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Effects of industrial pollution and ambient air temperature on larval performance and population dynamics of *Eriocrania* leafminers (Lepidoptera)

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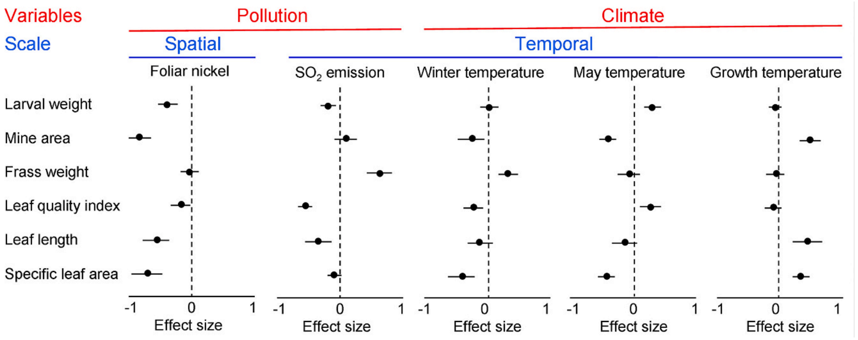
HIGHLIGHTS

- Pollution and temperature affect leaf-miner populations through multiple pathways.
- Larval weight increased with a decrease in pollution levels in both space and time.
- Warm springs increased leaf quality, allowing larvae to attain greater weight.
- The rate of population change did not correlate with larval weight.
- Severe pollution disrupted the effects of temperature on population dynamics.

GRAPHICAL ABSTRACT



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ABSTRACT

Pollution is an integral part of global environmental change, yet the combined and interactive effects of pollution and climate on terrestrial ecosystems remain inadequately understood. This study aims to explore whether pollution alters the impacts of ambient air temperature on the population dynamics of herbivorous insects. Between 1995 and 2005, we studied populations of two closely related moths, *Eriocrania semipurpurella* and *E. sangii*, at eight sites located 1 to 64 km from a large copper-nickel smelter in Monchegorsk, Russia. We found that pollution and temperature influence the performance of *Eriocrania* larvae mining in the leaves of mountain birch, *Betula pubescens* var. *pumila*, through multiple pathways. This is evident from the inconsistent changes observed in larval and frass weight, mine area, and leaf size. We found increases in both leaf quality and larval weight with decreasing pollution levels at both spatial and temporal scales and attributed these to the impact of sulphur dioxide, rather than trace elements (nickel and copper). The quality of birch leaves increased with spring (May) temperatures, enabling *Eriocrania* larvae to achieve greater weight while consuming less biomass. During the larval growth period (early June to early July), *Eriocrania* larvae increased their consumption with rising temperatures, presumably to compensate for increased metabolic expenses. Contrary to our expectations, the per capita rate of population change did not correlate with larval weight and did not vary along the pollution gradient. Nevertheless, we detected interactive effects of pollution and climate on the rate of population change. This rate decreased with rising winter temperatures in slightly polluted and unpolluted sites but remained

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unchanged in heavily polluted sites. We conclude that pollution disrupts mechanisms regulating the natural population dynamics of *Eriocrania* moths.

1. Introduction

Long-term studies conducted near industrial polluters have significant, yet often overlooked, potential to advance fundamental ecology (Liebhold, 2019) and global change biology (Kozlov and Zvereva, 2011). These studies are particularly valuable for examining the combined and interactive effects of pollution and climate on terrestrial ecosystems, as information on these effects is in short supply (De Marco et al., 2022).

This research gap is especially concerning, given current reports on rapid insect decline worldwide (Wagner, 2020), because environmental pollution is suspected to contribute to this decline (Kehoe et al., 2021; Ryalls et al., 2022). To test this suspicion, we examined spatial, temporal, and spatiotemporal variation in larval weight and feeding efficiency of two closely related species of leafmining moths, *Eriocrania semipurpurella* (Stephens) and *E. sangii* (Wood), within the impact zone of a large copper-nickel smelter in Monchegorsk, Russia. This study, conducted during a period of substantial emission decline and rapid climate warming (Zvereva et al., 2016; Marshall et al., 2016), focuses on the bottom-up effects of pollution and climate on the population dynamics of herbivorous insects; it complements a previous study of top-down regulations (Zvereva and Kozlov, 2006a).

Our study is unique in addressing the feeding efficiency of herbivores, a perspective that has been previously underexplored in global change research. This opportunity arises from the peculiar combination of life history traits exhibited by *Eriocrania* larvae (Koricheva and Haukioja, 1992, 1994). First, these larvae produce blotch mines, the size of which can be accurately measured and used as a proxy for biomass consumption. Second, the larval frass remains within these mines, enabling precise weighing. As a result, *Eriocrania* leafminers allow for a more comprehensive and detailed examination of bottom-up effects in natural environments compared to defoliating insects.

Pollution affects plant-feeding insects through various pathways, acting both directly and indirectly at different spatial and temporal scales (Hughes, 1988; Riemer and Whittaker, 1989; Koricheva and Haukioja, 1994). Furthermore, the magnitudes of the pollution effects on terrestrial biota change with mid-summer temperature, emission levels, and time since the onset of pollution (Zvereva and Kozlov, 2010; Kozlov and Zvereva, 2011). Nevertheless, despite the multiplicity of the variation sources and the complexity of their interactions, some predictions regarding the overall effects of pollution on populations of herbivorous insects can still be made.

Odum (1985) and Rapport et al. (1985) independently proposed that a reduction in organism size is a common ecosystem response to stress. This hypothesis gained support from a meta-analysis of data on body size of insects collected from industrial pollution gradients (Zvereva and Kozlov, 2010). Therefore, we predict that (1) at a spatial scale, the average weight of *Eriocrania* larvae will decrease with increasing pollution levels, being lower near the smelter than in more distant localities; and (2) at a temporal scale, the average weight of *Eriocrania* larvae will rise as aerial emissions decline, being lower at the start of our study period (1995) than at the end of it (2005).

The size of *Eriocrania* mines is only slightly smaller than the average leaf size of mountain birch (*Betula pubescens* var. *pumila* (G. Zanoni ex Murray) Govaerts) in our subarctic study region. Thus, leaf size often constrains the growth of a leafmining *Eriocrania* larva, because this larva, in contrast to defoliating insects, cannot move to another leaf after consuming the current one. Given the pronounced decline in leaf size of woody plans near industrial polluters (Zvereva et al., 2010), we predict that (3) the reduction in leaf size of mountain birch in heavily polluted sites explains a decrease in site-specific weight of *Eriocrania* larvae. However, we cannot predict the direction of the pollution impact on leaf quality, because SO_2 and trace elements co-occurring in our study region exert opposing effects. Sulphur dioxide generally enhances plant quality for herbivores (Hughes, 1988; Whittaker and Warrington, 1990), whereas plants contaminated by trace elements are toxic to insects (Boyd and Martens, 1994; Heliövaara et al., 1989).

Ambient temperature, akin to pollution, imposes direct and indirect effects on plant-feeding insects (Bale et al., 2002; Bauerfeind and Fischer, 2013; Lemoine et al., 2014), and it is challenging to disentangle these effects. A meta-analysis revealed that insect performance generally improves with experimental temperature elevation (Zvereva and Kozlov, 2006b). Similarly, bioassays with field-collected plants demonstrated that elevated spring temperatures enhance leaf quality for an insect herbivore (Zvereva et al., 2016). Integrating these findings, we predict that (4) the quality of mountain birch leaves will positively correlate with spring temperatures, resulting in a higher weight of *Eriocrania* larvae in years with warmer springs. By contrast, the direct impact of warm weather on herbivores could be adverse, as their metabolic demands increase with rising temperatures (Gillooly et al., 2001). Consequently, consumers typically escalate food intake or switch to higher quality food to offset the rising metabolic costs (O'Connor, 2009; Lemoine et al., 2014). However, the latter mechanism is impossible for leafminers, leading us to predict that (5) *Eriocrania* larvae growing at higher ambient temperatures (within realistic limits) will consume more foliar biomass (i.e., produce greater mines) to attain the same weight as larvae growing at lower ambient temperatures.

Temperature can modify pollution impacts on biota (Kozlov and Zvereva, 2011); however, the supportive evidence is generally scarce and indirect (Posch, 2002). Nonetheless, based on the increase in the rate of chemical and physical processes with rising temperature, we predict that (6) an increase in ambient temperature, by enhancing both mobility and toxicity of pollutants (Cairns et al., 1975; Leung et al., 2000; Öncel et al., 2000), will amplify their direct adverse effects on the growth and feeding efficiency of *Eriocrania* larvae.

The examination of larval weight holds significance primarily because it could provide insights into the processes shaping herbivore population dynamics. Assuming that larger females of insects, which do not feed during their adult stage (including *Eriocrania* moths), produce more eggs than smaller females (Haukioja and Neuvonen, 1985; Honěk, 1993), we predict that (7) the rate of *Eriocrania* population change will increase with rising larval weight, and (8) this bottom-up effect on *Eriocrania* population dynamics will be particularly notable in heavily polluted sites, where top-down regulation of *Eriocrania* populations is disrupted (Zvereva and Kozlov, 2006a). The ultimate goal of the present study is to explore how pollution alters the impacts of ambient temperature on the population dynamics of herbivorous insects.

2. Materials and methods

2.1. Study system

Eriocrania semipurpurella and *E. sangii* (Lepidoptera: Eriocraniidae) are tiny (wing span 9–16 mm) moths emerging at the time of birch budbreak, typically occurring from late May to early June in our study area. Females oviposit in the tips of unfolding leaves, and larval feeding distorts leaf growth. Larvae of both species are solitary and feed exclusively on birches. They develop in approximately 2–3 weeks, forming large (ca. 2 cm^2) blotch mines with long, intertwining threads of frass. After abandoning the mine, larvae overwinter in the soil and pupate the next spring. While larvae of *E. sangii* are dark grey, and easily distinguishable from the white larvae of *E. semipurpurella*, the abandoned mines of these species cannot be differentiated (Heath, 1976). The biology of all birch-feeding *Eriocrania* species is quite similar, and these species are frequently combined in ecological studies (Koricheva and Haukioja, 1992, 1994; Bylund and Tenow, 1994; Valladares and Hartley, 1994).

Mountain birch, a tree-line variety of downy birch, *B. pubescens* Ehrh., is a deciduous pioneer tree species. It is native and abundant throughout the study area and exhibits a wide range of growth forms, from low multistemmed shrubs in heavily polluted industrial barrens to 10–15 m tall trees in unpolluted forests. Mountain birch plays a crucial role in both pristine and disturbed subarctic forests, providing food and shelter to many organisms.

2.2. Study area and study sites

The copper-nickel smelter in Monchegorsk (67°56′ N, 32°49′ E), located in the central part of the Murmansk region in north-western Russia, is one of the largest industrial polluters in the Northern hemisphere. Throughout the study period (1995–2005), emissions of SO_2 and dust containing trace elements, primarily nickel and copper, declined two- to three-fold. This decline resulted from both a decrease in production and an increase in emission control (Kozlov et al., 2009). However, emissions into the ambient air remained high compared to industrial enterprises in EU countries: annual SO_2 emissions from the Monchegorsk smelter (Table S1) accounted for as much as 0.6 % of the total SO_2 emissions in Europe (calculated from Zhong et al., 2020).

Data were collected at the eight sites located 1 to 64 km from the smelter. These sites (Table 1) were systematically chosen to represent various stages of pollution-induced deterioration of coniferous forests of Norway spruce, *Picea abies* (L.) H. Karst. and Scots pine, *Pinus sylvestris* L. For a map showing site positions within the study region and for photographs of selected sites, see Kozlov et al. (2022).

Ambient concentrations of SO_2 and deposition of dust containing trace elements decreased immediately following the decline in emissions. In contrast, natural leaching of trace elements from severely contaminated soils can take several decades or even centuries (Tyler, 1978; Barcan, 2002). Consequently, nickel concentrations in birch foliage did not change during our study period despite the decline in emissions (Kozlov, 2005). Therefore, to measure pollution load at the spatial scale, we used the average nickel concentrations in mountain birch leaves across the study period. The four sites located in industrial barrens (Table 1) were classified as heavily polluted, in contrast to four slightly polluted forested sites.

Table 1
The characteristics of study sites.

Site code[a]	Latitude (N)	Longitude (E)	Habitat	Nickel[b], μg g^{-1}	SO_2[c], μg m^{-3}
1N	67°56′13″	32°50′07″	Industrial barren	195	151
4S	67°52′59″	32°46′43″	Industrial barren	177	162
6S	67°52′05″	32°48′16″	Industrial barren	243	186
8S	67°51′01″	32°48′03″	Industrial barren	155	150
13S	67°48′03″	32°46′36″	Birch- and willow-dominated community	90	76
27S	67°40′39″	32°49′32″	Slightly damaged spruce forest	32	36
35S	67°37′56″	32°45′04″	Slightly damaged spruce forest	29	44
64SE	67°32′16″	33°57′52″	Undamaged spruce forest	10	2

[a] The site codes indicate approximate distance from the smelter in km and direction to the north (N) or to the south (S) of the smelter.

[b] In unwashed samples of mountain birch foliage; averaged from 1991 to 2003 (after Kozlov, 2005).

[c] Measured by passive lead dioxide absorbers in summer of 1995 (after Kozlov, 2002).

2.3. Sampling and processing of mined birch leaves

We monitored the growth of *Eriocrania* larvae and commenced collecting mined leaves when more than half of the mines exceeded an area of 1.5 cm^2, reaching about 75 % of the final mine size. The dates of sampling varied among years, from 13 June to 12 July (Table S1). We collected shoots (most of which were short vegetative shoots with three leaves each) hosting *Eriocrania* mines that had reached this size and contained live larvae. These shoots were individually placed into 50 mL plastic vials tightly closed by caps to maintain air moisture. Our aim was to obtain 50 mined leaves from each site during each study year (1995–2005). However, logistical challenges and extreme density fluctuations impeded our plans.

The vials containing mined leaves were transported to the laboratory in Apatity and stored at room temperature (ca. 22 °C) under natural light. We anticipated that our protocol might affect both leaf quality and larval feeding efficiency. Therefore, we recorded larval growth duration in detached leaves (rounded to the nearest day) and incorporated this variable into the data analysis. Each vial was inspected three times a day, and emerged larvae were promptly transferred to individual 1.5 mL vials. Abandoned mines were opened, and frass was collected into individual vials. In cases where some frass adhered tightly to mine walls, we visually estimated the percentage of non-collected frass and adjusted for this loss in our calculations; this adjustment was applied to 2.2 % of all mines. When the unmined part of the mined leaf was sufficiently large, we punched out a disk 8 mm in diameter for the estimation of specific leaf area (SLA). All samples were dried for 24 h at 105 °C and then weighed to the nearest 0.01 mg. SLA was calculated by dividing the disk area (50.24 mm^2) by its dry weight (mg).

The mined leaves were affixed to sturdy paper and press-dried like standard herbarium specimens. The mine area was measured using a 5 × 5 mm grid to the nearest half of the grid cell. Additionally, we visually estimated the proportion of the mined leaf area and measured the length of the leaf lamina (leaf length hereafter) with a ruler to the nearest 1 mm. We used mine area as a proxy of consumed plant biomass and the larval mass to frass mass ratio as an index of leaf quality. This index, introduced by Koricheva and Haukioja (1992), reflects the efficiency of converting ingested food into insect body mass.

2.4. Monitoring of population densities

In late June to early July of each year from 1995 to 2005, at each study site, we recorded the number of *Eriocrania* mines on each of 25 haphazardly chosen mountain birch trees ranging from 30 to 300 cm tall. Leaf area (S, m^2) of each surveyed birch tree was calculated from its diameter (d, mm) using the equation: $S = 1.234 \times 10^{-3} \times d^2$. The site-specific densities of *Eriocrania* (two species combined due to impossibility to identify empty mines to the species) were expressed as the number of mines per 1 m^2 of birch leaf area. From these data, we calculated the per capita rate of population change (RPC) as follows: $RPC = \log(N_{t+1}/N_t)$, where N_t and N_{t+1} represent the site-specific densities of *Eriocrania* in two consecutive years, t and t + 1. In rare situations when $N_t = 0$, its value was replaced by 0.1.

2.5. Meteorological data

We used meteorological records collected in Monchegorsk from 1994 to 2005. Based on previous experience (Zvereva et al., 2016), we employed mean temperatures of winter (from November of the preceding year to April of the current year) and spring (May) to explore effects of weather conditions on *Eriocrania* populations. As an additional explanatory variable, we used the average temperature of the larval growth period, i.e. of the 15 days preceding the median collection date of mined birch leaves (Table S1).

2.6. Data analysis

We used ANCOVA to examine (i) the effects of larval growth duration in detached leaves on larval weight, frass weight, mine area and leaf quality index (fixed variable: *Eriocrania* species; covariate: time; SAS GLM procedure, type 3 sum of squares); and (ii) the spatial and temporal (annual) variations in these variables, leaf length and SLA (fixed variable: study year; random variable: study site; covariate: average concentration of nickel in mountain birch leaves; SAS GLIMMIX procedure: SAS Institute, 2009). Both models included the interaction between the fixed variable and the covariate. We included both site and pollution load in the second set of analyses because our sites differ not only in pollution load but also in other characteristics, such as habitat type, plant community composition, and mountain birch biomass.

Spatial variation analyses were based on Pearson's product moment correlation coefficients between site-specific values of six response variables (larval weight, frass weight, leaf quality index, mine area, leaf length, and SLA) and average foliar nickel concentrations. These correlations were calculated separately for each *Eriocrania* species for each of the ten study years. The correlations between RPC (two species combined) and nickel were calculated for each of ten study years. Temporal variation analyses were based on correlations of year-specific values of response variables with annual SO_2 emission and ambient air temperature during winter, spring, and larval growth period. These correlations were calculated separately for each *Eriocrania* species for each of eight study sites.

To calculate effect sizes (ESs), individual correlation coefficients were z-transformed and weighted by their sample sizes. Mean ESs were computed and compared using the MetaWin 2.0 program (Rosenberg et al., 2000). An effect was considered statistically significant if the 95 % confidence interval of the mean ES (CI95) did not include zero. The variation in the ESs among classes of categorical variables (study species, response variables, and pollution levels) was explored by calculating the heterogeneity index Q_B, which was then tested against the χ^2 distribution. We searched for the effect of pollution on population dynamics by calculating mean ES across ten year-specific correlations between RPC and foliar nickel concentrations. Interactions between spatial and temporal variations were examined by (i) contrasting ESs reflecting temporal patterns in response variables between heavily polluted and slightly polluted sites and (ii) meta-regressing ESs reflecting spatial patterns in response variables to SO_2 emissions and ambient air temperature. All analyses were performed using random effects models, assuming that the ESs differed not only due to sampling error but also due to random variation.

We further investigated the direct effects of climate on population dynamics by calculating mean ES across eight site-specific correlations between RPC and ambient air temperature. The expected bottom-up effect on *Eriocrania* population dynamics was searched for by calculating mean ES across eight site-specific correlations between RPC and the average weight of all *Eriocrania* larvae collected at the given site in the given year. The interactive effects were explored by contrasting ESs within each group between heavily polluted and slightly polluted sites.

3. Results

3.1. Data overview

We collected and processed 1713 leaves mined by *E. semipurpurella* larvae and 1521 leaves mined by *E. sangii* larvae. Our data include the weight of 3124 larvae, the weight of frass extracted from 3101 mines, the area of 3085 mines, the length of 3088 mined leaves, and the weight of disks punched from 1658 leaves (Data S1). This variation explains why the performed analyses are based on samples of different sizes.

3.2. Variation in measured characters

The length of a mined leaf varied from 8 mm to 52 mm (median value: 24 mm). The mine area in these leaves varied from 50 mm^2 to 450 mm^2 (median value: 200 mm^2), and the proportion of mined leaf area varied from 10 % to 100 % (median value: 65 %). A nine-fold difference in mine area occurred because 9 % of all leaves were completely consumed by *Eriocrania* larvae, and thus the size of these leaves constrained mine area. This variation may also reflect variation in SLA, because the weight of leaf disks 8 mm in diameter punched from intact parts of the leaf lamina varied from 1.39 mg to 5.56 mg (median value 2.80 mg). Dry weight of larvae varied between 0.27 mg and 3.93 mg (median value 1.84 mg), and dry weight of their frass varied between 0.54 mg and 11.63 mg (median value 4.59 mg) (Data S1).

3.3. Growth of larvae in detached leaves

The larvae of *E. semipurpurella* that emerged from mines on the day of collection or the following day were 3 % heavier than the larvae of *E. sangii* (Table 2; Fig. 1a). Nevertheless, the larvae of *E. semipurpurella* produced 4 % less frass while creating mines of the same size as the larvae of *E. sangii* (Table 2; Fig. 1b, c). The weight of larvae that emerged from mines on the fifth day after collection or later was reduced to 70 % in *E. semipurpurella* and to 76 % in *E. sangii* relative to the weight of larvae that emerged from mines on the day of collection (Fig. 1a), whereas frass weight remained unaffected (Table 2; Fig. 2c). This decrease in larval weight was accompanied by a small but significant increase in mine area (Table 2; Fig. 2b). The leaf quality index declined to 59 % in *E. semipurpurella* and to 75 % in *E. sangii* (Table 2; Fig. 1d).

Based on these findings, we excluded from all subsequent analyses the data on larvae that emerged from mines later than next day after collection and calculated all correlations separately for *E. semipurpurella* and *E. sangii*.

3.4. Spatial variation in feeding performance of Eriocrania larvae

All six response variables significantly varied among study sites in both *Eriocrania* species (Table 3). However, this variation was explained by foliar nickel concentrations in only seven out of 12 tests (2 species × 6 characters; Table 3), and only 23 of 120 individual correlations (2 species × 6 characters × 10 years) between response variables and foliar nickel concentrations appeared statistically significant (Table S2).

The meta-analysis revealed that correlations between studied characters and foliar nickel concentrations did not differ between *E. semipurpurella* and *E. sangii* ($Q_B = 0.01 \ldots 0.51$, df = 1, $P = 0.51 \ldots 0.92$). Therefore, these species were combined in the following analyses addressing spatial variation.

The studied characters showed different spatial correlations with pollution load ($Q_B = 40.8$, df = 5, $P = 0.001$). Larval weight significantly

Table 2

Effects of *Eriocrania* species and days elapsed from leaf collection date (covariate) on characteristics of *Eriocrania* larvae and mined leaves (ANCOVA, type 3 sum of squares; all years and sites combined).

Character	Source of variation	Statistics
Larval weight	Species	$F_{1,\ 3120} = 14.1, P = 0.0002$
	Days	$F_{1,\ 3120} = 316.0, P < 0.0001$
	Species × Days	$F_{1,\ 3120} = 5.55, P = 0.02$
Frass weight	Species	$F_{1,\ 3097} = 12.1, P = 0.0005$
	Days	$F_{1,\ 3097} = 2.23, P = 0.14$
	Species × Days	$F_{1,\ 3097} = 0.71, P = 0.40$
Mine area	Species	$F_{1,\ 3081} = 0.71, P = 0.40$
	Days	$F_{1,\ 3081} = 8.61, P = 0.0034$
	Species × Days	$F_{1,\ 3081} = 2.83, P = 0.09$
Leaf quality index	Species	$F_{1,\ 2996} = 46.8, P < 0.0001$
	Days	$F_{1,\ 2996} = 175.1, P < 0.0001$
	Species × Days	$F_{1,\ 2996} = 9.01, P = 0.0027$

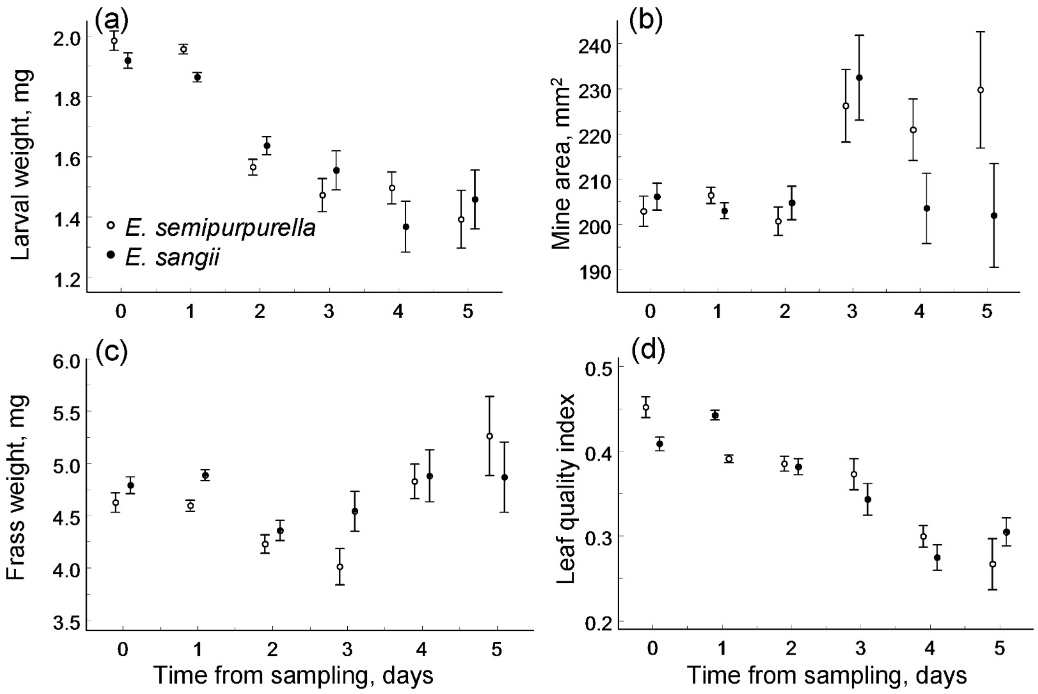

Fig. 1. Changes in study traits (means ± S.E.) with time elapsed from the leaf collection date to the day of larval emergence from a mine: (a) larval weight, (b) mine area, (c) frass weight, and (d) leaf quality index. For statistical analyses, see Table 2. Sample sizes for days 0–5: *Eriocrania semipurpurella*, 221, 905, 306, 72, 84, 28; *E. sangii*, 310, 833, 205, 47, 42, 25.

decreased as foliar nickel concentrations increased (Fig. 2a; ES = −0.40, CI95 = −0.58 … −0.23, $n = 20$), thus confirming prediction (1) regarding the spatial pattern in the weight of *Eriocrania* larvae. The mine area decreased with an increase in pollution (Fig. 2b; ES = −0.83, CI95 = −1.01 … −0.67, $n = 20$) greater than the larval weight did, in terms of both effect sizes (Fig. 2a, b; $Q_B = 7.78$, df = 1, $P = 0.005$) and the magnitude of changes (to 93 % and 83 % in the two most polluted sites relative to the two least polluted sites, respectively). Frass weight did not change along the pollution gradient (Fig. 2c; ES = −0.03, CI95 = −0.17 … 0.12, $n = 20$); consequently, the leaf quality index significantly decreased (to 90 %) with an increase in pollution (Fig. 2d; ES = −0.16, CI95 = −0.30 … −0.04, $n = 20$).

Both length of mined leaves (Fig. 2e; ES = −0.56, CI95 = −0.76 … −0.36, $n = 20$) and SLA (Fig. 2f; ES = −0.69, CI95 = −0.86 …−0.47, $n = 20$) decreased with an increase in pollution load, being in heavily polluted sites 84 % of that observed in slightly polluted sites. Consistently with the decrease in leaf size, proportion of birch leaves that were completely or nearly completely consumed by *Eriocrania* larvae (mine area >90 % of leaf area) significantly ($r = 0.79$, $n = 8$ sites, $P = 0.02$) increased with an increase in pollution load, from 15.3 % in the least polluted site to 30.0 % in the most polluted site. These findings, combined with the positive association between larval weight and the length of the mined leaf ($r = 0.26$, $n = 2184$ leaves, $P < 0.0001$), confirmed the prediction (3) that the decrease in birch leaf size with an increase in pollution contributed to the decrease in larval weight.

3.5. Temporal variation in feeding performance of *Eriocrania* larvae

All response variables significantly varied among study years (Table 3). However, only 25 of 384 individual correlations reflecting temporal patterns in studied characters (2 species × 6 characters × 8 sites × 4 explanatory variables) appeared statistically significant (Table S3). The four explanatory variables (SO_2 emissions and temperatures of winter, spring, and larval growth period) varied independently from each other ($R^2 = 0.0008$ … 0.38, $n = 10$ years, $P = 0.10$ … 0.93).

The meta-analysis revealed that correlations reflecting temporal patterns in the studied traits did not differ between *E. semipurpurella* and *E. sangii* ($Q_B = 0.00$ … 2.65, df = 1, $P = 0.052$ … 0.97). Therefore, these species were combined in the following analyses addressing annual variation in performance and feeding efficiency of *Eriocrania* larvae.

All studied traits exhibited different changes with the decline in emissions (Fig. 3; $Q_B = 85.1$, df = 5, $P < 0.001$). Larval weight increased by 25 % with a decrease in annual SO_2 emission from 129,400 metric tons (t) to 41,100 t, thus confirming prediction (2) regarding the temporal pattern in the weight of *Eriocrania* larvae. Simultaneously, leaf length increased by 10 %, while frass weight decreased by 16 % (Fig. 4c). Consequently, leaf quality index increased by 48 % (Fig. 4d), whereas mine area and SLA did not change with SO_2 emission decline (Fig. 3).

The ambient air temperature in winter, spring, and the larval growth period showed variable associations with the studied traits (Fig. 3; $Q_B = 5.84$ … 54.2, df = 2, $P = 0.001$ … 0.004). Larval weight increased by 13 % with an increase in spring temperature from −0.1 °C to 5.8 °C (Fig. 4a), but was not significantly associated with the temperature of either the winter or the larval growth period (Fig. 3). Mine area decreased by 13 % with an increase in spring temperature (Fig. 3), decreased by 7 % with an increase in winter temperature from −10.8 °C to −5.4 °C (Fig. 3), and increased by 14 % with an increase in temperature of larval growth period from 8.7 °C to 14.8 °C (Fig. 4b). Frass weight increased by 20 % with an increase in winter temperature, but did not correlate with the temperature of either the spring or the larval growth period (Fig. 3). The leaf quality index decreased by 17 % with an increase in winter temperature, increased by 26 % with an increase in spring temperature, but was not related to the temperature of the larval growth period (Fig. 3). The length of a mined leaf increased by 22 % with an increase in the temperature of the larval growth period (Fig. 4e), but did not correlate with the temperature of either winter or spring (Fig. 3). SLA declined by 25 % and 10 % with increases in winter (Fig. 4f) and spring temperatures, respectively, and increased by 9 % with an increase in the temperature of the larval growth period (Fig. 3).

The combination of these findings suggests that elevated spring temperatures, in line with prediction (4), increase leaf quality, allowing

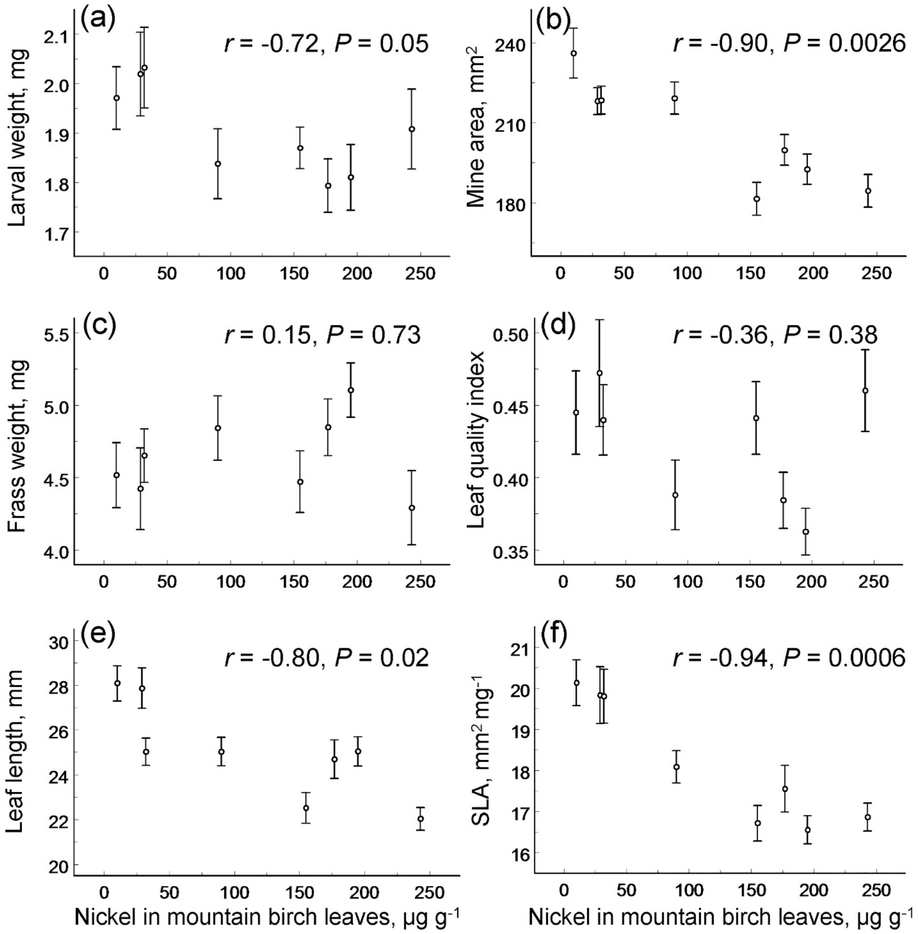

Fig. 2. Spatial associations between study traits (means ± S.E., based on 16–20 samples each) and pollution, quantified by the average concentration of nickel in mountain birch leaves: (a), larval weight, (b) mine area, (c) frass weight, (d) leaf quality index, (e) length of mined leaf, and (f) specific leaf area.

Eriocrania larvae to attain a larger weight while consuming less biomass, as indicated by the smaller mine area. Consistent with spatial variation, the increase in larval weight corresponds to an increase in leaf size. The increase in mine area with an elevation in the temperature of the larval growth period supports prediction (5) regarding an increase in metabolic expenses, because at higher ambient temperatures *Eriocrania* larvae consumed more biomass of the same quality to attain the same weight as they do at lower ambient temperatures.

3.6. Interactions between spatial and temporal variation in feeding performance of Eriocrania larvae

Interactive effects of spatial (pollution load) and temporal (annual) variation were significant in nine out of 12 tests (2 species × 6 characters; Table 3). Meta-regression revealed that the strength of the spatial association between pollution and the weight of *Eriocrania* larvae increased with rising winter temperature ($Q = 2.02$, $P = 0.03$), whereas the spatial association between pollution and frass weight increased with rising spring temperature ($Q = 2.65$, $P = 0.02$) but decreased with an increase in temperature during the larval growth period ($Q = 2.01$, $P = 0.05$). The length of a mined leaf showed different associations with spring temperature in heavily and slightly polluted sites ($Q_B = 2.99$, df $= 1$, $P = 0.02$): leaf length did not change with spring temperature in slightly polluted sites (ES $= 0.04$, CI95 $= -0.14 \ldots 0.20$, $n = 4$) but significantly decreased with an increase in spring temperature in heavily polluted sites (ES $= -0.31$, CI95 $= -0.46 \ldots -0.14$, $n = 4$). Hence, four out of 24 analyses support prediction (6) on the existence of interactive effects of pollution and climate on herbivorous insects.

3.7. Factors affecting Eriocrania population dynamics

The RPC did not correlate with foliar nickel concentrations (ES $= 0.16$, CI95 $= -0.21 \ldots 0.52$, $n = 10$) but significantly decreased with rising air temperatures (winter: ES $= -0.36$, CI95 $= -0.56 \ldots -0.12$, $n = 8$; spring: ES $= -0.43$, CI95 $= -0.62 \ldots -0.25$, $n = 8$; larval growth period: ES $= -0.18$, CI95 $= -0.34 \ldots -0.01$, $n = 8$). Furthermore, the strength of the negative association between RPC and winter temperatures differs between heavily and slightly polluted sites ($Q_B = 3.57$, df $= 1$, $P = 0.03$), being significant in slightly polluted sites (ES $= -0.62$, CI95 $= -0.82 \ldots -0.49$, $n = 4$) but not significant in heavily polluted sites (ES $= -0.11$, CI95 $= -0.35 \ldots 0.03$, $n = 4$). However, the RPC appeared independent from the previous-year larval weight (ES $= -0.13$, CI95 $= -0.31 \ldots 0.05$, $n = 8$ sites). This pattern (Fig. 5) did not differ between heavily and slightly polluted sites ($Q_B = 0.01$, df $= 1$, $P = 0.88$). Thus, our data provided no support for predictions (7) and (8) regarding the existence and strength of bottom-up impacts on *Eriocrania* population dynamics.

4. Discussion

4.1. Effects of pollution on feeding performance of Eriocrania larvae

Our study highlights several significant findings regarding the impact of pollution on *Eriocrania* larvae: (i) consistency in responses to pollution load between spatial and temporal scales, (ii) association of these responses with SO_2 rather than with trace elements, and (iii) identification of leaf size as a mediator of pollution impact on larval

Table 3

Effects of study year and foliar nickel concentration in mountain birch leaves (covariate) on characteristics of *Eriocrania* larvae and mined leaves (GLIMMIX procedure, type 3 sum of squares). The data are restricted to larvae that emerged from their mines no later than next day after sampling.

Character	Source of variation	*E. semipurpurella*	*E. sangii*
Larval weight	Year	$F_{9,\ 1119} = 18.0$, $P < 0.0001$	$F_{9,\ 1126} = 5.15$, $P < 0.0001$
	Nickel	$F_{1,\ 6.5} = 7.25$, $P = 0.03$	$F_{1,\ 6.1} = 3.36$, $P = 0.12$
	Year × Nickel	$F_{9,\ 1115} = 2.86$, $P = 0.0024$	$F_{9,\ 1134} = 1.49$, $P = 0.15$
	Site (random)	$\chi^2 = 13.8$, df = 1, $P = 0.0001$	$\chi^2 = 8.28$, df = 1, $P = 0.0020$
Frass weight	Year	$F_{9,\ 1118} = 9.62$, $P < 0.0001$	$F_{9,\ 1120} = 5.36$, $P < 0.0001$
	Nickel	$F_{1,\ 6.5} = 0.11$, $P = 0.75$	$F_{1,\ 7.5} = 0.00$, $P = 0.97$
	Year × Nickel	$F_{9,\ 1119} = 2.66$, $P = 0.0047$	$F_{9,\ 1126} = 1.65$, $P = 0.10$
	Site (random)	$\chi^2 = 43.4$, df = 1, $P < 0.0001$	$\chi^2 = 15.2$, df = 1, $P < 0.0001$
Mine area	Year	$F_{9,\ 1114} = 7.17$, $P < 0.0001$	$F_{9,\ 1106} = 6.80$, $P < 0.0001$
	Nickel	$F_{1,\ 8.1} = 20.4$, $P = 0.0019$	$F_{1,\ 7.3} = 25.2$, $P = 0.0013$
	Year × Nickel	$F_{9,\ 1111} = 2.18$, $P = 0.02$	$F_{9,\ 1111} = 3.76$, $P = 0.0001$
	Site (random)	$\chi^2 = 22.5$, df = 1, $P < 0.0001$	$\chi^2 = 10.5$, df = 1, $P = 0.0006$
Leaf quality index	Year	$F_{9,\ 1062} = 13.1$, $P < 0.0001$	$F_{9,\ 1100} = 8.34$, $P < 0.0001$
	Nickel	$F_{1,\ 6.0} = 0.30$, $P = 0.60$	$F_{1,\ 6.5} = 1.12$, $P = 0.33$
	Year × Nickel	$F_{9,\ 1063} = 3.30$, $P = 0.0005$	$F_{9,\ 1100} = 1.16$, $P = 0.32$
	Site (random)	$\chi^2 = 72.9$, df = 1, $P < 0.0001$	$\chi^2 = 48.1$, df = 1, $P < 0.0001$
Leaf length	Year	$F_{9,\ 1115} = 6.34$, $P < 0.0001$	$F_{9,\ 1110} = 5.26$, $P < 0.0001$
	Nickel	$F_{1,\ 7.6} = 10.1$, $P = 0.01$	$F_{1,\ 6.7} = 11.7$, $P = 0.01$
	Year × Nickel	$F_{9,\ 1114} = 2.71$, $P = 0.0040$	$F_{9,\ 1114} = 2.15$, $P = 0.02$
	Site (random)	$\chi^2 = 45.5$, df = 1, $P < 0.0001$	$\chi^2 = 14.0$, df = 1, $P < 0.0001$
Specific leaf area	Year	$F_{9,\ 616} = 8.04$, $P < 0.0001$	$F_{9,\ 606} = 7.24$, $P < 0.0001$
	Nickel	$F_{1,\ 6.7} = 29.7$, $P = 0.0011$	$F_{1,\ 6.0} = 10.3$, $P = 0.02$
	Year × Nickel	$F_{9,\ 608} = 1.18$, $P = 0.30$	$F_{9,\ 605} = 4.51$, $P < 0.0001$
	Site (random)	$\chi^2 = 3.01$, df = 1, $P = 0.04$	$\chi^2 = 39.5$, df = 1, $P < 0.0001$

weight.

The negative relationship between pollution load and larval weight at the spatial scale supports prediction (1) and aligns with the results of the meta-analysis (Zvereva and Kozlov, 2010), which revealed a general pattern of decreased insect performance near pollution sources. Additionally, our study revealed a noteworthy increase in the weight of *Eriocrania* larvae from 1995 to 2005. This finding supports prediction (2) and holds particular significance as it represents the first evidence of rapid, unassisted recovery of the individual performance of invertebrate herbivores following emission control measures.

Industrial emissions comprise numerous substances, many of which are toxic, and their depositions exhibit strong spatial and temporal correlations (Freedman and Hutchinson, 1980; Barkan, 1993). These correlations complicate the identification of the immediate drivers behind observed biotic effects. However, despite significant emission declines during our study period, there were no significant changes in concentrations of nickel and copper in mountain birch foliage—a phenomenon known as a legacy effect (Kozlov, 2005). This led us to attribute both spatial and temporal patterns explained by pollution to changes in concentrations of SO_2 rather than trace elements. Nevertheless, we cannot entirely exclude the contribution of trace elements to shaping the observed patterns, as combined exposure to SO_2 and trace elements may result in synergistic (Krause and Kaiser, 1977) or antagonistic effects (Toivonen and Hofstra, 1979) on plants. We propose that pollution indirectly affects the feeding performance of *Eriocrania* larvae through birch leaf quality, considering that the concentration of SO_2 in our most polluted site (186 μg m^{-3}: Kozlov, 2002) was lower than the lowest concentration known to cause direct toxicity effects on herbivorous insects (250 μg m^{-3}: Whittaker and Warrington, 1990; Kozlov et al., 1996).

The consistent response direction of *Eriocrania* larval weight to pollution at both spatial and temporal scales supports the frequent use of space-for-time substitution in pollution research. However, the magnitudes of the detected effects relative to changes in pollution load differ nearly 50-fold between spatial and temporal scales. The ambient SO_2 concentration at the most polluted site at the beginning of our study was 90 times greater than at the least polluted site (Table 1), while the weight of *Eriocrania* larvae at the most polluted site was reduced only to 90 % relative to the least polluted site (Fig. 2a). At the same time, a three-fold decline in SO_2 emissions from the Monchegorsk smelter during the study period was accompanied by a 25 % increase in the weight of *Eriocrania* larvae. This discrepancy hints that pollution effects observed at spatial and temporal scales could be mediated by different, yet unknown mechanisms.

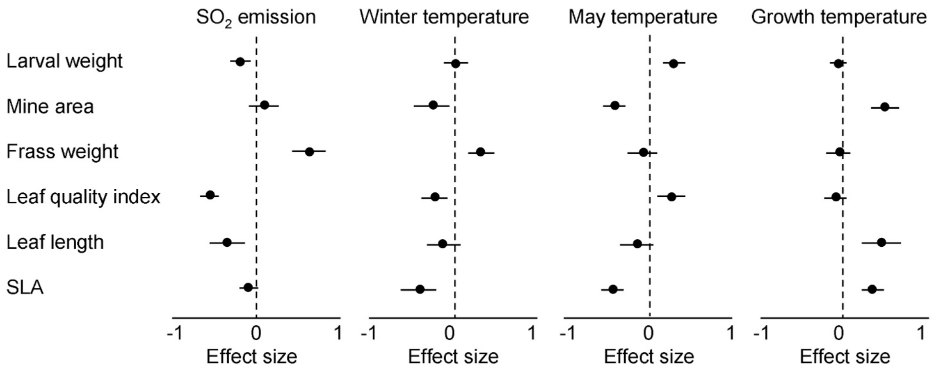

Fig. 3. Temporal associations between study traits and explanatory variables (results of meta-analysis). Mean values (dots) are each based on 16 effect sizes; horizontal lines denote 95 % confidence intervals (CI95). An effect is statistically significant if CI95 does not include zero. The positive effect size indicates an increase in the study trait with an increase in SO_2 emission or ambient temperature. For statistical analyses, see the main text.

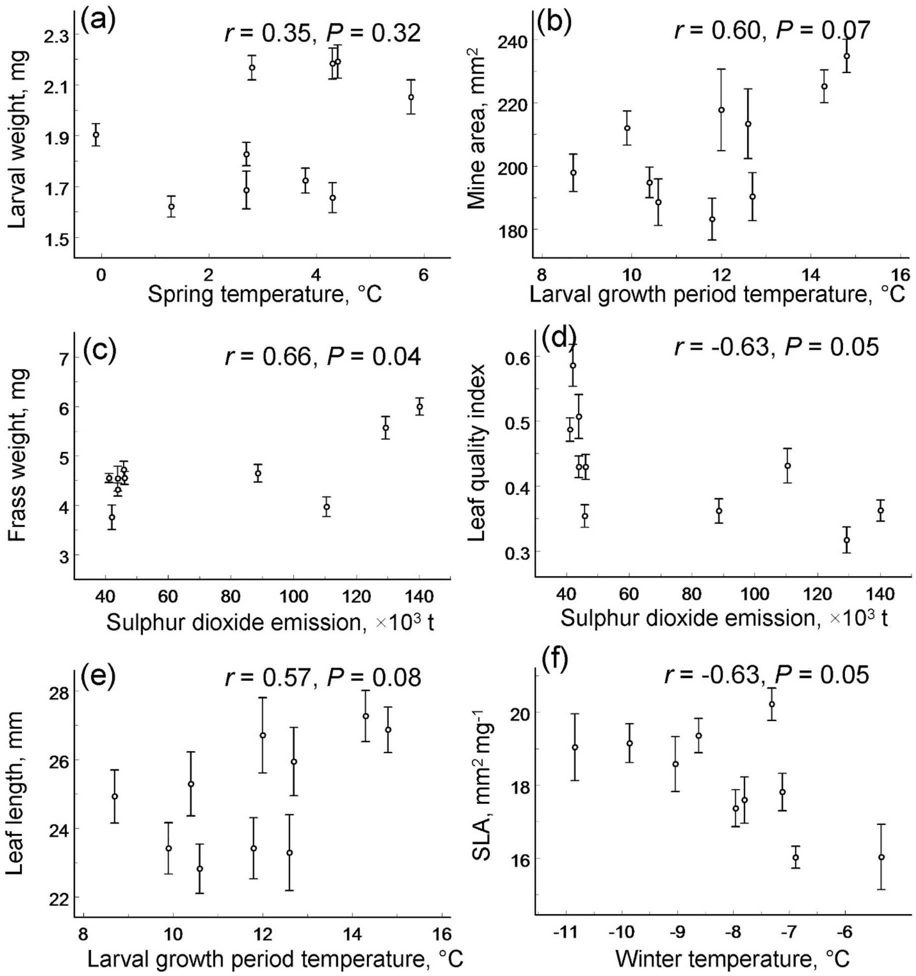

Fig. 4. The strongest temporal associations between study traits (means ± S.E., based on 13–16 samples each) and explanatory variables: (a), larval weight, (b) mine area, (c) frass weight, (d) leaf quality index, (e) length of mined leaf, and (f) specific leaf area.

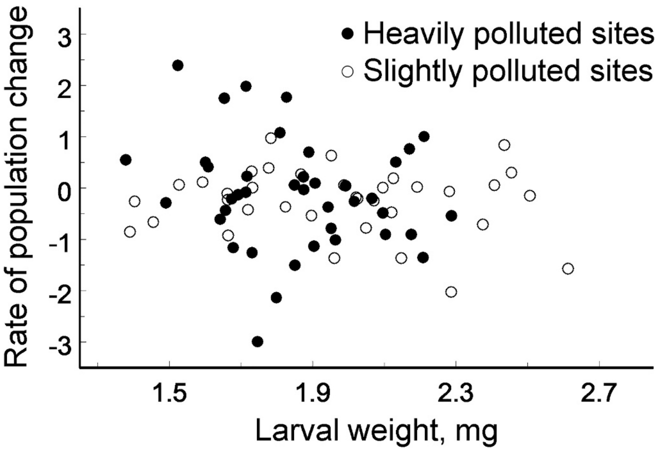

Fig. 5. Associations between the per capita rate of population change (RPC) and the average weight of *Eriocrania* larvae in four heavily polluted sites ($r = -0.19$, $P = 0.24$) and four slightly polluted sites ($r = -0.10$, $P = 0.55$) during the observation period (1995–2005). The positive RPC indicates an increase in population density.

A better performance of mining insects within larger leaves (Bultman and Faeth, 1986; Low et al., 2009; current study) suggests that pollution effects on the larval weight of *Eriocrania* could be mediated by changes in birch leaf size. The mountain birch leaves in unpolluted forests around Monchegorsk during our study years were 4–10 mm longer than in heavily polluted industrial barrens, and their length increased by 7–8 mm from 1995 to 2005 (Zverev, 2012). Thus, spatial and temporal changes in pollution effects on the length of birch leaves have similar magnitudes and, in agreement with prediction (3), may potentially explain similar pollution effects on *Eriocrania* performance in space and time.

Nevertheless, some *Eriocrania* larvae attained an average (or even larger) weight despite the size of the mined leaves being rather small, so that the mine area reached only half of its average value (Data S1). This seemingly paradoxical observation, contrasting the general opinion that mine size provides an effective cue to larval size (Springett and Matthiessen, 1975; Boomsma et al., 1987; Low et al., 2009), could be explained by an exceptionally early infestation of these leaves by *Eriocrania* larvae. Rapid consumption of leaf tissues by a larva prevents the infested leaf from attaining its programmed size, but the high quality of a young leaf (Ayres and MacLean, 1987; Martel and Kause, 2002) allows the larva to grow disproportionately large relative to the consumed biomass (as estimated from mine size).

4.2. *Effects of ambient air temperature on feeding performance of Eriocrania larvae*

Our most important findings related to the impacts of ambient air temperature on *Eriocrania* larvae are as follows: (i) larval weight is independent of ambient air temperature at the time of larval growth, (ii) larvae exposed to higher temperatures create larger mines (i.e., consume more biomass) to attain the same weight as larvae exposed to lower temperatures, and (iii) temperature and pollution sometimes modify each other's effects on the feeding performance of *Eriocrania* larvae.

Temperature is a key environmental factor for ectothermic organisms, including insects (Bale et al., 2002). Nevertheless, despite decades of research, our understanding of the effects of elevated temperatures on insect-plant interactions remains insufficient to predict the behaviour of a particular study system. The only exception is a consistent decrease in developmental time with an increase in ambient temperature, which has been reported in both natural and laboratory environments (Wagner et al., 2011; Bauerfeind and Fischer, 2013).

The effect of temperature on the body size of terrestrial arthropods varies with voltinism and body mass (Horne et al., 2015). Our *Eriocrania* species are univoltine, and the final body mass of their larvae is around 2 mg. Based on equations provided by Horne et al. (2015), we estimated that *Eriocrania* larvae would gain 3 % greater weight in our warmest year (when the ambient air temperature during the larval growth period was 14.8 °C) relative to our coldest year (when this temperature was 8.7 °C). However, we did not detect this effect in among-year comparisons. At the same time, the mine area in the warmest year was 17 % greater than in the coldest year, paralleling our previous finding that larvae of another leafminer, *Stigmella lapponica*, consumed less foliar biomass at higher (and cooler) latitudes than at lower (and warmer) latitudes to reach the same size (Kozlov et al., 2023). Based on the overall consistency between the effects of latitude and temperature on body size in arthropods (Horne et al., 2015), we attribute both of these patterns to an increase in metabolic demands of insects with temperature elevation (Lemoine et al., 2014; Parsons and Joern, 2014).

The positive effect of spring temperature on birch leaf quality, evidenced by an increase in the weight of *Eriocrania* larvae accompanied by a decrease in mine area, supports prediction (5) and is consistent with changes in the survival of the leaf beetle *Chrysomela lapponica* with an increase in spring temperatures (Zvereva et al., 2016). While it is tempting to attribute this effect to a negative correlation between leaf growth rate (which increases with temperature) and the foliar content of defensive metabolites (Herms and Mattson, 1992), this explanation is hindered by studies reporting a decrease in leaf quality with rising growth temperature (Bauerfeind and Fischer, 2013; Jamieson et al., 2015). A plausible explanation for the observed enhancement of birch leaf quality is that elevated temperature hampers the uptake of trace elements from the soil (Waughman et al., 1983), and the decrease in plant toxicity overcomes the adverse direct effects of temperature.

A high SLA can indicate better leaf quality for herbivores due to the positive correlation between SLA and foliar nitrogen (Wright et al., 2004), the concentration of which is of prime importance for herbivores, including leaf miners (Cornelissen and Stiling, 2006; Uesugi, 2015). The leaf quality index (i.e., the larval mass to frass mass ratio) was previously found to positively correlate with foliar nitrogen in the surroundings of the Harjavalta smelter in Finland (Koricheva and Haukioja, 1995). However, in our study, the leaf quality index and SLA demonstrated inconsistent responses to all explanatory variables at both spatial and temporal scales (Figs. 2, 3). Meanwhile, changes in mine area were consistent with changes in SLA (Figs. 2, 3), suggesting that mine size is affected more by leaf thickness than by leaf quality. However, this conclusion should be considered tentative, as small leaves were completely consumed by *Eriocrania* larvae, and therefore, SLA was measured only in large leaves.

4.3. Combined effects of pollution and climate on Eriocrania population dynamics

Environmental ecology rarely addresses density-dependent processes, thus limiting our knowledge on the combined impacts of pollution and climate on insect population dynamics and the mechanisms behind these impacts (Kozlov, 2022). This gives particular importance to our findings that (i) RPC of *Eriocrania* is independent of larval weight, (ii) RPC decreases with increases in ambient air temperatures during spring and the larval growth period, both in slightly and heavily polluted sites, and (iii) a decrease in RPC with an increase in winter temperatures occurs only in slightly polluted sites.

Demographic studies typically use fecundity (or body size as its proxy: Haukioja and Neuvonen, 1985; Honěk, 1993) to explore factors driving population changes (Tenan et al., 2021), or infer these changes based on fecundity estimates (Tammaru et al., 1996). Therefore, our discovery of the independence of RPC from larval weight, which contradicts prediction (7), is somewhat surprising. We propose that the average larval weight at emergence from a mine appeared to be a poor predictor of population-wide fecundity (and consequently, of RPC) due to size-dependent mortality (Ohgushi, 1996; Schröder, 2013). This mortality could have distorted the expected correlation between the weights of larvae and females due to among-site variation in the proportion of *Eriocrania* larvae that have emerged from insufficiently sized birch leaves.

The differences in the association of RPC with winter temperatures between heavily and slightly polluted sites could be explained by the thickness of snow cover, which in heavily polluted sites is reduced approximately to one-third of that in slightly polluted sites (Kozlov, 2001). Consequently, soil temperatures in winter are lower in heavily polluted sites (Kozlov and Haukioja, 1997), exposing insects hibernating in the soil to low temperatures even during warm winters. In contrast, insects at unpolluted sites during warm winters may experience temperatures favourable for completing diapause, which could have adverse effects on their survival (Bale et al., 2002). This finding adds to the rare reports of disruption or alteration of regulatory mechanisms in populations of herbivorous insects persisting in polluted environments (Zvereva and Kozlov, 2006a; Hunter and Kozlov, 2019).

4.4. Growth of leafmining insects in detached leaves: methodological implications

The practice of rearing leafminers in laboratory conditions is standard in taxonomic and faunistic studies, but existing protocols (Hering, 1951; Lopez-Vaamonde et al., 2021) pay no attention to the duration of leafminer growth in detached leaves. Our data, for the first time, demonstrated a rapid and substantial decline in the final larval weight of leafminers with an increase in time from the leaf collection date, highlighting the potential bias this uncontrolled variation may introduce in ecological studies. This decline likely results from rapid changes in the quality of detached leaves. For instance, research shows that five days after harvest, asparagus kept at 20 °C contains only 10–50 % of soluble carbohydrates and protein relative to the harvest date (Renquist et al., 2005).

We recommend that ecological studies involving the collection of mined leaves containing live insect larvae take the utmost care to minimize the duration of larval growth in detached leaves, record this duration, and account for it in data analysis. Researchers exploring insect size should be aware that miners reared from detached leaves may be smaller than their field-collected counterparts.

5. Conclusion

Our study advanced the understanding of the combined and interactive effects of pollution and climate on the population dynamics of herbivorous insects. We demonstrated that industrial pollution and ambient air temperature affect leafminer populations through multiple pathways. We found that larval weight consistently increased with a decrease in pollution, both spatially and temporally. Larvae attained greater weight in years with warm springs due to an increase in leaf quality; however, we observed no correlation between larval weight and the per capita rate of population change. High pollution disrupted the negative impact of winter temperatures on the rate of population change. Our findings suggest that the current level of knowledge is insufficient to predict climate-driven changes in herbivore population dynamics in polluted habitats.

CRediT authorship contribution statement

Mikhail V. Kozlov: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Vitali Zverev:** Writing – review & editing, Visualization, Methodology, Investigation.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve language and readability of our text. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data are provided in the supplementary.

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Appendix A. Supplementary data

Supplementary data to this article – annual atmospheric emissions of principal pollutants from the smelter at Monchegorsk from 1995 to 2005, climate variables in Monchegorsk, and collection dates of mined birch leaves (Table S1), Pearson correlation coefficients between response variables and average nickel concentrations in mountain birch foliage used in meta-analysis of spatial patterns in characteristics of *Eriocrania* larvae and the mined leaves (Table S2), Pearson correlation coefficients between response variables, annual SO_2 emissions and temperatures of winter, spring and larval growth periods used in meta-analysis of temporal patterns in characteristics of *Eriocrania* larvae and the mined leaves (Table S3), densities of *Eriocrania* larvae used in analyses of per capita population growth rates (Table S4), Pearson correlation coefficients between per capita population growth rates, larval weight and temperatures of winter, spring and larval growth periods used in meta-analysis of temporal patterns in *Eriocrania* population dynamics (Table S5), and data on *Eriocrania* larvae and mined birch leaves (Data S1) – can be found online at https://doi.org/10.1016/j.scitotenv.2024.174342.

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