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Combined effects of environmental disturbance and climate warming on insect herbivory in mountain birch in subarctic forests: Results of 26-year monitoring

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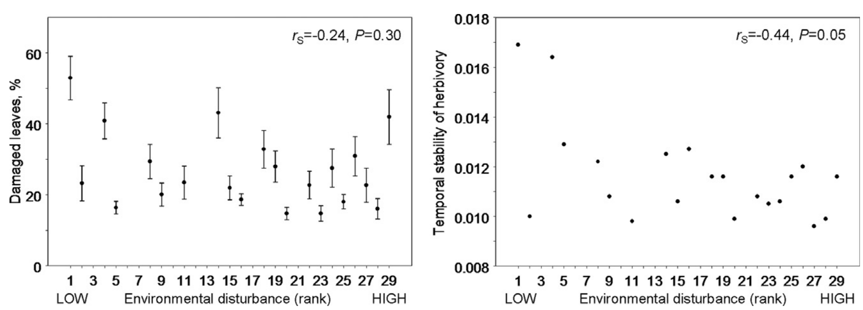
HIGHLIGHTS

- We explored the combined effects of pollution and climate on insect herbivory.
- Leaf-eating insects demonstrated variable responses to both these factors.
- Insect herbivory levels did not depend on the level of environmental disturbance.
- Temporal changes in herbivory differed between pristine and disturbed forests.
- Stability of insect-plant interactions decreased in habitats disturbed by pollution.

GRAPHICAL ABSTRACT



Insect damage to mountain birch leaves was unchanged along the gradient of pollution-induced environmental disturbance (left), but temporal stability of this damage (inverse of the coefficient of variation) decreased with an increase in disturbance (right).

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ABSTRACT

Both pollution and climate affect insect–plant interactions, but the combined effects of these two abiotic drivers of global change on insect herbivory remain almost unexplored. From 1991 to 2016, we monitored the population densities of 25 species or species groups of insects feeding on mountain birch (*Betula pubescens* ssp. *czerepanovii*) in 29 sites and recorded leaf damage by insects in 21 sites in subarctic forests around the nickel–copper smelter at Monchegorsk, north-western Russia. The leaf-eating insects demonstrated variable, and sometimes opposite, responses to pollution-induced forest disturbance and to climate variations. Consequently, we did not discover any general trend in herbivory along the disturbance gradient. Densities of eight species/species groups correlated with environmental disturbance, but these correlations weakened from 1991 to 2016, presumably due to the fivefold decrease in emissions of sulphur dioxide and heavy metals from the smelter. The densities of externally feeding defoliators decreased from 1991 to 2016 and the densities of leafminers increased, while the leaf roller densities remained unchanged. Consequently, no overall temporal trend in the abundance of birch-feeding insects emerged despite a 2–3 °C elevation in spring temperatures. Damage to birch leaves by insects decreased during the observation period in heavily disturbed forests, did not change in moderately disturbed forests and tended to increase in pristine forests. The temporal stability of insect-plant interactions, quantified by the inverse of the coefficient of among-year variations of herbivore population densities and of birch foliar damage, showed a negative correlation with forest disturbance. We conclude that climate differently affects insect herbivory in heavily stressed versus pristine forests, and that herbivorous insects demonstrate diverse responses to environmental disturbance and climate variations. This diversity of responses, in combination with the decreased stability of insect–plant interactions, increases the uncertainty in predictions on the impacts of global change on forest damage by insects.

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1. Introduction

Changes in ecosystem structure and functions following various disturbances have long been—and still remain—of central concern in ecology. The current intensification of disturbance-related research is associated with two co-occurring processes. First is the increasing frequency of natural disturbances due to climate change (Thom and Seidl, 2016). Second is the increasing worldwide recovery of ecosystems from anthropogenic disturbances (Moreno-Mateos et al., 2017). However, while extensive research has evaluated the changes in biodiversity occurring under disturbance impacts and in the course of the subsequent recovery, information on the respective changes occurring in biotic interactions is still in short supply. This, in turn, hampers the understanding of the consequences of interplay between disturbance and recovery processes for ecosystem services.

Environmental pollution—one of the most severe environmental stressors—is an integral part of global change; nevertheless, the research addressing biotic effects of global change has overlooked the pollution issue until very recently (Kozlov and Zvereva, 2015a). At the same time, none of over 500 data sources reporting quantitative information on the responses of terrestrial biota to industrial pollution have addressed the impacts of climate warming on these responses (Kozlov and Zvereva, 2011). However, meta-analyses have revealed a positive correlation between the magnitude of pollution effects on terrestrial biota and the climate of study sites. Based on this finding, the harmful impacts of pollution are suggested to increase with climate warming (Zvereva et al., 2008; Kozlov and Zvereva, 2011). This increase may result from both the enhancement of pollution effects in a warming climate and from differential responses of trophic groups to temperature elevation in polluted environments. In particular, increases in temperature could enhance the adverse effects of pollution on producers and decomposers, while mitigating the adverse effects on primary and secondary consumers (Kozlov and Zvereva, 2011), thereby potentially leading to 'ecological surprises' (sensu Paine et al., 1998). However, these possibilities have not yet been verified, in particular due to an acute shortage of long-term monitoring data.

Research addressing the consequences of environmental disturbance for terrestrial biota has frequently targeted leaf-eating insects, due to their profound effects on ecosystem structure and functions, including the composition and productivity of plant communities and carbon and nutrient cycling (reviewed by Kozlov and Zvereva, 2017). The historically accepted opinion is that pollution may favour outbreaks of many insect herbivores, in particular forest pests (Baltensweiler, 1985; Führer, 1985), and meta-analysis of published data (Zvereva and Kozlov, 2010) has demonstrated significant increases in herbivore abundances near industrial polluters. However, the magnitude of this effect may have been overestimated due to a number of research and publication biases, including preferential documentation of theoretically predicted patterns and selective publication of supportive evidence (Zvereva and Kozlov, 2010; Kozlov, 2015). The proof for this overestimation was provided by the analysis of data collected in unbiased way. This analysis revealed no effects of pollution on the density of birch-feeding insects; moreover, background insect herbivory was found to decrease near industrial polluters (Kozlov et al., 2009). Thus, additional data, and especially long-term observations on the entire community of herbivorous insects, are required to clarify the effects of environmental disturbance on insect-plant relationships and to explore the effects of climate variations on these relationships.

We initiated our exploration of insects feeding on mountain birch (*Betula pubescens* ssp. *czerepanovii* [Orlova] Hämet-Ahti) in the impact zone of a large nickel–copper smelter in Monchegorsk, in northwestern Russia, in 1981 (Kozlov, 1985), when the smelter discharged extreme amounts of emissions into the ambient air (Kozlov et al., 2009). Subsequent studies conducted in 1984–1990 allowed the development of research methodology and served as a basis for a monitoring program implemented from 1991 to 2016. During the observation period, the spring and fall temperatures in our study area increased by 2.5–3 °C, while emissions of sulphur dioxide and heavy metals from the smelter decreased fivefold (Zvereva et al., 2016). These environmental changes provided an excellent opportunity to explore the combined effects of climate warming and pollution decline on insect herbivory.

In this paper, we test whether the densities of insect herbivores sharing the same host plant show similar spatial and temporal patterns, whether these patterns are explained by pollution and/or climate and whether environmental disturbance affects the stability of herbivore populations and their responses to climatic variations. More specifically, we predict that (1) background insect herbivory decreases with increase in pollution-induced environmental disturbance; (2) temporal variations in herbivore densities and in damage to birch leaves by insects increase with this disturbance; (3) declines in emissions weaken the correlation between insect herbivory and environmental disturbance; (4) climate warming increases insect herbivory; and (5) the effects of climate warming on herbivory differ between heavily polluted and pristine forests.

2. Materials and methods

2.1. Study area and study sites

The study was conducted in the central part of the Kola Peninsula, which is located in the north-west of Russia, next to Finland and Norway, to the north of the Polar Circle (Fig. 1). The nickel–copper smelter in the town of Monchegorsk (67°56′ N, 32°49′ E), about 150 km south of the tree line, was one of the largest polluters in the Northern hemisphere for decades. The smelter began production in 1937–1938 and had no air-cleaning facilities until 1968. The annual emissions of sulphur dioxide reached a maximum of 278,000 metric tons (t) in 1983, steadily declined to about 100,000 t by the mid-1990s, dropped to 45,000 t in 1999 and have remained at about this level since then (Table S1). Metal emissions during the 1980s–1990s were 3000–8000 t of nickel and 1000–6000 t of copper annually and then declined in concert with declines in SO_2 (Table S1). For the history of pollution impacts on the study region and the levels of environmental degradation, consult Kozlov and Barcan (2000), Kozlov et al. (2009) and Manninen et al. (2015).

Our study sites were selected in both pristine (unpolluted) subarctic Norway spruce (*Picea abies* (L.) Karst.) forests and in forests exhibiting

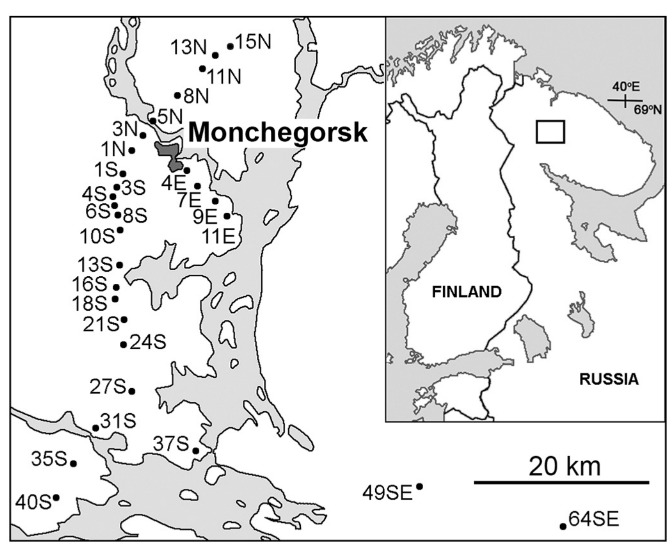

Fig. 1. Location of study sites (dots) in the vicinity of the Monchegorsk nickel–copper smelter, Kola Peninsula. Site codes indicate the approximate distance (km) and direction (to the north, south or south-east) from the smelter. Coordinates of the study sites are provided in Table S2. Insert: position of the study area in Northern Europe.