

Observed electric charge of insect swarms and their contribution to atmospheric electricity

Article

Published Version

Creative Commons: Attribution-Noncommercial-No Derivative Works 4.0

Open access

Hunting, E. R., O'Reilly, L. J., Harrison, R. G. ORCID: <https://orcid.org/0000-0003-0693-347X>, Manser, K., England, S. J., Harris, B. H. and Robert, D. (2022) Observed electric charge of insect swarms and their contribution to atmospheric electricity. iScience. 105241. ISSN 2589-0042 doi: 10.1016/j.isci.2022.105241 Available at <https://centaur.reading.ac.uk/107575/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1016/j.isci.2022.105241>

Publisher: Cell Press

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

Article

Observed electric charge of insect swarms and their contribution to atmospheric electricity



Ellard R. Hunting,
Liam J. O'Reilly, R.
Giles Harrison,
Konstantine
Manser, Sam J.
England, Beth H.
Harris, Daniel
Robert

e.r.hunting@bristol.ac.uk
(E.R.H.)
liam.oreilly@bristol.ac.uk
(L.J.O.)

Highlights

Aerial insects carry an
electric charge

Swarming honeybees
have a density-dependent
effect on atmospheric
electricity

Insects can have similar
effects on atmospheric
electricity as weather
events

Article

Observed electric charge of insect swarms and their contribution to atmospheric electricity

Ellard R. Hunting,^{1,3,4,*} Liam J. O'Reilly,^{1,3,*} R. Giles Harrison,² Konstantine Manser,¹ Sam J. England,¹ Beth H. Harris,¹ and Daniel Robert¹

SUMMARY

The atmosphere hosts multiple sources of electric charge that influence critical processes such as the aggregation of droplets and the removal of dust and aerosols. This is evident in the variability of the atmospheric electric field. Whereas these electric fields are known to respond to physical and geological processes, the effect of biotic sources of charge has not hitherto been considered. Here, we combine theoretical and empirical evidence to demonstrate that honeybee swarms directly contribute to atmospheric electricity, in proportion to the swarm density. We provide a quantitative assessment of this finding, by comparing the electrical contribution of various swarming insect species with common abiotic sources of charge. This reveals that the charge contribution of some insect swarms will be comparable with that of meteorologically induced variations. The observed transport of charge by insects therefore demonstrates an unexplored role of biogenic space charge for physical and ecological processes in the atmosphere.

INTRODUCTION

The Earth's atmosphere is always electrified to a greater or lesser extent, even in fair weather away from thunderstorms. Fossil evidence of paleolightning (Harland and Hacker, 1966) indicates this is unlikely to be a new phenomenon geologically, and therefore the atmospheric electric field can be regarded as a fundamental atmospheric property. It is conventionally observed as the vertical Potential Gradient (PG), essentially the voltage difference between the Earth's surface and a point (often 1 m) above it (Everett, 1868; Fdez-Arroyabe et al., 2021; Whipple, 1929). The atmospheric PG has proved important in understanding large-scale drivers of the global atmospheric electric circuit (e.g. from climate and space weather) (Harrison, 2015), and in causing migration of biologically relevant ions (e.g., nitrate, sulphate, radon) (Hunting et al., 2019, 2021a, 2021b) as well as facilitating animal dispersal or navigation (Clarke et al., 2013; Hunting et al., 2022; England and Robert, 2022; Morley and Robert, 2018). The continuous monitoring of atmospheric electric fields is therefore essential in developing a detailed understanding of a wide array of atmospheric, biological, and geological processes.

Various drivers of variations in atmospheric electricity have been identified. On a large scale, PGs in fair-weather regions are a consequence of global electric current flows driven by thunderstorm regions (e.g., Haldoupis et al., 2017; Rycroft et al., 2000). On a local scale, the PG is influenced by local atmospheric electrical processes such as cloud electrification, lightning initiation, precipitation, aerosol charging, and radioactivity (Anisimov et al., 2017; Hamilton, 1965; Harrison and Aplin, 2002; Pierce, 1972; Takeda et al., 2011), and is sensitive to anthropogenic pollution (Matthews et al., 2019), volcanism and potentially earthquakes (Harrison et al., 2010; Kamogawa et al., 2004). Yet, while these various abiotic drivers have been identified, they can still fail to explain commonly observed variations in atmospheric PGs, suggesting a comprehensive understanding of the causes and consequences of spatio-temporal variability in atmospheric electricity is still incomplete.

We propose a new perspective based on the idea that organisms that inhabit the lower atmosphere can act as a source of atmospheric space charge and associated atmospheric electrical variability. Insects are well-known to be ubiquitous in the global atmosphere (Hu et al., 2016; Reynolds et al., 2017), and they can occur in large densities in the lower (~0–5 km altitude) atmosphere. Moreover, a wide array of airborne insect species have been shown to carry an electric charge, which ranges from picocoulombs to nanocoulombs

¹School of Biological Sciences, University of Bristol, Bristol, UK

²Department of Meteorology, University of Reading, Reading, UK

³These authors contributed equally

⁴Lead contact

*Correspondence: e.r.hunting@bristol.ac.uk (E.R.H.), liam.oreilly@bristol.ac.uk (L.J.O.)

<https://doi.org/10.1016/j.isci.2022.105241>

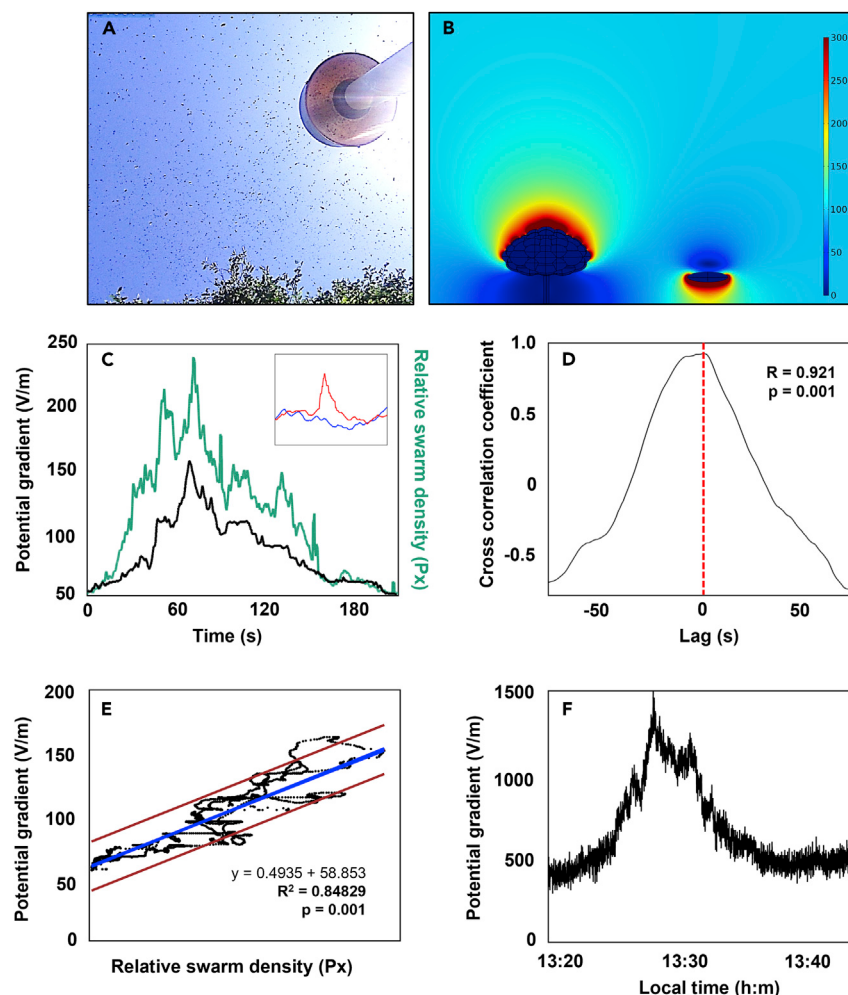


Figure 1. Effect of honeybee swarms on the atmospheric potential gradient, PG

(A) Honeybees passing the electric field monitor at the experimental site.
 (B) Finite element model illustrating the potential effect of a honeybee swarm on atmospheric PG (in V/m). Color scale truncated above 300 V/m.
 (C) Atmospheric PG and honeybee swarm density (expressed as the pixel density, Px). Inset shows dynamics in PG for both the honeybee swarm (red) and open field conditions (blue).
 (D) Cross-correlation analysis between atmospheric PG and honeybee swarm density.
 (E) Linear regression analysis between atmospheric PG and honeybee swarm density.
 (F) Changes in atmospheric PG in response to another honeybee swarming event.

per individual (Edwards, 1962; England and Robert, 2022; Erickson, 1975). These observations support the hypothesis that large aggregations of aerial insects provide an important source of space charge in the atmosphere. Here, a honeybee swarm is investigated as an emblematic example of such an insect aggregation, as honeybees have predictable swarming behavior, and the existence of individual bee charges has been well documented. We provide model-based and empirical evidence that bee swarms make a density-dependent contribution to the atmospheric PG, and explore the broader significance of insect swarms by offering a comparison with known abiotic sources of atmospheric electricity.

RESULTS AND DISCUSSION

Effect of honeybee swarms on atmospheric electricity

Insect swarms can occur at different altitudes and with different densities, and often consist of a single species (e.g., honeybees, locusts, butterflies, see Figures 1A and 2A). Using published charge measurements of honeybees (Edwards, 1962; Erickson, 1975) and our own calibrated measurements, we developed a

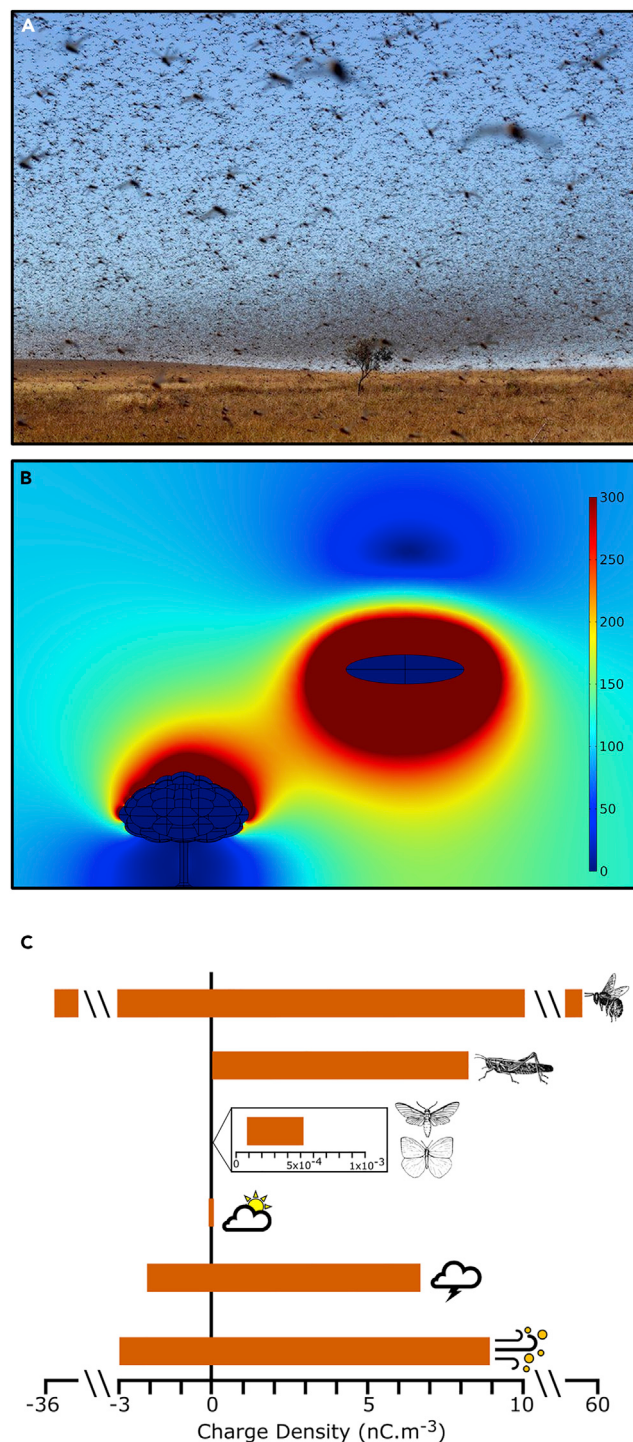


Figure 2. Effect of a locust swarm on the atmospheric potential gradient and the significance of insect swarm compared with meteorological conditions

(A) Example of a locust swarm (Courtesy: Bilal Tarabey-AFP).

(B) Finite element model showing the effect of a locust swarm on atmospheric PG (in V/m). Color scale truncated above 300 V/m.

(C) Charge densities of several swarming insect species and meteorological phenomena – from top to bottom, honeybee (*Apis mellifera*), Lepidoptera (*Tyria jacobaeae* and *Aglais io*) (England and Robert, 2022), desert locust (*S. gregaria*), semi-fair-weather clouds, thunderstorm clouds, and electrified dust storms.

three-dimensional finite element analysis model to computationally evaluate the effect of swarming honeybees on local atmospheric electric fields. These models of the electric fields around honeybee swarms highlight the appreciable perturbing influence that they can have on their local electrical environment (Figure 1B).

To test whether honeybee swarms can indeed cause observable atmospheric PG variations, measurements were carried out at our field station at the University of Bristol, School of Veterinary Sciences, Langford, United Kingdom. The site contains several honeybee hives used for research, which, in the event of overcrowding, exhibit their typical swarming behavior. Such an event provided an opportunity to assess the electrical effect of a honeybee swarm, by placing an electric field monitor (Boltek EFM 100 Field Mill) and an upward viewing camera near the swarm to assess swarm density. For about three minutes, part of the migrating swarm passed over the electric field monitor (Figure 1A). This revealed a net positive PG increase of 100 Vm^{-1} at peak density (Figure 1C). This effect was not observed in a second control field mill positioned in the open field 50 m away from the swarm (Inset Figure 1C). Cross-correlation indicates that bee swarm density (expressed as relative pixel density) was highly correlated with atmospheric PG ($R^2 = 0.92$, $p < 0.001$; Figure 1D). Regression analysis suggests a linear correlation between relative swarm density and atmospheric PG ($R^2 = 0.85$, $p < 0.001$; Figure 1E). Collectively, this evidence suggests that a honeybee swarm contains enough charge to affect the atmospheric PG, proportional to the swarm density. In several other swarming events, net positive increases in atmospheric PG have been observed up to $\sim 1,000 \text{ Vm}^{-1}$ at peak density (Figure 1F). The observed magnitude of the density-dependent effects thus falls within the expected ranges predicted in our model (Figure 1B).

Relevance of insect swarms for atmospheric electricity

Various insects swarm, including Hymenoptera (e.g., wasps and flying ants), Isoptera (e.g., termites), Orthoptera (e.g., locusts), Lepidoptera (e.g., migrating butterflies and moths), Diptera (e.g., mosquitoes, midges, and cluster flies), Ephemeroptera (e.g., mayflies), and Coleoptera (e.g., Australian soldier beetles). Gregarious grasshoppers, or locusts (Acrididae), can form swarms on a *biblical* scale (covering land areas of up to $1,000 \text{ km}^2$ (Uvarov, 1977); (Figure 2A), causing severe damage to agriculture and subsistence farming by decimating crops (Zhang et al., 2019). We therefore also estimated the effect of swarming locusts on local atmospheric electric fields based on our measurements of locusts' charges ($805 \pm 295.5 \text{ pC}$, median $\pm \text{SD}$, $N = 8$) and published densities ($0.001\text{--}10 \text{ insects m}^{-3}$; Rainey, 1958). Using a similar rationale to that used here for honeybees, our analysis reveals that locust swarms have the potential to alter their local electrical environment with a magnitude comparable with meteorological events (Figure 2B).

To provide context between insect swarm charges and meteorological phenomena, we estimated charge densities of swarms of three different swarming insects and compared these to meteorological charge densities (semi-fair-weather clouds, storm clouds, and electrified dust storms) reported in the literature (Harrison et al., 2018; Marshall and Stolzenburg, 1998; Nicoll and Harrison, 2016). Our calculations show that desert locust (*Schistocerca gregaria*) swarms are capable of exceeding charge densities reported for electrical storms and clouds (Figure 2C) (Marshall and Stolzenburg, 1998). In contrast, Lepidoptera (moths and butterflies) (England and Robert, 2022) do not appear to represent substantial sources of atmospheric charge when compared with meteorological phenomena owing to their low average densities ($\sim 0.01 \text{ insects m}^{-3}$) reported in the literature (Figure 2C; Johnson, 1969). However, extreme swarming incidents have been reported (Callahan and Mankin, 1979), in which it can be estimated that variations in PG resulting from such densities could potentially be commensurate with the PG changes associated with fair-weather clouds.

Concluding remarks and limitations of the study

The presented evidence that swarming, migrating insects transport charge in the lower atmosphere indicates that large collections of charged insects will contribute to a hitherto unrecognized source of electrical variability in the atmosphere. This recognition potentially carries various physically- and biologically relevant implications. For instance, entomogenic space charge is not considered in current climate models aimed at capturing the complex interplay between radiation and particulate matter, such as the atmospheric transport of dust. As atmospheric space charge enhances the aggregation and movement of aerial particles (Toth et al., 2020), it is conceivable that insect-derived space charges will also contribute to spatial changes in aerial particles. For example, it could be speculated that insect-driven charged particle collection and transport could contribute to long-range transport of desert dust, providing alternative

explanations for the transport of large particles, which cannot be explained by physical processes alone (Toth et al., 2020; Does Van der et al., 2018). Further, insects are not the only source of biogenic charge in the atmosphere, as birds and microorganisms also carry charge and abound in the lower atmosphere (Badger et al., 2015; de Groot et al., 2021). The observed presence and magnitude of biogenic space charge invites further interdisciplinary research into the dynamic electrical interactions between physical and biological entities in the atmosphere.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead contact
 - Materials availability
 - Data and code availability
- METHOD DETAILS
 - Finite element analysis
 - Measurements of swarms, insect charges, and electric fields
- QUANTIFICATION AND STATISTICAL ANALYSIS

ACKNOWLEDGMENTS

E.H. received financial support from the Swiss National Science Foundation, SNF (CRSK-2 190855), supporting L.O. D.R. acknowledges funding by UKRI BBSRC (Grant BB/T003235/1) and the European Research Council (ERC-ADG 743093 ELECTROBEE), supporting E.H., L.O., K.M., B.H., and S.E. We thank Tom O'Neil for technical assistance. Artwork designed and produced by Nubia Hunting.

AUTHOR CONTRIBUTIONS

E.H. conceived the study, collected empirical data, and performed data analysis. B.H. collected empirical data. L.O. and K.M. performed data analysis and S.E. collected empirical data and developed the model. E.H. drafted the manuscript, and all authors contributed to study design and developing the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

Received: May 30, 2022

Revised: September 20, 2022

Accepted: September 27, 2022

Published: October 24, 2022

REFERENCES

- Anisimov, S.V., Galichenko, S.V., and Mareev, E.A. (2017). Electrodynamic properties and height of atmospheric convective boundary layer. *Atmos. Res.* 194, 119–129. <https://doi.org/10.1016/j.atmosres.2017.04.012>.
- Badger, M., Ortega-Jimenez, V.M., Von Rabenau, L., Smiley, A., Dudley, R., and Gruverman, A. (2015). Electrostatic charge on flying hummingbirds and its potential role in pollination. *PLoS One* 10, e0138003. <https://doi.org/10.1371/journal.pone.0138003>.
- Bennett, A.J., and Harrison, R.G. (2007). Atmospheric electricity in different weather conditions. *Weather* 62, 277–283. <https://doi.org/10.1002/wea.97>.
- Paw U, K.T., and Mankin, R.W. (1979). Insects as unidentified flying objects: comment. *Appl. Opt.* 18, 2723–2724. <https://doi.org/10.1364/ao.18.002723>.
- Clarke, D., Whitney, H., Sutton, G., and Robert, D. (2013). Detection and learning of floral electric fields by bumblebees. *Science* 340, 66–69. <https://doi.org/10.1126/science.1230883>.
- Does Van der, M., Knippertz, P., Zschenderlein, P., Giles Harrison, R., and Stuu, J.B.W. (2018). The mysterious long-range transport of giant mineral dust particles. *Sci. Adv.* 4, eaau2768. <https://doi.org/10.1126/sciadv.aau2768>.
- Edwards, D.K. (1962). Electrostatic charges on insects due to contact with different substrates. *Can. J. Zool.* 40, 579–584. <https://doi.org/10.1139/z62-051>.
- England, S.J., and Robert, D. (2022). The ecology of electricity and electroreception. *Biol. Rev. Camb. Philos. Soc.* 97, 383–413. <https://doi.org/10.1111/brv.12804>.
- Erickson, E.H. (1975). Surface electric potentials on worker honeybees leaving and entering the

hive. *J. Apic. Res.* 14, 141–147. <https://doi.org/10.1080/00218839.1975.11099818>.

Everett, J.D. (1868). XI. Results of observations of atmospheric electricity at kew observatory, and at king's college, windsor, nova scotia. *Philos. Trans. R. Soc. London, A* 158, 347–361.

Fdez-Arroyabe, P., Kourtidis, K., Haldoupis, C., Savoska, S., Matthews, J., Mir, L.M., Kassomenos, P., Cifra, M., Barbosa, S., Chen, X., et al. (2021). Glossary on atmospheric electricity and its effects on biology. *Int. J. Biometeorol.* 65, 5–29. <https://doi.org/10.1007/s00484-020-02013-9>.

Fell, R.D., Ambrose, J.T., Burgett, D.M., De Jong, D., Morse, R.A., and Seeley, T.D. (1977). The seasonal cycle of swarming in Honeybees. *J. Apic. Res.* 16, 170–173. <https://doi.org/10.1080/00218839.1977.11099883>.

de Groot, G.A., Geisen, S., Wubs, E.R.J., Meulenbroek, L., Laros, I., Snoek, L.B., Lammertsma, D.R., Hansen, L.H., and Slim, P.A. (2021). The aerobiome uncovered: multi-marker metabarcoding reveals potential drivers of turnover in the full microbial community in the air. *Environ. Int.* 154, 106551. <https://doi.org/10.1016/J.ENVIINT.2021.106551>.

Haldoupis, C., Rycroft, M., Williams, E., and Price, C. (2017). Is the “Earth-ionosphere capacitor” a valid component in the atmospheric global electric circuit? *J. Atmos. Sol. Terr. Phys.* 164, 127–131. <https://doi.org/10.1016/j.jastp.2017.08.012>.

Hamilton, R.A. (1965). Secular and other changes of atmospheric electrical potential gradient at Lerwick. *Q. J. R. Meteorol. Soc.* 91, 348–352. <https://doi.org/10.1002/qj.49709138910>.

Harland, W.B., and Hacker, J.L. (1966). Fossil lightning strikes 250 million years ago. *Rep. Br. Assoc. Adv. Sci.* 22, 663–671.

Harrison, R.G. (2015). *Meteorological Measurements and Instrumentation* (John Wiley & Sons, Ltd).

Harrison, R.G., and Aplin, K.L. (2002). Mid-nineteenth century smoke concentrations near London. *Atmos. Environ. X* 36, 4037–4043. [https://doi.org/10.1016/S1352-2310\(02\)00334-5](https://doi.org/10.1016/S1352-2310(02)00334-5).

Harrison, R.G., Aplin, K.L., and Rycroft, M.J. (2010). Atmospheric electricity coupling between earthquake regions and the ionosphere. *J. Atmos. Sol. Terr. Phys.* 72, 376–381. <https://doi.org/10.1016/j.jastp.2009.12.004>.

Harrison, R.G., Nicoll, K.A., Marlton, G.J., Ryder, C.L., and Bennett, A.J. (2018). Saharan dust plume charging observed over the UK. *Environ. Res. Lett.* 13, 054018. <https://doi.org/10.1088/1748-9326/aabed9>.

Hu, G., Lim, K.S., Horvitz, N., Clark, S.J., Reynolds, D.R., Sapir, N., and Chapman, J.W. (2016). Mass seasonal bioflows of high-flying insect migrants. *Science* 354, 1584–1587. <https://doi.org/10.1126/science.aah4379>.

Hunting, E.R., Harrison, R.G., Bruder, A., Van Bodegom, P.M., Van Der Geest, H.G., Kampfraath, A.A., Vorenhout, M., Admiraal, W., Cusell, C., and Gessner, M.O. (2019). Atmospheric electricity influencing biogeochemical processes in soils and sediments. *Front. Physiol.* 10, 1–10. <https://doi.org/10.3389/fphys.2019.00378>.

Hunting, E.R., England, S.J., and Robert, D. (2021a). Tree canopies influence ground level atmospheric electrical and biogeochemical variability. *Int. J. Biometeorol.* 65, 1–3. <https://doi.org/10.3389/fearth.2021.671870>.

Hunting, E.R., Matthews, J., de Arróyabe Hernáez, P.F., England, S.J., Kourtidis, K., Koh, K., Nicoll, K., Harrison, R.G., Manser, K., Price, C., et al. (2021b). Challenges in coupling atmospheric electricity with biological systems. *Int. J. Biometeorol.* 65, 45–58. <https://doi.org/10.1007/s00484-020-01960-7>.

Hunting, E.R., England, S.J., Koh, K., Lawson, D.A., Brun, N.B., and Robert, D. (2022). Synthetic fertilizers alter floral biophysical cues and bumblebee foraging behavior. *PNAS Nexus*.

Johnson, C.G. (1969). *Migration and Dispersal of Insects by Flight* (Methuen).

Kamogawa, M., Liu, J.Y., Fujiwara, H., Chuo, Y.J., Tsai, Y.B., Ohtsuki, Y.H., Hattori, K., Nagao, T., Uyeda, S., and Ohtsuki, Y.H. (2004). Atmospheric field variations before the March 31, 2002 M6.8 earthquake in Taiwan. *Terr. Atmos. Ocean Sci.* 15, 397–412. [https://doi.org/10.3319/TAO.2004.15.3.397\(EP\)](https://doi.org/10.3319/TAO.2004.15.3.397(EP)).

Lighthart, B., Prier, K.R.S., and Bromenshenk, J.J. (2005). Flying honey bees adsorb airborne viruses. *Aerobiologia* 21, 147–149. <https://doi.org/10.1007/s10453-005-4185-9>.

Marshall, T.C., and Stolzenburg, M. (1998). Estimates of cloud charge densities in thunderstorms. *J. Geophys. Res.* 103, 19769–19775.

Matthews, J.C., Wright, M.D., Clarke, D., Morley, E.L., Silva, H., Bennett, A.J., Robert, D., and Shallcross, D.E. (2019). Urban and rural measurements of atmospheric potential gradient. *J. Electrostat.* 97, 42–50. <https://doi.org/10.1016/j.elstat.2018.11.006>.

Morley, E.L., and Robert, D. (2018). Electric fields elicit ballooning in spiders. *Curr. Biol.* 28, 2324–2330.e2. <https://doi.org/10.1016/j.cub.2018.05.057>.

Nicoll, K.A., and Harrison, R.G. (2016). Stratiform cloud electrification: comparison of theory with multiple in-cloud measurements. *Q. J. R. Meteorol. Soc.* 142, 2679–2691. <https://doi.org/10.1002/qj.2858>.

Pierce, E.T. (1972). Radioactive fallout and secular effects in atmospheric electricity. *J. Geophys. Res.* 77, 482–487. <https://doi.org/10.1029/jc077i003p00482>.

Rainey, R.C. (1958). Some observations on flying locusts and atmospheric turbulence in eastern Africa. *Q. J. R. Meteorol. Soc.* 84, 334–354.

Reynolds, D.R., Chapman, J.W., and Drake, V.A. (2017). Riders on the wind: the aerocology of insect migrants. In *Aerocology* (Springer), pp. 145–178.

Rycroft, M.J., Israelsson, S., and Price, C. (2000). The global atmospheric electric circuit, solar activity and climate change. *J. Atmos. Sol. Terr. Phys.* 62, 1563–1576. [https://doi.org/10.1016/S1364-6826\(00\)00112-7](https://doi.org/10.1016/S1364-6826(00)00112-7).

Suojanen, M., Lederle, C., Heim, R., Keikko, T., Kuusiluoma, S., and Korpinen, L. (2001). The effect of trees on calculation of electric fields near 400 kV transmission lines. *WIT Trans. Model. Simul.* 30, 935–944.

Takeda, M., Yamauchi, M., Makino, M., and Owada, T. (2011). Initial effect of the Fukushima accident on atmospheric electricity. *Geophys. Res. Lett.* 38. <https://doi.org/10.1029/2011GL048511>.

Toth III, J.R., Rajupet, S., Squire, H., Volbers, B., Zhou, J., Xie, L., Sankaran, R.M., and Lacks, D.J. (2020). Electrostatic forces alter particle size distributions in atmospheric dust. *Atmos. Chem. Phys.* 20, 3181–3190. <https://doi.org/10.5194/acp-20-3181-2020>.

Uvarov, B. (1977). *Grasshoppers and Locusts: A Handbook of General Acridology2* (Centre for Overseas Pest Research). Behaviour Ecology, Biogeography, Population Dynamics.

Whipple, F.J.W. (1929). On the association of the diurnal variation of electric potential on fine weather with the distribution of thunderstorms over the globe. *Q. J. R. Meteorol. Soc.* 55, 1–18. <https://doi.org/10.1038/115657a0>.

Wilson, C.T.R. (1903). Atmospheric electricity. *Nature* 68, 102–104. <https://doi.org/10.1038/068102d0>.

Zhang, L., Lecoq, M., Latchinsky, A., and Hunter, D. (2019). Locust and grasshopper management. *Annu. Rev. Entomol.* 64, 15–34. <https://doi.org/10.1146/annurev-ento-011118-112500>.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Other	Boltek EFM 100	N/A
Other	AKASO V50x	N/A
Other	John Chubb Instrumentation Ltd. Cheltenham, UK	N/A
Software and Algorithms	COMSOL Multiphysics® v. 5.4 (COMSOL AB, Stockholm, Sweden)	N/A
Deposited Data	Mendeley Data	https://doi.org/10.17632/wzxpnc9r55.1
Deposited Data	Mendeley Data	https://doi.org/10.17632/5bm5cj7jf7.1

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Ellard Hunting, e.r.hunting@bristol.ac.uk/e.r.hunting@gmail.com.

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data have been deposited at Mendeley Data, and are publicly available as of the date of publication. DOI is listed in the [key resources table](#). Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.
- All codes have been deposited at Mendeley Data, and are publicly available as of the date of publication. DOI is listed in the [key resources table](#). Any additional information required to use the code reported in this paper is available from the [lead contact](#) upon request.

METHOD DETAILS

Finite element analysis

Modelling of electric fields was performed using finite element analysis within COMSOL Multiphysics® v. 5.4 (COMSOL AB, Stockholm, Sweden) utilising the “Electrostatics” interface within the “AC/DC” module. The three-dimensional geometry consisted of a 60 m × 60 m × 40 m (length, width, height) cuboid within which the model operated. The two runs made for differently sized and charged ellipsoids represented insect swarms of honeybees and locusts. The honeybee swarm was represented as an ellipsoid with semi-axes 2 m × 1 m × 0.5 m ellipsoid at a height of 3 m, and the locust swarm an ellipsoid with semi-axes 4 m × 1 m × 1 m at a height of 15 m. The swarm charge was distributed evenly as a volume charge within the ellipsoids, with the total charge calculated respectively as the sum of 500 bees each carrying +100 pC (order of magnitude from (England and Robert, 2022)) and 1000 locusts carrying +850 pC each. An approximately 8 m tall deciduous tree was included in each model to provide scale and an electrical landmark for comparison (Hunting et al., 2021a). The remainder of the model domain was assigned as air. The upper surface of this air column was given an electrical potential typical of a 40 m altitude in fair-weather conditions (+4 kV), with the bottom surface defined as zero potential, equivalent to the established surface (first meter) atmospheric potential gradient of 100 V/m (Bennett and Harrison, 2007; Wilson, 1903). The surface of the tree was also defined as ground (Hunting et al., 2021a). Meshing of the geometry was physics-controlled, set to “extremely fine”. The relative permittivity, ϵ_r , was defined as $\epsilon_r = 12$ for living trees (Hunting et al., 2021a; Suojanen et al., 2001), $\epsilon_r = 1$ for air, and $\epsilon_r = 80$ inside the insect swarms (likely an overestimate, based on the permittivity of water). Model outputs presented for this study were produced by plotting data from two-dimensional slices through the centre of the three-dimensional dataset.

Measurements of swarms, insect charges, and electric fields

Observations were carried out at our field station at the University of Bristol, School of Veterinary Sciences, Langford United Kingdom, which is equipped with an electric field monitor to continuously measure atmospheric PG (Boltek EFM 100 Field Mill, calibrated in a capacitor plat setup). This site features several honeybee hives that are used for research. In the event of overcrowding of a beehive, the original queen leaves the hive with a fraction of the workers (on average around 12,000 bees) (Fell et al., 1977), resulting in occasional swarming events near PG measuring equipment at our study site. When honeybees swarm, they usually cluster on a limb of a tree for several days while scout bees search for suitable cavities to nest in. After an appropriate nest is found, the swarm will collectively migrate. An electric field monitor was placed near the swarm. A camera (AKASO V50X, 30 fps) was positioned next to the field mill with an upward orientation to record the swarm in flight (Figure 1B). A second electric field monitor was placed in an open field, 50m away from the other electric field monitor and swarm to ascertain any dynamics in the electric field monitor was caused by the presence of a swarm. For about three minutes, part of the swarm passed over the electric field monitor.

QUANTIFICATION AND STATISTICAL ANALYSIS

The video recording capturing the swarm event was cropped to a 500 by 220-pixel window to remove foreground objects obstructing the view of the swarm and was analysed using a custom script in Python 3.8.1. The video was converted to black and white pixels such that the background was white and any non-background objects, comprising the swarm, were black. The ratio of black to white pixels was calculated for each frame of the video resulting in a proxy measure for bee density, defined as relative pixel density here. At points during the swarm's passage, flowering heads of grass entered the frame, increasing the relative pixel density. Such affected data were therefore removed. The relative pixel densities were filtered by a moving mean over 10 data points (corresponding to 0.5 s) to emphasise the long-term trend of the data. These data were compared to data collected by the electric field monitor using cross correlation and linear regression in PAST v.4. Since insect charges can be expected to influence PGs directly, data were aligned (zero lag) based on the highest cross correlation coefficient.

To compare the point charge densities of insect swarms with electrical meteorological phenomena, insect surface charges were combined with published insect swarm densities (Johnson, 1969; Rainey, 1958). Surface charges were either taken from the literature (England and Robert, 2022) or measured within Faraday cages in a laboratory setting. Each individual insect was treated as a point charge and 3-D distribution was assumed to be homogenous. Surface charges of the desert locust (*Schistocerca gregaria*) were measured using a manufacturer-calibrated JCI 147 Faraday pail and a JCI 140 static monitor (John Chubb Instrumentation Ltd. Cheltenham, UK), and those of one butterfly and one moth species (*Aglaia io*, Nymphalidae and *Tyria jacobaeae*, Erebididae, respectively) were measured using a calibrated induction ring electrode and custom-built picoammeter. Insects were dropped or flew into the pail or through the induction ring without any contact from the experimenter, the equipment, or electrically charged or conductive objects. As insects accumulate surface charge during flight (e.g., (Erickson, 1975)), we allowed for such charging prior to measurement. Charging either consisted of tethering the insect with fishing line and allowing the animal to fly for a minimum of 30 s or placing the insect in a wind tunnel consisting of a plastic tube with plastic mesh at both ends with a 120 mm USB-powered computer cooling fan at one end. The airflow over the insect simulated flight in terms of friction with air for a triboelectric charging effect, but also through collision with airborne ions for an ion adsorption charging effect (Lighthart et al., 2005).