

**THE ROLE OF POPULATION STRUCTURE IN PATHOGEN DIVERSITY IN WILD  
BAT POPULATIONS**

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## 1. Abstract

1.0.1. *One or two sentences providing a basic introduction to the field.* Bats are an important reservoir of zoonotic diseases. It is still unclear what factors determine the number of pathogens a wild bat species carries. But once understood, these factors could provide a way to priorities surveillance of bat populations.

1.0.2. *Two to three sentences of more detailed background.*

1.0.3. *One sentence clearly stating the general problem (the gap).*

1.0.4. *One sentence summarising the main result.*

1.0.5. *Two or three sentences explaining what the main result reveals in direct comparison to what was thought to be the case previously.*

1.0.6. *One or two sentences to put the results into a more general context.*

1.0.7. *Two or three sentences to provide a broader perspective,*

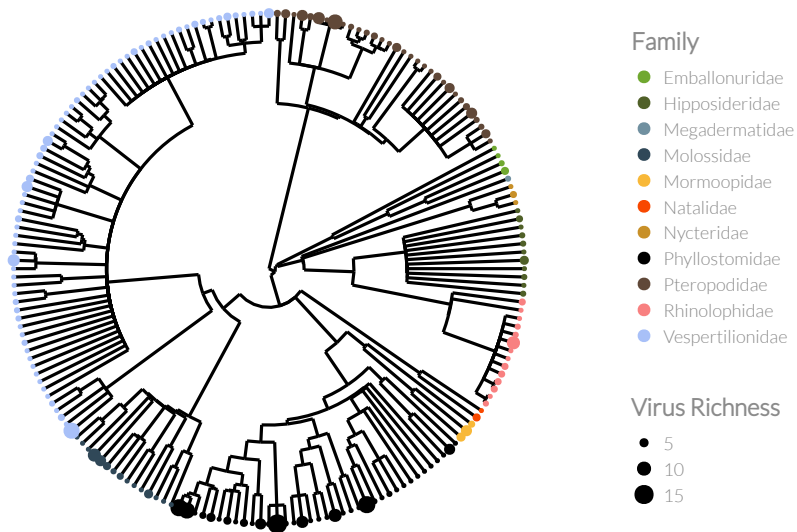


Figure 1. Pruned phylogeny with dot size showing number of pathogens and colour showing family.

## 2. Introduction

## 3. Methods

To measure pathogen richness I used data from (Luis et al. 2013). These simply include known infections of a bat species with a pathogen species. Only species with at least one pathogen were included in the analysis. Rows with host species that were not identified to species level were removed. Many viruses were not identified to species level or their identified species was not in the ICTV virus taxonomy (ICTV 2014). I counted a virus if it was the only virus, for that host species, in the lowest taxonomic level identified in the ICTV taxonomy. That is, if a host carries an unknown Paramyxoviridae virus, then it must carry at least one Paramyxoviridae virus. If a host carries an unknown Paramyxoviridae virus and a known Paramyxoviridae virus, then it is hard to confirm that the unknown virus is not another record of the known virus. In this case, this would be counted as one virus species.

I used two measures of population structure.  $F_{ST}$  and the number of subspecies. The number of subspecies was counted using the Wilson and Reeder taxonomy (Wilson and Reeder 2005).  $F_{ST}$  and other measures were collated from the literature. Studies are from a wide range of spatial scales, from local ( $\sim 10$  km) to continental. As  $F_{ST}$  inevitably increases with spatial scale I controlled for this by only using data from studies where a large proportion of the species range was studied. I used the ratio of the furthest distance between  $F_{ST}$  samples to the width of the species range and only used studies if this ratio was greater than 0.3. To allow comparison between different measures ( $F_{ST}$ ,  $\phi_{ST}$ ) and data from different molecular regions I converted all data to diploid gene flow. WILL ADD EXTRA METHODS LATER. These two measures of population structure were analysed separately as the number of subspecies has 192 data points while there is only  $F_{ST}$  data for  $\sim 30$  bat species.

To control for study bias I collected the number of Pubmed and Google Scholar citations for each bat species including synonyms from ITIS (*Integrated Taxonomic Information System* (ITIS) n.d.) via the taxize package (Chamberlain and Szöcs 2013). The counts were scraped using

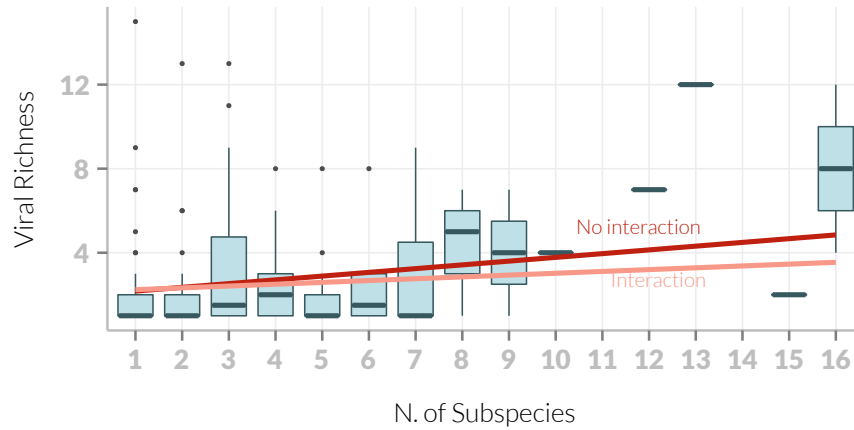


Figure 2. Number of virus species against number of subspecies. Data within a number of subspecies are plotted as boxplots with the dark bar showing the median, the box showing the interquartile range, vertical lines showing the range and outliers shown as separate points. Regression lines are from multivariate phylogenetic models with other independent variables set at their median value. The models shown are those with (pink) and without (red) an interaction between study effort and number of subspecies.

the *rvest* package (Wickham 2015). I log transformed these variables as they were strongly right skewed. The log number of citations on Pubmed and Google scholar were highly correlated (pgls:  $t = 18.69$ ,  $df = 190$ ,  $p = 0$ ). The results here are for analyses using only Google Scholar citations. See the appendix for analyses run using Pubmed citations.

Measures of body mass are taken from Pantheria (Jones et al. 2009) and primary literature (Canals et al. 2005; Arita 1993; López-Baucells et al. 2014; Orr and Zuk 2013; Lim and Engstrom 2001; Aldridge 1987; Ma et al. 2003; Owen et al. 2003; Henderson and Broders 2008; Heaney et al. 2012; Oleksy et al. 2015; Zhang et al. 2009). *Pipistrellus pygmaeus* was assigned the same mass as *P. pipistrellus* as they are indistinguishable by mass. They are log transformed due to the strong right skew.

To control for phylogenetic nonindependence I used the best-supported phylogeny from (Fritz et al. 2009) which is the supertree from (Bininda-Emonds et al. 2007) with names updated to match the Wilson & Reeder taxonomy (Wilson and Reeder 2005). Phylogenetic manipulation was performed using the *ape* package (Paradis et al. 2004). The importance of the phylogeny on each variable separately was estimated using (Revell 2012).

I ran two models using the *caper* package (D. Orme et al. 2012) testing the relationship between pathogen richness and log number of subspecies. All independent variables were log transformed. I ran phylogenetically controlled, multivariate linear models. This model was fitted both with and without an interaction term between number of subspecies and study effort.

Plots were created with a combination of (Wickham 2009; Lucas 2015; Solt and Hu 2015; Yu 2015)

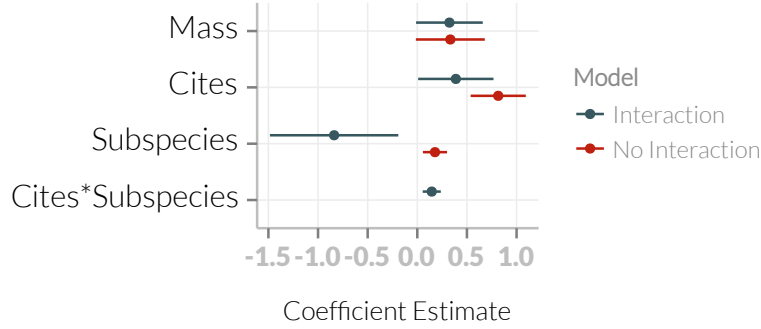


Figure 3. Plot of coefficient estimates and 95% confidence intervals for phylogenetic model with and without interactions between study effort and number of subspecies. Without interactions, number of subspecies is significant.

Covariate	Estimate (95% CI)	<i>p</i> value
Number of subspecies	0.18 (0.06 – 0.3)	$4.49 \times 10^{-3}$
Mass	0.33 (–0.01 – 0.68)	0.06
Study effort	0.82 (0.54 – 1.09)	$3.53 \times 10^{-8}$
Intercept	–4.08 (–6.06 – –2.11)	$7.33 \times 10^{-5}$

Table 1. Table of parameter estimates.

## 4. Results

### 4.1. Number of Subspecies.

4.1.1. *More descriptive.* After data cleaning there was data for 192 bat species in 11 families. The number of described virus species for a bat host ranged up to 15 viruses in *Carollia perspicillata*. Figure 1 shows the phylogeny used and the number of viruses for each species. The mean number of viruses across families is fairly constant with a lower range of 1.67 for Nycteridae. The highest mean is Mormoopidae with 5 virus species per bat species, but this is based on a sample size of 3. The Phyllostomidae have the second highest mean ( $n = 37$ ) of 3.49.

The small change in mean pathogen richness across families and the lack of clear pattern in Figure 1 implies that viral richness is not strongly phylogenetic. This is corroborated by the small estimated size of  $\lambda$  ( $\lambda = 0.05$ ,  $p = 0.1$ ). This fact implies that other factors must control pathogen richness. It also implies that pathogens are not directly inherited down the phylogeny, although this is to be expected by the fast evolution of viruses.

Of the explanatory variables, the number of subspecies has no phylogenetic autocorrelation ( $\lambda = 6.68 \times 10^{-5}$ ,  $p = 1$ ), study effort has weak but significant autocorrelation ( $\lambda = 0.06$ ,  $p = 0.04$ ) and mass is strongly phylogenetic ( $\lambda = 0.83$ ,  $p = 2.51 \times 10^{-43}$ ).

4.1.2. *Model results.* See Figure 3 for a display of estimated coefficients for the two models using number of viruses as the response variable. The main model with mass, study effort and number of subspecies as predictors found study effort to be highly significant ( $\beta = \text{NA}$ ,  $p = 1.18 \times 10^{-8}$ ). The number of subspecies was marginally significant ( $\beta = \text{NA}$ ,  $p = 0.03$ ). The effect of nonindependence due to phylogeny was very small ( $\lambda = 0.11$ ,  $p = 0.01$ ).

The interaction term between study effort and number of subspecies, when included, was significant ( $\beta = 0.15$ ,  $p = 2 \times 10^{-3}$ ).

#### 4.2. $F_{ST}$ .

## 5. Discussion

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