



# Climatic suitability influences species specific abundance patterns of Australian flying foxes and risk of Hendra virus spillover

Gerardo A. Martin<sup>a,\*</sup>, Carlos Yanez-Arenas<sup>b</sup>, Billie J. Roberts<sup>c</sup>, Carla Chen<sup>a</sup>, Raina K. Plowright<sup>d</sup>, Rebecca J. Webb<sup>a</sup>, Lee F. Skerratt<sup>a</sup>

<sup>a</sup> One Health Research Group, College of Public Health, Medical and Veterinary Sciences, James Cook University, Townsville, QLD, Australia

<sup>b</sup> Laboratorio de Conservación de la Biodiversidad, Parque Científico y Tecnológico de Yucatán, Universidad Nacional Autónoma de México, Mérida, Yucatán, México

<sup>c</sup> School of Environment, Griffith University, Brisbane, QLD, Australia

<sup>d</sup> Department of Microbiology and Immunology, Montana State University, Bozeman, MT, USA

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## ABSTRACT

Hendra virus is a paramyxovirus of Australian flying fox bats. It was first detected in August 1994, after the death of 20 horses and one human. Since then it has occurred regularly within a portion of the geographical distribution of all Australian flying fox (fruit bat) species. There is, however, little understanding about which species are most likely responsible for spillover, or why spillover does not occur in other areas occupied by reservoir and spillover hosts. Using ecological niche models of the four flying fox species we were able to identify which species are most likely linked to spillover events using the concept of distance to the niche centroid of each species. With this novel approach we found that 20 out of 27 events occur disproportionately closer to the niche centroid of two species (*P. alecto* and *P. conspicillatus*). With linear regressions we found a negative relationship between distance to the niche centroid and abundance of these two species. Thus, we suggest that the bioclimatic niche of these two species is likely driving the spatial pattern of spillover of Hendra virus into horses and ultimately humans.

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## 1. Introduction

Spillover of wildlife pathogens is a recurrent and often unpredictable phenomenon with important consequences for human and domestic animal health. Bats (Mammalia; Chiroptera) have been focus of considerable attention for their seemingly disproportionate diversity of viruses that are pathogenic to other mammal orders [1]. A few well known bat borne zoonotic viral diseases include Ebola, Marburg virus disease and SARS [2–4]. Despite their importance, spillover of these viral diseases is difficult to predict [5–7], partly due to the poor understanding of the viruses in their specific reservoir hosts and the ecological interaction of these hosts with the spillover hosts.

The abundance of reservoir hosts is an important determinant of the risk of pathogen spillover as it is a key driver of pathogen prevalence and disease transmission [8,9]. Spatial patterns of species abundance can be influenced by the climatic characteristics of the geographic areas inhabited by species [10]. At the very least, climate can predict where abundance is more likely to be higher [11].

Ecological niche modelling (ENM) is a field of ecology that studies the environmental requirements of species. By using spatially

referenced environmental and climatic data ENM is frequently used to identify geographic areas where species can survive and persist [12, 13]. The abundance patterns of species within the predicted geographic ranges are often related to its location within the ecological and climatic niche [10]. The different locations within climatic niches can be estimated by finding its multivariate centroid, which is formed by the mean of each environmental/climatic dimension of the niche. For instance the average of the maximum temperature or rainfall of wettest season across a species geographical range might represent a bi-variate niche centroid. Departures from the centroid in any direction are measured as environmental distance from the niche centroid (DNC).<sup>1</sup> Consequently the DNC of reservoir host species could be used to better understand and predict the risk of spillover of emerging zoonotic pathogens.

One of these emerging zoonoses is Hendra virus (HeV),<sup>2</sup> belonging to the genus *Henipavirus* (Paramyxoviridae). It was discovered in Australia in 1994 after a respiratory disease outbreak involving the death of 20 horses and one human [14]. Hendra virus has been found to naturally infect the four Australian fruit bat species (genus *Pteropus*, also known as flying foxes, FF),<sup>3</sup> the black flying fox, *P. alecto*; grey headed flying fox, *P. poliocephalus*; spectacled flying fox, *P. conspicillatus*; and

\* Corresponding author at: College of Public Health, Medical and Veterinary Sciences, James Cook University, James Cook Drive, DB41-106, 4810 Douglas, QLD, Australia.  
E-mail address: [gerardomm@gmail.com](mailto:gerardomm@gmail.com) (G.A. Martin).

<sup>1</sup> DNC = Distance to the niche centroid.

<sup>2</sup> HeV = Hendra virus.

<sup>3</sup> FF = Flying foxes.

the little red flying fox, *P. scapulatus* [15]. To date, infection in horses is rare and sporadic. Fifty-one spillover events have been recorded since September 1994, spanning nearly 1500 km of the east coast of Australia. The case fatality rates in horses and humans are approximately 75 and 50%, respectively [16].

Recent analyses suggest that black (*P. alecto*, BFF)<sup>4</sup> and spectacled FF (*P. conspicillatus*, SFF)<sup>5</sup> are more likely to be responsible for the HeV spillover events. This is based on the observation that the density of records of these two species is higher in areas where spillover has occurred [17,18], and that HeV is more likely to be detected in these species [19,20]. Spillover events seem to be expanding south, coinciding with the southwards expansion of *P. alecto* during the last few decades [21]. Although these correlations are statistically significant, an ecological explanation is still missing. For instance, the southwards increase of spillover cases can result from either the expanding range of *P. alecto*, or confounded by improved reporting and surveillance after the first New South Wales spillover case was detected in 2006 [22]. One way to address the uncertain role of these four FF species is to look at the ecological suitability of spillover sites for each of the four potential reservoir host species.

One of the key determinants of ecological suitability for FF are their preferred food resources, which are dependent on climate. For example, the flowering status of several *Eucalyptus* species, the main food source for FF, is determined by climatic factors [23]. In addition, the spillover pathway of Hendra virus from FF to horses is directly linked to FF food resources, as transmission appears to be due to FF shedding virus in trees inside horse paddocks while foraging [24,25]. This provides an ecological basis for investigating the spatial suitability and abundance patterns of FF in relation to climate with correlative methods. Moreover, it is well known that FF have limited thermal tolerance that differs among the four Australian species, indicating that their fundamental niche is a key component of their potential distribution, making climate an important factor limiting their geographic distribution [26,27].

Three previous studies have modelled the distribution of henipaviruses, first Peterson [28] sought to identify conditions that allow transmission and persistence of Nipah virus (NiV)<sup>6</sup> among hosts. Second, Daszak et al. [29] modelled the present and future potential distributions of *Henipavirus* hosts; and, Smith et al. [18] identified geographical correlates of HeV spillover. Other studies of bat borne zoonotic viruses have focused strictly on finding geographic areas of risk to human populations [e.g., [7,30]]. In this study we modelled the climatic requirements of HeV reservoir hosts. The models were then used to establish a relationship between suitability for FF and risk of HeV spillover based on the observed geography of spillover. Our results provide further evidence of the association of FF species with HeV spillover and potential drivers of the spatial pattern of spillover.

## 2. Methods

Predictions from niche models are a series of smoothed surfaces in the form of maps whose accuracy depends largely on the explanatory environmental variables [13,31]. Correlative niche modelling relies on statistical relationships between environmental characteristics and geographical records of species presence [32]. In many cases reliable records of species absence are not available which has led to the development of algorithms that use presence only data, like Maxent [32]. Similarly, validation techniques have been adapted to this kind of presence only data. For example some model testing methods use the proportion of the study area predicted to be occupied by the species and the proportion of predicted presences; like the Partial ROC and

Jackknife test [33,34]. These methods compare prediction rates of the model on testing data by comparing prediction rates with a random spatial predictor (proportion of area predicted to be occupied). Maxent is a machine learning algorithm based on maximum entropy, that is similar to a Poisson regression [35], but has a logistic-like output and is capable of fitting non-linear relationships. The result is a series of response functions that provide an estimate of probability of species presence in relation to the assumed proportion of grid cells occupied by the species [36]. Below we describe the methods we used to select the variables to model the niche of each FF species, validate the models and calculate the DNC of FF species of all pixels across the area where HeV spills over to horses and determine its relation to HeV spillover.

### 2.1. Niches of flying fox species

We obtained flying fox presence localities from the global biodiversity database (<http://www.gbif.org>), the Atlas of Living Australia (<http://www.ala.org.au>) and Roberts et al. [21]. The three databases were combined to maximise the number of records. We then used an iterative method to eliminate localities within a pre-specified threshold distance to reduce spatial autocorrelation. The filtered presence localities were then used to sample climatic raster data from the Worldclim bioclimatic variables (<http://www.worldclim.org>) [37]. In addition, points that were dubious or very far from the known distributional limits were removed. For each bat species we selected a set of layers based on pairwise correlations between climatic variables and how the presence points were distributed within each plot of variable pairs [13]. We sought to include the variables where presences had a unimodal distribution and occupied a limited range within the scope of possible values of the variable.

To validate models by means of measuring its performance on independent data we selected training and testing data spatially. To do so we created a chess board grid with squares of 40,000 km<sup>2</sup> approximately, and 200 km wide horizontal and vertical bands (along longitude and latitude). We used points lying within contiguous bands or squares for training and testing with a partial ROC analysis [33,38]. Given that we did not verify flying fox occurrence records for accuracy we allowed a 50% omission rate of testing points for the partial ROC analysis. Because the final data set for *P. conspicillatus* contained <30 occurrence records, we validated this model with a Jackknife test [34]. For the Jackknife test we calibrated  $N-1$  models ( $N$  = number of presence localities), leaving one of the presence localities out in each model run. Then from the scores assigned by the algorithm to each locality we used the minimum of these values as a threshold to see if the omitted locality had been predicted as present (had a probability of occurrence  $\geq$  threshold). The predictions/non-predictions and thresholds were used as probabilities to run the validation test with the “pValueCompute” tool from Pearson et al. [34].

Because niche models should only encompass the areas where species can move (areas colonisable by species = M [Movement]) [39,40], we assumed that the climatic regions of Australia (Bureau of Meteorology of Australia, <http://www.bom.gov.au>) occupied by each FF species are the boundaries of the areas accessible to colonise. The same assumption helped identify the HeV M area. All climatic regions containing at least one presence point of the final presence database were combined to mask the climatic variables for each species. All the FF niche models were generated with Maxent without clamping and extrapolation [32]. To generate the binary models necessary for the subsequent analyses we applied a threshold corresponding to the 50th percentile of model scores at presence localities, which represents the same criterion used in model testing. The resulting binary maps represent areas where each FF species has a probability  $\geq 0.5$  of being present. All models and analyses were performed with the statistical programming language R 3.1.1 [41] (R-Core-Team 2014) with packages “dismo” and “raster” [42,43].

<sup>4</sup> BFF = Black flying foxes.

<sup>5</sup> SFF = Spectacled flying foxes.

<sup>6</sup> NiV = Nipah virus.

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