Which factors explain lepidopteran larvae variance in seasonal guilds on some oaks?

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ABSTRACT: Differences between the oak lepidopteran communities were studied in Slovakia in 1993 and 1994. Sampling was undertaken between April and October on 3 oak species. Biological traits of larvae were examined in order to explain differences in seasonal guilds among oaks. Cluster analysis shows similarities between communities in the flush feeder guild where the results were influenced mainly by temporal variability; in the late spring guild mainly by site; factors influencing summer feeder and autumn feeder similarities remain unclear. Detrended Correspondence Analysis (DCA) was used to investigate the main gradients explaining variability in communities. Results indicated that the host specificity along axis 1 (A1) and larval ballooning along axis 2 (A2) were important in the flush feeder guild; larval feeding strategy along A1 and the degree of defoliation by *Lymantria dispar* along A2 were important in late spring feeders; the year of study along A1 and host specificity along A2 were important in the summer feeder guild; and adaptation to lower quality of food along A1 and host specificity along A2 for the autumn feeder guild. The results are discussed.

Keywords: cluster analysis; DCA; history-life traits of lepidopteran larvae; oaks; seasonal guilds

The study of forest insect communities is of interest to ecologists worldwide. As mentioned by Lowman and Wittman (1996), forest canopies contain a considerable portion of the species diversity on Earth. Thus, an understanding of the variables that determine species richness and composition should have a high importance for both theoretical and practical reasons. However, the completion of a reliable inventory list of canopy communities requires exhaustive mass-sampling (Stork et al. 1997).

Although descriptive studies have dominated canopy arthropod research, some recent studies have focused on statistical testing of hypotheses: e.g. vertical and seasonal variation in communities (Schowalter, Ganio 1998); several other studies were conducted to compare the community structure of Lepidoptera within and between various tree species (Neuvonen, Niemelä 1983; Kulfan 1990; Summerville et al. 2003).

Insect communities have also been used to estimate levels of forest disturbance (Tovar-Sanchez et al. 2003), and as a conservation tool to determine the value of natural reserves (Grill, Cleary 2003). In European forests the interspecific difference among host trees has been identified as a significant factor influencing the macrolepidopteran species richness. For example, a significant difference in caterpillar diversity was found between *Betula* sp. and *Fraxinus* sp., and also among other tree genera in Finnish forests (Neuvonen, Niemelä 1981, 1983). In North America Barbosa et al. (2000) compared caterpillar faunas from *Salix nigra* and *Acer negundo*

and confirmed a high proportion of caterpillars were host species specific. However, Summerville et al. (2003) argues that the degree to which species diversity found on any particular host tree varies due to random chance is unknown.

Despite the fact that oaks are a widely distributed group of trees with over 300–600 species worldwide (Tovar-Sanchez et al. 2003) and that they usually support a high abundance and diversity of insect species (Summerville et al. 2003), studies on the arthropod fauna of oaks are relatively scarce (Tovar-Sanchez et al. 2003).

Even less is known about host specific guild richness and factors that influence the annual variation in lepidopteran communities.

Niemelä and Haukioja (1982) studied lepidopteran species diversity on Finnish deciduous trees, and based on the availability of food resources in late summer they were able to define two main host tree groups. In addition experiments conducted in their study confirmed the importance of the host tree in determining the richness of seasonal guilds. Schowalter and Ganio (1998) found distinguishable arthropod communities on four coniferous tree species. They found significant differences between early (June) and late (August) seasons that explained (jointly with the canopy level) a high proportion of the variation in arthropod assemblages. In Mexico Tovar-Sanchez et al. (2003) described significant seasonal differences between lepidopteran communities on different oaks. Generally, the species diversity was higher in the rainy than in the dry season. Summerville and Crist (2003) and Summerville et al. (2003) confirmed significant compositional differences in moth communities sampled between early and late season. Summerville et al. (2003) found that the clustering of lepidopteran assemblages, on four deciduous trees, between early (June–July) and late (August–September) seasons was quite different. Differences in the phenology of lepidopteran species were considered the most significant factor affecting the similarity of caterpillar fauna (early and late season samples were only 18% similar). Kulfan and Degma (1999) found that communities in May had the highest species richness during both years of study, the maximum was found only occasionally in June.

There are several hypotheses why tree species sustain various communities of Lepidoptera. Previously, the pattern of associations between herbivores and their host plants has been considered as relationships between the quality of plants as food resources (Ehrlich, Raven 1964; Cates 1980), or as a result of plant nutrient composition (Scriber,

Feeny 1979), plant defence mechanisms (Courtney 1981; Becerra 1997) and phenology (Wood, Keese 1990). The assumption of high host specificity with studies revealing a lesser degree of high host specificity (Neuvonen, Niemelä 1983) or a high level of herbivore specificity has also been tested. The theory of available food resources (Niemelä, Haukioja 1982) suggests that the herbivore community diversity strongly depends on the type of tree, for example the *Quercus* type where new leaves are available for only a short time early in the season or the *Populus* type where new leaves are available all season. Lill et al. (2002) studied host plant–herbivore–parasitoid interactions and found that the host plant was the main variable influencing levels of lepidopteran parasitism. Neuvonen and Niemelä (1981) showed that host frequency, height and the number of relative host species explained a high proportion (71%) of lepidopteran species richness variance. Forkner et al. (2004) highlighted the role of tannin as an anti-herbivore defence on two oak species across seasons.

Our effort was focused on understanding the mechanisms that explain variance in lepidopteran communities in various seasonal guilds on different oaks. The main study goal was: to analyze the main life-history traits of lepidopteran larvae and other parameters that may explain species variance in seasonal guilds on different oak species via cluster analysis and ordination method.

STUDY SITES AND METHODS

Fundamental information about methodology of sampling, site description, and the separation of species to seasonal guild is in Turčáni et al. (2009).

In statistical analyses we used cluster analysis (Ward's procedure, Euclidean distances), STATISTICA 5 to compare differences between study sites using species abundance in seasonal assemblages. Prior to analysis, abundance data were transformed as $\log(x + 1)$.

Cluster analysis was performed on several different datasets:

(a) Twenty of the most abundant species the year round;
(b) Fifteen of the most abundant species classified as FlF;
(c) Ten of the most abundant species classified as LSF;
(d) All 10 species classified as SF;
(e) Five of the most abundant species classified as FaF.

Subsequently, we compared species assemblages using Detrended Correspondence Analysis (DCA), a method of ordination, which is an indirect gradient method. Values were detrended by segments, with a square root transformation using CANOCO 4.5 (Ter Braak, Šmilauer 2002). Results were plotted as biplot data with the scores for study sites, species and the main estimated gradients for two of the first axes in each of the seasonal guilds. Estimating the main gradients was done by the inspection of caterpillar life history traits and/or environmental parameters in relation to the DCA diagram. DCA was performed for the same datasets as in cluster analysis except for (a) Twenty of the most abundant species the year round.

RESULTS

Cluster analysis results

The cluster analysis of year round guilds (Fig. 1a) indicated a high similarity of *Quercus robur* stands, and a low similarity between *Q. robur* and the other two oak species. All guilds were clearly connected with studied oaks and there was an indication in the case of *Q. robur* that temporal rather than spatial variability played a greater role in guild clustering. This suggests that the communities were probably influenced more by stochastic factors like weather, enemies or competition than by the ecological parameters of stands. Among the 20 species taken for analysis 13 belonged to the FlF guild, five to LSF and two to FaF. No SF data were entered into this analysis, because of the low abundance of species feeding during summer.

Results of the cluster analysis of FlF data (Fig. 1b) were similar to those for the year round guild on *Q. robur*. Temporal variability also appeared more significant than the impact of the site (host tree). Communities on two different sites were grouped together by year, grouping by the same sites in different years was not found. A similar situation was found in the case of *Q. petraea* and *Q. rubra* where temporal variability also played a greater role in grouping the sites. This result indicates that differences between native (planted) and non-native host tree stands played a less important role than differences in conditions in various years. This cluster analysis reflects the situation at the beginning of the season, which is characterized by a lack of food if late frosts damage foliage (Patočka, Čapek 1971).

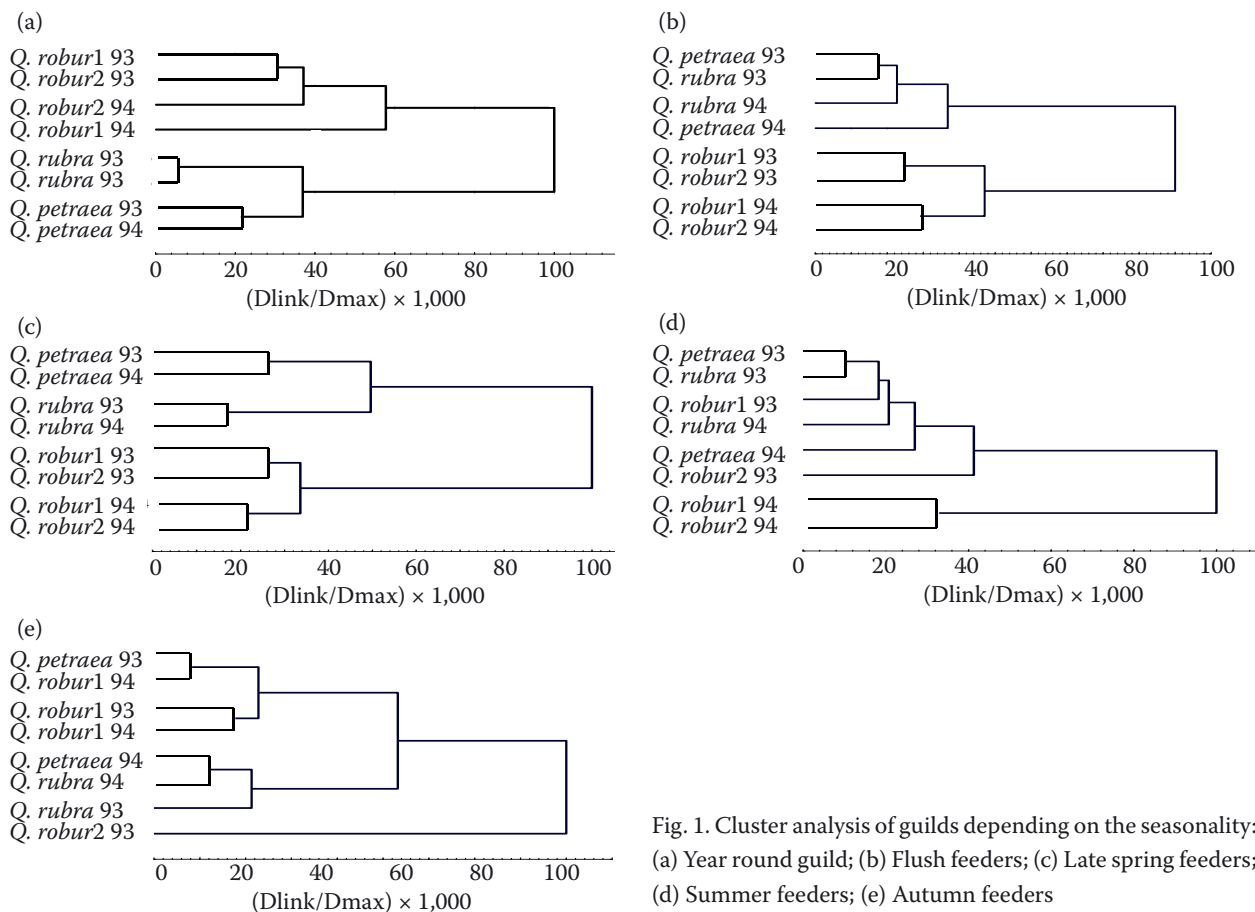LSF were clustered by host tree, and similarity of guilds on the same host tree was always higher

Fig. 1. Cluster analysis of guilds depending on the seasonality: (a) Year round guild; (b) Flush feeders; (c) Late spring feeders; (d) Summer feeders; (e) Autumn feeders

than among different host trees (Fig. 1c). The results suggested that the host tree played a greater role in the similarity of this guild than temporal variability. However, the similarity of guilds in the *Q. robur* cluster was determined more by temporal variability.

Clustering the guilds of SF was quite different from previous patterns (Fig. 1d). Summer is a time when the abundance of Lepidoptera larvae on oaks was the lowest during the vegetation season in our study at majority. Oak species showed only the presence of 0–4 species in 1993 and 2–7 species in 1994 per site. The number of individuals per 25 beatings (about 2,500 leaves) varied from 0 to 8 larvae in 1993 and from 2 to 24 larvae in 1994 per site. All 10 species (two of them with abundance of 1 larva per all sites) were taken to be analyzed. We also performed the analysis without rare species but the result of clustering was almost the same. Sites covered by *Q. robur* in 1994 are clearly separated from all other sites, so the year 1994 played a greater role on these sites. The abundance of larvae was much higher on these 2 sites than on all other sites. All other sites formed a big cluster combining variable sites. Guilds on various oak species were similar and the temporal variability did not play a visible role in these stands.

The results of FaF cluster analysis seem to be also influenced by the low abundance of species. Only 5 species were taken for analysis and it is possible to recognize 3 clearly defined groups.

(1) Guild on *Q. robur* 2 in 1993 was separated as the most abundant one;
(2) Cluster combining other *Q. robur* sites with the richer *Q. petraea* site;
(3) Cluster of *Q. rubra* with *Q. petraea* in 1994 (Fig. 1e).

There were no clear indications that the similarity of communities was influenced by food tree or temporal variability.

Detrended Correspondence Analysis results

The first two axes of Detrended Correspondence Analysis (DCA) (Fig. 2a) revealed the main gradients which form FlF communities. Two of the first axes explained 46.7% of species variance. There are two slightly overlapping clusters of sites along axis 1 (DCA-1, Fig. 2a).

These are:
(1) Planted stands of *Q. petraea* and *Q. rubra*;
(2) Well defined groups of *Q. robur* sites. The main ecological gradient along DCA-1 relates to the host specificity of FlF, which consists of three main groups:

(a) polyphagous species overwintering as eggs (*Lymantria dispar, Cosmia trapezina, Epirrita diluta,* and *Operophtera brumata*) from the left of axis 1 to its centre;
(b) oligophagous species in the central zone of axis one (*Lithophane ornitopus, Agriopis marginaria* and *Ypsolopha ustella*);
(c) relatively specialized species feeding only on oaks or only on some of the oak species (*Neozephyrus quercus, Nycteola revayana,* and *Tortrix viridana*).

Species in the 1st group are associated with *Q. rubra*, species of the 2nd group with *Q. petraea* and *Q. robur* and species from the 3rd group with *Q. robur*, but also *Q. petraea*. Species in the second group generally overwinter as pupae or adults, species of the third group as eggs (*T. viridana, N. quercus*) or adults (*N. revayana*). Another possible mechanism impacting the species variability is the timing of leaf flush. During this study *Quercus robur* was the earliest to present new leaves, followed by *Q. rubra* and lastly *Q. petraea*.

The presence/absence of wind-borne dispersal (known only for a minority of species involved in this analysis) was identified along axis 2 (DCA-2, Fig. 2a). There is only one species using ballooning on the bottom part of axis 2 (*Agriopis leucophaeria*), but there are several species on the upper part of axis 2 (*L. dispar, A. marginaria, Colotois pennaria,* and *O. brumata*). All these species are the main elements of the FlF guild on *Q. rubra*.

The FlF guild on *Q. robur* is characterized by a high incidence of specialized species (we do not consider miners) which occasionally occur also on *Q. petraea*. The communities on *Q. rubra* are composed of bigger species that are able to use wind-borne movement.

Two of the first DCA axes explained 66.8% of species variance in LSF. They revealed possible mechanisms which explain the species variance in this season. Along axis 1 (DCA-1, Fig. 2b) there are three slightly overlapping site clusters. These are clustered by host tree, and communities in this season are quite distinctively defined. The main gradient connected with axis 1 was feeding strategy (from left of axis 1 to the right: skeletonizers and leaf miners, feeders under webs and among spun leaves and free feeders). Free feeding larvae at this time use mimicry as a strategy of survival and skeletonize leaves as young larvae. We mentioned that leaf miners were not taken into consideration in this study, but *B. ulmella* is a leaf miner during the first larval stages and so later in development it is sensitive to beat sampling. Skeletonizers were mainly associated with *Q. robur*, the leaf architecture of which is the most suitable to partial miners like *Buc-*
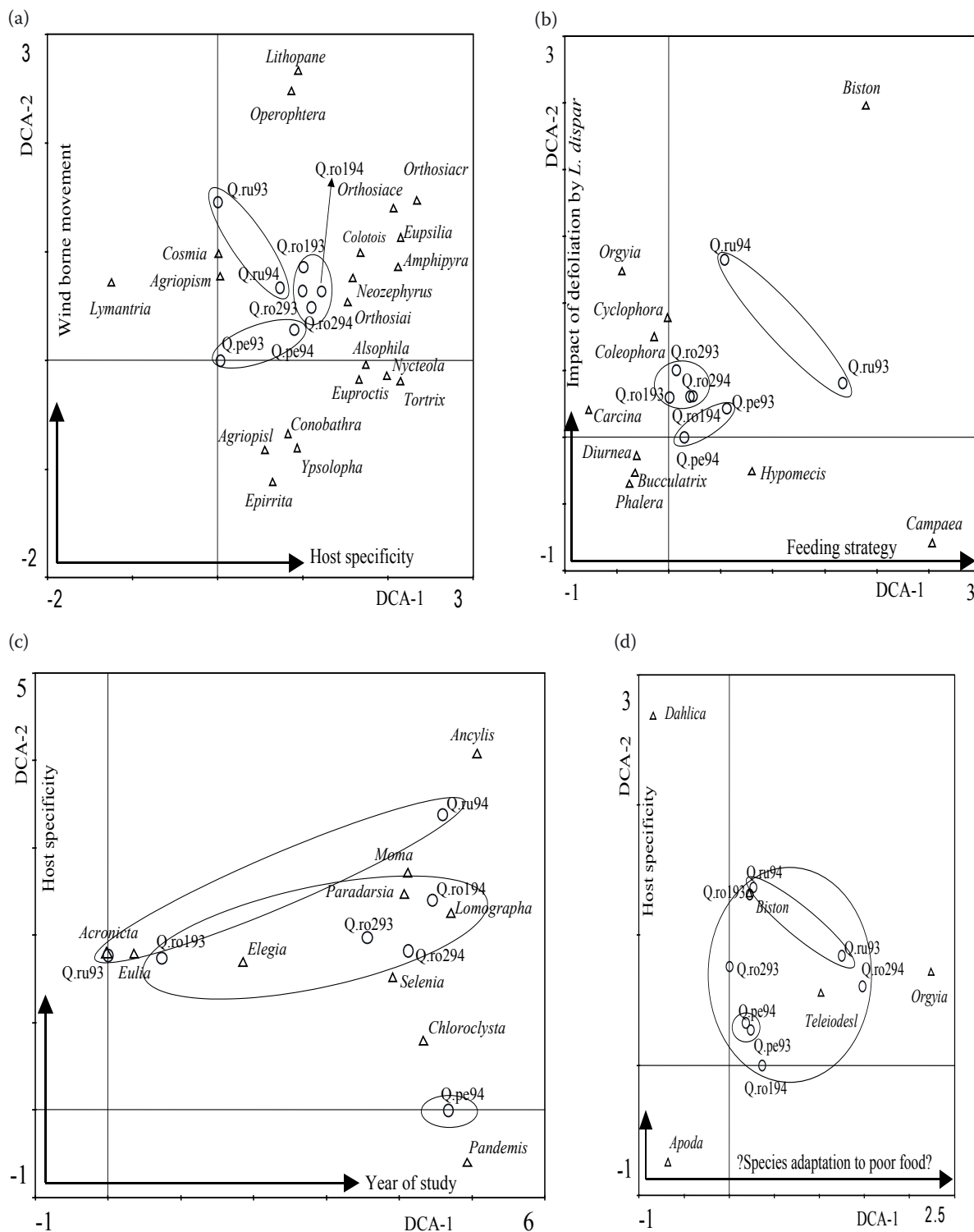
Fig. 2. DCA ordination diagrams of the sites and species score: (a) Flush feeders; (b) Late spring feeders; (c) Summer feeders; (d) Autumn feeders

culatrix ulmella and *Coleophora lutipenella*. Species feeding under webs were also mainly concentrated on *Q. robur*, but sometimes also on *Q. petraea* (*Diurnea fagella* and *Carcina quercana*). These oaks are also preferred by species feeding gregariously as young larvae (*Orgyia antiqua* and *Phalera bucephala*). Some free feeders, *Hypomecis punctinalis* and *Campaea*

margaritata, skeletonize leaves as young larvae. Free feeders occur on all oak species, but because the first two groups are either in low numbers or absent on *Q. rubra*, they played a greater role in the composition of guilds on this species.

The effect of defoliation intensity of gypsy moth (*L. dispar*), a flush feeder which was abundant in

both years of study, was identified along axis 2 (DCA-2, Fig. 2b). There is quite a clear gradient from stands of *Q. rubra* (upper part of axis 2) with a low proportion of defoliation by the gypsy moth, through to a middle level of defoliation on *Q. robur* to a relatively heavy defoliation on *Q. petraea* (lower part of axis 2). Free feeders such as *Biston strataria*, *O. antiqua* and *Cyclophora linearia* preferred *Q. rubra*, which with the least defoliation offered a rich supply of food. Smaller species are more specialized for feeding on *Q. robur* and were able to shelter among leaves because defoliation by *L. dispar* did not reach high levels. Several of the smaller free feeders were also able to use the limited resources left on *Q petraea*. It is also probable that partial production of new leaves allowed the survival of these species.

The first two DCA axes explained 62.8% of species variance in SF. The mechanisms which play the most important role are not very clear. Along axis 1 (DCA-1, Fig. 2c) there were three overlapping clusters (related *Q. rubra* and *Q. robur* sites and 1 separate site of *Q. petraea*). No larvae were found on the *Q. petraea* site in 1993. The main gradient connected with axis 1 was found to be the year of study (from the left of axis 1 to the right: 1993 samples are concentrated to the left, 1994 ones to the right). The year 1993 was evidently less favourable for SF which formed poorer guilds in all samples: *Q. petraea* 93 – 0 species, 0 specimen, 94 – 2 species, 3 specimens; *Q. rubra* 93 – 1 species, 1 specimen, 94 – 2 species, 2 specimens; *Q. robur* 1 93 – 3 species, 3 specimens, 94 – 5 species, 20 specimens; *Q. robur* 2 93 – 4 species, 8 specimens, 94 – 7 species, 16 specimens. The same temporal differences were found also in the case of FlF, but the number of species remained stable in LSF in both years and in the case of FaF the pattern was opposite, when more species and also more individuals were found in 1993.

Host specificity was identified along axis 2 (DCA-2, Fig. 2c). The gradient is not quite clear, because of the low number of species, but polyphagous species (*Pandemis cerasana*, *Chloroclysta miata*, *Selenia tetralunaria*, and *Eulia ministrana*) are present on the lower part of axis 2, and specialized species (*Elegia similella*, *Moma alpinum*, and *Ancylis mitterbacheriana*) on the upper part of the same axis.

Only five species of FaF were entered for analysis, because of the low abundance of individuals in this guild the results of the DCA are not quite clear. The first two DCA axes explain 52.9% of species variance. All sites were clustered jointly and without any separation based on site/host tree, year or other known parameters.

Like summer feeders, host specificity was identified along axis 2 (DCA-2, Fig. 2d). More polyphagous species are located on top of axis 2 (*Dahlica* sp., *Biston betularia* and *Orgyia recens*) and more specialized species on the bottom of axis 2 (*Apoda limacodes* and *Teleiodes luculellus*).

DISCUSSION

Our main goal was to investigate if the variability of Lepidoptera in different seasonal guilds was explained by the same factors across the host growing season. In tropical forest systems Tovar-Sanchez et al. (2003) found that seasonality significantly influenced the number of insect species on oaks present in dry and wet seasons. Similarly in temperate forests recent studies by Summerville et al. (2003) and Summerville and Crist (2003) also confirmed significant differences in the structure of communities in early and late seasons. Our study area is characterized by a continental climate with cold winters and hot dry summers. This has resulted in Lepidoptera adapting to variable conditions. We sorted the species into four groups which live in different climatic conditions and on food of variable quality. The classification was different from that used by Patočka (1954), because leaf miners were not included in our study. Leaf miners are generally highly specialized for feeding on individual oak species and adapted to tolerate the accumulation of tannins; as a result their abundance has the opposite pattern to non-leaf-mining species being scarce in spring and most numerous in autumn.

FlF is the seasonal guild in which differences in individual tree phenology play an important role (Hunter et al. 1997). The results of cluster analysis suggest the existence of this mechanism and results from DCA explain the caterpillar life-history characteristics relating to the differences in communities on various oaks. Host specificity and/or differences in budburst timing between oak species were the main gradients explaining the variance in the FlF guild. It was not clear from our results which factor was dominant. However the host specificity gradient had a more visible pattern than differences in budburst timing. Larger polyphagous species are not as sensitive to synchrony as smaller highly specialized species but there are several exceptions.

Because two of the study sites were relatively isolated the diversity and composition of Lepidoptera in these stands was probably influenced by patch size but we did not study this phenomenon. The differences in moth communities explained by patch size were found by Summerville and Crist (2003). In

our study only *Lepidoptera* species feeding on woody plants were taken for analysis, in this case the species richness of smaller stands should be lower than expected by chance (Summerville, Crist 2003).

We found a high similarity between exotic (*Q. rubra*) and artificially planted (*Q. petraea*) oak species. One possible explanation is that guilds on both these host tree species (*Q. petraea* and *Q. rubra*) were composed of polyphagous species (more than 50% of individuals recorded); in addition, some also disperse by ballooning (40% of recorded individuals, e.g. *L. dispar*) (Hunter, Elkinton 1999). It is probable that their distribution is accidental and influenced by stochastic processes rather than by the specific host plant. Ballooning was identified as the main gradient along axis 2 explaining 16.4% of species variance.

The LSF guild starts feeding when the majority of leaves have developed and the accumulation of tannin is in progress (Forkner et al. 2004). These species tend to be influenced by the impact of FlF activity (high defoliation or induced feeding resistance as a result of defoliation). We have no information about the efficiency of natural enemies in this season compared with FlF, however when Lill et al. (2002) analyzed the role of the host plant as a factor influencing the parasitism of forest caterpillars they found that some host plants induced a higher rate of parasitism than expected by chance, and the opposite was true of other families and genera which reduced parasitism of the same species more than expected by chance.

Another important factor that plays a role in the lepidopteran species composition and diversity on oak species is the effect of plant architecture. Marquis et al. (2002) found that *Q. alba*, which naturally has more leaves touching, had a greater number of leaves woven together by lepidopteran larvae. Manipulated experiments confirmed an increased number of woven leaves, damage and a higher number of individuals on trees when they artificially clustered leaves. We compared three oak species with quite different patterns of leaf architecture: *Q. rubra* has the petioles 25–50 mm in length (Dostál 1989), big leaves held apart from of each other. *Quercus petraea* has smaller leaves arranged close to each other with petioles 15–25 mm in length. *Q. robur* has the smallest leaves arranged in dense clusters with petioles only 2–5 mm in length. The last oak species has many more leaves touching and is more suitable for smaller species which tie two or more leaves together. A similar mechanism was described by Lill and Marquis (2003). By creating white oak leaf shelters early in the season *Pseudotelphusa* sp. caterpillars had a large and persistent effect on seasonal patterns of herbivore recruitment to and/or retention by white oaks. We found feeding strategy as the main gradient explaining species variance in this group. It seems that in Central Europe when the weather does not play the main role, the leaf architecture is quite an important factor.

The number of species and also individuals in the SF guild was quite low. This guild tended to be influenced more by the poor quality of leaves and the increasing accumulation of tannin as reported by Feeny (1970) and also Forkner et al. (2004). Because of a lack of information about the quality of food and amount of tannin in leaves during our study we cannot precisely estimate the impact of these factors. There are however some indications that species variance in the SF guild is explained by the study year (DCA-1, Fig. 2c). However, these speculations should be considered as preliminary only and future research is needed.

The SF but mainly FaF guild is specialized to feed on tough low food quality leaves found later in the season. Adaptation is expressed by feeding strategy, when smaller species skeletonize leaves in all life stages (*Teleiodes lucullelus*) and larger species skeletonize leaves only in the first larval stages, later feeding externally. Another kind of adaptation is feeding on understorey plants or on the bottom part of the canopy. Forkner et al. (2004) found that the percentage of dry mass foliage condenzed tannins expressed as oak condenzed tannin equivalents was lower in autumn on understorey *Q. velutina* and *Q. alba* individuals than in the canopy of the same species. Almost all species in our analysis are occasionally bivoltine, but they were found only during autumn in our study. There was only one typical autumn feeder *T. lucullelus* on our study (accompanied occasionally by the similar but rare species *Teleiodes paripunctellus*). *T. paripunctellus* is probably an example of adaptation to autumn feeding, because it feeds not only on oaks but also on birch, where it can find available food. We have no information about the percentage of tannin in individual trees at study sites and we can only speculate that the adaptation of species to a higher amount of tannin should be the main gradient along axis 1 (DCA-1, Fig. 2d). This hypothesis was suggested also by Niemelä and Haukioja (1982), who found that *O. antiqua* probably does better on mature leaves. However, they conducted experiments with *O. antiqua* on birch while in our study the closely related species *O. recens* was found. One exception in this guild is *Dahlica* sp., which feeds on algae, lichens and mosses and its presence and abundance are not connected with oak foliage (and so independent of tannin ac-

cumulation). From this point of view species less adapted to high tannin concentrations were found to the left of axis 1 and more specialized to the right (DCA-1, Fig. 2d) (*T. paripunctellus*, *O. recens*).

Host specificity was identified along axis 2 (DCA-2, Fig. 2d) as in the case of autumn feeders. The gradient is not clear, because of the low number of species, but specialized species (*A. limacodes* and *T. luculle-lus*) are present on the bottom of axis 2, with widely polyphagous species (*O. recens*, *B. betularia*, and *Dahlica* spp.) on the upper part of the same axis. The higher abundance of FaF on *Q. robur* may be influenced by the differences in stands when this species in grown on plain forests with a higher soil water level which should improve the quality of leaves. Another mechanism responsible for the high abundance is the presence of tree species of the "*Populus* type" (Niemelä, Haukioja 1982) which continue to produce new leaves later in the season (e.g. birch). Several polyphagous species in this group are known to be regular members of plain forests for example *O. recens*, *S. alternaria*, and *A. limacodes* (Patočka et al. 1999).

Our results suggest that life-history traits play an important role in the explanation of species variance among guilds on closely related oak species. We can also conclude that explanatory factors in each seasonal guild are different, probably as a result of species adaptation to seasonal conditions and/or resource specialization on the genus *Quercus*.

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