Leaf-spinning moths (Lepidoptera) feeding on *Vaccinium uliginosum* L. along an ecological gradient of central European peat bogs

Karel Spitzer, Josef Jaroš & Aleš Bezděk

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The leaf-spinning moths (Lepidoptera: Tortricidae, Gelechiidae, Chimabachidae and Geometridae) associated with the boreal plant *Vaccinium uliginosum* L. were investigated in two different peat bogs (Mrtvý luh and Chalupská slat'), both situated in the Šumava Mts., Czech Republic. During four years (1998–2001) of collecting leaf spinnings, 19 species of moths were recorded from both localities. Their occurrence was clearly structured along a distinct ecological (mesoclimatic) gradient. Species closely associated with peat bogs (tyrphobiontic and tyrphophilous taxa) were found to be most abundant in the treeless centres of both peat bogs in comparison with marginal parts. *Vaccinium uliginosum* is the only food plant of stenotopic boreal moths *Pammene luedersiana* (Sorhagen) and *Athrips pruinosella* (Lienig & Zeller) recorded in the Šumava Mts.

Karel Spitzer & Josef Jaroš, Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic; E-mail: spitzer@entu.cas.cz & jaros@entu.cas.cz
Aleš Bezděk, Institute of Entomology, Academy of Sciences of the Czech Republic and Faculty of Biological Sciences, University of South Bohemia České Budějovice, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic; E-mail: bezdek@entu.cas.cz

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1. Introduction

The central European peat bogs are isolated (approx. 12 000 years ago) ancient habitats, closely related to the forest-tundra biome of early Holocene. A proportion of the cold-adapted flora and fauna of the late Glacial and early Holocene periods survived locally in peat bogs during the subsequent climatic changes (Peus 1932, Jankovská 1980). *Vaccinium uliginosum* L. appears to be the best example of an old relict boreo(arctic)-montane plant adapted only to high altitudes and latitudes (Connoly & Dahl 1970), with isolated azonal occurrences in peat bogs of the temperate zone.

Vaccinium uliginosum is a deciduous shrub associated with habitats of acid and peaty soils of cold circumboreal and mountain environments (Jacquemart 1996). It is a characteristic plant of

isolated peat bogs in central Europe and has a unique guild of herbivorous insects. The basic faunistic composition of the Lepidoptera guild of subarctic, boreal and temperate populations of *V. uliginosum* is treated in many literature sources (e.g. Peus 1932, Krogerus 1960, Seppänen 1970, Bradley *et al*. 1973, 1979, Mikkola & Spitzer 1983, Väisänen 1992, Spitzer & Jaroš 1993) with special reference to tyrphobiontic taxa. The subject of insect herbivory on *V. uliginosum* is poorly treated in ecological and botanical revisions dealing with this unique boreal plant (see Jacquemart 1996). For example, the only model example of a strictly monophagous boreo-montane species of Lepidoptera associated with *V. uliginosum* seems to be isolated populations of butterfly *Colias palaeno* (L.) (e.g. Maey 1986, Rüetschi & Scholl 1985). Other tyrphobiontic non-spinning Lepidoptera feeding on *V. uliginosum* in central Europe, e.g. *Anarta cordigera* (Thunberg), *Lithophane lamda* (F.), *Carsia sororiata* (Hübner), could not be analyzed quantitatively along an ecological gradient.

Populations of Lepidoptera associated with *V. uliginosum* in habitat islands of central European peat bogs are represented by characteristic local tyrphobiontic and/or tyrphophilous species of high conservation and scientific values (Spitzer 1981, 1994, Mikkola & Spitzer 1983, Spitzer & Jaroš 1993, Spitzer *et al.* 1999), but guild structures are poorly known.

Our aim in the present paper is to answer the following questions: (1) Are the Lepidoptera species associated with *V. uliginosum* distributed within the bog habitat island randomly or do they follow a distinct ecological gradient between bog margins and centre? (2) Where are the highest abundances and diversity of the most stenotopic Lepidoptera (= monophagous and oligophagous relict boreal taxa closely associated with the bog) located along the ecological gradient?

For our investigations, we selected an important part of the Lepidoptera guild (sensu Crawley 1983) associated with *V. uliginosum*, viz. the characteristic subguild of the leaf-spinning micromoths (mainly some Tortricidae and Gelechiidae). This subguild represents the characteristic type of peat bog herbivore group and is probably the best subject for larval quantitative samples along ecological gradients and their comparative numerical analyses of habitat preference.

2. Material and methods

2.1. Study sites

Leaf spinnings of moth larvae on *V. uliginosum* were collected in two montane isolated peat bogs of the Šumava (Böhmerwald) Mts., Šumava National Park, SW Bohemia (Czech Republic):

1. Mrtvy luh near Volary, 48°52´N, 13°52´E, 740 m a.s.l., montane oligotrophic valley peat — virgin bog habitat island of 310 ha, a number of tyrphobiontic taxa already recorded (Spitzer & Novák 1969, Šula & Spitzer 2000). The transect between margin and centre is characterized by minimal and maximal temperatures (see Table 1)

Table 1. Maximum and minimum temperatures (°C) measured in the centre and in the margin of Mrtvý luh bog, Šumava Mts.

	May		June		July		August	
	Centre	Margin	Centre	Margin	Centre	Margin	Centre	Margin
Year 2000								
Maximum temperature	32.2	31.4	36.5	33.7	31.1	29.2	35.7	32.2
Average maximum temperature	24.4	23.5	26.9	26.3	22.2	20.8	27.5	24.9
Minimum temperature	–5.8	–4.9	–5.8	–3.5	–2.2	–0.6	–4.0	–2.7
Average minimum temperature	0.3	0.9	2.0	2.9	5.0	5.4	5.4	5.9
Year 2001								
Maximum temperature	30.3	29.2	31.8	31.1	33.3	33.7	32.6	31.4
Average maximum temperature	23.0	22.3	20.9	19.7	25.0	24.3	25.5	24.1
Minimum temperature	–5.3	–4.0	–3.1	–1.8	–1.0	–1.0	–4.0	–2.7
Average minimum temperature	1.4	1.9	2.7	3.3	5.6	5.8	6.1	5.7

and it represents an ecological gradient from marginal elfin pine forest to treeless centre.

2. Chalupská slat' bog near Borová Lada, 49°00´N, 13°40´E, 910 m a.s.l., oligotrophic montane raised bog with a small central lake — bog habitat island of 116 ha with partial ancient human impact (Spitzer & Jaroš 1998, 2001, incl. a list of species). The gradient between marginal parts and the centre is not gradual, with only a very narrow intermediate zone partially changed by human activities.

Vaccinium uliginosum is very common in both peat bogs and represents one of the dominant or subdominant local shrubs within the bog plant community Pino rotundatae-Sphagnetum (cf. Neuhäusl 1972).

2.2. Sampling

Leaf spinnings on *V. uliginosum* were collected on both Šumava peat bogs by individual sampling along a transect (= ecological gradient) between the margins and the centre of the bog. The margins were mostly forested by small trees and shrubs (mostly various open elfin forest types of *Pinus mugo* Turra s. lat. = *Pinus rotundata* Link hybridogenic complex) and the centre was mostly treeless with dominant ericaceous shrubs. The cover of *V. uliginosum* was usually higher near the treeless centre. For comparison, the leaf spinnings were also collected in the lag zone (sensu Gore 1983) i.e. the ecotone of transitory outer parts of the bog margin which are covered by *Betula pubescens* Ehrh. and *Pinus sylvestris* L. The intermediate zone between marginal and central parts is gradually developed in the Mrtvý luh bog, but not well developed in the Chalupská slat' bog. The intermediate zone of the gradient is usually less sharp in lower elevations of valley bogs. The leaf spinnings were collected during June for four years (1998–2001) (Table 2). May was too early and July was already late for sampling. The dates, numbers of spinnings and reared moths are summarized in Tables 2 and 3. The method for a different plant species is also described by Spitzer and Jaroš (1998).

2.3. Data analysis

Community data were analyzed by means of (partial) Canonical Correspondence Analysis (CCA; CANOCO version 3.12 software by Ter Braak [1987]) to determine the habitat preferences of leaf-spinning moths in relation to particular biotopes.

Constrained ordinations roughly correspond to regressions, where both explanatory and response variables are multivariate (although a weighted average is used instead of least squares in CCA). The CCA method is based on the assumption that species abundances have unimodal responses along the studied environmental gradient. Traditionally, the explanatory variables are called environmental variables in constrained ordinations. Partial constrained ordinations correspond to partial regression, where the influence of covariables is first partialled out and the explanatory power of environmental variables is tested. For more details, see Jongman *et al*. (1987).

Data from four years (1998–2001) were analyzed together. The habitat type (particular successional stages of Chalupská slat' and Mrtvý luh peat bogs) was the only (categorial) explanatory variable. To disentangle the differences in species composition between years and seasonal associations of species during each year, the year of collecting, date of collecting during each year and number of collected spinning were used as covariables. Species data were log-transformed.

3. Results

During four years (1998–2001) of collecting the leaf spinnings, 19 species of moths (Tortricidae, Gelechiidae, Chimabachidae and one species of Geometridae) associated with *V. uliginosum* were found on both peat bogs. The species composition was very similar on both localities, with the

Table 2. Dates and numbers of leaf spinnings collected on *Vaccinium uliginosum* (1998–2001) of two peat bogs of the Šumava Mts. Abbreviations: mrg. = margin, int. = intermediate.

Collecting date	Mrtvý luh				Chalupská slat'	
	centre	int.	mrg.	lagg	centre	mrg. + lagg
2 June 1998	35	23	85	–	–	–
11 June 1998	94	69	107	66	85	172
23 June 1998	–	–	–	–	83	–
3 June 1999	49	133	156	168	–	–
8 June 1999	126	–	156	–	185	119
2 June 2000	132	–	183	90	–	–
1 June 2001	150	–	150	58	–	–
7 June 2001	108	–	88	26	102	85

exception of some opportunistic polyphagous species penetrating to peat bogs from surrounding habitats (e.g. *Cnephasia stephensiana*, *Argyrotaenia ljungiana*, *Pandemis heparana*). The complete list of species is given in Table 3. The boreal stenotopic species closely associated with bogs (= tyrphobiontic and tyrphophilous taxa) e.g. P*ammene luedersiana* and *Athrips pruinosella* are most abundant in the centres of both peat bogs (Fig. 1, Table 3) with much lower abundance in the margins. The tyrphoneutral moths (Table 3) of the margins seem to be usually oligophagous and polyphagous, but feeding on *V. uliginosum* is common too.

The statistical analysis and ordination provided significant evidence that stenotopic species spectrum of both bog centres (Mrtvý luh and Chalupská slat') are very similar (Fig. 2). Species composition dissimilarity is characteristic for bog margins and caused by tyrphoneutral species, which inhabit not only bogs but habitats of the surrounding montane landscape as well. The species distribution and their abundance correlate with the ecological (micro-mesoclimatic) gradient from centre to the margins (Table 1).

4. Discussion

The complicated historical affinities among northern, widely distributed species of tyrphobiontic moths, their food plants and "relict geographical

Table 3. Moth species reared from leaf spinnings on *Vaccinium uliginosum* (1998–2001) of two peat bogs of the Šumava Mts. The nomenclature follows Karlsholt and Razowski (1996). Abbreviations: mrg. = margin, int. = intermediate.

Species	Mrtvý luh				Chalupská slat'	
	centre	int.	mrg.	lagg	centre	mrg. + lagg
Chimabachidae						
Diurnea lipsiella (Denis & Schiffermüller)	3	1	1	1	1	2
Dasystoma salicella (Hübner)	–	–	3	1	–	–
Gelechiidae						
Athrips pruinosella (Lienig & Zeller) – t	62	2	4	–	17	14
Tortricidae						
Acleris laterana (Fabricius)	–	–	–	2	–	–
Acleris maccana (Treitschke) – t	16	28	27	5	18	4
Acleris lipsiana (Denis & Schiffermüller) – t	55	5	8	2	2	–
Cnephasia stephensiana (Doubleday)	–	–	–	–	1	–
Cnephasia asseclana (Denis & Schiffermüller)	2	–	–	–	2	–
Argyrotaenia ljungiana (Thunberg)	2	–	–	–	–	–
Pandemis cinnamomeana (Treitschke)	–	–	1	–	–	–
Pandemis heparana (Denis & Schiffermüller)	1	–	–	–	–	–
Clepsis senecionana (Hübner)	–	–	1	–	–	–
Adoxophyes orana (Fischer von Röslerstamm)	–	–	–	1	–	2
Apotomis sauciana (Frölich) – t	–	–	1	2	–	–
Celypha lacunana (Denis & Schiffermüller)	–	–	–	3	–	1
Phiaris bipunctana (Fabricius) – t	9	1	2	–	1	–
Rhopobota naevana (Hübner)	19	12	110	96	107	109
Pammene luedersiana (Sorhagen) – t	86	10	3	4	6	–
Geometridae						
Rhinoprora debiliata (Hübner)* – t	–	1	1	1	–	–
Number of leaf spinnings	694	225	925	408	455	376
Parasitoids and pathogens	439	165	763	290	300	244

t = boreal tyrphobiontic and tyrphophilous species.
* = *Rhinoprora debiliata* is recently classified in the genus *Pasiphila* Meyrick.

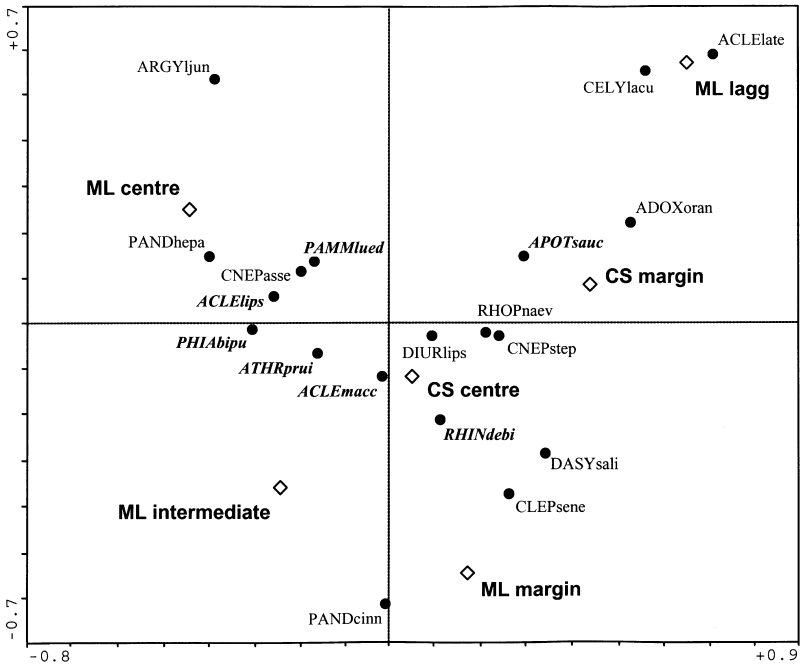

Fig. 1. CCA biplot representing the habitat associations of leaf-spinning moths of Mrtvý luh (ML) and Chalupská slat' (CS) peat bogs. Species closely associated with peat bogs are in bold italics. Abbreviations of species names are composed from the first four letters of genera and species names (see Table 3).

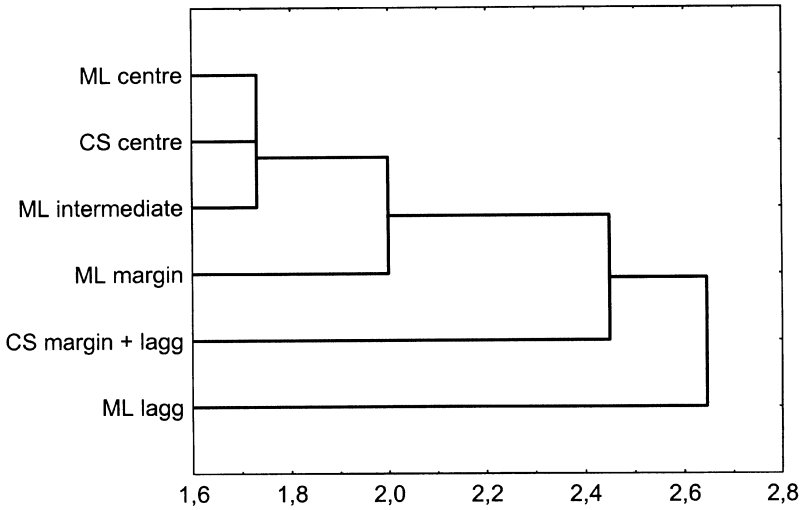

Fig. 2. Similarity of leaf-spinning moth communities (presence-absence data, single linkage, Euclidean distance) of Mrtvý luh (ML) and Chalupská slat' (CS) peat bogs.

races" in central European bogs are well illustrated by non-spinning species like *Eupithecia gelidata* Möschler and *Coenophila subrosea* (Stephens) (e.g. Peus 1932, Spitzer *et al.* 1991, Šula & Spitzer 2000). The structure and distribution of insect herbivore guilds within populations of the boreal plant *V. uliginosum* has never before been investigated (cf. Jacquemart 1996). Only various annotated lists of species and especially faunistic studies are available (cf. Peus 1932, Krogerus 1960, Spitzer & Jaroš 1993). There are no quantitative ecological studies of insect herbivores guilds of peat bog plants. The only exception is *Vaccinium vitis-idaea* L. and its peat bog Lepidoptera guild (Spitzer & Jaroš 1998). In the present paper, the larval leaf spinnings of the moth guild associated with *V. uliginosum* were investigated in two relict central European peat bogs (Šumava Mts.) along an ecological gradient from bog margin to the centre. The subguild of leaf spinning Lepi-

doptera is clearly structured along the ecological mesoclimatic gradient of bogs (Table 1, minimum and maximum temperature data from Mrtvý luh). The most stenotopic tyrphobiontic and tyrphophilous species of moths (*A. pruinosella*, *P. luedersiana*, *Acleris maccana*, etc.) are confined to and near the centres of the two investigated montane peat bogs. *Athrips pruinosella* and *P. luedersiana* seem to be strictly monophagous species associated with *V. uliginosum* (see also Svensson [1993] and Kaitila [1996] for Fennoscandia). Neither species was ever recorded outside peat bogs during our research (see also Bradley *et al*. 1979, Spitzer & Jaroš 2001). Some margins of the Mrtvý luh bog are dominated locally by shrubs of *Spiraea salicifolia* L., which were not colonized by larvae of *A. pruinosella* as recorded by some authors in central Europe (cf. Elsner *et al*. 1999). The tyrphoneutral Lepidoptera larvae feed on *V. uliginosum* near the margins and in lagg ecotone of the bog habitat island mainly, e.g. *Rhopobota naevana* (see the distribution especially in the Mrtvý luh bog) and several singletons (Table 3).

The only food plant of *P. luedersiana* in central Europe is *V. uliginosum* of the Šumava Mts. bogs (Spitzer & Jaroš 2001). *Vaccinium uliginosum* as a food plant of *P. luedersiana* has already been recorded by Palm (1982) from Denmark, but it is evidently an incorrect record of feeding on berries (Svensson 1993). Some records of *P. luedersiana* from southern Europe and Turkey are doubtful, concerning a different, probably undescribed taxon (cf. Danilevsky & Kuznetsov 1968). A food plant, *Myrica gale* L., of the boreal tortricid moth *P. luedersiana* was recorded by Bradley *et al*. (1979) for the first time from Scotland. *Myrica gale* does not occur in central Europe (Skene *et al*. 2000). Leaf spinnings of *Epinotia gimmerthaliana* (Lienig & Zeller) were not found in our present study, because the species is very rare in both investigated bogs. Nevertheless, the species is a common tyrphobiont associated with some bogs of the Šumava Mts. It is a monophagous species associated with *V. uliginosum* (our unpublished data from Šumava Mts., see also Svensson [1993]).

A weak trend of leaf spinnings was also observed in some geometrid moths. There are several records of *Rhinoprora debiliata* (recently classified in the genus *Pasiphila*) feeding on *Vaccinium* spp. of the Mrtvý luh bog (Weigt 1988), and several polyphagous geometrid moths have been found in other peatlands in the Czech Republic (e.g. *Hydriomena furcata* [Thunberg]).

The distribution of the leaf spinning moth larvae associated with *V. uliginosum* near bog centres seems to conform to habitat distribution of other tyrphobiontic and tyrphophilous species of central European peat bogs (e.g. Spitzer *et al*. [1999] and our unpublished light-trap data). It is likely that the most important dimension of the ecological niche of herbivorous tyrphobiontic species is not only a specific boreal food plant, but the meso- and microclimate ("eco-climate") of the peat bog (Table 1; see also Mikkola & Spitzer [1982] and Spitzer [1994] for further discussion). The guild of leaf-spinning moths is variable along the ecological gradient from margins to the bog centre (Väisänen 1992), which is dominated by highly specific taxa of ancient habitat island. In the case of *V. vitis-idaea*, the most stenotopic tyrphophilous tortricid moth *Argyroploce arbutella* (L.) was found in the bog centre only (Spitzer & Jaroš 1998). We may conclude that a complete habitat conservation of peat bog "islands" including their buffer zones is the only way of preserving the unique relict boreal biota of azonal biotopes situated within the temperate zone.

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