

# The relative strengths of rapid and delayed density dependence acting on a terrestrial herbivore change along a pollution gradient

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## Abstract

1. Animal populations vary in response to a combination of density-dependent and density-independent forces, which interact to drive their population dynamics. Understanding how abiotic forces mediate the form and strength of density-dependent processes remains a central goal of ecology, and is of increasing urgency in a rapidly changing world.
2. Here, we report for the first time that industrial pollution determines the relative strength of rapid and delayed density dependence operating on an animal population. We explored the impacts of pollution and climate on the population dynamics of an eruptive leafmining moth, *Phyllonorycter strigulatella*, around a coal-fired power plant near Apatity, north-western Russia. Populations were monitored at 14 sites over 26 years.
3. The relative strengths of rapid and delayed density dependence varied with distance from the power plant. Specifically, the strength of rapid density dependence increased while the strength of delayed density dependence decreased with increasing distance from the pollution source. Paralleling the increasing strength of rapid density dependence, we observed declines in the densities of *P. strigulatella*, increases in predation pressure from birds and ants, and declines in an unknown source of mortality (perhaps plant antibiosis) with increasing distance from the power plant.
4. In contrast to the associations with pollution, associations between climate change and leafminer population densities were negligible.
5. Our results may help to explain the outbreaks of insect herbivores that are frequently observed in polluted environments. We show that they can result from the weakening of rapid (stabilizing) density dependence relative to the effects of destabilizing delayed density dependence. Moreover, our results may explain some of the variation reported in published studies of animal populations in polluted habitats. Variable results may emerge in part because of the location of the study sites on different parts of pollution gradients. Finally, in a rapidly changing world, effects of anthropogenic pollution may be as, or more, important than are effects of climate change on the future dynamics of animal populations.

**KEYWORDS**

climate warming, density dependence, emission decline, insect–plant relationships, Kola Peninsula, pollution, population cycles, population dynamics

## 1 | INTRODUCTION

The dynamics of animal populations are driven by a combination of density-dependent (Lack, 1954; Nicholson & Bailey, 1935) and density-independent processes (Andrewartha & Birch, 1954), with interactions between them responsible for the fluctuations in animal numbers that we observe in nature (Royama, 1992; Stenseth et al., 1999; Varley, Gradwell, & Hassell, 1973). For example, water availability, a density-independent process, can determine the relative importance of resource limitation and predation pressure operating on animal populations (Price & Hunter, 2005, 2015). Likewise, spring temperatures (density-independent) can dictate the strength of competition between animal species (Hunter, 1998). Because density-dependent processes regulate animal populations and set limits on their population growth (Turchin, 1990), understanding how density-independent processes interact with density-dependent processes is important for the management of both beneficial and pest species (Berryman, 1981; Berryman, Stenseth, & Isaev, 1987). In the current period of rapid environmental change, predicting the impacts of abiotic forces on population regulation is of increasing urgency (Parmesan & Yohe, 2003; Walther et al., 2002). For example, if environment change alters the time-lag in the operation of density-dependent forces, it could have important implications for population dynamics. Typically, rapid density dependence enhances the stability of populations, whereas delayed density dependence is destabilizing (Turchin, 1990; Varley et al., 1973). Abiotic factors that increase the relative importance of delayed density-dependent processes should therefore increase population fluctuations (Hunter, Varley, & Gradwell, 1997; Stenseth et al., 2003; Turchin & Hanski, 1997).

The strength and form of density dependence operating on animal populations can vary substantially in space. For example, the relative strengths of rapid and delayed density dependence vary among populations of small mammals (Bjornstad, Stenseth, & Saitoh, 1999; Stenseth et al., 2003; Turchin & Hanski, 1997) and among populations of forest insects (Klemola, Tanhuanpaa, Korpimäki, & Ruohomäki, 2002; Liebhold, Johnson, & Bjornstad, 2006). Such spatial variation in negative feedback processes is often associated with latitudinal (seasonal) differences among populations, whereby delayed density dependence dominates at higher latitudes, inducing cyclic population dynamics (Klemola et al., 2002; Stenseth et al., 2003). However, differences in habitat type, such as stand composition, may also impact the form and strength of negative feedback operating on herbivores (Liebhold et al., 2006). Here, we ask whether pollution may act as an additional force generating spatial variation in density-dependent processes.

Anthropogenic effects of climate change on population dynamics continue to receive well-deserved attention in the literature (Altizer, Ostfeld, Johnson, Kutz, & Harvell, 2013; Jamieson, Schwartzberg, Raffa, Reich, & Lindroth, 2015; Valtonen et al., 2014). However, industrial pollution is a near-ubiquitous additional driver of environmental change in most ecosystems on Earth, with profound impacts on animal populations in aquatic and terrestrial ecosystems (Coleman, Crossley, & Hendrix, 2004; Hart & Fuller, 1979; Mirsal, 2008; Wulff, Rahm, & Larsson, 2001). Recent analyses suggest that effects of pollution on animal populations can exceed those of climate change (Zvereva, Hunter, Zverev, & Kozlov, 2016). Although it is well established that the impacts of pollution on animal populations may operate through biological forces such as competition and predation (Butler & Trumble, 2008), the effects of variation in pollution load on the relative strengths of density-dependent processes remain poorly understood.

Accepted opinion is that pollution favours outbreaks of many herbivores, in particular forest pests (Baltensweiler, 1985; Führer, 1985). Meta-analysis (Zvereva & Kozlov, 2010) has supported a pattern of consistent increases in herbivore abundance near point polluters, although this effect may be overestimated due to various biases in published data (Kozlov, Zvereva, & Zverev, 2009). The positive association between industrial pollution and herbivore outbreaks was supported recently by the analysis of long-term data on population densities of the willow-feeding leaf beetle, *Chrysomela lapponica*. Outbreaks of *C. lapponica* near a large non-ferrous smelter between 1990s and 2000s attenuated as pollution levels declined, associated with the re-establishment of top-down control by predators and parasitoids (Zvereva et al., 2016). However, over the same period, average densities of birch-feeding insects around the same smelter did not covary with pollution load either in space or in time (Kozlov, Zverev, & Zvereva, 2017).

Contrasting effects of pollution on the population dynamics of herbivores may be reconciled if we understand the effects of pollution on density-dependent processes. Most studies to date have focused on single biotic or abiotic drivers of population density (Alstad, Edmunds, & Weinstein, 1982; Butler & Trumble, 2008; Riemer & Whittaker, 1989; Selikhovkin, 1988; Zvereva & Kozlov, 2010), while studies that explore the effects of pollution on multiple negative feedback processes simultaneously (Zvereva et al., 2016) remain rare. Our limited understanding of how pollution interacts with sources of negative feedback is at least partly explained by the shortage of data suitable for the analysis of density dependence. Time series of at least 30–40 steps are ideal for analysing ecological factors that influence populations (Royama, 1992). Notably, the maximum length of population time series of herbivorous insects collected from pollution gradients, reported in studies published by

2009, was only 12 years (Zvereva & Kozlov, 2010). Since 2009, longer (19–26 years) time series from multiple sites around a copper-nickel smelter in Monchegorsk, north-western Russia, have been published (Kozlov et al., 2017; Zvereva et al., 2016). However, the vast majority of herbivorous insects monitored at these sites did not show clear population cycles during the observation period, and signals of delayed density dependence were only found in populations of two leaf beetle species, *C. lapponica* and *Phratora vitellinae*, around this smelter (Zvereva et al., 2016).

In 1991, M.V.K. started to monitor population densities of the leafmining moth *Phyllonorycter strigulatella* (Lienig et Zeller) (Lepidoptera, Gracillariidae) around a coal-fired power plant (which at that time emitted 20,000–29,000 metric tons of sulphur dioxide annually) near Apatity, north-western Russia. After ten years of data collection, it appeared that densities of this leafminer varied nearly 200-fold during the course of its population cycle, with peak population densities much higher near the power plant (Kozlov, 2003). Because of the apparent interaction between population cycles and pollution load, monitoring was continued until 2016. Here, we report the outcomes of time-series analyses of this unique dataset (23–26 years at 14 study sites), asking whether the strength of rapid and/or delayed density dependence operating on populations of the leafmining moth *P. strigulatella* varies along the pollution gradient. Additionally, we ask whether declines in pollution and climate warming, which have occurred simultaneously during the observation period, have affected the population dynamics of *P. strigulatella*.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area, insects and host plants

The study was conducted in the central part of the Murmansk region of Russia, in an area covered predominantly by secondary birch-dominated forests scattered among the remnants of primary coniferous forests. Daily values of temperature and precipitation in Apatity are freely available (at [www.rp5.ru](http://www.rp5.ru)) only from 2012, and therefore, we used climate data from Monchegorsk (Supporting Information Table S1; described in detail by Kozlov et al., 2017), which is located 43 km NNW from Apatity.

Speckled alder, *Alnus incana* (L.) Moench, is common over the entire study area, where it grows mainly in disturbed habitats along roads. Very small (wing expanse about 7 mm) moths of *P. strigulatella* fly in mid-June. Caterpillars make blotch epidermal mines (one larva in each) on the lower side of alder leaves from the end of June up to pupation in the end of July–beginning of August. Mine size at pupation is 1.2–1.8 cm<sup>2</sup>, and 5–15 larvae may successfully complete their development in a single alder leaf.

### 2.2 | Emission source and pollution load

The coal-fired power plant, situated some 1.5 km N of the city of Apatity (67°35'51"N, 33°25'08"E), is the only local point source of sulphur dioxide and some metals, such as Fe, Zn, Cr, Cd and Pb. The

station mainly uses coal from Inta, northern Ural (sulphur content 1.5%–1.9%), and sometimes from Spitsbergen or Khakassia (sulphur content 0.7%–1.0%). The height of the smokestack is 100 m; for more details, consult Kozlov et al. (2009). During the observation period, emissions of sulphur dioxide and dust from the station decreased nearly fivefold, whereas emission of nitrogen oxides did not change (Supporting Information Table S2). Concentrations of pollutants decline to regional background levels at a distance of approximately 5 km from the power plant (Kozlov, 2003).

### 2.3 | Leafminer densities

In total, fourteen sites were studied over the 26-year period. Sites were located along roads leading either SE or NW from the power plant, and ranged in distance from 0.3 to 7.2 km from the power plant (Supporting Information Table S3); the two directions from the power plant provided spatial replications of pollution load. Of the 14 sites sampled during the course of the study, 10 were sampled in 1991, while 13 were sampled in 1992 and 1994. All 14 sites were sampled in all remaining years (Supporting Information Table S3). Raw count data are available from the Dryad Digital Repository (Hunter & Kozlov, 2018: <https://doi.org/10.5061/dryad.sn0cn43>).

Densities of *P. strigulatella* were monitored once per growth season, during the first week of August in 1991–2016. Ten trees of speckled alder 2–5 m high were chosen at each site on a “first found, first sampled” basis. The trees were not tagged, so observations in different years were conducted on different sets of trees. One branch in the lower part of the crown (at about breast height) was haphazardly selected in each tree, and the total number of mines was counted in a sample of 25 leaves, starting from the tip of the branch. Care was taken to count even the smallest mines, which were 2–3 mm<sup>2</sup> size. Leaf size of speckled alder did not change systematically along the pollution gradient (Kozlov, 2003); thus, this method returned the number of mines per constant unit of host plant resource.

### 2.4 | Leafminer mortality

On 19 August 2017, we collected ca. 50 mines (range 49–71) haphazardly from each of the 14 sites. At this point during the season, over 90% of surviving leafminers have reached their final size (Kozlov, 2003). In each sample, we calculated the number of mines that had died during early stages of their development (reaching not more than one-third of the final size) and mines that had been opened by predators (wood ants and birds). All remaining mines were kept outdoors in large Petri dishes until 4 November 2017. On this date, we counted the numbers of mines that contained live pupae, those from which parasitoids had emerged, and any remaining miners that had died of unknown causes. On the basis of this information, each collected larva was assigned to one of four categories: pupated (alive), killed by predators, killed by parasitoids or death from unknown causes.

## 2.5 | Data analysis

### 2.5.1 | General patterns

Leafminer distributions were clumped on individual trees, such that around 40% of trees examined had counts of zero. Consequently, in our initial analysis, we used a negative binomial distribution and log link function (Proc GENMOD, SAS Institute 2009) to quantify the extent to which leafminer densities varied among sites and years. Counts from individual trees were the dependent variable, while year, site, and their interaction were independent variables.

Because we observed what appeared to be synchronous peaks in leafminer abundance among study sites, we tested for synchronous dynamics (Bjornstad, Ims, & Lambin, 1999) using the community.sync function in the synchrony package in R (Gouhier, 2018; Loreau & de Mazancourt, 2008). We compared among-site synchrony against 1,000 Monte Carlo randomized permutations of population data, with Kendall's coefficient as our measure of synchrony. We ran the synchrony analysis twice. First, we assessed synchrony among all 14 sites from 1995 to 2016 (years in which all 14 sites were sampled). Second, we assessed synchrony among the 10 sites for which we had leafminer counts for all 26 years (1991 to 2016).

Having established that leafminer densities varied significantly among sites and years and that their dynamics were synchronous among sites (Results), we then used averages of the 10 trees per site to explore temporal and spatial variation in more detail (below).

### 2.5.2 | Temporal patterns

First, we explored simple patterns of temporal change in leafminer densities using average densities of leafminers for each sample year; averaging across sites yielded 26 density estimates, one for each sample year. To assess effects of pollution load and climate on temporal patterns of leafminer density, we used principal component analysis (PCA) to combine 16 climate variables (Supporting Information Table S1: four variables for each of four seasons) into PCA axes w1–w4. Each of these axes had an eigenvalue exceeding 1, and they combined to explain 79.3% variation in the climate data. However, only w1 correlated with year ( $r = 0.64$ ,  $n = 26$  years,  $p = 0.0004$ , Supporting Information Figure S1), so w1 is the only PCA axis that represents systematic climate change. Similarly, we combined pollution data (Supporting Information Table S2: annual emissions of sulphur dioxide, dust and nitrogen oxides) into a single PCA axis (p1). This axis had an eigenvalue >1 and explained 72.8% of the variance in pollution emissions during the study period. This pollution axis correlates very strongly with year ( $r = -0.88$ ,  $n = 26$  years,  $p < 0.0001$ ) and so represents the combined declines in all three pollutants over time (Supporting Information Table S2). We used Proc GLM (SAS Institute, 2009) to correlate average leafminer densities among years (dependent variable, log-transformed) with PCA axes w1 and p1 in a multiple regression model. PCA p1 was log-transformed prior to analysis to linearize the exponential relationship.

Because we observed evidence of periodic fluctuations in leafminer density over time that might obscure effects of pollution or climate, we also used time-series analysis (Box & Jenkins, 1970; Royama, 1992) to account for any systematic variation in leafminer densities. Following previously published procedures (Forchhammer, Stenseth, Post, & Langvatn, 1998; Price & Hunter, 2005; Turchin, 1990), we regressed leafminer per capita rates of change ( $r = \text{natural log of } \lambda$ ), calculated between each pair of years in the time series, with their population densities at time  $t-1$  and  $t-2$  (natural log-transformed). With those factors held in the model, we then asked whether pollution (PCA axis p1) or climate change (PCA axis w1) could explain any additional variation in leafminer per capita rates of change. Models were built using Proc GENMOD (SAS Institute, 2009).

### 2.5.3 | Spatial patterns

Second, we explored some simple spatial patterns in the data. Here, we averaged across years to generate average leafminer densities for each site (14 sites total). Unlike the temporal data available on annual emissions from the power plant (Supporting Information Table S2), we do not have spatial data on pollution loads at each study site over the entire study period. Therefore, in our spatial analyses, we followed previous studies (Kozlov et al., 2009; Zvereva et al., 2016) and used distance from the polluter as a proxy for pollution load. The validity of this assumption has been confirmed previously for these sites by a significant negative correlation between distance and iron concentration in the leaves of speckled alder (Kozlov, 2003). Here, we used Proc GLM (SAS Institute, 2009) to correlate (a) leafminer counts for each site (log-transformed) and (b) the temporal stability of leafminer populations (calculated as the inverse of the coefficient of among-year variation) with distance from the polluter.

### 2.5.4 | Spatio-temporal patterns

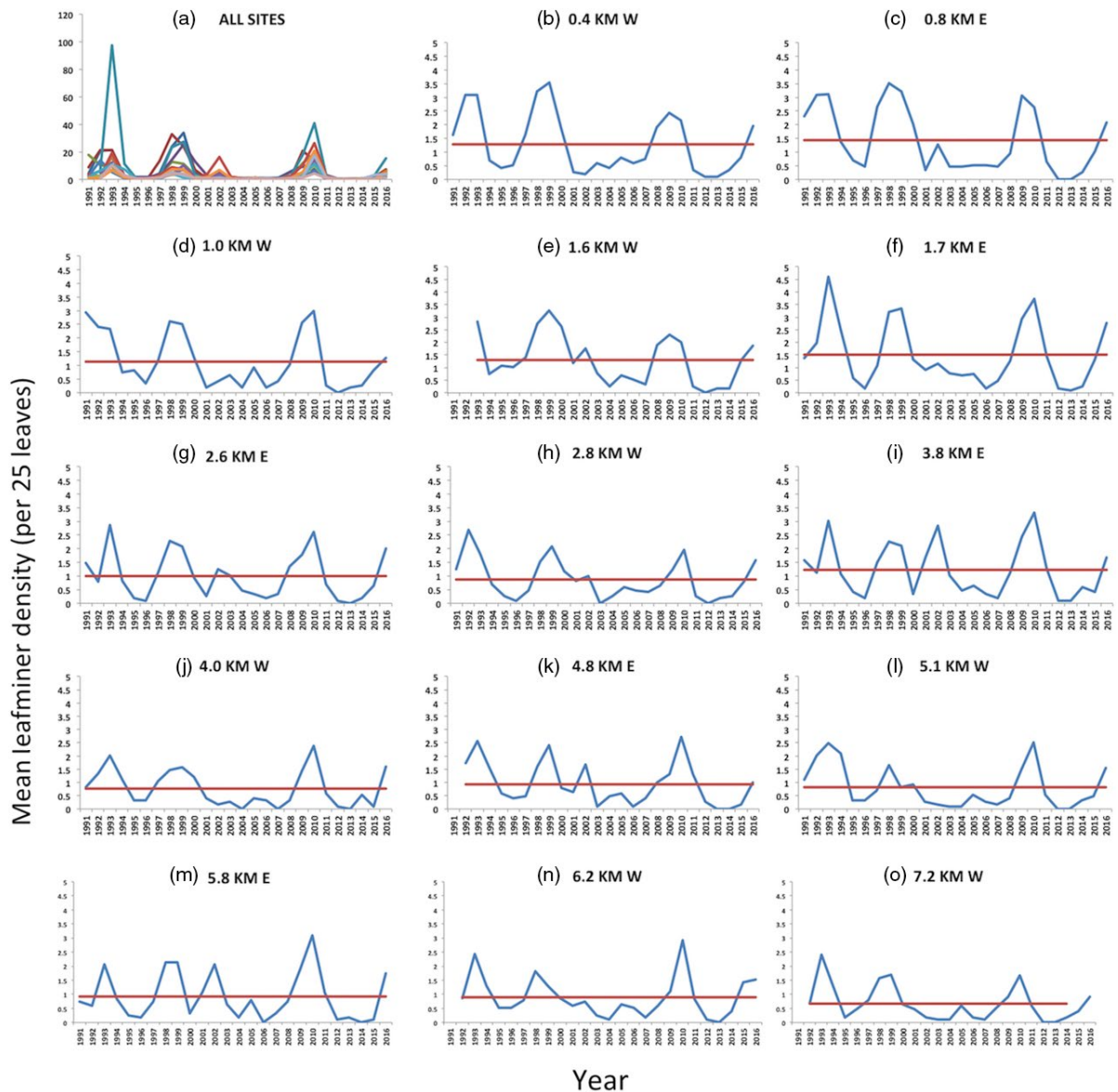
We then explored how temporal patterns of leafminer density varied in space. Separately for each site, we conducted time-series analysis (Hunter et al., 2014; Redfern & Hunter, 2005; Royama, 1992) to estimate the strength (slope) of any rapid and/or delayed density dependence acting on leafminer population dynamics. First, we fitted multiple regression models to the relationships between per capita rates of change and densities at time  $t-1$  and  $t-2$  (Proc GENMOD; SAS Institute, 2009) to generate maximum likelihood parameter values of the regression slopes. There is inherent autocorrelation in time-series analysis; per capita rates of change are not independent of population densities at time  $t-1$ , inflating the probability of detecting statistically significant regression slopes (Dennis & Taper, 1994; Royama, 1992). However, we are interested here in the magnitude of the slopes and how they vary with distance from the polluter, rather than in the  $p$ -values associated with those slopes. Next, because observation and sampling error can cause significant bias in the estimates of density dependence (Dennis, Ponciano, Lele, Taper, & Staples, 2006; Freckleton, Watkinson, Green, & Sutherland,

2006), we used a simulation extrapolation (SIMEX) procedure (Cook & Stefanski, 1994) to help mitigate effects of census error on our estimates of density dependence. Specifically, we used the standard error associated with our mean counts from 10 sample trees per year at each site to simulate the effects of census error on our estimates (see Supporting Information Table S4 for details). While our estimates of density dependence were generally robust to the effects of simulated error (Supporting Information Table S4), we have used the SIMEX-corrected estimates in subsequent analyses. Specifically, we correlated (using Proc GLM) the estimated slopes of rapid and delayed density dependence at each site with distance from the polluter. Finally, to investigate any systematic variation in

the periodicity in leafminer fluctuations among sites, we conducted spectral analyses (Bloomfield, 2000) on the log-transformed counts of leafminers from each site, using the spectrum function in R.

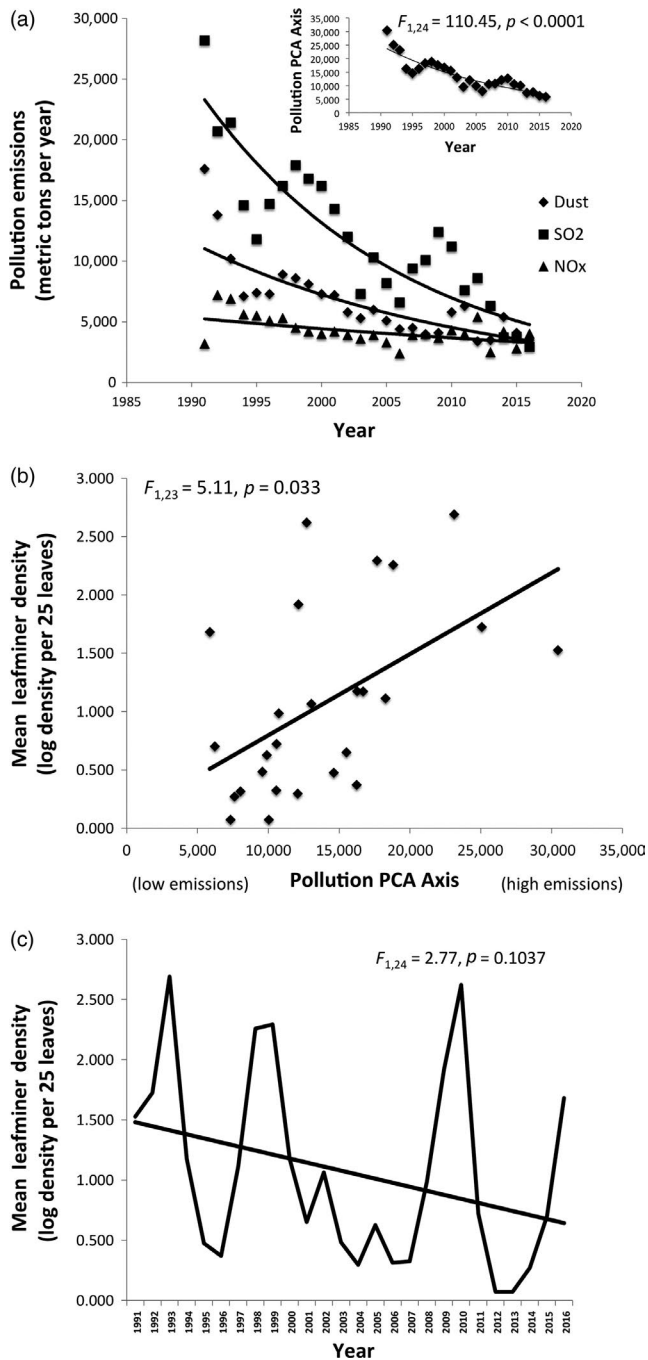
### 2.5.5 | Mortality patterns

Given that we observed differences in patterns of negative feedback with distance from the polluter (see Results), we investigated whether sources of leafminer mortality might also vary with pollution load. Using the sources of mortality that we had measured from mines collected in 2017, we assessed whether the proportion of leafminers dying from each mortality factor varied with distance from the power plant.



**FIGURE 1** (a) Synchronous population dynamics of the leafmining moth, *Phyllonorycter strigulatella*, over 26 years at 14 study sites around a coal-fired power plant near Apatity, north-western Russia. Densities are the average number of leafminers per 25 leaves ( $N = 10$  trees per site). (b–o) Average leafminer densities (natural log scale) at each of the 14 study sites, ordered by increasing distance from the power plant. E and W refer to sites east and west of the power plant, while horizontal lines represent mean densities at each site





**FIGURE 2** (a) Temporal declines in pollution emissions from a coal-fired power plant near Apatity, north-western Russia (the insert illustrates the PCA axis that combines all three pollutants). Data were log-transformed prior to analysis, but are shown here in raw form. (b) The relationship between pollution load (PCA axis) and the density of the leafmining moth, *Phyllonorycter strigulatella*, averaged across 14 study sites. Each point represents a single year. (c) Average leafminer densities (log scale) did not decline systematically over the course of the study

We analysed the proportions using binomial models with logit link functions in the GENMOD procedure in SAS (Littell, Stroup, & Freund, 2002), with mortality factors as dependent variables and distance from the power plant as the independent variable.

### 3 | RESULTS

#### 3.1 | Overall patterns

Densities of *P. strigulatella* varied 235-fold among years and 20-fold among sites, with the magnitude of difference among sites much more pronounced during population peaks (Figure 1a). Fluctuations in leafminer populations were synchronous among sites, whether we compared all 14 sites from 1995 to 2016 (Synchrony = 0.758,  $p = 0.001$ ), or the 10 sites for which had counts from 1991 to 2016 (Synchrony = 0.701,  $p = 0.001$ ).

#### 3.2 | Temporal patterns

Pollution emissions declined over the period of the study (Figure 2a), with a sixfold decline in SO<sub>2</sub> emissions, a halving of dust emissions and more modest declines in NO<sub>x</sub> emissions. These simultaneous declines in pollution are reflected in declines in the scores of PCA axis p1 (Year  $F_{1,24} = 110.45, p < 0.0001$ , Figure 2a insert). In turn, low pollution emissions were correlated with low leafminer densities among years (p1  $F_{1,23} = 5.11, p = 0.033$ , Figure 2b). Our estimate of climate change (PCA w1) was not a significant predictor of leafminer density (w1  $F_{1,23} = 0.16, p = 0.89$ ) in the simple multiple regression model. Despite declines in pollution emissions over time, we observed no clear reductions in leafminer densities between 1991 and 2016 (Year  $F_{1,24} = 2.77, p = 0.1037$ , Figure 2c).

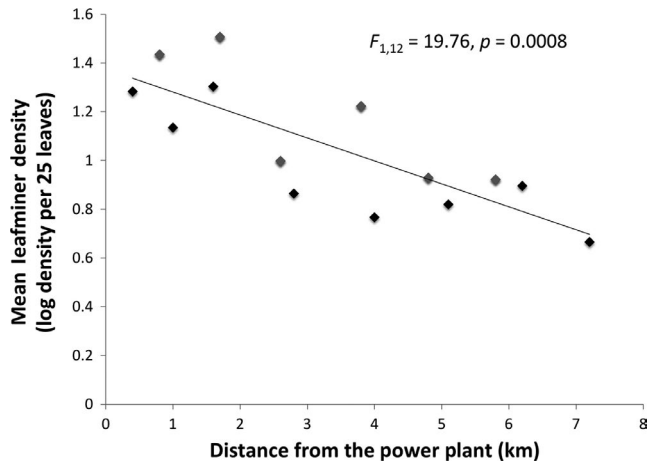
To further investigate any impacts of climate change or pollution on moth dynamics, we first accounted for the effects of leafminer densities at time  $t-1$  and  $t-2$  on leafminer per capita rates of change (see Methods). With densities included in the time-series models, we then assessed whether any of the residual variance in per capita rates of change was associated with climate or pollution data. After accounting for variation in leafminer densities, there was still no effect of our climate change estimate on leafminer per capita rates of change (w1  $F_{1,20} = 0.29, p = 0.595$ ). As with their impact on density (above), pollution emissions were associated positively with leafminer per capita rates of change (PCA p1  $F_{1,20} = 4.38, p = 0.0494$ ).

#### 3.3 | Spatial patterns

When averaged across years, leafminer densities declined by 45% over the 7.2 km from the site closest to the power plant to the most distant site ( $F_{1,12} = 19.76, p = 0.0008$ , Figure 3). The temporal stability of leafminer populations (i.e., inverse of the coefficient of among-year variation) was unrelated to distance from the power plant ( $F_{1,12} = 0.64, p = 0.438$ ).

#### 3.4 | Spatio-temporal patterns

The strength of rapid density dependence increased ( $F_{1,12} = 19.81, p = 0.0008$ ), while the strength of delayed density dependence

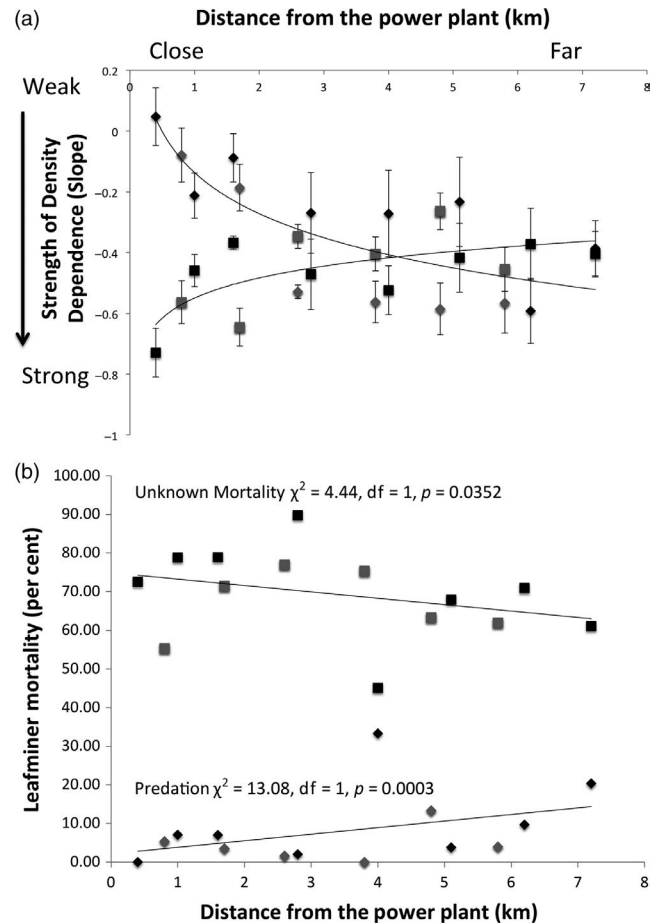


**FIGURE 3** Densities of the leafmining moth, *Phyllonorycter strigulatella*, decline with increasing distance from a coal-fired power plant near Apatity, north-western Russia. Each point represents a single study site, with densities averaged across 23 to 26 years of sampling. Grey symbols refer to sites east of the power plant, while black symbols refer to sites west of the power plant

decreased ( $F_{1,12} = 9.95, p = 0.0083$ ), with increasing distance from the power plant (Figure 4a). At distances  $>3$  km from the power plant, rapid and delayed density dependence became equally powerful forces acting on *P. strigulatella* per capita rates of change (Figure 4a). Because delayed density dependence remained pervasive among sites (Supporting Information Table S4), the combined values of rapid and delayed density dependence across all sites (Figure 4a) remained within ranges that should favour population cycles (see ‘Royama’s Triangle’; Royama, 1992), explaining the apparent presence of cycles in the leafminer time series at all sites (Figure 1). However, while the periodic fluctuations were similar among sites, average population sizes and the magnitude of outbreaks declined with increasing distance from the power plant (Figures 1b–o and 3). The periodograms from spectral analyses (Supporting Information Figure S2) illustrated pervasive high spectral densities at a frequency of 0.11–0.12, consistent with apparent 8–9 year cycles in the time-series data (Figure 1), and consistent with the action of delayed density dependence. While there were additional higher frequencies typical of more rapid cycles observed at some of the sites more distant from the power plant, there was no unequivocal evidence for a systematic change in outbreak periodicity with distance from the power plant (Supporting Information Figure S2).

### 3.5 | Mortality patterns

Across all sites, only 6.2% of *P. strigulatella* larvae survived until pupation in 2017 (Supporting Information Table S5). Most larvae (69.3%) died of unknown causes, either when their mines were small or just prior to pupation. Parasitoids (several species of Braconidae and Ichneumonidae, some of which may have been super-parasitoids)



**FIGURE 4** (a) Systematic changes in the strengths of rapid (diamonds) and delayed (squares) density dependence operating on populations of the leafmining moth, *Phyllonorycter strigulatella*, at 14 study sites around a coal-fired power plant near Apatity, north-western Russia. In (a), the strengths of density dependence are SIMEX estimates of the slopes of regressions between leafminer per capita rates of change and population densities at time  $t-1$  (rapid) and  $t-2$  (delayed), with more negative numbers representing stronger effects. (b) The effects of distance from the power plant on predation (diamonds) and an unknown mortality source (squares) operating on populations of *P. strigulatella*. Each point represents mortality at a single site from a sample of 49 to 71 leafminers per site. Statistics refer to binomial models of proportional mortality against distance. In both (a) and (b), grey symbols refer to sites east of the power plant, while black symbols refer to sites west of the power plant

emerged from 16.5% mines, while 8.0% of mines were opened by predators (birds and ants).

The proportion of leafminers killed by predators increased nearly fivefold with increasing distance from the power plant (Chi-square = 12.62,  $df = 1, p = 0.0004$ , Figure 4b). In contrast, mortality caused by unknown factors declined by about 10% with increasing distance from the power plant (Chi-square = 4.44,  $df = 1, p = 0.0353$ , Figure 4b), driven primarily by failed development early in life (Chi-square = 2.95,  $df = 1, p = 0.0860$ ). No other mortality factors that we measured were related to the distance from the power plant.

## 4 | DISCUSSION

Based on time-series analyses of long-term data, we report for the first time that the order of the negative feedback processes operating on an animal population varies predictably with distance from a pollution source. Population dynamics of the leafmining moth, *P. strigulatella*, are dominated by delayed density-dependent processes close to a coal-fired power plant. With increasing distance from the pollution source, the impact of delayed density dependence declines while the impact of rapid density dependence increases, so that they become equally powerful forces acting on leafminer dynamics at distances >3 km from the power plant (Figure 4a). From a single year of mortality data, we note that the change in the relative strengths of negative feedback is associated with increases in predation pressure, and declines in an unknown mortality factor, with increasing distance from the power plant (Figure 4b).

Density-dependent processes impose negative feedback, thereby maintaining a limit on population growth (Berryman, 1991; Varley et al., 1973). However, it is the interaction between density-dependent and density-independent forces that determines the temporal dynamics of animal populations (Forchhammer et al., 1998; Hunter, 2016; Stenseth et al., 1999; Turchin & Hanski, 1997). While previous studies have focused on the impacts of climatic factors on the form and strength of density dependence (Hunter et al., 1997; Price & Hunter, 2015; Stenseth et al., 1999), our results add another abiotic driver, pollution, to the list of factors that can mediate the relative strengths of density-dependent processes.

Moreover, our results may explain some of the variation that has been reported previously in the effects of pollution on animal population dynamics. For example, studies have differed in their conclusions on the relative importance of direct pollutant toxicity, changes in plant quality, and changes in predation pressure in determining herbivore population dynamics under pollution stress (Butler & Trumble, 2008; Kozlov et al., 2009; Zvereva & Kozlov, 2010). Our data suggest that the relative importance of ecological factors varies with distance from the pollution source and may generate different lags in the action of density dependence. It is therefore possible that apparent differences in dynamics among studies partly reflect differences in the distance from the polluter at which the study was conducted, rather than intrinsic differences based on the study system.

What density-dependent factors varied in response to changing pollution loads? Unfortunately, we do not have the long-term data on predation pressure or plant quality that would be necessary to determine whether and how they impose density dependence on leafminer populations. The suggestions that follow are therefore speculative. However, in the current study, generalist predators that tear open leaf mines (wood ants and birds) imposed higher rates of mortality at sites far from the power plant (Figure 4b). High levels of pollution can influence the morphology, physiology, density and behaviour of ants (Eeva, Belskii, Gilyazov, & Kozlov, 2012; Grześ, 2010; Grześ, Okrutniak, & Woch, 2015), including reducing the aggressiveness of wood ants (Sorvari & Eeva, 2010). Likewise, high pollution

levels can compromise the physiology (Geens, Dauwe, Bervoets, Blust, & Eens, 2010) and abundance (Eeva et al., 2012; Morelli, Benedetti, Mousseau, & Møller, 2018) of birds. Because both ants and birds can show rapid behavioural and numerical responses to variation in prey density (Holldobler & Wilson, 1990; Perrins, 1979), they may be responsible for the increasing importance of rapid density dependence with increasing distance from the power plant (Figure 4a). Previous studies of both insects and small mammals have illustrated that increases in the relative strength of rapid density dependence can emerge from increasing predation by generalist predators (Klemola et al., 2002; Stenseth et al., 2003; Turchin & Hanski, 1997). Our studies of *P. strigulatella* populations are therefore consistent with the suggestion that increases in the abundance of generalist predators impose strong rapid density dependence on herbivores. Moreover, our results suggest that a weakening of rapid density-dependent mortality may explain the frequently reported (Zvereva & Kozlov, 2010) increase in abundance of plant-feeding insects in polluted habitats. Critically, delayed density dependence is destabilizing relative to rapid density dependence (Royama, 1992; Turchin, 1990), and a dominance of delayed density dependence near sources of pollution may facilitate insect outbreaks.

The results presented here support previous work, in which we reported the re-establishment of predation pressure on an insect herbivore following temporal declines in pollution load (Zvereva et al., 2016). Specifically, populations of the willow-feeding leaf beetle, *C. lapponica*, near a copper-nickel smelter declined over time as the combined impacts of predation and parasitism increased. Our current results are similar, but occur over space rather than over time. Because we measured sources of mortality on *P. strigulatella* only in a single year, we are unable to assess any temporal changes in natural enemy impacts in the current study. However, we note that any temporal declines in the densities of *P. strigulatella* are much weaker (Figure 2c) than were the dramatic temporal declines we reported for *C. lapponica* (Zvereva et al., 2016). For *P. strigulatella*, the effects of spatial variation in pollution load appear much stronger than the effects of temporal variation. In support of that premise, we found no significant correlation between distance from the pollution source and the magnitude of density fluctuations (coefficient of variation) in *P. strigulatella* populations. This contrasts with the pattern that was observed around the copper-nickel smelter in Monchegorsk, where the magnitude of density fluctuations of birch-feeding insects correlated positively with pollution load (Kozlov et al., 2017). This difference may be explained by the lower environmental impact of the Apatity power plant relative to the Monchegorsk smelter, which emitted ten times more sulphur dioxide than the power plant (Kozlov et al., 2009).

In addition to changes in rapid density dependence, we observed increases in the strength of delayed density dependence under higher pollution loads. However, delayed density dependence was still apparent across a majority of our study sites (Supporting Information Table S4), occurring at levels that should promote cyclic dynamics (Royama, 1992), irrespective of distance to the power plant. Accordingly, such forces may have been responsible for the



synchronous population fluctuations that we observed at our sites (Figure 1). While we cannot rule out the possibility that density-independent processes generated the apparent cycles in leafminer populations (as described by Williams & Liebhold, 1995; Hunter & Price, 1998; Louca & Doebeli, 2014), there is no evidence of periodicity in climatic factors over the study period (Supporting Information Figure S1).

Why did our populations of *P. strigulatella* remain synchronous, despite systematic variation in the relative strengths of rapid and delayed density dependence? Previous work with spatially disjunct gypsy moth, *Lymantria dispar*, populations may help to answer this question. Like *P. strigulatella*, gypsy moth populations exhibit substantial spatial variation in the relative importance of rapid and delayed density dependence operating on their dynamics, likely due to variation in forest composition (Liebhold et al., 2006). Importantly, the authors developed a stochastic population model that included both rapid and delayed density dependence to explore how variation in the form and strength of density dependence influenced synchrony among disjunct populations. The authors concluded that variation in the strengths of negative feedback had minimal impact on population synchrony that was generated by dispersal among populations; variation in the strength of rapid density dependence could diminish synchrony that was generated primarily by stochastic forcing (Liebhold et al., 2006). This suggests that our populations of *P. strigulatella* may retain synchrony across space primarily through dispersal mechanisms rather than stochastic forcing. It has also been suggested that the dispersal of predators can maintain synchrony among sites (Bjornstad, Stenseth, et al., 1999); unfortunately, we lack data to compare the potential importance of dispersal by *P. strigulatella* or its enemies on population synchrony.

Although the spatial variation in negative feedback processes among our *P. strigulatella* populations was insufficient to influence gross dynamics (i.e., all populations were cyclic), effects are much stronger in some other systems. For example, populations of grey-sided voles, *Clethrionomys rufocanus*, in Japan suffer increases in the strength of delayed density dependence in northern sites where winters are long, which causes those populations to exhibit cyclic dynamics (Stenseth et al., 2003). In that example, spatial variation in the strength of predation during winter months drives differential dynamics among sites, and we suggest that similar patterns may occur near some larger polluters.

Although delayed density dependence operated at most of our study sites, its relative importance for population dynamics declined with distance from the power plant (Figure 4a) in concert with declines in leafminer mortality from unknown causes (Figure 4b). When insects that feed within their host plants die from unknown causes prior to completing their development, authors often invoke the operation of plant antibiosis (induced plant defence, poor nutritional quality) as a contributing factor (Haukioja, 1974; Connor, Adams-Manson, Carr, & Beck, 1994; Price & Hunter, 2005). We therefore suggest that the delayed density-dependent force that declined with distance from the polluter could have been plant-mediated. However, the possibility remains that other hidden sources of

mortality, such as pathogen attack, may have generated the delayed density dependence that we observed. For example, in some small mammal and insect populations, the switch from stable to cyclic dynamics with increasing latitude is associated with a relative increase in the role of specialist predators at higher latitudes, which induce delayed density dependence (Turchin & Hanski, 1997; Klemola et al., 2002; Stenseth et al., 2003).

The climate of our study region has changed rapidly over the past decades. The annual surface air temperature in the Kola Peninsula has increased by 2.3°C over the past 50 years, due to warming in spring and fall. Furthermore, springs are wetter and falls are drier than before (Marshall, Vignols, & Rees, 2016). Predictions suggest that increasing temperatures will cause larger increases in herbivory than in plant productivity (Ayres & Lombardero, 2000; O'Connor, 2009; DeLucia, Nability, Zavala, & Berenbaum, 2012), thereby increasing overall plant damage by insects. Studies conducted along latitudinal climatic gradients predict that increases in herbivory will be greater at high latitudes than at low latitudes (Kozlov, Lanta, Zverev, & Zvereva, 2015; Kozlov, Stekolshchikov et al., 2015). However, contrary to expectations, rising temperatures in our study region have not caused significant increases in the population density of *P. strigulatella* (Figure 1) and we observed no correlation between leafminer density and the PCA w1 axis for climate change. This result is consistent with the absence of positive effects of climate warming on willow- and birch-feeding insects in the Kola Peninsula (Kozlov et al., 2017; Zvereva et al., 2016). It is also consistent with the general absence of changes in foliar losses of temperate woody plants to insects in natural ecosystems between 1952 and 2013 (Kozlov & Zvereva, 2015).

Pollution imposes substantial environmental stress on organisms including birds (Morelli et al., 2018; Radhouani et al., 2012), insects (Bonisoli-Alquati et al., 2018; Butler & Trumble, 2008) and mammals (Drouhot et al., 2014; Fritsch et al., 2010). Our data confirm that effects of pollution on animal population dynamics can be stronger than those of climate change (Zvereva et al., 2016), and highlight the importance of studying pollution as an integral component of global change research (Batty & Hallberg, 2010; Sun & Zhou, 2002). By understanding how different density-dependent processes respond to pollution load, we may be better able to predict population change and manage species of economic and cultural importance. Finally, we note that pollution research can provide fundamental insights of general importance to population dynamics theory, by explaining temporal variation (Zvereva et al., 2016) and spatial variation (data presented here) in the relative strengths of negative feedback processes.

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## AUTHORS' CONTRIBUTIONS

M.V.K. designed the study and conducted the fieldwork; M.D.H. conducted the data analysis and interpretation; M.V.K and M.D.H. co-wrote the manuscript.

## DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sn0cn43> (Hunter & Kozlov, 2018).

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## SUPPORTING INFORMATION

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

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