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ORIGINAL ARTICLE

Poleward increase in feeding efficiency of leafminer *Stigmella lapponica* (Lepidoptera: Nepticulidae) in a latitudinal gradient crossing a boreal forest zone

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Abstract Damage to plant communities imposed by insect herbivores generally decreases from low to high latitudes. This decrease is routinely attributed to declines in herbivore abundance and/or diversity, whereas latitudinal changes in per capita food consumption remain virtually unknown. Here, we tested the hypothesis that the lifetime food consumption by a herbivore individual decreases from low to high latitudes due to a temperature-driven decrease in metabolic expenses. From 2016 to 2019, we explored latitudinal changes in multiple characteristics of linear (gallery) mines made by larvae of the pygmy moth, *Stigmella lapponica*, in leaves of downy birch, *Betula pubescens*. The mined leaves were larger than intact leaves at the southern end of our latitudinal gradient (at 60°N) but smaller than intact leaves at its northern end (at 69°N), suggesting that female oviposition preference changes with latitude. No latitudinal changes were observed in larval size, mine length or area, and in per capita food consumption, but the larval feeding efficiency (quantified as the ratio between larval size and mine size) increased with latitude. Consequently, *S. lapponica* larvae consumed less foliar biomass at higher latitudes than at lower latitudes to reach the same size. Based on space-for-time substitution, we suggest that climate warming will increase metabolic expenses of insect herbivores with uncertain consequences for plant–herbivore interactions.

Key words *Betula pubescens*; climate change; food quality; insect herbivory; metabolic expenses; oviposition preference

Introduction

The poleward decrease in background insect herbivory, which is especially pronounced within the boreal forest zone (Zvereva & Kozlov, 2021), is routinely attributed to the declines in abundance of plant-feeding insects (Salazar & Marquis, 2012). However, latitudinal studies addressing both plant damage and herbivore density are rare and have yielded inconsistent patterns, ranging from negative (Salazar & Marquis, 2012) to positive (Kozlov *et al*., 2013) correlations between these variables. Therefore, other factors can be suggested to contribute to latitudinal decrease in plant losses to herbivores, for example, changes in the amount of plant tissue consumed by an individual insect (i.e., per capita consumption) during its lifetime.

Latitudinal changes in per capita food consumption by plant-feeding insects may occur for several reasons. First, the quality of host plants for herbivores may change with latitude. In particular, leaf size, which is linked to leaf toughness and biochemistry (Wright *et al*., 2004), decreases with increasing latitude in both across- and

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within-species comparisons (Wright *et al.*, 2017; Zverev & Kozlov, 2020). Plant defenses against herbivory were also repeatedly suggested to change systematically with latitude (Coley & Aide, 1991; Schemske *et al.*, 2009), although the evidence remains mixed (Moles *et al.*, 2011; Stevens *et al.*, 2016). Second, herbivore metabolic expenses depend on ambient temperatures (Lemoine *et al.*, 2014; Parsons & Joern, 2014), which may result in latitudinal changes in consumption of plant tissues. Third, climate and plant traits may have interactive effects on herbivores. For example, food quality modifies a herbivore's responses to temperature (Huey & Kingsolver, 2019). Nevertheless, we are not aware of any study addressing latitudinal changes in the lifetime per capita food consumption by plant-feeding insects or in their feeding efficiency.

A simultaneous collection of data on food quality, food consumption by individual defoliating insects and their performance at multiple sites along an extensive latitudinal gradient is logistically challenging. However, this information could easily be obtained for leafminers (i.e., for insects that live within a plant leaf and consume its internal tissues). This is because mined leaves can be collected at any time between the completion of larval development and the beginning of seasonal leaf fall, and investigation of these leaves allows tracing of the fate of each larva. Furthermore, comparisons between mined and intact leaves and measurements of leaf and mine characteristics provide reliable information on the behavior of both ovipositing females and larvae (e.g. on their preferences of a particular part of a leaf), as well as on the amount of food consumed by a larva and on its size at the end of larval development (Boomsma *et al.*, 1987; Zvereva & Kozlov, 2006; Morton & Pereyra, 2011). Previous studies have suggested that different factors, such as leaf fluctuating asymmetry (FA) and mine shape, can serve as indicators of leaf quality for a miner (Cornelissen & Stiling, 2005; Kozlov & Zvereva, 2016). Therefore, leafmining insects are ideally suited for studying plant–herbivore interactions along geographical gradients.

In this study, we hypothesize that the lifetime food consumption by a herbivore individual decreases from low to high latitudes, thereby contributing to the overall latitudinal decline in plant damage by insect herbivores. We tested this hypothesis by exploring latitudinal changes in the characteristics of mines made by larvae of the pygmy moth, *Stigmella lapponica* (Wocke), in leaves of downy birch, *Betula pubescens* Ehrhart, and in characteristics of the mined leaves that could reflect their quality as a food for this leafminer.

Materials and methods

Study species

Stigmella lapponica (Lepidoptera: Nepticulidae) is a small moth (5–7 mm wingspan) widely distributed in the Holarctic. The species is univoltine; in northern Europe, the females oviposit from June to the beginning of July, when leaves of birches, their only host plants, have reached their full size. The larva constructs a linear (gallery) mine (Fig. 1), the first third of which is filled with diffuse greenish-brown frass. The frass pattern then changes to a very narrow, continuous dark line, and this change allows reliable identification of the species. The mature larva leaves the mine (usually in the second half of July in our study region), prepares a cocoon in plant litter, hibernates, and then pupates in the spring (Johansson *et al.*, 1990).

In northern Europe, mines of *S. lapponica* are equally frequent on *B. pubescens* and *B. pendula*, and the mine densities (per unit of host biomass) decrease toward the north (Kozlov *et al.*, 2013). Females preferentially oviposit on the basal half of a leaf, but they relax this preference in areas affected by severe industrial pollution (Kozlov & Zvereva, 2016).

Study region and study sites

This study was conducted at ten sites (Fig. 2A) located in unevenly aged, unmanaged old-growth coniferous forests of a similar type (Fig. 2B), ranging in latitude from 60°N near St Petersburg to 69°N close to Murmansk in NW Russia. The mean annual temperature decreases latitudinally from +4.24 °C in the southernmost site to −0.53 °C in the northernmost site. The mean summer (June–August) temperature decreases from +16.98 °C to 10.84 °C, and the mean annual precipitation varies from 611 to 799 mm (Table 1). For species composition and foliar biomass of most common woody plants in our sites, consult Zvereva *et al.* (2020b).

Sampling and processing of intact leaves

At each site, between 8 and 29 August 2016–2019, we haphazardly selected five mature *B. pubescens* trees growing at least 10 m apart from others of this species. From each birch tree, we collected a haphazardly selected branch with approximately 80–120 leaves. To minimize the impact of unconscious biases on leaf traits, the

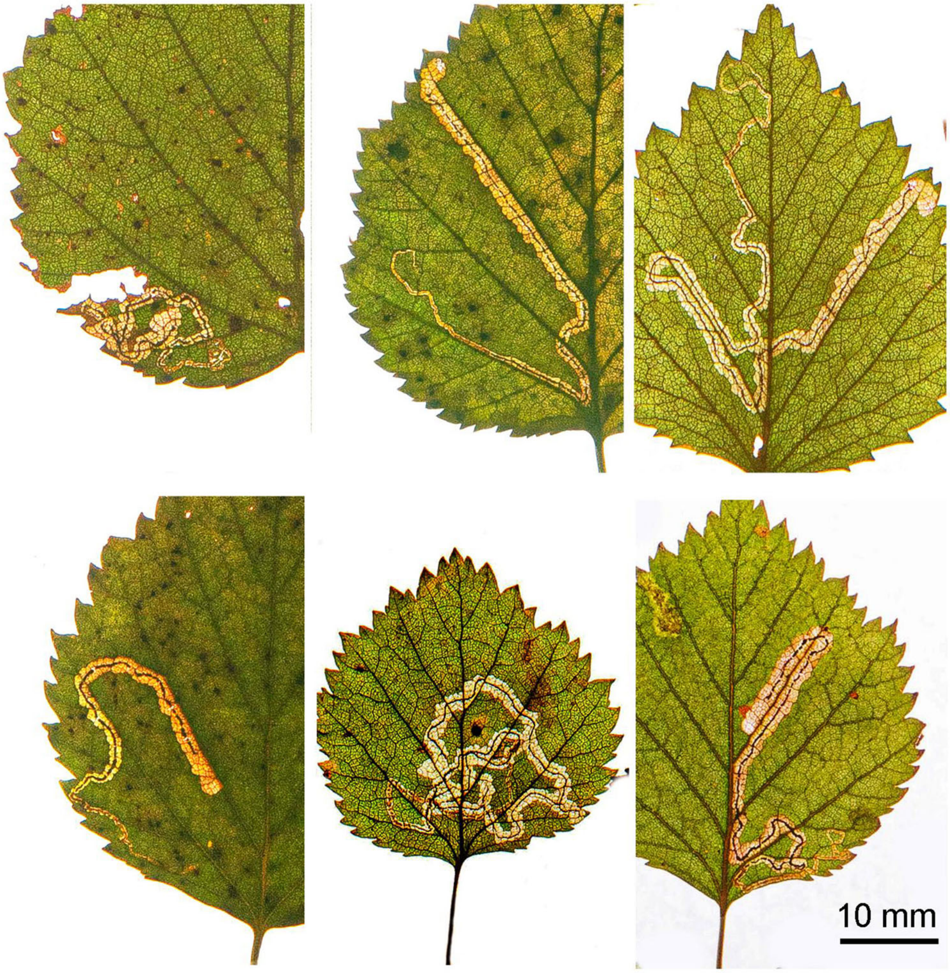

Fig. 1 Variation in the size, shape, and position of *Stigmella lapponica* mines in leaves of *Betula pubescens.*

branches were selected while standing at a distance of 5−10 m away to preclude any visual evaluation of leaf traits or leaf damage by insects. The collected branches were coded with random numbers and transported to the laboratory.

From each branch, we haphazardly collected five (in 2016 and 2017) or ten (in 2018 and 2019) medium-sized, short-shoot leaves bearing no traces of insect feeding. When the collected leaves were fresh, we punched one disc 13.3 mm in diameter outside the midrib from each leaf. The leaves and discs were dried for 48 h at +105 °C and weighed to the nearest 0.1 mg. The specific leaf area (SLA) was calculated by dividing the disc area by the disc weight. Subsequently, the area of the leaf lamina was estimated by multiplying the leaf weight by the SLA (Data S1).

Sampling and processing of mined leaves

We collected birch leaves mined by *Stigmella* spp. larvae after the collection of intact leaves. The same experienced persons (V.Z. and M.V.K.) jointly searched for mined leaves at all sites and during all study years. We attempted to obtain 20−50 mines from each study site annually; however, extremely low population densities in some years distorted these plans. All discovered mines (1273 in total) were collected, press-dried, mounted with adhesive tape on strong paper, numbered and photographed against the light. Based on these photographs, E.J.v.N. attributed most of the mines to individual insect species. We obtained 512 mines of *S. lapponica* in leaves of *B. pubescens*. Among those, 13% of the larvae were killed by ants, 5% were killed by parasitoids and

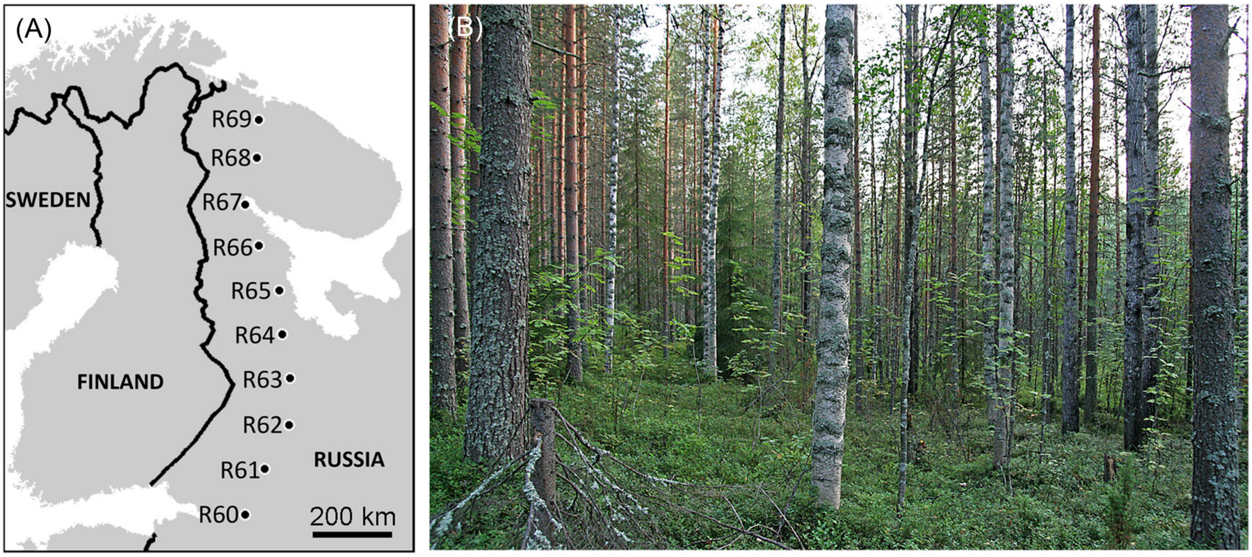

Fig. 2 Study sites: (A) location (for site characteristics consult Table 1); (B) forest type.

20% died from unknown causes (Zvereva *et al.*, 2020a). From the 318 mines that had successfully completed their development, we blindly (i.e., without examination of the leaves) selected 196 mines (always a single mine per leaf) to obtain similar numbers of mines collected from different sites and during different years.

Leaf and mine measurements

The images of the 196 selected leaves were processed blindly so that the persons conducting measurements were not aware of leaf origin. In each leaf, we measured the length of lamina and quantified the relative position of the oviposition site (i.e., the starting point of the mine) as the distance from the leaf base (along the midrib; Fig. 3A) divided by the length of the leaf lamina. Mine size provides an effective cue to larval size (Springett & Matthiessen, 1975; Boomsma *et al.*, 1987; Low *et al.*, 2009); therefore, we used the width of the terminal part of a mine (Fig. 3B) as a proxy for the final weight of the larva that emerged from this mine.

The dry weight of a leaf disc 8 mm in diameter punched from an unmined part of the leaf lamina outside the midrib was used to calculate the SLA, as explained above. This calculation accounted for shrinkage of the dry leaf area to 0.925 of its fresh value, as has been estimated from measurements of 200 birch leaves before and after drying. The mine area and the total area of the leaf lamina were measured by weighing their images cut out from standard office paper (80 g m^{-2}) on which they were printed. This method was preferred to image processing because the margins of the mine were poorly distinguished by the Adobe PhotoShop 2020 program, and the leaf margins were often damaged by defoliating insects. The biomass consumed by a larva was approximated by dividing the mine area by the SLA; this approximation assumed that the proportion of leaf epidermis (which was not consumed by the larva) in the foliar biomass did not change with latitude. The efficiency of conversion of ingested foliar biomass into larval biomass (feeding efficiency, hereafter) was quantified by dividing the width of the terminal part of the mine by the square root of the consumed biomass. The latter transformation was selected to achieve normality of the residuals.

Mine shape, which potentially reflects quality of different parts of a leaf for a leafminer (Kozlov & Zvereva, 2016), was explored by V.Z. The mine was approximated by a broken line made up of straight segments that followed the line of excrements as closely as possible (9–42 segments per mine; Fig. 3C). The standard instruments of Adobe PhotoShop 2020 were used to measure the length of each segment (to the nearest 0.06 mm) and the angle between two adjacent segments (to the nearest 1°). The segment length and the angles of the turns of the mine (excluding those at the intersections with leaf veins) were averaged for each mine prior to analysis following the protocol developed by Kozlov and Zvereva (2016).

A multivariate measure describing the FA in leaf shape, which is supposedly related to leaf quality for a herbivore (Cornelissen & Stiling, 2005; Kozlov *et al.*, 2018), was based on five landmarks: (1) the leaf apex, (2) the point

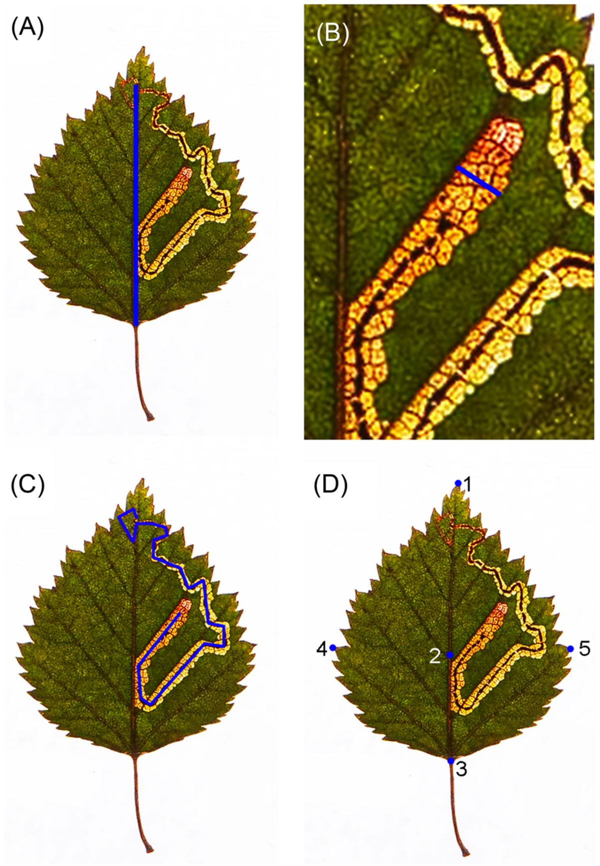

Fig. 3 Measurements of a *Stigmella lapponica* mine and of a *Betula pubescens* leaf: (A) distance between the oviposition site and the base of the leaf measured along the midrib; (B) the width of the terminal part of a mine; (C) the length of mine segments and angles of turns; (D) position of landmarks (1–5) used to quantify leaf FA.

where the sixth lateral vein diverges from the midrib, (3) the base of the leaf (i.e., the point where the petiole joins the lamina), and (4 and 5) the two points where the first two lateral veins arrive at the leaf margin (Fig. 3D). The coordinates of these landmarks were obtained by T.S. using ImageJ software (Rasband, 2017). Variations in leaf shape were analyzed using the MorphoJ software (Klingenberg, 2011), as described by Sandner *et al.* (2019), and this analysis resulted in a Mahalanobis FA measure of the asymmetric components of leaf shape (Data S2) corrected for nonisotropic variation (Klingenberg & Monteiro, 2005).

Data analysis

The effects of latitude on all studied characteristics were analyzed by general linear mixed models employing type 3 tests (GLIMMIX procedure; SAS Institute, 2009). In these models, latitude was treated as a covariate, whereas study site and year were treated as random intercept effects. In addition, the models comparing the size of mined and intact leaves or leaves in which larvae had completed their development or died for various reasons, included one more fixed factor, namely the presence or the fate of the mine, and the interaction of this factor with latitude. The simultaneous involvement of both site and latitude in our analyses is justified by the fact that our sites differ not only in latitude, but also in a number of other characteristics (Zvereva *et al.*, 2020a, b). We adjusted the standard errors and denominator degrees of freedom following Kenward & Roger (2009), and we evaluated the significance of random effects by testing the likelihood ratio against the chi-squared distribution (Littell *et al.*, 2006). The association between characteristics of mines and of the mined leaves were quantified by Pearson linear correlation coefficients.

Results

Selection of leaves and leaf parts by ovipositing females

Mined leaves were larger than intact leaves at the southern end of our latitudinal gradient, but smaller than intact leaves at its northern end (interaction term in Table 2; Fig. 4A). By contrast, SLA did not differ between mined and intact leaves and did not change with latitude (Table 2; Fig. 4B). Neither the oviposition site within a leaf ($F_{1,\,7.12} = 0.31$, $P = 0.59$) nor the FA of the mined leaves ($F_{1,\,4.94} = 0.11$, $P = 0.75$) changed with latitude. The size of leaves in which larvae completed their development did not differ from the size of leaves in which larvae died for various reasons (main effect: $F_{1,\,489.5} = 0.38$, $P = 0.53$) along the entire latitudinal gradient (interaction term: $F_{1,\,489.5} = 0.37$, $P = 0.54$).

Mine size and shape

The width of the terminal part of a mine, a proxy for the final weight of a larva that emerged from this mine, did not correlate with the length of the mine ($r = -0.03$, $n = 187$ leaves, $P = 0.66$). Larvae constructed longer mines in thinner leaves ($r = 0.75$, $n = 189$ leaves, $P < 0.0001$), but attained greater weight in thicker leaves ($r = -0.17$, $n = 181$ leaves, $P = 0.02$). None of the mine characteristics were associated with leaf FA ($r = -0.06$ to 0.02, $P = 0.39$ to 0.92).

No latitudinal changes were observed in the width of the terminal part of a mine (Fig. 5A), mine length

Table 1 Characteristics of study sites.

Site code	Latitude (N)	Longitude (E)	Elevation (m above sea level)	Mean annual temperature (°C)[†]	Mean summer temperature (°C)[†]	Total annual precipitation (mm)[†]
R60	60° 05′	32° 22′	25	4.24	16.98	749
R61	61° 00′	33° 03′	15	3.30	16.32	799
R62	61° 58′	34° 14′	45	2.68	16.11	662
R63	63° 00′	34° 22′	160	1.74	15.08	719
R64	64° 01′	34° 04′	100	1.53	14.40	674
R65	65° 01′	34° 00′	60	1.23	13.63	611
R66	66° 01′	32° 59′	105	0.98	13.60	614
R67	66° 56′	32° 12′	85	0.11	12.79	670
R68	68° 01′	32° 57′	155	−1.22	11.20	669
R69	68° 52′	33° 07′	100	−0.53	10.84	639

[†] The long-term (2001–2020) mean annual air temperature and precipitation and summer (June–August) temperature extracted from NASAPOWER archive (power.larc.nasa.gov).

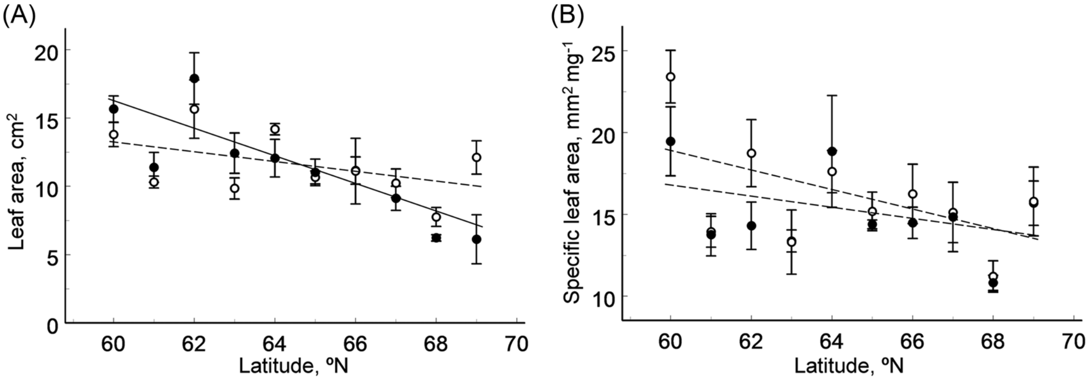

Fig. 4 Latitudinal changes in the area (A) and specific leaf area (B) of mined (filled circles) versus intact (open circles) birch leaves. Solid lines: significant models; dashed lines: nonsignificant models.

(Fig. 5B), mine area ($F_{1,\,7.72} = 1.53$, $P = 0.25$) or the mean angle of the turns of the mine (Fig. 5C), whereas the length of mine segments decreased toward the north (Fig. 5D). The proportion of leaf area consumed by an individual larva significantly increased toward the north (Fig. 5E) due to a poleward decrease in leaf area. The per capita food consumption was independent of latitude ($F_{1,\,6.99} = 0.05$, $P = 0.83$), but larval feeding efficiency increased with increasing latitude, being approximately 10% greater at 69°N than at 60°N (Fig. 5F).

Discussion

Our study found no support for the hypothesis that the lifetime food consumption by a herbivore individual decreases from low to high latitudes. At the same time, our results provide the first demonstration that feeding efficiency of insect herbivores increases with latitude in natural populations: to reach the same size, herbivorous insects consumed approximately 10% less foliar biomass at high-latitude localities than at low-latitude localities within the boreal forest zone. In combination, these two results suggest that larvae of *S. lapponica* should attain larger size at high latitudes. In line with this suggestion, earlier observations show that *S. lapponica* specimens from northern Scandinavia are usually larger than specimens from southern Scandinavia (Johansson *et al.*, 1990). In our study, latitudinal changes in *S. lapponica* size followed the same trend, although these changes did not reach the level of statistical significance (Fig. 5A). The lack of significance may be due to variation associated with preference of different leaves at different parts of our latitudinal gradient (Fig. 4A) or due to the insufficient accuracy of mine width as a measure of larval weight.

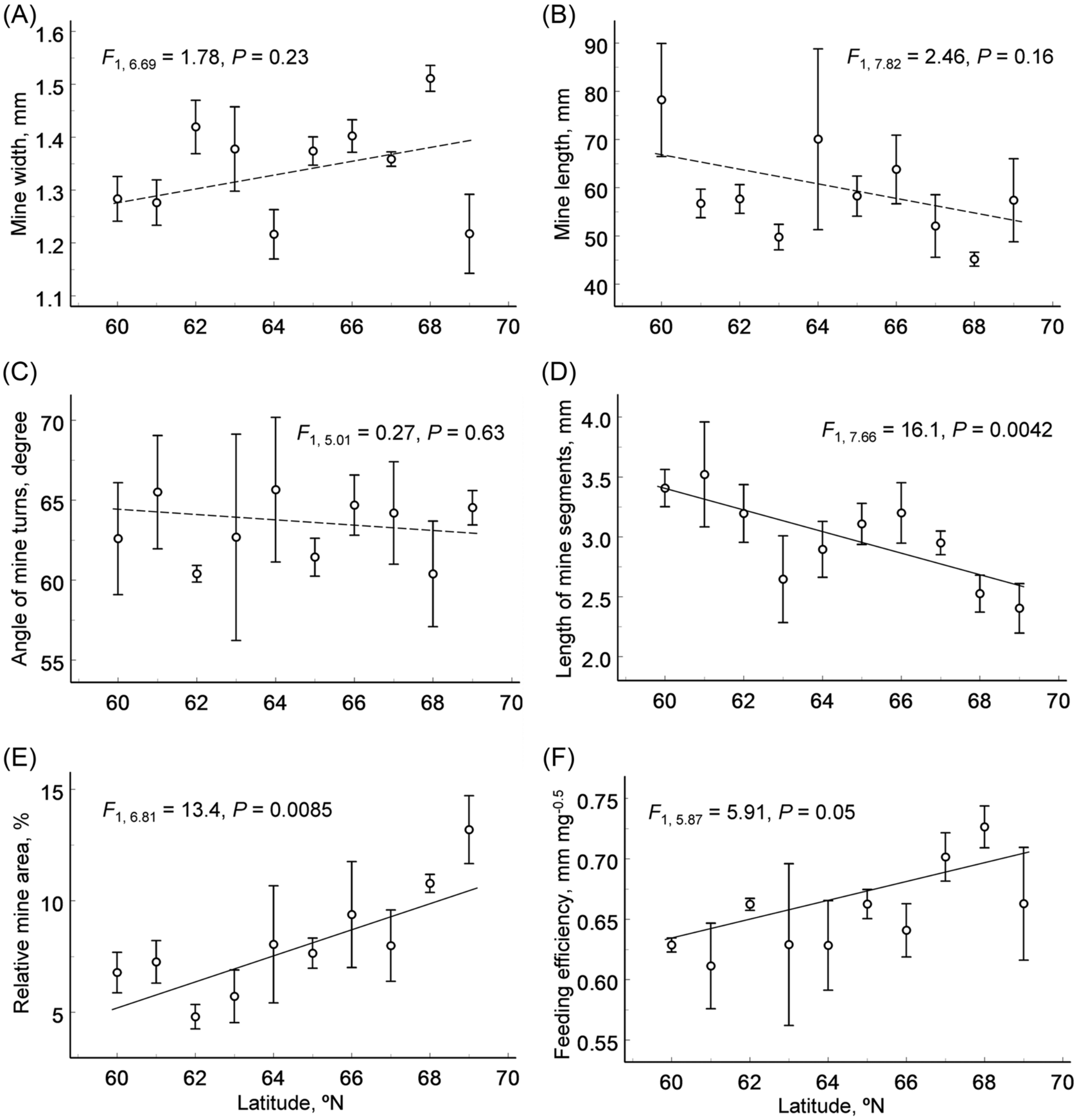

Fig. 5 Latitudinal changes in characteristics of *Stigmella lapponica* mines: (A) width of the terminal part of a mine; (B) length of the mine; (C) mean angle of the turns of the mine; (D) the length of mine segments; (E) percentage of the leaf area consumed by an individual larva; (F) larval feeding efficiency (measured in arbitrary units).

The poleward increase in feeding efficiency of *S. lapponica* larvae could arise if food quality increases from low to high latitudes, as proposed, for example, by the hypothesis that plants are better defended from herbivores at low latitudes than at high latitudes (Coley & Aide, 1991). However, two lines of evidence suggest that changes in plant quality as food for herbivores are unlikely to explain the discovered poleward increase in the feeding efficiency of *S. lapponica* larvae. First, the SLA of *B. pubescens* (which strongly correlates with foliar nitrogen and with several other biochemical characteristics; Wright *et al.*, 2004) showed no statistically significant poleward decline (Fig. 4B). Second, the total concentration of defensive compounds in leaves of *B. pubescens*, the host plant of *S. lapponica*, does not change between 60°N and 69°N (Stark *et al.*, 2008).

Despite previously published reports linking the FA of individual leaves with their quality for and their preference by herbivorous insects (Cornelissen & Stiling, 2005; Kozlov *et al.*, 2018), we found no correlation between the characteristics of *S. lapponica* mines and the FA of the mined leaf. This finding suggests that either high FA is not indicative of better leaf quality for *S. lapponica* larvae (expressed e.g. in lower concentrations of tannins

Table 2 Latitudinal changes in area and specific leaf area of *Betula pubescens* leaves with and without *Stigmella lapponica* mines.

		Leaf area		Specific leaf area	
Effect type	Explanatory variable	Test statistics	P	Test statistics	P
Fixed	Presence of a mine (M)	$F_{1,\,60.7} = 11.9$	0.001	$F_{1,\,60.2} = 2.71$	0.10
	Latitude (L)	$F_{1,\,8.09} = 10.2$	0.01	$F_{1,\,8.06} = 2.43$	0.16
	M × L	$F_{1,\,60.7} = 12.1$	0.001	$F_{1,\,60.2} = 2.43$	0.12
Random	Site	$\chi^2{}_1 = 15.1$	<0.0001	$\chi^2{}_1 = 26.4$	<0.0001
	Year	$\chi^2{}_1 = 0.03$	0.16	$\chi^2{}_1 = 19.7$	<0.0001

and higher concentrations of nitrogen relative to low-FA leaves; Cornelissen & Stiling, 2005) or that the larval behavior and/or the explored performance traits of *S. lapponica* do not change with leaf quality.

Previously, we associated the increases in both the angle of turns of the *S. lapponica* mine and in the length of the mine segments with feeding in low quality leaves (Kozlov & Zvereva, 2016). Thus, the absence of latitudinal changes in the angle of turns of the mine (Fig. 5C) could be interpreted as the absence of latitudinal changes in leaf quality for *S. lapponica*. Keeping in mind that this conclusion is consistent with the absence of latitudinal changes in other leaf traits also indicative of leaf quality for a herbivore (SLA and defensive chemistry), we attribute the latitudinal decrease in the length of the mine segments (Fig. 5D) to the more than 2-fold decrease in the area of a mined leaf (Fig. 4A), which constrains the shape of the mine, rather than ascribing it to the poleward increase in leaf quality. Thus, we conclude that the poleward increase in feeding efficiency of *S. lapponica* is not associated with changes in leaf quality and should therefore be explained by other factors.

An experiment with a butterfly, *Pieris napi*, revealed that the larvae converted food into body matter two to three times more efficiently at 17 °C than at 25 °C (Bauerfeind & Fischer, 2013). As metabolic demands increase exponentially with rising temperatures, consumers generally either increase food intake or switch to higher quality diets to offset the rising costs of metabolism (O'Connor, 2009; Lemoine *et al.*, 2014). Since we did not detect changes in birch leaf quality in our gradient, we conclude that our finding of an increase in feeding efficiency of *S. lapponica* larvae from low to high latitudes is likely explained by the lower metabolic demands of herbivores at lower ambient temperatures (O'Connor, 2009; Vucic-Pestic *et al.*, 2011).

Insects may change their behavior to avoid increased metabolic expenses caused by elevated temperatures (Abram *et al.*, 2017), and these changes may be especially important for leafminers, because within-mine temperatures can be much greater than ambient air temperatures (Pincebourde & Casas, 2006). Our study provides an interesting example of latitudinal changes in leafminer's oviposition behavior, which may be interpreted as adaptation aimed at regulation of temperature within a mine. We found that *S. lapponica* females preferentially oviposit on smaller-than-average birch leaves at higher latitudes, whereas at lower latitudes, they prefer larger-than-average birch leaves. Keeping in mind that sun-exposed trees usually produce small leaves, and shaded trees produce large leaves, we suggest that this oviposition preference may increase the temperature of leafmining larvae in cold subarctic regions and prevent overheating of larvae in warmer temperate climates.

Direct effects of climate warming on ectotherms are generally positive (Bale *et al.*, 2002), which is expected to increase plant damage by herbivorous insects (DeLucia *et al.*, 2012). However, our latitudinal study, in combination with some manipulative studies (Bauerfeind & Fischer, 2013; Lemoine *et al.*, 2014), suggests that also some negative effects of climate warming on insect herbivores will occur due to increases in their metabolic expenses, and these increases will have uncertain consequences for plant–herbivore interactions.

Acknowledgments

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Data availability

The data supporting the results are included in this article as Supporting Information Data S1 and Data S2.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Characteristics of intact (tree-specific values) and mined (leaf-specific values) leaves of *Betula pubescens*.

Data S2. Characteristics of *Betula pubescens* leaves and of *Stigmella lapponica* mines in these leaves.