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

[1]Mark D. Hunter and [2]Mikhail V. Kozlov

[1]Department of Ecology and Evolutionary Biology, 3010 Biological Sciences Building, 1105 North University Avenue, University of Michigan, Ann Arbor, MI 48109-1085, USA. mdhunter@umich.edu

[2]Section of Ecology and Evolutionary Biology, Department of Biology, University of Turku, Turku 20014, Finland. mikoz@utu.fi

**Corresponding Author:** Mark D. Hunter, Department of Ecology and Evolutionary Biology, 3010 Biological Sciences Building, 1105 North University Avenue, University of Michigan, Ann Arbor, MI 48109-1085, USA. mdhunter@umich.edu

**Statement of Authorship:**

MVK designed the study and conducted the fieldwork. MDH conducted the data analysis and interpretation. MVK and MDH co-wrote the manuscript.

**Short Running Title:** Pollution affects density dependence

**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, northwestern 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.

2

4. In contrast to the associations with pollution, associations between climate change and leafminer populations 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 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 on a pollution gradient. 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.

# 1. Introduction

The dynamics of animal populations are driven by a combination of density dependent (Nicholson & Bailey 1935; Lack 1954) and density independent processes (Andrewartha & Birch 1954), with interactions between them responsible for the fluctuations in animal numbers that we observe in nature (Varley *et al.* 1973; Royama 1992; Stenseth *et al.* 1999). 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; Price & Hunter 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 *et al*. 1987). In the current period of rapid environmental change, predicting the impacts of abiotic forces on population regulation is of increasing urgency (Walther *et al.* 2002; Parmesan & Yohe 2003). 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 (Varley *et al.* 1973; Turchin 1990). Abiotic factors that increase the relative importance of delayed density dependent processes should therefore increase population fluctuations (Hunter *et al*. 1997; Turchin & Hanski 1997; Stenseth et al. 2003).

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 (Turchin & Hanski 1997; Bjornstad et al. 1999b; Stenseth et al. 2003) and among populations of forest insects (Klemola et al. 2002; Liebhold et al. 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 *et al.* 2013; Valtonen *et al.* 2014; Jamieson *et al.* 2015). 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 (Hart & Fuller 1979; Wulff *et al*. 2001; Coleman *et al*. 2004; Mirsal 2008). Recent analyses suggest that effects of pollution on animal populations can exceed those of climate change (Zvereva *et al.* 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 favors outbreaks of many herbivores, in particular forest pests (Baltensweiler 1985; Führer 1985). Meta-analysis (Zvereva & Kozlov 2010) has supported consistent increases in herbivore abundance near point polluters, although this effect may be overestimated due to various biases in published data (Kozlov et al. 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 1990–2000s 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 et al. 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 et al. 1982; Selikhovkin 1988; Riemer & Whittaker 1989; Butler & Trumble 2008; 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 analyzing 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, northwestern Russia, have been published (Zvereva et al. 2016; Kozlov et al. 2017). However, the vast majority of herbivorous insects monitored at theses 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, northwestern 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 data set (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

7

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) only from 2012, and therefore we used climate data from Monchegorsk (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$^2$, 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 five-fold, whereas emission of nitrogen oxides did not change (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 0.3–7.2 km from the power plant (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 (Table S3).

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$^2$ 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 to 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 from 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 by synchronous peaks in leafminer abundance among study sites, we tested for synchronous dynamics (Bjornstad et al. 1999a) using the community.sync function in the synchrony package in R (Loreau & de Mazancourt 2008; Gouhier 2018). 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 (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, $P = 0.0004$, Fig. S1), so w1 is the only PCA axis that represents systematic climate change. Similarly, we combined pollution data (Table S2: annual emissions of sulphur dioxide, dust and nitrogen oxides) into a single PCA axis (p1). This axis had an eigenvalue greater than 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 (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

11

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 (Turchin 1990; Forchhammer et al. 1998; Price & Hunter 2005), we regressed leafminer per capita rates of change (r = 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 (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 (Royama 1992; Redfern & Hunter 2005; Hunter et

al. 2014) 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 (Royama 1992; Dennis & Taper 1994). 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 (Freckleton et al. 2006; Dennis et al.

2006), we used a simulation extrapolation (SIMEX) procedure (Cook & Stefanski 1994) to

estimate the bias in 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 error on our estimates (See Table S4 for details). While our estimates of density dependence

were generally robust to the effects of simulated error (Table S4), we have used the bias-

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. We analysed the proportions using binomial models with logit link functions in the GENMOD procedure in SAS (Littell et al. 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 (Fig 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

14

Pollution emissions declined over the period of the study (Fig. 2a), with a six-fold decline in $SO_2$ emissions, a halving of dust emissions, and more modest declines in NOx emissions. These simultaneous declines in pollution are reflected in declines in the scores of PCA axis p1 (Year $F_{1,24} = 110.45$, $P < 0.0001$, Fig. 2a insert). In turn, low pollution emissions were correlated with low leafminer densities among years (p1 $F_{1,23} = 5.11$, $P = 0.033$, Fig. 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 $F_{1,24} = 2.77$, $P = 0.1037$, Fig. 2c).

After accounting for the effects of periodic fluctuations in leafminer density using time-series models, there was still no effect of our climate change estimate on leafminer per capita rates of change (PCA 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 $F_{1,20} = 4.38$, $P = 0.0494$).

3.2. Spatial patterns

When averaged across years, leafminer densities declined around 45% with increasing distance from the power plant ($F_{1,12} = 19.76$, $P = 0.0008$, Fig. 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 ($r_S = 0.40$, $n = 14$ sites, $P = 0.15$).

3.3. 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 decreased ($F_{1,12} = 9.95$, $P = 0.0083$), with increasing distance from the power plant (Fig. 4a). At distances greater than 3km from the power plant, rapid and delayed density dependence became equally powerful forces acting on *P. strigulatella* per capita rates of change (Fig. 4a). Because delayed density dependence remained pervasive among sites (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 (Fig. 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 (Figs. 1B-O, Fig. 3). The periodograms from spectral analyses (Fig. 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 (Fig. 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 (Fig. S2).

3.4. Mortality patterns

Across all sites, only 6.2% of *P. strigulatella* larvae survived until pupation in 2017 (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) 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 five-fold with increasing distance from the power plant (Chi-square = 12.62, d.f. = 1, $P$ = 0.0004, Fig. 4b). In contrast, mortality caused by unknown factors declined by about 10% with increasing distance from the power plant (Chi-square = 4.44, d.f. = 1, $P$ = 0.0353, Fig. 4b), driven primarily by failed development early in life (Chi-square = 2.95, d.f. = 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 vary 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 greater than 3km from the power plant (Fig. 4a). 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 (Fig. 4b).

Density dependent processes impose negative feedback, thereby maintaining a limit on population growth (Varley *et al.* 1973; Berryman 1991). However, it is the interaction between density dependent and density independent forces that determines the temporal dynamics of animal populations (Turchin & Hanksi 1997; Forchhammer *et al.* 1998; Stenseth *et al.* 1999; Hunter 2016). While previous studies have focused on the impacts of climatic factors on the form and strength of density dependence (Hunter *et al.* 1997; Stenseth *et al.* 1999; Price & Hunter 2015), 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 reflect differences in the distance from the polluter at which the study was conducted, rather than intrinsic differences based on the species under study.

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 if and how they impose density-dependence on leaf miner populations. The

18

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 (Fig. 4b). High levels of pollution can influence the morphology,

physiology, density, and behavior of ants (Grześ 2010; Eeva et al. 2012; Grześ et al. 2015),

including reducing the aggressiveness of wood ants (Sorvari & Eeva 2010). Likewise, high

pollution levels can compromise the physiology (Geens et al. 2010) and abundance (Eeva et al.

2012; Morelli et al. 2018) of birds. Because both ants and birds can show rapid behavioral and

numerical responses to variation in prey density (Perrins 1979; Holldobler & Wilson 1990), they

may be responsible for the increasing importance of rapid density dependence with increasing

distance from the power plant (Fig. 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 (Turchin & Hanski 1997; Klemola et al. 2002;

Stenseth et al. 2003). 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 (Turchin 1990; Royama 1992), 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 nickel-copper 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 (Fig. 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 (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 (Fig. 1). While we cannot rule out the possibility that density

independent processes generated the apparent cycles in leafminer populations (as demonstrated by Williams & Liebhold 1995; Hunter & Price 1998; Louca & Doebeli 2014), there is no evidence of periodicity in climatic factors over the study period (Fig. 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 explain why. 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 et al. 1999b); 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 gray-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 (Fig. 4a) in concert with
declines in leafminer mortality from unknown causes (Fig. 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 et al. 1994; Price & Hunter 2005. We therefore
suggest that the delayed density dependent force that declined with distance from the polluter
was plant-mediated. However, the possibility remains that other hidden sources of mortality,
such 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 et al. 2016). Predictions suggest that increasing temperatures will cause larger increases in herbivory than in plant productivity (Ayres & Lombardero 2000; O'Connor et al. 2009; DeLucia et al. 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 et al. 2015a,b). However, contrary to expectations, rising temperatures in our study region have not caused significant increases in the population density of *P. strigulatella* (Fig. 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 (Zvereva et al. 2016; Kozlov et al. 2017). 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 (Radhouani et al. 2012; Morelli et al. 2018), insects (Butler & Trumble 2008; Bonisoli-Alquati et al. 2018), and mammals (Fritsch et al. 2010; Drouhot et al. 2014). 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 (Sun & Zhou 2002; Batty & Hallberg 2010). 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.

## Data Accessibility

Data will be made available in the Dryad Digital Repository and the DOI will be provided, should the manuscript be accepted for publication.

## References

Alstad, D.N., Edmunds, G.F. & Weinstein, L.H. (1982). Effects of air pollutants on insect populations. *Annual Review of Entomology,* 27, 369-384.

Altizer, S., Ostfeld, R.S., Johnson, P.T.J., Kutz, S. & Harvell, C.D. (2013). Climate change and infectious diseases: From evidence to a predictive framework. *Science*, 341, 514-519.

Andrewartha, H.G. & Birch, C. (1954). *The distribution and abundance of animals*. Chicago University Press, Chicago.

Ayres, M.P. & Lombardero, M.J. (2000). Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of The Total Environment*, 262, 263-286.

Baltensweiler, W. (1985). Waldsterben: forest pests and air pollution. *Journal of Applied Entomology*, 99, 77-85.

Batty, L.C. & Hallberg, K.B. (2010). Ecology of Industrial Pollution. In: *Ecological Reviews*. Cambridge University Press, Cambridge.

Berryman A.A. (1981). *Population systems: a general introduction*. Plenum, New York.

Berryman, A.A. (1991). Vague notions of density-dependence. *Oikos*, 62, 252-254.

Berryman, A.A., Stenseth, N.C. & Isaev, A.S. (1987). Natural regulation of herbivorous forest insect populations. *Oecologia*, 71, 174-184.

Bjornstad, O.N., Ims, R.A. & Lambin, X. (1999a). Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution*, 14, 427-432.

Bjornstad, O.N., Stenseth, N.C. & Saitoh, T. (1999b). Synchrony and scaling in dynamics of voles and mice in northern Japan. *Ecology*, 80, 622-637.

Bloomfield, P. (2000). Fourier analysis of time series. An introduction. Second edition. John Wiley and Sons, Inc. New York.

Bonisoli-Alquati, A., Ostermiller, S., Beasley, D.A.E., Welch, S.M., Møller, A.P. & Mousseau, T.A. (2018). Faster Development Covaries with Higher DNA Damage in Grasshoppers

(*Chorthippus albomarginatus*) from Chernobyl. *Physiological and Biochemical Zoology*, 91, 776-787.

Box, G., & Jenkins, G. (1970). *Time series analysis: Forecasting and control*. Holden-Day, San Francisco.

Butler, C.D. & Trumble, J.T. (2008). Effects of pollutants on bottom-up and top-down processes in insect–plant interactions. *Environmental Pollution*, 156, 1-10.

Coleman, D.C., Crossley, D.A. & Hendrix, P.F. (2004). *Fundamentals of soil ecology*. Elsevier Academic Press, Amsterdam.

Connor, E.F., Adams-Manson, R.H., Carr, T.G. & Beck, M.W. (1994). The effects of host plant phenology on the demography and population dynamics of the leaf-mining moth, *Cameraria hamadryadella* (Lepidoptera: Gracillariidae). *Ecological Entomology*, 19, 111-120.

Cook, J.R. & Stefanski, L.A. (1994). Simulation-extrapolation estimation in parametric measurement error models. *Journal of the American Statistical Association*, 89, 1314-1328.

DeLucia, E.H., Nabity, P.D., Zavala, J.A. & Berenbaum, M.R. (2012). Climate change: resetting plant–insect interactions. *Plant Physiology*, 160, 1677-1685.

Dennis, B. & Taper, M.L. (1994). Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs*, 64, 205-224.

Dennis, B., Ponciano, J.M., Lele, S.R., Taper, M.L. & Staples, D.F. ( 2006). Estimating density dependence, process noise, and observation error. *Ecological Monographs*, 76, 323-341.

Drouhot, S., Raoul, F., Crini, N., Tougard, C., Prudent, A.-S., Druart, C. *et al.* (2014). Responses of wild small mammals to arsenic pollution at a partially remediated mining site in Southern France. *Science of The Total Environment*, 470-471, 1012-1022.

Eeva, T., Belskii, E., Gilyazov, A.S. & Kozlov, M.V. (2012). Pollution impacts on bird population density and species diversity at four non-ferrous smelter sites. *Biological Conservation*, 150, 33-41.

Forchhammer, M.C., Stenseth, N.C., Post, E. & Langvatn, R. (1998). Population dynamics of Norwegian red deer: density dependence and climatic variation. *Proceedings of the Royal Society of London, Series B*, 265, 341-350.

Freckleton, R.P., Watkinson, A.R., Green, R.E. & Sutherland, W.J. (2006). Census error and the detection of density dependence. Journal of Animal Ecology, 75, 837-851.

Fritsch, C., Cosson, R.P., Cœurdassier, M., Raoul, F., Giraudoux, P., Crini, N. *et al.* (2010). Responses of wild small mammals to a pollution gradient: Host factors influence metal and metallothionein levels. *Environmental Pollution*, 158, 827-840.

Führer, E. (1985). Air pollution and the incidence of forest insect problems. *Journal of Applied Entomology*, 99, 371-377.

Geens, A., Dauwe, T., Bervoets, L., Blust, R. & Eens, M. (2010). Haematological status of wintering great tits (Parus major) along a metal pollution gradient. *Science of The Total Environment*, 408, 1174-1179.

Gouhier, T.C. (2018). Methods for computing spatial, temporal, and spatiotemporal statistics. *CRAN* http://github.com/tgouhier/synchrony.

Grześ, I.M. (2010). Ants and heavy metal pollution – A review. *European Journal of Soil Biology*, 46, 350-355.

Grześ, I.M., Okrutniak, M. & Woch, M.W. (2015). Monomorphic ants undergo within-colony morphological changes along the metal-pollution gradient. *Environmental Science and Pollution Research*, 22, 6126-6134.

Hart, C.W.J. & Fuller, S.L.H. (1979). Pollution ecology of estuarine invertebrates. Academic Press, New York.

Haukioja, E. (1974). Measuring consumption in *Eriocrania* (Eriocraniidae, Lep.) miners with reference to interaction between the leaf and the miner. *Reports of the Kevo Subarctic Research Station*, 11, 16-21.

Holldobler, B. & Wilson, E.O. (1990). *The Ants*. Belknap Press of Harvard University, Cambridge, MA.

Hunter, M.D. (1998). Interactions between *Operophtera brumata* and *Tortrix viridana* on oak: new evidence from time-series analysis. *Ecological Entomology*, 23, 168-173.

Hunter, M.D. (2016). *The phytochemical landscape. linking trophic interactions and nutrient dynamics.* Princeton University Press, Princeton, NJ, USA.

Hunter, M.D. & Price, P.W. (1998). Cycles in insect populations: delayed density dependence or exogenous driving variables? *Ecological Entomology*, 23, 216-222.

Hunter, M.D., Kozlov, M.V., Itämies, J., Pulliainen, E., Bäck, J., Kyrö, E.-M. *et al.* (2014). Current temporal trends in moth abundance are counter to predicted effects of climate change in an assemblage of subarctic forest moths. *Global Change Biology*, 20, 1723-1737.

Hunter, M.D., Varley, G.C. & Gradwell, G.R. (1997). Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: A classic study revisited.

*Proceedings of the National Academy of Sciences of the United States of America*, 94, 9176-9181.

Jamieson, M.A., Schwartzberg, E.G., Raffa, K.F., Reich, P.B. & Lindroth, R.L. (2015). Experimental climate warming alters aspen and birch phytochemistry and performance traits for an outbreak insect herbivore. *Global Change Biology*, 21, 2698-2710.

Klemola, T., Tanhuanpaa, M., Korpimäki, E. & Ruohomäki, K. (2002). Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos*, 99, 83-94.

Kozlov, M.V. (2003). Density fluctuations of the leafminer *Phyllonorycter strigulatella* Lepidoptera: Gracillariidae) in the impact zone of a power plant. *Environmental Pollution*, 121, 1-10.

Kozlov, M.V. & Zvereva, E.L. (2015). Changes in the background losses of woody plant foliage to insects during the past 60 years: are the predictions fulfilled? *Biology Letters*, 11, 20150480.

Kozlov, M.V., Zvereva, E.L. & Zverev, V. (2009). *Impacts of point polluters on terrestrial biota: comparative analysis of 18 contaminated areas*. Springer, Dordrecht.

Kozlov, M.V., Stekolshchikov, A.V., Söderman, G., Labina, E.S., Zverev, V. & Zvereva, E.L. (2015a). Sap-feeding insects on forest trees along latitudinal gradients in northern Europe: a climate-driven pattern. *Global Change Biology*, 21, 106-116.

Kozlov, M.V., Lanta, V., Zverev, V.E. & Zvereva, E.L. (2015b). Global patterns in background losses of woody plant foliage to insects. *Global Ecology & Biogeography*, 24, 1126-1135.

Kozlov, M.V., Zverev, V. & Zvereva, E.L. (2017). Combined effects of environmental
    disturbance and climate warming on insect herbivory in mountain birch in subarctic
    forests: results of 26-year monitoring. *Science of the Total Environment*, 601-602, 802-
    811.

Lack, D. (1954). *The natural regulation of animal numbers.* Clarendon Press, Oxford, UK.

Liebhold, A.M., Johnson, D.N. & Bjornstad, O.N. (2006). Geographic variation in density-
    dependent dynamics impacts the synchronizing effect of dispersal and regional
    stochasticity. *Population Ecology*, 48, 131-138.

Littell, R.C., Stroup, W.W. & Freund, R.J. (2002). *SAS for Linear Models*. 4th edn. SAS
    Institute, Cary, New York.

Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: Neutral and
    nonneutral community dynamics in fluctuating environments. *The American Naturalist*,
    172, E48-E66.

Louca, S. & Doebeli, M. (2014). Distinguishing intrinsic limit cycles from forced oscillations in
    ecological time series. *Theoretical Ecology*, 7, 381-390.

Marshall, G.J., Vignols, R.M. & Rees, W.G. (2016). Climate change in the Kola Peninsula,
    Arctic Russia, during the last 50 years from meteorological observations. *Journal of
    Climatology*, 29, 6823-6840.

Mirsal, I. (2008). *Soil Pollution. Origin, Monitoring, & Remediation*. Springer-Verlag, Berlin.

Morelli, F., Benedetti, Y., Mousseau, T.A. & Møller, A.P. (2018). Ionizing radiation and
    taxonomic, functional and evolutionary diversity of bird communities. *Journal of
    Environmental Management*, 220, 183-190.

Nicholson, A.J. & Bailey, V.A. (1935). The Balance of Animal Populations.Part I. . *Proceedings of the Zoological Society of London*, 105, 551-598.

O'Connor, M.I. (2009). Warming strengthens an herbivore-plant interaction. *Ecology*, 90, 388-398.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.

Perrins, C.M. (1979). *British Tits*. Collins, London, UK.

Price, P.W. & Hunter, M.D. (2005). Long-term population dynamics of a sawfly show strong bottom-up effects. *Journal of Animal Ecology*, 74, 917-925.

Price, P.W. & Hunter, M.D. (2015). Population dynamics of an insect herbivore over 32 years are driven by precipitation and host-plant effects: Testing model predictions. *Environmental Entomology*, 44, 463-473.

Radhouani, H., Poeta, P., Gonçalves, A., Pacheco, R., Sargo, R. & Igrejas, G. (2012). Wild birds as biological indicators of environmental pollution: antimicrobial resistance patterns of Escherichia coli and enterococci isolated from common buzzards (*Buteo buteo*). *Journal of Medical Microbiology*, 61, 837-843.

Redfern, M. & Hunter, M.D. (2005). Time tells: long-term patterns in the population dynamics of the yew gall midge, *Taxomyia taxi* (Cecidomyiidae), over 35 years. *Ecological Entomology*, 30, 86-95.

Riemer J. & Whittaker, J.B. (1989). Air pollution and insect herbivores: observed interactions and possible mechanisms. In: Bernays, E.A. (ed) *Insect-plant interactions*. CRC, Boca Raton, Florida, USA, pp 73–105.

Royama, T. (1992). *Analytical Population Dynamics*. Springer, New York.

Sas Institute, I. (2009). *SAS User's Guide*. SAS Institute, Cary, NY.

Selikhovkin, A.V. (1988). Impact of industrial aerial pollution on herbivorous insects. In: Narchuk, E.P. (ed.), *Lectures on 39th annual meeting in memory of N.A. Cholodkovsky*. Nauka, Leningrad, pp. 3-42 (in Russian).

Sorvari, J. & Eeva, T. (2010). Pollution diminishes intra-specific aggressiveness between wood ant colonies. *Science of The Total Environment*, 408, 3189-3192.

Stenseth, N.C., Chan, K.-S., Tong, H., Boonstra, R., Boutin, S., Krebs, C.J. *et al.* (1999). Common Dynamic Structure of Canada Lynx Populations Within Three Climatic Regions. *Science*, 285, 1071-1073.

Stenseth, N.C., Viljugrein, H., Saitoh, T., Hansen, T.F., Kittilsen, M.O., Bolviken, E. & Glockner, F. (2003). Seasonality, density dependence, and population cycles in Hokkaido voles. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 11478-11483.

Sun, T. & Zhou, Q. (2002). Retrospect and prospect of pollution ecology. *The journal of applied ecology*, 13, 221-223.

Turchin, P. (1990). Rarity of density dependence or population regulation with lags? *Nature*, 344, 660-663.

Turchin, P. & Hanski, I. (1997). An empirically based model for latitudinal gradient in vole population dynamics. *American Naturalist*, 149, 842-874.

Valtonen, A., Leinonen, R., Pöyry, J., Roininen, H., Tuomela, J. & Ayres, M.P. (2014). Is climate warming more consequential towards poles? The phenology of Lepidoptera in Finland. *Global Change Biology*, 20, 16-27.

Varley, G.C., Gradwell, G.R. & Hassell, M.P. (1973). *Insect population ecology: An analytical approach*. Blackwell Scientific Publications Oxford, UK.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002). Ecological responses to recent climate change. *Nature*, 416, 389-395.

Williams, D.W. & Liebhold, A.M. (1995). Detection of delayed density dependence: effects of autocorrelation in an exogenous factor. *Ecology*, 76, 1005-1008.

Wulff, F.V., Rahm, L.A. & Larsson, P. (2001). A Systems Analysis of the Baltic Sea. Springer-Verlag Berlin.

Zvereva, E.L. & Kozlov, M.V. (2010). Responses of terrestrial arthropods to air pollution: a meta-analysis. *Environmental Science & Pollution Research*, 17, 297-311.

Zvereva, E.L., Hunter, M.D., Zverev, V. & Kozlov, M.V. (2016). Factors affecting population dynamics of leaf beetles in a subarctic region: The interplay between climate warming and pollution decline. *Science of the Total Environment*, 566-567, 1277-1288.

# Figure Legends

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, northwestern Russia. (B-O) Densities (log scale) at each of the 14 study sites, ordered by increasing distance from the power plant. Horizontal lines represent mean densities at each site.

Figure 2. (A) Temporal declines in pollution emissions from a coal fired power plant near Apatity, northwestern 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.

Figure 3. Densities of the leafmining moth, *Phyllonorycter strigulatella*, decline with increasing distance from a coal fired power plant near Apatity, northwestern 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.

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, northwestern 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.
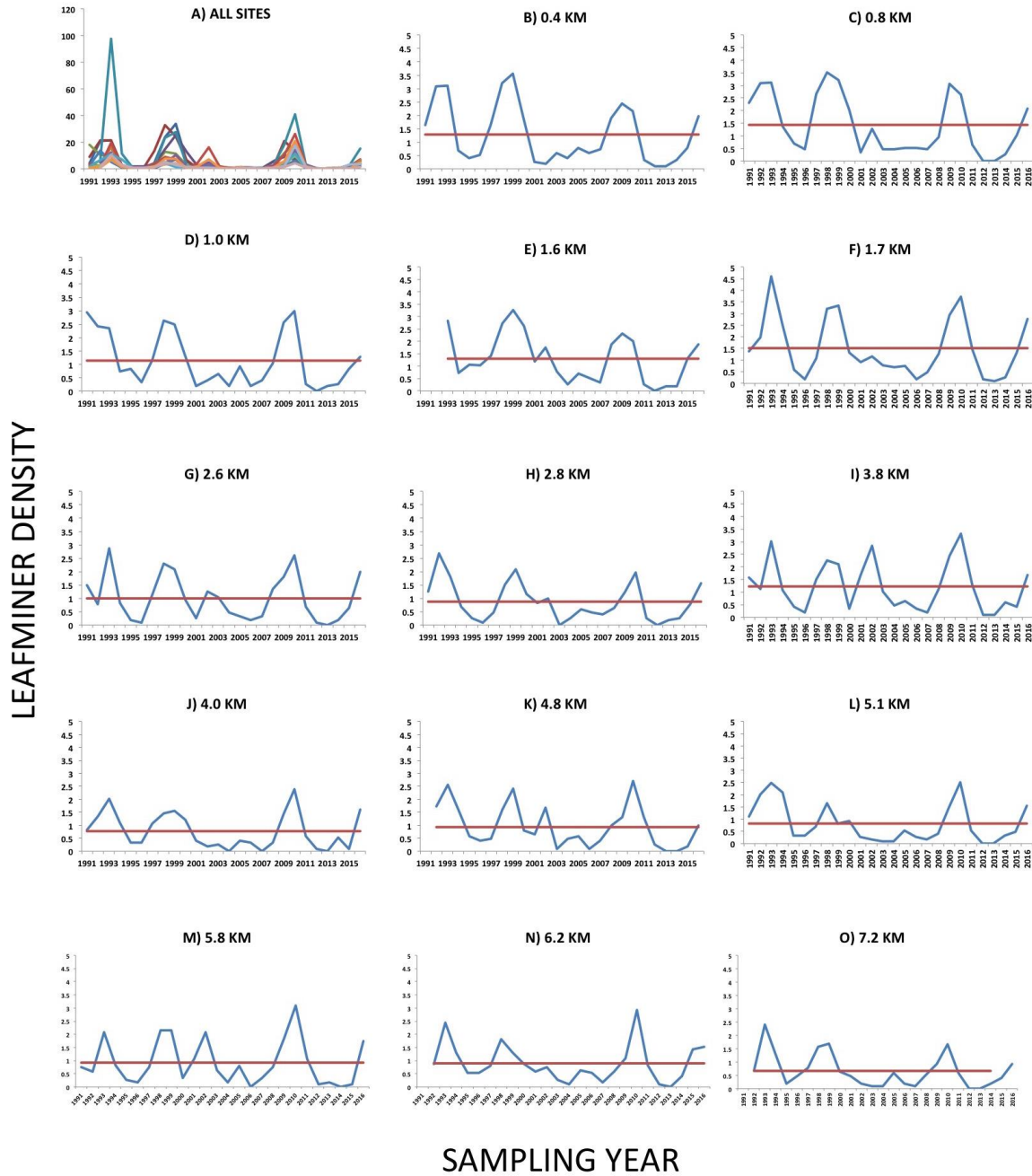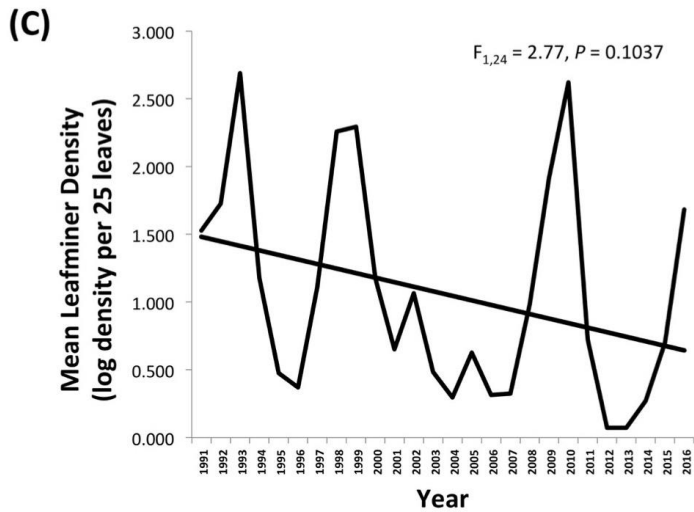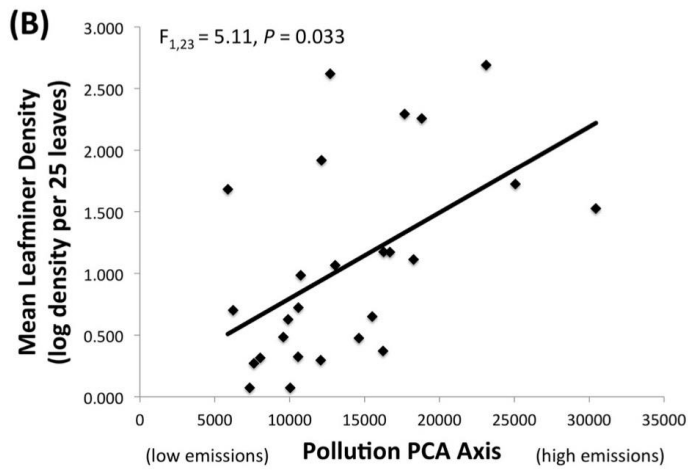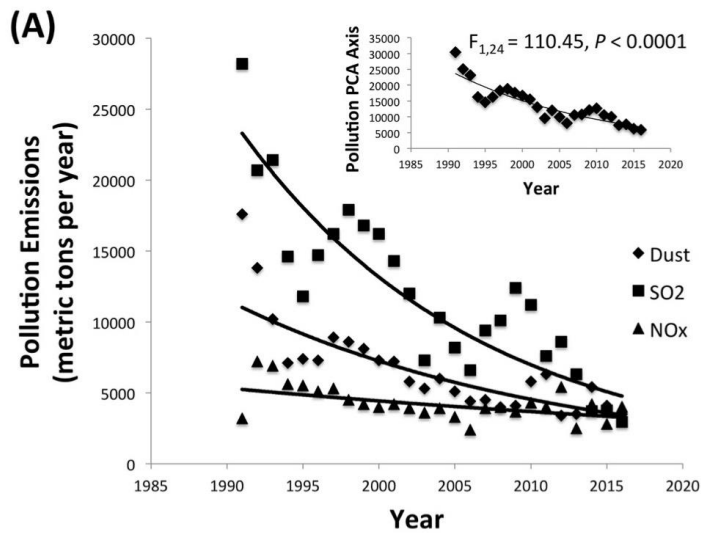
Figure 1.

Figure 2.



(A)

$F_{1,24} = 110.45, P < 0.0001$

(B)

$F_{1,23} = 5.11, P = 0.033$

(C)

$F_{1,24} = 2.77, P = 0.1037$

Figure 3.



$F_{1,12} = 19.76$, $P = 0.0008$

Figure 4.

**(A)**



**(B)**