Experimental data**

To confirm the causal relationship between patterns observed in time and space and feeding damage by the FTC, we conducted a small-scale laboratory experiment with final-instar FTC larvae, the stage which, by virtue of its size, causes most of the defoliation. Groups of 10 FTC larvae were each confined to 22-L plastic containers with a screen cover and offered fresh aspen foliage including galls of three different taxa: gall midges in the genus Harmandia, gall mites of the species Phyllocnistis populiella, and gall mites of the species Vasates dispar. Due to limited availability and similarity in both structure and limited availability, we would expect the highest damage to be inflicted by fresh foliage was invaded by galls or leaf-mines.

**Statistical models**

We used generalized linear mixed-effects models (glimm; Breslow & Clayton, 1993; Littell et al., 1996) to analyze the data. Using the full set of 27 sites sampled across the landscape (cf. Spatial data), we focused on three different responses to assess the impact of FTC densities on the abundance and distribution of sympatric arthropod species: 1) the total number of species present on individual trees; 2) the abundance (count of a given species on individual trees, and 3) the presence or absence of a species on individual trees.

Response (1) is a single count of species numbers per tree. Hence, it was modelled as a function of FTC density in the previous year, 2001 (henceforth “FTC2001”), assuming Poisson-distributed errors and a log link function (cf. McCullagh & Nelder, 1989; Littell et al., 1996). Individual trees were treated as repeated samples within sites, and the identity of the SITE hence modelled as a random effect. By explicitly modelling variation at the site level, we also accounted for local variation in resource quality as caused, for instance, by the distribution of individual aspen clones (Lindroth & Hwang, 1996; Hwang & Lindroth, 1997).

For response (2), the basic unit of observation is the count of a species on a given tree. Hence, this response was modelled as a function of SPECIES (adjusting for differences in the average abundance of different species), FTC2001, and the interaction between the two (SPECIES × FTC2001, allowing for different responses to FTC density by different species). Here, we had several observations per tree (several species counted on the same tree) and modelled both SITE and TREE within...
SITE as random effects. Positive and zero counts were equally included in the analysis.

For response (3), the response variable is a proportion (i.e., the number of trees occupied out of number of trees examined). Therefore, we assumed a logit link function and binomially distributed errors (cf. McCullagh & Nelder, 1989; Littell et al., 1996). Again, the response was modelled as a function of SPECIES (now adjusting for differences in the average incidence of different species), FTC2001, and the interaction between the two (SPECIES × FTC2001). As several species were observed in the same sites, SITE was modelled as a random effect.

For species that occurred on only a small number of trees or sites, there was an obvious lack of power in the analyses of responses (2) and (3). Hence, we restricted these analyses to the set of species that occurred on at least five sites.

Data on Phyllocoptes didelphis were modelled separately. Here, we used the number of branch tips occupied by the species (out of 10 branch tips sampled) on each tree as a measure of local abundance (cf. Spatial data, above). With one observation per tree, we modelled abundance as a function of FTC2001, including SITE as a random effect. Since the response is a proportion, we assumed a logit link function and a binomial error structure (cf. McCullagh & Nelder, 1989; Littell et al., 1996).

To disentangle the role of local and regional processes (that is, site-specific birth and death rates versus immigration to and emigration from the site; cf. Thomas & Kunin, 1999) in the recovery of local arthropod communities in the aftermath of an FTC outbreak, we focused on the seven sites that had been fully defoliated in 2001. We started with a model including the three terms assessed above (SPECIES, FTC2001, and SPECIES × FTC2001), and then tested the explanatory power of two more: the distance from the undefoliated edge of the outbreak zone into the defoliated area (DISTANCE), and the interaction between SPECIES and DISTANCE. Here, an increase in DISTANCE was assumed to reflect a decreasing probability of immigration and recolonization from populations outside the defoliated area, whereas SPECIES × DISTANCE would show differential responses to distance by different species. To increase the power of the tests, we retained only the species present on at least two of the seven sites in these analyses (for a list of species, see Table I). We used the same response variables as defined above, making identical assumptions regarding error structures and link functions. Again, data on Phyllocoptes didelphis were modelled separately from the rest. We used each tree as a unit of observation and the number of branch tips occupied by the species (out of 10 tips examined) as our response. The impact of immigration from other sources was evaluated based on the effect of DISTANCE in a model also including FTC2001 (to control for uneven FTC densities within the outbreak area).

To assess whether progressing defoliation by the FTC caused similar changes in the local abundance of different taxa, we used data from the 10 trees monitored throughout the summer (the Temporal data). Here, we applied simple $\chi^2$ statistics to test whether the ratio between galls still present on the trees versus galls disappeared from the trees.
showed a positive response to increasing FTC densities (Lepidoptera: Gracillariidae) and \( \text{P} = 0.0001 \) among individual trees (range 30-98\% among individual trees).

Our \textit{a priori} prediction, that the probability of damage would be lower in the resistant species \textit{Vasates dispar} than in the susceptible \textit{Harmandia} spp. and \textit{Phyllocopites didelphis} (cf. above under Experimental data), was evaluated based on regular \( t \)-tests of the appropriate contrasts (Littell \textit{et al.}, 1996).

All glmm models were fitted using the GLIMMIX macro implemented in SAS System for Windows 8.02, PROC MIXED (Littell \textit{et al.}, 1996; SAS Institute, 2001). The significance of independent variables was assessed based on standard type 3 \( F \)-statistics (Littell \textit{et al.}, 1996).

Results

\textbf{Spatial data}

The local diversity of gall-making and leaf-mining arthropod taxa decreased with an increasing density of FTC in the previous year (Table IIa; Figure 2a). This was due to a general decrease in the incidence of six out of 10 species with an increasing abundance of FTC (Figure 2b).

The same pattern of predominantly negative effects of increasing FTC densities but highly variable responses across individual species also extended to the local abundance of species (Table IIc; Figure 2c). Again, \textit{Vasates dispar} showed a positive response to increasing FTC densities, whereas two other species, the leaf-mining moth \textit{Phyllocnistis populiella} (Lepidoptera: Gracillariidae) and the cecidomyiid \textit{Harmandia} sp 2, were basically unaffected by FTC density. The mite \textit{Phyllocopites didelphis}, which was modelled separately from the rest, also showed a negative response to FTC, with local incidence at the branch tip level decreasing with increasing FTC densities (Figure 2b).

Within the defoliated area, the negative effects of FTC varied with the distance from the undefoliated edge of the outbreak zone. Among the seven sites fully defoliated in 2001, population densities of gallers and miners in 2002 generally decreased with an increasing distance into the defoliated forest tract (Table IIIc), even though we had compensated for spatial variation in the exact FTC density. However, the impact of distance varied among species (Table IIIc; the interaction \textit{SPECIES} \( \times \) \textit{DISTANCE}). The same pattern was also evident in the distribution of the species: the incidence of most species declined with increasing distance from the edge, but in this case the effect was only marginally significant (Table IIIib) and the difference among species was non-significant (Table IIIib; the interaction \textit{SPECIES} \( \times \) \textit{DISTANCE}).

Finally, in \textit{Phyllocopites didelphis}, we did not detect any significant association between the distance from the edge and local abundance (Table IIIId).

\textbf{Temporal data}

The 10 trees followed over the summer grew within two sites characterized by particularly high densities of FTC in 2002 and were almost completely defoliated by the FTC: on average, the caterpillars consumed 80\% of the total leaf volume (SD = 24\%, range 30-98\% among individual trees). During the same time period, the mite \textit{Phyllocopites didelphis} went from highly abundant to very rare. In mid-June, the species was present on a total of nine out of 10 sampled trees and 54 out of 100 sampled branch tips. By mid summer, the numbers were down to three trees and 14 branch tips. Finally, in late July, the species was only recorded on two branch tips on a single tree.

Similar changes were observed in other taxa. Of 80 other galls initially present on the leaves, only 36 survived defoliation by FTC. Thirty-five of the surviving galls were induced by the mite \textit{Vasates dispar}, whereas all but one midge gall were destroyed by feeding FTC caterpillars. Hence, the proportion of galls disappearing from the twigs was much higher for midge than for mite galls (\( \chi^2 = 6.47, \text{P} = 0.04 \)).

At the tree level, there was a clear-cut relation between defoliation by the FTC and later refoliation. On
TABLE III. Generalized linear mixed-effects models of arthropod assemblage structure as a function of distance into a defoliated forest area. The following response variables were modeled: a) the total number of species present on individual trees, b) the presence or absence of a species on individual trees, c) the abundance (count) of a given species on individual trees, and d) the presence or absence of the mite Phyllocopetes didelphis at the level of individual branch tips. For fixed effects, we provide Type 3 F-statistics with associated degrees of freedom and P-values. For random effects, we show variance estimates and associated standard errors.

<table>
<thead>
<tr>
<th>Source</th>
<th>Variance</th>
<th>F-ratio</th>
<th>df, df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) FTC2001</td>
<td>9.47</td>
<td>3.62</td>
<td>1, 28</td>
<td>0.005</td>
</tr>
<tr>
<td>SITE</td>
<td>0.00 ± 0.00</td>
<td>0.74 ± 0.18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td>0.00</td>
<td>1.33</td>
<td>1, 20</td>
<td>0.98</td>
</tr>
<tr>
<td>SPECIES</td>
<td>1.33</td>
<td>3.20</td>
<td>5, 20</td>
<td>0.29</td>
</tr>
<tr>
<td>FTC2001 × SPECIES</td>
<td>1.33</td>
<td>3.20</td>
<td>1, 20</td>
<td>0.09</td>
</tr>
<tr>
<td>SITE</td>
<td>0.00 ± 0.00</td>
<td>1.00 ± 0.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c)</td>
<td>0.89</td>
<td>3.05</td>
<td>1, 159</td>
<td>0.35</td>
</tr>
<tr>
<td>SPECIES</td>
<td>3.05</td>
<td>15.42</td>
<td>5, 159</td>
<td>0.0001</td>
</tr>
<tr>
<td>FTC2001 × SPECIES</td>
<td>3.78</td>
<td>6.12</td>
<td>5, 159</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>SITE</td>
<td>0.85 ± 0.85</td>
<td>5.41 ± 0.51</td>
<td>1.03 ± 0.11</td>
<td></td>
</tr>
<tr>
<td>TREE(SITE)</td>
<td>0.54 ± 0.28</td>
<td>1.03 ± 0.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>1.03 ± 0.11</td>
<td>1.73 ± 0.47</td>
<td></td>
<td></td>
</tr>
<tr>
<td>d)</td>
<td>0.99</td>
<td>0.25</td>
<td>1, 28</td>
<td>0.33</td>
</tr>
<tr>
<td>DISTANCE</td>
<td>5.29 ± 4.36</td>
<td>1.25 ± 0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SITE</td>
<td>5.29 ± 4.36</td>
<td>1.25 ± 0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>1.73 ± 0.47</td>
<td>1.73 ± 0.47</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

July 29, the three trees that had lost the smallest proportion of leaves (30-60%) showed no or little refoliation, whereas all of the truly defoliated trees (with ≥ 80% leaf damage) showed substantial refoliation (Figure 3). In a sample of n trees of which k show refoliation, the probability of these k trees being the most severely defoliated by chance alone is \( P = \binom{n}{k}/n^{!} \), in this case \( P = 0.008 \). Hence, either the trees respond actively to defoliation by the FTC or the FTC prefer trees that are later particularly likely to refoliate.

Despite the production of new leaves, the trees retained the majority of old and damaged foliage. Even in the trees that showed the strongest flush of refoliation, damaged leaves were still in ample supply by late July. No new galls were observed on the fresh leaves.

**Experimental data**

The laboratory choice experiment suggested a causal link between interference competition by the FTC at a local scale and patterns in the abundance and distribution of aspen galler in both space and time. Overall, the probability of feeding damage differed significantly among galler species (Table IV; Figure 4). While galls of Vasates dispar were offered in the highest numbers and

**Discussion**

Our results suggest a strong relationship between outbreaks by the FTC and the structure of phytophagous arthropod communities on trembling aspen. Across the landscape we examined, the previous-year abundance of FTC was strongly related not only with the local rank order of different community members, but also with the presence and absence of individual species at a site and with local species richness. But how do these relationships arise? Below, we evaluate the agreement between the observed patterns and different mechanisms of interference and exploitation competition, stressing that multiple mechanisms may be involved at the same time.

**Interference competition**

The general decline in both the regional distribution and local abundance of most taxa with increasing FTC densities could be due to local interference competition. If feeding FTC larvae damaged galls and leaf-mines of sympatric arthropods, variation in the response of different
taxa might stem from differences in the edibility of galls and leaf-mines of different morphology. This hypothesis is directly supported by our results from the 10 trees monitored throughout the summer and from the laboratory choice experiment. On the 10 trees, feeding by the FTC was accompanied by a strong reduction in the overall density of galls. The rate of decline differed substantially between species, with the mite Vasates dispar being less affected than gall midges in the genus Harmania and mites of the species Phyllocopites didelphus. As the galls themselves are integral parts of the leaves and do not drop off before leaf abscission, the pattern seemed directly attributable to differences in feeding damage caused by FTC. This notion was confirmed by the laboratory choice experiment, where galls by V. dispar suffered much less damage than galls of Harmania spp. and P. didelphus. Hence, the strength of interference competition exerted by FTC varies among species, accounting for some of the patterns observed in local community structure. Nevertheless, a low competitive pressure on V. dispar cannot account for the actual increase in this species with increasing FTC densities; some other force must also be involved. Hence, we turn to mechanisms of exploitation competition.

Exploitation competition

The patterns observed at the landscape scale could be mediated by the host plant. If the aspen trees responded actively to feeding damage inflicted by the FTC, the observed patterns might reflect species-specific responses to induced changes in the quantity or quality of the leaf resources.

Quantitatively, the FTC could induce premature leaf abscission and/or the production of new foliage to replace damaged leaves. The 10 trees that were followed throughout the summer did show a high rate of defoliation. Nevertheless, the old leaves were not abscised: the trees simply added new units to their battered foliage. Because the leaves were not individually marked, we cannot rule out the abscission of some leaves. However, the retention of a vast number of damaged leaves argues against FTC-induced leaf abscission as a major mortality factor among gallers or leaf-miners.

On the other hand, the production of new foliage did not favour any arthropod species. When inspected by the end of the summer, the fresh leaves were free of any galls or leaf-mines. Apparently, the new foliage was produced too late to be colonized by the gallers or leaf-miners, the adults of which appear relatively early in the season (F. Roslin, unpubl. data). Of course, these refoliated leaves may also differ in quality from the original leaves (Faeth, 1992), with a so far unknown effect on subsequent generations of herbivores.

Qualitatively, herbivore damage may modify the defensive and nutritive contents of foliar resources (Karban & Baldwin, 1997). In some cases, such induced responses result in heightened resistance to herbivores (“induced resistance”: Agrawal, 1998; Stout et al., 1998; Traw & Dawson, 2002a), but in others it reduces it (“induced susceptibility”: Carroll & Hoffman, 1980; Williams & Myers, 1984; Danell & Huss-Danell, 1985; Roland & Myers, 1987; Karban & Niño, 1995). Given species-specific variation among arthropods in their sensitivity to induced plant responses (Stout et al., 1998; Agrawal & Karban, 2000; Traw & Dawson 2002b; Van Zandt & Agrawal, 2004), changes in plant quality have been predicted to alter the composition of the herbivore community on previously damaged plants (Van Zandt & Agrawal, 2004). Hence, induced plant responses may have contributed to the observed patterns. In sites with a high FTC density, the main mechanism of competition will presumably be interference competition (cf. above), since here, the majority of foliage is directly consumed by FTC larvae (up to 98% in the trees monitored by us). However, responses induced in such years may carry over in time, influencing subsequent patterns of arthropod abundance and distribution (Kaitaniemi et al., 1998; 1999). We suggest that induced responses (and induced susceptibility in particular) could account for the increase observed in Vasates dispar, but further experimental work will be needed to assess this prediction.

Recovery of local populations

Within the area defoliated by the FTC in 2001, local population densities of other arthropods were higher the closer they were to undefoliated, non-outbreak sites (i.e., to the edge of the outbreak). This effect was evident even

<table>
<thead>
<tr>
<th>Source</th>
<th>Variance</th>
<th>F-ratio</th>
<th>df, df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPECIES</td>
<td>1.21 ± 0.67</td>
<td>14.18</td>
<td>2, 311</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>REPLICATE</td>
<td>0.94 ± 0.07</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 4. The total fraction of galls per taxon destroyed by FTC herbivory in the laboratory choice experiment.
after compensation for dissimilar FTC densities within the outbreak area. As the observations were made in 2002, following the maturation and dispersal of the 2001 cohort(s), this suggests an important role for immigration for local population recovery. If local population growth had been much faster than the gain of individuals from elsewhere, we would not have found any effect of distance. If, on the other hand, a substantial proportion of individuals emanates from elsewhere, immigrants will prop up population densities at sites closer to the outbreak edge – hence the effect seen.

The interaction between distance and species identity might suggest varying dispersal capacities among species, with migrating individuals reaching different distances into the defoliated area. However, the observed variation in the strength of the distance effect could not be linked to any differences in the dispersal mode or taxonomic affinity of the species (Nieminen, Rita & Uuvana, 1999): the one mite species included (Vasates dispar) was no more different from five species of gall midges than the midges were from each other. Alternatively, the observed differences may be caused by local population processes: even if the distribution of dispersal distances had been the same across species, interspecific variation in local population growth rates might still have created different gradients in density with the distance from the outbreak edge. For species where the local population rebounds to its initial level within a single generation following the FTC outbreak, local abundance should be independent of distance (cf. above). In species where local growth is particularly slow, we would expect a steep gradient. As dispersal capacity and local population growth are intimately entangled in defining the slope of the gradient (and we lack independent data on either factor), we cannot distinguish between the two. Nevertheless, the existence of a steep gradient in several species provides clear evidence for the importance of regional processes, and variation in the exact slope of this gradient opens up intriguing avenues for future experimental research.

Conclusion

This study suggests an important role for the FTC in structuring the phytophagous arthropod communities on trembling aspen. The density of FTC in a given year was strongly related to the rank order of local community members in the next year, and to the presence and absence of these members – hence to the structure of the full assemblage.

To understand the implications of the current results, we should examine the spatial scale to which they apply. Over the last 3 y alone, 91,000 km² of Alberta’s aspen forests were defoliated by forest Lepidoptera (including Malacosoma disstria, Operophtera bruceata, and Choristoneura conflictana), an area as large as an average European country (calculations based on Alberta Sustainable Resource Development, 2003; see also Figure 1). The FTC itself defoliated continuous areas of up to 3,000 km², and individual outbreaks tended to move in space.

The extent of the outbreak areas, their repeated nature, and their movement in space all contribute to one fact: a large fraction of all aspen forests will spend much of their time either defoliated or recovering from the previous outbreak. Hence, insect outbreaks will regularly affect a substantial proportion of temperate forests, and competition is likely to be an important and widespread structuring force among forest arthropods.

Acknowledgements

E. Robinson, D. Roth, C. Schmidt, and D. Sjostrom did most of the field work, and D. Sjostrom coordinated the laboratory experiment. R. Gagné identified the lecideyiids to genera, and H. Proctor helped us confirm the identification of some mites. G. Pohl provided invaluable information on the insect fauna of Alberta. D. Lux and C. Kominke at Alberta Sustainable Resource Development provided access to official databases on FTC outbreaks, and E. Meyke and C. Popplewell helped us process the digital maps. B. O’Hara gave invaluable statistical advice, and comments by anonymous referees helped us improve an earlier version of the manuscript. The contribution of T. Roslin was funded by the Academy of Finland (project number 51789) and by the Ella and Georg Ehrnrooth Foundation; the contribution of J. Roland was funded by a Natural Sciences and Engineering Research Council of Canada Discovery Grant.

Literature cited


