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In the wind: Invasive species travel along predictable atmospheric pathways

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Abstract

Invasive species such as insects, pathogens, and weeds reaching new environments by traveling with the wind, represent unquantified and difficult-to-manage biosecurity threats to human, animal, and plant health in managed and natural ecosystems. Despite the importance of these invasion events, their complexity is reflected by the lack of tools to predict them. Here, we provide the first known evidence showing that the long-distance aerial dispersal of invasive insects and wildfire smoke, a potential carrier of invasive species, is driven by atmospheric pathways known as Lagrangian coherent structures (LCS). An aerobiological modeling system combining LCS modeling with species biology and atmospheric survival has the potential to transform the understanding and prediction of atmospheric invasions. The proposed modeling system run in forecast or hindcast modes can inform high-risk invasion events and invasion source locations, making it possible to locate them early, improving the chances of eradication success.

KEYWORDS

aerobiology, biosecurity, fall armyworm, invasive species, Lepidoptera migration, long distance dispersal

INTRODUCTION

It is widely recognized that invasive species (insects, pathogens, and weeds) threaten human, animal, and plant health; managed and natural ecosystems; food security; and livelihoods (Diagne et al., 2021; Pyšek et al., 2020). Invasive species can reach new environments through a variety of pathways but invasions via the long-distance (hundreds to thousands of kilometers) wind-assisted pathway is the least understood and, therefore, is a challenging pathway to actively manage (Hulme, 2015). The invasive pest problem is on the rise, because the ranges of many important pests are expanding as a result of climate change (Bebber, 2015). Any tool that increases the likelihood of detecting a pest arriving in a new environment will represent a major advance for biosecurity management.

A new type of atmospheric transport modeling, namely Lagrangian coherent structure (LCS) modeling (Peacock & Haller, 2013), has the potential to improve the understanding and prediction of biological invasions. The LCS approach provides insights into the fundamental underlying structures that govern complex mixing patterns in the atmosphere (Haller, 2015). Two types of LCS are considered—attracting and repelling. Attracting LCS in the aerial long-distance dispersal context can be thought of as "air bridges" that concentrate airborne particles (insects, pathogens, seeds, and smoke) along the LCS. Conversely, repelling LCS can be thought of as atmospheric "walls", which act as boundaries between air masses (Peacock & Haller, 2013). Subsequent references to LCS herein relate to attracting LCS unless otherwise stated.

Observations are rarely available of the exact time of arrival of invasive species in countries or locations where they are not already present because their presence is usually only noticed some time after a population establishes, often when damage or symptoms are observed on humans, animals, or host plants. Isolated islands make ideal study sites for these events because other forms of transport (such as human assisted pathways) and/or background sources can largely be excluded. We had the rare opportunity to investigate the linkages between long-distance dispersal of invasive Lepidoptera (which are readily trapped by light traps) and LCS using two datasets from two isolated islands. Two publications associated with these datasets robustly document long-distance, trans-oceanic dispersal of invasive Lepidoptera, in circumstances where the atmospheric pathway was the only reasonable mechanism for their arrival:

1. Eight events of invasive Lepidoptera movement from Australia to New Zealand's west coast (~2000 km east of mainland Australia across the Tasman Sea) (Fox, 1978).
2. Two events of Lepidoptera transport from Australia or New Zealand to the remote sub-Antarctic Macquarie Island (~2000 km SE of mainland Australia, ~1500 km SE of Tasmania and ~1000 km SE of New Zealand) (Greenslade et al., 1999).

Long-distance migration usually takes place at high altitudes—a few hundred meters above the relatively calm surface layer, where insects move around to feed and reproduce (Chapman et al., 2015). In these higher layers, migrations occur in directions close to downwind because the insects' flight speeds are lower than the wind speed (Chapman et al., 2015; Drake & Farrow, 1988). During long-distance migration, insects are often concentrated into stratified vertical layers, especially at night when the Planetary Boundary Layer is stable (Reynolds et al., 2008). Concentration of insects also occur horizontally in regions of flow convergence that are associated with atmospheric processes at a range of atmospheric scales. The most important of these for long-distance migration are mesoscale phenomena (weather systems that are around 5 km to several hundred kilometers in size) such as density currents, sea breezes, and storm outflows and synoptic-scale features (weather systems that span 1000 km or more) like fronts and cyclones (Drake & Farrow, 1988). The concentration of insects in regions of convergence is of particular importance to the LCS application, as attractive LCS are regions of flow convergence.

The relationship between LCS and long-distance dispersal was further evaluated by investigating trans-oceanic smoke transport emitted by major south-eastern Australian wildfires in 2020. Smoke plumes are known to transport a rich diversity of biological material ranging from microbes to seeds and insects (Fox, 1978; Kobziar & Thompson, 2020) and, therefore, could provide a mechanism for invasive species to reach a new environment.

METHODS

LCS modeling

To estimate the locations of LCS in a spatiotemporally varying velocity field, $\mathbf{v}(\mathbf{x},t)$, we calculated the ridges of the Finite-Time Lyapunov Exponent (FTLE) field (Nolan et al., 2020),

$$\sigma(\boldsymbol{x},t,T)=\frac{1}{2|T|}\log(\lambda_{\max}(\boldsymbol{C}(\boldsymbol{x}))) \tag{1}$$

where $\lambda_{\max}$ is the maximum eigenvalue of the right Cauchy-Green deformation tensor.

$\boldsymbol{C}=(\nabla\mathbf{F})\times(\nabla\mathbf{F})$, and $\mathbf{F}$ is the flow map, which gives the location of an air parcel initially located at position $\boldsymbol{x}$ at time t after being advected via the velocity field $\mathbf{v}$ for a duration T (which could be positive or negative). The FTLE backward time is a measure of how fast closely-spaced particle trajectories converge, and in forward time, conversely, is a measure of trajectory divergence (Shadden et al., 2005). Ridges in the backward-time FTLE field are regions of fastest trajectory convergence, known as attracting LCS. Conversely, ridges of the forward-time FTLE field indicates repelling LCS. The ridges of a FTLE field are calculated from a continuum of closely spaced particles (in our case, spaced 0.05°, roughly 5500 m) advected in a flow field (for our purposes, wind fields obtained from meteorological reanalysis datasets).

Attractive LCS concentrate material transported by the flow field (Shadden et al., 2005). Conversely, repelling LCS act as atmospheric "walls" which act as boundaries between air masses (Peacock & Haller, 2013). Since attracting and repelling LCS curves in a 2D flow are material curves, according to the Picard–Lindelof theorem, material cannot cross them (Meiss, 2007). Even though repelling LCS play an important role in atmospheric transport dynamics, we did not include them in our analysis. The reason for this is that an analysis showed (see Appendix S1 and Video S1) that the crossing point between attractive and repelling LCS are constantly on the move. It is, therefore, more conservative for a biosecurity analysis to not disqualify attractive LCS pathways because of a cross with a repelling LCS. In other words, for effective risk mitigation, false positives are more acceptable than false negatives.

The advection (the amount of time particles are transported in the flow field) time T used in the calculation of the FTLE field is application dependent; a reasonable approximation of T is the half-life of the transport phenomenon in question (Tallapragada et al., 2011). In this study, the advection period was chosen as 48 h for the Australia to New Zealand modeling and 12 h for the Macquarie Island case studies.

LCS are 2D surfaces in 3D flow fields. However, long-distance dispersal in the troposphere can be reasonably assumed to occur on 2D atmospheric surfaces of constant pressure (Tallapragada et al., 2011; Zdunkowski & Bott, 2003). Therefore, to avoid the complexity of dealing with 3D flow fields, this article focuses on detecting LCS on constant-pressure atmospheric levels where LCSs are approximated as continuous, smooth curves of fluid elements advected by the flow (Peacock & Haller, 2013). For an in-depth overview of the mathematical derivation of FTLE fields, refer to Shadden et al. (2005) and Haller (2015).

Meteorological and spatial data

The computation of LCS requires wind fields at a constant atmospheric pressure. We used the European Centre for Medium-Range Weather Forecasts Reanalysis ERA5 global atmospheric reanalysis data (Hersbach et al., 2018). This dataset covers the period January 1950 to present, at a horizontal spacing of 0.25° with a vertical resolution of 137 model layers at hourly intervals; it is the best available dataset that covers the periods of interest for our case studies (1971–2020).

To capture large-scale LCS and to reduce small scale noise, we tested several spatial and temporal resolutions of the ERA5 wind fields:

1. Australia to New Zealand: we found that identification of large-scale LCS associated with transport of material from Australia across the Tasman Sea to New Zealand requires coarser resolution data than the native dataset. Therefore, we used wind fields at a 1° horizontal spacing and at 6-h intervals.
2. Australia/New Zealand to Macquarie Island: we used the 0.25° data at hourly intervals as Macquarie Island is a small geographical feature with a surface area of 130 km^2, therefore, we considered smaller-scale structures would be more relevant.

For the lepidopteran case studies, we used wind data from the 950 hPa level, corresponding to roughly 500 m above mean sea level. This height corresponds to an atmospheric level already documented for bulk Lepidoptera migration (Wood et al., 2009) although some Lepidoptera are known to migrate at higher altitudes (Riley et al., 1995). For the case-studies of smoke transport, we used data from two atmospheric levels, 950 and 850 hPa (corresponding to roughly 1500 m above mean sea level) as the exact height of smoke transport is unknown. For the calculation of approximate travel-times along LCS pathways, interpolated wind speed values from 0.25° ERA5 data were used and averaged over the 48-h LCS advection period.

The natural geographical range of the lepidopteran case study species was determined from observations made by the public between 2008 and 2020 on a citizen science platform called iNaturalist (https://www.inaturalist.org), a joint initiative of the California Academy of Sciences and the National Geographic Society.

Fall armyworm case study

LCS modeling was performed at 6-h increments, with advection times of 48 h, over a period of 5 years (2017 to 2021, inclusive) using ERA5 wind fields. The analysis was conducted for the 950, 850, and 700 hPa atmospheric levels (roughly corresponding to 500 m, 1500 and 3000 m above mean sea level) since fall armyworm (FAW) are known to migrate at a range of altitudes (Ma et al., 2019; Wu et al., 2019). The LCS pathways between Australia and the North Island of New Zealand were reduced to single-pixel lines and summed.

Biological constraints

Climatic suitability modeling suggests that FAW populations are confined to north Australia during the months of May to October and spread south during the months of November to April (Maino et al., 2021). The modeled source locations reflected these distributions (Figure 4). The South Island of New Zealand is not currently climatically suitable to FAW establishment (Tepa-Yotto et al., 2021) and was therefore excluded from the modeling.

Little is known about FAW atmospheric survival and the length of time they can survive aloft. We assumed that they could survive a journey of 120 h (not taking in account the flight speed of the moths), based on the estimated travel times of the lepidopteran incursions investigated in Figure 1. If FAW flight speed is taken in account

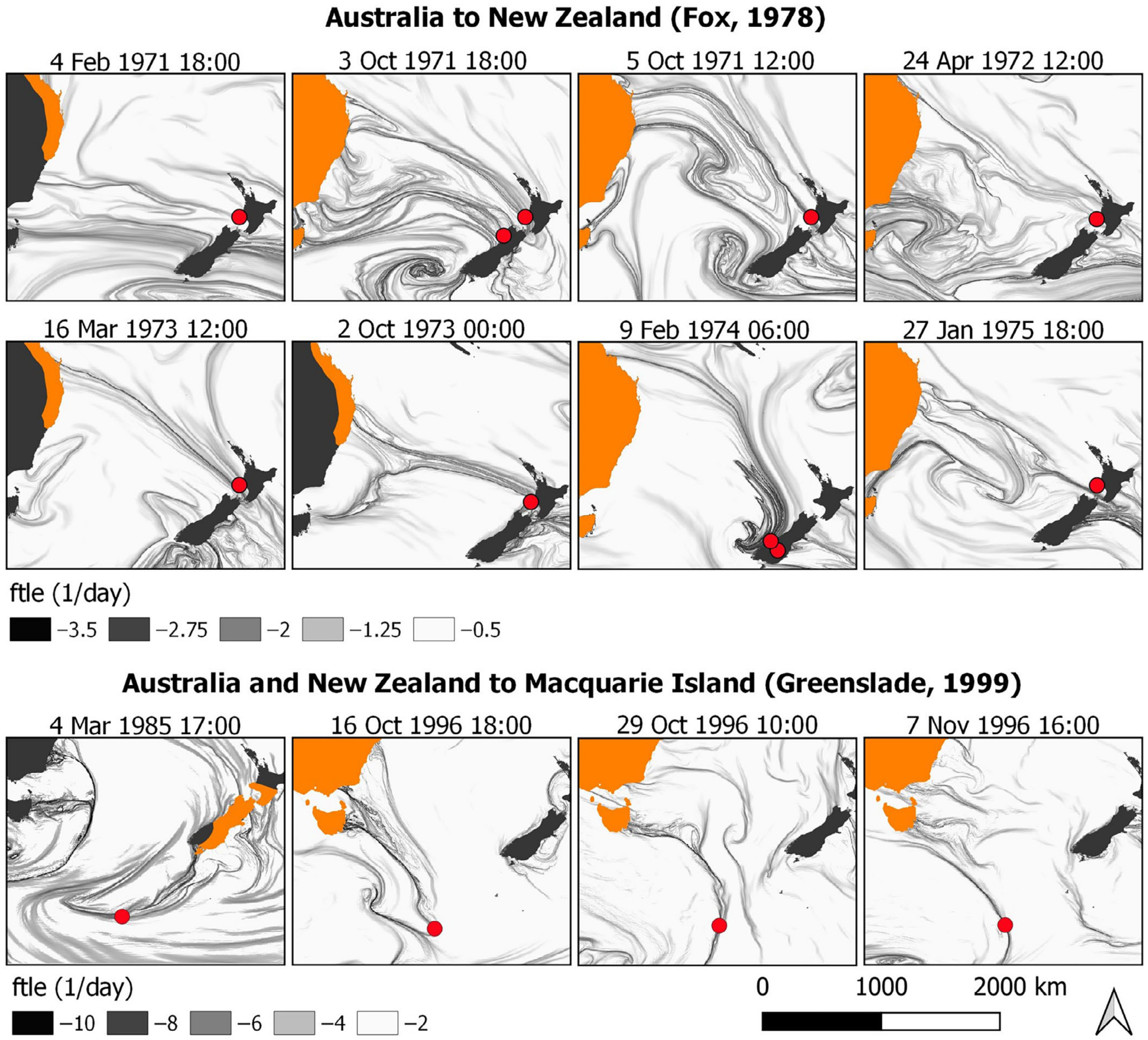


FIGURE 1 Lagrangian coherent structures (LCS) (gray shading) calculated for each of the documented Lepidoptera incursion events. The maps shown provide a "snapshot" view of the dynamic, sweeping LCS motion. The native geographical range of the invasive species is highlighted in orange. Places where migratory Lepidoptera specimens were captured or observed are shown as red dots. Times are New Zealand Standard Time (Greenwich Mean Time + 12) for the New Zealand incursions and in Macquarie Island Standard Time (Greenwich Mean Time + 10) for the Macquarie Island incursions.

(~4.5 m/s for noctuids) (Westbrook, 2008), this reduces the approximate travel time constraint to <~90–100 h. The approximate travel time along LCS pathways were calculated from interpolated wind speed values from 0.25° ERA5 data, averaged over the 48-h LCS advection period.

FAW is a tropical species, and adults are known to initiate migratory flights on sufficiently strong and warm winds (Maino et al., 2021). Pathways were therefore limited to those with a surface-level ambient temperature of 20°C or above as laboratory experiments showed optimal flight temperatures for FAW ranges between 20 and 25°C (Ge et al., 2021). Take-off temperatures were calculated as the maximum temperature over the 48-h LCS advection period from interpolated 0.25° ERA5 data 2 m above the surface.

Laboratory experiments show that FAW flight performance weakens significantly at temperatures below 10°C (Ge et al., 2021). Pathways were therefore removed if the average temperature along the pathway, calculated from

0.25° ERA5 data and averaged over the 48-h advection time, was below 10°C.

RESULTS

Invasive Lepidoptera travel along LCS

We simulated LCS for all the cases of documented Lepidoptera incursions into New Zealand's western coastline and Macquarie Island as described in Fox, 1978 and Greenslade et al., 1999, respectively:

1. Australia–New Zealand: LCS connections were present each time an invasive Lepidoptera species was trapped (Figure 1). In all but one of these incursion events, the estimated home range of the Lepidoptera species (i.e., the source population) that traveled (orange coloring, Figure 1) was either close to, or overlapped by the air bridge, meaning that the Lepidoptera had access to an LCS for trans-oceanic transport to New Zealand.
2. Australia/New Zealand to Macquarie Island: An LCS air bridge occurred in early March 1985 between NZ and Macquarie Island (Figure 1), the time of the first documented incursion. Air bridges were also present between Australia-Macquarie Island at the time of the second event, which occurred between October and November 1996 (Figure 1). These air bridges originated in Tasmania/South Australia, a known host range for the trapped species. Three possible incursion dates were identified, namely, 16 October, 29 October, and 7 November 1996.

In all cases, there were strong associations between the arrival of the Lepidoptera and the presence of LCS. The LCS pathways originated in regions that would provide a source population for the Lepidoptera and extended all the way to the trapping location (Figure 1). All the species identified in the incursions are either documented migrants, are long-lived as adults, or, if not documented, have related species in the same genus with the capability to undertake the flight times interpreted from LCS data:

1. Australia to New Zealand: 53 to 150 h with assumed flight speed of 3 m/s.
2. Australia/New Zealand to Macquarie Island: 20 to 43 h with assumed flight speed of 3 m/s.

Smoke dispersal along LCS

In early January 2020, smoke from bushfires in south-eastern Australia reached New Zealand over several days. The smoke plumes were so dense that they were captured by the Himawari-8 geostationary satellite (Japan Meteorological Agency, 2015). In addition, the smoke plume footprints were captured as an Aerosol Index by the Ozone Mapping and Profiler Suite Nadir-Mapper instrument on the Suomi-NPP satellite (Torres, 2019). The satellite imagery provides a rare opportunity to visualize the entire trans-oceanic pathway of long-distance material transport from Australia to New Zealand. Because the exact height of the smoke plume was unknown, LCS were calculated for two atmospheric heights, at 950 hPa, roughly 500 m above sea level, and 850 hPa, roughly 1500 m above sea level. One or more LCS were present at both atmospheric levels during each of the days smoke was transported from Australia to New Zealand (Figure 2). The smoke footprint shows strong similarities to the shape and locations of the LCS (Figure 2) and provides evidence of particulate concentration and transport in LCS.

DISCUSSION

LCS modeling for biosecurity management

We described that LCS are the atmospheric transport mechanisms that allow invasive species to reach new landmasses. LCS modeling was used to establish the likely source areas of the invasions. At present, conventional air-trajectory modeling is used to determine the risk of invasion of aerial invasive species, source locations, and migration routes, for example, the FAW studies by Ma et al. (2019), Qi et al. (2021), and Wu et al. (2022). However, it was shown that, in comparison to conventional air-trajectory modeling, novel LCS modeling is robust to wind field uncertainties and errors, and provides deeper insights by defining the fundamental underlying structures that organize complex mixing patterns in unsteady air flow (Haller, 2015).

The implications of these findings are globally applicable and suggest that LCS modeling could improve existing biosecurity systems for a pest invasion pathway that is currently unmanaged. LCS pathways are expected to occur more frequently than the number of successful incursions; therefore, LCS modeling will be most valuable for biosecurity management as part of an integrated aerobiological process modeling framework. The framework would combine LCS modeling with available knowledge on pest phenology, lifting and deposition mechanisms for the pest to enter and exit the LCS, atmospheric survival, distribution of host species or suitable habitat at the point of arrival, and climate suitability (Figure 3).

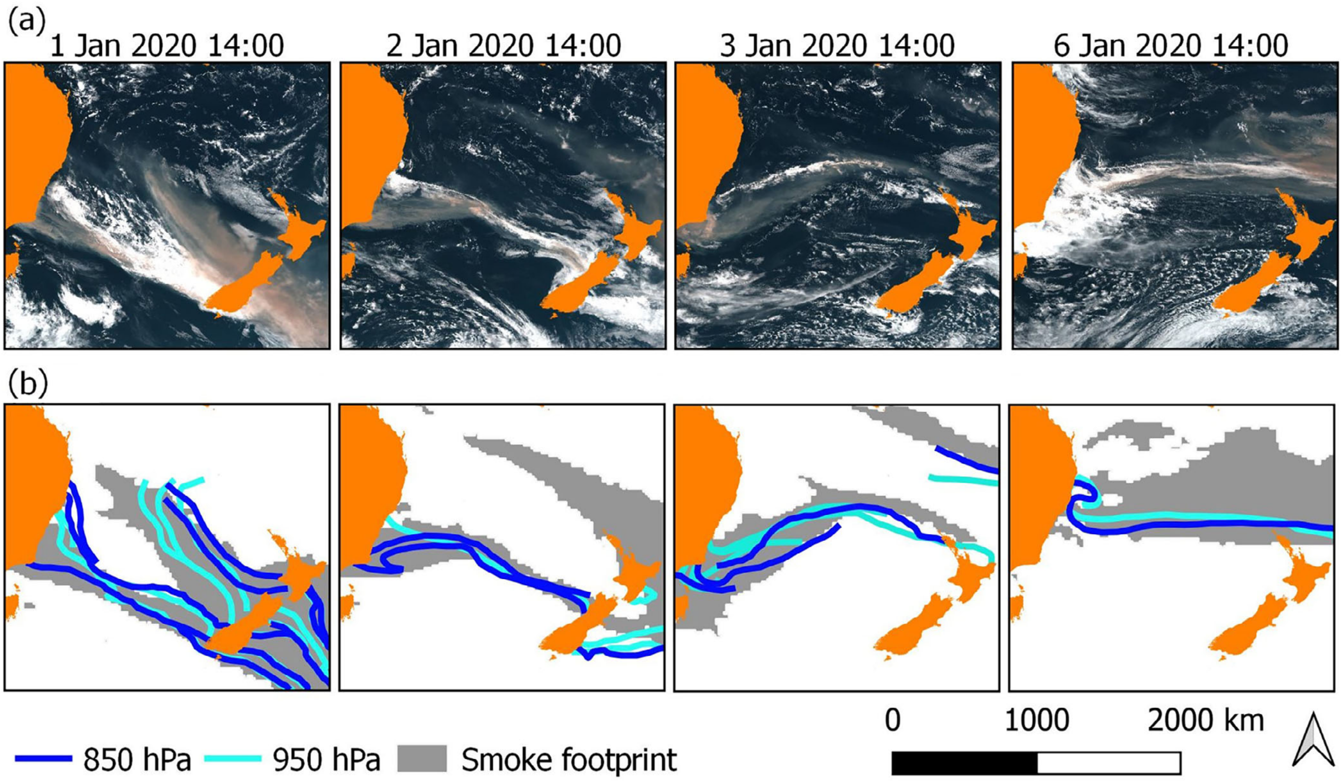


FIGURE 2 (a) Himawari-8 satellite imagery of trans-oceanic smoke dispersal from Australia to New Zealand, during early January 2020. Smoke appears reddish brown. (b) The smoke plume footprint, as observed by the Ozone Mapping and Profiler Suite (gray). The Lagrangian coherent structures associated with the smoke transport for the 950 hPa level (light blue) and for the 850 hPa level (dark blue). Times are New Zealand Standard Time (Greenwich Mean Time + 12). Orange coloring indicates landmass.

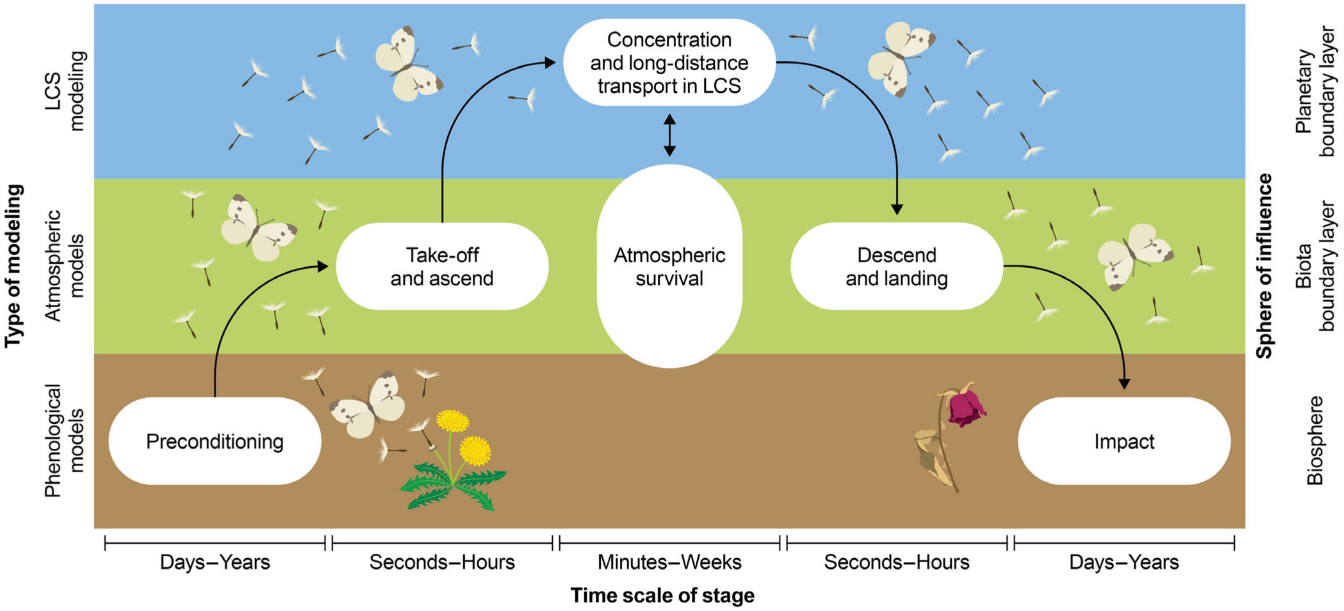
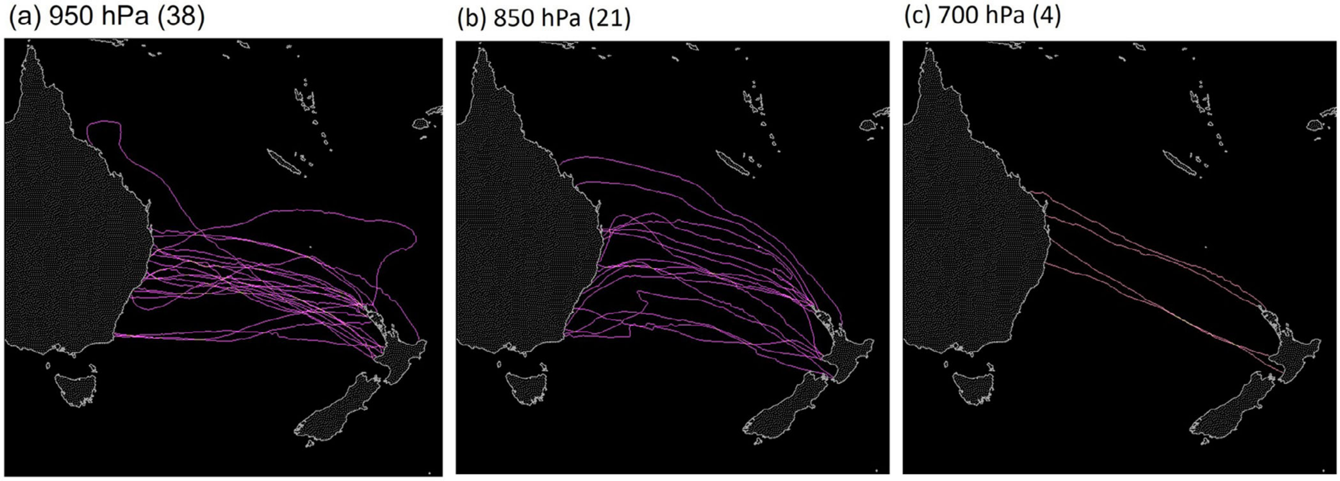


FIGURE 3 The role of Lagrangian coherent structures (LCS) modeling in an integrated aerobiological process modeling framework. Adapted from published work (Edmonds, 1979; Isard et al., 2005).

November–April, 2017–2021: Australia mainland source-region

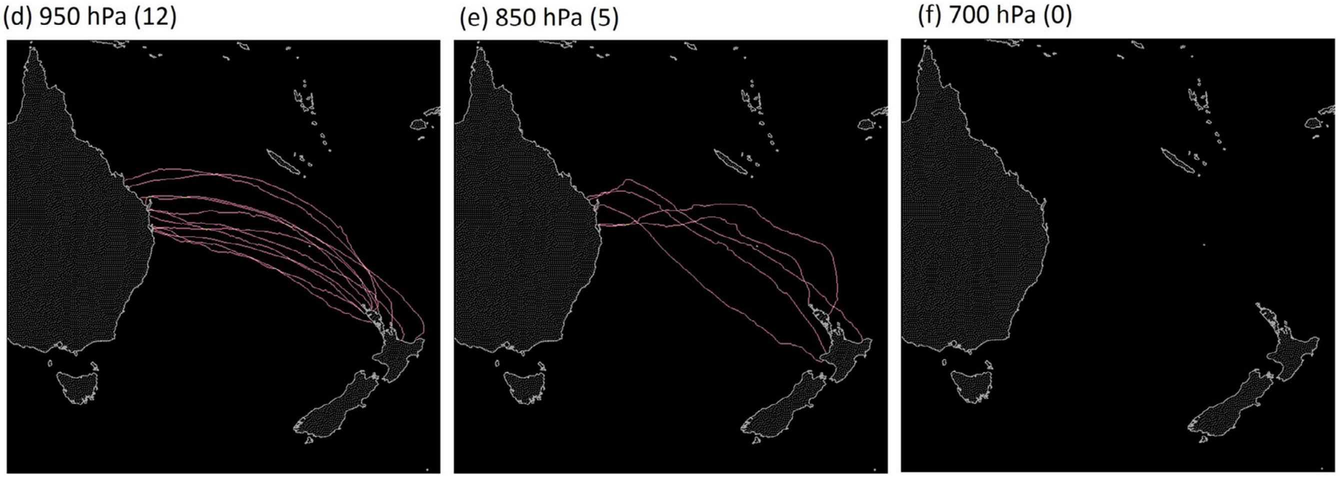


(a) 950 hPa (38)

(b) 850 hPa (21)

(c) 700 hPa (4)

May–October, 2017–2021: Northern Australia source-region



(d) 950 hPa (12)

(e) 850 hPa (5)

(f) 700 hPa (0)

FIGURE 4 The number of pathways that could result in a FAW incursion from Australia to New Zealand over the period 2017 to 2021 (inclusive) is given in brackets for each scenario. (a) All pathways meeting the FAW biological constraints at the 950 hPa atmospheric level, November to April. (b) All pathways meeting the FAW biological constraints at the 850 hPa atmospheric level, November to April. (c) All pathways meeting the FAW biological constraints at the 700 hPa atmospheric level, November to April. (d) All pathways meeting the FAW biological constraints at the 950 hPa atmospheric level, May to October. (e) All pathways meeting the FAW biological constraints at the 850 hPa atmospheric level, May to October. (f) All pathways meeting the FAW biological constraints at the 700 hPa atmospheric level, May to October.

Fall armyworm case-study

The damaging and highly invasive crop pest, FAW spreads widely by means of atmospheric dispersal, and reached Australia in February 2020 (Maino et al., 2021). Subsequently, it was expected that FAW could migrate to New Zealand. The first detections of FAW were made in March 2022 in New Zealand (Biosecurity New Zealand, 2022). FAW is used as an example to illustrate how the LCS modeling framework of Figure 3 can be used to identify potential high-risk FAW invasion events from Australia to New Zealand.

When biological constraints were applied to LCS modeling, the number of pathways of concern over the 5-year period, 2017–2021 (inclusive) are as follows for the different atmospheric levels and source regions modeled (Figure 4):

1. November–April (Australia mainland FAW source region): 950 hPa—38 pathways; 850 hPa—21 pathways; 700 hPa—4 pathways
2. May–October (Northern Australia source-region): 950 hPa—12 pathways, 850 hPa—5 pathways, 700 hPa—0 pathways

This modeling can inform biosecurity management in two ways:

1. The maps produced in Figure 4 can inform optimized targeted surveillance by identifying high-risk locations and times for FAW arrival in New Zealand.
2. Pathways of concern can be forecasted using meteorological parameters produced by numerical weather prediction models. The number of potential pathways (between 50 and 4 per atmospheric level over 5 years, when all months are considered) are sufficiently low for biosecurity systems to realistically respond.

The biosecurity of managed and natural ecosystems worldwide is under threat from airborne invasions of insects, pathogens and weeds (Diagne et al., 2021; Pyšek et al., 2020). Wind-assisted transport is a critically important pest-incursion pathway yet is poorly studied and difficult to manage, with few tools currently available for predicting airborne pest incursions (Hulme, 2015). Here we demonstrate that invasive pests can travel vast distances along predictable atmospheric pathways known as LCS. When LCS modeling is combined with knowledge on pest biology and atmospheric survival, high-risk areal invasion events can be predicted, making it possible to optimize surveillance efforts and detect pests early. Early detection simultaneously improves eradication potential and reduces eradication costs (Liebhold et al., 2016).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Custom code (Schou & Pretorius, 2022) developed for the fall armyworm case study is provided in Zenodo at https://doi.org/10.5281/zenodo.7324857. The python package Lagrangian was not developed by the authors of this paper and is available on the Github repository https://github.com/CNES/aviso-lagrangian. European Centre for Medium-Range Weather Forecasts Reanalysis ERA5 global atmospheric reanalysis data (Hersbach et al., 2018) are available from the Copernicus Climate Change Service Climate Data Store at https://doi.org/10.24381/cds.bd0915c6; these data were downloaded by searching for the U and V components of wind and temperature. Natural geographic range data were retrieved from iNaturalist https://inaturalist.nz/ by searching for the species observed by historical studies, listed in Appendix S1, and filtering for observations between 2008 and 2020.

REFERENCES

Bebber, D. P. 2015. "Range-Expanding Pests and Pathogens in a Warming World." *Annual Review of Phytopathology* 53: 335–56.

Biosecurity New Zealand. 2022. "FAW Response: Situation Report 18 as at 1300 Hours Thursday June 23, 2022." MPI Situation Report 18. Ministry for Primary Industries.

Chapman, J. W., D. R. Reynolds, and K. Wilson. 2015. "Long-Range Seasonal Migration in Insects: Mechanisms, Evolutionary Drivers and Ecological Consequences." *Ecology Letters* 18: 287–302.

Diagne, C., B. Leroy, A. C. Vaissière, R. E. Gozlan, D. Roiz, I. Jarić, J. M. Salles, C. J. A. Bradshaw, and F. Courchamp. 2021. "High and Rising Economic Costs of Biological Invasions Worldwide." *Nature* 592: 571–6.

Drake, V. A., and R. A. Farrow. 1988. "The Influence of Atmospheric Structure and Motions on Insect Migration." *Annual Review of Entomology* 33: 183–210.

Edmonds, R. L. 1979. *Aerobiology: The Ecological Systems Approach*. Straudsburg, PA and Oxford: Academic Press.

Fox, K. J. 1978. "The Transoceanic Migration of Lepidoptera to New Zealand — A History and a Hypothesis on Colonisation." *New Zealand Entomologist* 6: 368–80.

Ge, S. S., L. M. He, W. He, R. Yan, K. A. G. Wyckhuys, and K. M. Wu. 2021. "Laboratory-Based Flight Performance of the Fall Armyworm, *Spodoptera frugiperda*." *Journal of Integrative Agriculture* 20: 707–14.

Greenslade, P., R. A. Farrow, and J. M. B. Smith. 1999. "Long Distance Migration of Insects to a Subantarctic Island." *Journal of Biogeography* 26: 1161–7.

Haller, G. 2015. "Lagrangian Coherent Structures." *Annual Review of Fluid Mechanics* 47: 137–62.

Hersbach, H., B. Bell, P. Berrisford, G. Biavati, A. Horányi, J. Muñoz Sabater, J. Nicolas, et al. 2018. "ERA5 Hourly Data on Pressure Levels from 1959 to Present." Copernicus Climate Change Service (C3S) Climate Data Store (CDS). https://doi.org/10.24381/cds.bd0915c6.

Hulme, P. E. 2015. "Invasion Pathways at a Crossroad: Policy and Research Challenges for Managing Alien Species Introductions." *Journal of Applied Ecology* 52: 1418–24.

Isard, S. A., S. H. Gage, P. Comtois, and J. M. Russo. 2005. "Principles of the Atmospheric Pathway for Invasive Species Applied to Soybean Rust." *BioScience* 55: 851–61.

Japan Meteorological Agency. 2015. *Himawari-8/9 Standard Data User's Guide*. Tokyo: Japan Meteorological Agency.

Kobziar, L. N., and G. R. Thompson. 2020. "Wildfire Smoke, a Potential Infectious Agent." *Science* 370: 1408–10.

Liebhold, A. M., L. Berec, E. G. Brockerhoff, R. S. Epanchin-Niell, A. Hastings, D. A. Herms, J. M. Kean, et al. 2016. "Eradication of Invading Insect Populations: From Concepts to Applications." *Annual Review of Entomology* 61: 335–52.

Ma, J., Y. P. Wang, M. F. Wu, B. Y. Gao, J. Liu, G. S. Lee, A. Otuka, and G. Hu. 2019. "High Risk of the Fall Armyworm Invading Japan and the Korean Peninsula Via Overseas Migration." *Journal of Applied Entomology* 143: 911–20.

Maino, J. L., R. Schouten, K. Overton, R. Day, S. Ekesi, B. Bett, M. Barton, P. C. Gregg, P. A. Umina, and O. L. Reynolds. 2021.

"Regional and Seasonal Activity Predictions for Fall Armyworm in Australia." *Current Research in Insect Science* 1: 100010.

Meiss, J. D. 2007. *Differential Dynamical Systems*. Philadelphia, PA: Society for Industrial and Applied Mathematics.

Nolan, P. J., H. Foroutan, and S. D. Ross. 2020. "Pollution Transport Patterns Obtained through Generalized Lagrangian Coherent Structures." *Atmosphere* 11: 1–14.

Peacock, T., and G. Haller. 2013. "Lagrangian Coherent Structures: The Hidden Skeleton of Fluid Flows." *Physics Today* 66: 42–7.

Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, J. T. Carlton, W. Dawson, et al. 2020. "Scientists' Warning on Invasive Alien Species." *Biological Reviews* 95: 1511–34.

Qi, G. J., J. Ma, J. Wan, Y. L. Ren, S. McKirdy, G. Hu, and Z. F. Zhang. 2021. "Source Regions of the First Immigration of Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) Invading Australia." *Insects* 12: 1104.

Reynolds, D. R., A. D. Smith, and J. W. Chapman. 2008. "A Radar Study of Emigratory Flight and Layer Formation by Insects at Dawn over Southern Britain." *Bulletin of Entomological Research* 98: 35–52.

Riley, J. R., D. R. Reynolds, A. D. Smith, A. S. Edwards, X. X. Zhang, X. N. Cheng, H. K. Wang, J. Y. Cheng, and B. P. Zhai. 1995. "Observations of the Autumn Migration of the Rice Leaf Roller *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) and Other Moths in Eastern China." *Bulletin of Entomological Research* 85: 397–414.

Schou, W. C., and I. Pretorius. 2022. "Using Lagrangian Coherent Structures to Determine Dispersal of Invasive Species (1.1.0.0)." Zenodo. https://doi.org/10.5281/zenodo.7324857.

Shadden, S. C., F. Lekien, and J. E. Marsden. 2005. "Definition and Properties of Lagrangian Coherent Structures from Finite-Time Lyapunov Exponents in Two-Dimensional Aperiodic Flows." *Physica D: Nonlinear Phenomena* 212: 271–304.

Tallapragada, P., S. D. Ross, and D. G. Schmale. 2011. "Lagrangian Coherent Structures Are Associated with Fluctuations in Airborne Microbial Populations." *Chaos* 21: 033122.

Tepa-Yotto, G. T., H. E. Z. Tonnang, G. Goergen, S. Subramanian, E. Kimathi, E. M. Abdel-Rahman, D. Flø, et al. 2021. "Global Habitat Suitability of *Spodoptera frugiperda* (JE Smith) (Lepidoptera, Noctuidae): Key Parasitoids Considered for its Biological Control." *Insects* 12: 273.

Torres, O. 2019. *OMPS-NPP L2 NM Aerosol Index Swath Orbital V2*. Greenbelt, MD: Goddard Earth Sciences Data and Information Services Center (GES DISC).

Westbrook, J. K. 2008. "Noctuid Migration in Texas within the Nocturnal Aeroecological Boundary Layer." *Integrative and Comparative Biology* 48: 99–106.

Wood, C. R., D. R. Reynolds, P. M. Wells, J. F. Barlow, I. P. Woiwod, and J. W. Chapman. 2009. "Flight Periodicity and the Vertical Distribution of High-Altitude Moth Migration over Southern Britain." *Bulletin of Entomological Research* 99: 525–35.

Wu, M. F., G. J. Qi, H. Chen, J. Ma, J. Liu, Y. Y. Jiang, G. S. Lee, A. Otuka, and G. Hu. 2022. "Overseas Immigration of Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), Invading Korea and Japan in 2019." *Insect Science* 29: 505–20.

Wu, Q. L., L. M. He, X. J. Shen, Y. Y. Jiang, J. Liu, G. Hu, and K. M. Wu. 2019. "Estimation of the Potential Infestation Area of Newly-Invaded Fall Armyworm *Spodoptera frugiperda* in the Yangtze River Valley of China." *Insects* 10: 298.

Zdunkowski, W., and A. Bott. 2003. *Dynamics of the Atmosphere: A Course in Theoretical Meteorology. Page Thermodynamics of the Atmosphere*. New York: Cambridge University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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