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# A geospatial model of entry pathways of lumpy skin disease virus introduction into Australia

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## Abstract

Lumpy skin disease (LSD) is a disease of bovines resulting from the mechanical transmission of lumpy skin disease virus (LSDV) by arthropod vectors.

While LSD has never been reported in Australia, the disease has spread through Asia and recently expanded to neighbouring countries such as Indonesia. The detection of LSD in Australian cattle would likely lead to trade restrictions, resulting in Australian cattle industries experiencing severe economic losses. There is a need for geospatial decision support tools to support border and post border surveillance efforts through the identification of areas which would be more vulnerable to a LSDV introduction. Previous risk assessments have calculated that overall risk of introduction into Australia is negligible to very low after evaluating four entry pathways, including windborne dispersal of arthropod vectors, commercial vessels carrying hitchhiker arthropod vectors (excluding live export vessels), returning live export vessels carrying hitchhiker arthropod vectors, and movements in Torres Strait Treaty area leading to the transport of hitchhiker arthropod vectors. However, the studies also reported very high uncertainty given a lack of robust empirical data for many of the model parameters and only described risk in terms of each pathway as a whole rather than describing spatial variation in risk.

This study aimed to develop a novel integrated geospatial model for simulating the likelihood of LSDV-carrying vectors entering Australia via two different entry pathways: transport of vectors through shipping channels and vectors being carried long distances by strong wind currents. This model was used to explore the spatial variation in suitability for LSDV-carrying vectors entering Australia for each pathway independently and combined to identify geographical areas with the highest suitability. Furthermore, the study incorporated species distribution modelling and current bovine LSD case data in neighbouring countries to better model the current suitability of LSD in livestock, which were not included in the previous risk assessments.

Pathway one showed the ports at Port Hedland and Dampier as having the highest suitability for LSDV-carrying vectors entering Australia compared to the rest of the country. Pathway two showed highest comparative suitability in Far North Queensland, with suitability extending as far as 25 degrees south. Furthermore, likelihood of vectors being carried by wind currents into Australia was highest in the summer months. A model combining both pathways highlighted areas along the northern tip of Far North Queensland and around Port Hedland in Western Australia as having the highest suitability for LSDV-carrying vectors entering Australia compared to the rest of the country. These findings may assist future modelling of exposure and spread of LSDV in the Australian bovine population following a successful incursion event, which may help guide local authorities with planning and prioritisation of integrated surveillance activities.

## Keywords

Lumpy skin disease, geospatial modelling, wind dispersal, insect vectors

## Introduction

Lumpy skin disease (LSD) affects bovines such as cattle and buffalo and represents a significant risk to Australia's cattle industry<sup>1</sup>. As of November 2025, Australia remains free of LSD with no reports of the disease in the country to date<sup>2</sup>. However, since 2019 LSD has been reported in east and south Asian countries<sup>3,4</sup>, and cases have been reported across neighbouring Indonesia since 2022<sup>5,6</sup>.

Lumpy skin disease is caused by lumpy skin disease virus (LSDV), which is a virus in the *Poxviridae* family<sup>7-9</sup>. The virus is spread primarily through mechanical transmission via vectors such as biting arthropod vectors, with experimental evidence demonstrating this for *Aedes aegypti* mosquitoes<sup>10</sup>, stable flies (*Stomoxys calcitrans*)<sup>11,12</sup> and ticks (*Rhipicephalus appendiculatus*<sup>13</sup> and *Amblyomma hebraeum*<sup>14</sup>). Probabilistic models developed by Sanz-Bernardo et al.<sup>15</sup> indicated that *C. nubeculosus* may also play an important role in LSDV transmission, although transmission from midges to bovines has never been directly demonstrated<sup>15</sup>.

Previous LSDV outbreaks in Asia are considered to be linked with cross-border cattle movement between neighbouring countries<sup>3,16</sup>, however, Australia is an island nation and therefore any importation of cattle is restricted to seaports, where strict biosecurity measures are in place<sup>1</sup>. A literature review conducted by Owada et al.<sup>17</sup> identified wind patterns as a possible vehicle for long distance transportation of LSDV-carrying vectors. Eagles et al.<sup>18</sup> applied the generic spatial insect model (GenSIM) and Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) models to demonstrate the potential for bluetongue virus-competent *Culicoides* midges being carried by wind currents from the island of Timor into north-western and northern Australia<sup>18</sup>. More recently, Hall et al.<sup>19</sup> used a HYSPLIT model to evaluate the risk of LSDV-carrying flying vectors being carried by wind into north-western and northern Australia from Indonesia, Papua New Guinea, and Timor-Leste<sup>19</sup>. This evidence highlights the importance of this pathway for the introduction of LSDV into Australia from neighbouring countries where LSD is present rather than cattle importation.

The detection of LSD in Australian cattle would likely lead to the introduction of trade restrictions on exports of both live cattle and meat and dairy products<sup>1</sup>. The World Organisation for Animal Health (WOAH) recommends that importing countries should not place conditions on exporting countries where LSD is present for imports of skeletal muscle meat<sup>20</sup>, however, it may not be possible to anticipate how importing countries would react to LSD being detected in Australia. Australian beef and dairy exports were worth A\$9.2 billion in 2021<sup>21</sup> and A\$3.8 billion in 2021-2022<sup>22</sup>, respectively. Australia exported 771,931 live cattle in 2021<sup>23</sup>, with the value of live cattle exports estimated at A\$1.3B in 2019-20 to the national economy<sup>24</sup>. Consequently, any trade restrictions would result in great economic losses for the Australian cattle industry.

This threat to Australia's cattle industries has prompted assessments of the risk of LSDV entering Australia<sup>25,26</sup>. Notably, risk assessments investigating the potential for LSDV to enter Australia and cause disease in cattle used probabilistic modelling to evaluate four different unregulated pathways: 1) windborne dispersal of arthropod vectors, 2) commercial vessels carrying hitchhiker arthropod vectors (excluding live export vessels), 3) returning live export vessels carrying hitchhiker arthropod vectors, and 4) Torres Strait Treaty movements carrying hitchhiker arthropod vectors<sup>25,26</sup>. These risk assessments identified the most likely overall risk of incursion as being negligible to very low, although with very high uncertainty given a lack of robust empirical data for many of the model parameters<sup>25,26</sup>.

The number of annual LSDV incursions leading to clinical LSD cases in Australian cattle through windborne dispersal of arthropod vectors was estimated for each Northern Australia Quarantine Strategy (NAQS) risk zone, as well as three areas representing the remainder of northern Western Australia, Northern Territory, and western Queensland. While the NAQS risk zones along the coastline provide a relatively high degree of spatial granularity, the inland NAQS risk zones span large geographical areas, making it difficult to assess the localised variation in risk within these inland areas. Maps describing the NAQS risk zones can be found elsewhere<sup>19</sup>. The

modelling of the risk of commercial vessels carrying hitchhiker arthropod vectors estimated the probability of LSDV-carrying vectors entering Australia through Australian seaports. The model factored in country-level totals for bovine and vector population data, LSDV transmission probabilities, such as number of vectors biting each bovine per infectious day, commercial vessel speed and travel distance, and trade volumes between Australia and origin countries. With the exception of Indonesia, the model did not take into account spatial variation within origin countries for bovine and vector populations.

The LSD outbreak situation in Australia's neighbouring countries is continually changing, and therefore there is a need to incorporate up-to-date LSD case data to better model the distribution of potentially infected bovines and vectors carrying LSDV in these neighbouring countries. These species distributions in the origin countries are an important factor in modelling the entry pathways into Australia.

The aim of the current study was to develop an integrated geospatial model, which incorporates the latest species data and bovine LSD case data, to identify the areas of Australia with the highest suitability for incursion by LSDV-carrying vectors via two potential entry pathways: 1) the transporting of LSDV-carrying mechanical vectors through shipping channels and 2) LSDV-carrying mechanical vectors being carried long distances by strong wind currents. This model assesses the suitability for incursion by LSDV-carrying vectors, which will provide valuable input to future modelling of the spatial variation in the risk of Australian cattle being infected with LSDV following the successful incursion of LSDV-carrying vectors into the country. Such modelling may be beneficial in designing geospatial decision support tools that support targeted border and post border surveillance efforts in Australia.

## Results

All species distribution model (SDM) raster maps for the selected vector species were found to have a receiver operating characteristic (ROC) area under the curve (AUC) value of greater than 0.9 and therefore the models were considered to exhibit strong discriminative performance on the occurrence data used to train the models.

### Animal and vector distribution modelling

The SDM vector distribution probability maps generated for *Ae. aegypti*, *Cx. quinquefasciatus*, *A. stephensi*, *Stomoxys spp.*, and *Culicoides spp.* showed spatial variation between species across the selected 16 countries (Supplementary Figures S1–S5). *Aedes aegypti* were estimated to be the most common vector species in South-east Asia. *Stomoxys spp.* were estimated to be common in localised areas in China and Indonesia. *Culicoides spp.* were estimated to be present in a wide geographical area across the selected 16 countries.

The combined bovine population estimate map estimated the highest density of bovine population in northern India. Density was considerably lower in all other 15 countries compared to India (Supplementary Figure S6).

### Suitability of potentially infected bovines

The WOA World Animal Health Information System (WAHIS) online database contained data for 1,389 outbreaks of LSD, representing 526,996 cases of LSD over the period of 1 January 2018 to 30 June 2024. The vast majority of the cases were for cattle and buffalo (526,979), with the remaining 17 cases describing LSD cases in *Bos frontalis*, *B. gaurus*, and *B. javanicus*.

The structural equation modelling (SEM) produced for suitability of bovines potentially infected with LSDV had a Comparative Fit Index (CFI) value of 1.0 and a Root Mean Square Error of Approximation (RMSEA) value of less than 0.001 and therefore was considered valid.

The SEM suitability map indicated that LSDV-infected bovines were most likely to be present in India, southern Vietnam, Thailand, and Cambodia, and in the Indonesian island of Java (Supplementary Figure S7).

## Suitability of vectors potentially carrying LSDV

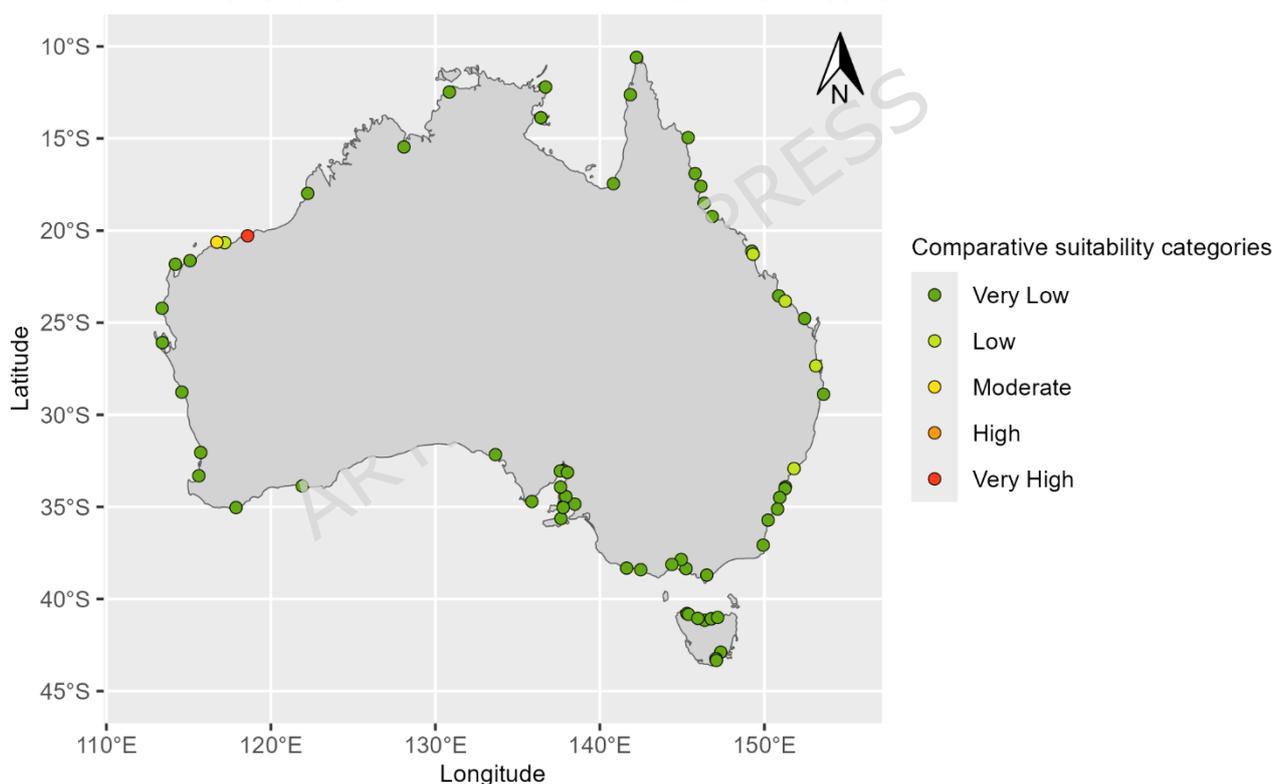
The multiple-criteria decision analysis (MCDA) raster suitability map suggested that flying mechanical vectors were most likely to be present in southern India, Hong Kong, south-east Asia, and Indonesian island of Java (Supplementary Figures S8).

### LSDV introduction via LSDV-carrying flying mechanical vectors entering through shipping ports (Pathway 1)

Of the identified 138 shipping ports in the selected 16 countries, the country with the greatest number of shipping ports was Indonesia (29), followed by China (26) and India (19). According to the OEC export volumes for 2023, in terms of trade value, 27.3% of Australia's imports originated in China, followed by the Republic of Korea (6.4%), and Singapore (5.0%).

The variation in comparative suitability for vector incursion in the current analysis suggests that trade volume influenced suitability for vector incursion more than shipping distance, with the comparative suitability categorised as very high in Port Hedland and moderate in Dampier, both Western Australian ports in the list of top ten port calls for Australia in the 2018–2019 financial year (Figure 1). The other 64 ports were categorised as low (5) and very low (59).

Map of comparative suitability for LSDV introduction into Australia via LSDV-carrying flying mechanical vectors entering through shipping ports



[Figure created by Owada (2024)]

Figure 1. Map of comparative suitability for LSDV introduction into Australia via shipping ports (Pathway 1)

### LSDV introduction through LSDV-carrying flying mechanical vectors carried by wind currents (Pathway 2)

The forward projection of wind trajectories from 195 coordinates across Indonesia, Papua New Guinea, and Timor-Leste demonstrated the potential for vectors to be carried by wind currents from multiple locations in these countries to a wide range of areas across northern Australia (Figure 2). Furthermore, it was found that the forward projected wind trajectories were most likely to intersect with Australia in the summer months of December, January, and February. This period is referred to as the wet season in the Monsoonal North by the Australian Bureau of

Meteorology<sup>27</sup>. The likelihood of vector incursion dropped significantly in autumn and the average monthly total number of intersections below five for the period of June–September across all five modelled years (Figure 3).

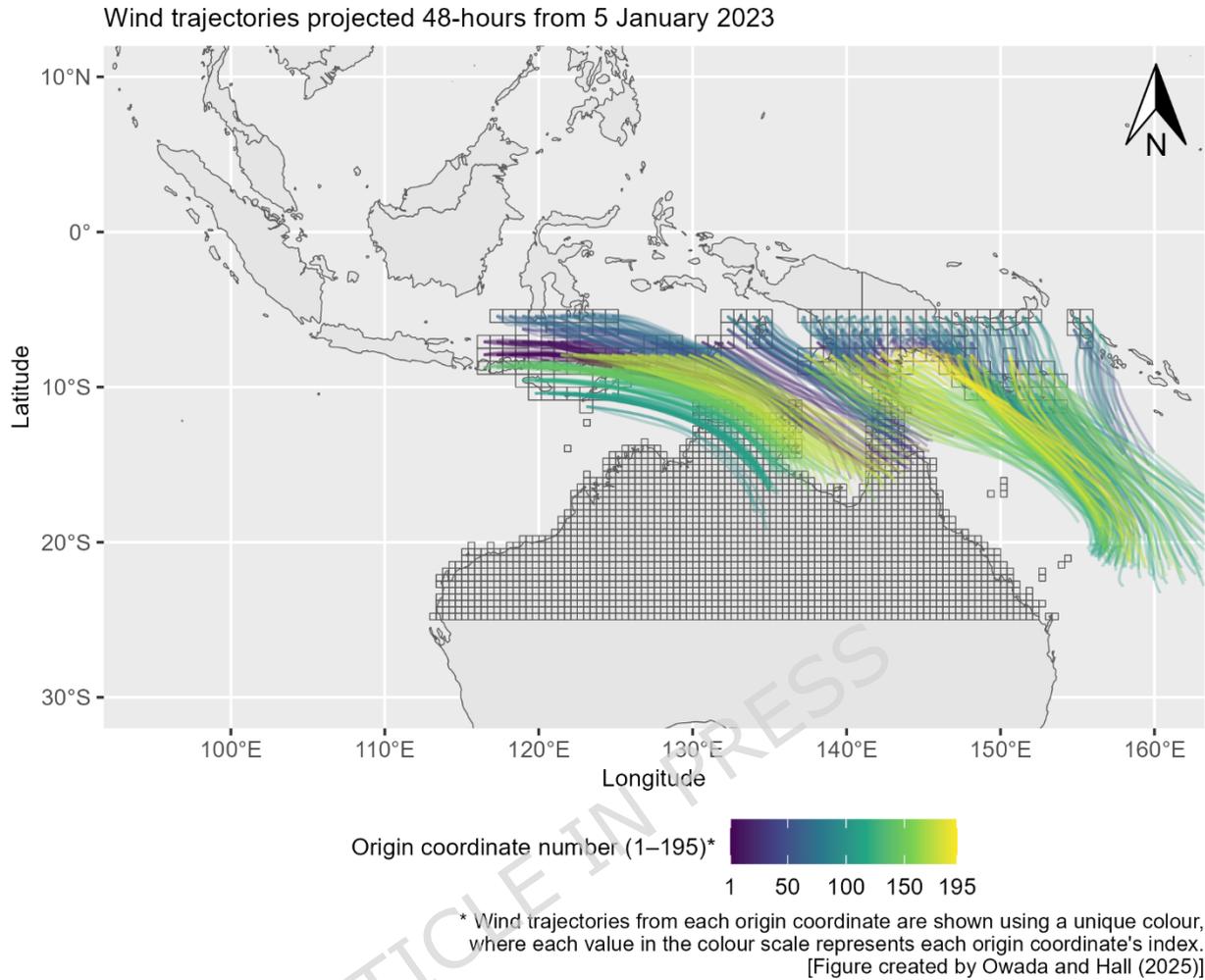


Figure 2. Example of projected 48-hour wind trajectories from 195 coordinates in Indonesia, Papua New Guinea, and Timor-Leste on 5 January 2023. This date was chosen to demonstrate a day on which wind trajectories intersected with Australia.

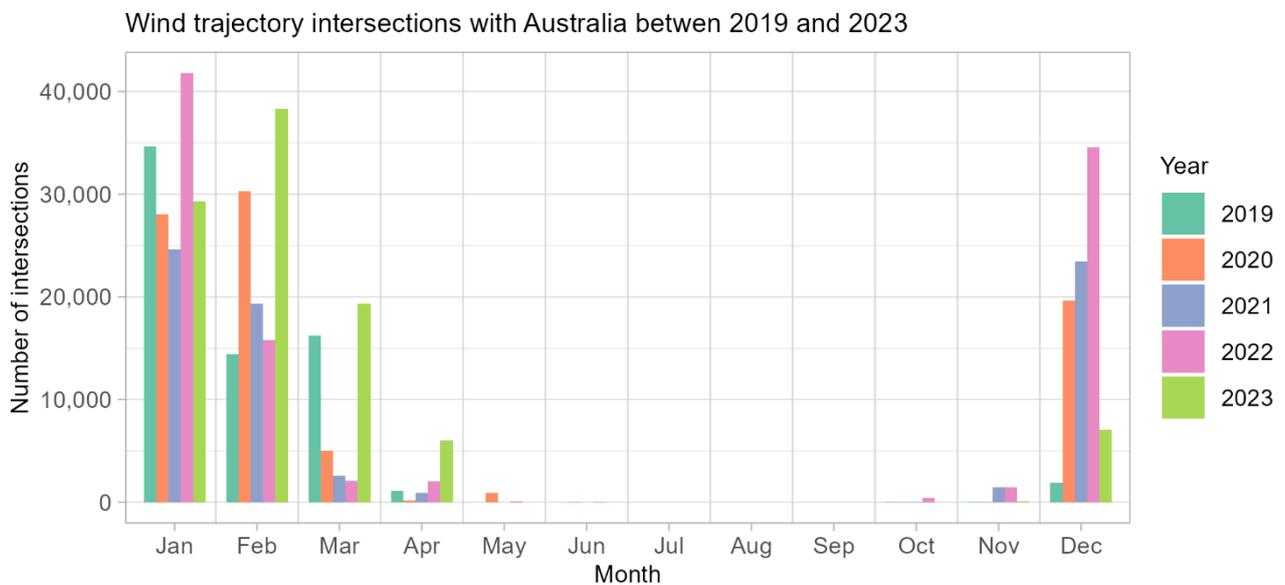
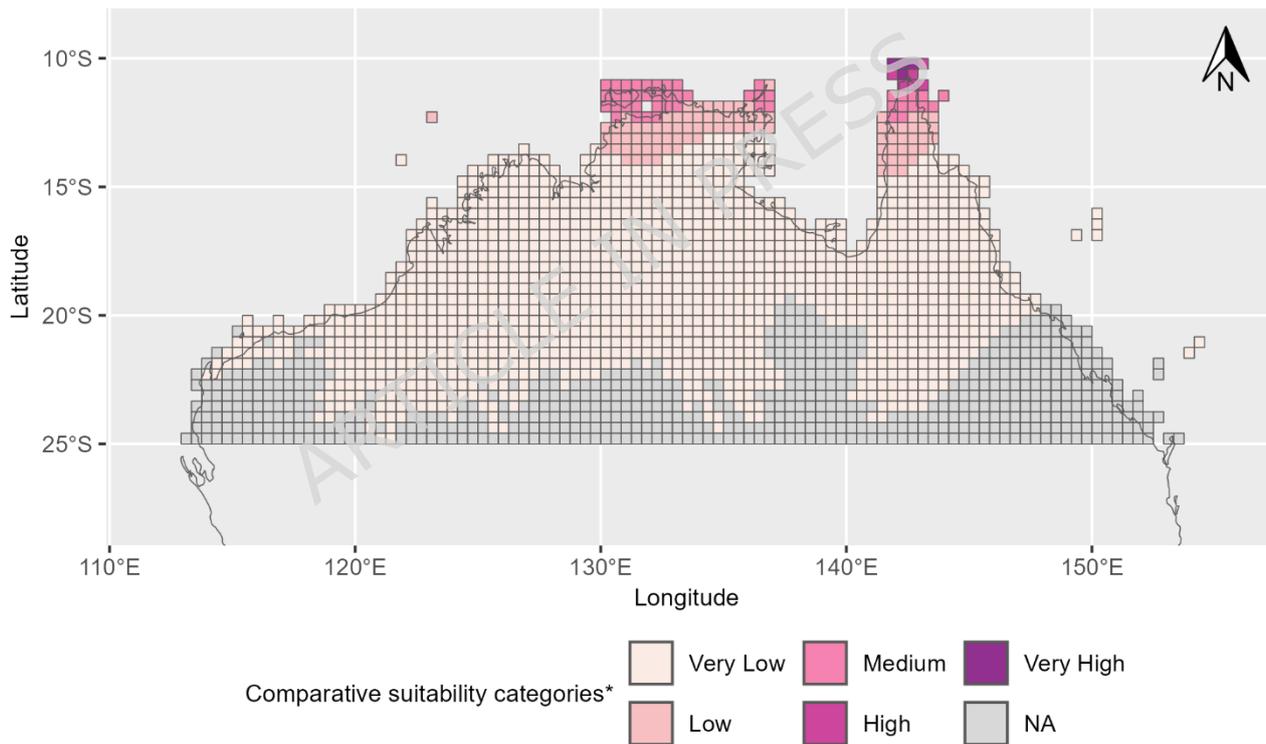


Figure 3. Monthly variation in wind trajectories intersecting with Australia between 2019 and 2023

Combining the total numbers of forward projected wind trajectories intersecting Australia over 2019–2023 with the MCDA raster data for suitability of flying mechanical vectors potentially carrying LSDV in Indonesia, Papua New Guinea, and Timor-Leste, shows the highest comparative suitability for vector incursion in Far North Queensland, followed by the northern areas of Northern Territory and Queensland, with suitability extending as far as 25 degrees south in Western Australia and to a slightly lesser extent in Northern Territory and Queensland (Figure 4). The projection of all wind trajectories over this five-year period indicated that it is unlikely that LSDV-carrying vectors could be transported further south than 25 degrees south by wind currents over a 48-hour period.

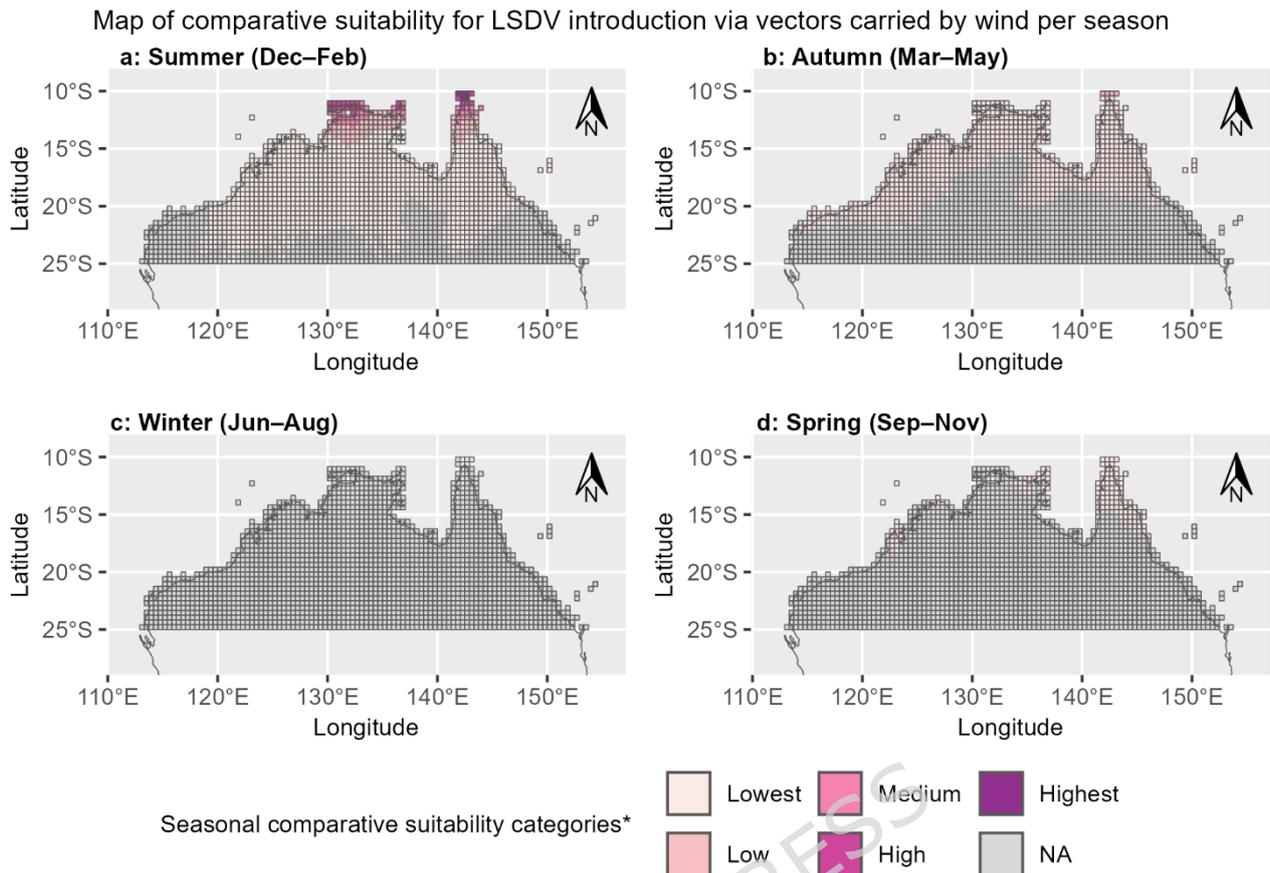
When looking at the comparative suitability for vector incursion at a seasonal level, the summer months (December–February) showed a similar spatial distribution to that of the 5-year total comparative suitability map (Figure 5 Panel A). The spatial extent contracts in Autumn (March–May) and is mostly categorised as seasonal lowest (Figure 5 Panel B). In winter (June–August), the few numbers of wind trajectory intersections resulted in areas categorised as seasonal lowest in a localised area in Far North Queensland (Figure 5 Panel C). In spring (September–November), the spatial extent of suitability expanded slightly into northern Queensland, north-eastern Northern Territory, and northern Western Australia, but with all areas categorised as seasonal lowest (Figure 5 Panel D).

Map of comparative suitability for LSDV introduction via vectors carried by wind based on 2019–2023 wind trajectories



[Figure created by Owada (2024)]

Figure 4. Map of comparative suitability for LSDV introduction into Australia via vectors carried by wind currents (Pathway 2)



\* All seasons use comparative suitability categories based on the consistent scale of incursion risk values.

[Figure created by Owada (2024)]

Figure 5. Maps of comparative suitability for LSDV introduction into Australia via vectors carried by wind currents (Pathway 2 – per season)

## Combined suitability for LSDV introduction into Australia via two pathways

The final map combining the two introduction pathways shows that the highest comparative suitability for LSDV-carrying vector introduction into Australia is in the tip of Far North Queensland, with suitability ranging from very high to moderate, in comparison to the rest of Australia. The incursion suitability in Port Hedland and Dampier in Western Australia was also being categorised as very high and moderate, respectively (Figure 6). The comparative suitability for the north western and north eastern tips of Northern Territory are categorised as low with the comparative suitability category falling to very low for most of the inland area of the northern half of Australia. The comparative suitability is categorised as very low for most all ports in the southern half of Australia and in all of Tasmania (Figure 6).

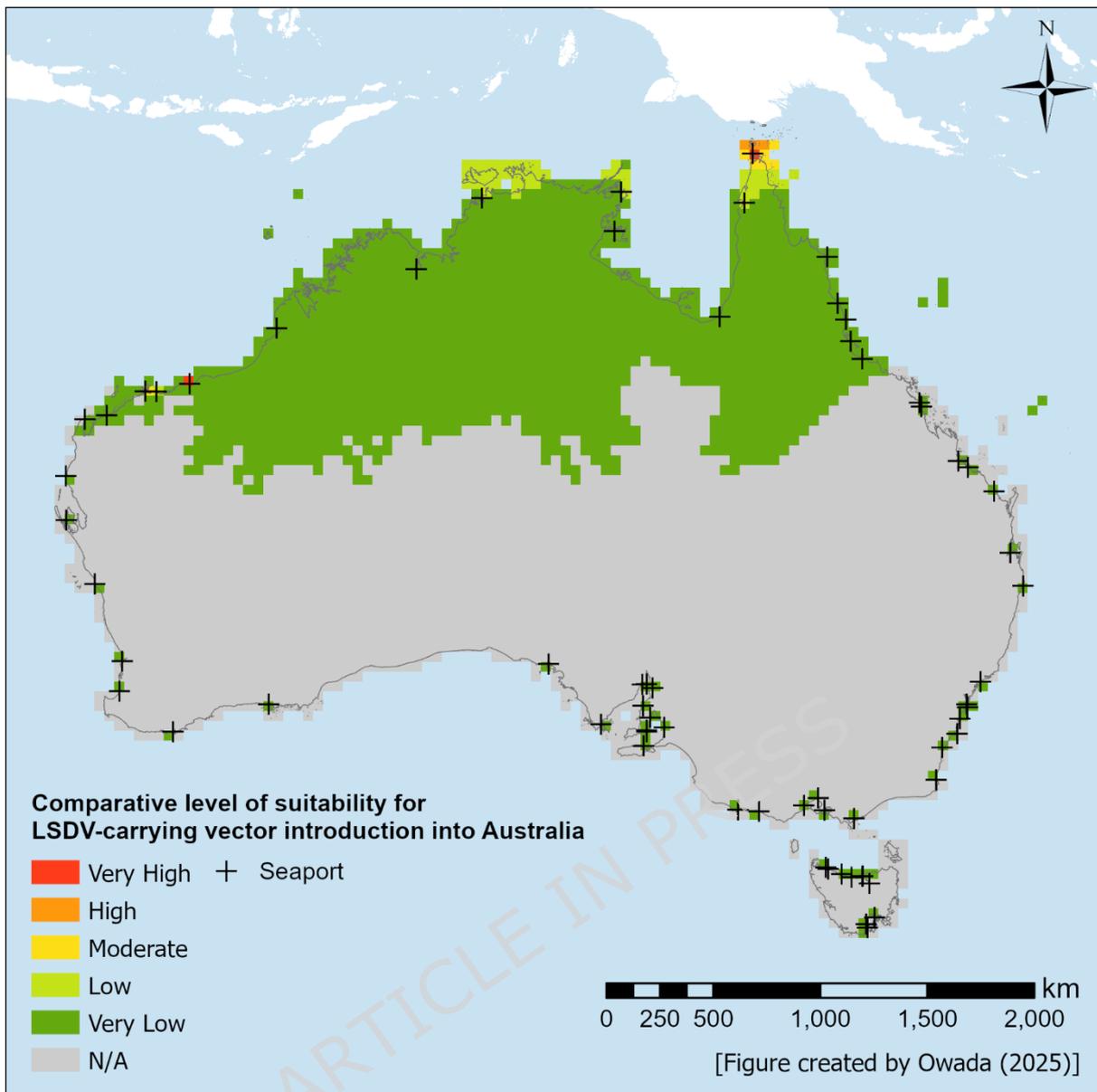


Figure 6. Map of comparative suitability for LSDV introduction via two pathways combined

## Sensitivity analysis results

The sensitivity analysis produced differences in the geographical distribution of suitability for bovines potentially infected with LSD and the flying mechanical vector potentially carrying LSDV, however, the geographical distribution described by the map of combined comparative suitability for LSDV introduction suitability did not change compared to the map produced by the full model.

## Discussion

The geographical spread of LSDV through South East Asia in recent years has seen the virus come into close proximity to Australia<sup>3-6</sup>. To mitigate the risk of LSDV introduction, Australia applies strict biosecurity measures at all international ports, including disinsection of vessels, to minimise the probability of LSDV-carrying vectors from entering the country<sup>1</sup>. From a policy perspective, Australia developed an LSD action plan detailing activities being undertaken to enhance Australia's preparedness for a potential incursion of LSD, including surveillance, as well as response activities in the event of LSD being detected in Australia<sup>28</sup>. A major geographical focus of surveillance comprises risk areas under the Northern Australian Quarantine Strategy (NAQS) which have been the focus of previous LSDV risk assessments

using probabilistic modelling<sup>25,26</sup>. These studies have estimated the overall risk of LSDV being introduced into the Australian cattle population as being negligible to very low. The risk estimates were attributed a high level of uncertainty partly due to the difficulty in measuring geospatial changes in the role of underlying risk factors, which in turn are likely to influence the suitability of some areas in Australia to be receptors of LSD-carrying vectors<sup>25,26</sup>. The present study employed a geospatial modelling approach that supplements existing biosecurity risk assessments through exploring the spatial variation in suitability of LSDV-carrying vectors successfully entering Australia. The output of the current model may complement the action plan by guiding more spatially-targeted surveillance and preparedness activities based on areas with highest comparative suitability for incursion for LSDV-carrying vectors. Additionally, the various risk factors associated with the two potential pathways for LSDV-carrying vector introduction investigated in this study highlight the need for conducting integrated vector surveillance.

Previous risk assessments evaluated the risk of LSDV introduction via wind dispersal of vectors into Northern Australian Quarantine Strategy (NAQS) risk zones rather than all areas of Australia reachable by wind currents within 48 hours of Australia's neighbouring countries<sup>25,26</sup>. The risk zones with the highest reported risk in the previous risk assessments spanned the Tiwi Islands and the areas between Darwin and the Cobourg Peninsula in the Northern Territory, which were also found to represent a high comparative suitability for LSDV-carrying vector introduction in the current study<sup>25,26</sup>.

Our results of the model for the introduction pathway considering LSDV-carrying flying mechanical vectors being transported by shipping vessels into Australia (Pathway 1) indicated the highest comparative suitability for incursion was at the busiest Australian ports, including Port Hedland and Dampier. The port-level trade volume may have impacted the calculation of comparative suitability for LSDV-carrying vector incursion more than distances between Australian ports and ports in the selected 16 countries as all other ports of equal or less distance than Port Hedland and Dampier had very low comparative suitability. This is in line with a study on the spread of mosquito species by the cargo ships in the United States Gulf Coast, which found a positive association between number of cargo ship arrivals and the risk of introduction of mosquito species including *Ae. aegypti*<sup>29</sup>. In the current study, this pathway only considered vectors within a 30 km radius of origin port as being potentially capable for arriving at a port and boarding a shipping vessel based on the maximum flight distance of the stable fly (*S. calcitrans*)<sup>30</sup>. It may be possible for vectors to arrive at origin ports from greater distances by hitchhiking on trucks or trains<sup>31</sup>. A modelling study on LSD control and surveillance estimated that LSD could potentially spread up to 80 km from an infected area<sup>32</sup>.

Our findings for an introduction pathway considering LSDV-carrying flying mechanical vectors being carried by wind currents from Indonesia, Papua New Guinea, and Timor-Leste into Australia (Pathway 2) highlighted that over the period of 2019–2023, wind currents originating in these three countries most frequently reached Australia within 48 hours during the summer months of December, January, and February. Furthermore, when combining these wind trajectories with MCDA suitability data for flying mechanical vectors potentially carrying LSDV in these origin countries, the highest comparative suitability of LSDV-carrying flying mechanical vectors entering Australia was found in a discrete set of locations in Far North Queensland and northern areas of Northern Territory. A limited number of wind trajectories reached as far as 25 degrees south in Western Australia and to a slightly lesser extent in Northern Territory and Queensland, suggesting that there is potential for these areas to experience an LSDV incursion by vectors. Furthermore, in the event of LSDV-carrying flying mechanical vectors successfully entering Australia, there is potential for these vectors to be spread rapidly across Australia by inland wind patterns and weather events. Previous studies identified wind and weather as influencing the long distance spread of vectors carrying bovine ephemeral virus, bluetongue virus, and Akabane virus from northern Australia to southern and eastern regions of Australia<sup>33,34</sup>.

While the current model does not evaluate the temporal variation in vector population potentially carrying LSDV, several sources of evidence suggest that LSDV-carrying vectors may

be most common during the summer months in Indonesia. For example, Central and Eastern Indonesia usually record their highest levels of rainfall during the period of December–March, with average mean and maximum temperatures of around 25 degrees Celsius and 30 degrees Celsius, respectively<sup>35</sup>. Previous studies in other parts of the world have reported LSD cases to be more common during warmer months<sup>36,37</sup> and after periods of increased rainfall<sup>38</sup>. Evidence suggests that mosquito and stable fly activity is highest during warmer periods<sup>39,40</sup>.

Interestingly, out of the 16 LSD outbreaks in Indonesia recorded by WOA/WAHIS as at 12 November 2025, 13 outbreaks started between the December to March period<sup>41</sup>. Combined with the frequency of wind currents with trajectories intersecting with Australia during this period, these findings suggest that it may be beneficial to heighten LSDV vector surveillance in Far North Queensland and northern areas of Northern Territory during the summer months, if detection of LSDV-carrying insects is important. Furthermore, the Australian Bureau of Meteorology reported 36 tropical cyclones during the modelled period of 1 January 2019 to 31 December 2023, with all cyclones occurring between the months of December and May and 25 cyclones being tracked between the months of January and March<sup>42</sup>. The average radius size of the outermost closed isobar for cyclones during this five year period was 259 m with a standard deviation of 127 m, with cyclone Oma in February 2019 having the largest recorded outermost closed isobar radius of 1148 m<sup>43</sup>. These extreme weather events are significant because a number of vector species are reportedly detected in Northern Australia following cyclones<sup>44</sup>, although the survivability of these vectors is not reported. Future modelling could investigate potential effect of cyclone size and trajectory on flying mechanical vector species incursion into Australia.

The map of overall LSD incursion suitability in this study shows that most areas of Australia are of very low to low suitability for LSD introduction in comparison to the few discrete areas in northern and western Australia. Similarly, the findings of the previous risk assessment concluded that the overall risk of LSDV introduction into Australia is negligible to very low<sup>25,26</sup>. The map of overall LSDV incursion suitability in the current study predicted discrete areas in Far North Queensland, Port Hedland in Western Australia as having the highest comparative suitability. These areas represent geographical locations likely to be vulnerable to incursion and therefore requiring the most attention for targeted surveillance.

The findings of our study need to be interpreted considering a few methodological limitations. First, our modelling for the LSDV-introduction pathway via shipping vessels was limited by the availability of data associated with shipping volume and duration. The current model used trade value as a proxy for trade volume, however, details of frequency of ships travelling between origin ports and Australian ports could provide a better estimate of trade volume. Estimation of travel time of cargo ships could be improved by incorporating actual shipping routes, as well as details of stopovers between origin port and Australia. Furthermore, details of duration of docking at origin port could also be relevant as increased docking duration may allow for more vectors to board docked cargo ships. However, the increased time between boarding and arriving in Australia may impact virus retention in and survivability of vectors. A quantitative risk assessment of Japanese encephalitis virus (JEV)-infected mosquitoes carried on cargo ships from nine different regions in Asia arriving at United States shipping ports found negligible risk of JEV-infected mosquitoes arriving from each region in Asia regardless of varying numbers of cargo ship arrivals between regions<sup>45</sup>. The authors of this risk assessment assumed this pathway to be viable given that the expected time to travel from Asia to the United States is shorter than the potential JEV retention period in mosquitoes and therefore other factors such as temperature and humidity shifts may impact on mosquito survivability during long ocean voyages<sup>45</sup>. Notably, JEV is biologically vectored by insect hosts, unlike LSDV. Further studies on the survivability of LSDV vectors during ocean voyages may assist in the modelling of the risk of LSDV-carrying vectors arriving by ship.

Second, the lack of temporal variation in vector population data, with constant spatial data applied across the five-year period (2019–2023) is a simplification that overlooks potential seasonal or yearly fluctuations in vector populations. Third, the use of the HYSPLIT model to estimate wind trajectories introduces its own constraints<sup>46</sup>. HYSPLIT is designed for modelling

the dispersion of gases and particulates, and as such vector-specific factors like weight, flight behaviour, or self-guided movement are not fully captured by the model presented in this study<sup>19,25</sup>. In the present study, the use of HYSPLIT models was considered appropriate as it has been used extensively for wind-borne insect trajectory modelling for the dispersal of insect vectors, including the introduction of LSDV into Australia, the introduction of bluetongue virus into northern Australia, Sicily in Italy, and France, as well as the spread of epizootic haemorrhagic disease virus (EHDV) into France<sup>18,19,47-49</sup>. Furthermore, the HYSPLIT model used to evaluate the wind dispersal of EHDV-carrying *Culicoides* midges in France was considered appropriate for the current model as it was able to predict EHDV outbreak areas with an area under the curve (AUC) of the receiver operating characteristic (ROC) curve value of 0.96<sup>48</sup>. Fourth, our model does not predict the probability of vectors entering wind currents or being deposited at specific locations in Australia, as all areas through which wind trajectories pass were treated equally. A more sophisticated approach that randomizes the likelihood of vector deposition could improve the accuracy of the assessment of this entry pathway. Furthermore, the reliance on historical wind data from 2019–2023 limits the model to past conditions. Real-time monitoring of wind patterns and the inclusion of meteorological forecasts could enhance the model's ability to predict future suitability and help target vector control efforts more effectively. Finally, the species distribution models used observational data from GBIF<sup>50</sup>, which will likely introduce spatial biases, as some species may be underrepresented in less accessible areas. The study also relied on genus-level data for some vector species, potentially reducing the accuracy of their modelled distribution. Additionally, the bovine population model did not account for species-specific differences in susceptibility to LSDV, such as the greater resilience of *B. indicus* cattle compared to European *B. taurus* breeds<sup>51,52</sup>, nor did it include feral bovine populations due to a lack of reliable data. Nevertheless, our results were robust to changes in species distribution parameters since the sensitivity analysis did not produce any differences in the geographical distribution of comparative introduction suitability after varying the selection of bovine and vector species included in the model.

## Conclusions

The current model provides spatially-explicit output to assist with spatially-targeted surveillance and preparedness activities under the National LSD Action Plan based on the identification of areas suitable for the incursion of LSDV-carrying vectors. While consistent with the findings from previous risk assessments in finding a majority of areas in Australia as having comparatively low suitability for LSDV-carrying vector introduction, this study identified areas in Far North Queensland and Port Hedland in Western Australia as having the highest suitability for LSDV-carrying vector introduction compared to the rest of the country. Each individual pathway's incursion suitability map, along with the combined incursion suitability map, will be valuable to inform targeted surveillance in shipping areas, on livestock properties, and feral bovine populations within and adjacent to areas identified in the study. Additionally, the various risk factors associated with the two potential pathways for LSDV-carrying vector introduction investigated in this study highlight the need to conduct integrated vector surveillance.

An extension of the current study could include an evaluation of areas suitable for LSDV becoming established in Australia. Subsequent modelling could incorporate the effect of Australia's unique environmental conditions on the survivability of vectors, and include animal movement data as a basis for exploring the spatial variation in suitability for LSDV spreading to the bovine population in Australia. Such modelling may assist in the development and implementation of spatially-targeted response activities of any potential LSD outbreaks in Australia.

## Methods

The LSDV geospatial model evaluated two risk pathways of LSDV introduction into Australia using the findings of the literature review conducted by Owada et al.<sup>17</sup>, modelling approaches

applied in the quantitative risk assessment performed by Hall et al.<sup>25</sup>, and previous LSDV experimental and observational studies as the basis for the model framework. For the purpose of this study, LSDV introduction is defined as one or more LSDV-carrying vectors successfully entering Australia. The two pathways modelled were: a) LSDV-carrying mechanical vectors being transported by ships arriving in Australia from overseas, and b) LSDV-carrying mechanical vectors being carried by wind currents from neighbouring countries into Australia.

The spatial distribution of vector species potentially carrying LSDV and bovines potentially infected with LSDV in selected countries in Asia and Oceania were modelled and then combined with other risk factors to create maps visualising the spatial variation in suitability for LSDV introduction into Australia via these two different pathways.

## Model framework

As an initial step in the development of the geospatial model for LSDV introduction, a causal diagram was designed based on the findings of the literature review (Supplementary Figure S9)<sup>17,53</sup>. The causal diagram described the scenarios of LSDV being introduced into Australia via the two considered possible pathways and helped provide a framework for quantifying and identifying suitable areas of incursion in Australia. Additional details of the model framework are contained in the Supplementary methods section.

## Geographical extent of origin areas for LSDV introduction

The scope of the geographical extent considered for areas from which LSDV could be brought into Australia was primarily based on the set of countries included in a previous quantitative risk assessment for LSDV introduction into Australia<sup>25</sup>. The factors included in selecting countries to include in the geographical extent were LSDV virus retention duration in vectors, maximum flight potential of vectors, and official reports of LSD cases. Additional details on these selection criteria are described in the Supplementary methods section. The following 16 countries were selected as potential original areas for LSDV introduction: Bangladesh, Cambodia, China and associated autonomous regions (Hong Kong, Taiwan), India, Indonesia, Malaysia, Myanmar, Pakistan, Papua New Guinea, Republic of Korea, Russian Federation, Singapore, Sri Lanka, Thailand, Timor-Leste, and Vietnam (Supplementary Figure S10).

## Model parameter database

Data associated with LSDV geospatial risk factors were extracted primarily from studies identified in a recent literature review<sup>17</sup>. These data were supplemented by incorporating risk factors identified in previous risk assessments for LSDV introduction into Australia<sup>25,26</sup>, as well as additional data on the biting insect vector transmission mechanisms extracted from other studies. Data for environmental and climatic risk factors, biting insect vector transmission mechanisms, animal and vector populations, bovine LSD cases, and shipping port locations were extracted from publicly available sources (Supplementary Table S1).

## Animal and vector population modelling

Current evidence on vectors either definitively or potentially capable of mechanical transmission of LSDV was used to identify vector species for inclusion in modelling. The vector species identified were: midges (*Culicoides nubeculosus*), flies (*Stomoxys calcitrans*, *S. sitiens*, *S. indica*), mosquitoes (*Aedes Aegypti*, *Anopheles stephensi*, *Culex quinquefasciatus*). While tick species, including *Amblyomma hebraeum*, *Rhipicephalus annulatus*, *R. appendiculatus*, *R. decoloratus*, were identified as potentially capable of mechanical transmission of LSDV, only flying vectors were considered as capable of introducing LSDV into Australia via the two entry pathways. Due to a lack of empirical data on the spatial distribution of vector populations within the selected 16 countries, occurrence data were used to create population distribution models.

The Global Biodiversity Information Facility (GBIF) was used to retrieve occurrence data for the identified vector species<sup>50</sup>. Species data were retrieved for *Cx. Quinquefasciatus*, *A. stephensi*, and *Ae. aegypti*. Genus level data were used for species where insufficient species-specific

data were available within the selected 16 countries. Namely, *Culicoides* genus was used for *C. nubeculosus* and *Stomoxys* genus was used for *S. calcitrans*, *S. sitiens*, and *S. indica*. The individual GBIF datasets are listed in Supplementary Table S1.

Species distribution modelling (SDM) was used to estimate the spatial distribution of the selected vector species and genera. This approach was used due to a lack of empirical spatial distribution data for vectors. It should be noted that the output of the SDM generated measure species distribution in terms of probability of the species being present rather than estimating actual population. Probability raster maps were produced for vectors in the selected 16 origin countries using R software (version 4.4.1; R Core Team, 2024, URL: <https://www.R-project.org/>) with the *ggplot2* plotting library (version 3.5.1; Thomas Lin Pedersen, 2024, URL: <https://www.rdocumentation.org/packages/ggplot2/versions/3.5.1>). Details of the specific data sources for SDM parameters and the process for performing SDM are described in the Supplementary methods section and Supplementary Table S1.

Owada et al.<sup>17</sup> identified that bovine species including cattle (*Bos taurus*), domestic water buffalo (*Bubalus bubalis*), wild water buffalo (*Bubalus arnee*), banteng (*Bos javanicus*), and zebu (*Bos indicus*) can be infected with LSDV, however, the differences in susceptibility to LSD between species is not well understood. The Gridded Livestock of the World (GLW) raster maps, which provide population estimate maps for both cattle and domestic water buffalo, were used for estimating bovine population<sup>54</sup>. Similar data were unavailable for other bovine species, and therefore, the total bovine population was estimated by calculating the sum of the cattle and domestic water buffalo GLW maps.

### Modelling of suitability of potentially infected bovines

A suitability map of potentially infected bovines was generated using structural equation modelling (SEM) to estimate the spatial distribution of the likelihood of bovines infected with LSDV using the bovine population distribution probability map, environmental variables, and LSD case data used as inputs. Details of the specific data sources for SEM and the process for performing SEM are described in the Supplementary methods section.

### Modelling of suitability of vectors potentially carrying LSDV

A suitability map of all flying mechanical vector species potentially carrying LSDV was generated using multiple-criteria decision analysis (MCDA) to estimate the spatial distribution of the likelihood of flying mechanical vectors potentially carrying LSDV using the vector population distribution probability maps, environmental variables, and potentially infected bovine suitability map used as inputs. Details of the specific data sources for MCDA and the process for performing MCDA are described in the Supplementary methods section.

### Modelling of LSDV introduction via LSDV-carrying flying mechanical vectors entering through shipping ports (Pathway 1)

The first pathway modelled for introduction of LSDV-carrying flying mechanical vectors into Australia was via shipping ports. It was assumed that flying mechanical vectors carrying LSDV could potentially be transported by ship to Australia<sup>25,26</sup>. The suitability for LSDV introduction via this pathway was modelled at 66 Australian shipping ports using 138 overseas shipping ports as points of origin.

The suitability for an LSDV-carrying flying mechanical vector arriving at a specific Australian shipping port was calculated by first evaluating the product of each overseas port suitability for LSDV-carrying flying mechanical vectors arriving at the port, the overseas port's country's export volume to Australia, and the proportion of port calls between the overseas port's country and the corresponding Australian shipping port. This product was then divided by the product of the total number of ports in the country of the overseas port and the distance to corresponding Australian port. The sum of these values for all overseas ports was then finally multiplied by the proportion of days each year above the minimum vector survivable temperature at the corresponding Australian shipping port. Division is used for distance

between overseas ports and Australian ports because greater distance is assumed to translate to lower suitability for vectors arriving due to increased travel duration and limited duration of retention of LSDV in vectors. Additional details of the calculations for estimating the suitability via this pathway are described in the Supplementary methods section. The equation for the suitability for an LSDV-carrying flying mechanical vector arriving at a specific Australian shipping port is defined in equation (1).

$$R(\text{Port})_i = T_i \sum_{j=1}^{j=J} \frac{V_j E_j P_i}{D_{ij} N_j} \quad (1)$$

Where:

$i$  is one of the 66 Australian shipping ports

$R(\text{Port})_i$  is the suitability for an LSDV-carrying flying mechanical vector arriving at Australian shipping port  $i$

$T_i$  is the proportion of days each year with a minimum temperature of 14.4 degrees Celsius or warmer at Australian shipping port  $i$

$j$  is one of the 138 overseas shipping ports  $j$

$V_j$  is the suitability for LSDV-carrying flying mechanical vectors reaching overseas shipping port  $j$

$E_j$  is the export volume for the country of overseas shipping port  $j$

$P_i$  is the proportion of port calls to Australian shipping port  $i$

$D_{ij}$  is the distance between Australian shipping port  $i$  and overseas shipping port  $j$

$N_j$  is the total number of overseas shipping ports in the country where shipping port  $j$  exists

The vector incursion suitability values were divided into five equal intervals over the result value range and grouped into the suitability categories of very high, high, moderate, low, very low. These categorised results for each port were plotted on a map to visualise which ports represent the highest comparative suitability for LSDV-carrying flying mechanical vector introduction into Australia via commercial shipping. This suitability map was generated using R software (version 4.4.1; R Core Team, 2024, URL: <https://www.R-project.org/>) using the *ggplot2* plotting library (version 3.5.1; Thomas Lin Pedersen, 2024, URL: <https://www.rdocumentation.org/packages/ggplot2/versions/3.5.1>).

## Modelling of LSDV introduction through LSDV-carrying flying mechanical vectors carried by wind currents (Pathway 2)

### Wind trajectory forward projection and intersection with Australia

A wind trajectory model was developed to model the suitability for LSDV being introduced into Australia through LSDV-carrying flying mechanical vectors being carried by wind currents from neighbouring countries by using HYSPLIT software version 5.3.0<sup>55</sup> via the *splitr* library version 0.4 (Iannone, 2022) for R.

The land area of Indonesia, Papua New Guinea, and Timor-Leste was divided in grid squares with a resolution of 50 minutes (approximately 92.5 km) and the centroids of the 195 grid squares south-east of 5 degrees south and 116 degrees east were used as origin locations for wind trajectory forward projection. For each origin coordinate, wind trajectories were forward-projected for 48 hours from four starting time points each day (12AM, 6AM, 12PM, and 6PM) over the period of 2019–2023.

The spatial distribution of wind trajectories entering Australia was estimated by dividing the area of Australia north of 25 degrees south into 2016 grid squares with a resolution of 25 minutes (approximately 46.3 km) and calculating the number of times each wind trajectory

intersected with each grid square over the five-year period of 2019–2023. A southern-most latitude of 25 degrees south was chosen based on the furthest extent of the wind trajectory forward projection (Supplementary Figure S11). These wind trajectories were visualised using R software (version 4.4.1; R Core Team, 2024, URL: <https://www.R-project.org/>) using the *ggplot2* plotting library (version 3.5.1; Thomas Lin Pedersen, 2024, URL: <https://www.rdocumentation.org/packages/ggplot2/versions/3.5.1>). Further details of wind trajectory forward projection and intersection calculations and *splitr* function parameters used for forward projection are contained in the Supplementary methods section.

### Calculation of suitability for LSDV-carrying flying mechanical vectors entering Australia by wind

For each of the 2016 grid squares in Australia and each day during the period of 2019–2023, the suitability for LSDV-carrying flying mechanical vectors being carried by wind to this area was evaluated by calculating the sum product of the number of times a projected wind trajectory from each origin coordinate intersected with that Australian area and the average value of the combined MCDA suitability map for all LSDV-carrying flying mechanical vectors within the 50-minute grid square centred at the same origin coordinate. For each wind trajectory, a vector could only land within a single 25-minute grid square, however, this approach counts the intersections with every 25-minute grid square along the wind trajectory's path because it is not possible to predict where a vector will land with this model. Further details of suitability calculations for this pathway are contained in the Supplementary methods section. The equation for the suitability for an LSDV-carrying flying mechanical vector being carried by wind currents into Australia is defined in equation (2).

$$R(\text{Wind})_{ij} = \sum_{k=1}^{k=K} W_{ijk} S_k(2)$$

Where:

$i$  is one of the 2016 unique 25-minute areas in Australia

$j$  is a single day during the period of 2019–2023

$R(\text{Wind})_{ij}$  is the suitability for an LSDV-carrying flying mechanical vector being carried by wind from overseas to location  $i$  in Australia on day  $j$

$k$  is one of the 195 origin coordinates  $K$  across Indonesia, Papua New Guinea, and Timor-Leste

$W_{ijk}$  is the number of times wind trajectories originating from origin coordinate  $k$  intersects with Australian area  $i$  on day  $j$

$S_k$  is the average value of the combined MCDA suitability map for all flying mechanical vectors potentially carrying LSDV within the 50-minute area centred at origin coordinate  $k$

The results of these calculations were then summed for the cumulative suitability for all days within the period of 2019–2023. These cumulative vector incursion suitability values were divided into five equal intervals over the result value range and grouped into the suitability categories of very high, high, moderate, low, very low. These categorised results were plotted on a map to visualise areas with the highest comparative suitability for LSDV-carrying flying mechanical vector introduction into Australia via this pathway.

Furthermore, the daily suitability values were divided into three-month groups representing Australia's seasons (Summer: December–February, Autumn: March–May, Winter: June–August, Spring: September–November) and summed for each season. The cumulative suitability values for each season were divided into five equal intervals over the value range of lowest seasonal suitability value and highest seasonal suitability value across all four seasons, and grouped into the suitability categories: seasonal highest, high, moderate, low, seasonal lowest. These were

then plotted on separate maps using a common scale bar for each season to visualise the variation in comparative suitability for LSDV introduction between each season.

All suitability maps for this pathway were generated using R software (version 4.4.1; R Core Team, 2024, URL: <https://www.R-project.org/>) using the *ggplot2* plotting library (version 3.5.1; Thomas Lin Pedersen, 2024, URL: <https://www.rdocumentation.org/packages/ggplot2/versions/3.5.1>).

## Modelling of combined suitability of the two LSDV introduction pathways

In order to create a model of the combined suitability for LSDV introduction into Australia via the two pathways, the coordinates for the ports in shipping port pathway model and their associated suitability values were converted into a raster map with the same resolution as the wind current pathway model map. Where multiple ports existed within the same raster pixel, their suitability values were summed together to produce the pixel value. The values in the rasterised version of the port suitability map were then grouped into categories using the same method as described in the methods section for the original port suitability map.

The five main suitability categories were assigned values of 1–5 for very low to very high. These category values at each pixel in Australia were summed across the suitability maps for the two LSDV introduction pathways, resulting in a maximum potential suitability value of 10.

Finally, the resulting summed values were divided equally into the same five categories for values between 1 and the maximum value in the map. The combined LSDV introduction raster data were plotted on a map to visualise areas with the highest comparative suitability for LSDV introduction into Australia when taking into account the combined suitability of both introduction pathways of shipping ports and wind currents. The combined suitability map was generated using Esri ArcGIS Desktop software (version 10.8.1; Esri, 2020, URL: <https://desktop.arcgis.com/en/arcmap/index.html>).

## Sensitivity analysis of combined suitability model

The sensitivity of the final combined suitability model was tested by changing the selection of species included in the modelling of suitability of potentially infected bovines and modelling of suitability of vectors potentially carrying LSDV. This analysis was conducted to assess the robustness of our findings. Further details of the sensitivity analysis are contained in the Supplementary methods section.

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## Author contributions

Conceptualisation, K.O., A.C.-C., R.N.H., R.K.A., B.J.H., T.J.M., and R.J.S.M.; methodology, K.O., A.C.-C., R.N.H., R.K.A., B.J.H., T.J.M., and R.J.S.M.; validation, K.O., A.C.-C., R.N.H., R.K.A., B.J.H., T.J.M., and R.J.S.M.; formal analysis, K.O., R.N.H., and R.J.S.M.; investigation, K.O., A.C.-C., R.N.H., R.K.A., B.J.H., T.J.M., and R.J.S.M.; data curation, K.O., A.C.-C., R.N.H., and R.J.S.M.; writing—original draft preparation, K.O.; writing—review and editing, K.O., A.C.-C., R.N.H., R.K.A., B.J.H., T.J.M., and R.J.S.M.; visualisation, K.O. and R.N.H.; supervision, B.J.H., T.J.M., and R.J.S.M.; project administration, B.J.H. and R.J.S.M. All authors read and agreed to the published version of the manuscript.

## Code availability

The code used for the modelling conducted in this study are contained in the Supplementary methods section.

## Data availability statement

The data presented in this study are based on publicly available datasets. All sources are specified in the Methods and Supplementary methods sections.

## Competing interests

Kei Owada, Ben J. Hayes, Timothy J. Mahony, and Ricardo J. Soares Magalhães are employees of the University of Queensland. Adam C. Castonguay is an employee of the Commonwealth Scientific and Industrial Research Organisation. Robyn. N. Hall is an employee of Ausvet Pty. Ltd. Rebecca K. Ambrose is an employee of the Queensland Government Department of Primary Industries.