Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in
Insect Science

Population dynamics of herbivorous insects in polluted landscapes

Mikhail V Kozlov

Environmental pollution is one cause of insect decline in the Anthropocene, but the underlying mechanisms remain obscure due to a paucity of pollution-impact studies on insects that address density-dependent processes. Long data series (19–26 years) are available only for a few species monitored around two industrial polluters in north-western Russia. A particularly exciting current finding is that industrial pollution determines the relative strength of rapid (stabilising) and delayed (destabilising) density dependence operating on a herbivore population. Most studies address acute effects of traditional pollutants (e.g. sulphur dioxide and trace elements) and nitrogen deposition on agricultural pests, whereas the effects of realistic concentrations of ozone, particulate matter and emerging pollutants on insects feeding on noncultivated plants are unknown. The accumulated evidence remains insufficient to predict the effects of pollutants of global concern on the population dynamics of herbivorous insects.

Address
Department of Biology, University of Turku, 20014 Turku, Finland

Corresponding author: Mikhail V Kozlov (mikoz@utu.fi)

Current Opinion in Insect Science 2022, **54**:100987

This review comes from a themed issue on **Ecology**

Edited by **Kyle Haynes, Derek Johnson** and **Andrew Liebhold**

For complete overview about the section, refer “Ecology 2023”

Available online 25th October 2022

https://doi.org/10.1016/j.cois.2022.100987

Introduction

Pollution, the introduction of contaminants into an environment that causes instability, disorder, harm or discomfort to the physical systems or living organisms, has long been recognised as a serious environmental and social problem. The current generation has inherited large areas disturbed or destroyed by industrial pollution, and the destruction continues today in many countries [1]. However, industrial development, environmental legislation and public attitude during the past 10–20 years have shifted the focal research topics of pollution ecology from the exploration of acute local damage caused by traditional pollutants (e.g. sulphur dioxide, fluorine and trace elements) associated with large industrial enterprises (Figure 1) to studies of the regional effects of ozone (O_3), nitrogen (N) deposition, particulate matter (PM) and several groups of emerging pollutants [2•].

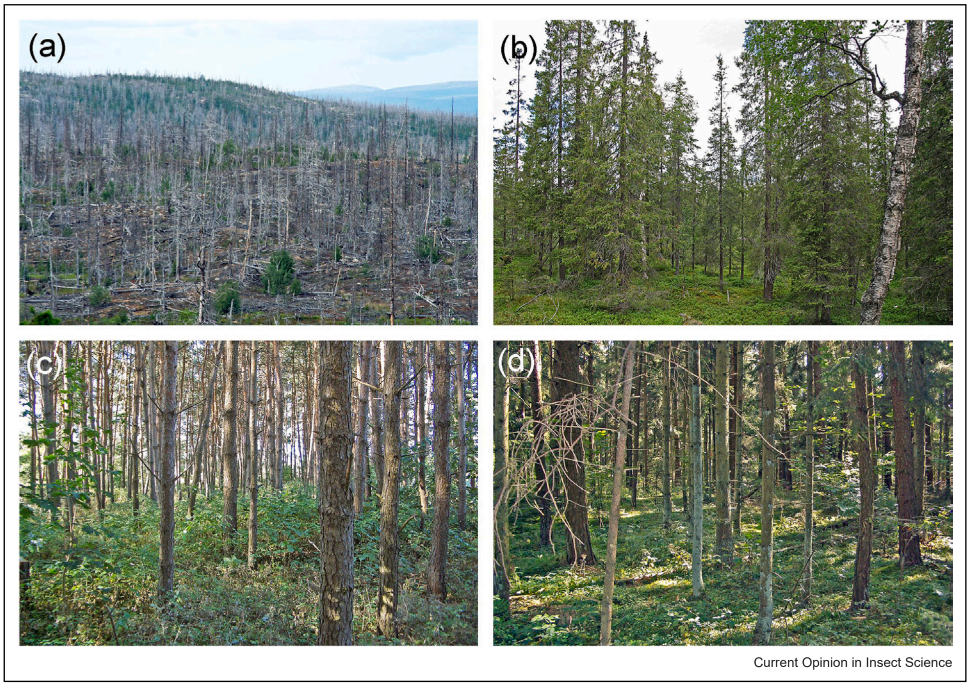
Environmental pollution is a major driver of global biodiversity decline [3], including losses of insect diversity and abundance [4]. However, pollution-related concerns are primarily linked with excessive use of pesticides and fertilisers, along with light and noise pollution [5,6]. By contrast, photochemically formed ground-level ozone and industrial pollutants — despite their global importance [2•] and overall negative impact on biodiversity [7] — are rarely considered in conservation planning and management [8]. The neglect of chemical pollution in insect-conservation agendas likely reflects the shortage of empirical information regarding pollutant effects on insect community structure and dynamics [9•]. Here, I summarise the current findings on chemical pollutant effects on fecundity, mortality, migration and other factors that directly or indirectly affect insect population dynamics (Figure 2).

Despite the overall adverse effects of pollutants on insect fitness, abundance and diversity [10,11], industrial pollution was repeatedly reported to favour many plant-feeding species, particularly forest pests [12,13]. Meta-analysis confirmed a consistent increase in herbivorous insect abundance near industrial polluters [11], although this effect may be overestimated due to various biases in published data [1]. Here, I focus on factors affecting variations in herbivorous insect responses to chemical pollution.

Changes in herbivore population dynamics

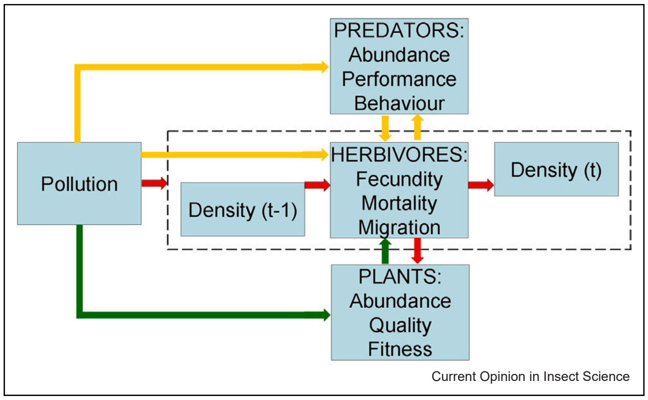
Exploration of pollution effects on population dynamics requires simultaneous monitoring of several populations, replicated within both polluted and unpolluted regions over multiple (preferably 30–40) generations, coupled with monitoring and/or manipulation of factors potentially affecting the study population density and structure. Not surprisingly, data of this kind are limited to a few herbivorous insect species. A search in the ISI Web of Science Core Collection on 9 July 2022 for insect* AND herbivor* AND pollut* AND ‘population dynamic*’ revealed only 11 studies of direct relevance to

Figure 1



Examples of pollution-induced transformation of forested landscapes. **(a)** Industrial barren located 4 km S of the copper–nickel smelter at Monchegorsk, north-western Russia, which had evolved from spruce forest **(b)** following 80 years of severe impacts of sulphur dioxide and deposition of trace elements. **(c)** Scots pine forest with extensive nitrophilous vegetation located 1 km W of the fertiliser factory at Jonava, Lithuania, which had evolved from forest with low-stature, sparse field-layer vegetation **(d)** following 40 years of intensive deposition of nitrogen-containing emissions. Photo: V. Zverev.
Reproduced with permission from [1].

Figure 2



The relative level of knowledge (green: high; yellow: intermediate; red: low) on direct and indirect impacts of chemical pollution on individual and population characteristics of insect herbivores. The effects of pollution on the resulting population dynamics (within the dashed box) are illustrated as changes in herbivore population density between generation t-1 and generation t shaped by a combination of density-dependent and density-independent processes. The figure reflects the author's subjective opinion on the relative numbers of case studies addressing individual links and on the consistency between the results of these studies. This opinion is based on all evidence on this topic.

the present review topic, and only one of these studies [14•] appeared in the past five years.

Pollution impacts on herbivore population dynamics are best exemplified in a willow-feeding leaf beetle, *Chrysomela lapponica*, as multiple populations have been monitored for over 20 years at different distances from a copper–nickel smelter in subarctic European Russia. Spring and fall temperatures increased by 2.5–3 °C during the observation period, while smelter emissions of sulphur dioxide and heavy metals decreased fivefold. Despite a discovered increase in host-plant quality with increased temperatures, the *C. lapponica* density showed a rapid 20-fold decline in the early 2000s, remaining at very low levels thereafter. Time-series analysis and model selection indicated an association between this abrupt population decline and the smelter's decreased aerial emissions, and this was explained by increases in insect mortality from natural enemies as a consequence of climate warming and declining pollution [15•].

Consistent with these results, 26 years of monitoring of an eruptive leafmining moth, *Phyllonorycter strigulatella*, at 14 sites located at different distances from a coal-fired power plant near Apatity, north-western Russia, revealed a decrease in the strength of rapid density dependence but an increase in the strength of delayed density dependence with decreasing distance from the pollution source [14•]. This is the most exciting current finding regarding pollution impacts on the landscape-level population dynamics of plant-feeding insects, because it suggests that insect herbivore outbreaks in polluted environments can reflect a weakening of rapid (stabilising) density dependence relative to delayed (destabilising) density dependence [14•].

Population densities of insects feeding on birch leaves demonstrated variable, and sometimes opposite, responses to industrial pollution gradients near the Monchegorsk copper–nickel smelter [16]. The response direction and strength are linked with herbivore life history traits: the abundances of oligophagous and polyphagous moth and butterfly species that fed externally on plants and hibernated as larvae generally declined near the smelter, whereas the abundances of monophagous Lepidoptera species that fed inside live plant tissues and hibernated as imagoes or pupae were unaffected by pollution [9•].

We know of no study reporting long-term observations on the abundance of herbivorous insects and/or on the intensity of herbivory in spatial gradients of O_3, N or PM (except for dust containing trace elements). Therefore, the landscape-level effects of these pollutants on plant-feeding insects can only be predicted from accumulated evidence of their direct and indirect impacts on insect fecundity, survival and dispersal.

Changes expected from direct pollutant effects on herbivores

The direct impact of chemical pollutants on the individual performance of herbivorous insects is generally negative [11], especially when pollutant-contaminated food is ingested. The most representative information is accumulated for trace elements. Realistic concentrations of lead, zinc, manganese and cadmium reduce larval growth, survival and/or fecundity in several moth and beetle species [17–20]. However, these effects are often species-specific: zinc in an artificial diet reduced monarch butterfly (*Danaus plexippus*) survival but enhanced cabbage white butterfly (*Pieris rapae*) survival [21]. Similarly, the same manganese concentrations applied to birch leaves affected food consumption by *Cabera pusaria* [22] but not by *Phyllobius arborator* [23]. The sources of this variation should be identified to broaden our understanding of pollution tolerance in insect species of conservation concern.

Airborne PM is a significant threat to human health, but PM deposition effects on plant-feeding insects are insufficiently understood. Feeding on leaves of *Prunus padus* and *P. serotina* artificially dusted with cement and roadside PM decreased the performance of the leaf beetle *Gonioctena quinquepunctata* [24]. Similarly, consumption of gypsum- and coal-dusted leaves by *Gloveria medusa* [25] and *Helicoverpa armigera* larvae [26], as well as exposure of *Bicyclus anynana* butterfly larvae to artificially generated smoke [27], significantly increased insect mortality. Conversely, external treatment of *G. medusa* larvae with PM [25] and tarsal contact of *Oncopeltus fasciatus* with TiO_2 and Al_2O_3 nanoparticles [28] did not modify their survival or fecundity.

Most data on high O_3 toxicity for insects originate from studies using O_3 to control stored-product pests, and these studies generally use O_3 concentrations that exceed concentrations observed in nature by factors of 100–10 000 [29]. However, realistic O_3 episodes (80 ppb and greater) also increase the mortality of tiny insects [30].

Pollution was recently demonstrated to dampen insect migratory abilities. The distance covered by adults painted lady butterflies (*Vanessa cardui*) declined by 65% during the first 20 min of flying in air polluted with combustion-generated PM2.5, and flight speed strongly declined with increases in airborne PM2.5 concentration [31•]. Similarly, short-term O_3 exposure (80–200 ppb) decreased motility of the fig wasp *Blastophaga psenes* [30]. Combined with a strong positive correlation between concentrations of trace elements (nickel and copper) in butterflies and in plants within the Monchegorsk pollution gradient [32], these results suggest that migration to or from polluted sites contributes little to herbivore population dynamics compared with pollution effects on insect fecundity and mortality.

Changes expected from feeding on polluted plants (bottom-up effects)

The current studies addressing indirect effects of pollutants on herbivorous insects are dominated by the effects of N fertilisation on host-plant quality. This dominance is likely explained by N being the primary limiting nutrient of herbivorous insects [33] and N deposition having an increasing global importance in natural and agricultural ecosystems [2•].

The brown rice planthopper *Nilaparvata lugens* showed greater fecundity when feeding on N-fertilised than on nonfertilised rice plants [34•]. *Tuta absoluta* miners produced more eggs and had a higher intrinsic rate of population increase when they developed in leaves from N-fertilised plants than in leaves from nonfertilised plants [35]. Consistently, N fertilisation increased population growth rates of two aphid species, *Sitobion avenae* and *Acyrthosiphon pisum* [36]. Conversely, N fertilisation decreased larval survival in six butterfly species, although the underlying mechanisms remain unknown [37]. A decrease in survival and reproduction of a locust, *Oedaeleus senegalensis*, feeding on N-fertilised plants, was associated with an increasing plant protein-to-carbohydrate ratio [38].

Exposure of host plants to O_3 induces diverse responses in insect herbivores. In a choice experiment, Eri silkmoth (*Samia ricini*) larvae did not distinguish between plants exposed to ambient and elevated O_3 concentrations (20 ppb vs. 55 ppb), but larval growth was inhibited, whereas mortality was unaffected, by feeding on plants exposed to elevated O_3 [39•]. By contrast, growth of *Chrysomela populi* on poplar leaves exposed to 80-ppb O_3 increased relative to control leaves, but this effect was significant only on one of two poplar clones [40•]. When given the choice, *Pieris brassicae* butterflies laid 49% fewer eggs on plants exposed to 120-ppb O_3 than on control plants. Consistently, O_3 decreased the growth of *P. brassicae* larvae, but only at high temperatures, whereas egg survival was greater on O_3-exposed than on control plants [41].

Reactive N from human sources (e.g. NO_2) is taken up by plant roots following deposition in soils, but it can also be assimilated by leaves directly from the atmosphere. This assimilation was recently found to increase the N-based defensive metabolites in leaves of *Nicotiana tabacum* and consequently reduce food consumption and growth of tobacco hornworm (*Manduca sexta*) larvae [42].

The accumulated evidence suggests that the bottom-up effects of pollutants on individual and population performance of plant-feeding insects are more variable than the direct effects, ranking from strongly positive to strongly negative. The sources of this variation require further exploration to allow justified generalisations regarding possible consequences of these effects for herbivore population dynamics.

Changes expected from pollution effects on predators and parasitoids (top-down effects)

An increase in herbivorous insect abundance in polluted areas is routinely explained by a combination of beneficial changes in host-plant quality (discussed above) and enemy-free space (i.e. decreased abundance of natural enemies) [10,14•,15•,43]. However, meta-analysis revealed that a significant overall decrease in abundance of predatory invertebrates with an increase in industrial pollution was driven by a rapid decline in epigeic predators. By contrast, the abundance of predators feeding in plant canopies (e.g. wasps, ladybirds, bugs and hoverfly larvae) was independent of the pollution load [11].

Recent studies demonstrated that pollution may both enhance and weaken top-down control on insect herbivores. In particular, N fertilisation can increase prey nutritional quality to the point that it alters predator foraging and feeding behaviour, resulting either in slower rates of prey (*Aphis gossypii*) consumption and longer prey handling times by ladybugs (*Hippodamia variegate*) [44] or in increased fecundity and longevity of parasitic wasps (*Habrobracon hebetor*) feeding on tomato fruit worm (*Helocoverpa armigera*) larvae [45•]. Both zinc and N transferred through food chains increased predator (*Harmonia axyridis* ladybug) mortality [46], thereby releasing aphids (*Aphis medicaginis* and *Acyrthosiphon pisum*) from top-down control. Nitrogen benefited both brown rice planthoppers and predatory mirid bugs (*Cyrtorhinus lividipennis*), however, the difference in N effects on these species resulted in weakening of top-down control of the planthopper by the mirid bug as rice leaf N concentrations increased [34•]. Similarly, high N fertilisation releases cereal aphids (*Sitobion arvense* and *Rhopalosiphym padi*) from the control of Aphidiinae parasitoids [47].

The only study of pollution impacts on mutualistic interactions revealed a positive effect of N enrichment on the abundance of sap-feeding insects (aphids, mealybugs and treehoppers) that are mutualist partners of predaceous ants (primarily *Formica obscuripes*). The abundance of ants in N-treated plants did not change, nevertheless, ants provided greater antipredator protection for mutualist herbivores on these plants than on control plants [48].

The uncertainties in predicting pollution impacts on herbivore population dynamics via top-down control are enhanced by the recent finding that the ratio between rapid (stabilising) and delayed (destabilising) density dependence is more important than the absolute intensity of the top-down impact [14•]. This interplay between different forces shaping herbivore population dynamics stresses the need for simultaneous exploration of pollution impacts on both bottom-up and top-down drivers.

Methodological implications

Disturbance-induced changes in ecosystems are a central concern in ecology, and from this perspective, the impacts of pollutants on natural ecosystems can be seen as unintentional large-scale disturbance experiments. Ecologists can make use of the results of these experiments to pinpoint the factors that affect the resilience of community structures and ecosystem functions [49]. However, researchers preferentially use results from unintentional experiments associated with extreme levels of industrial pollutants (as illustrated by Figure 1a, c). Consequently, the current shift in research priorities of pollution-oriented studies [2•] has greatly decreased the number of unintentional experiments that can be used to explore pollution effects on natural communities, because spatial gradients of O_3, N and PM are generally much shallower than spatial gradients of traditional industrial pollutants and are rarely accompanied by landscape-level changes, such as forest decline. Nevertheless, regions with elevated N deposition can be used as testing grounds to study herbivorous insect population dynamics and particularly the effects of microclimatic cooling triggered by N-induced increases in plant biomass [50,51•].

Research needs and future directions

Despite decades of research, we know surprisingly little regarding pollution impacts on the population dynamics of insect herbivores (Figure 2). Especially disappointing is acute shortage of studies addressing density-dependent processes in herbivore populations experiencing different loads of pollutants of global concern. In the absence of long-term data, the only solution is to use a 'space-for-time' substitution to invoke temporal changes in herbivore abundance from contemporary spatial patterns [9•,52], as done to explore N-deposition effects on moth and butterfly abundances in Switzerland [51•]. For this purpose, monitoring populations of key species of herbivorous insects should be added to programmes of relevant networks assessing the effects of various pollutants (O_3, in particular) on natural ecosystems. The data obtained in this way could be used to (i) test the hypothesis of a general similarity in the effects of different pollutants on herbivore population dynamics and (ii) suggest new hypotheses on mechanisms underlying the observed effects.

Although environmental pollution is an integral part of global change, most research addressing the biotic effects of climate change does not consider pollution issues. Furthermore, most studies on both the distribution of pollutants and the biotic effects of pollution have neglected the issue of climate change [2•]. Consequently, studies exploring the combined effects of air pollution and climate change remain uncommon, although in a rapidly changing world, the effects of anthropogenic pollution on the dynamics of animal populations may be at least as important as the effects of climate change [14•]. I therefore recommend intensification of experimental studies that address the combined effects of pollution and climate on plant-feeding insects. These studies should preferably explore insects feeding on noncultivated plants to assure a better representation of taxonomic and functional diversity of herbivorous insects in the published data and a greater generality of the resulting conclusions.

Conflict of interest statement

The author declares no conflict of interest.

Data Availability

No data were used for the research described in the article.

Acknowledgements

The study was supported by the Academy of Finland (project 316182).

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest

1. Kozlov MV, Zvereva EL, Zverev VE: **Impacts of Point Polluters on Terrestrial Biota: Comparative Analysis of 18 Contaminated Areas**. Springer; 2009.

2. • De Marco A, Sicard P, Feng Z, Agathokleous E, Alonso R, Araminiene V, Augustaitis A, Badea O, Beasley JC, Branquinho C, *et al.*: **Strategic roadmap to assess forest vulnerability under air pollution and climate change**. *Glob Change Biol* 2022, **28**:5062-5085, https://doi.org/10.1111/gcb.16278.

This review, which threats insect herbivory as one of multiple stresses compromising forest health, summarizes the current knowledge on combined air pollution and climate change effects on global forest ecosystems and identifies research priorities as a roadmap for the future. These priorities, in particular, include the extension of the network of monitoring sites, intensification of experimental studies addressing the combined effects of different abiotic factors on forests, and improving representation of taxonomic and functional diversity of biota in both observational and experimental studies.

3. IPBES: **Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services**. IPBES Secretariat; 2019.

4. Cardoso P, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima CS, Gaigher R, Habel JC, Hallmann CA, *et al.*: **Scientists' warning to humanity on insect extinctions**. *Biol Conserv* 2020, **242**:108426.

5. Harvey JA, Heinen R, Armbrecht I, Basset Y, Baxter-Gilbert JH, Bezemer TM, Böhm M, Bommarco R, Borges PAV, Cardoso P, *et al.*: **International scientists formulate a roadmap for insect conservation and recovery**. *Nat Ecol Evol* 2020, **4**:174-176.

6. Warren MS, Maes D, van Swaay CAM, Goffart P, van Dyck H, Bourn NAD, Wynhoff I, Hoare D, Ellis S: **The decline of butterflies in Europe: problems, significance, and possible solutions**. *Proc Natl Acad Sci USA* 2021, **118**:e2002551117.

7. Lu Y, Yang Y, Sun B, Yuan J, Yu M, Stenseth NC, Bullock JM, Obersteiner M: **Spatial variation in biodiversity loss across China under multiple environmental stressors**. *Sci Adv* 2020, **6**:eabd0952.

8. Lovett GM, Tear TH, Evers DC, Findlay SEG, Cosby BJ, Dunscomb JK, Driscoll CT, Weathers KC: **Effects of air pollution on ecosystems and biological diversity in the eastern United States**. *Ann N Y Acad Sci* 2009, **1162**:99-135.

9. • Kozlov MV, Castagneyrol B, Zverev V, Zvereva EL: **Recovery of moth and butterfly (Lepidoptera) communities in a polluted region following emission decline**. *Sci Total Environ* 2022, **838**:155800.

This study revealed that responses of each individual species of moths and butterflies to industrial pollution (sulphur dioxide and trace elements) were associated with its life history traits. The abundances of monophagous species that fed inside live plant tissues and hibernated as imagoes or pupae were not affected by emissions from the copper-nickel smelter at Monchegorsk, whereas the abundances of oligophagous and polyphagous species that fed externally on plants and hibernated as larvae generally declined near this smelter.

10. Heliövaara K, Väisänen R: Insects and Pollution. CRC; 1993.

11. Zvereva EL, Kozlov MV: **Responses of terrestrial arthropods to air pollution: a metaanalysis**. *Environ Sci Pollut Res* 2010, **17**:297-311.

12. Baltensweiler W: **Waldsterben: forest pests and air pollution**. *J Appl Entomol* 1985, **99**:77-85.

13. Führer E: **Air pollution and the incidence of forest insect problems**. *J Appl Entomol* 1985, **99**:371-377.

14. • Hunter MD, Kozlov MV: **The relative strengths of rapid and delayed density dependence acting on a terrestrial herbivore change along a pollution gradient**. *J Anim Ecol* 2019, **88**:665-676.

This study discovered that the strength of rapid density dependence operating on populations of an eruptive leafmining moth, *Phyllonorycter strigulatella*, increased while the strength of delayed density dependence decreased with increasing distance from a coal-fired power plant. The increasing strength of rapid density dependence was paralelled by declines in herbivore densities, increases in predation pressure from birds and ants, and declines in an unknown source of mortality (perhaps plant antibiosis).

15. • Zvereva EL, Hunter MD, Zverev V, Kozlov MV: **Factors affecting population dynamics of leaf beetles in a subarctic region: the interplay between climate warming and pollution decline**. *Sci Total Environ* 2016, **566–567**:1277-1288.

The fivefold decline of emissions of sulfur dioxide and heavy metals from the nickel-copper smelter at Monchegorsk did not affect densities of either *Phratora vitellinae* or *Plagiodera versicolora*, whereas densities of both *Chrysomela lapponica* and *Gonioctena pallida* showed a simultaneous rapid 20-fold decline in the early 2000s. Time series analysis and model selection indicated that these abrupt population declines were associated with decreases in aerial emissions from the smelter, which increased beetle mortality from natural enemies.

16. Kozlov MV, Zverev V, Zvereva EL: **Combined effects of environmental disturbance and climate warming on insect herbivory in mountain birch in subarctic forests: results of 26-year monitoring**. *Sci Total Environ* 2017, **601–602**:802-811.

17. Ali S, Ullah MI, Saeed MF, Khalid S, Saqib M, Arshad M, Afzal M, Damalas CA: **Heavy metal exposure through artificial diet reduces growth and survival of *Spodoptera litura* (Lepidoptera: Noctuidae)**. *Environ Sci Pollut Res* 2019, **26**:14426-14434.

18. Wei ZH, Wang XQ, Li PR, Tan XL, Yang XQ: **Diet-mediated effects of cadmium on fitness-related traits and detoxification and antioxidative enzymes in the oriental armyworm, *Mythimna separata***. *Entomol Gen* 2020, **40**:407-419.

19. Ullah MI, Ali S, Khalid S, Mehmood N, Aatif HM, Sajjad A, Saeed MF, Hanif MS, Muqaddas H, Ahmad MH, *et al.*: **Risk assessment of heavy metal induced toxicity in hadda beetle, *Epilachna vigintioctopunctata* (Coccinellidae; Coleoptera)**. *Fresenius Environ Bull* 2021, **30**:103-111.

20. Zeng JY, Guo JX, Shi JH, Shi ZB, Zhang GC, Zhang J: **Stress response of *Lymantria dispar asiatica* (Lepidoptera: Erebidae) larvae and its gut microbiota to manganese ion**. *J Res* 2021, **32**:1241-1251.

21. Shephard AM, Mitchell TS, Henry SB, Oberhauser KS, Kobiela ME, Snell-Rood EC: **Assessing zinc tolerance in two butterfly species: consequences for conservation in polluted environments**. *Insect Conserv Divers* 2020, **13**:201-210.

22. Martinek P, Hedbavny J, Kudlacek T, Stasta M, Kula E: **Adverse responses of *Cabera pusaria* caterpillars to high dietary manganese concentration**. *Entomol Exp Appl* 2020, **168**:635-643.

23. Martinek P, Kula E, Hedbavny J: **Reaction of leaf weevil *Phyllobius arborator* (Coleoptera: Curculionidae) to manganese content in diet**. *Environ Entomol* 2017, **46**:131-136.

24. Lukowski A, Popek R, Jagiello R, Maderek E, Karolewski P: **Particulate matter on two *Prunus* spp. decreases survival and performance of the folivorous beetle *Gonioctena quinquepunctata***. *Environ Sci Pollut Res* 2018, **25**:16629-16639.

25. Osborne KH, Longcore T: **Effect of gypsum dust on lepidopterous larvae**. *Ecotoxicol Environ Saf* 2021, **228**:113027.

26. Vanderstock AM, Latty T, Leonard RJ, Hochuli DF: **Mines over matter: effects of foliar particulate matter on the herbivorous insect, *Helicoverpa armigera***. *J Appl Entomol* 2019, **143**:77-87.

27. Tan YQ, Dion E, Monteiro A: **Haze smoke impacts survival and development of butterflies**. *Sci Rep* 2018, **8**:15667.

28. Lopez-Munoz D, Ochoa-Zapater MA, Torreblanca A, Garcera MD: **Evaluation of the effects of titanium dioxide and aluminum oxide nanoparticles through tarsal contact exposure in the model insect *Oncopeltus fasciatus***. *Sci Total Environ* 2019, **666**:759-765.

29. Boopathy B, Rajan A, Radhakrishnan M: **Ozone: an alternative fumigant in controlling the stored product insects and pests: a status report**. *Ozone Sci Eng* 2022, **44**:79-95.

30. Vanderplanck M, Lapeyre B, Lucas S, Proffit M: **Ozone induces distress behaviors in fig wasps with a reduced chance of recovery**. *Insects* 2021, **12**:995.

31. • Liu V, Wooster MJ, Grosvenor MJ, Lim KS, Francis RA: **Strong impacts of smoke polluted air demonstrated on the flight behaviour of the painted lady butterfly (*Vanessa cardui* L.)**. *Ecol Entomol* 2021, **46**:195-208.

The tethered flight mill experiment demonstrated that the total flight distance covered by adult painted lady butterflies (*Vanessa cardui*) flying in air with combustion-generated PM2.5 declined by 65% during the first 20 min of flying, and flight speed strongly declined with an increase in airborne PM2.5 concentration. Thus, pollution can affect insect population dynamics by dampening their migratory abilities.

32. Zverev V, Kozlov MV: **Decline of *Eulia ministrana* (Lepidoptera: Tortricidae) in polluted habitats is not accompanied by phenotypic stress responses**. *Insect Sci* 2021, **28**:1482-1490.

33. Rode M, Lemoine NP, Smith MD: **Prospective evidence for independent nitrogen and phosphorus limitation of grasshopper (*Chorthippus curtipennis*) growth in a tallgrass prairie**. *PLoS One* 2017, **12**:e0177754.

34. • Zhu PY, Zheng XS, Xu HX, Johnson AC, Heong KL, Gurr GM, Lu ZX: **Nitrogen fertilization of rice plants improves ecological fitness of an entomophagous predator but dampens its impact on prey, the rice brown planthopper, *Nilaparvata lugens***. *J Pest Sci* 2020, **93**:747-755.

Nitrogen fertilization of rice plants benefited their key pest, brown planthopper *Nilaparvata lugens*, both directly and indirectly. Planthopper females preferentially oviposited on N-fertilised plants, and feeding with these plants enhanced female fecundity. At the same time, the number of prey eggs attacked per predatory mirid bug, *Cyrtorhinus lividipennis*, decreased when its host was fed in high-N plants, signalling a weakening of top-down control of a planthopper.

35. Blazheyski S, Kalaitzaki AP, Tsagkarakis AE: **Impact of nitrogen and potassium fertilization regimes on the biology of the tomato leaf miner *Tuta absoluta***. *Entomol Gen* 2018, **37**:157-174.

36. Wang LY, Cui HY, Chang XY, Zhu MM, Zhao ZH: **Increased nitrogen fertilization inhibits the biocontrol activity promoted by the intercropping partner plant**. *Insect Sci* 2021, **28**:1179-1190.

37. Kurze S, Heinken T, Fartmann T: **Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species**. *Oecologia* 2018, **188**:1227-1237.

38. Le Gall M, Word ML, Thompson N, Beye A, Cease AJ: **Nitrogen fertilizer decreases survival and reproduction of female locusts by increasing plant protein to carbohydrate ratio**. *J Anim Ecol* 2020, **89**:2214-2221.

39. • Agathokleous E, WaiLi Y, Ntatsi G, Konno K, Saitanis CJ, Kitao M, Koike T: **Effects of ozone and ammonium sulfate on cauliflower: emphasis on the interaction between plants and insect herbivores**. *Sci Total Environ* 2019, **659**:995-1007.

In a choice experiment, cauliflower (*Brassica oleracea*) plants exposed to ambient and elevated O_3 concentrations (20 ppb vs 55 ppb) for about one month were not distinguished by Eri silkmoth larvae (*Samia ricini*), but feeding on plants exposed to elevated O_3 inhibited larval growth, although did not increase mortality.

40. • Cotrozzi L, Conti B, Lorenzini G, Pellegrini E, Nali C: **In the tripartite combination ozone-poplar-*Chrysomela populi*, the**

pollutant alters the plant-insect interaction via primary metabolites of foliage. *Environ Res* 2021, **201**:111581.

The leaf beetle (*Chrysomela populi*) larvae fed with poplar leaves that were exposed to 80 ppb of O_3 during 10 consecutive days attained higher weight relative to larvae fed with poplar leaves exposed to charcoal-filtered air; however, this effect was significant only in one of two studied poplar clones.

41. Duque L, Poelman EH, Steffan-Dewenter I: **Plant-mediated effects of ozone on herbivores depend on exposure duration and temperature**. *Sci Rep* 2019, **9**:19891.

42. Campbell SA, Vallano DM: **Plant defences mediate interactions between herbivory and the direct foliar uptake of atmospheric reactive nitrogen**. *Nat Commun* 2018, **9**:4743.

43. Riemer J, Whittaker JB: **Air pollution and insects herbivores: observed interactions and possible mechanisms**. In *Insect-Plant Interactions*. Edited by Bernays EA. CRC Press; 1989:73-105.

44. Hosseini A, Hosseini M, Michaud JP, Awal MM, Ghadamyari M: **Nitrogen fertilization increases the nutritional quality of *Aphis gossypii* (Hemiptera: Aphididae) as prey for *Hippodamia variegata* (Coleoptera: Coccinellidae) and alters predator foraging behavior**. *J Econ Entomol* 2018, **111**:2059-2068.

45. Gharekhani G, Salehi F, Shirazi J, Vaez N: **Tri-trophic interactions among nitrogen-fertilized tomato cultivars, the tomato fruit worm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) and the ectoparasitoid, *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae)**. *Egypt J Biol Pest Control* 2020, **30**:6.
•

Fecundity and longevity of adult ectoparasitoid wasps *Habrobracon hebetor* that have emerged from *Helicoverpa armigera* larvae increased with N fertilization of their host plants.

46. Shi ZK, Wang SS, Pan BY, Liu YK, Li Y, Wang SG, Wang S, Tang B: **Effects of zinc acquired through the plant-aphid-ladybug food chain on the growth, development and fertility of *Harmonia axyridis***. *Chemosphere* 2020, **259**:127497.

47. Qiao F, Yang QF, Hou RX, Zhang KN, Li J, Ge F, Ouyang F: **Moderately decreasing fertilizer in fields does not reduce populations of cereal aphids but maximizes fitness of parasitoids**. *Sci Rep* 2021, **11**:2517.

48. Grinath JB: **Chronic, low-level nitrogen deposition enhances abundances of ant-protected herbivores inhabiting an imperiled foundation species**. *Acta Oecol* 2021, **110**:103706.
•

This study experimentally revealed a positive effect of N enrichment on abundance of sap-feeding insects that are mutualist partners of predaceous ants. The abundance of ants in N-treated plants did not change, but ants on these plants provided greater antipredator protection for mutualist herbivores.

49. Liebhold AM: **Air pollution as an experimental probe of insect population dynamics**. *J Anim Ecol* 2019, **88**:662-664.

50. Yang YHS, Xi XQ, Zhong XT, Eisenhauer N, Sun SC: **N addition suppresses the performance of grassland caterpillars (*Gynaephora alpherakjj* [sic!]) by decreasing ground temperature**. *Ecosphere* 2017, **8**:e01755.

51. Roth T, Kohli L, Rihm B, Meier R, Amrhein V: **Negative effects of nitrogen deposition on Swiss butterflies**. *Conserv Biol* 2021, **35**:1766-1776.
•

The data from the Swiss biodiversity monitoring program demonstrated that abundance of 86% of 113 Lepidoptera (mostly butterfly) species was negatively related to the modelled N deposition. The strongest negative effects were found for species of conservation concern (near-threatened and vulnerable).

52. Blois JL, Williams JW, Fitzpatrick MC, Jackson ST, Ferrier S: **Space can substitute for time in predicting climate-change effects on biodiversity**. *Proc Natl Acad Sci USA* 2013, **110**:9374-9379.