

# **Sampling and domestication, but not wildlife trade, drive zoonotic viral richness in mammals: response to Shivaprakash *et al.***

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## **Abstract**

A recent study by Shivaprakash *et al.* suggests that mammal species involved in the wildlife trade disproportionately host zoonotic viruses. We identify concerns about data quality and the reproducibility of the analysis, as well as the role of sampling bias in the interpretation of the results. We reanalyze their data and the closely-related Global Virome in One Network (VIRION) dataset, using a path analysis that includes citations as a proxy for scientific research effort. We find that citations and domestication are significant positive predictors of species-level zoonotic virus diversity, but traded status is not. In conclusion, we are unable to show that wildlife trade has substantially restructured the mammalian virome.

## Introduction

In their recent study in *Current Biology* (“Mammals, wildlife trade, and the next global pandemic”), Shivaprakash *et al.* have presented a novel analysis of global viral diversity<sup>1</sup> in mammal species affected by the legal and illegal wildlife trade. This is an important and high-profile topic, particularly given the ongoing search for the wildlife origins of SARS-CoV-2. Using an updated copy of a widely-used database of host-virus associations (termed an edgelist), they report that mammals involved in the wildlife trade are associated with more zoonotic viruses than nontraded mammals, and conclude that traded species pose a much greater risk to human health. Here, we identify several major issues with the data quality, analyses, and scientific interpretation provided by that study.

## The data

Taxonomic reconciliation of host-virus association data requires extensive manual curation and quality control, particularly given the unique challenges of constantly-changing viral taxonomy. Previous work shows that differences in curation and cleaning between datasets can measurably skew estimates of host-level viral richness (Gibb *et al.*, 2021).

The Shivaprakash *et al.* study expands the widely-cited edgelist of host-virus associations published by Olival *et al.* (2017), adding the USAID PREDICT program’s publicly-available data (36% of all associations) and a literature review of other sources (17%). The latter component is oversampled for hosts involved in the wildlife trade (Traded: 291; Nontraded: 241), and their viral associations (Traded: 758; Nontraded: 485), artificially inflating the effects of wildlife trade on viral diversity<sup>2</sup>. Nevertheless, in the full dataset, this only creates a marginal difference in per-species viral richness between traded species (mean: 5.30 viruses, 2.19

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<sup>1</sup> Throughout Shivaprakash *et al.*’s study, viral richness or viral diversity (a concept at the level of both viral “species” and host species) is sometimes incorrectly referred to as “viral load,” a term used in disease ecology to describe the intensity of active infection within an individual host. This could create particular confusion if propagated outside of the study, as it might incorrectly suggest the study used data that profiled active infections of traded animals.

<sup>2</sup> For comparison, even data from the PREDICT project - which, over several years, actively targeted zoonotic reservoirs in wildlife markets and supply chains for disease surveillance - does not show a comparable level of oversampling in hosts (Traded: 67; Nontraded: 152) and viral associations (Traded: 478; Nontraded: 510).

zoonotic; median: 2 viruses, 1 zoonotic) and nontraded species (mean: 3.42 viruses, 1.55 zoonotic; median: 2 viruses, 1 zoonotic), particularly compared to domesticated species (mean: 18.6 viruses, 10.9 zoonotic; median: 9 viruses, 5 zoonotic).

However, this newly-compiled host-virus edgelist<sup>3</sup> also contains many inconsistencies and errors, including duplications (a zoonotic “Reston\_ebolavirus” with four associated hosts, and a non-zoonotic misspelled “Riston \_Ebola” with 22 hosts<sup>4</sup>), inconsistent taxonomic ranks (e.g., “Filovirus” and “Pestiviruses”, which are family and genus-level descriptors, respectively, rather than species), or both (e.g., “corona” vs. “Bat CoV” vs. “bat coronavirus HKU6” vs. “BatCoV HKU6”; “Influenza A” vs. “Influenza A, subtype H18N11” vs. “Influenza\_A\_virus”; “Venezuelan equine encephalitis virus” vs. “VEE \_(IE)”, which refers to VEEV subtype IE). The summary spreadsheets, which should reflect variations on the same data, also include discrepancies and errors. For example, the host summary sheet<sup>5</sup> includes a “domestic” *Canis familiaris* (27 viruses reported, 22 zoonotic), a “domestic” *Canis lupus familiaris* (26 viruses, 22 zoonotic), and a “traded” *Canis lupus* (9 viruses, 5 zoonotic). Similarly, *Manis pentadactyla* and *Rattus leucopus* are recorded in this summary spreadsheet with more zoonotic viruses than total viruses, and have negative values of non-zoonotic viral diversity reported (-1 and -5 viruses, respectively); both species are notably unrecorded in the edgelist.

One major conflict between the edgelist and summary files is particularly notable. After manual matching name conflicts with the host and virus metadata files, the edgelist includes 1,076 unique hosts, 1,679 unique viruses, and 5,025 unique associations, but a total of 8,762 associations including duplications. Duplicated records in the edgelist are propagated into the viral richness statistics given in the host summary file. As a result, only 903 of 1,076 hosts have the correct number of viruses reported in the summary files<sup>6</sup>. For example, there are 438 rows

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<sup>3</sup> Data S1B in the supporting information of Shivaprakash *et al.*

<sup>4</sup> In the virus metadata summary (Data S1C), the host range of “Reston\_ebolavirus” is given as 26 hosts, while “Riston \_Ebola” is correctly given as 22. There are no duplications for “Reston\_ebolavirus” in the edgelist to explain this difference (see below). The host range of “Reston\_ebolavirus” in the viral metadata therefore appears to be the sum of the 22 and 4 given in Data S1B, possibly a manual correction.

<sup>5</sup> Data S1A in the supporting information of Shivaprakash *et al.*

<sup>6</sup> One additional species, *Mus minutoides*, has two viruses recorded in the edgelist, both non-zoonotic, but is recorded twice in the host metadata: once as “Mus minutoides” with two viruses, both non-zoonotic, and once as “Mus\_minutoides”, with one virus, which is recorded as zoonotic. This conflicted record is the only “decrease” in total reported viral richness found in the host metadata.

in the edgelist that match *Eidolon helvum*, and 438 viruses reported in the summary, but only 35 *distinct* viruses in the edgelist; the association between *Eidolon helvum* and Eidolon bat coronavirus alone is reported identically 383 times. The origin of this duplication, in a dataset with only two columns (host and virus), is unclear; it may be as simple as a failure to collapse unique data after removing metadata that is no longer attached to the database.

However, the repercussions of these duplications for the analysis are notable. Traded species are not disproportionately represented in the set of duplicated species; however, on average, traded species have a higher resulting inflation of reported viral richness (mean: +30 virus spp.) than nontraded (+19 spp.) and domestic species (+6 spp.). This has a “ripple” effect on zoonotic virus richness, where traded species tend to gain zoonotic viruses (+1: 15 spp.; +2: 1 sp.; +3: 1 sp.; -1: 4 spp.), and nontraded species tend to lose them (+1: 1 sp.; -1: 7 spp.). Although these inflations can also be explained by duplication, the origins of these losses are unknown. For example, *Akodon simulator* is a nontraded species with two viruses in the edgelist (Andes virus and Laguna Negra virus); both are recorded as zoonotic in the virus metadata summary<sup>7</sup>, but the species is only recorded as having one zoonotic virus in the host summary sheet. These adjustments are less readily explained<sup>8</sup>.

Given how few viruses are associated with most species, errors of this scale are likely to have measurably impacted the results of the analysis. Without detailed supporting code for both the data generation and analysis, the scope of these impacts is difficult to assess.

## The analysis

The study by Shivaprakash *et al.* explores several ways of using descriptive statistics to test for a relationship between viral richness and host domestication or traded status. For example, a central claim of the paper is that a disproportionately high three-quarters of all zoonotic viruses

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<sup>7</sup> Data S1C in the supporting information.

<sup>8</sup> Cumulatively, these inconsistencies slightly increase the differences in means between traded species (9.34 viruses, 2.28 zoonotic; median: 2 viruses, 1 zoonotic) and nontraded species (6.29 viruses, 1.57 zoonotic; median: 2 viruses, 1 zoonotic) as reported in the host summary data.

are hosted by a small subset (reported as 26.5%<sup>9</sup>) of mammals involved in the wildlife trade. This framing, however, is misleading. In the study's edgelist, traded species actually account for 39% (421 of 1,076) of all hosts in the sample, and only appear to host 68% (153 of 224<sup>10</sup>) of zoonotic viruses in the sample<sup>11</sup>. Due to the convex, power law-like scaling of subsampled bipartite ecological networks (Carlson et al., 2019), any random draw of 39% of hosts from these data is expected to capture an even higher percent of zoonotic viruses (mean: 78.7%, s.d.: 4.1%, n: 1000 draws). This suggests that traded species actually host *fewer* total zoonotic viruses than expected. By comparison, 3.3% (35 of 1,076) of mammals in the edgelist dataset are domesticated, and these host 51.3% (115 of 224) of known zoonotic viruses; a random draw of 3.3% of hosts would be expected to only capture 22.0% (s.d.: 6.0%) of zoonotic viruses.

The main oversight, however, is a lack of statistical correction for sampling biases. It should be unsurprising that traded species may be better sampled for viruses, given international coordination on biosecurity and endangered species surveillance in these settings. The authors acknowledge the possibility that sampling bias impacted their results, noting a strong correlation between the number of individual animals tested and the number of viruses detected in a subset of the data. However, the study makes no correction for sampling effort in the main analyses, which are largely descriptive. This is a fundamental omission: recent studies have found that species-level viral richness estimates can be largely driven by sampling effort (Wille *et al.*, 2021), and that jointly adjusting for sampling effort and total viral richness removed the effect of a comparable driver (adaptation to urban environments) on zoonotic viral richness (Albery *et al.*, 2021).

We reanalyzed Shivaprakash *et al.*'s edgelist using a path analysis that adjusts for the effect of host sampling effort (measured using PubMed citation counts for species' Latin names) and

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<sup>9</sup> We cannot reproduce the 26.5% figure. The authors have explained its derivation as 400 species with at least one zoonotic virus (358 traded and 42 future traded) out of 1441 total species known to be involved in the wildlife trade, for a total of 27.75% (*pers. comm.*, K. Shivaprakash).

<sup>10</sup> The study and virus metadata report 226 known zoonotic viruses; however, six viruses are present in the virus metadata but absent from the edgelist: two are zoonotic (Bangui virus and Lake Victoria marburgvirus, a redundancy with "Marburg Virus (MARV)") and four are non-zoonotic (Gossas virus, Kolente virus, Menekre virus, and Ntaya virus). These absences may also be connected to differences in the 75% statistic.

<sup>11</sup> Including the "future traded" species - predictions of which species might be involved in future wildlife trade - raises this to 158 of 224 (70.5%). Here, we have chosen not to address the use of future trade as a speculative variable, and focused on species currently known to be traded.

the covariance between total and zoonotic viral richness. We found that domesticated and traded species both have higher apparent research effort; further, better-studied and domesticated species had greater total and zoonotic viral richness, while traded status had no significant effect on either. When reproducing this analysis with the multi-source, taxonomically-standardised The Global Virome in One Network (VIRION) dataset, we confirmed that domesticated species had greater total and zoonotic viral richness; although traded species had a higher reported total viral richness even after adjusting for citations (likely indicating an additional layer of sampling effects or latent phylogenetic effects), we found no evidence of their having significantly higher zoonotic viral richness. This finding is consistent with the premise that domestication's impact on viral sharing with humans has been gradual over time (Morand et al. 2014). While the global wildlife trade is rapidly growing, on the scale of human history, it has only relatively recently begun to influence zoonotic emergence, and its role in major outbreaks has only been established in a handful of high-profile instances (e.g., monkeypox or SARS-CoV).

### **The interpretation**

Different permutations of these analyses (e.g., incorporating phylogenetic or geographic bias) may recover different drivers of viral richness, and change the relative statistical importance of individual terms. (For example, in the supplement, a second path analysis is provided that replaces zoonotic viral diversity with proportion of zoonotic viruses as the outcome of interest; findings relating to wildlife trade are largely the same for both datasets.) However, the explanatory role of wildlife trade is clearly confounded by research effort, and is notably weaker than the effect of domestication. As such, the role of the wildlife trade in zoonotic emergence has been overstated in this study.

This is concerning given the obvious policy implications, and public-facing communications around the study. For example, in a press release accompanying the paper, one author posits: "From our findings, it is conceivable that wildlife trade...is the key risk factor driving the global spread of zoonotic and emerging infectious diseases." However, these data and analyses fail to support this idea. In fact, component datasets used by this study directly contradict it: for example, a detailed study by Johnson *et al.* (2015) found that only six out of 162 zoonotic viruses (~4%) could be definitively linked to the wildlife trade. This highlights the gap between

knowing a species involved in the wildlife trade can potentially host a given virus – which Shivaprakash *et al.*'s study focuses on – and actually finding that virus in traded animals, demonstrating a link between trade pathways and higher viral prevalence, or connecting traded animals to spillover into human populations<sup>12</sup>.

Given unprecedented interest in using ecological levers to mitigate the risks of zoonotic spillover, policymakers need impartial, evidence-based assessments of the circumstances in which wildlife trade may exacerbate zoonotic risks. Globally-aggregated viral richness data are often a poor and biased proxy for pathogen spillover and emergence risk (Wille *et al.* 2021), and offer limited contextual information that could inform specific interventions. In contrast - despite the authors' claim that "there are no studies quantitatively assessing zoonotic disease risk associated with wildlife trade" - disease surveillance data from the wildlife trade have been used to show that, for example, coronaviruses become more prevalent in and along these supply chains (Anthony *et al.*, 2017; Huong *et al.*, 2020). These types of targeted investigations are much more likely to conclusively resolve the zoonotic risks posed by the wildlife trade, and result in policy interventions that help to both prevent future pandemics and protect endangered species.

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<sup>12</sup> It also stands in contrast to claims made by Shivaprakash *et al.*, who appear to incorrectly suggest that MERS-CoV and Nipah virus, among others, reached domestic animals - camels and pigs respectively - through contact between these animals and traded wildlife.

## **Acknowledgements**

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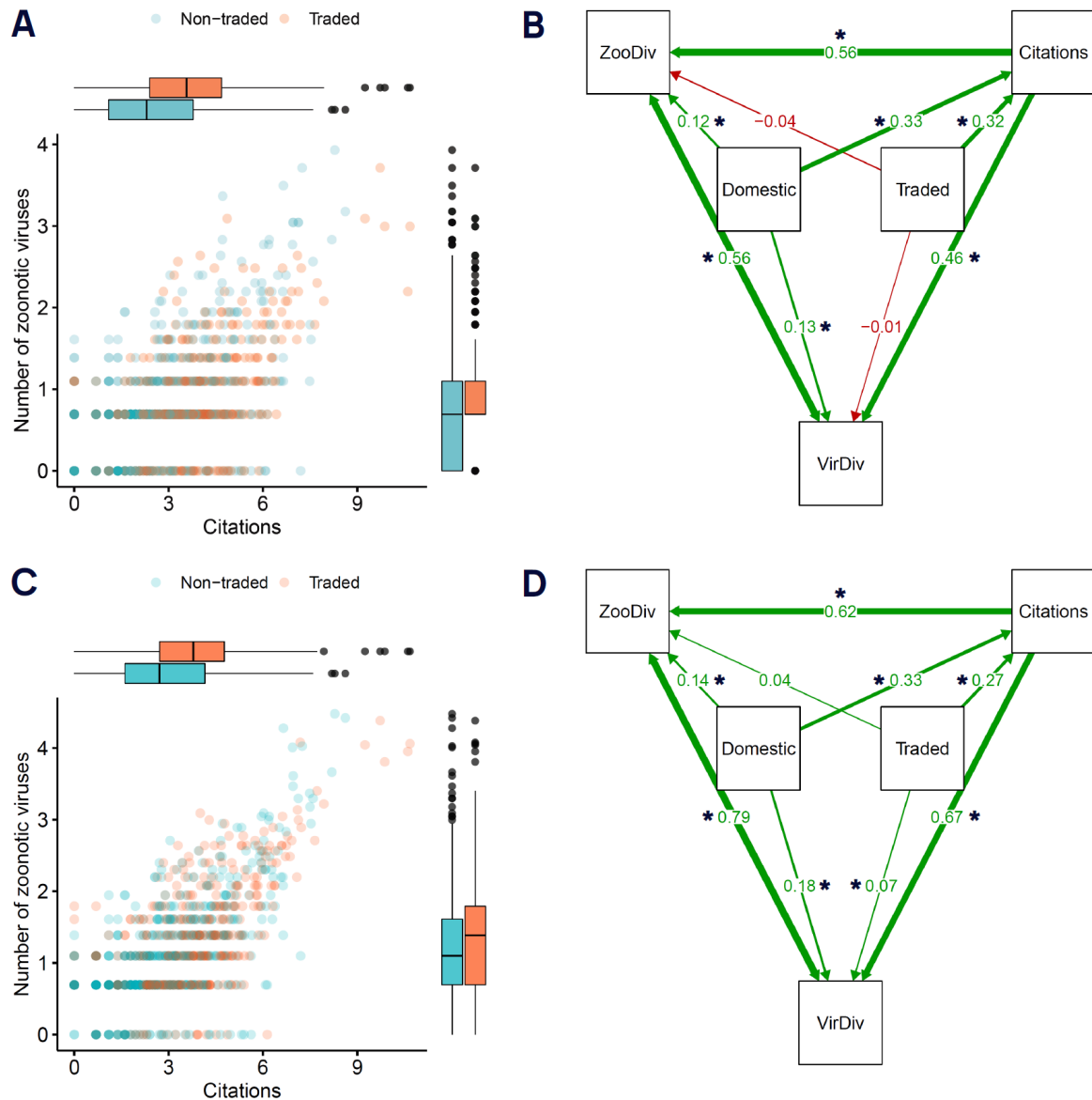
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**Figure 1.** In both the internally-reconciled Shivaprakash *et al.* dataset (A,B) and the VIRION dataset (C,D), species involved in the wildlife trade (orange) have much higher citation counts than those that are not (blue); this explains patterns in total and zoonotic viral richness better than wildlife trade does. Citation counts and richness estimates have all been  $\log_{10}$  transformed. (ZooDiv = zoonotic virus richness, VirDiv = total viral richness; \* indicates statistical significance at the level  $p < 0.05$ ; edge thickness proportional to standardized estimates of effect size from the structural equation model, and color of arrows indicates directionality of effect).



## Supplement

### Methods

**Host-virus edgelists:** For analyses, including both the path analyses and all main-text statistics (unless otherwise specified), we used the Shivaprakash *et al.* edgelist instead of the summarized data, which contained some known anomalies. We used a version of this edgelist with five host names and one virus name adjusted to be compatible with the other files provided in the Shivaprakash *et al.* supplement, but made no additional effort to correct errors.

We also used the Global Virome in One Network (VIRION) dataset release 0.1.1-beta, which contains most of the same data sources as the Shivaprakash *et al.* edgelist but has been subject to extensive taxonomic reconciliation. For consistency, we limited the dataset to mammal hosts that were resolved in the NCBI taxonomy at species level, and to viruses resolved in the same way that have been additionally ratified by the International Committee on the Taxonomy of Viruses (ICTV). At this level of filtering, the VIRION dataset includes 2.4 million metadata-rich records, including 1,322 unique hosts, 1,357 unique viruses, 506 unique zoonotic viruses (any that can infect humans and another animal), and 7,424 unique associations. The VIRION dataset is experimental and pre-publication; a preprint describing the full method of compilation is forthcoming. The VIRION dataset is available at [github.com/viralemergence/virion](https://github.com/viralemergence/virion).

**Citation counts:** We obtained citation counts using the ‘easyPubMed’ package (v2.13) in R, searching for a species’ full Latin name, based on every species in the host metadata spreadsheet. We downloaded the citation counts on July 15, 2021.

**Path analyses:** Analyses were implemented using the ‘lavaan’ (v0.6-9) and ‘semPlot’ packages (v1.1.2) in R. We first tested a model where domestication and traded status drove citations, all three were jointly allowed to drive total viral diversity and zoonotic virus diversity, and a covariance term was specified between total and zoonotic virus diversity. Model outputs are given in Table S1 and S2 and in Figure 1B and 1D.

In a supplementary analysis (Table S3 and S4, Figure S1 and S2) we use the same datasets but fit the proportion of viruses that are zoonotic as the outcome variable in place of zoonotic viral richness, and included total viral diversity in the predictors as a unidirectional

response. As with the main analyses, we found that traded status drove viral diversity in the VIRION dataset but not the Shivaprakash *et al.* dataset; and found no significant effect of traded status or domestication on proportion of zoonotic viruses. Citations positively predicted proportion zoonotic (better studied species had a higher proportion of zoonotic viruses) in the Shivaprakash *et al.* dataset but not the VIRION dataset; and total viral diversity negatively predicted proportion zoonotic (when few viruses are known for a species, they tend to be zoonoses) in both datasets.

**Reproducibility:** All code to produce the analyses included in this paper is available from the Verena Consortium institutional repository at [github.com/viralemergence/WildlifeTrade](https://github.com/viralemergence/WildlifeTrade). The VIRION dataset is available from [github.com/viralemergence/virion](https://github.com/viralemergence/virion).

**Table S1.** Path analysis results on zoonotic diversity using Shivaprakash *et al.* edgelist

## Regressions:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Citations ~						
Traded	1.236	0.109	11.331	0.000	1.236	0.317
Domestic	3.623	0.304	11.934	0.000	3.623	0.333
VirDiv ~						
Citations	0.179	0.011	15.708	0.000	0.179	0.456
Traded	-0.010	0.043	-0.243	0.808	-0.010	-0.007
Domestic	0.572	0.121	4.735	0.000	0.572	0.134
ZooDiv ~						
Citations	0.207	0.010	20.959	0.000	0.207	0.565
Traded	-0.061	0.037	-1.632	0.103	-0.061	-0.043
Domestic	0.474	0.104	4.546	0.000	0.474	0.119

## Covariances:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Traded ~~						
Domestic	-0.012	0.003	-4.689	0.000	-0.012	-0.145
.VirDiv ~~						
.ZooDiv	0.200	0.013	15.984	0.000	0.200	0.559

## Variances:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
.Citations	2.970	0.128	23.152	0.000	2.970	0.819
.VirDiv	0.415	0.018	23.152	0.000	0.415	0.740
.ZooDiv	0.309	0.013	23.152	0.000	0.309	0.638
Traded	0.238	0.010	23.152	0.000	0.238	1.000
Domestic	0.031	0.001	23.152	0.000	0.031	1.000

## R-Square:

	Estimate
Citations	0.181
VirDiv	0.260
ZooDiv	0.362

**Table S2.** Path analysis results on zoonotic diversity using VIRION edgelist

## Regressions:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Citations ~						
Traded	1.014	0.115	8.791	0.000	1.014	0.274
Domestic	3.277	0.307	10.676	0.000	3.277	0.333
VirDiv ~						
Citations	0.309	0.011	27.875	0.000	0.309	0.668
Traded	0.115	0.040	2.894	0.004	0.115	0.067
Domestic	0.817	0.108	7.567	0.000	0.817	0.179
ZooDiv ~						
Citations	0.274	0.012	23.522	0.000	0.274	0.624
Traded	0.061	0.042	1.466	0.143	0.061	0.038
Domestic	0.619	0.113	5.463	0.000	0.619	0.143

## Covariances:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Traded ~~						
Domestic	-0.015	0.003	-4.918	0.000	-0.015	-0.167
.VirDiv ~~						
.ZooDiv	0.257	0.014	18.509	0.000	0.257	0.790

## Variances:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
.Citations	2.826	0.134	21.119	0.000	2.826	0.844
.VirDiv	0.310	0.015	21.119	0.000	0.310	0.432
.ZooDiv	0.342	0.016	21.119	0.000	0.342	0.529
Traded	0.245	0.012	21.119	0.000	0.245	1.000
Domestic	0.035	0.002	21.119	0.000	0.035	1.000

## R-Square:

	Estimate
Citations	0.156
VirDiv	0.568
ZooDiv	0.471

**Table S3.** Path analysis results on proportion zoonotic using Shivaprakash *et al.* edgelist

## Regressions:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Citations ~						
Traded	1.236	0.109	11.331	0.000	1.236	0.317
Domestic	3.623	0.304	11.934	0.000	3.623	0.333
VirDiv ~						
Citations	0.179	0.011	15.708	0.000	0.179	0.456
Traded	-0.010	0.043	-0.243	0.808	-0.010	-0.007
Domestic	0.572	0.121	4.735	0.000	0.572	0.134
PropZoo ~						
Citations	0.073	0.008	9.570	0.000	0.073	0.343
Traded	-0.036	0.026	-1.386	0.166	-0.036	-0.043
Domestic	0.011	0.074	0.152	0.879	0.011	0.005
VirDiv	-0.082	0.018	-4.454	0.000	-0.082	-0.151

## Covariances:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Traded ~~						
Domestic	-0.012	0.003	-4.689	0.000	-0.012	-0.145

## Variances:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
.Citations	2.970	0.128	23.152	0.000	2.970	0.819
.VirDiv	0.415	0.018	23.152	0.000	0.415	0.740
.PropZoo	0.151	0.007	23.152	0.000	0.151	0.915
Traded	0.238	0.010	23.152	0.000	0.238	1.000
Domestic	0.031	0.001	23.152	0.000	0.031	1.000

## R-Square:

	Estimate
Citations	0.181
VirDiv	0.260
PropZoo	0.085

**Table S4.** Path analysis results on proportion zoonotic using VIRION edgelist

## Regressions:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Citations ~						
Traded	1.014	0.115	8.791	0.000	1.014	0.274
Domestic	3.277	0.307	10.676	0.000	3.277	0.333
VirDiv ~						
Citations	0.309	0.011	27.875	0.000	0.309	0.668
Traded	0.115	0.040	2.894	0.004	0.115	0.067
Domestic	0.817	0.108	7.567	0.000	0.817	0.179
PropZoo ~						
Citations	0.012	0.009	1.408	0.159	0.012	0.068
Traded	-0.006	0.023	-0.273	0.785	-0.006	-0.009
Domestic	-0.029	0.063	-0.468	0.640	-0.029	-0.017
VirDiv	-0.098	0.019	-5.195	0.000	-0.098	-0.258

## Covariances:

	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
Traded ~~						
Domestic	-0.015	0.003	-4.918	0.000	-0.015	-0.167

## Variances:

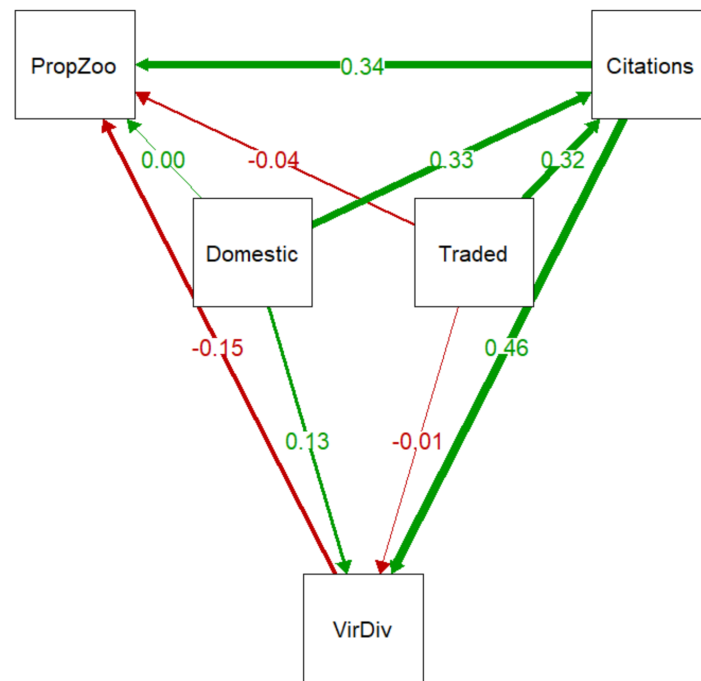
	Estimate	Std.Err	z-value	P(> z )	Std.lv	Std.all
.Citations	2.826	0.134	21.119	0.000	2.826	0.844
.VirDiv	0.310	0.015	21.119	0.000	0.310	0.432
.PropZoo	0.098	0.005	21.119	0.000	0.098	0.951
Traded	0.245	0.012	21.119	0.000	0.245	1.000
Domestic	0.035	0.002	21.119	0.000	0.035	1.000

## R-Square:

	Estimate
Citations	0.156
VirDiv	0.568
PropZoo	0.049



**Figure S1.** Path analysis on proportion zoonotic using Shivaprakash *et al.* edgelist



**Figure S2.** Path analysis on proportion zoonotic using VIRION edgelist

