RESEARCH ARTICLE

Environmental variation across multiple spatial scales and temporal lags influences Hendra virus spillover

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Abstract

1. Pathogens can spill over and infect new host species by overcoming a series of ecological and biological barriers. Hendra virus (HeV) circulates in Australian flying-foxes and provides a data-rich study system for identifying environmental drivers underlying spillover events. The frequency of spillover events to horses has varied interannually since the virus was first discovered in 1994. These observations suggest that HeV spillover events are driven, in part, by environmental factors, including loss of flying fox habitat and climate variability.

2. We explicitly examine the impact of environmental variation on the risk of HeV spillover at three spatial scales relevant to this system. We use a dataset of 60 spillover events and boosted regression tree methods to identify environmental features (including concurrent and lagged temperature, rainfall, vegetation indices, land cover, and climate indices) at three spatial scales (1-km, 20-km, 100-km radii) associated with horse contacts and reservoir species ecology.

3. We find that temperature, local (1-km radius) human population density, and landscape (100-km radius) forest cover and pasture are the most influential environmental features associated with HeV spillover risk. By including multiple spatial scales and temporal lags in environmental features, we can more accurately quantify risk across space and time than with models that use a single scale. For example, high quality vegetation at the local scale and within a foraging radius (20-km) in the concurrent month and previous years, combined with poorer quality vegetation at the landscape scale in the concurrent month increase risk of HeV spillover. These and other environmental associations likely influence the dynamic foraging behaviour of reservoir flying foxes and drive contacts that facilitate spillover into horse populations.

4. *Synthesis and application*: Current management of HeV spillover focuses on local-scale interventions – primarily through vaccination and detection of infected horses. Our study finds that HeV spillover risk is also driven by environmental changes over much larger scales and demonstrates management practices would benefit from incorporating landscape interventions alongside local interventions.

1 | INTRODUCTION

Outcomes of pathogen spillover into new hosts range from asymptomatic dead-end infections to global pandemics. Identifying drivers of pathogen spillover is critical for mitigating zoonotic (animal-to-human) disease burden and preventing large outbreaks (Bogich et al., 2012). The incidence of zoonotic spillover is increasing globally (Marani et al., 2021), in part driven by environmental change (Jones et al., 2008). Spillover risk can be quantified as the force of infection—the product of pathogen prevalence in reservoir populations, reservoir-recipient contacts, and likelihood of recipient infection given contact (Lloyd-Smith et al., 2009; Lo Iacono et al., 2016). Spillover only occurs with sufficient force of infection (Lloyd-Smith et al., 2009) and when pathogens overcome a series of ecological and biological barriers (Plowright et al., 2017). There are several examples showing that environmental change can facilitate higher force of spillover infection and reduce barriers across a diversity of pathogen systems (Allen et al., 2017; Gottdenker et al., 2014; Jones et al., 2008). Mechanisms underlying changes in spillover concomitant to climate change include shifts in host and vector distributions (Ryan et al., 2019) and environmental conditions that increase transmission (Harvell et al., 2002). Conversion of natural environments to human-modified landscapes can increase competent zoonotic host diversity and density (Gibb et al., 2020) and contact between reservoirs and recipients (Bloomfield et al., 2020). However, because there are many ecological, physiological, and behavioural conditions that must align, explicit links between spillover and environmental change have proved difficult to identify, thus limiting our ability to forecast risk accurately (Lloyd-Smith et al., 2015; Washburne et al., 2019).
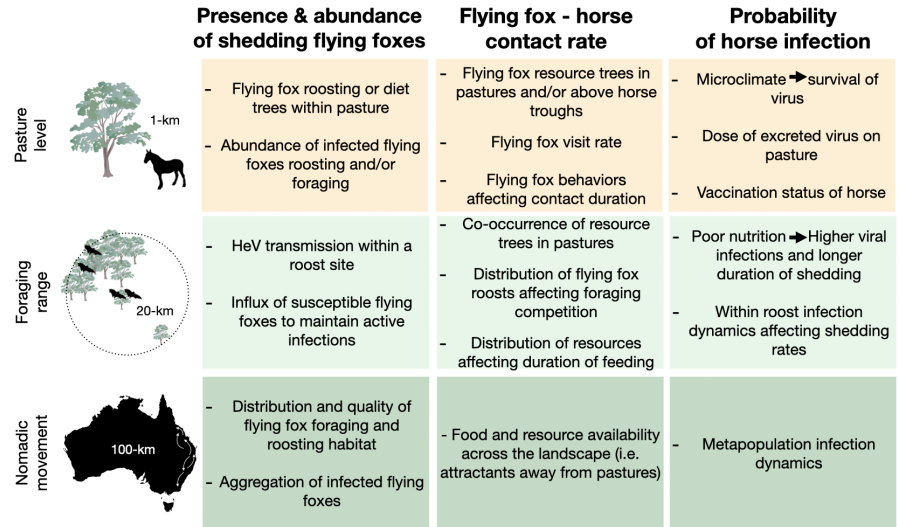
Hendra virus (HeV) spillover provides an excellent study system for understanding how environmental change affects force of spillover infection. HeV (genus *Henipavirus*, family *Paramyxoviridae*) is a single stranded RNA virus that naturally circulates and causes minimal observable pathogenesis in reservoir Australian *Pteropus* (flying fox) species. Nearly three decades of investigations have focused on the originally described HeV (HeV-g1; Murray et al., 1995), yet a new variant has recently been discovered (HeV-g2; Annand et al., 2022; Wang et al., 2021). *Pteropus alecto* and *P. conspicillatus* are the likely key reservoirs of HeV-g1 (Edson, Field, McMichael, Vidgen, et al., 2015; Smith et al., 2014), while *P. poliocephalus* likely also plays a role as a reservoir of HeV-g2 (Peel et al., 2022; Wang et al., 2021). One hypothesis is that HeV persistently infects its hosts and physiological and/or environmental factors drive intermittent shedding of virus in urine (Plowright et al., 2016). HeV spills over into horses which are bridge hosts for onward infections, including humans (Field, 2016; Murray et al., 1995). Because HeV is not viable in the environment for extended periods (Fogarty et al., 2008), spillover

occurs when horses feed on pasture or from troughs underneath a tree that was recently used as a roost or feeding site of actively shedding *Pteropus* (Edson, Field, McMichael, Vidgen, et al., 2015; Martin et al., 2015, 2017). Humans are subsequently infected when they contact an infectious horse (Mahalingam et al., 2012). Infection in recipient hosts (both horses and humans) is associated with severe acute febrile encephalitis, respiratory disease and high case fatality rates (Field et al., 2000). Spillover events are clustered spatiotemporally, suggesting a link between the environment and the timing and location of spillovers (Plowright et al., 2015).

Current management of HeV spillover relies heavily on horse vaccination and horse case detection—placing the burden of disease control on individual owners and veterinarians. Early control strategies attempted to disperse flying fox roosts and move them away from humans, however these strategies did not lead to lasting impacts on flying fox distributions (Roberts et al., 2012). There was also concern that disturbance of roosts could lead to an increase in stress and virus shedding in remaining bats—but sufficient studies have not been carried out to quantify the impacts of these interventions. A study of another zoonotic disease reservoir (vampire bats) concluded that bat dispersal in response to roost culling facilitates rabies virus spread (Viana et al., 2023), lending evidence for displacement strategies increasing overall risk. Identifying key environmental mechanisms preceding HeV spillover, including any temporal lags and influential spatial scales, would facilitate forecasting and inform management strategies for prevention, early detection, and rapid response of horse infections and, ultimately, human cases.

Environmental change can impact force of HeV spillover infections by affecting the distribution of infectious reservoirs, contact between reservoirs and horses, and likelihood of horse infection given contact (Figure 1). Temporally dynamic changes in the environment affect where flying foxes congregate in daytime roosts and forage nocturnally on diverse native and introduced species' pollen, nectar and fruits (Eby, 1991; Eby & Law, 2008; McWilliam, 1986; Palmer, 1997; Richards, 1990). Habitat loss and land use change across the range of flying foxes are associated with an increase in the number of roosts in human-populated areas (Eby et al., 2023; Plowright et al., 2011; Williams et al., 2006), potentially increasing contact with horses (bridge hosts). Environmental changes can also alter prevalence and rates of viral shedding in reservoirs, directly affecting distribution of infectious reservoirs and likelihood of infection. HeV prevalence is often measured through pooled urine samples collected from underneath flying fox roosts and is an inexact reflection of population level prevalence. Prevalence is higher under roosts which have a high proportion of key reservoir species (roosts can be multi-species; Edson, Field, McMichael, Jordan, et al., 2015; Goldspink et al., 2015; Smith et al., 2014). Lower precipitation and colder weather in spring has been associated with higher

FIGURE 1 Hypothesized influences of environmental features that impact Hendra virus spillover risk. Where and when HeV spills over into horses is affected by multiple spatial scales that reflect pasture-level, nightly foraging range, and nomadic reservoir movement. This schematic illustrates potential environmental and ecological factors affecting components of force of spillover infection (presence and abundance of shedding flying foxes, flying fox-horse contact rates and probability of horse infection).

	Presence & abundance of shedding flying foxes	Flying fox - horse contact rate	Probability of horse infection
Pasture level (1-km)	- Flying fox roosting or diet trees within pasture - Abundance of infected flying foxes roosting and/or foraging	- Flying fox resource trees in pastures and/or above horse troughs - Flying fox visit rate - Flying fox behaviors affecting contact duration	- Microclimate → survival of virus - Dose of excreted virus on pasture - Vaccination status of horse
Foraging range (20-km)	- HeV transmission within a roost site - Influx of susceptible flying foxes to maintain active infections	- Co-occurrence of resource trees in pastures - Distribution of flying fox roosts affecting foraging competition - Distribution of resources affecting duration of feeding	- Poor nutrition → Higher viral infections and longer duration of shedding - Within roost infection dynamics affecting shedding rates
Nomadic movement (100-km)	- Distribution and quality of flying fox foraging and roosting habitat - Aggregation of infected flying foxes	- Food and resource availability across the landscape (i.e. attractants away from pastures)	- Metapopulation infection dynamics

rates of underroost HeV (Paez et al., 2017). Sub-optimal foraging conditions in the prior year increases the amount and duration of HeV detected under new overwintering roosts (Becker et al., 2023). A recent analysis demonstrated that clusters of subtropical HeV spillovers likely result from interactions between long-term flying fox habitat loss and acute nutritional stress linked to El Niño events (Eby et al., 2023). While not all studies have found associations between the environment and HeV shedding (Edson et al., 2019; Peel et al., 2019), there is often variation in the spatial and temporal scales of environmental variables considered for predictions (Table S3).

Characterizing mechanisms affecting HeV spillover is key to forecasting risk and designing mitigation and prevention policies in a changing world. Multiple spatial scales can drive changes in risk (local weather and regional vegetation productivity) at various temporal lags (Becker et al., 2019). Flying foxes are highly mobile, meaning that environmental change across hundreds of kilometres can affect reservoir distribution and density across the landscape (Welbergen et al., 2020). Additionally, native flying fox dietary plant species flower in episodic events (Eby et al., 2019) that are largely consistent seasonally but are unpredictable annually. Conditions that increase abundance of shedding bats will not result in spillover if horses are not present but data on horse distribution across Australia is currently insufficient (Cowled et al., 2009). Despite these challenges, there are opportunities to leverage advances in predicting disease occurrence (in this case spillover), building on methods in machine learning and species distribution modelling (Brock et al., 2019; Elith et al., 2008).

In this study, we aim to identify the temporal lags, spatial scales and types of environmental variation that are strongly predictive of HeV spillover from bats to horses in Australia. We use a 20-year dataset of spillover locations to identify environmental features, temporal lags, and spatial scales associated with HeV spillover to help forecast areas at future risk. This work will help guide management efforts for this important zoonotic disease in a region affected by ongoing loss of natural habitats and climate change.

2 | MATERIALS AND METHODS

2.1 | Machine learning approach

We used boosted regression trees (BRTs; Elith et al., 2008) to identify important environmental features, temporal lags and spatial scales that are predictive of HeV spillover. Boosted regression trees utilize recursive binary splits in data and combine multiple regression trees into an ensemble model. They can fit complex, non-linear relationships, which can result in superior predictive performance compared to traditional statistical models. In the last decade, there has been significant development of these methods and applications to spatiotemporal disease predictions (Brock et al., 2019; Childs et al., 2019; Elith et al., 2008; Pigott et al., 2016).

2.2 | HeV spillover data

We curated a dataset of all known HeV spillovers based on symptomatic and laboratory-confirmed cases in horses ($n=63$ spillovers). Locations of each infected property (accurate to 0.1 decimal degrees) and dates of horse euthanasia following diagnosis of HeV disease were gathered from news reports and government databases. Only spillover events occurring after 1999 ($n=60$) were included in our analysis because environmental data were available at a higher temporal frequency (annual vs 5-year) from 2000 onwards. We focused on HeV-g1 and its known reservoirs as this is still poorly defined for HeV-g2, and because of a mismatch in diagnostic assays (Annand et al., 2022), it is likely that HeV-g2 spillover events have been missed over this time.

2.3 | Pseudo-negative data

For species distribution models, ecological niche models, and other classification and regression analyses of spatially explicit presence

data, BRTs require points representing a contrast class (i.e. pseudo-absences or pseudo-negatives; Phillips et al., 2009). For comparison to spillover locations, we sampled 'absence' data (we refer to these as pseudo-negative points) by identifying where spillovers could occur but were not reported for all 240 months from January 2000 to December 2020. To define the spatial extent of these pseudo-negative points, we first identified a maximum spatial extent where spillover is possible by quantifying where HeV-g1 reservoir species, *P. alecto* and P. *conspicillatus*, have been observed. We identified 'reservoir roosts' where at least one *P. alecto* or *P. conspicillatus* has been observed using Flying Fox Monitoring Project data from 2002 to 2020 (Westcott et al., 2011; Flying Fox Monitoring Program, 2020). We apply a 20-km buffer around this subset of roosts to account for the typical foraging range (McWilliam, 1986). The extent of the total foraging range of reservoir roosts covers 115,308 km^2 in Queensland and New South Wales and encompasses most observed HeV spillovers (61/63; Figures S2 and S3). For each month, we randomly sampled 50 pseudo-negative points from the total foraging range of reservoir roosts. In months with spillover events, we identified and removed foraging radii of roosts that overlapped with the infected property (Figure S4). For months without any spillover events, we randomly sampled locations among the total reservoir roost foraging area. Random sampling yields more accurate results than stratified sampling for boosted regression trees with small numbers of presence points (Barbet-Massin et al., 2012).

2.4 | Features for environmental variation

We calculated values for a suite of environmental features for each point (spillover and pseudo-negative). Selection of these variables was based on previous research examining environmental impacts on nectar availability (Table S1); distribution of flying foxes (Table S2); rates of HeV shedding (Table S3); viral survival outside hosts (Table S4); and spillover locations (Table S5). Measurement frequency of environmental features varied from daily to biannually (Tables S6 and S7). Briefly, we included precipitation, temperature, normalized difference vegetation index (NDVI), land cover, human population density, and flying fox data for spatially dependent environmental features. Most features were available on a monthly basis for the entire period and extent; however, land cover only was available annually from 2000 to 2015 and flying fox data was only available for a subset of training data (Supporting Information Table S6).

In horses, HeV incubation periods, or the time between infection and the onset of symptoms, range from 4 to 16 days (Murray et al., 1995). To estimate a range of dates around each spillover event that would encompass influencing environmental conditions preceding spillover, we calculate an average of 36 to 6 days prior to the day of death or euthanasia for daily environmental data. For monthly environmental data, if the day of the horse's death was less than 10 days into a month, we assumed spillover occurred or was influenced by the environmental factors in the previous month and used values from the previous month for calculations—otherwise

the month of the spillover was used. We also calculated environmental features at three spatial scales, calculating 1-km, 20-km, and 100-km buffers around each location (Figure 1). The smallest spatial scale (1-km) comprises environmental variation that horses experience and likely reflects pasture conditions that affect flying fox presence and contact with horses (Figure 1), and likelihood of horse infection related to virus survival (Martin et al., 2017). The moderate spatial scale (20-km) includes the nightly foraging range of flying foxes (Eby, 1991; Giles et al., 2018; McWilliam, 1986). The largest spatial scale (100-km) encompasses the median monthly travel distance for *P. alecto* (Welbergen et al., 2020). Environmental features can be highly correlated across these three scales. Correlation was assessed using Kendall's tau correlation coefficient and any variables with values >0.7 were only included in the analysis at the local (1-km) scale (Table S6). Although multi-collinearity of predictor variables in boosted regression trees does not affect model performance, inclusion of highly correlated variables can lead to incorrect inferences of feature importance. To avoid misidentifying important spatial scales, we only included the local scale (1-km radius) for variables that were highly correlated across spatial scales (Table S6).

Finally, to incorporate climatic oscillations that impact local meteorological conditions in many regions of Australia (Fasullo et al., 2018), we use the El Niño Southern Oscillation Index (SOI; Trenberth, 1984) to identify current and cumulative months with La Niña and El Niño events. These were included as global environmental features (Table S7). In total, 70 environmental features were calculated and included in model formulation (Tables S6 and S7).

2.5 | Assessing model predictive ability and identification of important predictor variables

Boosted regression tree models were bootstrapped using 100 training datasets, each including spillovers through 2015 ($n=49$, 82% of spillover events) and 144 randomly sampled (without replacement) pseudo-absence points from the same period. The dataset was split temporally—the frequency of HeV spillovers is not different between the two periods and by using only the earlier spillovers (2000–2015) for training, we could ensure all environmental data for training reflected the contemporaneous conditions. For 2016 onwards, landcover is not available on an annual basis (Table S6). Additionally, by including few pseudo-absence points but increasing the number of datasets, we are able to better balance the influence of presence and pseudo-absence points (Barbet-Massin et al., 2012). We initially performed a grid search on three hyperparameters, including tree complexity (1–4 nodes), learning rates (0.0001–0.002), and bagging rates (50%–85%). The final hyperparameters (2 nodes, 0.0005 learning rate, 65% bagging) were selected with mean deviance explained to minimize prediction error and avoid overfitting. We fit the models by 10-fold cross-validation implemented with *gbm.step* in the package DISMO (Hijmans et al., 2020) in *R* (R Core Team, 2021). We fit four sets of models: one using all three spatial scales, and three

sets only using one of each of the spatial scales (local-, foraging- or landscape-scale). We assessed model predictive ability using area under the receiver operator curve (AUC) on withheld testing data from 2016 to 2020. In addition, we predicted the probability of spillover across the entire study region for each month from 2016 to 2020. We then calculated the mean predicted probability for each month across this time period to visualize where spillover risk is predicted to be highest on average. To compare risk between years, we calculated anomalies $\left(\frac{\rho-\mu}{\mu}\right)$, where ρ is the predicted probability in each month and μ is the monthly mean probability from 2016 to 2020.

We used relative variable importance (RVI) to identify environmental features accurately classifying historical HeV spillover events. RVI measures the number of times a variable is selected for splitting during the construction of a model, weighted by the squared improvement of the model owing to the split, and is averaged over all trees in the model (Elith et al., 2008). For important variables, we used partial dependence plots to visualize the marginal effect of an environmental feature on predicted HeV spillover (Friedman, 2001).

We calculated partial dependence plots using the *R* package PDP (Greenwell, 2017).

3 | RESULTS

The 60 spillover events from 2000 to 2021 included in our analyses ranged from −16.53 to −32.00 latitude (1800 km apart) and spanned subtropical and tropical regions in eastern Australia (Figure S1). Spillover events were documented in every month (Figure 3a). Boosted regression trees fitted to spillover cases and pseudo-negative locations identified concurrent and lagged environmental features at multiple spatial scales associated with spillover (Figure 2).

Despite the small dataset, our models were able to discriminate spillover events from non-spillover locations in space and time (mean AUC on test data = 0.92; Figure 3). Mean seasonal spatio-temporal predictions for 2016–2020 accurately differentiated HeV spillover risk without using HeV spillover events from these years in model training (Figure 3e,f). Among winters (June–August), the
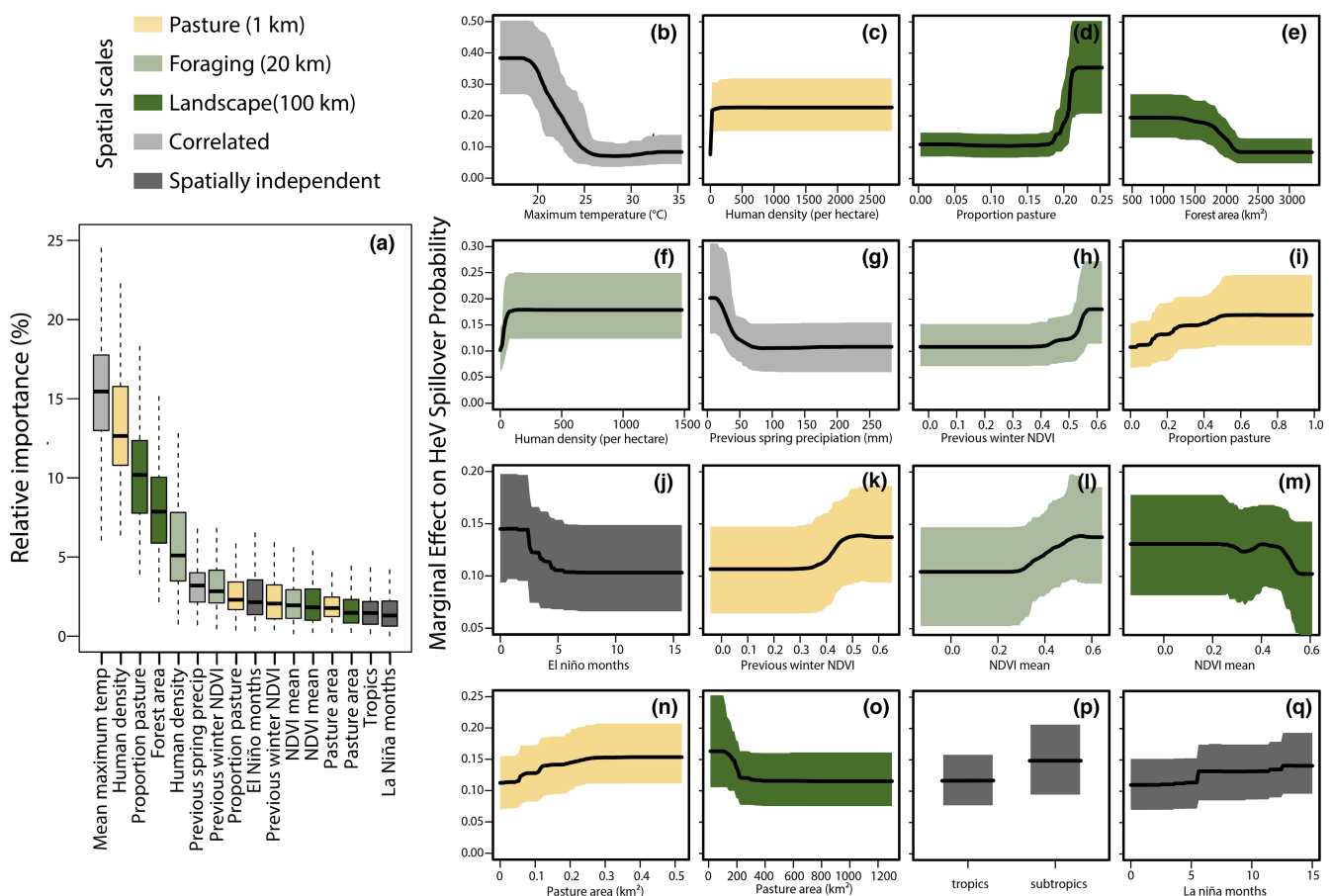

FIGURE 2 Sixteen most impactful environmental features. (a) The relative influence of the sixteen most important environmental features and the distribution of relative importance across the 100 datasets. (b–q) The partial dependence plots show the median (black) and 95% CI (shading) across 100 datasets. Credible intervals are shaded by the spatial scale—including variables that are correlated across spatial scales (light grey) or are spatially independent (dark grey). Log-odds are transformed into probability—note the range of probabilities on the y-axes change between rows.
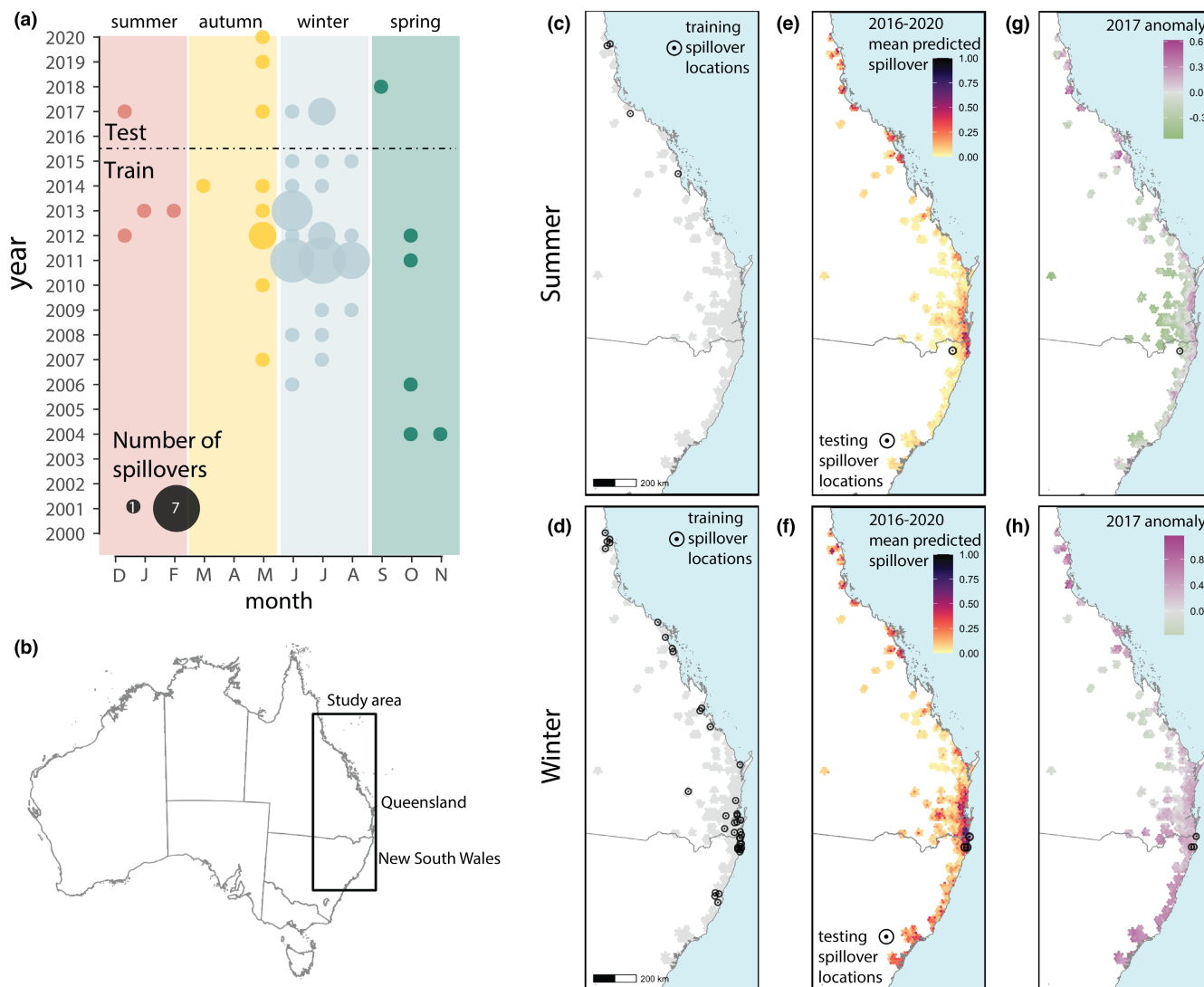
FIGURE 3 HeV spillover predictions. (a) HeV spillovers have occurred in each season and are proportionally represented in training (n = 49) and testing (n = 11) datasets. (b) HeV spillovers are limited to coastal regions of Queensland and New South Wales. (c–h) Model inputs and outputs for both summer (top row) and winter (bottom row): (c, d) grey highlights reservoir roosts foraging area and points indicate training spillovers, (E/F) average prediction of spillover from 2016 to 2020, and (g, h) 2017 anomalies with testing spillover points indicated. For anomalies, negative values (green) indicate lower spillover risk than average for that location, whereas positive values (pink) indicate higher spillover risk than average.

highest predicted risk was in winter 2017 (Figure 3h), which coincided with the highest frequency of spillovers in the testing dataset (n = 3). Only one spillover was observed in summer (in 2017) and the region was highlighted as higher risk in space (Figure 3e) and relative risk in 2017 (Figure 3g), despite no summer spillover events in New South Wales in the training dataset.

Mean monthly maximum temperatures had the highest median relative importance in predicting spillover (mRVI = 15.4%, Figure 2a). Mean temperatures below 20°C were more associated with spillover occurrence (Figure 2b), which occurs south of −26° latitude in the winter months. Because mean temperatures were highly correlated across spatial scales, we only included the local scale in the analysis and were therefore unable to identify the most influential spatial scale in which this feature impacted spillover. A non-zero human

population within a 1-km radius was associated with higher spillover risk and was also important in most BRTs (mRVI = 12.8%; Figure 2c). Higher proportions of pasture cover (mRVI = 10.2%, Figure 2d) and greater amounts of forest cover (mRVI = 7.9%, Figure 2e) at the landscape scale (100-km radius) were associated with higher spillover risk.

Additional environmental features at the landscape level that were associated with spillover include low mean NDVI (Figure 2m) and the proportion of certain land cover classes (higher proportions of pasture cover). NDVI at the two smaller scales were also important (Figure 2k,l); these effects demonstrated that higher NDVI, or greener vegetation, at local and foraging scales were associated with higher risk of spillover both in the previous winter and the concurrent month. While NDVI is important at each scale, the effects are

contrasting—spillover was associated with good vegetation at smaller scales (likely reflecting foraging behaviours) but concurrent poorer vegetation at larger scales (potentially affecting aggregation of foraging across the landscape). Low precipitation during the previous spring was also associated with elevated spillover risk (Figure 2g). Precipitation metrics were also strongly correlated across the spatial scales we examined (>0.9 tau), so we only included it at the local level, and it is not possible to infer at what scale this is most influential. Lower frequency of El Niño months and higher frequency of La Niña events in the preceeding 18 months were associated with spillover, though RVI was low (mRVI: 1.3–2.1%, Figure 2j,q). Data on reservoir species presence/absence and abundance was not strongly correlated with spillover. Subtropical and tropical categories were included as a feature, and this was found to be significant, but have a low relative importance (mRVI: 1.5%) and did not have a significant interaction with other features.

Models were also run with all environmental features at a single spatial scale but AUCs were all lower than the multi-scale model. Of the models run at a single spatial scale, models fit to 100-km (landscape) radius have the highest mean predictive power (AUC = 0.83) and models fit to 20-km (foraging) radius have the lowest mean predictive power (AUC = 0.78) for single spatial scales.

4 | DISCUSSION

By using a flexible modelling framework, we were able to identify environmental features at various spatial scales and temporal lags that reliably predict HeV spillover. Spillovers were more likely to occur in the months and areas where mean monthly maximum temperatures were <20°C, there was a measurable human presence at the local scale, and there was low forest cover at the landscape scale. The different spatial and temporal scales reflect the dynamic and large-scale movements of reservoir hosts in this system and highlight the complexity of HeV spillover. A preventative management strategy incorporating landscape-scale interventions and targeted vaccination of horses in local, high-risk areas would provide a focused, multi-scale policy for managing spillover risk.

By combining multiple spatial scales and including variables that discriminate across spatial scales, we are able to overcome limitations of previous studies of HeV spillover risk that used fixed spatial (Wardrop et al., 2014) and temporal scales (Martin et al., 2018). Inconsistencies between local environment and spillover locations have raised doubts about the influence of smaller scale environmental conditions on spillover risk (Martin et al., 2015). However, here we confirm previous expectations (Smith et al., 2014), and show that local environment can be influential in combination with landscape-level environment variation. Predictive models that include multiple spatial scales performed better than any of the fixed spatial scale models using the same environmental features. Variation in forest loss and fragmentation at multiple spatial scales has been previously shown to drive zoonotic malaria risk (Brock et al., 2019). We found that environmental features within

a 100-km radius influence HeV spillover. We expect that this reflects a protective impact of native forests and high-quality resources that are attractive to *Pteropus* and draw reservoirs away from pastures where they contact bridge hosts (horses).

Several variables that were most important in predicting HeV spillover at the smallest spatial scale could be influencing the likelihood of transmission and contacts between reservoir and bridge hosts (Figure 1) and provide important fine-scale indicators for spillover risk. Presence of human populations is likely a proxy for horses on the landscape and is supported by findings that higher proportions of pasture on the local scale is associated with increased spillover risk. We found that spillover was significantly more likely when average monthly maximum temperatures did not exceed 20°C. Because mean maximum temperature is highly correlated across different spatial scales, we were unable to identify at which spatial scale temperature is affecting spillover risk, but previous research provides several mechanisms that could operate at different scales. Experimental data demonstrates that temperatures below 22°C facilitate longer *Henipavirus* survival outside the host (Fogarty et al., 2008), suggesting temperatures at the pasture level may affect infection probability of horses. However, because other temperature metrics (i.e. number of days with maximum temperature < 22°C) did not have predictive power, it is possible that mean monthly temperature is a proxy for an alternative mechanism, aside from environmental persistence on pastures, that facilitates spillover. For example, in one study in southeast Queensland, time spent foraging at a single location for GPS-tracked grey-headed flying foxes increased significantly when temperature was below 20°C (Giles et al., 2018). Longer foraging times at lower temperatures may be related to aggregation of limited resources across space during winter (Eby & Law, 2008) and may impact spillover risk by leading to an increase in the amount of urine underneath a particular tree, given a spatial overlap of foraging trees, infected bats, and horse pasture in a foraging radii. These temperature conditions are observed in winter, which is consistent with other studies that found more spillovers (Eby et al., 2023; Martin et al., 2018; McFarlane et al., 2011) and increased underroost viral shedding (Paez et al., 2017) in the winter.

These smaller-scale predictors can be used to target resources to inform and support horse owners and veterinarians and identify key local governmental areas to develop policies in areas most at risk for HeV spillover. Pasture-level interventions can include covering feeding troughs, removing water and feed troughs from underneath trees, and removing fruit trees from grazing pastures. There are costs to individuals for adopting these interventions (Kung et al., 2013), but providing evidence-based risk estimations may lend confidence in the value of implementing preventative measures. An equine vaccine for HeV was released in 2012 and reduced the probability of infection following exposure (Middleton et al., 2014), but vaccination coverage is highly variable across space (Goyen et al., 2017). Better targeting vaccination campaigns may increase the coverage in key areas that are the most at risk of HeV spillover.

In addition to local features, several landscape level environmental features had high relative importance. We expect these

features to affect the movement and location of reservoirs across the landscape, which can either prevent or facilitate overlap between horse pastures and areas where reservoir species forage or roost. Research on grey-headed flying foxes shows that poor local foraging conditions encourage dispersal (Eby et al., 2023; Westcott et al., 2015) and nutritional resource pulses encourage aggregation of individuals (Eby et al., 1999; Giles et al., 2018). We found that HeV spillover across Australia is associated with lower NDVI at the landscape scale and higher local and foraging NDVI conditions. Our results also showed that greater amounts of forest cover in a 100-km radius reduced spillover suggesting that in these landscapes bats have sufficient natural resources and likely reduce foraging in pastures and infectious contacts. It is important to note that forest cover only corresponds with food availability if dietary species are present and flowering and producing nectar, but species-specific data on flower and nectar production at this scale are not available.

These important landscape-level features emphasize that policies to reduce zoonotic risk must also be implemented at state, or even federal levels. Vegetation quality and land use are associated with HeV spillover. This finding is corroborated by a recently published 25-year study that demonstrated spillover events are most common in years following food shortages and in mosaic agricultural landscapes with intermediate levels of forest cover in roost foraging areas (Eby et al., 2023). Our findings also support increasing forest cover at regional scales and we interpret this as increased habitat to increase resilience of flying fox populations. Eby et al. (2023) identified planting critical winter diet species as a key recommendation for the prevention of HeV spillovers in the long-term. Multiple lines of evidence now underscore the importance of managing HeV spillover at the landscape scale, beyond individual horse owners and veterinarians, and better aligned with observed foraging ecology of reservoir species.

In addition to identifying concurrent environmental features, we also find that environmental conditions across the previous 18 months play a role in spillover risk. Precipitation and temperature across various time lags have been found to influence flower timing and nectar availability (Hawkins et al., 2018; Hudson et al., 2010; Keatley et al., 2021), including some diet species of *Pteropus alecto* and *P. conspicillatus* (Table S1). Higher rates of HeV shedding have been recorded in years following a dry spring (Paez et al., 2017) and following resource scarcity (Becker et al., 2023). El Niño events, associated with hot and dry conditions, have been shown to precede clusters of spillover in altered landscapes when native winter flowering does not occur (Eby et al., 2023). Altogether, these results demonstrate there is sufficient time to direct and reallocate resources to enhance vaccination and preventative measures in seasons favouring spillover.

There are several limitations to model performance that could be improved in future studies. Detection of HeV spillovers is variable across the spatial extent of documented cases (Smith et al., 2016) in part because the case definition expanded and led to higher testing rates concurrent with an increase in the sensitivity of molecular assays (Smith et al., 2016). Horse density and horse vaccination rates are expected to be highly variable across space and time, thus additional data on these important bridge hosts would serve to improve spatiotemporal predictions. A final limitation of the work is that we focus on HeV-g1 spillovers—as more is discovered about HeV-g2 epidemiology, it will be important to include this new variant.

5 | CONCLUSIONS

We highlight the complex spatial and temporal scales that affect HeV spillover by using machine learning methods to identify non-linear responses to environmental features at multiple scales that increase the likelihood of spillover events. Previous work on species distribution models has emphasized the utility of including multiple spatial and temporal scales in distribution modelling (Fernandez-Gonzalez et al., 2013). Here we show that considering multiple spatial scales improves model predictions and provides valuable information for management of HeV spillovers. Current HeV management focuses on small spatial scales—such as encouraging individuals to vaccinate their horses. These results highlight the importance of management actions conducted at the landscape scale and provide risk profiles for targeting vaccination at local levels.

AUTHOR CONTRIBUTIONS

Christina L. Faust, Nita Bharti, Barbara A. Han and Raina K. Plowright conceived the ideas and methodology. Christina L. Faust, Allison J. Peel and Peggy Eby collected the data. Christina L. Faust and Adrian A. Castellanos conducted the analysis. Christina L. Faust led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

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

Table S1. Environmental variables associated with flying fox diet species (Eucalypts in general).

Table S2. Environmental variables associated with flying fox distribution.

Table S3. Environmental variables associated with HeV shedding.

Table S4. Environmental variables associated with HeV survival.

Table S5. Environmental variables associated with HeV spillover locations.

Table S6. Environmental features calculated at multiple spatial scales.

Table S7. Global environmental features: not calculated at multiple scales.

Figure S1. Spillover events over space and time.

Figure S2. Range of Hendra virus natural reservoir species.

Figure S3. Frequency of spillover events by season and region.

Figure S4. Cumulative map of reservoir foraging roosts.