Received: 14 February 2019 | Accepted: 25 February 2019
DOI: 10.1111/1365-2656.12992

IN FOCUS

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

Air pollution as an experimental probe of insect population dynamics

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Handling Editor: Jennifer Gill

Abstract

In Focus: Hunter, M. D., & Kozlov, M. V. (2019) The relative strengths of rapid and delayed density-dependence acting on a terrestrial herbivore change along a pollution gradient. *Journal of Animal Ecology, 88*, 665–676.

Teasing apart the interactions between biotic and abiotic factors affecting animal population dynamics is a difficult task when based solely on the analysis of natural populations. Experimental manipulations of systems using microcosm studies can be powerful tools for probing such interactions, but microcosms are ultimately limited by their lack of complexity compared with nature. Hunter and Kozlov (2019) take a novel field-based experimental approach to studying abiotic influences on biotic interactions by quantifying how the presence of a pollutant source alters biotic processes driving populations of a forest leaf miner. They find that populations in proximity to a pollutant source show weaker direct density dependence and stronger delayed density dependence than more distant populations unaffected by pollution. These differences in density dependence cause higher equilibrium densities near the pollution source but surprisingly they do not alter leaf miner oscillatory dynamics. This creative study provides useful insight into how abiotic forces alter biotic population processes and how density dependence shapes the spatial dynamics of animal populations.

KEYWORDS
abiotic factors, density dependence, ecological experiment, generalist predator, pollution

The quest to understand the processes driving temporal changes in animal abundance has been a pursuit of ecologists for many years but remains only partially resolved. The role of biotic vs. abiotic factors is central to this problem, but often difficult to disentangle. During the first half of the 20th century, there was great debate over which of these factors played a more important role but a general consensus emerged that both biotic and abiotic factors interact to produce observed dynamic patterns (Berryman, 1999; Royama, 2012). Nevertheless, the way in which these factors interact is often not clear and an ability to predict interactions would improve our understanding of climate change impacts on animal population dynamics. While empirical studies have shed considerable light on this problem, experimental approaches are needed to fully understand these interactions.

In this issue, Hunter and Kozlov (2019) exploit a "fortuitous" experiment, the construction of a massive coal-fired power plant that has altered adjoining birch–alder forests, to test how such an abiotic influence alters the biotic density-dependent dynamics of a leaf-mining insect species (Figure 1). *Phyllonorycter strigulatella* is a common leaf miner on speckled alder and exhibits quasi-regular population oscillations through much of the Russian taiga. The 415-megawatt power plant, built in 1959, has historically emitted 20,000–30,000 metric tons of SO_2 per year as well as copious amounts of Fe, Zn, Cr, Cd and Pb into the atmosphere; these pollutants affect various components of nearby forest ecosystems, including speckled alder, insect predators and indirectly affect leaf miners. From 26 years of sampling at 14 sites at varying distances around

FIGURE 1 (a) The Apatitskaya coal-fired plant is the largest thermal power plant in the Murmansk region of northwest Russia (photograph by Vitali Zverev). (b) Blotch leaf mine created by *Phyllonorycter strigulatella* (photograph by Aleksandrs Balodis, licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license). (c) Adult *P. strigulatella* (photograph by Ilia Ustyantsev, licensed under the Creative Commons Attribution-Share Alike 2.0 Generic license)

the factory, Hunter and Kozlov (2019) found that the strength of direct density dependence increased with distance from the plant, while the importance of delayed density dependence decreased. Parallel with these trends, they found that predation by generalist predators increased with distance from the plant. They hypothesize that observed patterns of spatial variation in density dependence are caused by pollution adversely affecting populations of generalist predators. Another fascinating result was that there was a strong spatial trend of declining leaf miner abundance with increasing distance from the plant. Apparently, the diminished direct density dependence associated with proximity to the plant causes populations to equilibrate at higher levels in areas that experience great pollution levels. The tendency of air pollution to trigger higher densities has previously been observed in several systems but mechanisms for such trends have largely remained mysterious (Führer, 1985).

Recognizing the need for a more experimental approach to the study of population ecology, many researchers have used microcosm experiments to explore interactions between abiotic influences and density-dependent processes (Benton, Solan, Travis, & Sait, 2007). For example, microcosm experiments have shed light into interactions of pollution with density-dependent predation (Gergs, Zenker, Grimm, & Preuss, 2013), resource quality (Hanazato & Hirokawa, 2004) and resource quantity (Takahashi & Hanazato, 2007). In a recent microcosm study, Reyes, Ramos-Jiliberto, Arim, and Lima (2018) found that exposure of *Daphnia* to pollutants altered the effect of predator host size specificity on equilibrium dynamics. Experimental manipulations in such microcosm studies provide insight into the way abiotic factors (such as pollution and climate change) alter density-dependent biotic population interactions but the value of such studies is ultimately constrained by the unrealistic simplicity of experimental settings (Carpenter, 1996). Exploitation of large-scale field "experiments", as carried out by Hunter and Kozlov (2019), offers insight that otherwise is not possible in microcosm experiments.

In other systems, there has been a success in quantifying variation in the strength of density dependence in relation to naturally occurring variation in abiotic factors and this has contributed to our knowledge of the role these density-dependent factors play in producing observed population behaviour. For example, generalist predators are a major cause of direct density dependence in host populations but their diversity and abundance typically decrease across gradients from warm to cold climates (Turchin & Hanski, 1997). This phenomenon is believed to be responsible for observed gradients in the strength of direct density dependence in small mammals (Lambin, Petty, & Mackinnon, 2000; Stenseth, Bjørnstad, & Saitoh, 1996) and forest insects (Klemola, Tanhuanpää, Korpimäki, & Ruohomäki, 2002). In these systems, gradients in periodicity are also typically found to be coincident with the gradient in density dependence. However, in the density dependence gradient observed in leaf miner populations observed by Hunter and Kozlov (2019), no corresponding gradient in population periodicity was found. Relatively strong spatial synchrony was observed among densities of these periodically oscillating leaf miner populations. Spatial synchrony can arise either from dispersal among populations or from regional (synchronous) stochastic effects (Liebhold, Koenig, & Bjørnstad, 2004). In most systems, it is difficult to determine which of these play a more dominant role in synchronizing populations and similarly the cause of synchrony in this leaf miner system remains unknown. However, it is interesting to speculate that the unknown factor that is driving synchrony in this system may also be forcing geographical homogeneity in periodicity despite the gradient in density dependence, a phenomenon predicted by theoretical studies (Liebhold, Johnson, & Bjørnstad, 2006).

The study by Hunter and Kozlov (2019) provides a good example of how unintended alteration of ecological communities can be exploited as accidental ecological experiments. In this system, the novel approach yielded new insight into how generalist predator abundance affects the population dynamics of herbivore populations. In the future, as humans continue to alter their environment, other opportunities for exploiting similar ecological experiments may arise and provide useful insight into basic ecological problems (Lee, 1998).

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REFERENCES

Benton, T. G., Solan, M., Travis, J. M., & Sait, S. M. (2007). Microcosm experiments can inform global ecological problems. *Trends in Ecology & Evolution*, *22*, 516–521.

Berryman, A. A. (1999). *Principles of population dynamics and their application*. Cheltenham, UK: Stanley Thornes.

Carpenter, S. R. (1996). Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology*, *77*, 677–680.

Führer, E. (1985). Air pollution and the incidence of forest insect problems. *Zeitschrift für Angewandte Entomologie*, *99*, 371–377.

Gergs, A., Zenker, A., Grimm, V., & Preuss, T. G. (2013). Chemical and natural stressors combined: From cryptic effects to population extinction. *Scientific Reports*, *3*, 2036.

Hanazato, T., & Hirokawa, H. (2004). Changes in vulnerability of *Daphnia* to an insecticide application depending on the population phase. *Freshwater Biology*, *49*, 402–409.

Hunter, M. D., & Kozlov, M. V. (2019) The relative strengths of rapid and delayed density-dependence acting on a terrestrial herbivore change along a pollution gradient. *Journal of Animal Ecology*, *88*, 665–676.

Klemola, T., Tanhuanpää, 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.

Lambin, X., Petty, S. J., & Mackinnon, J. L. (2000). Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, *69*, 106–119.

Lee, J. A. (1998). Unintentional experiments with terrestrial ecosystems: Ecological effects of sulphur and nitrogen pollutants. *Journal of Ecology*, *86*, 1–12.

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

Liebhold, A., Koenig, W. D., & Bjørnstad, O. N. (2004). Spatial synchrony in population dynamics. *Annual Review of Ecology Evolution & Systematics*, *35*, 467–490.

Reyes, C. A., Ramos-Jiliberto, R., Arim, M., & Lima, M. (2018). Disentangling demographic co-effects of predation and pollution on population dynamics. *Oikos*, *128*, 286–296.

Royama, T. (2012). *Analytical population dynamics*. London, UK: Chapman & Hall.

Stenseth, N. C., Bjørnstad, O. N., & Saitoh, T. (1996). A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proceedings of the Royal Society of London B*, *263*, 1117–1126.

Takahashi, H., & Hanazato, T. (2007). Synergistic effects of food shortage and an insecticide on a Daphnia population: Rapid decline of food density at the peak of population density reduces tolerance to the chemical and induces a large population crash. *Limnology*, *8*, 45–51.

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

How to cite this article: Liebhold AM. Air pollution as an experimental probe of insect population dynamics. *J Anim Ecol*. 2019;88:662–664. https://doi.org/10.1111/1365-2656.12992