PNAS LETTER

Erratic spatiotemporal vegetation growth anomalies drive population outbreaks in a trans-Saharan insect migrant

Roger López-Mañas[a,1], Joan Pere Pascual-Díaz[a,1], Aurora García-Berro[a], Farid Bahleman[b], Megan S. Reich[c], Lisa Pokorny[a], Clément P. Bataille[c,d], Roger Vila[e], Cristina Domingo-Marimon[f,2], and Gerard Talavera[a,2]

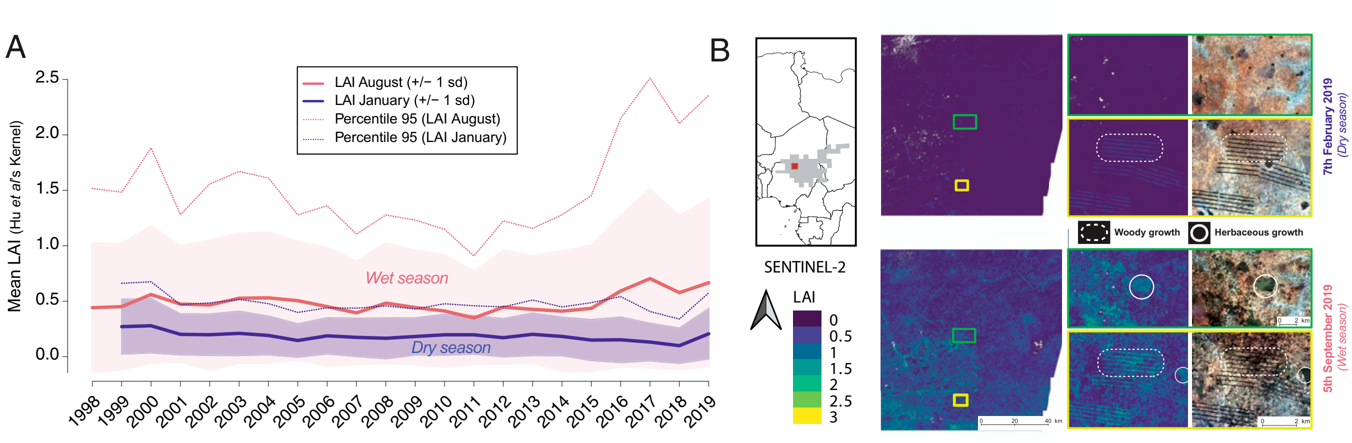

Fig. 1. (*A*) Comparative Copernicus LAI (6) values for Hu et al.'s (1) kernels across years (1998–2019) during the wet (August) and the dry (January) seasons. LAI values indicate the degree of vegetation coverage. Dry season values are steadily lower across time, showing no transient herbaceous growth comparable to that of the wet season. A wider SD interval in the wet season illustrates the presence of both areas covered by contiguous herbaceous growth (high LAI) and areas covered by only patchy woody growth (low LAI), whereas the narrow SD interval of the dry season is attributable to areas with active woody plants alone. (*B*) Illustrative example of high-resolution Sentinel-2 images (10 m) for a quadrant of Hu et al.'s eastern kernel. LAI values for two nested areas are plotted for specific days during both seasons, showing a contrasting signal between herbaceous and woody growth, reinforcing the evidence that Hu et al.'s vegetation growth detection is probably mostly driven by woody plants across their kernels.

Hu et al. (1) propose that vegetation growth in "kernel" regions of the Savanna/Sahel during January/February is key to explain population abundances of the painted lady butterfly (*Vanessa cardui*) in Europe. We identify issues in their rationale and provide evidence toward an alternative scenario.

First, Hu et al. (1) conjecture that, in exceptional years, substantial breeding of *V. cardui* occurs in the African Savanna/Sahel at the peak of the dry season, but no ground-truthed evidence is provided. This hypothesis challenges previous research in Africa, including models based on breeding data (2, 3), and the authors refer to their results as "counterintuitive." We inspected the leaf area index (LAI) in Hu et al.'s kernels and show that the values are steadily low, with no peaks in the dry season that may indicate substantial herbaceous coverage at any scale (Fig. 1*A*). We argue that the low signal of vegetation growth found by Hu et al. likely corresponds to woody plants (Fig. 1*B*), which may store water (4, 5) but are not *V. cardui* larval hosts (2, 3).

Second, Hu et al.'s (1) approach assumes that key breeding localities explaining outbreaks are recurrent across events, excluding the possibility that migratory steps and breeding groups from successive generations could be linked every year to slightly different configurations. Additionally, their models were constrained to account for only a few predetermined regions and months. Given the low philopatry of *V. cardui* and the erratic nature of exceptional climatic events, we demonstrate a different approach that avoids a predetermined spatiotemporal partition. We inferred monthly, highly positive vegetation growth anomalies in the species' African range, using a suite of satellite-derived layers, for the 1994–2020 period, and visually inspected their geographical distribution (Fig. 2). We find that 1) the four major butterfly abundance peaks documented in Europe were closely preceded by vegetation growth anomalies outside the kernels; 2) these anomalies were located at different suitable spatiotemporal breeding grounds in North Africa, the Middle East, and the Afrotropics

Author affiliations: [a]Institut Botànic de Barcelona, Consejo Superior de Investigaciones Científicas and Ajuntament de Barcelona, Barcelona, 08038 Catalonia, Spain; [b]SOS Savane - NGO, Tanguiéta, BP: 145, Benin; [c]Department of Biology, University of Ottawa, Ottawa, ON K1N 6N5, Canada; [d]Department of Earth and Environmental Sciences, University of Ottawa, Ottawa, ON K1N 6N5, Canada; [e]Institut de Biologia Evolutiva, Consejo Superior de Investigaciones Científicas and Universitat Pompeu Fabra, Barcelona, 08003 Catalonia, Spain; and [f]Centre for Ecological Research and Forestry Applications (CREAF), Grumets Research Group, Cerdanyola del Vallès, 08193 Catalonia, Spain

Author contributions: R.L.-M., J.P.P.-D., C.D.-M., and G.T. designed and performed research; R.L.-M., J.P.P.-D., and C.D.-M. analyzed data; and R.L.-M., J.P.P.-D., A.G.-B., F.B., M.S.R., L.P., C.P.B., R.V., C.D.-M., and G.T. discussed data and wrote the paper.

The authors declare no competing interest.

Copyright © 2022 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

[1]R.L.-M. and J.P.P.-D. contributed equally to this work.

[2]To whom correspondence may be addressed. Email: cristina.domingo@uab.cat or gerard.talavera@csic.es.

Published May 5, 2022.

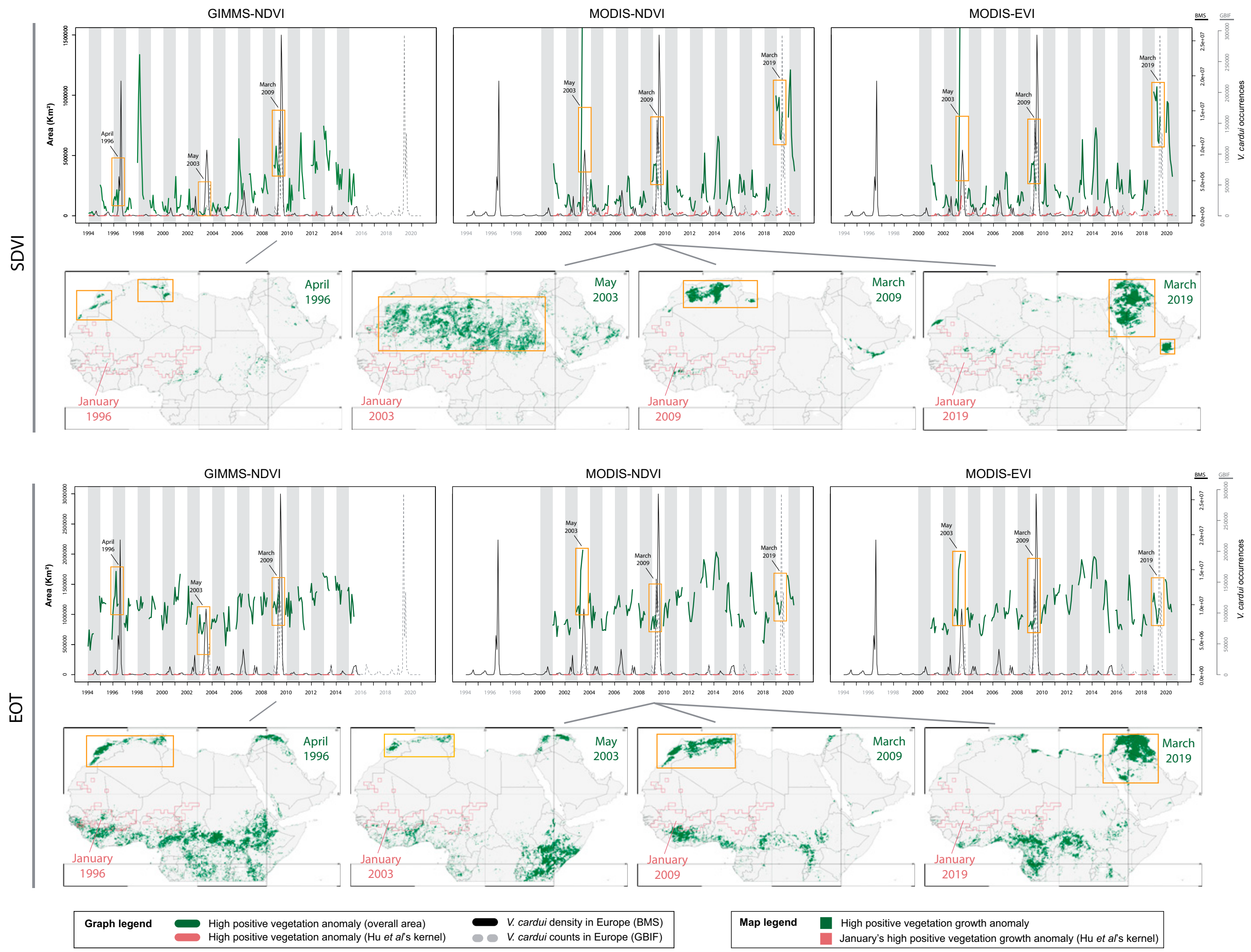

Fig. 2. Time series plots of butterfly abundance in Europe (1994–2020): Butterfly Monitoring Scheme (BMS) densities (black lines) and Global Biodiversity Information Facility (GBIF) overall counts (dashed gray lines). High positive vegetation growth anomalies (Z score $\geq$ 3/EOT $\geq$ 500; green lines) in Africa and the Middle East from November to June consistently predate outbreaks (orange rectangles). Vegetation anomalies are based on the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI) from the global inventory monitoring and modeling system (GIMMS) (7) and the moderate resolution imaging spectroradiometer (MODIS) (8) satellite databases (0.08° and 0.05° spatial resolution, respectively), and two algorithms: standardized difference vegetation index (SDVI) and empirical orthogonal teleconnection (EOT) (9). Vegetation growth anomalies at Hu et al.'s (1) kernels (red lines) are also shown, but no peaks are detected preceding outbreaks. Maps indicating high positive vegetation anomalies (green pixels) are shown for the four main historical outbreaks in Europe. Red polygons delimit Hu et al.'s kernels, depicting the very few monthly vegetation growth anomalies (red pixels) in January of the outbreak year.

(3); 3) the contribution of the kernels to the overall winter and early spring vegetation growth in Africa was minimal; and 4) remarkable variability exists between remote sensing methods, which could affect correlations.

Hu et al.'s (1) modeling exercise, although limited by arguable assumptions, illustrates that climate in Africa could explain abundances of insects migrating to Europe, a view that we share. However, we dispute the nature and strength of the correlation found in their kernels. Based on our analyses, we argue that it is highly unlikely that this correlation represents substantial breeding and the source of outbreaks, although it could represent a side effect of biologically meaningful climatic anomalies occurring in other areas/times. Our results provide a grounded alternative scenario where the strongest vegetation growth events preceding butterfly outbreaks in Europe constitute the most logical environmental drivers, even if their unpredictable localization renders them hardly detectable using pixel-based correlations. This pattern agrees with the view that populations of migratory insects are dynamic and opportunistically exploit vegetation within their suitable seasonal range, making them true spatiotemporal riders of erratic vegetation resources.

ACKNOWLEDGMENTS. R.L.-M. was supported by the program Junta para la Ampliación de Estudios (JAE-intro) from the Consejo Superior de Investigaciones Científicas (Grant JAEICU-21-IBB-005). A.G.-B. was supported by the program Formación de Profesorado Universitario (FPU) (Grant FPU19/01594). C.P.B., M.S.R., and G.T. were supported by Grant NFRE-2018-00738 of the New Frontiers in Research Fund (Government of Canada). C.D.-M. was supported by the Catalan Government under Grant SGR2017-1690. G.T. was supported by the Spanish Ministry of Science and Innovation (Grants PID2020-117739GA-I00/AEI/10.13039/501100011033 and RYC2018-025335-I) and by Grant WW1-300R-18 of the National Geographic Society.

1. G. Hu *et al.*, Environmental drivers of annual population fluctuations in a trans-Saharan insect migrant. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2102762118 (2021).
2. G. Talavera, R. Vila, Discovery of mass migration and breeding of the painted lady butterfly *Vanessa cardui* in the sub-Sahara: The Europe–Africa migration revisited. *Biol. J. Linn. Soc. Lond.* **120**, 274–285 (2016).
3. M. Menchetti, M. Guéguen, G. Talavera, Spatio-temporal ecological niche modelling of multigenerational insect migrations. *Proc. Biol. Sci.* **286**, 20191583 (2019).
4. S. de Bie, P. Ketner, M. Paasse, C. Geerling, Woody plant phenology in the West Africa Savanna. *J. Biogeogr.* **25**, 883–900 (1998).
5. S. Horion, R. Fensholt, T. Tagesson, A. Ehammer, Using earth observation-based dry season NDVI trends for assessment of changes in tree cover in the Sahel. *Int. J. Remote Sens.* **35**, 2493–2515 (2014).
6. A. Verger, F. Baret, M. Weiss, Algorithm theoretical basis document: LAI, fAPAR, fCOVER Collection 1 km, Version 2, Issue I1.41. https://land.copernicus.eu/global/sites/cgls.vito.be/files/products/CGLOPS1_ATBD_LAI1km-V2_I1.41.pdf. Accessed 25 October 2021.
7. C. J. Tucker *et al.*, An extended AVHRR 8 Km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *Int. J. Remote Sens.* **26**, 4485–4498 (2005).
8. K. Didan, MOD13C2 MODIS/Terra Vegetation Indices Monthly L3 Global 0.05 Deg CMG V006. https://doi.org/10.5067/MODIS/MOD13C2.006. Accessed 19 October 2021.
9. T. Appelhans, F. Detsch, T. Nauss, remote: Empirical orthogonal teleconnections in R. *J. Stat. Softw.* **65**, 1–19 (2015).