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Research

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Abundance and diversity of birch-feeding leafminers along latitudinal gradients in northern Europe

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Latitudinal patterns in biotic interactions, including herbivory, have been widely debated during the past years. In particular, recent meta-analysis questioned the hypothesis that herbivory increases from the poles towards the equator. Our study was designed to verify this hypothesis by exploring latitudinal patterns in abundance and diversity of birch-feeding insect herbivores belonging to the leafminier guild in northern Europe, from 59° to 69°N. We collected branches from five mature trees of two birch species (*Betula pendula* and *B. pubescens*) at each study site (ten sites for each of five latitudinal gradients) twice per season (in early and late summer of 2008–2011) and attributed all mines found on leaves of these branches to a certain taxon of insects. Latitudinal patterns were quantified by calculating Spearman rank correlation coefficients between both abundance and diversity of leafmining taxa and latitudes of sampling sites. In general, both abundance and diversity of leafminers significantly decreased with latitude. However, we discovered pronounced variation in patterns of latitudinal changes among study years and leafminer taxa. Variation among study years was best explained by mean temperatures in July at the northern ends of our gradients. During cold years, abundance of leafminers significantly decreased with latitude, while during warm years the abundance was either independent of latitude or even increased towards the pole. In the northern boreal forests (66° to 69°N), herbivores demonstrated larger changes in densities in response to temperature variations than in the boreo-nemoral forests (59° to 62°N). Our data suggest that climate warming will result in a stronger increase in herbivory at higher latitudes than at lower latitudes.

Latitudinal patterns in different characteristics of ecosystem structure and function have fascinated biologists over centuries. While an increase in species richness from the poles towards the equator is now seen as a general regularity (Willig et al. 2003), the existence of latitudinal patterns of biotic interactions, in particular herbivory, remains controversial. For decades, it was widely accepted that herbivory is greater in the tropics than in the temperate zone (Coley and Aide 1991, Coley and Barone 1996). However, recent meta-analysis (Moles et al. 2011) found that, on average, herbivory is independent from latitude. Since the idea that more herbivory occurs at lower latitudes underpins several dominant theories in biogeography (as discussed by Moles et al. 2011), the question arises whether the results of this meta-analysis are sufficiently robust to influence the development of basic ecology.

The meta-analysis performed by Moles et al. (2011) is based on 38 latitudinal comparisons of herbivory from all around the world. The low number of studies did not allow for controlling of even the most obvious sources of variation, such as the group of herbivores that caused plant damage (e.g. insects or vertebrates; individual species or the entire community), plant functional type (e.g. woody or herbaceous), ontogenetic stage (e.g. seedlings or mature individuals), damaged part of the plant (e.g. leaves or reproductive organs) and methods used to estimate the level of herbivory. These and many other characteristics of study systems and of methodological approaches have been identified in earlier meta-analyses as important sources of variation in the results of studies addressing different aspects of plant–herbivore interactions (Nykänen and Koricheva 2004, Zvereva et al. 2010, Zvereva and Kozlov 2012), which allows us to suggest that they may have influenced also the outcomes of studies that explored latitudinal patterns in herbivory. This non-controlled variability may be one of the reasons behind difficulties in discovering the general pattern, and thus exploration of variation in latitudinal patterns of herbivory becomes a very important task.

A vast majority of the studies considered by Moles et al. (2011) were performed in regions with temperate climate, between the 30th and 50th parallels in both hemispheres. Insects living at these latitudes have relatively broad thermal tolerance and are expected to show only minor responses to temperature increase (Deutsch et al. 2008). Therefore it is not surprising that latitudinal patterns in herbivory averaged across these latitudes yielded zero net effect. In contrast, insects living at higher latitudes, often close to their distributional limits, are generally controlled by temperatures (Bale et al. 2002, Deutsch et al. 2008). Therefore we hypothesized that latitudinal changes in herbivory are stronger at high latitudes. The first empirical support for this hypothesis was found in white birch *Betula pendula*, in which the foliar damage caused by defoliating insect herbivores decreased with latitude between 60°N and 69°N, but was independent of latitude between 48°N and 60°N (Kozlov 2008). Thus, one of the critical gaps in knowledge that became evident from the meta-analysis by Moles et al. (2011) is the acute shortage of data on latitudinal changes in herbivory at high latitudes.

Only six of 38 studies used by Moles et al. (2011) were based on data collected during three or more years. However, even in these studies the data from different years were either collected from different sets of study sites (Garcia et al. 2000, Kelly et al. 2008) or averaged prior to the analysis (Pennings et al. 2009). We are not aware of any study reporting variation in latitudinal patterns of herbivory among the study years. Moreover, this variation cannot be explored by meta-analysis; it requires collecting data from the same latitudinal gradient for several years.

Insects living at higher latitudes are more responsive to changes in ambient temperature than insects from more southern regions (Bertram 1935, Deutsch et al. 2008). As a result, during warm years the correlation between herbivore abundance and latitude may be weakened due to the larger response of northern populations to elevated temperatures. Therefore, we aimed not only at finding general patterns in latitudinal changes in herbivory by averaging observations from 2008 to 2011, but also at quantifying the annual variation in correlations between the latitudes of study sites and the levels of herbivory.

Studies of latitudinal patterns in background insect herbivory generally report total losses of foliage caused by feeding of an unknown number of unidentified species (Kozlov 2008, Pennings et al. 2009, Zhang et al. 2011). This method, although fully justified from the plants' perspective, complicates data interpretation and hampers uncovering of the mechanisms behind the observed patterns. In particular, asynchronous fluctuations in the densities of individual herbivore species and their individualistic responses to both weather conditions and biotic environment do not allow conclusions about the mechanisms underying the higher foliar losses observed at some study site(s). These losses could be the result of 1) a higher abundance of a single species, 2) higher abundances of all species in the community, or 3) a higher number of species in the community. Importantly, none of the primary studies included in the meta-analysis by Moles et al. (2011) addressed this problem. Leafminers, the feeding patterns of which often allow species-level identification (Ellis 2012), represent a unique model to study variation in latitudinal patterns among coexisting herbivore species on the same host.

Birches support an exceptionally large diversity of leafminers: 55 species were recorded in Britain (Atkinson 1992) and 71 are listed for Europe (Ellis 2012). The ecology of several birch-feeding leafminers has been studied extensively (Tuomi et al. 1981, Boomsma et al. 1987, Bylund and Tenow 1994, Digweed et al. 2009), including both their interactions with other feeding guilds of herbivorous insects (Valladares and Hartley 1994, Fisher et al. 1999, Johnson et al. 2002) and their effects on host plant performance (Kozlov 2005, Kozlov et al. 2012). Both the diversity of birch-feeding leafminers and the amount of available ecological information substantiate the choice of this group as a model to compare latitudinal patterns in abundance among different taxa of herbivores.

Our study is based on the results of an extensive monitoring program implemented during 2008–2011 in northern Europe, from 59 to 69°N and from 10 to 60°E. In this study we asked: 1) whether abundance and diversity of leafminers change with latitude; 2) whether latitudinal patterns differ among geographical regions, study years, birch species and leafminer taxa; 3) whether the variation in latitudinal patterns of abundance among leafminer taxa can be explained by differences in their life histories; and 4) whether among-year variation in latitudinal patterns of the overall abundance can be explained by differences in weather conditions.

Material and methods

Study area and sampling sites

Sampling was conducted along five latitudinal gradients which were between 750 and 1300 km in length (Fig. 1: N, between Olso and Andselv, Norway; F, between Turku and Nuorgam, Finland; R, between St Petersburg and Murmansk, Russia; A, between Vologda and Arkhangelsk, Russia; K, between Vologda and Inta, Russia). All gradients were located in Scandinavian and Russian taiga, an ecoregion within the taiga and boreal forests biome. Typical coniferous forests of this ecoregion are dominated by Scots pine *Pinus sylvestris* or Norway spruce *Picea abies* but also have significant numbers of downy and white birches *Betula pubescens* and *B. pendula*, respectively.

The sampling sites were located in forests typical for each locality; care was taken to select a representative site where both *B. pubescens* and *B. pendula* grow naturally. This was impossible in some areas, and therefore in 13 of 50 sampling sites we collected samples only from *B. pubescens* (Fig. 1, Supplementary material Appendix 1). The northernmost site in the F gradient was excluded from the analysis, because during the study year the birches at this site were completely defoliated by the larvae of autumnal moth *Epirrhita autumnata*. In most study sites the sampled area did not exceed 2000 m^2. Each site was sampled twice a year. The R gradient was sampled each year (23–29 July and 21–25 August 2008, 24–29 June and 24–28 August 2009, 22–27 June and 29 July–2 August 2010, 12–16 June and 10–14 August 2011), while all other gradients were each sampled during one year (N gradient: 29 June–2 July and 27–30 August 2011; F gradient: 25–26 June and 2–4 September 2008; A gradient: 16–18 June and 7–9 August 2010; K gradient: 18–20 June and 1–3 September 2009).

Mean temperatures in July were calculated from the web-based archive of weather data for each study year (<www.rp5.ru>); multiyear averages were obtained using New_LocClim (FAO 2006).

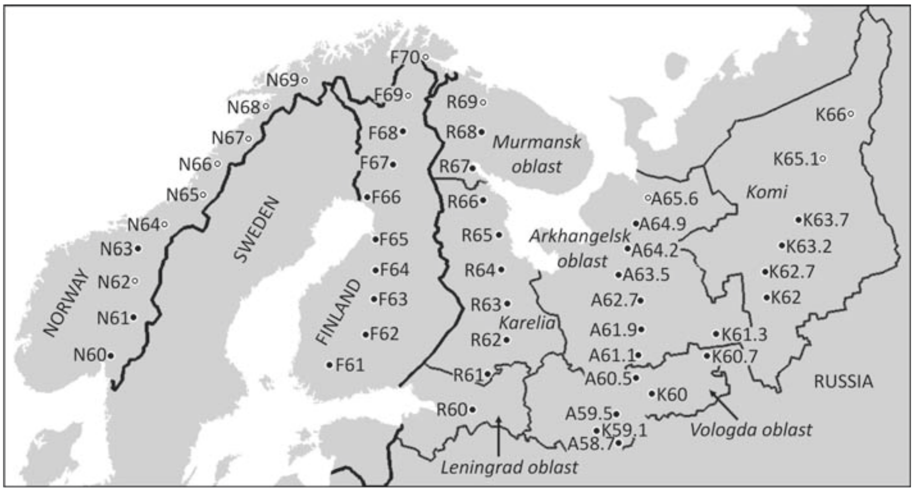

Figure 1. Study area and study sites. Name of each study site contains the code of the gradient and the approximate latitude (for the coordinates of study sites see Supplementary material Appendix 1). Open circles denote study sites where the samples were collected only from *Betula pubescens*. Note that only the R gradient was sampled during all four consecutive years.

Sampling and processing

Mature trees (generally aged 20 yr or more) with lower branches that can be reached from the ground (i.e. within 2 m height) were selected on a 'first found, first sampled' basis. One branch about 50 cm in length (with approximately 80 leaves) was collected from each of the five trees of each birch species at each site on each sampling date. The sampled trees were not tagged and therefore early and late summer samples were generally collected from different trees.

In the laboratory, the leaves on each branch were counted, and each leaf was carefully inspected for damage caused by insect feeding. Mines of the most abundant taxa (*Caloptilia* sp., *Coleophora* sp., *Eriocrania* sp., *E. sparrmannella*, *Incurvaria pectinea*, *Parornix* sp. and *Phyllonorycter* sp.) were identified and counted by MVK during the sorting of fresh samples, and only a fraction of these mines was retained. When the larva was alive, we attempted rearing the adult. All the mines made by other, less abundant taxa, were preserved and then identified by EvN, mostly using the European leafminer site (Ellis 2012). Many mines were checked or re-identified by W. N. Ellis. Identification of mines is not always straightforward as they are a product of the activity of the insect, rather than a character of the insect itself. The shape of the mines can be influenced by external factors such as weather or disease. As a result, some of mines (presumably $< 1\%$) may have been misidentified. In total, we have processed 5824 mines made by 30 species or groups of closely related congeneric species that cannot be distinguished on the basis of their mines (taxa hereafter) from four insect orders (Table 1, Supplementary material Appendix 2). The voucher specimens of leaf mines are deposited in the Naturalis Biodiversity Center (Leiden); the reared adults are deposited in the Finnish Museum of Natural History (Helsinki).

Ten undamaged leaves randomly selected from each branch were dried at +80°C for 24 h and weighed to the nearest 0.001 g. Branch-specific weight of foliage was calculated by multiplying mean leaf weight by the number of leaves. Abundance of leafminers was expressed in mines kg^{-1} (d.w.) of foliage. This measure of abundance was favoured over the proportion of mined leaves, because leaf size decreased and specific leaf weight increased with latitude (data not shown). Average leaf weight across our samples was 0.054 g, thus an average proportion of mined leaves can be obtained by dividing the reported abundance values by 18 520 (average number of leaves in 1 kg of dry foliage).

As a measure of diversity, we used Shannon's index ($H = -\Sigma[p_i \times \ln p_i]$, where p_i = the proportion of *i*th species of the total abundance), calculated from the site-specific numbers of mines separately for each birch species. For sites with no leafminers H was set to 0. We also calculated the number of taxa recorded in each study site; note that this method underestimates actual species richness, because the five recognizable taxonomic units used in our study (*Caloptilia* sp., *Coleophora* sp., *Eriocrania* sp., *Parornix* sp. and *Phyllonorycter* sp.) each contain more than one species (Table 1). Since we applied similar sampling efforts at each site and leafminers were not randomly distributed over the study area, the rarefaction method was not used (Gotelli and Colwell 2001).

Data analysis

Distribution of individual leafminers both among branches and among study sites was greatly skewed: no mines were found in 426 of 1430 collected branches, and the maximum number of mines recorded in one branch was 225. Therefore for all taxon-specific data we used non-parametric methods of statistical analysis. In contrast, the log-transformed overall abundance of leafminers (all taxa pooled and averaged per study site × study year × birch species) met the normality assumption, thus justifying the use of parametric statistics (ANOVA and regression analysis).

Table 1. Characteristics of leafminers.

Order	Taxon	Number of mines	Timing of damage[1]	Change of life habit[2]	Hibernating stage	Hosts other than birches[3]
Coleoptera	*Anoplus plantaris* (Naezen)	52	early	no	imago	yes
	Orchestes rusci (Herbst)	149	early-mid	no	imago	no
	Orchestes testaceus (Müller)	33	early	no	imago	yes
	Ramphus pulicarius (Herbst)	57	late	no	imago	yes
Lepidoptera	*Atemelia torquatella* (Lienig and Zeller)	9	late	yes	larva	no
	Bucculatrix demaryella (Duponchel)	464	late	yes	pupa	no
	Caloptilia sp.[4]	1257	early-mid	yes	imago	no
	Coleophora sp.[5]	500	early-mid	yes	larva	yes
	Ectoedemia minimella (Zetterstedt)	75	mid-late	no	prepupa	no
	Ectoedemia occultella (Linnaeus)	11	mid-late	no	prepupa	no[6]
	Eriocrania sp.[7]	846	early	no	prepupa	no
	Eriocrania sparrmannella (Bosc)	96	early-mid	no	prepupa	no
	Heliozela hammoniella (Sorhagen)	2	late	yes	pupa	no
	Incurvaria pectinea (Haworth)	1099	early-mid	yes	pupa	yes
	Parornix sp.[8]	535	mid-late	yes	pupa	no
	Phyllonorycter sp.[9]	29	mid-late	no	pupa	–
	Phylloporia bistrigella (Haworth)	25	mid-late	no	pupa	no
	Recurvaria nanella (Denis and Schiffermüller)	1	late	yes	larva	yes
	Stigmella betulicola (Stainton)	51	late	no	prepupa	no
	Stigmella confusella (Wood)	46	mid-late	no	prepupa	no
	Stigmella continuella (Stainton)	7	mid-late	no	prepupa	no
	Stigmella lapponica (Wocke)	209	mid	no	prepupa	no
	Stigmella luteella (Stainton)	46	late	no	prepupa	no
Hymenoptera	*Fenusa pumila* (Leach)	100	early-late	no	prepupa	no
	Fenusella nana (Klug)	26	early-late	no	prepupa	no
	Heterarthrus nemoratus (Fallén)	4	mid-late	no	pupa	no
	Profenusa thomsoni (Konow)	3	late	no	prepupa	no
	Scolioneura betuleti (Klug)	25	early-late	no	prepupa	no
	Scolioneura vicina (Konow)	1	early	no	pupa	no
Diptera	*Agromyza alnibetulae* (Hendel)	30	mid-late	no	pupa	no
–	unknown miner	36	–	–	–	–

[1] Early: before termination of leaf growth; mid: between termination of leaf growth and termination of long-shoot growth; late: after termination of long-shoot growth.

[2] Yes: only the first instar(s) are mining in leaves, then change the feeding habit; no: all instars are leafminers.

[3] Refers only to the study region.

[4] The majority (ca 85%) of reared adults belonged to *C. suberinella* (Tengström), 15% to *C. betulicola* (Hering) and 1 specimen to *C. populetorum* (Zeller).

[5] The vast majority ($>95\%$) of collected larvae belonged to *C. serratella* (Linnaeus). Note that each larva produces multiple mines.

[6] Although *E. occultella* was once found on *Salix pentandra* in Finland, this seems a single incidence, and thus we regard this species as monophagous.

[7] Primarily *E. semipurpurella* Stephens (s.l.) and *E. sangii* Wood.

[8] Includes *P. betulae* (Stainton) and *P. loganella* (Stainton).

[9] Three species were reared to adults: *P. cavella* (Zeller), *P. ulmifoliella* (Hübner) and *P. coryfoliella* (Hübner).

Seven species that were each represented by less than ten mines (Table 1) were excluded from taxon-specific analyses. However, these species were accounted for in the analyses of total abundance and diversity of leafminers in latitudinal gradients.

All leafminers feeding on birch in our study region produce one generation per year. Thus, the differences between two censuses may indicate either late infestation by some leafminers (higher abundance recorded in late summer) or premature abscission of mined leaves (higher abundance recorded in early summer). To determine which census gave a better density estimate of a particular leafminer, we compared (by Kruskal–Wallis test) abundance of each taxon between two censuses using gradient × study year × birch species combinations as replicates. The 2008 and 2010 data from the R gradient were excluded from these comparisons because of the deviating dates of the first census in 2008 and of the second census in 2010 (both were conducted in mid-summer). If the differences between the censuses were significant ($p < 0.05$), then the analysis of latitudinal patterns was based on the census that yielded the higher estimate of abundance. If the differences were not significant, then the analysis was based on the mean abundance (averaged from two censuses). Abundance of leafminers was also compared (by Kruskal–Wallis test) between the two birch species.

Latitudinal patterns in both abundance and diversity were quantified by calculating Spearman rank correlation coefficients with latitudes of sampling sites. For abundance, individual correlations refer to gradient × study year × birch species combination (249 coefficients). For Shannon diversity index, correlations were calculated separately for early and late summer censuses (32 coefficients). Latitudinal change in another measure of diversity, the number of leafminer taxa recorded during all study years, was explored only for the R gradient. Sources of variation in the relationships of both abundance and diversity with latitude were explored using meta-analysis. To calculate effect sizes (ES) individual correlation coefficients were *z*-transformed and weighted by their sample size using the standard procedure in the MetaWin program (Rosenberg et al. 2000). In our study the positive ES values indicate increases in abundance or diversity with latitude. If the number of ES in an individual group was nine or less, a bootstrap estimate of the 95% confidence interval (CI_{95}) was used. The effect was considered statistically significant if its CI_{95} did not include zero.

Meta-analysis was performed using random effects categorical models that compared ES between censuses, birch species, community-level and taxon-specific responses, individual species and groups of closely related species, as well as among groups of taxa that differ in life history traits. The variation in the ES among the classes of categorical variables was explored by calculating the heterogeneity index (Q_B) and testing it against the χ^2 distribution (Gurevitch and Hedges 2001).

The sources of variation in overall abundance of leafminers were explored by ANCOVA (SAS GLM procedure). We used a model selection approach to identify which of the temperature variables (multiyear average or current-year temperatures in July at both the northern and the southern end of the latitudinal gradient, or the differences in current-year temperatures in July between the ends of the gradient) explained the largest part of annual variation in ES. We also compared the magnitudes of annual variations (quantified by coefficients of variation) in overall abundance of leafminers and in temperature in July between the northern and southern ends of the R gradient.

Results

Differences between early and late summer censuses

Most of the leafminers demonstrated significant differences in abundance between samples collected in early and in late summer (Table 2). The average (per study site × birch species) number of leafminer taxa increased from 3.17 in early summer to 4.57 in late summer ($\chi^2 = 27.9$, DF = 1, $p < 0.0001$). Consistently, the Shannon diversity index (Supplementary material Appendix 3) increased from 0.72 to 1.08 ($\chi^2 = 36.1$, DF = 1, $p < 0.0001$). However, total abundance of leafminers (Supplementary material Appendix 3: 1050 and 817 mines kg^{-1} of foliage, respectively; $\chi^2 = 0.01$, DF = 1, $p = 0.96$), as well as latitudinal changes in their diversity ($Q_B = 0.26$, DF = 1, $p = 0.62$) and abundance ($Q_B = 0.60$, DF = 1, $p < 0.49$), did not differ between two censuses.

Differences between birch species

Neither the total abundance of leafminers ($\chi^2 = 0.00$, DF = 1, $p = 0.98$) nor the number of their taxa ($\chi^2 = 0.15$, DF = 1, $p = 0.70$) differed between birch species. However, four of 23 taxa of leafminers were more abundant on

Table 2. Differences in abundance of leafminers between two birch species and between two censuses, and census selected for subsequent analyses.

	Abundance, mines kg^{-1}		Differences between birch species		Abundance, mines kg^{-1}		Differences between censuses		
Taxon	*B.pendula*	*B.pubescens*	χ^2	p	Early summer	Late summer	χ^2	p	Census selected for the analyses
Agromyza alnibetulae	17.4	0	14.6	0.0001	1.4	8.8	4.74	0.03	2
Anoplus plantaris	6.3	8.6	1.64	0.20	17.6	4.2	1.58	0.21	1 + 2
Bucculatrix demaryella	113.3	182.9	0.01	0.94	0.9	174.1	50.4	< 0.0001	2
Caloptilia sp.	347.6	229.3	1.52	0.22	313.0	108.5	9.01	0.0027	1
Coleophora sp.	110.5	156.0	1.15	0.28	159.1	18.1	21.7	< 0.0001	1
Ectoedemia minimella	10.2	30.7	7.25	0.0071	0	24.0	34.9	< 0.0001	2
E. occultella	1.6	5.6	0.07	0.80	0	5.2	5.14	0.02	2
Eriocrania sp.	261.0	186.8	9.98	0.0016	232.0	74.1	17.7	< 0.0001	1
E. sparrmannella	22.5	11.1	1.32	0.25	21.6	11.7	0.09	0.77	1 + 2
Fenusa pumila	52.3	2.9	18.1	< 0.0001	2.7	31.6	13.2	0.0003	2
Fenusella nana	3.6	9.1	1.19	0.28	0.2	5.9	8.0	0.0047	2
Incurvaria pectinea	310.9	63.7	1.54	0.21	288.8	93.0	0.88	0.35	1 + 2
Orchestes rusci	42.0	25.3	1.04	0.31	40.8	10.0	14.3	0.0002	1
O. testaceus	11.7	6.4	1.61	0.20	11.2	2.2	3.07	0.08	1
Parornix sp.	154.4	130.2	0.24	0.62	28.9	123.1	36.7	< 0.0001	2
Phyllonorycter sp.	2.68	6.21	0.67	0.41	4.69	7.3	2.04	0.15	1 + 2
Phylloporia bistrigella	0	14.7	13.5	0.0002	0.5	9.6	11.1	0.0009	2
Ramphus pulicarius	12.0	24.2	1.01	0.32	0	25.5	22.1	< 0.0001	2
Scolioneura betuleti	13.9	2.9	3.81	0.05	0	9.1	8.35	0.0039	2
Stigmella betulicola	10.5	13.3	0.08	0.78	0.5	12.4	16.8	< 0.0001	2
Stigmella confusella	2.1	21.9	8.62	0.0033	1.0	11.4	9.89	0.0017	2
Stigmella lapponica	30.3	30.2	0.05	0.82	26.2	24.2	1.77	0.18	1 + 2
Stigmella luteella	12.0	13.6	0.13	0.72	0	15.0	22.1	< 0.0001	2
All leafminers combined	1095.0	792.4	0.00	0.99	1170.0	819.7	0.19	0.66	1 + 2

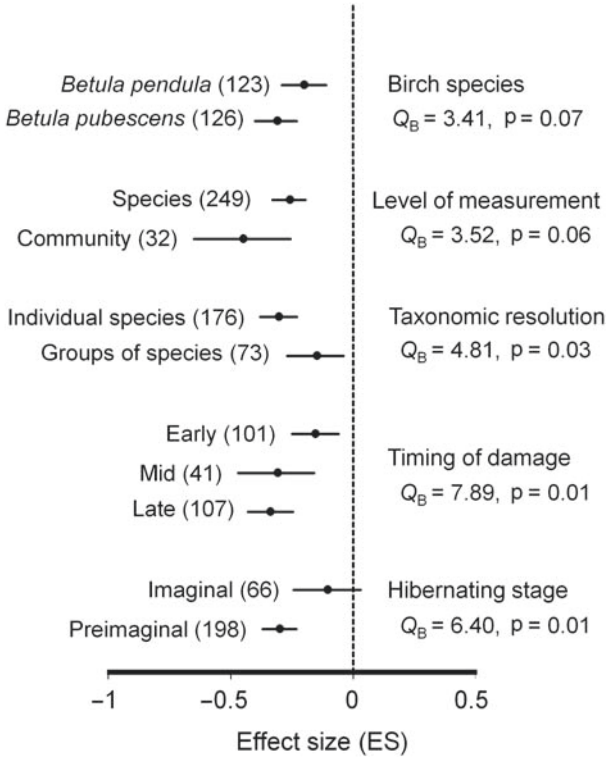

Figure 2. Sources of variation in latitudinal patterns of abundance of leafminers (results of meta-analysis). The negative ES values indicate decrease in abundance with latitude. Horizontal lines denote 95% confidence intervals; sample sizes are shown in brackets; Q_B, between-class heterogeneity.

B. pendula, and another three taxa were more abundant on *B. pubescens* (Table 2).

Latitudinal changes in the abundance of leafminers tended to be larger for *B. pubescens* than for *B. pendula* (Fig. 2). Diversity of leafminers on both birch species decreased with latitude to a similar extent (Table 3; $Q_B = 1.40$, DF = 1, $p = 0.22$).

Differences among geographical gradients and study years

The total abundance of leafminers varied among the geographical gradients and study years (Supplementary material Appendix 3, Table 4). Diversity was lowest in the F gradient and highest in the N gradient (Supplementary material Appendix 3: $\chi^2 = 11.3$, DF = 4, $p = 0.02$).

Latitudinal patterns in the abundance of individual leafminers ($Q_B = 31.8$, DF = 4, $p = 0.001$), as well as in their overall abundance ($Q_B = 23.9$, DF = 4, $p = 0.002$) and diversity ($Q_B = 29.8$, DF = 4, $p = 0.001$), differed among the five geographical gradients. However, these differences are more likely a result of the annual differences in weather conditions (as indicated by the significant interaction between the study year and the latitude within the R gradient: $F_{3,\,140} = 2.95$, $p = 0.035$), rather than a result of the geographical variation.

Variation in the overall abundance of leafminers among the study years in the three northernmost study sites of the R gradient was nearly twice as large as in the three southernmost sites (coefficients of variation: 18.8 and 10.0%, respectively; $F_{1,\,9} = 5.53$, $p = 0.04$). During the same years variation in July temperatures in the southernmost sites was larger than in the northernmost sites (11.9 and 16.7%, respectively; $F_{1,\,4} = 92.3$, $p = 0.0007$).

Comparison between the linear regression models with different temperature variables demonstrated that variation in ES reflecting changes in overall abundance of leafminers with latitude (Fig. 3) was best explained by current-year temperature in July at the northern end of the gradient. During cold years, abundance of leafminers significantly decreased with latitude, while during warm years it was either independent from latitude or even increased towards the north (Fig. 4). Effects of temperature on latitudinal patterns in diversity of leafminers did not reach the level of significance (*B. pendula*: $r_S = 0.60$, $n = 8$, $p = 0.12$; *B. pubescens*: $r_S = 0.36$, $n = 8$, $p = 0.38$).

Latitudinal patterns in abundances of individual leafminers

We have obtained 249 correlation coefficients for 368 taxon × gradient × study year × birch species combinations. Among these coefficients, 33 were significant at the probability level $p = 0.05$ (Table 3). In general, abundance of individual taxa decreased with latitude: an overall effect was negative (ES = −0.26, $CI_{95} = -0.32$ to −0.20). This conclusion remained valid when the ES based on the limited number of records (i.e. the single record per gradient) or study sites (data for *B. pendula* from the N gradient consisting of three study sites only) were excluded from the analysis (data not shown).

We detected significant heterogeneity in changes of abundance of individual taxa with latitude ($Q_B = 88.5$, DF = 22, $p = 0.001$). The abundance of 14 taxa decreased with latitude and increased with latitude for one group (*Caloptilia* sp.). The remaining eight taxa showed no latitudinal pattern (Supplementary material Appendix 4). This variation was not explained by either absolute abundance of different taxa (contrast between taxa represented by more vs less than 100 mines: $Q_B = 0.02$, DF = 1, $p = 0.51$) or insect order ($Q_B = 2.29$, DF = 3, $p = 0.51$). However, individual species showed stronger latitudinal changes in abundance than groups of congeneric species (Fig. 2). Species feeding early in the season demonstrated weaker correlations between densities and latitudes of sampling sites than species feeding in mid and late summer (Fig. 2). Species hibernating at pre-imaginal stages showed stronger decline with latitude than species hibernating as imago (Fig. 2). Species whose larvae change life habit during their development demonstrated the same latitudinal patterns as species with larvae that spend their entire life in the mine ($Q_B = 0.20$, DF = 1, $p = 0.65$). Specialist leafminers, i.e. those feeding only on birches, showed the same latitudinal patterns in abundance as generalist leafminers ($Q_B = 0.14$, DF = 1, $p = 0.71$).

Table 3. Latitudinal patterns (Spearman rank correlation coefficients with latitudes of study sites) in abundance and diversity of leafminer taxa.

	N, 2011		F, 2008		R, 2008		R, 2009		R, 2010		R, 2011		A, 2010		K, 2009	
Taxon	*pen* n = 3	*pub* n = 10	*pen* n = 8	*pub* n = 9	*pen* n = 9	*pub* n = 10	*pen* n = 9	*pub* n = 10	*pen* n = 9	*pub* n = 10	*pen* n = 9	*pub* n = 10	*pen* n = 9	*pub* n = 10	*pen* n = 8	*pub* n = 10
Agromyza alnibetulae	–	–	–	–	(−0.41)	–	(−0.41)	–	(−0.55)	–	(0.27)	–	(−0.64)	–	**−0.72**	–
Anoplus plantaris	(−0.87)	−0.05	(−0.25)	–	–	–	−0.11	–	–	–	(−0.55)	–	0.27	–	−0.58	−0.28
Bucculatrix demaryella	–	(−0.52)	**−0.76**	**−0.87**	−0.51	−0.55	**−0.76**	−0.51	−0.34	−0.47	−0.39	**−0.85**	**−0.76**	**−0.76**	**−0.95**	**−0.87**
Caloptilia sp.	0.50	−0.37	–	–	0.46	−0.02	0.18	−0.17	0.49	0.03	0.47	−0.06	**0.97**	**0.68**	0.47	0.11
Coleophora sp.	–	−0.12	−0.45	**−0.66**	−0.27	−0.29	−0.48	0.03	−0.63	(−0.29)	**−0.73**	0.16	−0.24	−0.53	−0.49	0.04
Ectoedemia minimella	–	0.57	−0.11	−0.32	–	–	0.69	0.51	0.05	0.22	–	(0.06)	–	(−0.41)	(−0.41)	0.29
E. occultella	–	(0.06)	–	**−0.73**	–	–	–	–	–	–	–	–	–	–	−0.23	–
Eriocrania sp.	−0.50	0.48	**−0.79**	−0.55	(0.00)	−0.34	−0.63	−0.82	−0.17	**−0.71**	0.45	**−0.73**	**0.79**	0.35	−0.30	−0.48
E. sparrmannella	(0.00)	−0.08	**−0.73**	−0.14	−0.07	−0.48	−0.14	−0.25	−0.20	−0.37	0.08	–	0.29	0.23	0.10	−0.11
Fenusa pumila	(0.00)	–	–	–	**−0.68**	–	**−0.74**	–	–	–	**−0.76**	(−0.52)	−0.24	(−0.17)	−0.16	(−0.52)
Fenusella nana	–	–	(−0.58)	−0.55	(0.27)	(−0.17)	–	−0.53	–	(−0.29)	(0.14)	−0.22	–	–	(0.08)	–
Incurvaria pectinea	–	**−0.70**	0.33	0.09	−0.59	–	(−0.41)	–	0.03	−0.19	−0.03	−0.32	(0.55)	0.37	(0.08)	–
Orchestes rusci	–	−0.16	−0.55	(−0.54)	–	–	−0.24	−0.53	−0.11	−0.17	−0.11	**−0.79**	−0.11	−0.20	0.08	−0.17
O. testaceus	–	–	(−0.24)	–	–	–	–	–	(−0.14)	(−0.41)	−0.32	(−0.41)	0.59	−0.07	(0.25)	–
Parornix sp.	(−0.87)	0.19	**−0.89**	**−0.80**	−0.08	−0.21	−0.55	−0.19	0.53	(0.62)	−0.55	−0.52	0.42	−0.50	**−0.76**	−0.30
Phyllonorycter sp.	(0.87)	0.16	(−0.58)	(−0.41)	–	−0.12	0.04	(−0.41)	–	(0.17)	–	–	(0.27)	(0.29)	−0.20	−0.31
Phylloporia bistrigella	–	(−0.29)	–	(−0.55)	–	(−0.29)	–	−0.35	–	(−0.29)	–	**−0.70**	–	**−0.72**	–	**−0.70**
Ramphus pulicarius	–	–	−0.52	−0.82	–	–	−0.43	−0.59	–	–	(0.00)	–	(0.00)	−0.24	–	−0.02
Scolioneura betuleti	–	–	(−0.41)	(−0.41)	−0.32	–	0.14	−0.39	(−0.14)	–	–	–	–	–	(−0.25)	–
Stigmella betulicola	–	−0.24	**−0.76**	–	(−0.41)	–	–	−0.53	−0.64	−0.32	–	–	−0.18	0.09	0.51	0.18
Stigmella confusella	–	–	–	−0.46	–	(−0.05)	–	−0.53	(−0.14)	**−0.70**	–	−0.57	–	−0.32	−0.19	(−0.52)
Stigmella lapponica	−1.00	−0.26	−0.06	−0.28	−0.37	−0.16	0.42	−0.44	−0.35	−0.26	−0.34	−0.53	0.53	0.07	−0.54	−0.56
Stigmella luteella	**1.00**	−0.01	–	–	–	–	(−0.14)	−0.16	−0.15	0.07	–	(−0.52)	–	–	0.60	−0.23
Diversity, first census	**1.00**	−0.08	**−0.91**	**−0.75**	−0.57	−0.65	−0.65	−0.58	−0.65	−0.26	−0.24	**−0.75**	0.62	−0.16	0.19	−0.45
Diversity, second census	−0.50	−0.24	**−0.80**	**−0.97**	**−0.80**	−0.62	−0.38	**−0.83**	−0.57	−0.57	**−0.82**	**−0.92**	0.20	−0.18	0.29	−0.24

Missing values indicate absence of leafminer in the particular data set (gradient × study year × birch species); coefficients significant at p = 0.05 are shown in bold; *pen, Betula pendula*; *pub, B. pubescens*; n = number of study sites within the gradient. Values based on observations of species in a single plot within the gradient are shown in parentheses.

Table 4. Sources of variation in overall abundance of leafminers.

Source of variation	DF	Type III sum of squares	*F*	p
Gradient	4	10.0	2.82	0.0255
Study year	3	23.6	8.86	<0.0001
Latitude	1	19.3	21.67	<0.0001
Latitude × study year	3	24.5	9.20	<0.0001
Error	263	233.8		

Structure of data (consult text) does not allow the analysis of interactions between gradient and study year.

Latitudinal patterns in leafminer community characteristics

The latitudinal patterns in overall abundance and diversity of leafminer community greatly varied among study years and gradients (Fig. 3; Table 3). Although the proportions of negative correlations with latitude were only 44% for the abundance data (Fig. 3) and 33% for the diversity data (Table 3), meta-analysis demonstrated that both these characteristics generally decreased with latitude (abundance: $ES = -0.45$, $CI_{95} = -0.68$ to -0.23; diversity: $ES = -0.57$, $CI_{95} = -0.80$ to –0.35). The magnitudes of the latitudinal changes did not differ ($Q_B = 0.08$, $DF = 1$, $p = 0.77$) between the number of leafminer taxa ($ES = -0.62$, $CI_{95} = -0.85$ to –0.38) and the Shannon diversity index ($ES = -0.57$, $CI_{95} = -0.81$ to -0.34). The latitudinal pattern in overall abundance was expressed better than in abundances of individual taxa (Fig. 2). The numbers of leafminer taxa recorded in the northernmost study sites of the R gradient (selected for this analysis because of a significantly larger amount of collected material relative to all other gradients) were between one-half and one-third of the numbers recorded in the southernmost study sites (Fig. 5). In other words, the decrease in the total abundance of leafminers towards the north resulted from decrease in both the number of taxa and the abundance of most of taxa.

Discussion

Latitudinal patterns in abundance and diversity of birch-feeding leafminers

Our study provides one of the very first comprehensive assessments of large-scale geographical variation in abundance of herbivorous insects, that is based on a properly replicated sampling design. In spite of pronounced variation among latitudinal gradients, study years and taxa of leafminers in both absolute densities and patterns of latitudinal changes, the overall conclusion of our study is straightforward: abundance of leafminers feeding on two birch species in boreal forests of northern Europe significantly decreases with latitude. This result is consistent with several earlier studies that show decrease in the abundance of leafminers feeding on *Nothofagus pumilio* along altitudinal gradients in the northern Patagonian Andes, Argentina (Garibaldi et al. 2011) and the decrease in foliar loss of birches (resulting from feeding of all groups of herbivorous insects) between 58° and 69°N in Scandinavia (Kozlov 2008). However, our finding contradicts the conclusions of other studies of leafminers, which found either no geographical pattern (in Australia: Sinclair and Hughes 2008) or an increase in leafminer abundance with latitude (in Europe: Gaston et al. 2004). This inconsistency in outcomes of individual studies may reflect the differences among study systems, geographical regions, or weather conditions during the study years.

The diversity of leafminers feeding on birch also decreases with latitude (Fig. 5). Although this conclusion is in line with the general regularity, i.e. with an overall increase in species richness from the poles towards the equator (Gaston and Williams 1996, Willig et al. 2003), this pattern has never been demonstrated for a community of insects feeding on the same host (discussed by Adams et al. 2010). Thus, we provide the first direct evidence that the southern populations of a certain tree species are attacked by a larger number of herbivore species than its northern populations. A similar conclusion was reached by Adams et al. (2010); however, it was based on counting types of foliar damage rather than herbivore taxa.

The lower abundance of leafminers feeding on birches in northernmost regions results not only from the lower diversity, but also from the lower abundances of more than half (14 of 23) of the studied taxa. The latter effect is most likely associated with the direct impact of climate on insects: lower summer temperatures decrease the fitness of insect herbivores both directly (Bale et al. 2002) and indirectly. In particular, low temperatures cause an increase in developmental time of insects, which may lead to a higher risk of being killed by enemies (Lawton and McNeill 1979, Häggström and Larsson 1995). However, we cannot exclude the effects of latitudinal change in plant quality for herbivores. Two meta-analyses showed that overall, chemical defences were significantly higher in plants from higher latitudes (Moles et al. 2011), and that feeding on plants grown at elevated temperatures generally improved herbivore performance (Zvereva and Kozlov 2006). Although the latter effect obviously results from integrated changes in leaf physical and chemical traits (Zvereva and Kozlov 2006), tentatively it can be associated with the decrease in total foliar concentrations of phenolics with temperature, which was discovered in white birch (Kuokkanen et al. 2001).

The observed geographical variation in the abundance of leafminers may also reflect heritable differences in leaf quality for herbivores between birch populations from different parts of latitudinal gradients. A reciprocal transplant experiment with *Nothofagus pumilio* between low- and high-elevation sites demonstrated that at both planting sites, plants from a low-elevation origin experienced higher damage than plants from a high-elevation origin (Garibaldi et al. 2011). Similarly, birches from the northern populations can be more resistant to herbivory, as indicated by common garden trials with white birch from localities in Finland, Sweden, Estonia, Scotland and Russia, ranging in latitudes from 53° to 67°N, where browsing by moose decreased with increasing latitude of seed origin (Vihera-Aarnio and Heikkila 2006).

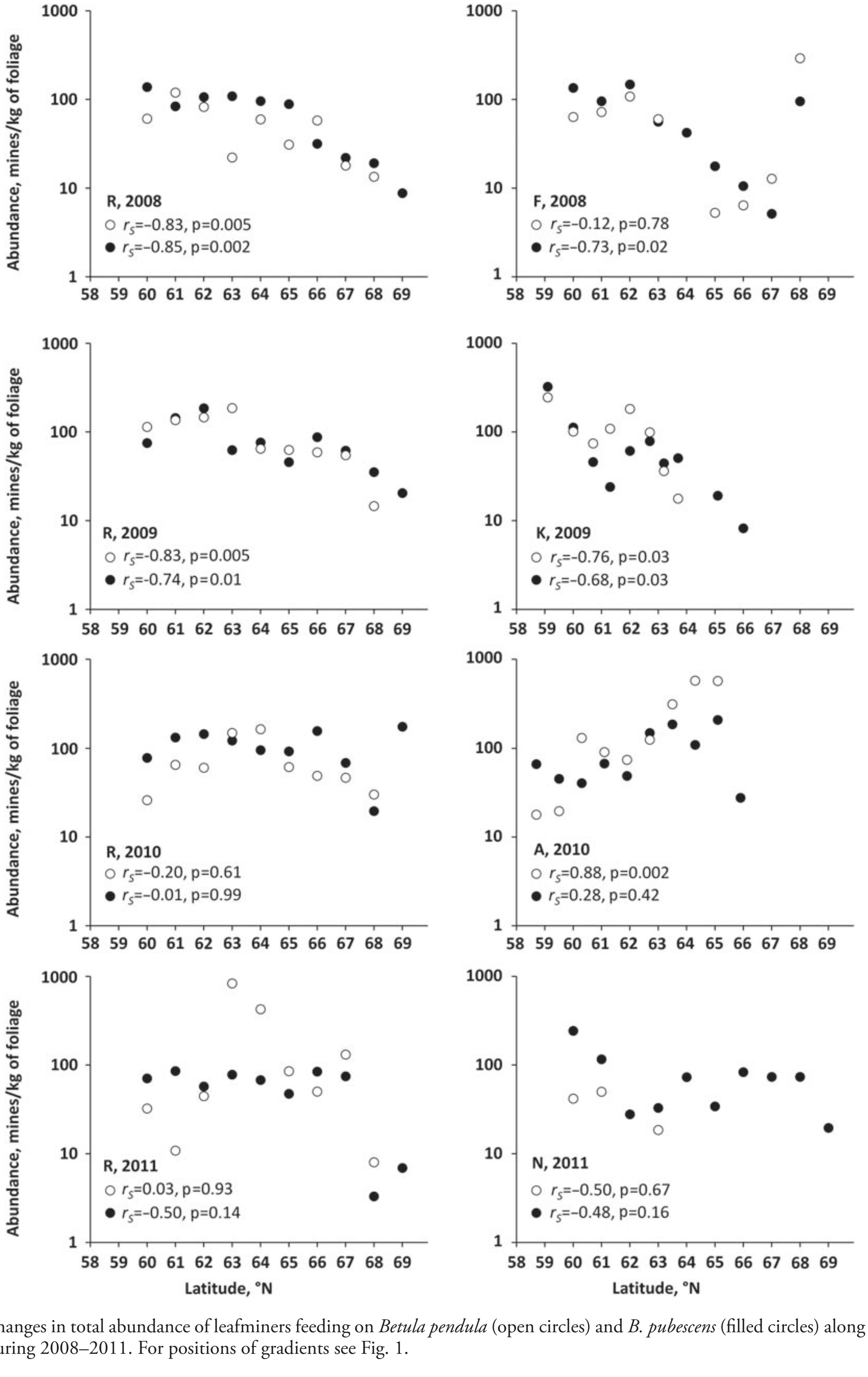

Figure 3. Changes in total abundance of leafminers feeding on *Betula pendula* (open circles) and *B. pubescens* (filled circles) along latitudinal gradients during 2008–2011. For positions of gradients see Fig. 1.

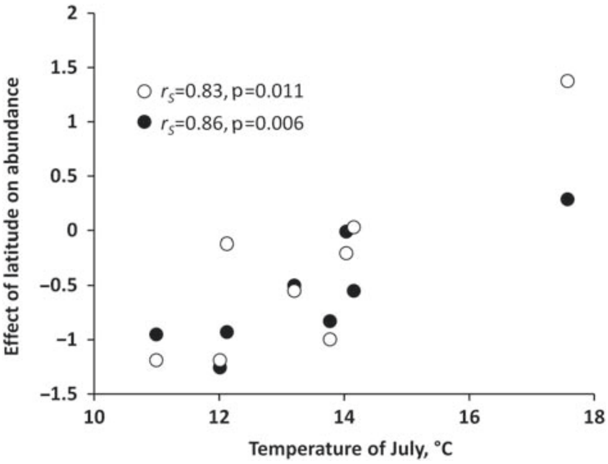

Figure 4. Correlation between effect sizes (ES) reflecting changes in total abundance of leafminers feeding on *Betula pendula* (open circles) and *B. pubescens* (filled circles) along latitudinal gradients and temperatures in June at the northern ends of the gradients (data of 2008–2011). The negative ES values indicate decrease in abundance with latitude.

Sources of variation in latitudinal patterns of herbivory

Spatial and temporal replication of data collection from the same study system allows identification of several sources of variation which are crucial for revealing the general regularities (Kozlov et al. 2009). Using this approach, we demonstrated for the first time that latitudinal patterns in herbivory on the same host plant differed among geographical regions, study years and herbivores. In spite of the significant general trend, one third to two thirds of individual data sets showed either no correlation with latitude or an increase in abundance towards the north (Fig. 3, Table 3, Supplementary material Appendix 4). The detected variation stresses the need to collect more information on latitudinal changes in herbivory from different study systems in different parts of the globe before the existence of the general pattern can be either confirmed or rejected with a sufficient level of confidence.

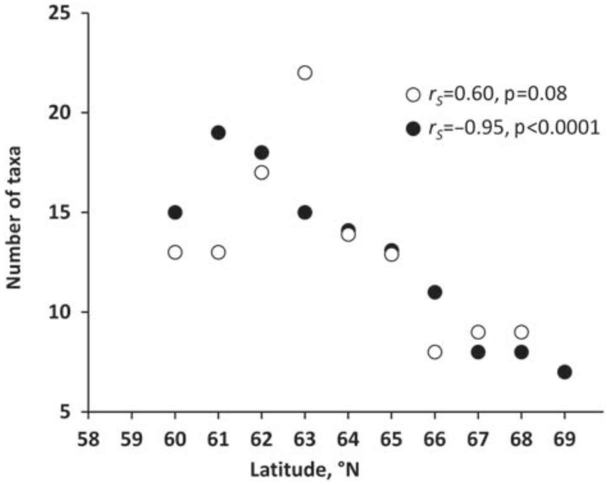

Figure 5. Changes in total number of taxa of leafminers feeding on *Betula pendula* (open circles) and *B. pubescens* (filled circles) along the R gradient (data of 2008–2011). For the list of taxa consult Table 1.

The importance of temperature in shaping latitudinal patterns of herbivory was supported by the pronounced differences between cold and warm years (Fig. 4). In addition, variation in the abundance of leafminers was higher at the northern sites than at the southern sites of the R gradient, although the respective variation in summer temperatures showed the opposite pattern. In an exceptionally warm year we even observed inversion of the latitudinal pattern, i.e. an increase in leafminer abundance with latitude (Fig. 3: A gradient). Thus, changes in herbivore abundance in response to summer temperatures depended on the latitude of the locality, and the highest responses occurred in the north. This result agrees well with the predictions of Deutsch et al. (2008), who concluded that insects living at high latitudes, often below their thermal optima, are constrained by temperature and therefore will benefit from temperature increase. In contrast, at lower latitudes insects live at or even above their thermal optima and therefore the effect of temperature increase will be smaller or even negative (Deutsch et al. 2008).

The pronounced variation in latitudinal patterns of abundances between the leafminer taxa points to the need to clearly distinguish between studies reporting individual (i.e. species-specific) and community-level data in the analyses of latitudinal patterns in herbivory. First, the pattern detected in one herbivore species may differ from the community-wide pattern. For example, abundance of *Bucculatrix demaryella* on white birch in the A gradient decreased with latitude (Table 3), while the total abundance of leafminers increased (Fig. 3). Second, the same herbivore species may show opposite latitudinal trends in different parts of its distribution range or in different study years (Table 3).

The discovered variation in latitudinal patterns of abundance between the taxa of leafminers was not random: it was associated with several life history traits, such as timing of damage and hibernating stage. Although causal relationships cannot be invoked from our data, we do suggest that weaker latitudinal changes in the abundance of species hibernating as adults (Fig. 2) hint at lower sensitivity of imagos (relative to pre-imaginal stages) to climate. Larger effects of latitude on species feeding in late summer (Fig. 2) may be associated with a stronger seasonal decline in suitability of birch foliage for herbivores at higher latitudes due to the effects of temperature on the accumulation of phenolics (Kuokkanen et al. 2001, Riipi et al. 2002).

Conclusions

We demonstrated that, in general, both abundance and diversity of birch-feeding leafminers in boreal forests of northern Europe significantly decreased with latitude. However, we discovered pronounced variation among regions, study years and herbivores in both absolute values and patterns of latitudinal change. The disparities, found within one guild of insect herbivores feeding on the same host plant, indicate that the data from latitudinal gradients should be used with caution when predicting levels of herbivory under future climate scenarios. Variation in latitudinal patterns of leafminer abundance was best explained by the mean temperatures in July at the northern ends of the gradients. During years with cold summers, the abundance decreased with latitude, while during warm years this correlation weakened, and during an exceptionally warm year, the abundance increased with latitude. In the northern boreal forests (66° to 69°N) leafminer populations demonstrated larger changes in densities in response to annual temperature variations than in the boreo-nemoral forests (59° to 62°N), suggesting that climate warming is likely to cause a larger increase in herbivory at higher latitudes than at lower latitudes.

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Supplementary material (Appendix ECOG-00272 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.