EcoHealth
https://doi.org/10.1007/s10393-017-1309-y

ECOHEALTH

Original Contribution

Hendra Virus Spillover is a Bimodal System Driven by Climatic Factors

Gerardo Martin,[1] Carlos Yanez-Arenas,[2] Raina K. Plowright,[3] Carla Chen,[4]
Billie Roberts,[5] and Lee F. Skerratt[1]

[1] *One Health Research Group, College of Public Health, Medical and Veterinary Sciences, James Cook University, Townsville, QLD, Australia*
[2] *Laboratorio de Conservación de la Biodiversidad, Parque Científico y Tecnológico de Yucatán, Universidad, Universidad Nacional Autónoma de México, Mérida, Yucatán, Mexico*
[3] *Bozeman Disease Ecology Lab, Department of Microbiology and Immunology, Montana State University, Bozeman, MT*
[4] *Australian Institute of Marine Sciences, Townsville, QLD, Australia*
[5] *Griffith School of Environment, Griffith University, Nathan, QLD, Australia*

Abstract: Understanding environmental factors driving spatiotemporal patterns of disease can improve risk mitigation strategies. Hendra virus (HeV), discovered in Australia in 1994, spills over from bats (*Pteropus* sp.) to horses and thence to humans. Below latitude − 22°, almost all spillover events to horses occur during winter, and above this latitude spillover is aseasonal. We generated a statistical model of environmental drivers of HeV spillover per month. The model reproduced the spatiotemporal pattern of spillover risk between 1994 and 2015. The model was generated with an ensemble of methods for presence–absence data (boosted regression trees, random forests and logistic regression). Presences were the locations of horse cases, and absences per spatial unit (2.7 × 2.7 km pixels without spillover) were sampled with the horse census of Queensland and New South Wales. The most influential factors indicate that spillover is associated with both cold-dry and wet conditions. Bimodal responses to several variables suggest spillover involves two systems: one above and one below a latitudinal area close to − 22°. Northern spillovers are associated with cold-dry and wet conditions, and southern with cold-dry conditions. Biologically, these patterns could be driven by immune or behavioural changes in response to food shortage in bats and horse husbandry. Future research should look for differences in these traits between seasons in the two latitudinal regions. Based on the predicted risk patterns by latitude, we recommend enhanced preventive management for horses from March to November below latitude 22° south.

Keywords: Hendra virus, Horses, Spatiotemporal risk, Flying foxes, Emerging diseases, Spillover

INTRODUCTION

Infectious diseases have temporal patterns of incidence, some of which might present as seasonal cycles (Fisman 2007). However, incidence can also vary over space,

---

Electronic supplementary material: The online version of this article (https://doi.org/10.1007/s10393-017-1309-y) contains supplementary material, which is available to authorized users.

Correspondence to: Gerardo Martin, e-mail: gerardommc@gmail.com

resulting in spatiotemporal patterns (Ostfeld et al. 2005). These patterns have mostly been studied in single-host–single-pathogen systems and vector-borne diseases (Ostfeld et al. 2005; Bacaër and Guernaoui 2006; Altizer et al. 2006; Cuong et al. 2013). The biological mechanisms regulating spatiotemporal patterns of incidence can result from interactions between the host, pathogen and climate (Dowell 2001; Sultan et al. 2005; Fisman 2007). A typical consequence is the climatic regulation of incidence cycles that can result in longer and larger outbreaks when environmental conditions are more suitable for disease (e.g. cholera, dengue and influenza) (Pascual and Dobson 2005; Sultan et al. 2005; Grassly and Fraser 2006; Cuong et al. 2013).

Pathogen transmission between species, known as spillover (Plowright et al. 2017), requires the integration of spatiotemporal patterns of biotic and abiotic conditions across more than one host species (Lo Iacono et al. 2016; Plowright et al. 2017). For spillover to occur and result in a diseased individual, several ecological processes at different scales of organisation need to converge (e.g. pathogen survival in the environment, presence of infectious reservoirs and presence and susceptibility of spillover hosts) (Estrada-Peña et al. 2014; Plowright et al. 2015, 2017). Climate could influence all of these drivers of spillover risk. Therefore, the climatic factors associated with spatiotemporal patterns of spillover might be used for risk prediction, mitigation and guidance of further research. One of such diseases is the bat-borne Hendra virus (HeV) in Australia (Plowright et al. 2015).

Hendra virus is a Paramyxovirus, genus *Henipavirus*, first detected to infect and cause disease in horses and humans in 1994 (Murray et al. 1995a, b). In these spillover hosts, HeV causes severe respiratory and nervous system illness with mortality rates of 50% in horses and 75% in humans. The latter estimate is uncertain as there have only been seven cases in humans. The four Australian flying fox bat species (*Pteropus alecto, P. conspicillatus, P. poliocephalus* and *P. scapulatus*) are the only wild animals that have been found with antibodies (Halpin and Field 1996). Of the four bat species, evidence suggests *P. alecto* (black flying foxes) and *P. conspicillatus* (spectacled flying foxes) *are* the natural reservoir host and more likely to transmit HeV to horses (Edson et al.): firstly, because these species are statistically associated with the spatial pattern of spillover (Smith et al. 2014); secondly they are the only bat species from which the virus has been isolated (Edson et al. 2015); and thirdly, spillover events consistently occur in the geographical areas that are climatically more suitable for these two bat species (Martin et al. 2016). These areas are the northern wet tropics inhabited primarily by *P. conspicillatus* and to a lesser degree by *P. alecto*, and from the dry tropics to the temperate wet forests of central New South Wales inhabited by *P. alecto* (Martin et al. 2016). None of the bat species develop or show signs of disease as a result of HeV infection (Williamson et al. 1998, 2000; Halpin et al. 2011).

During the time frame since emergence of HeV, and particularly after a large cluster of spillover events in 2011, a spatiotemporal pattern of spillover has become evident. HeV is transmitted to horses in eastern Australia, during the southern hemisphere winter between May and September below latitude 22° south (34 spillover events) with one exception in November 2016 (ProMED archive number 20170107.4747872). Above this line, transmission has been recorded in all seasons (the remaining 21 of a total of 55 events) (McFarlane et al. 2011; Plowright et al. 2015).

Several environmental factors could be related to the spatiotemporal patterns of spillover. Bats feed exclusively on nectar and fruit of native and introduced plants (Richards 1990; Palmer et al. 2000). Nectar production by native *Eucalyptus* spp. trees depends on present and recent climatic conditions (Hudson et al. 2010). Pulses of nectar production regulate the number of bats present in certain geographical areas (Giles et al. 2016). Moreover, nutritional stress, driven by low plant production that is common during winter in subtropical areas (McFarlane et al. 2011), could result in increased susceptibility to diseases in general (Eby 1991) and to HeV infection in particular (Plowright et al. 2008, 2016). The temporal dynamics of food for bats in horse paddocks might also align with these climatically driven pulses of nectar production that occur at larger spatial scales. Climate also influences the longer-term geographical distribution and density of bats (Martin et al. 2016). All of the ecological interactions between bats, climate, and plants could have direct consequences for the dynamics of HeV in bats (Plowright et al. 2011, 2015, 2016). However, it is still unclear which climatic factors and biological mechanisms could regulate the observed seasonal pulses of HeV excretion and spillover risk (Field et al. 2015; Plowright et al. 2015)

Transmission from bats to horses is thought to occur through contact with infectious bat excreta or possibly ingestion of urine contaminated feed in the environment (Edson et al. 2015; Plowright et al. 2015; Martin et al. 2015). Because the cumulative number of spillover events matched the seasonal survival pattern of HeV in the environment, increased environmental survival of HeV was thought to contribute to spillover seasonality (Scanlan et al. 2014). However, an analysis of the spillover events in space and time found that HeV spillover did not occur when and where survival was higher (Martin et al. 2015, 2017). These results suggest that longer virus survival is not necessary for transmission and that increased environmental survival does not contribute to spillover seasonality.

A common approach to investigate disease seasonality consists of regression procedures to identify statistically significant correlations between disease incidence and an environmental or climatic factor. These associations between disease incidence and climate are often weak and provide little insight into underlying mechanisms driving seasonality (Dowell 2001; Pascual and Dobson 2005). Therefore, to gain more biological insights we used methods capable of finding nonlinear relationships, statistical associations and geographical patterns between a series of factors and HeV spillover risk. We investigated the spatiotemporal pattern of HeV incidence in horses in a niche modelling framework: we identified environmental requirements for spillover occurrence in space and time using an ensemble of presence–absence methods (Marmion et al. 2009). The aim of this study was to develop a consensus statistical model that identified climatic requirements or correlates that reproduce the observed spatiotemporal pattern of HeV spillover. We included the presence and abundance of bats and horses in the model, which are key determinants of HeV spillover dynamics.

METHODS

We generated a model that predicts the monthly distribution of HeV spillover risk using presence–absence data (case–non-case) per 2.7 × 2.7 km raster pixels. Presence pixels (cases or HeV events as they are generally called) were defined as laboratory confirmed cases of clinically ill horses with HeV, and absences (non-cases) were defined as pixels where no HeV cases had been reported during the month of interest, but were at risk of spillover given the potential presence of bats. Environmental data of the month and year of each spillover event were extracted from raster layers using the longitude and latitude coordinates of the events using the database maintained by Biosecurity Queensland. Absence pixels were sampled within a series of buffers with variable minimum and maximum distances from the presence pixels, as described in more detail below. Distances were measured from the coordinates of the centroid of the horse paddocks associated with each spillover event, as recorded in the 2007 horse census of Queensland and New South Wales (Moloney 2011). Hence, if the longitude and latitude of a HeV case or non-case lied within the upper and lower boundaries of a pixel, such pixel was classified as case or non-case. The extracted data were used to fit three models with different regression methods that were combined to generate a consensus model.

EXTRACTING DATA

Prior to extracting the environmental data, we thinned the data set with the coordinates of the spillover events to reduce spatial autocorrelation from 55 spillover events to 42 (Hijmans 2012). We used a recursive filtering algorithm based on a physical distance threshold of 0.05° between points. This was necessary because point data and environmental rasters have strong spatial dependence even more so in the presence of sampling bias which might be true for HeV spillover events. [Prevalence has remained stable, while samples for HeV testing have increased in numbers since discovery in 1994 (Smith et al. 2016)]. Besides, autocorrelated data sets compromise the assessment of a model's performance (Veloz 2009), as they violate the assumption of independence between observations. In addition to this adjustment, we assumed a 2-week delay between the registered date of the report and actual spillover, to account for an incubation period and therefore to capture the climatic conditions that were more likely to have occurred during or before the actual transmission from a bat to a horse. The values for monthly climatic variables for the estimated month of spillover of the filtered database were extracted from the pixels of the raster files using the geographical coordinates of each HeV case.

We selected explanatory variables according to our current knowledge of the HeV spillover system; bat species (distance to bat camps or roosting site, and environmental distance to the niche centroid as surrogate of abundance, see supplementary materials), density of horses (number of horses per grid cell) and variables representing climatic variability (corresponding to the average conditions of the recorded month of spillover compared with seasonal extremes). For instance, the variables, minimum temperature difference from minimum temperature of coldest month

Table 1. Variables Used for Hendra Virus Spillover Distribution Models.

Variable	Short name	Source
Distance to closest flying fox camp	*Distbats*	Model-generated
Distance to the niche centroid of flying foxes	DNC	Model-generated
Horse density	*Horsedens*	Generated from Queensland and New South Wales departments of primary industries horse census database
Normalised Difference Vegetation Index average (month)	NDVI	Bureau of meteorology (BOM)
Average minimum temperature (month)	*Mintemp*	BOM
Temperature range (month)	*Temprange*	Generated from BOM data
Rainfall		BOM
Difference between observed minimum and minimum temperature of coldest month	*mindif*	Generated from BOM data
Difference between observed maximum and maximum temperature of hottest month	*Maxdif*	Generated from BOM data
Difference between observed rainfall and average rainfall of the wettest month	*Raindifwet*	Generated from BOM data
Difference between observed rainfall and average rainfall of the dryest month	*Raindifdry*	Generated from BOM data
Solar exposure	*Solex*	BOM

(*mindif*, Table 1), maximum temperature difference from maximum temperature of warmest month (*maxdif*), rainfall difference from wettest month (*raindifwet*) and rainfall difference from driest month (*raindifdry*), represent the amplitude of seasonal variability.

The variables "distance to closest bat camp" and "environmental distance to the niche centroid of bats" were generated with similarity index methods (described in detail in the supplementary materials) (Farber and Kadmon 2003; Martínez-Meyer et al. 2013). Distance to the closest bat camp represents the physical distance (in a straight line) to a pixel with similar climatic characteristics to those occupied by bats. Climatic distance to the niche centroid represents a measure of similarity with an optimum defined by the multivariate centroid of the climatic conditions occupied by bat roosts.

To generate the horse density model, we repeated the coordinates of the property centroid by the number of horses reported. Then we added statistical uniformly distributed noise equivalent to half of the pixel size of the environmental data on each of the repeated property coordinates. After noising the coordinates, we counted the number of points per pixel and repeated the process 100 times. When iterations were completed, we averaged the 100 raster layers to obtain the final horse density model. A more detailed description is given in the supplementary materials.

While these types of analyses are correlational, the variables related to bat and horse presence and abundance could represent mechanistic relationships. The variables of climatic variability were used to represent other biological phenomena that might influence spillover risk but for which we have no data, such as plant phenology, bat and horse behaviour and HeV levels in bats (Plowright et al. 2015).

Sampling Absence Data

The process to obtain absence data comprised model validation simultaneously, although validation is described in detail below. To sample absence data, we randomly selected 15–16 non-case properties (756 in total) from the horse census database per spillover event. From this database we randomly selected the three to four properties per spillover event for the testing/validating data set. The data set used to fit the models comprised 42 presences and 600 absences (15–16 per spillover event). This ratio of absences/presence is the minimum of the recommended range of ratios for generalised linear models, boosted regression trees and random forests for use in species distribution models (Barbet-Massin et al. 2012). All sampled absence pixels lay within two buffers of different radius size around each spillover event. One radius was used to limit the minimum

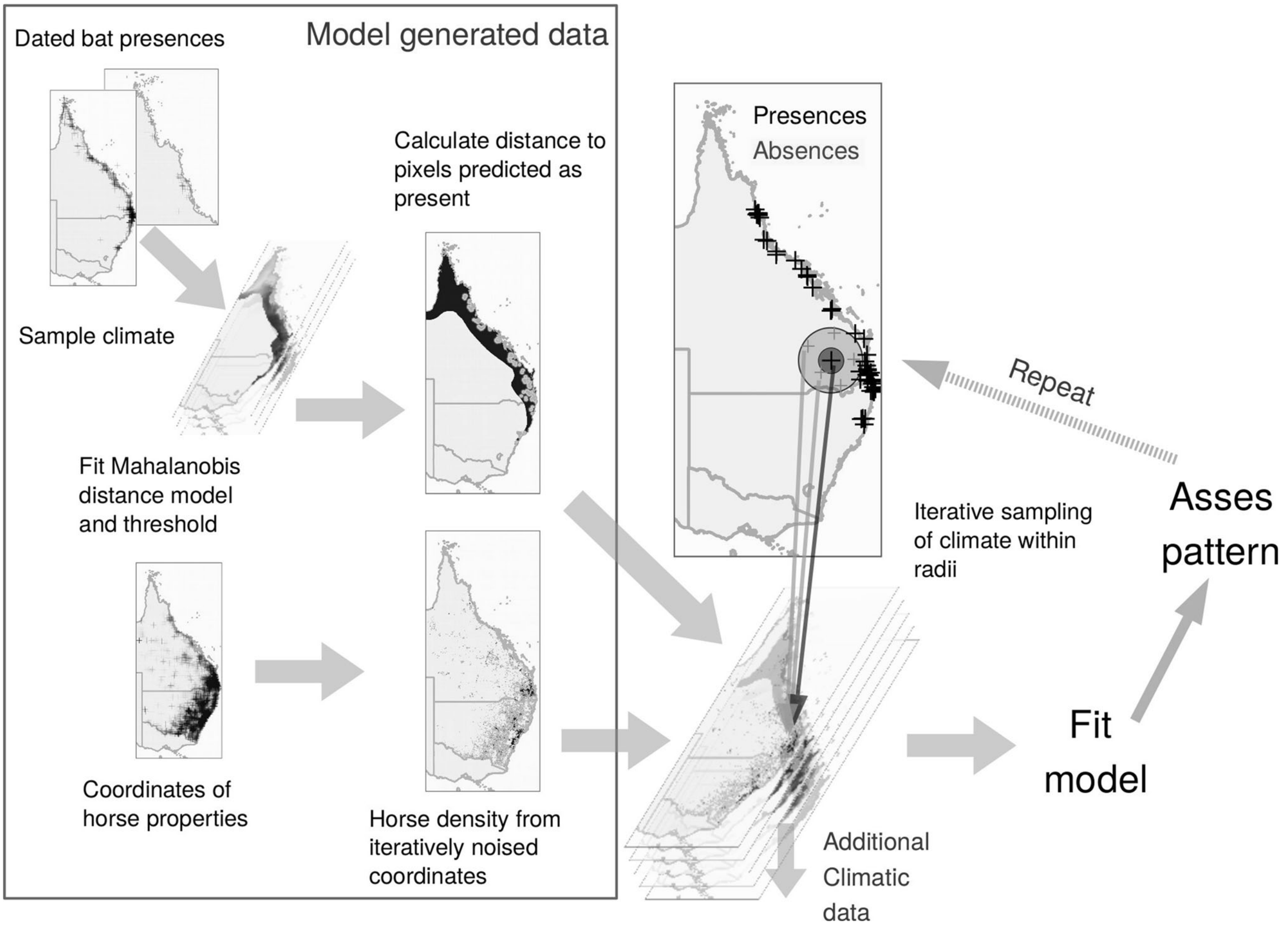

Fig. 1. Workflow followed to generate data and fit the model that reproduced the spatiotemporal pattern of spillover. The variables that were model-generated can represent causal associations because they are conditional for spillover (presence of reservoir and spillover hosts). Additional climatic data influence variability of spillover risk.

distance allowed around the spillover event (10–20 km), and the other buffer was used to limit the maximum distance (50–250 km). Then we implemented an iterative process that consisted of (1) increasing or decreasing the size of both buffers, (2) randomly sampling environmental data lying between the two buffers, (3) fitting the models with the sampled data and (4) testing the fitted model's performance on independent data (Fig. 1).

To test the model's performance (validation) in each iteration, we (1) partitioned the data set into 8 subsets for testing and training such that every event was used in either training or testing; (2) assessed its discriminative ability between presences and absences with the area under curve (AUC) of the receiver operator characteristic (ROC, specific details on model testing are given below), using the 150 absences that were sampled previously; and (3) assessed whether the model had reproduced the observed spatiotemporal pattern of spillover risk. To do the latter, models fitted in each iteration were projected to the average conditions of the months between discovery in 1994 and 2015 where spillover has been recorded (e.g. average conditions for each January from 1995 to 2015). Then the predicted suitability for each month was averaged by rows of pixels by using only the pixels that were 75 km or closer from the coast. This was necessary to allow better visualisation of the spatiotemporal pattern. The resulting averages by rows of the projected maps were stacked together and compared with a kernel density estimation of spillover event densities by month and latitude (Plowright et al. 2015). Finally, we kept the absences sampled within the buffer sizes that maximised the AUC and allowed reproduction of the spatiotemporal pattern.

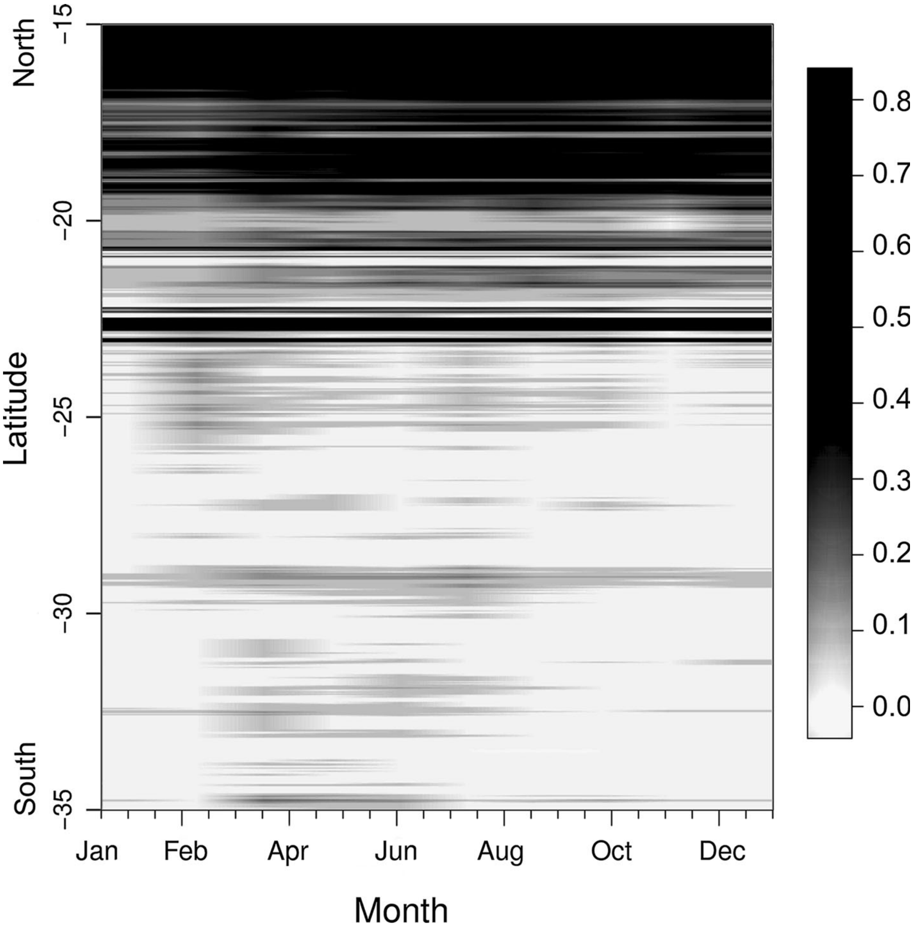

Fig. 2. Risk of spillover occurrence by month (*x* axis) and latitude (*y* axis) averaged across longitude. Darker shades indicate higher risk. In the southern spillover system risk increases in March and peaks in June at 28° south. In contrast, likelihood of spillover is more constant in higher latitudes across the year.

FITTING THE MODELS

Consensus or ensemble methods are algorithms that combine the predictions of a series of models fitted with different methods. The resulting distribution models after combining the different methods can exceed the performance of models generated with a single method depending on the combining algorithm (Marmion et al. 2009). Here we modelled the spatiotemporal pattern of HeV spillover risk with three regression methods, boosted regression trees, random forests and logistic regression, to create a consensus model with the AUC-weighted average of each model's predictions. All regression methods were implemented in R 3.1.1 (R-Development-Team 2014), using packages "gbm" and "RandomForest".

Boosted regression trees and random forests are extensions of classification and regression trees, which consist of the combination of multiple simple trees fitted to subsets of the data (bagging). The main difference between them is a process called gradient boosting, performed by boosted regression trees. Gradient boosting consists of sequentially adding simple regression tree models that are fitted to the residuals of previous models. When the sequential models are combined, the different splits give rise to smooth surfaces similar to those from traditional regression methods (Elith et al. 2008). We used these three methods because boosted regression trees and random forests have very high predictive accuracy (Breiman 2001; Elith et al. 2008); logistic regression is a transparent, well-understood and robust methodology, and because we could analyse presence–absence data with a logistic response with each of the methods.

The response variable for regression was presence or absence of spillover (logistic response). Each observation (presence or absence) was explained by additive terms of the variables listed in Table 1. We only used additive terms because boosted regression trees and random forests automatically determine the most relevant variable interactions (Breiman 2001; Elith et al. 2008), and because including interactions in the formulas of generalised linear models to generate species distributions does not usually improve their predictive performance (Thuiller et al. 2003).

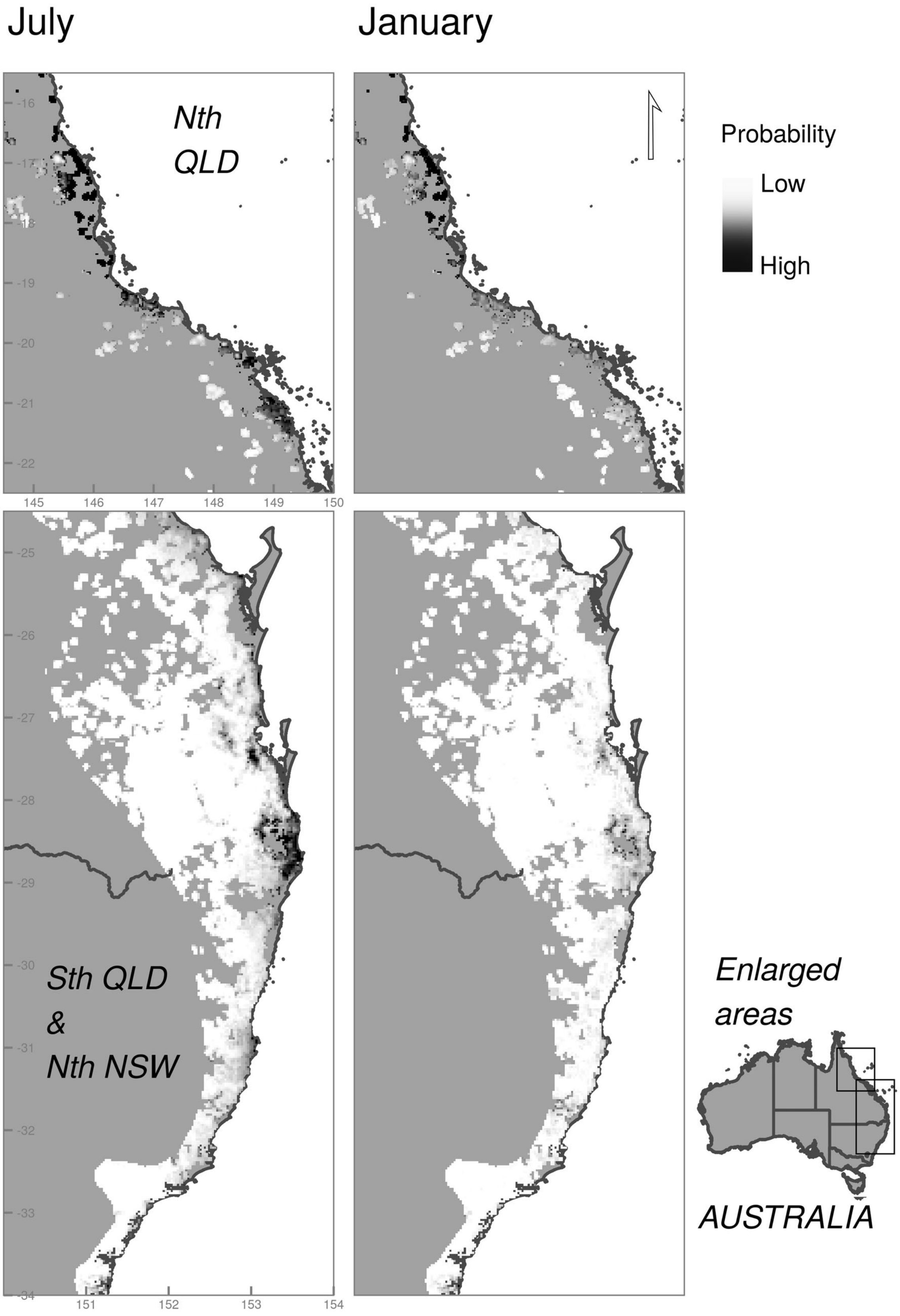

Fig. 3. Projections of the consensus model to the average conditions of the climatic variables of July and January between 1994 and 2014. Darker pixels indicate higher predicted suitability for spillover. The lower suitability in areas close to the border between Queensland and New South Wales during January represents the seasonal fluctuations.

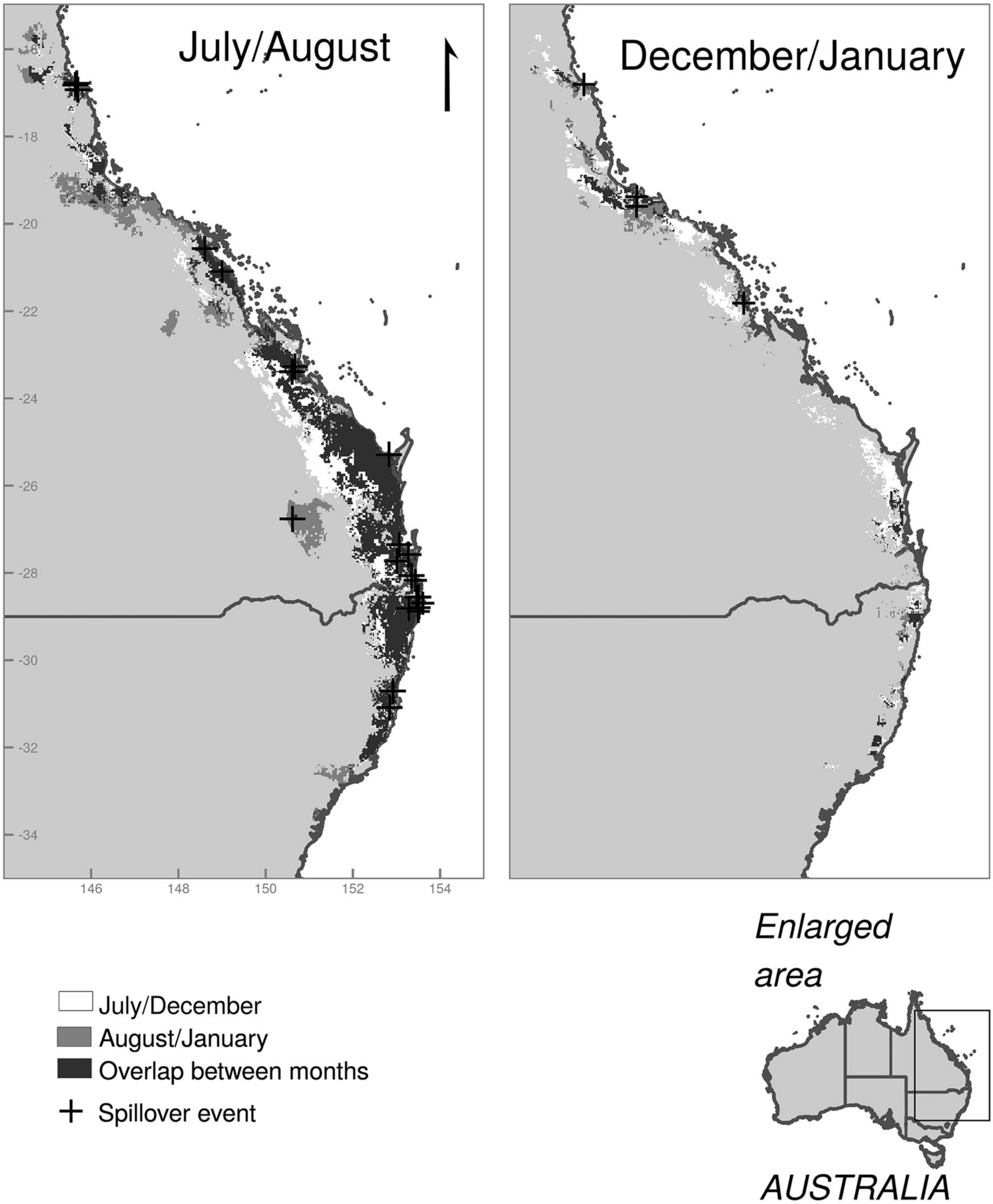

Fig. 4. Predictions of suitability according to the Mahalanobis distance model with climatic data only. Colours represent the month where areas at risk occur. In the left side July (white) and August (light grey), in the right side December (white) and January (light grey) and the overlap in risk that occurs between months (dark grey). Spillover localities correspond to those reported in July, August, December and January, respectively.

Validating the Models

We validated models fitted with individual methods with an AUC analysis at the same time that absences (non-cases) were being sampled. This method measured the model's ability to discriminate presences from absences (cases from non-cases), such that an AUC = 1 indicates perfect discrimination between presences and absences. Model's AUC scores on independent data were obtained by cross vali-

Table 2. Individual Variable's Contribution by Method and Consensus Model.

Variable	Method			
	Logistic regression	Random forest	Boosted regression trees	Consensus
NDVI	0.0265218138	0.0822897993	0.0581631333	0.055242626
Mintemp	0.1842491899	0.0824090844	0.0646522574	0.1109858062
Maxdif	0.1308561101	0.0535145893	0.026019653	0.0704994228
Mindif	0.3464459305	0.0763090204	0.0436831223	0.1569846931
Temprange	0.0332760371	0.0881916668	0.0954456208	0.0720005364
Solex	0.050221069	0.0652289297	0.043720652	0.052894018
rainfall	0.0018350817	0.0774999831	0.0304539593	0.0359838083
Distbats	0.0232535535	0.0843974006	0.0887695118	0.0651225297
DNC	0.0141872594	0.0704642356	0.0721045288	0.0519208851
Horsedens	0.1828075893	0.090664857	0.1947156795	0.156967504
Raindifwet	0.0022513437	0.1655746951	0.2545987897	0.1401336059
Raindifdry	0.004095022	0.0634557387	0.0276730919	0.0312645646

Variable influence has been de-scaled so that values represent proportions of the contribution metric for each method (explained deviance in logistic regression and incremental node purity in random forest, for instance).

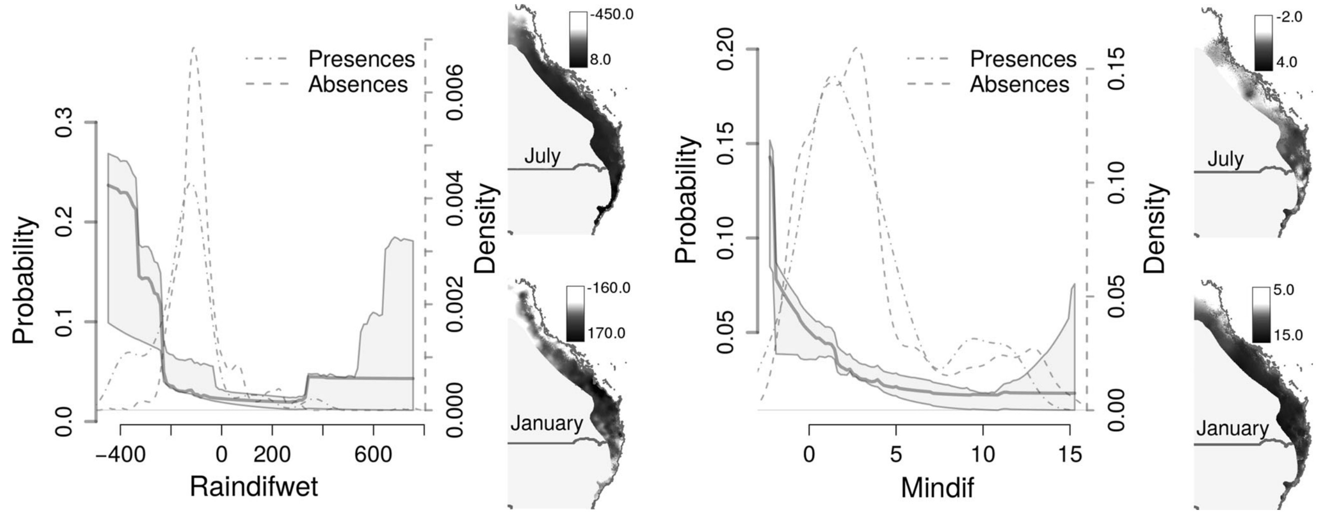

Fig. 5. Bold lines represent the partial dependence plots of the consensus model for two variables, *raindifwet* and *mindif*, which are the climatic factors that explained the majority of variability. The grey-shaded areas represent the average 1 weighted standard error of model predictions. The dashed lines are the density of the variables among presences and absences. The maps on the right side of each graph show the values of both variables in the two contrasting months, July and January.

dation; each of the eight partitioned data sets (described above) comprised of subsets of 70% of the presence data used to fit the model and then obtained the AUC with the remaining 30% of the data left behind. For each of the partitions of presences, we used the same 150 randomly sampled absences (3–4 absences per presence) to generate the AUC. The statistical significance of these performance tests was assessed by comparing the model's highest AUC with a distribution of AUC scores of 1000 null models fitted with 1000 sets of randomly fabricated presences and absences that were partitioned to generate the AUC (Raes and Ter Steege 2007). After obtaining the distribution of AUC values of the null models, we calculated the probability that the AUC of the tested model was significantly better than random by finding the proportion of null models that had a lower AUC.

The final model testing stage consisted of assessing the performance of the spatial projections of the model, for which we used the partial ROC test (Peterson et al. 2008). This modification of the traditional AUC analysis consists of calculating the area of a polygon formed by the proportion of the predicted geographical area (within a threshold of model predicted values) versus the proportion of predicted presence points. The calculated area under the polygon formed by the different fractions of predicted area and predicted points is then divided by the area under a random predictor based on the proportion of the geographical area predicted by the model. For this reason, the maximum value of this performance metric is 2. AUC ratios of 1 occur when the area under the polygon of proportion of area predicted vs proportion of predicted presences equals the area under the random prediction threshold (model predictions are not better than random) (Peterson et al. 2008). These model tests were accompanied by an extrapolation analysis that allowed us to identify geographical areas and points in time where the model predictions were affected by the projection data.

Extrapolation Analysis

To make sure that model predictions were as artefact free as possible, we sought for differences between fitting and projection data with an extrapolation detection analysis using ExDet (http://www.climond.org) (Mesgaran et al. 2014). When statistical models are used for prediction, they can face projection data that is different from the data used to fit the models. The differences between fitting and projection data can be values out of the range in the fitting data or different correlation structures between variables (Owens et al. 2013; Mesgaran et al. 2014). These differences can result in prediction artefacts of the model. Hence, we identified geographical areas in the raster maps generated with the models that could be spurious predictions based on the differences between fitting and projection data.

Interpreting the Model

We used two approaches to interpret the consensus model, variable partial effects curves derived from the consensus model and a similarity index model using only climatic variables (Table 1) from the Bureau of Meteorology (http://www.bom.gov.au) generated with the Mahalanobis distance algorithm (Farber and Kadmon 2003).

Variable partial effects curves show how predicted suitability responds to increases of an explanatory variable, while the remaining variables are kept constant at their mean value. More detailed information about the methods used can be found in the supplementary materials.

RESULTS

The final consensus model successfully reproduced the spatiotemporal pattern of spillover seen from 1994 until 2012 (Figs. 2, 3). This occurred when absences were sampled within a buffer of 20–250 km around spillover events. The spatiotemporal pattern consisted of a relatively constant risk of spillover in northern latitudes throughout the year, whereas below the tropics higher risk was during winter and early spring. At the time of these analyses, 32 events had occurred below 22° south latitude and all occurred in winter and early spring (May–November). Above this latitude, 23 events had been evenly distributed across seasons. Given the spatial autocorrelation of some events, the final data set for analysis contained only 42 events.

The largest seasonal differences occurred above and below latitude 22° south (Fig. 2) and between January and July (Figs. 3, 4). Suitability for spillover occurrence increased at lower latitudes from March and peaked in June at 28° south. By contrast, likelihood of spillover was more constant (white–blue tones in Fig. 2) in higher latitudes across the year. The apparent lower overall risk below 22° south in Fig. 2 was caused by the averaging across longitude necessary to produce the plot and the negative effect of horse density on spillover risk (see below and Figure S2).

The Mahalanobis distance model (fitted with climate data only, without horses and bats) also reproduced the spatiotemporal pattern of spillover risk. Its spatial projections show the change of size of areas to be at risk of spillover in relation to climate (Fig. 4). This model also allows better visualisation of the overlap in risk between months (areas that remain at risk in successive months, Fig. 4).

Minimum temperature difference from minimum temperature of coldest month (*mindif*, Table 2) and horse density were the most influential variables in the consensus model (32% of explained variability) with negative effects. *Mindif* is consistently lower during winter across latitudes. However, in summer it is much higher at southern latitudes. These levels of *mindif* result in the model estimating lower risk during summer in the south and more constant risk between months in the north. The negative effect of horse density indicated a lower risk of HeV spillover associated with higher density of horses. This effect reached a minimum at 200 horses per pixel and then increased until it remained stable at 220 horses and above (at about 50% of the maximum risk reached at 1 horse per pixel, Figure S2). Rainfall difference from the wettest month (*raindifwet*, Table 2) had a negative effect. Risk reached a minimum at -400 mm (drier conditions) and then increased to a stable point at 250, which was the maximum for positive values of *raindifwet*. Average minimum temperature had a positive effect and together with *raindifwet* accounted 26% of explained variability. The remaining variables had little explanatory power. A common feature among variables was the occurrence of bimodal responses (Figure S2).

From the four most influential variables mentioned above, *mindif* and *raindifwet* were the two climatic factors that had the most importance in the consensus model. The average value of *mindif* and *raindifwet* is lower among presences (events) than controls (absence of events), hence the negative relationships (density curves, Fig. 5). Distance to the niche centroid of bats was positively correlated with risk of spillover in the consensus model (Figure S2).

INDIVIDUAL MODELS

All individual models that were combined in the consensus model had a high discriminative ability, AUC = 0.936 (± 0.01) and performed significantly better than random when compared with the AUC of 1000 null models ($P < 0.05$). The logistic regression model had the highest AUC and explained 23% of the deviance. Of all variables, *mindif* (minimum temperature difference from the minimum temperature of coldest month) explained most of the deviance with a negative relationship. *mindif* was followed by horse density (negative relationship) and minimum temperature (positive). The boosted regression trees model had the second highest AUC (= 0.935). *Raindifwet* (rainfall difference from wettest month), distance to the niche centroid of bats and horse density explained most of the variability. The random forest model had an AUC = 0.92. It also found *raindifwet* was the most important variable in describing spillover events, followed by minimum average temperature, and distance to bat colonies. In contrast, the Mahalanobis distance model with climate-only data had the lowest performance with an AUC = 0.73 ($P = 0.01$) and was not included in the consensus model because it only included the climatic variables. The AUC scores of the models in relation to the distribution of the AUC scores of the null models are in the supplementary materials (Figure S3).

The algorithm or combination of algorithms that had the best performance in space of all according to the AUC ratio of the partial ROC test was the average of random forest and boosted regression trees (1.72, $P < 0.05$, P value indicates the probability that the calculated ratio is ≤ 1). As for individual models, random forest (1.64, $P < 0.05$) had a AUC ratio slightly higher than logistic regression (1.64, $P < 0.05$) and boosted regression trees (1.62, $P < 0.05$). The weighted average model that resulted from these three algorithms also performed better than a random prediction (1.58, $P < 0.05$) and clearly shows the lower suitability for spillover in southern regions during summer. The algorithms were slightly different in terms of how variability was explained by environmental factors, but their explanatory performance was very similar. For these reasons, the consensus model consisted of all three regression methods.

EXTRAPOLATION ANALYSIS

We identified areas where the consensus model faced extrapolation. This was located in the southernmost limit of the model projection. The type of extrapolation changed between months (extended variable range or inverted variable correlations) and in all cases increased the predicted spillover suitability. The only month in which the model did not face novel conditions in this area was February when it predicted low risk (Fig. 2). A comparison of these projections with the Mahalanobis distance model shows that the environmental conditions of this southern area are not similar to any of the conditions of the spillover events. By contrast, the small areas close to the border between Queensland and New South Wales that remained with higher probabilities of spillover during summer have similar environmental conditions to other events (Figs. 3, 4).

DISTANCE TO BAT CAMPS AND HORSE DENSITY

All the projections of the distance to bat camp models to spillover months after 2007 were predictions of the trained model. All of those models for which we had data for validation performed better than random with AUC ratios greater than 1.5 (maximum possible of 2). An example of the validated models is shown in Figure S1.

DISCUSSION

Our model reproduced the observed spatiotemporal pattern of HeV spillover between 1994 and 2015 (Plowright et al. 2015) with a number of differences. First, risk was lower in areas with a high density of spillover events; second, the model predicted areas at risk during summer below latitude 22° south. The pattern captured by the model suggests that the higher-risk period below latitude 22° south is from April to October. While no events have been reported to occur in April below this latitude, the longer predicted high-risk season may be explained by delays between HeV spillover, development of disease in horses and reporting of clinical cases in horses. Above 22° south, higher spillover suitability is more constant among months (Figs. 2, 4), which coincides with the density of spillover events by month and latitude (Plowright et al. 2015). Two climatic factors explained the majority of variability in the data with negative effects: the difference in minimum temperature from the minimum temperature of the coldest month (*mindif*) and difference of rainfall from rainfall of the wettest month (*raindifwet*). Minimum temperatures change more dramatically between seasons below latitude 22° south, close to the Tropic of Capricorn (Fig. 5), than above this area. This means that temperatures closer to the local minimum increase spillover risk when they are combined with low precipitation during a month.

Bimodal responses to rainfall levels (rainfall and *raindifwet*) indicate that either wet or dry conditions can increase spillover risk. Spillover in wet months occurs in northern areas; hence, wet conditions might only increase spillover risk in the north. These relationships also suggest that a single set of optimal conditions for spillover does not exist, coinciding with analyses of HeV shedding patterns in response to rainfall levels and temperature along the latitudinal range of spillover events. HeV shedding pulses are mainly explained by climatic conditions at small spatial scales (Páez et al. 2017). Therefore, we suggest that in the context of our study spillover risk is better represented by two systems, one in the north and another in the south. Spillover in the north seems to be correlated with both wet and dry conditions, and in the south it is related mostly to dry and cold climate. These two systems might well exist as a result of two different bat species involved in spillover, *P. conspicillatus* and *P. alecto* (Smith et al. 2014; Edson et al. 2015; Goldspink et al. 2015; Martin et al. 2016). The southern system could be driven by *P. alecto* and the northern by both *P. alecto* and *P. conspicillatus.*

We suggest that a basis to identify the two spillover systems in space be the estimated distributions of *P. alecto* and *P conspicillatus* (Martin et al. 2016). The climatic niche occupied by *P. conspicillatus* spans further south than its usual distribution in north-eastern Australia (Parsons et al. 2010), and its limits coincide with the area where there seem to be greater visual differences in our results and previous representations of the spillover pattern (Plowright et al. 2015). Given that disease systems could be subject to very high stochasticity, the threshold might be better described as a range around latitude 22° south, around the Tropic of Capricorn.

The suggested separate spatial locations of spillover systems implicate interactions with different plant communities (Eby and Law 2008) that potentially respond differently to climatic conditions and result in different HeV prevalence and shedding dynamics (Páez et al. 2017). In the northern system *P. alecto* and *P. conspicillatus* interact more frequently with a mixture of tropical rainforest and sclerophyll vegetation communities (Webb 1959; Eby and Law 2008). In the southern system, *P. alecto* interacts mostly with an ensemble of sclerophyll native plants dominated by *Eucalyptus* sp. and *Corymbia* sp. (Eby and Law 2008). The interactions with the different vegetation communities might regulate nutritional stress, body condition and susceptibility to HeV (Plowright et al. 2008, 2015; Páez et al. 2017; Peel et al. 2017), further providing plausible explanations for the different spillover patterns.

Migration of reservoir hosts could be one of the biological mechanisms driving spatiotemporal patterns. In some other bat virus spillover systems, migration contributes to spillover seasonality. For example, rabies spillover occurs when greater numbers of *Lasiurus cinereus* migrate to greener areas during winter (Escobar et al. 2013). However, the data we used to calibrate the distance to bat camp models indicate that there are bats still present in areas and seasons without recorded spillover events. In fact, recent analyses indicate that spillover has occurred when bat densities are low due to low food availability (Giles et al. 2016). Although the effects of food shortage in bats are not fully understood, nutritional stress has been associated with increased HeV seroprevalence (Plowright et al. 2008). Nutritional stress in that case was caused by flowering cessation of native plants after a cyclone. However, the relationship between seropositivity and HeV infectious status is unknown (Plowright et al. 2008; Field et al. 2011; Plowright et al. 2016). In general, HeV spillover has been related to low plant and crop productivity (McFarlane et al. 2011). Consequently, some of the potential scenarios by which bat–plant interactions could influence seasonal spillover risk below latitude 22° are: (1) poor nutrition leading to higher susceptibility which could lead to higher HeV infection levels and transmission among individual bats; (2) higher densities of bats feeding in more urbanised or agricultural landscapes when native plants are not in bloom (Plowright et al. 2015); or (3) a mixture of infection susceptibility in bats and switching of foraging habitat. Of these processes, there is stronger evidence for infection susceptibility because throughout the distribution of *P. alecto* there is a seasonal gradient of HeV excretion peaking in winter (Field et al. 2015; Páez et al. 2017). However, there are multiple alternative mechanisms that could be influencing seasonal excretion patterns (Plowright et al. 2016).

The negative response of spillover risk to horse density that we found contrasts with previous analyses that failed to demonstrate an effect of horse density (McFarlane et al. 2011; Smith et al. 2014). This effect might occur as a consequence of several different processes, ranging from bat foraging habitat availability, to husbandry practices in professionally managed properties associated with higher horse densities. Although not considered here, there could be a relationship between the number of horses per pixel and availability of bat food trees and the type and quality of management practices. This deserves further research to show how paddock management and structure might influence susceptibility to or likelihood of contact with HeV, because it could be one of the mechanisms influencing the spatiotemporal pattern of spillover. In other pathogen spillover systems, the same effect of apparent competition between host species arises when the spillover host is negatively affected by the pathogen (Holt and Pickering 1985; Power and Mitchell 2004). Horses are affected by HeV, but HeV spillover is too rare to reduce horse density. However, the same effect would arise from ecological competition between bats and horses (Power and Mitchell 2004). It is possible that domestic horses compete for habitat with bats because horses are linked to land clearing for grazing, whereas bats rely on flowering trees for food. Consequently, two factors could potentially create the relationship seen here; a negative effect of horses on bats' foraging habitat and a correlation between higher horse density and professional husbandry practises that reduce the risk of spillover. Regardless of the underlying cause, the resulting effect is lower spillover risk per horse as horse density increases.

The consensus model fitted a positive response to distance to the niche centroid of bats, our surrogate measure of bat abundance. The relationship between bat abundance and distance to the niche centroid is generally negative (Martin et al. 2016); hence, greater environmental distances from the niche centroid result in potentially smaller numbers of bats per pixel (Martínez-Meyer et al. 2013). This seemingly accurate prediction given Giles et al. (2016)'s recent findings of spillover occurring during low abundance of bats is, nevertheless, spatially confounded, by the behaviour of bats. This is because spillover occurs when bats are widely dispersed foraging at night time. These foraging areas are generally physically and environmentally distant from camp sites where bats are most abundant during the day (Vardon et al. 2001)

The differences between the climate-only Mahalanobis distance and the consensus model could be explained by the absence of the factors that are conditional for spillover like the presence of bats and horses. In addition the distributional estimates of environmental envelope methods, like those of Mahalanobis distance, are closer to the potential distribution than presence–absence methods that estimate the realised distribution (Soberón and Peterson 2005; Jiménez-Valverde et al. 2008). Alternative explanations for the wider areas predicted in the climate-only model could be related to the spatial resolution of the environmental data. It is possible that the spatial scale at which climate influences the biological mechanism driving the spatiotemporal spillover pattern is greater than the 2.7×2.7 km pixels used here. This is a common issue in species distribution and ecological niche modelling studies; ideally the grain size should match the scale at which species select their habitat (Peterson 2006). For instance, it has been suggested that the minimum area for a bat population to persist is 5000 km^2 (Vardon et al. 2001) and the foraging habitat of a bat camp is up to 40 km wide (Field et al. 2015). Therefore, the spatial scale at which climate influences risk of HeV spillover could be different than the one used here. The predictions of the climate-only model also represent a warning that adequate conditions for spillover occurrence are not completely absent during late spring and summer south of the 22° south area. For example, the late spring spillover event in November in Casino NSW (~ 29° south, ProMED archive number 20170107.4747872) was predicted by the full and climate-only models (Figs. 2, 4).

Our analyses have obvious limitations: (1) the absence of a strong link between climatic factors and a specific biological mechanism precludes the identification of the factors driving seasonality; (2) a poor understanding of bat foraging patterns and HeV transmission pathways to horses may result in misclassification of non-case properties; (3) the potential errors in the model-generated variables (distance to bat camps and DNC), regardless of their high performance, could accumulate uncertainty in the final spillover model; and (4) there could be alternative analytical methods more adequate and transparent than the consensus type of spatiotemporal analyses performed here.

The higher-risk season of HeV spillover below latitude 22° south has been from April to October. Whether this seasonal pattern is caused by immigration or emigration of bats is unclear. The number of bats in such areas depends mainly on food abundance, which has been previously suggested as a cause of increased susceptibility to HeV (Plowright et al. 2008). Consequently, our models could well be detecting these signals and the underlying mechanisms of seasonal spillover below latitude 22° south may be a mixture of seasonal movement and feeding of the reservoir host in horse paddocks (Pascual and Dobson 2005; Grassly and Fraser 2006). Impairment of the immune function of both reservoir and spillover hosts is also possible and could act in synergy with behavioural changes. One example of how these factors might increase risk is the spillover event in Casino NSW in November 2016 (ProMED archive number 20170107.4747872). This event occurred during a food shortage in late spring resulting in bats with poor body condition in the southern spillover system (Páez et al. 2017; Peel et al. 2017). An additional factor that could contribute to result in the observed spatiotemporal pattern is management of horses. For example, feed supplementation or stabling will reduce dependence on natural grass and exposure to HeV. These factors have been poorly studied and deserve future research.

Determining how the components of the HeV spillover system are affected by climate is beyond the scope of this analysis. Thus, further research is needed to understand the effects of climate on food availability and the consequent effects on bats and horse interactions and their immune function and management. However, good husbandry practices, like restriction of access of horses to trees (where flying foxes feed and excrete HeV) and vaccination against Hendra virus, can override the effect of many environmental factors (Haining 2003). We suggest that these practices should be more rigorously considered and followed in the areas and seasons that are at greater risk of Hendra virus spillover, while considering that areas and seasons that have not had spillover events might still pose low risk levels.

CONCLUSIONS

The mechanisms driving seasonality of Hendra virus spillover are likely influenced by the effects of the seasonal amplitude of minimum temperature and rainfall on food resources of bats and horses. Food resources might then regulate infection levels through changes in immune function (nutritional stress and body condition), behaviour and spatial population dynamics of bats. In horses, grass abundance might also influence immune function, behaviour and husbandry practices. Therefore, we suggest that future research focuses on determining how behaviour, immune function and management of both horses and bats change in response to food shortage driven by climate. Behavioural and immunological changes might be more evident when comparing areas north and south around latitude 22° south or the Tropic of Capricorn, which is where the major differences in seasonality seem to occur. However, we suggest that while the high-risk season below latitude 22° south occurred from April to October between 1994 and 2015, considering a longer-risk season such as from March to November could result in improved risk mitigation. Properties within and around the areas should be encouraged to improve mitigation by following the prevention guidelines of the Australian Veterinary Association (http://www.ava.com.au/hendra-virus), including vaccination, removing feed and water troughs from under trees, restricting access to trees during the night and removing grass or tall vegetation under trees that might provide better conditions for HeV survival and transmission in the environment.

ACKNOWLEDGEMENTS

The College of Public Health, Medical and Veterinary Sciences, James Cook University, was contracted by the Rural Industries Research and Development Corporation to undertake this research project. This research was funded by the Commonwealth of Australia, the State of New South Wales and the State of Queensland under the National Hendra Virus Research Program. HeV incident locations are by courtesy of the State of Queensland, through the Department of Agriculture, Fisheries and Forestry, Biosecurity Queensland, thanks to Dr. Craig Smith. We would also like to thank Dr David Páez and the reviewers for their valuable comments on the manuscript.

REFERENCES

Altizer S, Dobson A, Hosseini P, Hudson P, Pascual M, Rohani P (2006) Seasonality and the dynamics of infectious diseases. *Ecol Lett* 9:467–484. https://doi.org/10.1111/j.1461-0248.2005.00879.x

Bacaër N, Guernaoui S (2006) The epidemic threshold of vector-borne diseases with seasonality: The case of cutaneous leishmaniasis in Chichaoua, Morocco. *J Math Biol* 53:421–436. https://doi.org/10.1007/s00285-006-0015-0

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol Evol*. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Breiman L (2001) Random forests. *Mach Learn* 45:5–32

Cuong HQ, Vu NT, Cazelles B, Boni MF, Thai KTD, Rabaa MA, Quang LC, Simmons CP, Huu TN, Anders KL (2013) Spatiotemporal dynamics of dengue epidemics, Southern Vietnam. *Emerg Infect Dis* 19:945–953. https://doi.org/10.3201/eid1906.121323

Dowell SF (2001) Seasonal variation in host susceptibility and cycles of certain infectious diseases. *Emerg Infect Dis* 7:369–374. https://doi.org/10.3201/eid0703.010301

Eby P (1991) Seasonal movements of grey-headed flying-foxes, Pteropus poliocephalus (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. *Wildl Res* 18:547. https://doi.org/10.1071/WR9910547

Eby P, Law BS (2008) Ranking the feeding habitats of Grey-headed flying foxes for conservation management.

Edson D, Field H, McMichael L, Vidgen M, Goldspink L, Broos A, Melville D, Kristoffersen J, de Jong C, McLaughlin A, Davis R, Kung N, Jordan D, Kirkland P, Smith C (2015) Routes of Hendra Virus Excretion in Naturally-Infected Flying-Foxes: Implications for Viral Transmission and Spillover Risk. *PLoS One* 10:e0140670. https://doi.org/10.1371/journal.pone.0140670

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *J Anim Ecol* 77:802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Escobar LE, Peterson AT, Favi M, Yung V, Pons DJ, Medina-Vogel G (2013) Ecology and geography of transmission of two bat-borne rabies lineages in Chile. *PLoS Negl Trop Dis* 7:e2577. https://doi.org/10.1371/journal.pntd.0002577

Estrada-Peña A, Ostfeld RS, Peterson AT, Poulin R, de la Fuente J (2014) Effects of environmental change on zoonotic disease risk: An ecological primer. *Trends Parasitol* 30:205–214. https://doi.org/10.1016/j.pt.2014.02.003

Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance.

Field H, Jordan D, Edson D, Morris S, Melville D, Parry-Jones K, Broos A, Divljan A, McMichael L, Davis R, Kung N, Kirkland P, Smith C (2015) Spatiotemporal Aspects of Hendra Virus Infection in Pteropid Bats (Flying-Foxes) in Eastern Australia. *PLoS One* 10:e0144055. https://doi.org/10.1371/journal.pone.0144055

Field HE, de Jong C, Melville D, Smith C, Smith I, Broos A, Kung N, McLaughlin A, Zeddeman A (2011) Hendra virus infection dynamics in Australian fruit bats. *PLoS One* 6:e28678. https://doi.org/10.1371/journal.pone.0028678

Field HE, Smith CS, de Jong CE, Melville D, Broos A, Kung N, Thompson J, Dechmann DKN (2015) Landscape Utilisation, Animal Behaviour and Hendra Virus Risk. *Ecohealth* 13:26–38. https://doi.org/10.1007/s10393-015-1066-8

Fisman DN (2007) Seasonality of infectious diseases. *Annu Rev Public Health* 28:127–143. https://doi.org/10.1146/annurev.publhealth.28.021406.144128

Giles JR, Plowright RK, Eby P, Peel AJ, McCallum H (2016) Models of Eucalypt phenology predict bat population flux. *Ecol Evol*. https://doi.org/10.1002/ece3.2382

Goldspink LK, Edson DW, Vidgen ME, Bingham J, Field HE, Smith CS (2015) Natural Hendra Virus Infection in Flying-Foxes - Tissue Tropism and Risk Factors. *PLoS One* 10:e0128835. https://doi.org/10.1371/journal.pone.0128835

Grassly NC, Fraser C (2006) Seasonal infectious disease epidemiology. *Proc Biol Sci* 273:2541–2550. https://doi.org/10.1098/rspb.2006.3604

Haining R (2003) *Spatial data Analysis: Theory and Practice*, Edinburgh: Cambridge University Press

Halpin K, Field HE (1996) Identification of likely natural hosts for equine Morbillivirus. *Commun Dis Intell* 20:1996

Halpin K, Hyatt AD, Fogarty R, Middleton D, Bingham J, Epstein JH, Rahman SA, Hughes T, Smith C, Field HE, Daszak P (2011) Pteropid bats are confirmed as the reservoir hosts of henipaviruses: a comprehensive experimental study of virus transmission. *Am J Trop Med Hyg* 85:946–951. https://doi.org/10.4269/ajtmh.2011.10-0567

Hijmans RJ (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology* 93:679–688

Holt RD, Pickering J (1985) Infectious Disease and Species Coexistence: A Model of Lotka-Volterra Form. *Am Nat* 126:196–211

Hudson IL, Kim SW, Keatley MR (2010) Climatic Influences on the Flowering Phenology of Four Eucalypts: A GAMLSS Approach. In: *Phenological Research*, Hudson IL, Keatley MR (editors), London: Springer, pp 209–228

Jiménez-Valverde A, Lobo JM, Hortal J (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Divers Distrib* 14:885–890. https://doi.org/10.1111/j.1472-4642.2008.00496.x

Lo Iacono GL, Cunningham AA, Moses LM, Lo Iacono G, Cunningham AA, Fichet-calvet E (2016) A Unified Framework for the Infection Dynamics of Zoonotic Spillover and Spread. *PLoS One*. https://doi.org/10.1371/journal.pntd.0004957

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. *Divers Distrib* 15:59–69. https://doi.org/10.1111/j.1472-4642.2008.00491.x

Martin G, Plowright R, Chen C, Kault D, Selleck P, Skerratt L (2015) Hendra virus survival does not explain spillover patterns and implicates relatively direct transmission routes from flying foxes to horses. J Gen Virol vir.0.000073. https://doi.org/10.1099/vir.0.000073

Martin G, Webb RJ, Chen C, Plowright RK, Skerratt LF (2017) Microclimates Might Limit Indirect Spillover of the Bat Borne Zoonotic Hendra Virus. *Microb Ecol*. https://doi.org/10.1007/s00248-017-0934-x

Martin G, Yanez-Arenas C, Roberts BJ, Chen C, Plowright RK, Webb RJ, Skerratt LF (2016) Climatic suitability influences species specific abundance patterns of Australian flying foxes and risk of Hendra virus spillover. *One Heal* 2:115–121. https://doi.org/10.1016/j.onehlt.2016.07.004

Martínez-Meyer E, Díaz-Porras D, Peterson AT, Yáñez-Arenas C (2013) Ecological niche structure and rangewide abundance patterns of species. *Biol Lett* 9:20120637. https://doi.org/10.1098/rsbl.2012.0637

McFarlane R, Becker N, Field H (2011) Investigation of the climatic and environmental context of Hendra virus spillover events 1994-2010. *PLoS One* 6:e28374. https://doi.org/10.1371/journal.pone.0028374

Mesgaran MB, Cousens RD, Webber BL (2014) Here be dragons: a tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. *Divers Distrib n/a-n/a*. https://doi.org/10.1111/ddi.12209

Moloney BJ (2011) Overview of the epidemiology of equine influenza in the Australian outbreak. *Aust Vet J* 89(Suppl 1):50–56. https://doi.org/10.1111/j.1751-0813.2011.00748.x

Murray K, Rogers R, Selvey LA, Selleck P, Hyatt A, Gould A, Gleeson L, Hooper P, Westbury H (1995a) A Novel Morbillivirus Pneumonia of Horses and its Transmission to Humans. Emerg Infect Dis 1:31–3n oubr.

Murray K, Selleck P, Hooper P, Hyatt A, Gould A, Gleeson L, Westbury H, Hiley L, Selvey L, Rodwell B (1995) A morbillivirus that caused fatal disease in horses and humans. *Science* 268:94–97

Ostfeld RS, Glass GE, Keesing F (2005) Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends Ecol Evol* 20:328–336. https://doi.org/10.1016/j.tree.2005.03.009

Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, Ingenloff K, Lira-Noriega A, Hensz CM, Myers CE, Peterson AT (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol Modell* 263:10–18. https://doi.org/10.1016/j.ecolmodel.2013.04.011

Páez DJ, Giles J, McCallum H, Field H, Jordan D, Peel AJ, Plowright RK (2017) Conditions affecting the timing and magnitude of Hendra virus shedding across pteropodid bat populations in Australia. *Epidemiol Infect*. https://doi.org/10.1017/S0950268817002138

Palmer C, Price O, Bach C (2000) Foraging ecology of the black flying fox (Pteropus alecto) in the seasonal tropics of the Northern Territory, Australia. *Wildl Res* 27:169–178

Parsons JG, VanDerWal J, Robson SKA, Shilton LA (2010) The Implications of Sympatry in the Spectacled and Grey Headed Flying-Fox, Pteropus conspicillatus and P. poliocephalus (Chiroptera: Pteropodidae). *Acta Chiropterologica* 12:301–309. https://doi.org/10.3161/150811010X537882

Pascual M, Dobson A (2005) Seasonal patterns of infectious diseases. *PLoS Med* 2:e5. https://doi.org/10.1371/journal.pmed.0020005

Peel AJ, Eby P, Kessler M, Lunn T, Breed AC, Plowright RK (2017) Letter to the editor: Hendra virus spillover risk in horses: heightened vigilance and precautions being urged this winter.

Peterson AT (2006) Uses and requirements of ecological niche models and related distributional models. *Biodivers Informatics* 3:59–72

Peterson AT, Papes M, Soberon J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol Modell* 213:63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Plowright RK, Eby P, Hudson PJ, Smith I, Westcott D, Bryden W, Middleton DJ, Reid P, McFarlane R, Martin G, Tabor G, Skerratt LF, Anderson D, Cramery G, Quammen D, Jordan D, Freeman P, Lin-Fa W, Epstein JH, Marsh G, Kung N, McCallum H (2015) Ecological dynamics of emerging bat virus spillover.

Plowright RK, Field HE, Smith C, Divljan A, Palmer C, Tabor G, Daszak P, Foley JE (2008) Reproduction and nutritional stress are risk factors for Hendra virus infection in little red flying foxes (Pteropus scapulatus). *Proc Biol Sci* 275:861–869. https://doi.org/10.1098/rspb.2007.1260

Plowright RK, Foley P, Field HE, Dobson AP, Foley JE, Eby P, Daszak P (2011) Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus* spp.). Proc Biol Sci. https://doi.org/10.1098/rspb.2011.0522

Plowright RK, Parrish CR, McCallum H, Hudson PJ, Ko AI, Graham AL, Lloyd-Smith JO (2017) Pathways to zoonotic spillover. *Nat Rev Microbiol* 15:502–510. https://doi.org/10.1038/nrmicro.2017.45

Plowright RK, Peel AJ, Streicker DG, Gilbert A, McCallum H, Wood J, Baker ML, Restif O (2016) Transmission or within-host dynamics driving pulses of zoonotic viruses in reservoir-host populations. *PLoS Negl Trop Dis*. https://doi.org/10.1371/journal.pntd.0004796

Power AG, Mitchell CE (2004) Pathogen spillover in disease epidemics. *Am Nat* 164(Suppl):S79–S89. https://doi.org/10.1086/424610

R-Development-Team (2014) R: A language and environment for statistical computing.

Raes N, Ter Steege H (2007) A null-model for significance testing of presence-only species distribution models. *Ecography (Cop)* 30:727–736. https://doi.org/10.1111/j.2007.0906-7590.05041.x

Richards GC (1990) The spectacled flying-fox, Pteropus conspicillatus (Chiroptera: Pteropodidae), in north Queensland. 2. Diet, seed dispersal and feeding ecology. *J Aust Mammal* 13:25–31

Scanlan JC, Kung N, Selleck P, Field H (2014) Survival of Hendra Virus in the Environment: Modelling the Effect of Temperature. *Ecohealth*. https://doi.org/10.1007/s10393-014-0920-4

Smith C, Skelly C, Kung N, Roberts B, Field H (2014) Flying-fox species density - a spatial risk factor for hendra virus infection in horses in eastern australia. *PLoS One* 9:e99965. https://doi.org/10.1371/journal.pone.0099965

Smith CS, McLaughlin A, Field HE, Edson D, Mayer D, Ossedryver S, Barrett J, Waltisbuhl D (2016) Twenty years of Hendra virus: laboratory submission trends and risk factors for infection in horses. *Epidemiol Infect*. https://doi.org/10.1017/S0950268816001400

Soberón J, Peterson AT (2005) Interpretation of Models of Fundamental Ecological Niches and Species Distributional Areas. *Biodivers Informatics* 2:1–10. https://doi.org/10.1093/wber/lhm022

Sultan B, Labadi K, Guégan J-F, Janicot S (2005) Climate drives the meningitis epidemics onset in west Africa. *PLoS Med* 2:e6. https://doi.org/10.1371/journal.pmed.0020006

Thuiller W, Araújo Miguel B, Lavorel S (2003) Generalized models vs. classification tree analysis: predicting spatial distributions of plant species at different scales. *J Veg Sci* 14:669–680. https://doi.org/10.1111/j.1654-1103.2003.tb02199.x

Vardon MJ, Brocklehurst PS, Woinarski JCZ, Cunningham RB, Donnelly CF, Tidemann CR (2001) Seasonal habitat use by flying-foxes, Pteropus alecto and P. scapulatus (Megachiroptera), in monsoonal Australia. *J Zool* 253:523–535. https://doi.org/10.1017/S0952836901000486

Veloz SD (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *J Biogeogr* 36:2290–2299. https://doi.org/10.1111/j.1365-2699.2009.02174.x

Webb BYLJ (1959) A physiognomic classification of Australian rain forests. *J Ecol* 47:551–570. https://doi.org/10.2307/2257290

Williamson MM, Hooper PT, Selleck PW, Gleeson LJ, Daniels PW, Westbury HA, Murray PK (1998) Transmission studies of Hendra virus (equine morbilli-virus) in fruit bats, horses and cats. *Aust Vet J* 76:813–818. https://doi.org/10.1111/j.1751-0813.1998.tb12335.x

Williamson MM, Hooper PT, Selleck PW, Westbury HA, Slocombe RF (2000) Experimental hendra virus infectionin pregnant guinea-pigs and fruit Bats (Pteropus poliocephalus). *J Comp Pathol* 122:201–207. https://doi.org/10.1053/jcpa.1999.0364