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4 1 **Toward a general framework for predicting threat status of data-**
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6 2 **deficient species from phylogenetic, spatial and environmental**
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37 13
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40 14 Running head: Predicting species threat status
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57 20 * Authors contributed equally
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3 21 **Abstract**
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6 22 In taxon-wide assessments of threat status many species remain not included due to lack
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8 23 of data. Here we present a novel spatial-phylogenetic statistical framework that uses a
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10 24 small set of readily available or derivable characteristics, including phylogenetically
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12 25 imputed body mass and remotely-sensed human encroachment, to provide initial baseline
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14 26 predictions of threat status for data-deficient species. Applied to assessed mammal
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16 27 species worldwide the approach effectively identifies threatened species and predicts the
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18 28 geographic variation in threat. For the 483 data-deficient species the models predict
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20 29 highly elevated threat, with 69% 'at-risk' species in this set, compared to 22% among
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22 30 assessed species. This results in 331 additional potentially threatened mammals, with
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24 31 elevated conservation importance in rodents, bats and shrews, and countries like
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26 32 Colombia, Sulawesi, and the Philippines. These findings demonstrate the future potential
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28 33 for combining phylogenies and remotely sensed data with species distributions to identify
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30 34 species and regions of conservation concern.
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36 **Introduction**

37 Human activities continue to cause the loss of many species together with the function
38 and services they provide [1]. In the face of these mounting threats and limited resources
39 to conserve species [2], tools are required to identify those of greatest conservation
40 concern. Global IUCN Red List assessments [3] have provided important knowledge
41 about the state of biodiversity and have helped to identify priority species and regions for
42 conservation [4-7]. On this basis approximately 20% of mammal, bird and amphibian
43 species are currently identified as threatened [3]. In order to minimize potential biases in
44 perceived patterns of biodiversity threat, species should be assessed comprehensively or
45 at least representatively. In addition to undiscovered species [4, 8], species with too little
46 information for threat categorization ('data-deficient species') are thus a major concern.
47 The IUCN assessment process relies on available field-based knowledge of e.g.
48 population size, rate of decline, and range size of each species to assigned threat status
49 [9-12]. Paucity of data, e.g. due to financial or logistical limitations for field studies,
50 makes complete assessments impossible for some species, with little prospects for change
51 in the near future. The number of species lacking data may be substantial, with e.g. 2,436
52 of 11,806 recognized mammal and amphibians species classified as 'data-deficient' in
53 2011 [3], including 834 extant mammals. The potential for data-deficient species to
54 change absolute threat levels of taxa has been acknowledged [4, 7]. In the absence of
55 better knowledge, a risk-averse approach may be to simply assume that all data-deficient
56 species are threatened. But given the sheer number of data-deficient species the
57 implications for conservation prioritization may be substantial and carry a high cost if
58 large numbers are in fact not threatened. At the other extreme data-deficient species may

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3 59 be no more threatened than assessed species, for example as appears to be the case with
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5 60 data-deficient birds [13]. Model-based initial baseline threat predictions for data-deficient
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8 61 species and a general framework to provide them for groups assessed in the future would
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10 62 thus hold multiple benefits for conservation practice.
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16 64 The relative paucity of data on ecology and threats of many species stands in stark
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18 65 contrast to our rapidly growing detailed knowledge about species' phylogenetic
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20 66 relationships and geographic distributions. Technology now allows cost-effective and
21
22 67 rapid generation of phylogenies for thousands of species. While often remaining coarse in
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24 68 grain [14, 15] or even limited to type specimen and thus for some species a main reason
25
26 69 for data-deficient status, more faceted geographic distribution information is increasingly
27
28 70 becoming available for many species [15; see also mol.org]. Distribution data permits
29
30 71 two types of inference about potential threat status. First, statistical models can
31
32 72 quantitatively capture the association between range size and threat status in assessed
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34 73 species [16] and then can be applied to data-deficient species [17-19] to account for this
35
36 74 risk component. Second, geographic range information can be intersected with
37
38 75 environmental layers that inform about broad-scale environmental niches and associated
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40 76 life history signals (e.g. on fecundity, generation time) related to threat status [16, 20].
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42 77 And, more directly, remotely-sensed layers of land-cover can provide coarse estimates of
43
44 78 potential habitat loss due to human encroachment. Information of this kind has recently
45
46 79 been shown to successfully predict threat status in birds [20] and mammals [21]. Modern
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48 80 statistical tools allow the development of models of correlates of current threat levels that
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50 81 incorporate both phylogenetic and spatial data [17, 22-27].
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83 In previous work, modeled threat predictions for data-deficient species have been made
84 without environmental or phylogenetic information [19], or without habitat encroachment
85 information and using eigenvectors [17, 18] which are highly constrained in their ability
86 to appropriately represent both phylogenetic and spatial signals [28, 29]. A general
87 framework that readily capitalizes on the ever increasing availability of species
88 distribution and remote sensing data, and rigorously incorporates phylogenetic and
89 geographic information is thus still missing. In this study we build on our earlier work
90 linking spatial and phylogenetic models [27] and predicting threat data with GIS-derived
91 habitat information [20] to develop such a framework. We demonstrate the approach
92 applied to mammals by parameterizing models of threat status based on readily available
93 variables capturing key aspects of life history, rarity and range loss (body mass,
94 geographic range size, human encroachment on species' ranges) together with spatial and
95 phylogenetic dependency for 3,703 mammal species across 16 orders with sufficient
96 information to be assessed by the Red List. We then apply these models to 483 species
97 classified as data-deficient species. We show, that the presented framework may offer a
98 cost-effective way for initial baseline threat evaluation of many understudied (and
99 potentially at-risk) species.

100

101 **Methods**

102 **Data.** We analyzed data on 4,186 terrestrial mammal species from 16 orders in the IUCN
103 Red List [30] that could also be placed in the mammalian super tree phylogeny [31] (with
104 recent updates). Of these, 3703 species had been assessed (with 812 deemed threatened,

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3 105 i.e. categories “Vulnerable”, “Endangered” and “Critically Endangered”) and 483
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5 106 recognized but not assessed (category “Data-Deficient”) by IUCN. We gathered
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8 107 information on mammal body masses from [32] and from F. Smith (pers. comm.). One
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10 108 order (Perissodactyla) contained no data-deficient species. We selected native and
11
12 109 reintroduced resident and breeding ranges that were extant or probably extant from the
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14 110 IUCN expert range maps [30] which we extracted over a 110x110km grid in Equal Area
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17 111 Cylindrical projection. We overlaid each species range map with information on
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19 112 transformed habitats owing to anthropogenic activities. Specifically, we estimated
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21 113 ‘Encroachment’ as the proportion of expert range transformed by past human activities
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23 114 (i.e. cultivated or managed, mosaics, including cropland and urban areas) according to the
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25 115 Global LandCover 2000 land-cover classification [33]. At 1km native resolution this
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27 116 information is collected at much finer scale than expert range maps and analysis grid
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29 117 [14], but used as range summary measure it offers a concrete first-order estimate of
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31 118 overall range encroachment, and has recently been shown to be a strong correlate of
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33 119 expert-assessed IUCN threat status in birds [20]. We note that other high-resolution
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35 120 global land cover classifications exist and that all suffer from remaining classification
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37 121 errors [34]. As additional metric we also calculated the average Human Influence Index
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39 122 (‘HII’) value [35, 36] over the species ranges.
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49 124 **Summary of approach**

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52 125 To summarize our approach, we first imputed the body masses of species for which data
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54 126 are missing and then used Generalized Linear Models that include phylogenetic and
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56 127 spatial dependence to predict IUCN status. We account for statistical uncertainty in our
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3 128 estimates of body mass by using Multiple Imputation. In order to incorporate uncertainty
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5 129 in our overall predictions, we express the model outputs as threat probabilities; i.e. given
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8 130 the predictions of the model and the statistical uncertainty in these, what is the probability
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10 131 that each species is threatened (i.e. IUCN categories Vulnerable, Endangered or Critically
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12
13 132 Endangered) or not?
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18 134 **Statistical modelling framework**

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21 135 The starting point for our analyses is a linear statistical model relating the values of a trait
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23 136 of interest to a set of predictors [24, 26]. The errors are assumed to have a multivariate
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25 137 normal distribution with mean 0 and a variance-covariance matrix that is defined by the
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27 138 phylogeny [23, 24, 26] and spatial distances [27]. Predictions from our models were
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29 139 generated by using the fitted parameter values together with the degree of phylogenetic
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31 140 and spatial similarity of species using the approach described in [26]. Our predictions
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33 141 therefore account for the phylogenetic /spatial structure in the data, i.e. they have the
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35 142 property that closely related, or species that live in the same place, should be similar to
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37 143 each other. We calculated variances for predicted values using the formulae in [24].
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39 144 These variances are used to calculate the variance in estimates of body mass and IUCN
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41 145 status (below).
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50 147 **Phylogenetic and spatial models for trait covariances**

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53 148 We use the generalized least squares (GLS) approach described in Freckleton & Jetz [27]
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55 149 to account for both spatial and phylogenetic effects. A parameter ϕ is included in the
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3 150 model to account for the influence of space. According to this model, of the total
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6 151 variance, a proportion ϕ is attributed to spatial variance, $(1 - \phi)$ is due to the non-spatial
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8 152 component. We also used the λ transformation suggested by Pagel [22, 37]. In the
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10 153 context of modelling spatial and phylogenetic effects simultaneously, the λ statistic
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12 154 allows us to include trait variation independent of both phylogeny and space in our
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14 155 analysis: a proportion $\gamma = (1 - \phi) (1 - \lambda)$ of the trait variation is independent of phylogeny
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16 156 or space [27]. This approach is akin to including a ‘nugget’ in a spatial model [38]. We
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18 157 estimated ϕ and λ by maximum likelihood [39].
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27 159 The spatial matrix was calculated and tested using the approach described in Freckleton
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29 160 & Jetz [27]. The spatial matrix reduces the spatial configuration of the data to a series of
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31 161 pairwise distances that measure the distance between each species. Following Freckleton
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33 162 & Jetz [27] we did this by calculating the distances between the centroids of the ranges of
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35 163 each pair of species. The assumption is, therefore, that the variance between species’
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37 164 traits grows linearly with spatial distances. As we showed before, this assumption can be
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39 165 tested graphically and in the analyses reported here, as well as in Freckleton & Jetz [27],
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41 166 this assumption was found to be adequate. Following Freckleton & Jetz [27], in order to
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43 167 aid interpretation of the model we define λ' as the relative contribution of phylogeny (λ'
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45 168 $=\lambda (1 - \phi)$) once the effects of space have been accounted for. This parameterisation
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47 169 allows a simple interpretation of the joint estimates of ϕ and λ because, as shown in
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49 170 Freckleton & Jetz [27], the sum of γ , λ' , and ϕ is always 1. These parameters can be
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51 171 interpreted as the individual proportional contributions to variance of the different
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3 172 variance components.
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9 174 **Imputation of mammalian body mass**
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11 175 We used estimates of mammalian body masses of 3462 species in the 16 analyzed orders
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13 176 to predict the values for the 723 species without body mass data. For each order we used
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15 177 the GLS approach described above to predict body mass based on the species with body
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17 178 mass data along with phylogenetic and spatial information. We conducted this analysis at
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19 179 the level of orders as previous analysis has shown that the Brownian model, modified to
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21 180 allow for varying degrees of phylogenetic dependence, provides an adequate description
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23 181 of body mass variation within orders [40]. Body mass was log-transformed prior to
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25 182 analysis.
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34 184 For species missing body mass we used the predicted values predicted as estimates of log
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36 185 mass in the modeling of IUCN threat status. A problem with using single imputation of
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38 186 this sort is that although parameter estimates should be unbiased [41], there is a
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40 187 possibility of under-estimation of variances for parameters using this method. We
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42 188 therefore conducted significance tests for our models using multiple imputation. For this
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44 189 we calculated for all species lacking body mass data predicted values using the above
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46 190 GLS model, along with a variance for each prediction (using the method in [24], see
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48 191 above). These estimates formed the basis for the multiple imputations [for further
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50 192 background on the method see 42, 43, 44; for specific implementation here see also
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52 193 Nakagawa & Freckleton 2008]. We used 10 imputations, and the statistical tests reported
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3 194 in Table S1 are the outcome of this analysis. We found that in practice the variance
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5 195 across the imputations was very small indeed so that this step was not vital in this case,
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8 196 although this need not always be true.
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13 198 In order to evaluate the accuracy of the predictions of body mass we used a simple
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16 199 randomization. Estimates of λ and ϕ from the best fitting model for each order were used
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19 200 to construct a variance-covariance matrix. This variance matrix formed the basis for
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21 201 generating randomized multivariate normally distributed data (using the `rmvnorm` in the
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23 202 R `mvtnorm` package). Species originally missing data were then removed and their values
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26 203 imputed. The correlation of these imputed values with the true values was then
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28 204 calculated. Note that because this analysis is conducted on randomly generated data, this
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30 205 is different from a cross-validation which is based on removal of data from the original
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32 206 data and would not normally be conducted using single-species removals. This was
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35 207 repeated 1000 times per missing species per order. The results of this analysis are
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37 208 summarized in Table S2.
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41 42 43 210 **Application to IUCN categories**

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46 211 The IUCN categories were treated as a five point ordinal scale ranging from “Least
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48 212 Concern”, 1, to “Critically Endangered”, 5. Although the response variable is a discrete
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50 213 ordinal variable, the models described observed threat levels well, offering explanatory
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52 214 power equal to, or better than that found in previous studies (Table S1, Fig. S1). This
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55 215 same approach has been taken in other recent analyses of threat status [45]. We compared
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3 216 our results with those of generalized linear models in which responses are treated as
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5 217 multinomial or ordered logistic responses, which yielded very similar results, but are
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8 218 unable to address the spatial and phylogenetic covariance (see Figs S2, S3 and below).
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10 219 The main problem in generating an output from the model is that a fitted / predicted value
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12 220 is a point estimate and does not account for the statistical uncertainty in our estimates. To
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15 221 incorporate uncertainty, after the analysis we converted our predictions of IUCN status
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17 222 into probabilities of threat. Previous analyses have taken a similar approach in the
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19 223 analysis of threat status, but instead converting the threat to a binary variable before the
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21 224 regression analysis [17]. This has the disadvantage that information on the ordinal nature
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23 225 of the IUCN scale is ignored. Our analysis, however, retained the continuous information
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25 226 in the model fitting: for example we account for the fact that a species classified as
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27 227 category 5 (Critically Endangered) is more at risk than a species in category 3
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29 228 (Vulnerable).
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37 230 To produce these threat probabilities we calculated the probability that each species was
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39 231 threatened or not from the predictions of IUCN status. This was simply done by
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41 232 calculating:
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$$45 \quad 233 \quad P_i^{threatened} = Z\left(\frac{y_i^{pred} - 2.5}{\sigma_i}\right) \quad (1)$$

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48 234 where $Z()$ is the cumulative z (standardized normal) distribution, y^{pred} is the predicted
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50 235 value and σ is its standard deviation. This is the probability that the predicted value of
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52 236 species i is *greater* than 2.5 (see also [17, 20]). The choice of threshold in equation (1) is
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54 237 dependent on the interpretation of the categories and how these relate to continuous
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3 238 model predictions. With eqn. (1), a species with an IUCN status predicted to be 2.5 (i.e.
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5 239 in between “near threatened” and “vulnerable”) will have a threat probability of 0.5. We
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8 240 repeated the analysis using a threshold of 2 which yielded a visually clearer
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10 241 discrimination between the higher IUCN categories, but did essentially not affect the
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12 242 results of Fig. 1(Fig. S4), because the probabilities are simply rescaled such that the mean
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14 243 probability is 0.5 at a predicted value of 2 rather than 2.5. The results in Fig 2 are also
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16 244 extremely similar (Fig. S5), because the estimates of the proportions of species to be
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18 245 threatened or not are set by a threshold estimated from the data by receiver operator
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20 246 characteristic analysis (below). Thus, results were broadly invariant to the choice of
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22 247 threshold in equation (1).
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30 249 We used the full models in Table S1 for making predictions and did not attempt model
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32 250 reduction. There were several reasons for this. First, model reduction by elimination of
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34 251 variables (e.g. based on statistical significance) has undesirable consequences, such as
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36 252 degenerate sampling distributions and model selection bias [46]. Second, examination of
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38 253 the coefficients for the predictors indicated that, independent of statistical significance,
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40 254 the directions of effects were usually quite consistent between orders. For example 15 out
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42 255 of 16 coefficients for the effect of body mass are positive even if all are not statistically
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44 256 significant (Table S1); 12 of 16 coefficients for the encroachment variable are positive
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46 257 (Table S1). Finally, we checked predictions with and without the least significant
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48 258 variables and confirmed that the R^2 values were not unduly inflated and giving a false
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50 259 impression of good fit. In order to test the predictive ability of the threat probabilities we
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52 260 assessed how well the fitted threat probabilities predicted for assessed species were able
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3 261 to distinguish threatened from non-threatened species using the Area Under the Curve
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5 262 (AUC) in the Receiver Operating Characteristic (ROC) curve [47]. AUC varies between
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8 263 0.5, which indicates that the predictions are no better than random, and 1, which is
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10 264 perfect agreement between observed and predicted. As threshold for assigning
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12 265 probabilities into binary categories of threatened and non-threatened, we used the value at
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15 266 which sensitivity equaled specificity in a given order.
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21 268 **Model Approach and Limitations**

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24 269 The methodology we have used is based on currently available tools and will be
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26 270 improved by future developments that include techniques such as logistic and
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28 271 multinomial generalized linear mixed models that could account for phylogenetic and
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30 272 spatial dependence and would enable to better model the discrete ordinal state variable
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32 273 [48, 49]. However such tools require very large datasets: logistic regression requires large
33
34 274 amounts of data because binary observations contain relatively little information.
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36 275 Multinomial or ordered responses are an extension of logistic regression and as the
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38 276 number of states increases the data requirements increase. Given this, the approach taken
39
40 277 here to treat the data as continuous is unlikely to seriously compromise the results (see
41
42 278 also supplementary results). Moreover existing methods for such responses do not
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44 279 combine spatial and phylogenetic signals, and can be very difficult to implement and
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46 280 tune. In the future, faster methods for fitting phylogenetic models are under development
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48 281 and these should facilitate further methodological advances [50]. We have assumed that
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50 282 the variance scales linearly with both phylogenetic and geographic distances. This is
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52 283 supported by diagnostics (e.g. see [27] for a worked examples). The assumption of
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3 284 linearity is not terribly critical so long as variance increases with distance. In previous
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5 285 work we suggested how the assumption could be varied (Table 1 in [27]). However it
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8 286 should be noted that nonlinear transformations of variance matrices are potentially
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11 287 difficult to work with. For example we have recently shown that a commonly used
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13 288 transformation (the Ornstein Uhlenbeck) is severely biased under most circumstances for
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15 289 even large datasets (Thomas et al. in review).

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18 290 The models we developed are strongly dependent on range size as a predictor of IUCN
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20 291 status, which reflects the importance of range size in the formal assessment process. It is
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22 292 important to note that our predictive models are not aimed at *testing* the relevance of this
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24 293 variable (which would require variable elimination to avoid circularity), but to use this
25
26 294 formally recognized association for prediction. In other words, we use A (assessed
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28 295 species) modeled by B (novel framework and independent variables) to predict C (not yet
29
30 296 assessed species), not to make inference about A.
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36 37 38 298 **Results**

39 40 41 299 **Assessed species**

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44 300 For the 16 mammal orders analyzed the threat probabilities (whether a species is non-
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46 301 threatened or threatened) predicted by the models successfully explain observed variation
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48 302 in assessed threat score (R^2 values were typically ~40% or greater; Table S1) and
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50 303 effectively predict species threat category (Fig. 1A). Range size and body mass were
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52 304 generally strong correlates of threat status, with smaller ranging and larger species
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55 305 typically being subject to greater threat (Table S1). Given the inherent role of range size
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3 306 in the IUCN assessment process [11] these associations are not altogether unexpected and
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5 307 confirm previous findings [19, 20, 51, 52]. Less consistently than recently observed in all
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8 308 terrestrial birds [20], land-cover encroachment and human influence measures are
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10 309 strongly positively correlated with IUCN threat category in several orders. This
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12 310 contributes to the overall predictive ability of the models and confirms the relevance of
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15 311 such variables for threat predictions (Table S1).
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20 313 In addition to the strong phylogenetic dependence of body mass (Table S2), 9 of the
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22 314 orders showed phylogenetic or spatial dependence in the residuals of the models for
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24
25 315 IUCN threat. The degree of net phylogenetic signal in the residuals of the final models is
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27 316 generally low, with the phylogenetic effect estimated as zero for seven and very low (0.1
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29 317 or less) for five orders. Notably higher estimates are obtained for primates (0.66). Six
30
31 318 orders showed strong spatial signals, with estimates of the spatial coefficient, ϕ , as high
32
33 319 as 0.6-1.0 (Table S1). The threat probabilities resulting from our models are the
34
35 320 probabilities that each species is in one of the threatened states rather than not threatened,
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37 321 given the mean and variance predicted by the model (see methods). The Receiver
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39 322 Operating Characteristic plot (Fig 1B) indicates a very strong discrimination of
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41 323 threatened from non-threatened species with an AUC of 0.90 for the whole dataset and a
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43 324 median of 0.91 for all orders. These were associated with high degrees of sensitivity and
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45 325 specificity (typically ca. 0.8 - 0.9, Table S1). Predicted threat probabilities are remarkably
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47 326 effective in delimiting threat status, as especially illustrated by the most and least
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49 327 threatened IUCN classes: only 4% of species assessed to be of 'least concern' were
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51 328 predicted to have a threat probability of 0.5 or greater (Fig. 1C; see Fig. S1 for order-
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3 329 level plots) and only 11% of species assessed to be ‘critically endangered’ were assigned
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5 330 a threat probability lower than 0.5 (Fig. 1C). Across all threat categories, 61% of species
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8 331 assessed as being under some degree of threat had estimated threat probabilities greater
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10 332 than 0.6 and (with nearly 31% greater than 0.8) (Fig. 1C). Overall, our predicted threat
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12 333 probabilities are a strong discriminator of threat status with particularly high values
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15 334 (>0.8) extremely unlikely for species that are not actually threatened.
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20 336 The relative richness of species assessed as being threatened is geographically very
21
22 337 uneven (Fig. 3A). Applied to assessed species, our model predicts this observed pattern
23
24 338 very well (Fig. 3B). Overall, however, there is a strong association between the predicted
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26 339 average probability or predicted proportion of species threatened and the observed
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28 340 proportion of species assessed threatened ($r = 0.74$ and $r = 0.68$, respectively; Fig. 4A, B)
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30 341 as well as, expectedly, between predicted and observed threatened richness ($r = 0.82$, Fig.
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32 342 4C). This suggests that our models successfully capture the biogeography of assessed
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34 343 threatened species.
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41 42 43 345 **Data-deficient species**

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45 346 Data-deficient species are predicted to be substantially more likely to be threatened than
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47 347 assessed species (Fig. 1D), with an average predicted threat probability of 0.40 compared
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49 348 to 0.21 in assessed species. For data-deficient species 28% of threat probability estimates
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51 349 were greater than 0.6, whereas for assessed species it was only 11%. Overall threat
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53 350 probabilities were higher for data-deficient species in 10 orders, and statistically
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3 351 significantly so for 7 orders (Fig. 2). Classifying data deficient species into binary threat
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5 352 categories using a standardized order-specific threshold (the value at which sensitivity
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8 353 equals specificity) results in a total of 331 of 483 species predicted threatened, i.e. 69% of
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11 354 species threatened compared to 29% among assessed species. This difference is repeated
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13 355 among almost all orders, with a total of 298 potentially threatened data-deficient species
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15 356 identified among the Chiroptera, Rodentia and Eulipotyphla alone (for species-level
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17 357 results see Table S3).

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23 359 Geographically, data-deficient species are predicted to exhibit substantially higher
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25 360 average probabilities and proportions of species threatened (grid cell assemblage values
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28 361 of 0.12 and 0.17, respectively) than assessed species (0.06 and 0.06, respectively). At the
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30 362 grid cell level, the predicted average threat probabilities or proportion of data-deficient
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33 363 species shows barely any relationship with the proportion of species assessed to be
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35 364 threatened (Spearman rank correlations: $r = 0.30$ and $r = 0.29$, respectively; Figs. 4D,E).
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37 365 Equally, the richness of data-deficient species predicted to be threatened is only weakly
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40 366 correlated with that of species assessed to be threatened ($r = 0.30$, Fig. 4F). The
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42 367 discordance in geographic ‘hotspots’ of predicted assessed and data-deficient threat is
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44 368 apparent when comparing the maps of their predicted threat probabilities and species
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47 369 richness in Figure 3. Threat levels predicted for data-deficient species substantially
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49 370 exceed those of assessed species in many locations (note different color scales). Data-
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52 371 deficient species hold much higher predicted threat levels than assessed species in
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54 372 Colombia and Central America, Southern South America, and parts of Southeast Asia. In
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56 373 terms of species richness (Fig 3F, 4F), data-deficient species are predicted to strongly
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3 374 increase the number of at-risk species in Sumatra, New Guinea, Colombia, and especially
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6 375 Sulawesi, where in grid cell 10 likely threatened mammal species add to the known 16.
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8 376 This suggests that these regions are even more important for conservation than previous
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10 377 global conservation prioritization analyses may have suggested [53, 54]. In contrast, data-
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12 378 deficient species predicted *not* to be threatened occur both outside (e.g. Southern South
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14 379 America) and inside (e.g. Borneo, Central and West African forests) some main areas of
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16 380 known (assessed) high prevalence of threatened species (Fig 3D, E).
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26 383 **Discussion**

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29 384 In this study we have shown that data-deficient species are much more likely to be under
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31 385 threat than those that have already been assessed and that the geographic distribution of
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33 386 data-deficient species that are likely threatened is different to that of assessed threatened
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35 387 species. This may have important implications for global mammal conservation strategies
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37 388 [55]. According to our analysis it is extremely likely that well over three hundred
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39 389 additional mammal species (69% of those data-deficient) are threatened, many of them
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41 390 potentially severely so. This is over an order of magnitude more than suggested by
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43 391 Davidson et al [19] which identified 28 data-deficient mammal species as potentially
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45 392 threatened, but did not use environmental, spatial or phylogenetic information. Using
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47 393 eigenvectors, no encroachment data and model validation with only bats, Jones and Safi
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49 394 [18] estimated 35% of 481 data-deficient mammal species to be potentially threatened.
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51 395 Our statistically more robust approach [28, 29] that additionally uses remotely sensed
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53 396 encroachment information thus suggests much greater levels of threat in data-deficient
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3 397 species than previously thought. The relatively low degree of phylogenetic signal of
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5 398 IUCN status we found here contrasts with previous related results in carnivores [17]. This
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8 399 difference has two sources: firstly from the inclusion of species' body masses in our
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10 400 analyses, and secondly from the inclusion of spatial effects, which also has phylogenetic
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12 401 signal. In particular mean mass is both strongly phylogenetically determined in all orders
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15 402 and strongly related to IUCN status (Table S1). Accounting for body mass thus decreases
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17 403 the detectable phylogenetic signal.
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23 405 Our findings suggest that data-deficient species cannot be ignored in conservation threat
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25 406 assessments and in interpretation of threat status for policy setting. In mammals data-
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27 407 deficient species are clearly more likely than non data-deficient species to be under
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29 408 significant threat. The association between threat status and data deficiency arises,
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31 409 because narrow-ranged (and thus often scarce), large-bodied (that thus often low-density,
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33 410 long generation time) species, are also very likely to be those for which little data exist
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36 411 (Table S1, [see also 45]). There are notable exceptions: for instance, the threat probability
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38 412 of data-deficient primates is no higher than that of those that have been assessed, likely
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40 413 reflecting the relatively higher research effort directed at primates in the past. In contrast,
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42 414 rodents are much more difficult to study (they are small, live in inaccessible habitat and
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44 415 are frequently nocturnal) and for them over half of data-deficient species are predicted to
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46 416 be threatened whereas only 16% have been assessed as threatened (Fig 2). Our findings
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48 417 contrast with recent results for birds, where just 0.6% of species are data-deficient and
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50 418 where species that were recently moved from this category were found to be less
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52 419 threatened than non-data-deficient species [13]. However, these only recently assessed
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3 420 bird species are likely not a representative sample of data-deficient species as whole, as
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5 421 data-deficient species assessed first will likely be ones that are more easily studied (and
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8 422 thus face different, potentially lesser threats) than those assessed last. The statistical
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10 423 results gathered from all species may offer more reliable guidance.
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16 425 Our general aim was to demonstrate how readily-available information can be used to
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18 426 make initial predictions about the likely conservation status of species for which a formal
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20 427 assessment has not yet been possible. If a similar proportion of data-deficient yet
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22 428 threatened mammal species (69%) was to be found amongst data-deficient amphibians
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24 429 (1,600 out of 6,312 species are data-deficient, [3]), it would represent a very large
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26 430 increase of amphibian species at-risk. Such a scenario would add many new species to
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28 431 the threatened categories in the Red List with strong potential consequences for geographic
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30 432 conservation prioritization. The transferability of mammal-based estimates to other taxa
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32 433 is of course unclear, but this realization highlights the importance of expanding
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34 434 assessment work and seizing the increasing opportunities for rigorous statistical inference
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36 435 of threat status.
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45 437 The strong importance of select life history traits and range size for predicting threat
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47 438 status has previously been illustrated [16]. Recently the complementary power of
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49 439 remotely-sensed measures of human land encroachment to predict threat status has also
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51 440 been demonstrated for birds [20]. Combined with an increasingly thorough understanding
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53 441 of the spatial context of species [15] and ever-improving data on the phylogenetic signal,
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55 442 a general predictive framework is emerging that may be instrumental for statistically
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3 443 assessing the thousands of species for which an individual evaluation is time- or cost-
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5 444 prohibitive. By identifying already assessed species with highly over- or under-predicted
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8 445 threat status for further scrutiny, it may also someday help improve the Red Listing
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10 446 process which is not without human error. Clearly, the presented framework is no silver
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12 447 bullet to replace the need for expert assessment based on field ecological data. We expect
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15 448 that assessment data for at least 50% of species, depending on representativeness, is
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17 449 needed to provide reasonably reliable threat predictions, but this will vary by group and
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19 450 likely often be higher. But this does potentially free up resources and lower completion
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21 451 thresholds [56, 57] that would benefit the assessment of neglected taxa such as
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23 452 invertebrates and plants. More generally, a complementary approach to traditional expert-
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25 453 based assessment may emerge that combines available phylogenetic/biological data with
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27 454 improved species distribution knowledge linked to a remotely-sensed monitoring of land
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29 455 cover [15] – all facilitating a dynamic and continuous baseline assessment of the state of
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31 456 species.
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Figure Legends

Fig. 1. Explanatory and discriminative power of the fitted models of threat status for assessed species. (A), the relationship between fitted threat probability and IUCN status for assessed species. Threat probability is the probability a species is in one of the ‘threatened’ categories according to our spatial-phylogenetic multi-predictor model. (B), Receiver Operator Characteristic (ROC) curve, showing the relationship between true positive (sensitivity) and false positive (1 minus specificity) rate. The dashed line is the expected pattern if the threat probabilities were no better than random at discriminating threatened species. The AUC, which varies between 0.5 and 1, is the area highlighted in grey and is a measure of explanatory power. (C), the frequency distribution of fitted probabilities for species of contrasting conservation status. The green bars refer to species of ‘least concern’ (IUCN status 1 in *A*), whilst the red bars refer to species which are ‘critically endangered’ (IUCN status 5 in *A*). (D) Fitted / predicted threat probabilities shown separately for assessed species (grey) and data-deficient species (red).

Fig. 2. Prediction of threats for individual mammal orders. For each order the average fitted threat probabilities for assessed species (black points) and predicted threat probabilities for data-deficient species (red points) are shown (\pm standard errors). F-ratios and p-values refer to tests of differences between the mean fitted threat probabilities of assessed and data-deficient species. The numbers of assessed species is given for each order, together with the number of data-deficient and threatened (i.e. not ‘least concern’) species. The grey vertical bars show the threshold threat probability for each order (see Table S1), which is used to denote which data-deficient species are predicted to be threatened. The threshold is the point at which sensitivity = specificity (where

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3 threatened and non-threatened status have equal chance of being correctly predicted [58]). Based
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5 on this probability, the final column gives the number of data-deficient species which are predicted
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7 to be threatened. Note that there are no data-deficient species in Perrissodactyla and the orders is
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9 thus not included here.
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Fig. 3. The geography of observed and predicted mammal threat levels and richness. Panels
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17 illustrate the observed and predicted grid-cell proportions of all species assessed by IUCN to be
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19 threatened and analyzed here (A,B, 3,703 species, for model details see Table S1), and the
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21 predicted proportion of data-deficient species threatened (C, 483 species, for details see Fig 2).
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23 (D-F) show observed and predicted richness patterns: the richness of observed (assessed)
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25 threatened species (D, 812 of 3,703 species in analysis, i.e. all those assessed “vulnerable”,
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27 “endangered” or “critically endangered”), those data-deficient species predicted by the combined
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29 spatial, phylogenetic and environmental model to be non-threatened (E, N = 152 of 483 species),
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31 and those predicted to be threatened (F, 331 of 483 species). Quantile classification of values
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33 across 110km equal area grid cells in Behrman projection. Note that color scales vary to emphasize
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35 geographic differences.
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Fig. 4. Relationships between observed and predicted threat levels of grid cell assemblages.

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47 The model-based predictions of average probability (A) and total proportion (B) of species
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49 threatened successfully captures the observed variation in proportion species threatened (A,
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51 Spearman $r = 0.72$; B, $r = 0.66$; 3,703 species; cf. Fig 3A, B). Observed and predicted richness of
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53 threatened assessed species is tightly associated (C, $r = 0.77$, cf. Fig 3D). In contrast, the predicted
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55 average threat levels and proportions of data-deficient species (cf. Fig 3C) show only very weak
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3 association with the proportional threat patterns of assessed species (D, $r = 0.33$, E, $r = 0.23$; 843
4 data-deficient species). Equally, the areas with high richness of data-deficient species predicted to
5 be threatened shows little covariance with those of high assessed threatened richness (F, $r = 0.31$,
6 cf. Fig 3F). Darker gray represent higher density of points, line indicates 1:1 relationship. A total
7 of 11,331 110km equal area grid cells that had $\geq 50\%$ dry land or were oceanic islands and had \geq
8 2 assessed species were analyzed.
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For Review Only

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Figure 1







