

**Cover image**

Image © Jorge Paillao and Pablo Marquet.

---

Typeset by Nova Techset Private Limited, Bengaluru & Chennai, India. Printed in the UK by Latimer Trend.

This paper meets the requirements of ISO 9706:1994(E) and ANSI/NISO Z39.48-1992 (Permanence of Paper) effective with volume 335, issue 1273, 1992.

*Phil. Trans. R. Soc. B* (ISSN 0962-8436) is published 26 times a year for US\$6461 per year by the Royal Society, and is distributed in the USA by Agent named Air Business, C/O Worldnet Shipping USA Inc., 149-35 177th Street, Jamaica, New York, NY11434, USA. US Postmaster: Send address changes to *Phil. Trans. R. Soc. B*, C/O Air Business Ltd, C/O Worldnet Shipping USA Inc, 149-35 177th Street Jamaica, New York, NY11414.



The Royal Society is a self-governing Fellowship of many of the world's most distinguished scientists drawn from all areas of science, engineering, and medicine. The Society's fundamental purpose, as it has been since its foundation in 1660, is to recognise, promote, and support excellence in science and to encourage the development and use of science for the benefit of humanity.

The Society's strategic priorities emphasise its commitment to the highest quality science, to curiosity-driven research, and to the development and use of science for the benefit of society.

These priorities are:

- Promoting science and its benefits
- Recognising excellence in science
- Supporting outstanding science
- Providing scientific advice for policy
- Fostering international and global cooperation
- Education and public engagement

**For further information on the Royal Society**

The Royal Society  
6 – 9 Carlton House Terrace  
London SW1Y 5AG

**T** +44 20 7451 2500

**W** [royalsociety.org](http://royalsociety.org)

**For further information on *Philosophical Transactions of the Royal Society B***

**T** +44 20 7451 2602

**E** [philtransb@royalsociety.org](mailto:philtransb@royalsociety.org)

**W** [rstb.royalsocietypublishing.org](http://rstb.royalsocietypublishing.org)



0962-8436(20171205)372:1735

ISBN: 978-1-78252-291-1

ISSN 0962-8436

The Royal Society Registered Charity No 207043