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Science of the Total Environment 838 (2022) 155800

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Recovery of moth and butterfly (Lepidoptera) communities in a polluted region following emission decline

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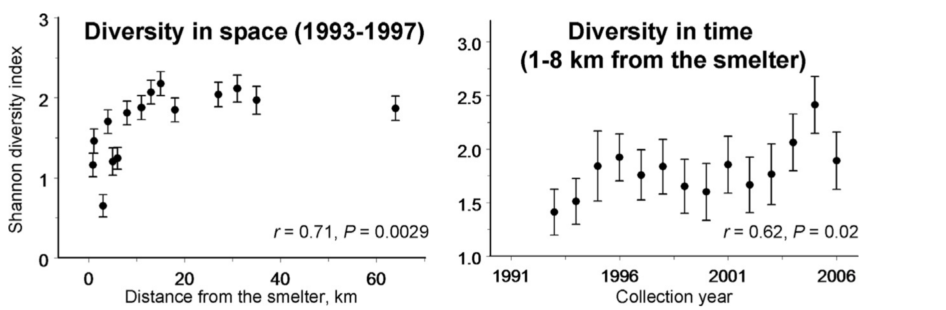
HIGHLIGHTS

- Diversity of Lepidoptera declined near the smelter while abundance did not change.
- Diversity, but not abundance, increased near the smelter after emission decline.
- Life history traits of a species indicate its vulnerability to pollution.
- Recovery trajectories of insect communities can be predicted from spatial patterns.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Elena Paoletti

Keywords:
Abundance
Biodiversity
Industrial pollution
Life history traits
Murmansk region
Natural recovery

ABSTRACT

Environmental pollution is one of the major drivers of the present-day decline in global biodiversity. However, the links between the effects of industrial pollution on insect communities and the underlying species-specific responses remain poorly understood. We explored the spatial pattern in insect communities by analysing 581 samples of moths and butterflies (containing 25,628 individuals of 345 species) collected along a strong pollution gradient in subarctic Russia, and we recorded temporal changes in these communities during the pollution decline that occurred from 1992 to 2006. In the 1990s, the diversity of the Lepidoptera community was positively correlated with the distance from the copper-nickel smelter at Monchegorsk. The overall abundance of Lepidoptera did not change along the pollution gradient, although the abundance of many species decreased with increasing pollution. The responses of each individual species to pollution were associated with its life history traits. The abundances of monophagous species that fed inside live plant tissues and hibernated as imagoes or pupae were not affected by pollution, whereas the abundances of oligophagous and polyphagous species that fed externally on plants and hibernated as larvae generally declined near the smelter. Substantial decreases in aerial emissions from the smelter between 1992 and 2006 resulted in an increase in the diversity of moths and butterflies in severely polluted habitats, whereas their overall abundance did not change. This recovery of the Lepidoptera community occurred due to the reappearance of rare species that had been previously extirpated by pollution and was observed despite the lack of any signs of recovery of the vegetation in the heavily polluted sites. We conclude that the recovery trajectories of insect communities following emission control can be predicted from studies of their changes along spatial pollution gradients by using space-for-time substitution.

1. Introduction

Insects—the most diverse group of living beings (Stork, 2018)—are crucial components of terrestrial ecosystems and they drive many important ecosystem functions. Consequently, alarming reports on global insect extinction (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019;

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http://dx.doi.org/10.1016/j.scitotenv.2022.155800
Received 4 February 2022; Received in revised form 14 April 2022; Accepted 5 May 2022
Available online 10 May 2022

Seibold et al., 2019; Wagner, 2020) have raised concerns regarding the healthy functioning of future ecosystems (Cardoso et al., 2020) and have forced scientists to develop conservation measures to combat this serious threat (Harvey et al., 2020).

Environmental pollution is now recognised as one of the major drivers of global biodiversity decline (IPBES, 2019), including losses of insect diversity and abundance (Cardoso et al., 2020). However, pollution-related concerns are primarily linked with the excessive use of pesticides and fertilisers, along with light and noise pollution (Harvey et al., 2020; Warren et al., 2021). By contrast, industrial pollution—despite its global importance (De Marco et al., 2022) and overall negative impact on biodiversity (Lu et al., 2020)—is rarely considered in conservation planning and management (Lovett et al., 2009). This neglect of industrial pollution in biodiversity conservation agendas has likely resulted from the shortage of empirical information regarding the effects of pollutants on insect communities.

A decrease in biodiversity is one of the general ecosystem responses to environmental disturbance (Odum, 1985; Rapport et al., 1985). However, community-wide studies of insects in polluted terrestrial ecosystems remain scarce: a meta-analysis of insect responses to industrial pollution involved only 13 effect sizes based on the Shannon diversity index (Zvereva and Kozlov, 2010), and only a handful of relevant studies have been published since then (Moroń et al., 2012; Belskaya et al., 2019; Ozaki et al., 2022). This number is astonishingly small and obviously insufficient to uncover any general pattern in the responses of insect communities to pollution. Although many species and some functional groups of insects show declines with an increase in pollution (Alstad et al., 1982; Heliövaara and Väisänen, 1993), others flourish in polluted habitats (Führer, 1985; Kozlov, 1997; Hunter and Kozlov, 2019) and decline following the implementation of pollution control measures (Zvereva et al., 2016). A better understanding of which species and functional groups are most vulnerable to pollution is badly needed to advance global insect conservation, and this task has now become a matter of urgency (Cardoso et al., 2020; Harvey et al., 2020).

Long-term studies conducted near industrial polluters have tremendous potential to contribute to the development of fundamental ecology (Liebhold, 2019). In the present study, we report new results of a large-scale, long-term, unintentional pollution experiment (as defined by Lee, 1998), which started in 1937 with the construction of a large copper-nickel smelter in a previously unpopulated territory and the establishment of the town of Monchegorsk nearby. This smelter, located in the centre of the Murmansk region of Russia, had no air-cleaning facilities until 1968, and the aerial emissions of sulphur dioxide and dust containing nickel, copper and other metals had created impressive 'moonscapes' (Fig. 1a, b) around Monchegorsk even by the 1960s and had deeply altered the adjoining coniferous forests (Fig. 1c–h; Kozlov et al., 2009).

A sharp toxicity gradient resulting from the deposition of airborne pollutants created gradients in plant productivity and, finally, in microclimate (Kozlov and Haukioja, 1997; Kozlov and Zvereva, 2007). The aboveground biomass of the plant communities near Monchegorsk is only ca. 2% of that in unpolluted forests (Manninen et al., 2015). This lack of vegetation would be expected to have particularly deleterious effects on Lepidoptera species, as the larvae of a vast majority of moths and butterflies feed on live plants (Scoble, 1992; Speight et al., 2008). In this study, we assumed that the biomass of herbivorous insects is controlled by primary productivity (McNaughton et al., 1989), and we predicted that the overall abundance of Lepidoptera will decline with increasing proximity to the smelter. Furthermore, the generally positive association observed between biodiversity and ecosystem productivity (Hutchinson, 1959; Brown, 2014), combined with the loss of plant diversity in the polluted areas (Zvereva et al., 2008), suggests that the diversity of moths and butterflies near the smelter will also be smaller than that in pristine forests.

Various insect species generally differ in their tolerance to pollutants (Butler et al., 2009; Spurgeon et al., 2020) and to climatic extremes (MacLean et al., 2019; Harvey et al., 2020); therefore, gradual changes in these factors with increasing proximity to the smelter are likely to filter out the most sensitive species from severely polluted areas. The majority (80–95%) of nickel and copper found in birch foliage in the heavily contaminated site near the Monchegorsk smelter was due to deposition of dust particles on leaf surfaces (Kozlov et al., 2000), indicating that external feeders face much greater toxicity problems than internal feeders do. We therefore predicted that the responses to pollution will be weaker for species feeding within plant tissues than for externally feeding species, as the latter are directly exposed to acid rain and to gaseous and particulate pollutants, than for species feeding within plant tissues.

Deep soil freezing in the industrial barrens during the winter (Kozlov and Haukioja, 1997) suggests that the declines near the smelter will be greater for species hibernating as larvae than for species hibernating at the imaginal or pupal stages, which are more tolerant to low (sub-zero) temperatures (Hain and Ben Alya, 1985; Gu, 2009; Aryal and Jung, 2018). The species richness of vascular plants in the industrial barrens is reduced by 20–40% relative to unpolluted forests (Kozlov et al., 1998), and the proportion of specialist herbivore insects is highest in the most diverse plant communities (Forister et al., 2015). Therefore, we also predicted that the abundance of polyphagous species will show a lesser decline towards the polluter compared with the abundance of monophagous or oligophagous species.

We started our observations on abundance and diversity of Lepidoptera at the beginning of the substantial emission decline (Table S1), and the rapid improvement in the air quality near the smelter added a new dimension to our study. We predicted that temporal changes in diversity and abundance of Lepidoptera following emission control would be consistent with spatial changes along the pollution gradient, thus confirming the validity of "space-for-time" substitution, which is widely used in ecology to invoke temporal changes in ecosystem structure and functions from contemporary spatial patterns (Blois et al., 2013; De Frenne et al., 2013). We tested all our predictions by analysing data on moths and butterflies, which were quantitatively collected from 1992 to 2006 at 15 study sites representing different stages of pollution-induced forest disturbance, ranging from nearly pristine forests to industrial barrens (Fig. 1).

2. Materials and methods

2.1. Study area and study sites

Our study area is located in the central part of the Murmansk region in north-western Russia (Fig. 2). For decades, the nickel–copper smelter at Monchegorsk (67°56′ N, 32°49′ E) was one of the largest industrial polluters in the Northern hemisphere. It emitted sulphur dioxide and dust containing heavy metals, primarily nickel and copper, into the ambient air. During the study period, emissions of these substances declined three- to five-fold, but still remained rather high relative to industrial enterprises in EU countries (Table S1). For the history of pollution impacts on the study area, consult Kozlov and Barcan (2000).

Prior to the start of smelter operations, the study area was covered by impenetrable forests of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Bobrova and Kachurin, 1936). Our study sites, located 1 to 64 km from the smelter (Fig. 2; Table S2), were systematically selected along the main roads of the study region to represent different stages of pollution-induced deterioration of these forests. The spread of the study area to the south-east (64 km) was greater than the spread to the north (15 km) as northern winds prevail during the summer, carrying pollution in the south-easterly direction (Doncheva, 1978). Since concentrations of pollutants decrease hyperbolically with an increase in distance from the smelter (Baklanov and Rodjushkina, 1993; Kozlov et al., 1995), we used shorter between-site distances close to the smelter than further away from it (Fig. 2). The concentrations of the main pollutants (measured from 1991 to 1994; Table S2) significantly and consistently declined with an increase in $\log_{10}$-transformed distance from the smelter (nickel: $r = -0.90$, $n = 15$ sites, $P < 0.0001$; copper: $r = -0.93$, $n = 15$ sites, $P < 0.0001$; sulphur dioxide: $r = -0.80$, $n = 15$ sites, $P = 0.0003$).

The two most distant sites are classified as undamaged spruce forest (Fig. 1h). They have dense stands, with <5% of spruce trees showing

Fig. 1. Landscape and the state of vegetation at the study sites: (a) site 1N, industrial barren; (b) site 8S, industrial barren; (c) site 1S, birch and willow-dominated community; (d) site 13S, severely damaged forest; (e) site 11N, severely damaged forest; (f) site 15N, moderately damaged forest; (g) site 27S, slightly damaged forest; (h) site 64SE, undamaged forest. For the positions of the study sites, consult Fig. 2 and Table S2.

dead upper canopies (for measurement of stand characteristics, consult Manninen et al., 2015). The natural regeneration of spruce is abundant, and the field layer vegetation has no gaps of bare ground. The concentrations of nickel in mountain birch (*Betula pubescens* var. *pumila*) foliage in these undamaged forests is below 20 μg g^{-1} dry weight (Kozlov et al., 1995, 2009).

By contrast, the slightly damaged pine (site 15 N) and spruce (sites 18–31S) forests (Fig. 1f, g) have sparse stands, which include 5–25% of coniferous trees with dead upper canopies. The natural regeneration of conifers is common, and the field layer vegetation is dense. The foliar nickel ranges from 15 to 60 μg g^{-1} (Kozlov et al., 1995, 2009). The severely damaged pine (11N) and spruce (13S) forests (Fig. 1d, e) have very sparse

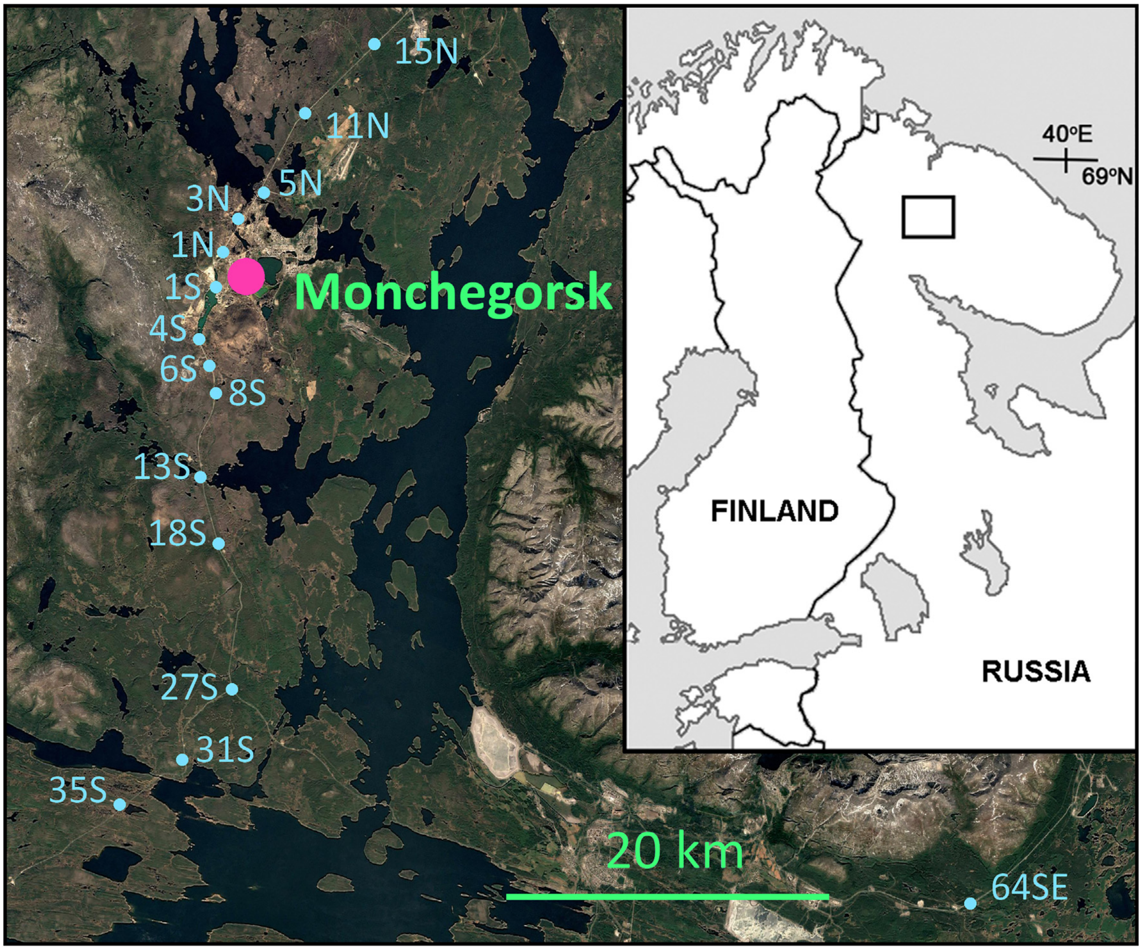

Fig. 2. Location of the study sites (blue dots) in the vicinity of the Monchegorsk copper-nickel smelter (pink circle). The satellite image (taken in 2001) illustrates vegetation decline near the smelter. The site codes indicate the approximate distance (km) and direction (to the north, south or south-east) from the smelter. Coordinates of the study sites are provided in Table S2. Insert: the position of the study area in Northern Europe.

stands, with more than 50% of the top-canopy trees killed by pollution. More than 25% of the living conifers have dead upper canopies, and natural regeneration of conifers is infrequent. The field layer vegetation is patchy, with gaps of bare ground. The foliar nickel ranges from 60 to 100 μg g^{-1} (Kozlov et al., 1995, 2009).

The secondary communities, which are dominated by mountain birch and willows (*Salix caprea*, *S. myrsinifolia*), are lacking top-canopy trees (Fig. 1c). The surviving trees have stunted, bush-like canopies, and natural regeneration of conifers is absent. The field layer vegetation is very sparse and scattered over bare ground. The foliar nickel ranges from 150 to 200 μg g^{-1} (Kozlov et al., 1995, 2009).

The most disturbed sites are classified as industrial barrens (Fig. 1a, b). Vegetation in these habitats consists of stunted, sparsely growing mountain birches, with rare additions of other tree species. The top-canopy trees are absent. The field layer vegetation persists in small patches scattered over bare ground. The foliar nickel ranges from 120 to 350 μg g^{-1} (Kozlov et al., 1995, 2009).

In our categorical data analyses, we classified proximate sites (1–8 km from the smelter) as severely polluted and distant sites (11–64 km from the smelter) as moderately polluted to unpolluted.

2.2. Collection and processing

In 1992, we developed the collection protocol and tested its effectiveness in five study sites. In 1993, 1994, 1996 and 1997, when the emissions were still high (Table S1), we repeatedly (4–7 times each year, from June to August) collected moths and butterflies across 15 study sites with different levels of pollution load. In 1995 and 1998–2006, we sampled (2–3 times each year) four heavily polluted and four slightly polluted sites (Table S4) to monitor the changes caused by emission decline. Each year, we planned our sampling in such a way that variations in day, time and collectors were not associated with the distance from the smelter (day: $r = -0.15$, $n = 15$ sites, $P = 0.60$; time: $r = -0.25$, $n = 15$ sites, $P = 0.37$; collector: $\chi^2 = 37.0$, df $= 42$, $P = 0.69$).

Moths and butterflies, with rare exceptions, were collected on days with favourable weather conditions, when the ambient air temperature was at least 10 °C, the wind did not exceed three on the Beaufort scale (gentle breeze, 3.4–5.5 m s^{-1}), and the last rain had fallen at least 2 h before sampling. Weather conditions (air temperature, wind speed and cloudiness) were recorded in the middle of each sampling session. The experienced collector(s) actively searched for adult moths and butterflies and captured them with a standard entomological net within a plot 200 × 200 m size during two person-hours, aiming to collect as many of the naturally flying individuals as possible. We estimate that, on average, ca. 80% of spotted individuals have been collected. When no flying moths and butterflies were seen, the collector disturbed them from both low-stature vegetation (herbs and dwarf shrubs) and from branches of trees and shrubs; these disturbed individuals contributed some 20% to the total catches.

The collected insects were transported to the laboratory, where M.V.K. identified and counted the individuals of common species and pinned all individuals of rare species and of species of uncertain identities. These pinned specimens, identified primarily by †J. Jalava (samples of 1992–2003) and by J. Kullberg (samples of 2004–2006), were deposited in the Zoological Museum, University of Helsinki (MZH). As in studies based on the lighttrap catches (Hunter et al., 2014; Keret et al., 2020), our data reflect the relative abundances of collected species rather than their population densities in the strict sense.

2.3. Life history traits

We restricted our analyses of the association between spatial patterns in the abundance of individual Lepidoptera species with their life history traits to the 96 most abundant species, for which we collected at least 25 individuals in 15 sites during 1993, 1994, 1996 and 1997 (Data S2). We classified these 96 species based on overwintering stage (egg, larva, pupa or imago), larval food (live vascular plants or any other substances, e.g. live mosses or decaying wood), feeding strategy (internal feeders, whose larvae develop inside live plant tissues, or external feeders) and feeding guild (internal feeders: leaf miners, stem borers and larvae feeding inside flowers or seeds; external feeders: defoliators and leaf-rollers, whose larvae feed inside a shelter constructed from plant leaves). For species feeding on vascular plants, we categorised their hosts as woody or herbaceous or both, and we classified their feeding specialisation as monophagous (feeding on plants of a single genus), oligophagous (feeding on plants of two genera) and polyphagous (feeding on plants of three or more genera). These life history traits of common Lepidoptera species (listed in Table S5) were obtained primarily from Kozlov et al. (2010), Hunter et al. (2014) and Keret et al. (2020), and they were complemented with information from multiple published and web-based data sources and from consultations with our colleagues. Classification of species as threatened or not threatened is based on the Finnish Red List (Nupponen et al., 2019), because the list of insects threatened in the Murmansk region of Russia is obviously incomplete and includes only five species of Lepidoptera (Konstantinova et al., 2003).

2.4. Data analysis

A sample, in terms of our study, consisted of all individuals of moths and butterflies collected from one site during two person-hours. Abundance was quantified by the number of individuals in a sample. Diversity was measured by the Shannon H index and was based on the numbers of individuals of each species in a sample. We also used individual rarefaction (PAST program: Hammer et al., 2001) to generate the numbers of species expected in a sample of 100 individuals for each of the study sites and in a sample of 1000 individuals for proximate and distant sites during the periods with high and low pollution. These rarefaction-based estimates were used to avoid obvious effects of sample size on actual species richness; they were considered significantly different if their 95% confidence intervals (CI_{95}) did not overlap. We used the $\log_{10}$-transformed distance from the smelter as a measure of the pollution-induced environmental disturbance (Kozlov et al., 2009).

We explored the spatial and temporal variation in the abundance (square-root transformed to normalise the distribution of the residuals) and diversity (Shannon index) of the Lepidoptera in individual samples using linear mixed models (SAS GLIMMIX procedure; SAS Institute, 2009) with a Gaussian error distribution. In these models, the distance from the polluter, year and their interaction, as well as collector, wind speed and temperature, were considered fixed effects, whereas the study site was treated as a random effect. We adjusted the standard errors and denominator degrees of freedom following Kenward and Roger (2009), and we evaluated the significance of a random effect by testing the likelihood ratio against the χ^2 distribution (Littell et al., 2006). We accounted for the variation in sampling conditions—especially for wind speed, as it was found to increase near the smelter (see Results)—by calculating the site-specific and year-specific least-square means of diversity and abundance, and we correlated (using Pearson coefficients) these estimates with the characteristics of study sites (nickel concentration, stand basal area and field vegetation cover; Table S2) and study years (previous-year emissions of sulphur dioxide and copper plus nickel, mean temperature and precipitation of July–August; Tables S1 and S3). For the calculation of the site-specific least-square means, we considered study site as a fixed factor.

The species-level spatial patterns were explored in the most abundant species based on samples collected in 1993, 1994, 1996 and 1997 (i.e. during the high-emission period). The data used in our species-level analyses (numbers of individuals in a sample averaged by study site or by collection year) contained 65% zero values. Therefore, we used Spearman rank correlation coefficients to quantify the associations of species abundance with the distance to the smelter, and we calculated the effect sizes (ES hereafter) by z-transforming these coefficients. We used meta-analysis (Koricheva et al., 2013) to identify the overall pattern and to uncover sources of variation in both spatial and temporal changes in the abundance of individual species.

We first tested the overall effect of the distance to the smelter on species abundance by calculating the grand mean effect size, i.e. the model coefficient parameter of an intercept-only hierarchical model with insect family and genus as nested random effects. We then compared ES among groups of species by calculating the between-group heterogeneity (Q_B) in a serie of multi-level (hierarchical) mixed-effects models, and we tested Q_B against the χ^2 distribution with the number of groups minus one degree of freedom. We tested the effects of the overwintering stage, host plant, feeding guild and feeding specialisation as fixed effects in separate models while controlling for non-independence among residuals arising from phylogentic structure by including insect family and genus as nested random effects. As for the insect feeding guild, we first tested the effect of feeding habit (internal vs. external feeder) and then the effect of feeding guild per se separately within internal and external feeders. We estimated coefficient parameters (and their CI_{95}) of each model and interpreted the average values of ES for each group of species. The effect of distance from the smelter or the collection year on the abundance of the selected group of species was considered significant when its CI_{95} did not include zero. We ran meta-analyses with the *R* statistical language software (R Core Team, 2021) using the function *rma.mv* in package *metafor* (Viechtbauer, 2010).

3. Results

3.1. Data overview

We obtained 581 samples of moths and butterflies from 15 study sites (Data S1). These samples, which were collected by ten persons (including the authors) during 1992–2006, contained 25,628 individuals, 25,606 of which were identified to the species level. Within 345 identified species (Data S2), *Argyresthia pygmaeella* (Argyresthiidae, 2390 individuals) and *Ancylis myrtillana* (Tortricidae, 2353 individuals) were most abundant. Half of the collected species (172 of 345) were represented by one to six individuals, and their overall contribution to our catches was 1.5%. Of these 172 species, 50 were collected from industrial barrens only. Surprisingly, the fauna of the severely polluted habitats included critically endangered *Eucosma saussureana* and vulnerable *Argyroploce concretana*, *Cydia cornucopiae* and *Erebia disa*. The larvae of two-thirds of the 96 most abundant species fed on birches, willows or dwarf shrubs (Ericaceae) (Table S5).

Lepidoptera were collected between 12 June and 17 August (median date 16 July), from 10 am to 12 pm (median time 4 pm). The ambient air temperature during the sampling sessions varied from 9 to 28 °C (median value 18 °C) and did not depend on the distance from the polluter ($r = 0.26$, $n = 15$ sites, $P = 0.34$). Cloudiness varied from 0 to 100% (median value 50%) and also did not depend on the distance from the polluter ($r = -0.37$, $n = 15$ sites, $P = 0.17$). Wind speed (Beaufort scale) varied from 0 to 4 (median value 2) and strongly increased near the smelter ($r = -0.72$, $n = 15$ sites, $P = 0.0023$).

3.2. Spatial patterns in community-wide abundance and diversity

Across the 325 samples collected during the high-emission period, both the abundance and diversity varied significantly among the 15 study sites (random effect in Table 1). However, this variation was explained by the distance from the smelter only for the Shannon diversity index (Fig. 3b; fixed effect in Table 1), whereas abundance did not depend on this distance

Table 1
Exploration of spatial patterns in the abundance and diversity of Lepidoptera (data from 15 sites collected in 1993, 1994, 1996 and 1997; SAS GLIMMIX procedure, type 3 tests).

Effect type	Explanatory variable	Abundance		Diversity	
		Test statistics	P	Test statistics	P
Fixed	Distance	$F_{1, 12.1} = 2.74$	0.12	$F_{1, 13.2} = 12.63$	0.0034
	Year	$F_{3, 293.6} = 3.17$	0.0246	$F_{3, 293.6} = 2.91$	0.0347
	Distance × year	$F_{3, 294.8} = 2.41$	0.07	$F_{3, 294.4} = 0.78$	0.51
	Collector	$F_{6, 294.6} = 7.95$	<0.0001	$F_{6, 294.1} = 1.97$	0.07
	Wind speed	$F_{4, 298.1} = 10.04$	<0.0001	$F_{4, 296.2} = 6.10$	0.0001
	Temperature	$F_{1, 297.2} = 1.17$	0.28	$F_{1, 295.7} = 11.45$	0.0008
Random	Site	$\chi^2_1 = 13.97$	<0.0001	$\chi^2_1 = 43.17$	<0.0001

(Fig. 3a; fixed effect in Table 1). These patterns were consistent across study years (interaction term in Table 1). The numbers of species expected in a sample of 100 individuals followed the same pattern as the Shannon diversity index (Fig. 3c), decreasing substantially in the most polluted sites.

The site-specific least-square means of abundance did not correlate with either nickel concentrations in birch leaves ($r = -0.42$, $n = 15$ sites, $P = 0.12$) or stand basal area ($r = 0.16$, $n = 15$ sites, $P = 0.57$); rather, it decreased with the decline in field vegetation cover ($r = 0.54$, $n = 15$ sites, $P = 0.04$). The site-specific least-square means of diversity correlated equally well with nickel concentrations in birch leaves ($r = -0.68$, $n = 15$ sites, $P = 0.0057$) and field vegetation cover ($r = 0.69$, $n = 15$ sites, $P = 0.0041$), but it varied independently of stand basal area ($r = 0.46$, $n = 15$ sites, $P = 0.08$).

3.3. Temporal pattern in community-wide abundance and diversity

Across the 403 samples collected in eight study sites (representing entire pollution gradient) from 1993 to 2006, the abundance did not change with the collection year, and this pattern was consistent across all study sites (Table 2). By contrast, the diversity varied with study year, and this variation depended on the distance to the polluter (Table 2).

The year-specific least-square means of abundance did not change from 1993 to 2006 (Fig. 4a) and did not correlate with either the previous-year emission of pollutants (sulphur dioxide: $r = -0.15$, $n = 14$ years, $P = 0.62$; metals: $r = 0.14$, $n = 14$ years, $P = 0.62$) or the weather conditions (temperature: $r = 0.11$, $n = 14$ years, $P = 0.71$; precipitation: $r = -0.17$, $n = 14$ years, $P = 0.56$). The year-specific least-square means of diversity in the heavily polluted sites significantly increased during the observation period (Fig. 4b) due to a substantial increase in species richness (Fig. 5), and this pattern was associated with a gradual decline in emissions (sulphur dioxide: $r = -0.51$, $n = 14$ years, $P = 0.06$; metals: $r = -0.74$, $n = 14$ years, $P = 0.0026$). By contrast, the diversity in moderately polluted to unpolluted sites did not change during the observation period (Figs. 4c, 5) and was independent of the emissions (sulphur dioxide: $r = -0.30$, $n = 14$ years, $P = 0.30$; metals: $r = -0.36$, $n = 14$ years, $P = 0.20$). The annual variation in the diversity of moths and butterflies did not correlate with the summer temperature and precipitation in either the heavily polluted or less polluted sites ($r = -0.17$ to 0.14, $n = 14$ years, $P = 0.57$ to 0.87).

3.4. Abundances of individual species in a pollution gradient during the high-emission period

The abundances of 45 of the 96 most frequent species during the high-emission period were significantly correlated with the distance from the polluter. The abundances of ten species (including the most common *A. pygmaeella*) increased, whereas the abundances of 35 species declined near the smelter. Consistently, meta-analysis of the species-specific correlations with distance demonstrated that, on average, the abundance of Lepidoptera decreased with a decrease in the distance from the smelter (ES = 0.28, $n = 96$ species, $CI_{95} = 0.08…0.48$).

The changes in the Lepidoptera abundance along the pollution gradient depended on the overwintering stage (Fig. 6a) and host plants (Fig. 6b). Specifically, in species that hibernate as pupae, the abundance increased near the smelter, whereas it declined in species that hibernate as larvae (Fig. 6a). No significant effect of the distance to the smelter was detected for species overwintering as eggs or imagoes. Species that fed on both herbaceous and woody plants appeared most sensitive to pollution, whereas the abundance of species that fed on herbaceous plants only did not change significantly along the pollution gradient (Fig. 6b). Another important predictor of a correlation between the abundance of a species and the distance from the smelter was the larval feeding habit ($Q_B = 14.00$, df = 1, $P < 0.001$): species whose larvae feed inside plant tissues showed no response to pollution, whereas externally feeding species showed declines near the smelter (Fig. 6c). Within these two contrasting feeding habits, we found no differences in responses of individual feeding guilds to pollution (Fig. 6c).

The decline in insect abundance towards the smelter tended to be stronger for oligophagous than for monophagous or polyphagous herbivores; however, this difference did not reach the conventional level of statistical significance (Fig. 6d). The spatial pattern in the abundance of moths and butterflies did not differ between species feeding on live vascular plants and on other substrates ($Q_B = 0.02$, df = 1, $P = 0.89$) and was not associated with insect size ($Q = 0.05$, df = 1, $P = 0.83$).

4. Discussion

4.1. Pollution effects on communities of moths and butterflies

Our conclusions are based on the abundances of 345 species; i.e., we collected 41.4% of the entire Lepidoptera fauna of the Murmansk region (which now totals 834 species: Kozlov et al., 2020) from 15 plots with the total area of 0.6 km^2. These plots were located close to the eastern border of the Lapland Nature Reserve, which covers 2784 km^2 of taiga and mountain tundra of the Murmansk region, but the fauna of which includes only 214 species of Lepidoptera (Gilyazova, 1997). A better studied fauna of the Kandalaksha nature reserve, which covers 210 km^2 of undisturbed taiga and tundra of the Murmansk region, includes 453 species of Lepidoptera (Shutova, 2008). We therefore conclude that our collection method is suitable for obtaining quantitative information on Lepidoptera communities and that our study area harbours exceptionally high diversity of Lepidoptera due to the overlapping of preindustrial variation in landscape characteristics and in plant communities with human-induced disturbance, with pollution foremost.

Previous studies on the pollution impacts on Lepidoptera were limited to several groups of these insects, including butterflies (Kozlov et al., 1996b; Mulder et al., 2005; Wallis De Vries and van Swaay, 2006; Meléndez-Jaramillo et al., 2021) and moths collected by bait traps (Kozlov et al., 1996a) or by pheromone traps (Kozlov and Haukioja, 1993; Ruohomäki et al., 1996; Zverev and Kozlov, 2021) and larvae sampled with foliage (Jones and Paine, 2006) or counted on host plants (Koricheva and Haukioja, 1992; Ruohomäki et al., 1996; Kulfan et al., 2002; Kozlov et al., 2017). These studies demonstrated variable responses of moths and butterflies to pollution, and this variation was difficult to explain. Pollution was often blamed for the decline in moths and butterflies (Barbour, 1986; Pescott et al., 2015; Nacua et al., 2020), but the evidence was mostly equivocal (Thomas, 1986; Warren, 1992). We demonstrated a

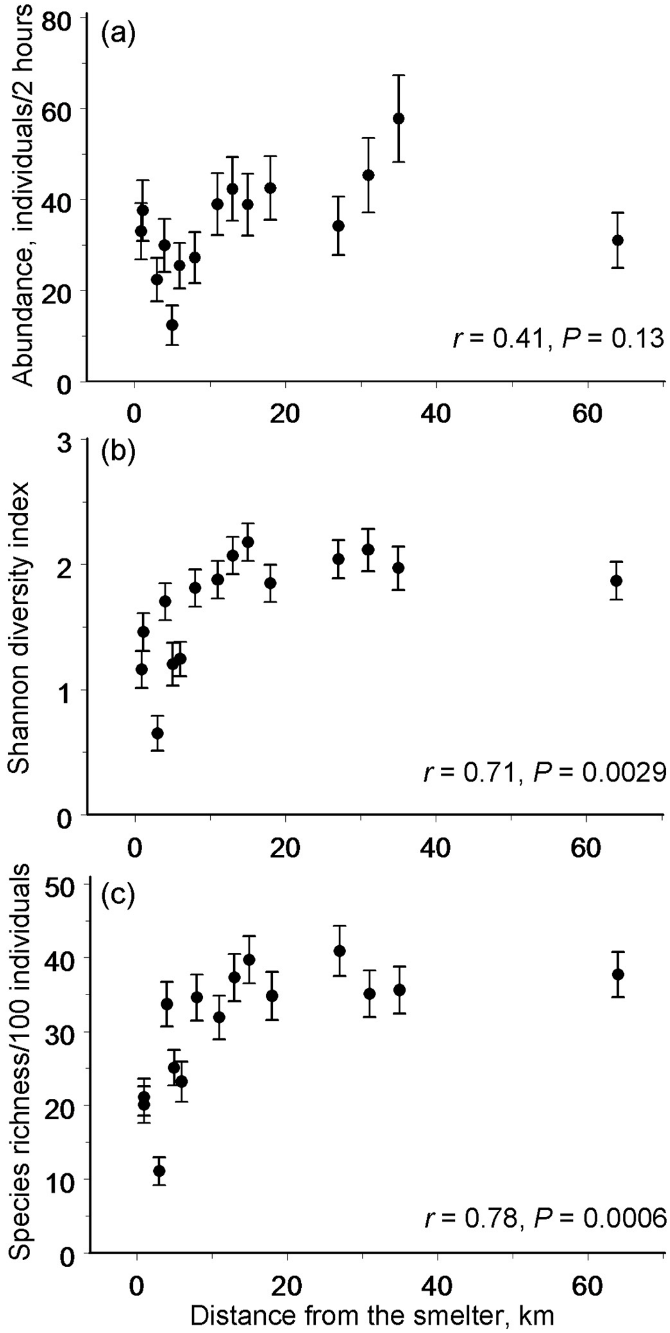

Fig. 3. Abundance (a), diversity (b) and species richness (c) of moths and butterflies in relation to the distance from the Monchegorsk copper-nickel smelter during the high-emission period (1993, 1994, 1996 and 1997). Values are least-square means (±SE) from the SAS GLIMMIX procedure (a, b) and the estimated means (±SE) from rarefaction analysis (c); the values of abundance are back-transformed. Correlations refer to $\log_{10}$-transformed distance; the correlation with abundance is based on the square-root transformed values.

substantial decline in the diversity of the entire Lepidoptera communities near the large non-ferrous smelter relative to the moderately polluted and unpolluted forests. This result was predictable, because the landscape in the vicinity of the smelter is highly devastated (Fig. 1a–c) and the vegetation cover is reduced in terms of both productivity and diversity (Kozlov et al., 2009; Manninen et al., 2015). This result is also in line with conclusions made for the stress responses of many groups of biota (Odum, 1985; Rapport et al., 1985; Kozlov and Zvereva, 2011). However, our 16-year-long study around the Monchegorsk smelter is unique, because we not only uncovered spatial pattern in Lepidoptera communities but we also observed temporal changes in these communities following a sharp pollutant emission decline.

Surprisingly, the overall abundance of moths and butterflies did not decline near the smelter even during the high-emission period. This could suggest that many individuals collected in heavily polluted sites are simply occasional migrants; however, the observation of increased concentrations of the two main metal pollutants, nickel and copper, in butterflies from heavily polluted sites allowed rejection of this hypothesis (Zverev and Kozlov, 2021). Furthermore, the airborne particles emitted by the smelter are likely to hamper the flight activity of Lepidoptera, thereby limiting their arrival at polluted areas (Liu et al., 2021). Therefore we conclude that moths and butterflies, similarly to bees (Sgolastra et al., 2018), are quite resilient to heavy metals emitted by different industries. This conclusion is in line with low effects of realistic concentrations of metal pollutants on performance of Lepidoptera. In particular, 50–200 μg g^{-1} of copper added to the larval diet slightly but significantly decreased the pupal weight of the oriental leafworm moth, *Spodoptera litura* (Huang et al., 2012), whereas 100 μg g^{-1} of nickel did not affect wing size in the cabbage white butterfly, *Pieris rapae* (Kobieva and Snell-Rood, 2018).

At the same time, the density of birch-feeding herbivores per unit of birch leaf area did not change along the Monchegorsk pollution gradient (Kozlov et al., 2017). The Lepidoptera comprise the greater part of these herbivores; therefore, the two-fold decline in the foliar biomass of deciduous shrubs and trees near the Monchegorsk smelter relative to the unpolluted forests (Manninen et al., 2015) could be expected to result in a two-fold decline in biomass of birch-feeding moths. However, this expectation was not met, as the abundance of herbivorous moths near the smelter (a proxy of biomass in the absence of association between moth size and changes in moth abundance along the pollution gradient) was just as high as in pristine forests, despite the environmental toxicity and limitations in resources. This lack of a decrease in Lepidoptera abundance, even in severely polluted sites, is presumably explained by the high survival of herbivores in these sites due to the strong decline in several groups of their natural enemies, which creates an enemy-free space for the herbivores (Zvereva and Kozlov, 2000, 2006; Eeva et al., 2012).

Abiotic factors may also contribute to an increase in the overall abundance of moth communities by extending the moth activity period (Keret et al., 2020) due to the earlier (up to 4 weeks) soil thawing and higher spring temperatures of the soil in heavily polluted sites (Kozlov and Haukioja, 1997). Lastly, the open landscapes of industrial barrens are quite unusual for the central part of the Murmansk region, which is covered by subarctic coniferous forests, and these open landscapes host specific insect fauna. In particular, populations of several infrequent species, such as *Sesia bembeciformis*, *Ancylis laetana*, *Plusia festucae*, *Saturnia pavonia* and *Lasiommata petropolitana*, have persisted in the barren sites for decades, sometimes reaching high densities (Kozlov and Kullberg, 2011). Consequently, rarity, as such, does not indicate the vulnerability of a species to pollution, and several species that are currently classified as threatened in Finland (Nupponen et al., 2019) were found in industrial barrens near the smelter.

4.2. Life history traits associated with species' responses to pollution

The heavily polluted industrial barren, due to combination of toxicity and harsh microclimate (Kozlov and Zvereva, 2007), is an excellent example of a habitat that should select for species (and genotypes) adapted to multiple co-occurring stressors, i.e. for species demonstrating the stress tolerance syndrome as defined by Chapin et al. (1993). This prediction was confirmed by our discovery of links between the life history traits of individual Lepidoptera species and the changes in their abundance along a spatial pollution gradient.

We found that those species whose larvae feed inside live plant tissues show relatively minor, if any, declines with increasing proximity to the smelter. Feeding inside plant tissues provides insects with partial protection from industrial pollutants, especially acid rain and metal-containing particles deposited on leaf surfaces. This feeding habit can also protect these

Table 2
Exploration of temporal patterns in the abundance and diversity of Lepidoptera (data from eight sites collected from 1993 to 2006; SAS GLIMMIX procedure, type 3 tests).

Effect type	Explanatory variable	Abundance		Diversity	
		Test statistics	*P*	Test statistics	*P*
Fixed	Distance	$F_{1,\ 6.4} = 3.47$	0.11	$F_{1,\ 6.4} = 4.88$	0.07
	Year	$F_{13,\ 358.3} = 0.69$	0.77	$F_{13,\ 356.3} = 2.92$	0.0005
	Distance × year	$F_{13,\ 358.3} = 1.15$	0.32	$F_{13,\ 356.3} = 2.02$	0.0188
	Collector	$F_{6,\ 359.1} = 4.29$	0.0003	$F_{6,\ 356.9} = 1.97$	0.07
	Wind speed	$F_{4,\ 362.0} = 7.97$	<0.0001	$F_{4,\ 359.1} = 1.23$	0.30
	Temperature	$F_{1,\ 359.5} = 6.36$	0.0121	$F_{1,\ 357.3} = 7.12$	0.0080
Random	Site	$\chi^2_1 = 7.97$	0.0024	$\chi^2_1 = 16.23$	<0.0001

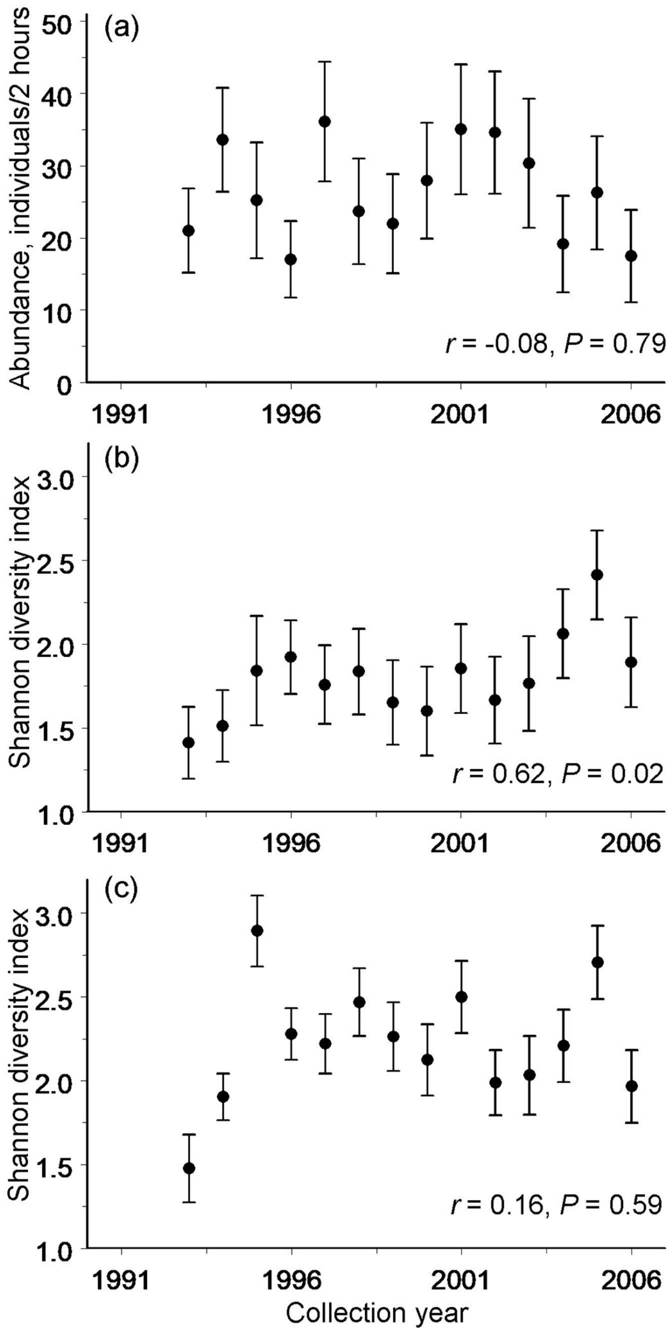

Fig. 4. Abundance (a) and diversity (b, c) of moths and butterflies in four heavily polluted sites (b), four moderately to slightly polluted sites (c) and in all eight sites combined (a) in relation to the collection year. Values are the least-square means (±SE) from the SAS GLIMMIX procedure; the values of abundance are back-transformed. Correlation with abundance is based on the square-root transformed values.

insects from desiccation (Tooker and Giron, 2020), which poses a greater risk in the industrial barrens than in forests due to the increased wind speed and higher temperatures in the barrens during the sunny days (Kozlov and Zvereva, 2007). The absence of density changes in internally feeding Lepidoptera species along the Monchegorsk pollution gradient is consistent with the results of meta-analysis (Zvereva and Kozlov, 2010), which revealed no significant differences in abundance of mining, galling or boring insects between industrially polluted and unpolluted sites. Similarly, leaf miners and borers were previously found to respond positively to plants subjected to abiotic environmental stressors, including pollution (Koricheva et al., 1998).

In contrast to the internally feeding species, Lepidoptera species with larvae externally feeding on plants generally decline in abundance near the smelter. This pattern is consistent with the negative responses of defoliators to experimentally stressed plants (Koricheva et al., 1998) but contrasts with the positive response of defoliators (and, to a certain extent, of leaf-rollers) to industrial pollution revealed by meta-analysis of published evidence (Zvereva and Kozlov, 2010). We suggest that the latter pattern is spurious and likely emerged due to a preferential documentation of pollution-induced outbreaks. By contrast, our study addressed background herbivory, which is likely driven by other factors. The decline in externally living species near the smelter can be explained by the direct toxic effects of airborne pollutants (Heliövaara and Väisänen, 1993; Kozlov et al., 1996c).

In agreement with our predictions, the species hibernating at the larval stage declined in abundance near the smelter, whereas the species hibernating as pupae showed the opposite pattern. We explain this variation by a differential sensitivity of insect developmental stages to the sub-zero soil temperatures (Hain and Ben Alya, 1985; Gu, 2009; Aryal and Jung, 2018) that are typical for industrial barrens in the winter due to snow removal

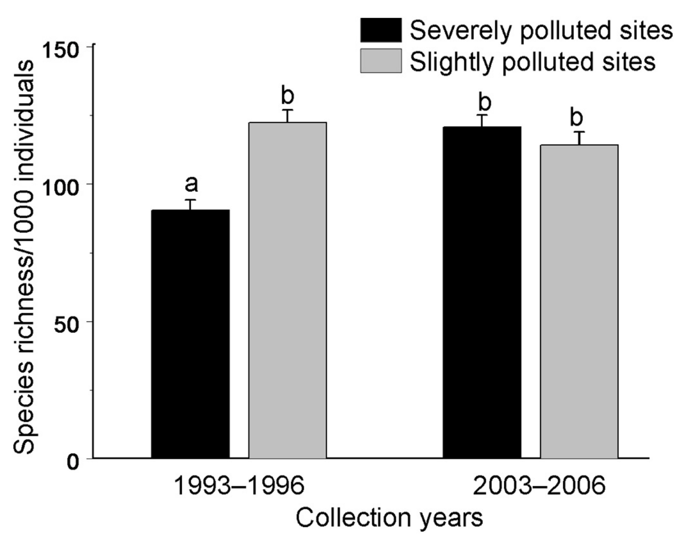

Fig. 5. Species richness (mean ± SE from individual rarefaction analyses) of moths and butterflies in four severely polluted and four slightly polluted sites during the periods of high (1993–1996) and low (2003–2006) aerial emissions from the copper-nickel smelter at Monchegorsk. For emission data, consult Table S1.

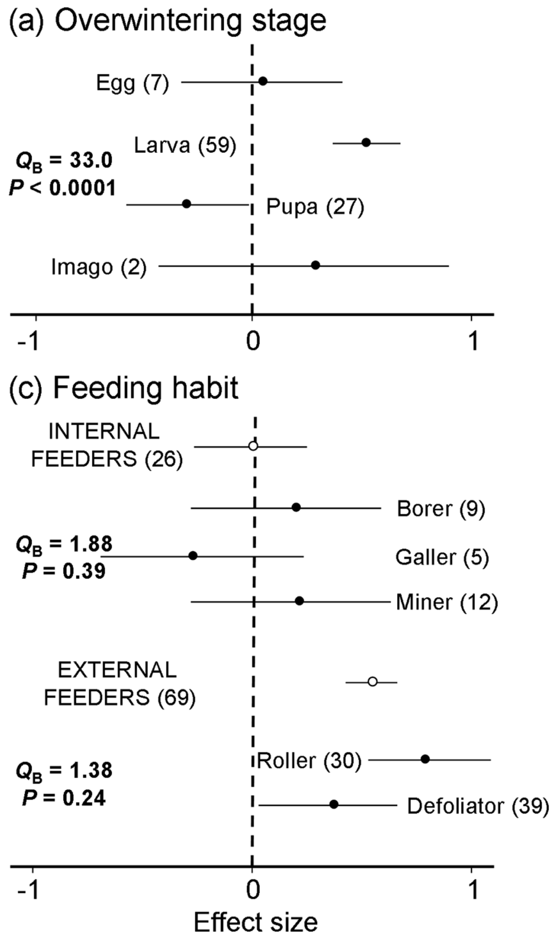

Fig. 6. Effects of leaf history traits of common species of moths and butterflies on the *z*-transformed Spearman rank correlation between species abundance and the distance from the smelter: the outcomes of categorical meta-analyses. Dots indicate mean effect sizes; lines indicate 95% confidence intervals; numbers of species in each group are shown in brackets. Positive effect sizes indicate an increase in abundance with an increase in the distance from the polluter.

by the strong winds (Kozlov and Haukioja, 1997). However, other mechanisms may also be involved, because grasslands affected by nitrogen deposition show greater declines in butterfly species that overwinter as eggs or larvae than in those overwintering as imagoes or pupae (Wallis De Vries and van Swaay, 2006), despite the absence of landscape-level changes in vegetation structure that could affect microclimate during the winter time. We found no statistically significant relationship between the distance to the smelter and the abundance of species overwintering as eggs or imagoes. This result was however only supported by a very limited number of species, which calls for particular caution when interpreting it.

Finally, we expected that the more specialised species, rather than the generalists, will face greater problems in locating their hosts in the sparse plant communities of the industrial barrens. This expectation was not met: we found no statistically significant evidence that Lepidoptera larvae with different levels of feeding specialisation had different response to pollution. This pattern contrasts one observed in plant-feeding bugs, in which the specialised species were less abundant and less diverse than the generalists near a polluter emitting calcareous dust (Brändle et al., 2001). The pattern discovered in our study also disagrees with the conclusion that species with narrow feeding niches are at the highest extinction risk (Chichorro et al., 2019); in our case, they are at the same risk as generalist species. The association between pollution tolerance and feeding on herbaceous plants is likely caused by an increased abundance of these plants (in particular *Epilobium angustifolium*, grasses and sedges) in the immediate vicinity of the Monchegorsk smelter, as they colonise bare ground after the decline in dwarf shrubs (Kozlov et al., 2009, and unpublished).

4.3. Recovery of Lepidoptera communities

Emissions from the Monchegorsk smelter declined substantially during the study period, and this decline was followed by an increase in the diversity of moths and butterflies in the heavily polluted sites near the smelter. The absence of similar temporal changes in slightly polluted sites suggests that the effect observed near the smelter was caused by the pollution decline and not by climate warming, which has also occurred in the study area during the past decades (Zvereva et al., 2016; Marshall et al., 2016). At the same time, the abundance of Lepidoptera did not change significantly from 1993 to 2006 in either the heavily polluted or the slightly polluted sites.

The rapid emission decline during our study period offered a unique opportunity to uncover mechanisms driving pollution impacts on Lepidoptera communities. The ambient concentrations of sulphur dioxide and the deposition of metal-containing particles decreased immediately following emission decline. By contrast, natural leaching of metal pollutants from severely contaminated soils may take several decades or even centuries (Tyler, 1978; Barcan, 2002). As a result, a time lag exists between the emission decline and the beginning of biotic changes in polluted habitats (Lovett et al., 2009; Berglund and Nyholm, 2011). In particular, the mountain birch populations near the Monchegorsk smelter (in the same sites where we collected moths and butterflies) continued to decline until at least 2006 (Zverev, 2009), and no natural regeneration of birch populations was observed in barren sites until 2019 (V.Z. and M.V.K., personal observation). Both the diversity and density of birds near the Monchegorsk smelter remained extremely low until at least 2009 (Eeva et al., 2012), and many birds, including insectivorous species, are unlikely to return to these sites until large trees reappear there.

We therefore assume that an increase in diversity of Lepidoptera communities, which we observed in severely polluted sites, resulted from a combination of the decrease in pollutant toxicity and the physiological changes in plants, which affect their quality as a food for insects (Riemer and Whittaker, 1989; Kozlov et al., 1996c), following decreases in ambient concentrations of sulphur dioxide and metal-containing particulate matter. This process rapidly shifted the balance between the negative and positive effects of pollution (including pollution-induced habitat changes) on insects, thereby initiating a natural recovery of their communities through colonisation of these sites by species that had been previously extirpated by pollutant toxicity. This process is illustrated by the disappearance of the difference in the species richness of moths and butterflies between the heavily polluted and slightly polluted sites over the ten years between 1993 and 1996 and 2003–2006. However, recovery may take decades for the Lepidoptera species whose host plants, and particularly the conifers, are missing from the heavily polluted sites (Lovett et al., 2009; Pescott et al., 2015).

4.4. Community-wide and species-specific patterns: do they match?

The majority of studies exploring pollution impacts on insects, including moths and butterflies, have reported changes in abundances of individual species along pollution gradients (Alstad et al., 1982; Heliövaara and Väisänen, 1993). Consequently, these species-level studies have shaped patterns uncovered by meta-analysis of insect responses to pollution (Zvereva and Kozlov, 2010). However, the question remains regarding whether community-wide responses to pollution can be reliably predicted from species-level responses.

Our meta-analyses of species-level responses revealed that the abundance of most common moths and butterflies, on average, decreased towards the smelter. By contrast, community-wide data demonstrated no pollution-related spatial changes in the abundance of moths and butterflies, because abundance of several common species (e.g. *Plutella xylostella* and *Argyresthia pygmaeella*) increased with pollution. Thus, as with the latitudinal changes in herbivory (Zvereva et al., 2020), the pollution-driven changes in Lepidoptera communities could not be adequately predicted by a simple summation of the species-level responses. This conclusion stresses the importance of community-wide studies that not only account for abundances of common species but also involve rare species, which form a substantial part of overall diversity, but whose responses to disturbance are difficult to quantify individually.

Our findings also question the concept of bioindication, as applied to Lepidoptera. Indeed, many (but not all) butterflies decline in polluted and/or urban habitats (Kozlov et al., 1996b; Meléndez-Jaramillo et al., 2021); however, as we demonstrated, the entire community of moths and butterflies showed no decline near the Monchegorsk smelter. Consequently, we support the suggestion by Hallmann et al. (2021) to re-evaluate hazards and conservation strategies that traditionally target rare and endangered species. In particular, the conservation of butterflies, considered a flagship group of insects (Podsiadlowski et al., 2021; Preston et al., 2021), may not ensure conservation of entire insect communities.

5. Conclusion

Our study, surprisingly, demonstrated a relatively high tolerance of moths and butterflies to extreme load of industrial pollution. The Lepidoptera communities showed an ability to persist in severely polluted and deteriorated (barren) habitats and started recovering soon after the emission decline, prior the appearance of any visible changes in the plant communities. The similarities between the spatial and temporal patterns in the community characteristics of moths and butterflies confirm the validity of the space-for-time substitution (Pickett, 1989), which is commonly used in environmental studies to predict impacts of pollution increases and declines on ecosystem structures and functions (Zvereva et al., 2008; Kozlov et al., 2009).

The significant decreases in diversity and species richness of the Lepidoptera in our study area are limited to extremely polluted sites, where the mean ambient concentrations of sulphur dioxide in the early 1990s exceeded 100 μg m^{-3} (Baklanov and Rodjushkina, 1993; Kryuchkov, 1993), and the soil concentrations of nickel and copper ranged 1000–9000 μg g^{-1} (Barcan and Kovnatsky, 1998). By contrast, in the sites with moderate or slight pollution (sulphur dioxide concentrations 5–50 μg m^{-3}), the insect diversity remained unchanged during the entire observation period. Keeping in mind that annual concentrations of sulphur dioxide in Europe are generally below 10 μg m^{-3} (EEA, 2020) and that soil concentrations of nickel and copper are below 100 μg g^{-1} (Tóth et al., 2016), we doubt that these industrial pollutants could be responsible for the recent regional declines in moths and butterflies in Europe and other parts of the world, although local effects (e.g. at historical smelting sites) cannot be excluded. The large-scale declines of moths and butterflies reported in earlier studies are likely associated with other pollutants, primarily agrochemicals, and light pollution (Conrad et al., 2006; Warren et al., 2021; Habel et al., 2019; Wepprich et al., 2019).

CRediT authorship contribution statement

Mikhail V. Kozlov: Conceptualization, Methodology, Investigation, Data analysis, Data curation, Visualization, Writing - Original Draft. Bastien Castagneyrol: Data analysis, Writing - Review & Editing. Vitali Zverev: Methodology, Investigation, Visualization, Writing - Review & Editing. Elena L. Zvereva: Conceptualization, Investigation, Writing - Review & Editing.

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.

Acknowledgements

We thank E. Haukioja and †K. Mikkola for methodological advices and for supporting the first phase of the project; A. Blashkevich, A. L. Lvovsky, E. Melnikov, A. V. Selikhovkin, I. A. Selikhovkin, A. Vassiliev and †I. Vishnyakov for participation in data collection; M. Mutanen and T. Muus for information on life histories of several moth species; and V. Barcan for providing meteorological and emission data. We are deeply indebted to †J. Jalava, J. Kullberg and L. Kaila for identification of problematic specimens and to five anonymous reviewers for their inspiring comments to an earlier version of the manuscript. The study was supported by the Academy of Finland (projects 122133, 211662, 213969, 214824, 316182, and researcher posts of M. Kozlov), EC through the BASIS and BALANCE projects carried out under contracts ENV4-CT97-0637 and EVK2-2002-00169, Turku University Foundation and Maj and Tor Nessling Foundation.

Appendix A. Supplementary data

Supplementary data to this article – annual atmospheric emissions of principal pollutants from the smelter at Monchegorsk from 1992 to 2006 (Table S1), the characteristics of study sites (Table S2), seasonal averages of climate variables in Monchegorsk from 1992 to 2006 (Table S3), the numbers of samples collected annually from individual study sites (Table S4), life history traits and size of most common Lepidoptera species and correlation of their abundances with distance from the smelter (Table S5), characteristics of individual samples (Data S1) and abundances of individual species in each sample (Data S2) – can be found online at https://doi.org/10.1016/j.scitotenv.2022.155800.

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