# **METHODS**

### **Trait data collection, processing, and transformations:**

As many trait databases use older taxonomic references (e.g., the third edition of Mammal Species of the World [(Wilson and Reeder, 2005)](https://paperpile.com/c/aI9Qxl/rReI), Birdlife V3 world list as modified by [(W. Jetz et al., 2012)](https://paperpile.com/c/aI9Qxl/ALmg)), species names were reverted to older synonyms associated with trait data when appropriate. We primarily sourced trait data from AnAge [(de Magalhães and Costa, 2009)](https://paperpile.com/c/aI9Qxl/tvZQ), Amniote Life History Database [(Myhrvold et al., 2015)](https://paperpile.com/c/aI9Qxl/9emK), and EltonTraits [(Wilman et al., 2014)](https://paperpile.com/c/aI9Qxl/5TOT) (Supplementary Table 1), and augmented these data with values from AmphiBIO [(Oliveira et al., 2017)](https://paperpile.com/c/aI9Qxl/e9gO), FishBase [(Froese and Pauly, 2019)](https://paperpile.com/c/aI9Qxl/XZnA), [(Meiri, 2018)](https://paperpile.com/c/aI9Qxl/AsZ2), [(Meiri, 2019)](https://paperpile.com/c/aI9Qxl/5Axs), and a database of CITES listed turtles and tortoises [(“Open Data,” n.d.)](https://paperpile.com/c/aI9Qxl/KMvO) to increase variable coverage across our species. We used the sf R package [(Pebesma, 2018)](https://paperpile.com/c/aI9Qxl/69NJ) to calculate range size from IUCN RedList [(IUCN, 2020)](https://paperpile.com/c/aI9Qxl/we1i) and Birdlife International species range polygons [(“BirdLife Data Zone,” 2021)](https://paperpile.com/c/aI9Qxl/cgX1) and Food and Agriculture Organization of the United Nations (FAO) polygons of Major Fishing Areas [(“FAO Fisheries & Aquaculture,” 2020)](https://paperpile.com/c/aI9Qxl/HDGF). To determine overlap with ecoregions, we used polygons of terrestrial ecoregions from The Nature Conservancy [(Olson and Dinerstein, 2002)](https://paperpile.com/c/aI9Qxl/JsMq) and marine ecoregions from the Marine Ecoregions of the World by the World Wildlife Fund [(Spalding et al., 2007)](https://paperpile.com/c/aI9Qxl/aaXG). These polygons were rasterized with a resolution of ~100 km2 using the R package fasterize [(Ross, 2020)](https://paperpile.com/c/aI9Qxl/UMx1). We counted the number of unique ecoregions each species overlapped. To enable comparison across species, we expressed ecoregion breadth as the percentage of all terrestrial ecoregions (for terrestrial and freshwater species), marine ecoregions (for marine species according to FAO code), or both (for species found in both marine and freshwater environments according to their FAO Major Fishing Area). Given the coarseness of fish polygon data, we instead gathered georeferenced point data for all fishes in our dataset from the Global Biodiversity Information Facility [(gbif.org, 2020)](https://paperpile.com/c/aI9Qxl/1sRh) and checked for ecoregion overlap with these points. Mass specific production as described by [(Hamilton et al., 2011)](https://paperpile.com/c/aI9Qxl/aV5s) was calculated using adult body mass, birth/hatching weight, litter/clutch size, and number of litters/clutches per year. We used a PROMALS3D [(Pei et al., 2008)](https://paperpile.com/c/aI9Qxl/7hdJ) alignment of our ACE2 sequences to extract residue identity at positions 30 and 83. We encoded whether the residue at position 30 was negatively charged and whether the residue at position 83 was a tyrosine, based on each of these residue traits correlating with a species being susceptible to SARS-CoV-2 in a previous structure-based study [(Rodrigues et al., 2020)](https://paperpile.com/c/aI9Qxl/Sgox). To account for potential effects on our models related to study effort, we used the wosr package [(Baker, 2018)](https://paperpile.com/c/aI9Qxl/xqok) to determine the number of publications with each species name in their title or abstract in Web of Science. As this citation count could itself be biased towards species with recent name changes or a high degree of taxonomic uncertainty, we determined synonyms for each of our species using the backbone taxonomy from GBIF [(GBIF Secretariat, 2019)](https://paperpile.com/c/aI9Qxl/NK18) and used a species’ name and all its synonyms to craft our queries.

To compare foraging strategy variables across birds and mammals and make these variables consistent across classes, we reclassified them from a continuous percentage to a binary variable. The bird specific EltonTraits variables of ForStrat-watbelowsurf and ForStrat-wataroundsurf were reclassified as ForStrat-ground to match with the definition given for this variable in the mammal EltonTraits data. Additionally, ForStrat-midhigh and ForStrat-canopy were merged with ForStrat-arboreal and ForStrat-pelagic with ForStrat-marine. For fishes, FAO Major Fishing Areas referencing inland and oceanic waters were used to determine values in ForStrat-ground (non-marine aquatic) and ForStrat-marine. As diet categories for fishes and terrestrial vertebrates did not match, the number of nonzero values in diet categories (e.g., fruit, seeds, invertebrates) for a species were counted and then divided by the total number of terrestrial or marine diet categories to enable comparison across classes. For any species without mean longevity information from Amniote Life History Database, we added values for maximum longevity if they existed. Incubation and gestation time showed a bias in coverage related to class, so we merged the two variables, taking the mean in the event that values for both variables existed. We log transformed values for any variable with a heavily skewed distribution as shown by a density curve. For trait sources, units, coverage, and transformation information, see Supplementary Table 1.

For prediction and imputation of missing values, the same trait variables mentioned in the main text for our mammal-only dataset (PanTHERIA traits, those from Amniote Life History Database, AnAge, EltonTraits, and those calculated for this study; Supplementary Table 2) were compiled for the 5,400 mammal species in the EltonTraits dataset. We chose this set of species because they followed the taxonomy of the 2005 edition of Mammal Species of the World [(Wilson and Reeder, 2005)](https://paperpile.com/c/aI9Qxl/rReI) and showed high coverage across their variables, making it an ideal starting point to add variables from other trait databases.

Given that cetaceans are the main taxonomic group in mammals with marine foraging strategies, we adjusted the ForStrat variables used with our mammal-only dataset to reduce possible bias. We condensed our foraging strategy variables into terrestrial and aquatic versions, with aquatic foraging strategies including those freshwater foraging species previously classified as ForStrat.ground (see Supplementary Table 2).

Imputation of missing mammal trait values

To boost the predictive power of our mammal dataset, we imputed missing values of variables. For variables with more than 1% and less than 95% coverage in the dataset of 5,400 mammals, we used boosted regression tree modeling to model each variable as a Gaussian outcome. As a relatively large sample size was typically present for training these models, parameterization explored learning rates of 0.001 and 0.01, maximum interaction depth of 1 through 4, and a minimum number of observations in the terminal nodes of 2, 5, and 10. Combinations of parameters were compared using pseudo-R2; those with the best performance were used with model evaluation through bootstrapping as described above. After model evaluation with all predictors and those with importance over one percent, we applied two filters to determine which variables to impute missing values for: 1) corrected mean test pseudo-R2 over 0.75 for either set of bootstrap runs, and 2) correlation over 0.8 between original values and mean values predicted by these same bootstrap iterations. We built models of the variables that passed these filters using the full dataset and used them to predict missing values in our mammal specific dataset.

A small number of imputed data values were biologically impossible: 107 data points (0.6% of all data), across 3 variables (female\_maturity\_d, mass\_specific\_production, and longevity\_y) had negative values. We retained these values to avoid introducing bias associated with constraining values [(Rodwell et al., 2014)](https://paperpile.com/c/aI9Qxl/IBGw).

**Modeling:**

We used generalized boosted regression to generate predictions using species’ trait data as predictors of the following labels: 1) HADDOCK score (with a continuous distribution), 2) zoonotic capacity (a binary label based on a HADDOCK score threshold, described in detail below under Modeling), 3) the charge at amino acid position 30 (a binary label, also described below under Modeling).

### Grid search for selecting hyperparameters

For all models, we applied a grid search to select optimal hyperparameters. This parameter search included fitting models with all possible combinations of learning rates of 0.001, 0.01, and 0.1, maximum interaction depths among variables of 2, 3, and 4, and minimum number of observations in a terminal node in the decision tree (n.minobsinnode) of 2 or 5. We chose values for the minimum number of observations in terminal nodes smaller than the default of 10 due to the small size of the dataset. Each model included a maximum of 100,000 trees. For each set of hyperparameters, we graphed the training and test deviance by number of trees. For some hyperparameters, the optimal number of trees, with the lowest test deviance, was reached rapidly, followed by rapid increase in deviance with increasing number of trees. Based on visual inspection, we selected the set of hyperparameters that had the highest test accuracy and stably decreasing deviance curves.

We produced three generalized boosted regression models. For the zoonotic capacity model (the main model described in this paper) and the amino acid 30 charge model, a Bernoulli error distribution was used for binary classification. We measured performance by the area under the receiver operating characteristic curve (AUC) on a hold-out test dataset. For the continuous binding strength model, which used a Gaussian error distribution, and performance was measured using pseudo-R2.

### Modeling

We began by modeling HADDOCK score for all vertebrates using boosted regression. When we found a relatively low pseudo-R2 for this model (Supplementary Table 3), we designed two simpler models. One simpler model classified whether a species’ HADDOCK score is at or below -129. This value is between two HADDOCK scores: the domestic cat (*Felis catus*), which is currently the species with weakest predicted binding among animals with confirmed conspecific transmission [(Bosco-Lauth et al., 2020)](https://paperpile.com/c/aI9Qxl/jWo5u), and the pig / wild boar (*Sus scrofa*), which shows the strongest predicted binding among species for which experimental inoculation failed to cause detectable infection [(Shi et al., 2020)](https://paperpile.com/c/aI9Qxl/YWye2). A second simpler model classified whether a species has a negative charge at amino acid residue 30 in ACE2, which appeared to be a useful proxy for susceptibility based on previous computational and empirical results suggesting that a negative charge at this residue is an important shared feature of species with strong binding to SARS-CoV-2 [(Rodrigues et al., 2020)](https://paperpile.com/c/0rfivF/Gh5n). We fit amino acid 30 charge models including HADDOCK score as a predictor. Our trait-based models predicted nearly all mammal species to have a negative charge at amino acid 30, thus the results of this model were relatively uninformative except to identify a few species with particularly low risk of binding SARS-CoV-2. For full model results, see Supplementary Table 3.

### Bootstrapping to describe precision and accuracy of models and predictions

Applying the set of hyperparameters selected by grid search, we performed model fitting 50 times for the zoonotic capacity model and 10 times for all other models, using different seeds each time for partitioning training and test datasets. Across these bootstrapping runs, we computed the mean training and test accuracy measure, AUC for binary classification and pseudo-R2 for models of the continuous HADDOCK score.

To gain a more realistic measure of accuracy, we completed a second set of bootstrapping runs to develop a null distribution of accuracy scores. Patterns in the structure of the predictor data, independent of their relationship to the label, have the potential to influence apparent model accuracy. To account for this possibility in a null model, we randomly permuted labels prior to modeling. We repeated this procedure 50 times (for the zoonotic capacity model) or 10 times (for the other models) to produce a null distribution of accuracy statistics. For binary classification models, we corrected the test AUC by the difference between the null model test AUC mean (across bootstrap runs) and 0.5, the latter being the performance expected by a model that performed no better than chance. For models with Gaussian distribution (for HADDOCK scores), we reached a corrected pseudo-R2 by subtracting the absolute value of the null model pseudo-R2 mean, which was in some cases negative, from the observed model pseudo-R2 mean.

We used all available data to train one model of zoonotic capacity that we used to make predictions for each of 5,400 mammal species. To develop confidence estimates around these zoonotic capacity predictions, for each of the 50 bootstrap iterations we used the model to make predictions on the full mammal dataset. Results can be found in Supplementary File 1.

### **Standardizing species susceptibility predictions across studies:**

To place our methods and predictions in context with the variety of existing approaches used to predict species susceptibility to SARS-CoV-2, we collated the results of previous studies that made predictions on multiple animal species. These studies made predictions through sequence-based methods (e.g., comparing species’ ACE2 amino acid sequence similarity with human ACE2), structure-based methods (e.g., creating three-dimensional representations of ACE2 orthologs), and laboratory experiments (e.g., characterizing cell entry using pseudotyped viruses). We collated the predictions made by the following studies: [(Ahmed et al., 2021)](https://paperpile.com/c/aI9Qxl/qK6f), [(Damas et al., 2020)](https://paperpile.com/c/aI9Qxl/NhWM), [(Huang et al., 2020)](https://paperpile.com/c/aI9Qxl/Ikj1), [(Kumar et al., 2020)](https://paperpile.com/c/aI9Qxl/ReNy), [(Lam et al., 2020)](https://paperpile.com/c/aI9Qxl/oCbY), [(Li et al., 2020)](https://paperpile.com/c/aI9Qxl/CxZs), [(Y. Liu et al., 2020)](https://paperpile.com/c/aI9Qxl/9eID), [(Z. Liu et al., 2020)](https://paperpile.com/c/aI9Qxl/n1sS), [(Luan et al., 2020)](https://paperpile.com/c/aI9Qxl/Lt9i), [(Mathavarajah et al., 2021)](https://paperpile.com/c/aI9Qxl/1EC8), [(Melin et al., 2020)](https://paperpile.com/c/aI9Qxl/cFZg), [(Rodrigues et al., 2020)](https://paperpile.com/c/aI9Qxl/Sgox), [(Yan et al., 2020)](https://paperpile.com/c/aI9Qxl/Sprg), and [(Zhao et al., 2020)](https://paperpile.com/c/aI9Qxl/KPZ9).

Some of these studies categorized species susceptibility as a gradient. For instance, [Damas et al., 2020](https://paperpile.com/c/aI9Qxl/NhWM) ranked species as a series of five categories from very high to very low, and Mathavarajah et al., 2020 ranked species as high, medium and low. Other studies categorized species susceptibility as a binary measure. For example, [Huang et al., 2020](https://paperpile.com/c/aI9Qxl/Ikj1) report whether each species is predicted to be susceptible or not. For those studies that did not assign species into explicit categories, we assigned categories based on the context of conclusions discussed by the authors of each study. For example, Rodrigues et al. 2020 discuss their species predictions by comparing each species’ HADDOCK score relative to empirical studies that confirm species as either positive or negative for SARS-CoV-2 infection. Based on the context of this discussion, we binned all of the species predictions from Rodrigues et al. 2020 into high (e.g., orangutan) and low (e.g., hedgehog) categories. For ease of comparison (Figure 1), we used three categories (low, medium, high) to organize predictions of species susceptibility across studies. Damas et al. 2020 was the only study that used categories outside of these. Very low and very high predictions from Damas et al. 2020 were recategorized as low and high, respectively. All other categorizations made by study authors were retained.

For the alluvial plot comparing species predictions by study method (Figure 5), all species predictions were transformed from a character value to a numeric value (e.g., low susceptibility translates to a 1 and high susceptibility translates to a 3). Species for which multiple predictions have been generated for a single method, predictions were averaged together and then rounded to the nearest whole number to create a single value for each species-method combination.

### **Mapping:**

To identify areas for future surveillance work, we mapped the top 10% of predictions from the zoonotic capacity threshold model (min probability = 0.748, mean = 0.889, max = 0.988). For representations of each species’ distribution, we used species range polygons from the IUCN Red List (IUCN 2020). Additionally, we focused on species found in human occupied or human modified landscapes because co-occurrence with humans may increase risk of spillback or secondary spillover. We used the IUCN API and the rredlist package in R version 4.0.0 to gather habitat associations for our subset of species predictions [(Chamberlain, 2020; IUCN, 2020; R Core Team, 2020)](https://paperpile.com/c/aI9Qxl/8PiN+we1i+xc6r), and subset to species listed by IUCN as having artificial terrestrial habitat associations (e.g., urban areas, crops or pastures, heavily degraded landscapes, etc.). We filtered these species distributions to only those areas overlapping with areas classified as ‘artificial terrestrial’ (according to classifications created by [(Jung et al., 2020)](https://paperpile.com/c/aI9Qxl/VsJ6).

Due to known issues matching high resolution environmental data with the much coarser resolution of range polygons (see [(Walter Jetz et al., 2012)](https://paperpile.com/c/aI9Qxl/JmNg) for a good explanation of the issue), we resampled the artificial terrestrial habitat raster from ~1 km to ~100 km in resolution using the resample function in the raster package in R [(Hijmans, 2020)](https://paperpile.com/c/aI9Qxl/OEMO). Polygons of species distribution data were rasterized at a resolution of ~100 km2 to match these data using the fasterize package in R [(Ross, 2020)](https://paperpile.com/c/aI9Qxl/UMx1). Small polygons may not be rasterized correctly using this method, so any polygon that produced an empty raster was converted to point data and rasterized using the rasterize function in the raster package [(Hijmans, 2020)](https://paperpile.com/c/aI9Qxl/OEMO). Any cells for rasterized species distributions that did not overlap a cell classified as artificial terrestrial were changed to NA.

Regions with higher numbers of human COVID-19 cases may pose a higher risk of spillback transmission to co-occurring animals. We gathered cumulative case count data from the COVID-19 Data Repository by the Center for Systems Science and Engineering (CSSE) at Johns Hopkins University [(Dong et al., 2020)](https://paperpile.com/c/aI9Qxl/YzQH). These data are mostly at the country level with the exception of state or province information for Australia, Brazil, Canada, Chile, Colombia, France, Germany, India, Italy, Japan, Mexico, the Netherlands, Pakistan, Peru, Russia, Spain, Sweden, Ukraine, the United Kingdom, and the United States of America. We considered hotspots as those administrative units (i.e., countries or states/provinces) with 100,000 or more cumulative COVID-19 cases. Species distributions were further restricted to areas within regions designated as hotspots to determine a final map of highest spillback risk (panel C of Figure 6 in the main text).

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