1 **Interannual climate variability data improves niche estimates in species**

2 **distribution models**

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12

13 **Abstract**

14 **Aim**

15 Climate is an essential element of species' niche estimates in many current ecological

16 applications such as species distribution models (SDMs). Climate predictors are often used in

17 the form of long-term mean values. Yet, climate can also be described as spatial or temporal

18 variability for variables like temperature or precipitation. Such variability, spatial or temporal,

19 offers additional insights into niche properties. Here, we test to what degree spatial variability

20 and long-term temporal variability in temperature and precipitation improve SDM predictions

21 globally.

22 **Location**

23 Global.

24 **Time period**

25 1979-2013

26 **Major taxa studies**

27 Mammal, Amphibians, Reptiles

28 **Methods**

29 We use three different SDM algorithms, and a set of 833 amphibian, 779 reptile, and 2211

30 mammal species to quantify the effect of spatial and temporal climate variability in SDMs. All

31   SDMs were cross-validated and accessed for their performance using the Area under the Curve

32   (AUC) and the True Skill Statistic (TSS).

33   **Results**

34   Mean performance of SDMs with climatic means as predictors was TSS=0.71 and AUC=0.90.

35   The inclusion of spatial variability offers a significant gain in SDM performance (mean

36   TSS=0.74, mean AUC=0.92), as does the inclusion of temporal variability (mean TSS=0.80,

37   mean AUC=0.94). Including both spatial and temporal variability in SDMs shows similarly

38   high TSS and AUC scores.

39

40   **Main conclusions**

41   Accounting for temporal rather than spatial variability in climate improved the SDM prediction

42   especially in exotherm groups such as amphibians and reptiles, while for endotermic mammals

43   no such improvement was observed. These results indicate that more detailed information about

44   temporal climate variability offers a highly promising avenue for improving niche estimates

45   and calls for a new set of standard bioclimatic predictors in SDM research.

Introduction

Climate is known to influence species' distributions (Woodward & Woodward, 1987) across different spatial and temporal scales, thus, detecting the impact of climate on species depends to a large degree on the spatial and temporal scale at which it is assessed (Wiens, 1989; Rahbek, 2005). While the effect of spatial variability in climate on species distributions has received heightened attention in recent years due to the ever increasing spatial resolution of freely available climate data (e.g. Hijmans *et al.*, 2005; Fick & Hijmans, 2017; Karger *et al.*, 2017), analyses of the effect of temporal climate variability on species ranges have been much less abundant (Zimmermann *et al.*, 2009). Analytically, an increase in resolution in one dimension often comes at the cost of decreased resolution in the other dimension due to computational limitations (Hourdin *et al.*, 2017; Schär *et al.*, 2019). However, a focus on ever increasing spatial resolution may leave time-dependent phenomena undetected (Wiens, 1989). This is especially of concern since one of the major components of climate change is an increase in climate variability and – in consequence – an increase of extremes (Rahmstorf & Coumou, 2011; Seneviratne *et al.*, 2012). Increasing frequencies and severities of extreme events may cause greater physiological stress and may thus result in rapid responses in many species with likely severe consequences for their spatial distribution (Reyer *et al.*, 2013; Alexander *et al.*, 2015).

The spatial ranges of species are commonly estimated using empirical species distribution models (SDMs), sometimes also termed bioclimatic envelope or habitat suitability models (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). SDMs characterize the environmental niche of a species (Hutchinson, 1957) usually with respect to a few key environmental factors, such as temperature and precipitation. It has become common practice to use a limited set of climate variables as predictor variables (Araújo & Guisan, 2006) based on long-term means (climatologies) alone (Ashcroft *et al.*, 2011). Such an aggregation of climate variability into long-term climatological means fully removes information on the temporal signal, including inter-annual variability. Species are known to strongly differ in degree to which they can tolerate climatic extremes, and this affects their life cycles, coping strategies through functional adaptations and, ultimately, their spatial distribution. Yet when using long term climatic means, our capacity to distinguish effects from differences in climate variability on species' distributions is basically removed.

Climatologies do not only smooth out temporal variabilities in climate but also reduce spatial variability. Spatial climate heterogeneity as a result of small-scale topography and other factors are not represented in gridded datasets of coarse spatial grain. Coarse spatial grains cannot

80   resolve the richness in topography, and thus climate, environment, and habitats, that are

81   essential for quantifying species' environmental niches (Stein *et al.*, 2014; Stein & Kreft, 2015).

82   Such misrepresentation of spatial heterogeneity when representing or aggregating climate

83   predictors at coarse grain might more strongly impact niche estimates in the tropics compared

84   to temperate or boreal zones (Janzen, 1967). In the tropics, species generally experience a lower

85   degree of intra- and interannual climatic variation due to the rather stable environmental

86   conditions they encounter throughout the year (Janzen, 1967; Wiens, 1989). In temperate

87   climates however, the conditions a species experiences are much more variable due to the larger

88   intra- and interannual variation in climate (Janzen, 1967). Species occurring in tropical

89   ecosystems, therefore often have a much narrower climatic niche (Stevens, 1989; Cadena *et al.*,

90   2012). In turn, this also implies that the influence of temporal variability might be greater in

91   areas where species are not well adapted to variation in climate. Therefore, along large-scale

92   geographic gradients both spatial and temporal variability can become important in estimations

93   of a species environmental niche.

94   Climate does not only influence the distribution of species, but also has a profound impact on

95   how specific traits evolve over time as adaptations to climate itself (Kozak & Wiens, 2010;

96   Rolland *et al.*, 2018; Liu *et al.*, 2020). While climate is an important factor in the diversification

97   of species (Liu *et al.*, 2020), many adaptations can also be directly linked to environmental

98   factors. A prominent example is the evolution of endothermy, which allows to some degree, the

99   decoupling of a species internal temperature from that of its surrounding habitat (McNab, 1978;

100 Ruben, 1995), which in turn leads to different responses of species to a climatic factor. Hence,

101 overall, spatial and temporal variabilities may not only act as species range determinants in

102 isolation, but also interact with each other. With climatic data becoming available at

103 increasingly higher spatial and temporal resolution, the opportunity arises to generate an

104 improved understanding of the role of spatial and temporal climatic variability on the

105 distribution of species. Here, we evaluate if considering temporal, and spatial variation in

106 addition to classical coarse-grained climate mean values improves the performance of SDMs

107 when using coarse-grained species distribution data.

108 Based on the potential effects of spatial and temporal climate variability on species discussed

109 before, we hypothesize that

110 i)   both the inclusion of spatial and temporal variability positively affect the

111   performance of SDMs,

112 ii)   the performance of ectotherm SDMs increases more strongly when accounting for

113   spatial and temporal variability than the performance of endotherm SDMs, and

114   iii)   SDMs for tropical and mountain species will benefit more strongly from including

115   variability than SDMs of species from other habitats.

116   We test these hypotheses by modelling the distribution of 833 amphibian, 779 reptile, and 2211

117   mammal species as a function of current climate using four different predictor groups composed

118   of different combinations of input variables: mean climate, spatial climatic variability and

119   temporal (interannual) climatic variability.

Methods

Species data

122   We used global distribution maps provided by the Amphibian, Mammal, and Reptile Red List

123   Assessment (IUCN, 2016). Grid cells within the distribution range of each species were

124   converted to 0.5° grid cells, which is close to 50 km at the equator, a resolution suggested as

125   appropriate (Hurlbert & Jetz, 2007) and often used (Fritz & Rahbek, 2012; Zurell *et al.*, 2018;

126   Thuiller *et al.*, 2019) when gridding polygon range maps at the global scale. Grid cells

127   intersecting with a range map polygon were assigned as presence cells, while those not

128   intersecting where treated as absence cells. We only considered species for which the presences

129   cover at least 72 0.5° grid cells so that a minimum of six data points per predictor variable

130   (including quadratic terms) was available for model building. We also removed domestic and

131   aquatic species.

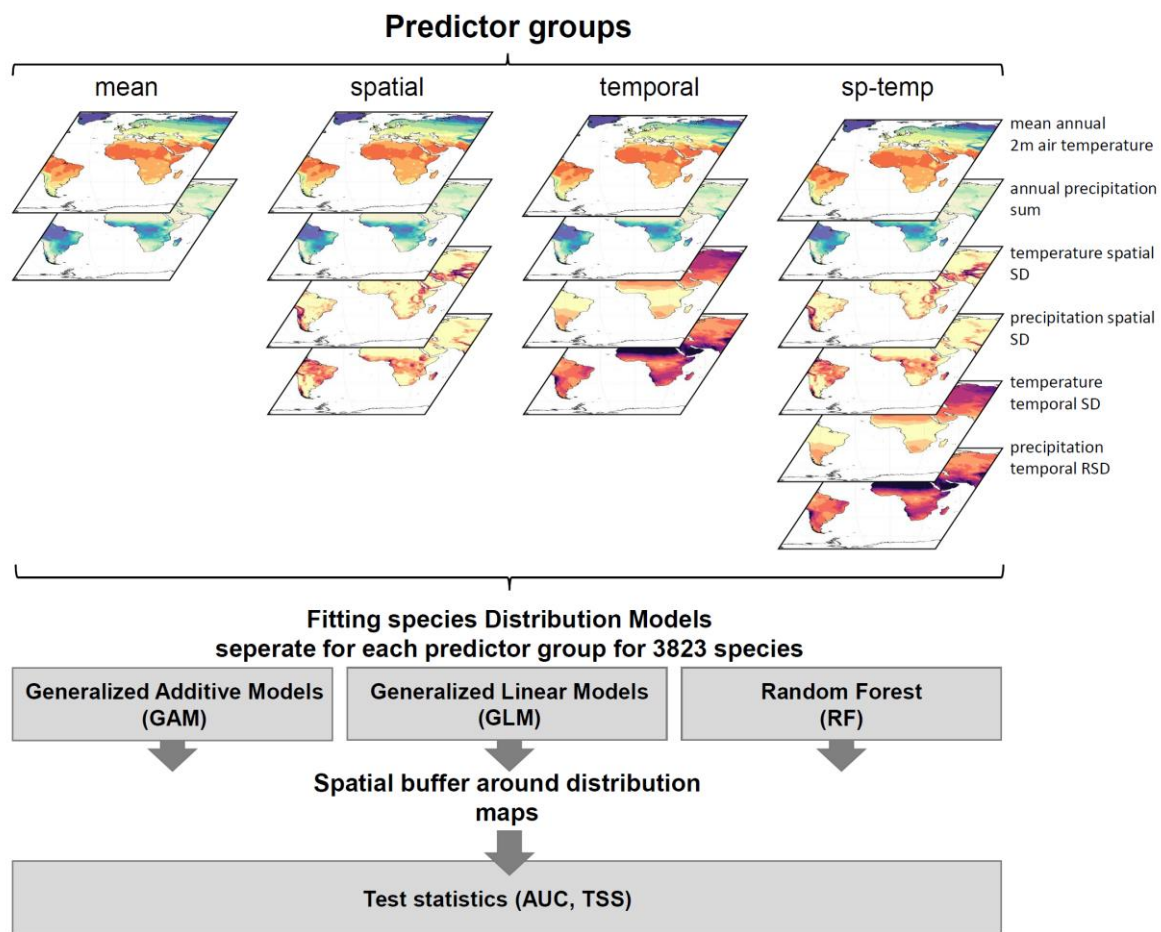### Climate predictor groups

133   We used global climate data from CHELSA V1.2 (Karger *et al.*, 2017a,b) and built several

134   groups of predictors (Fig. 1, Table 1) by aggregating CHELSA to the 0.5° grid of the species

135   data by taking the mean of all 30 arc second grid cells overlapping with a 0.5° grid cell. To

136   calculate sub-grid heterogeneity of a climatic variable (hereafter: spatial) within a 0.5° grid cell,

137   we used the standard deviation of all CHELSA 30 arc second grid cells overlapping with 0.5°

138   grid cells. To calculate the interannual variability (hereafter: temporal) we calculated the

139   standard deviation of mean annual 2m air temperature for each year from 1979 to 2013 from

140   CHELSA V1.2 per grid cell. For temporal precipitation variability we used the relative standard

141   deviation (temporal RSD, equivalent to the coefficient of variation) of the annual precipitation

142   sum across all years from 1979 to 2013 from CHELSA V1.2 per grid cell. Based on the data

143   aggregated as explained above, we generated four different groups of predictors for annual

144   temperature and precipitation, with different combinations of spatial and temporal variabilities

145   (Table 1).

146 **Table 1.** Characterization of the four predictor groups used with the respective variables
147 included in each group as well as the temporal or spatial unit over which they were aggregated.
148 All variables are based on CHELSA V1.2 (Karger *et al.*, 2017a).

Predictor group	variables included	aggregation unit
mean	mean annual 2m air temperature 1979-2013	-
	mean annual precipitation sum 1979-2013	-
spatial	mean annual 2m air temperature 1979-2013	-
	mean annual precipitation sum 1979-2013	-
	standard deviation mean annual 2m air temperature 1979-2013	all 0.0083334° grid cells within a 0.5° grid cell
	standard deviation mean annual precipitation sum 1979-2013	all 0.0083334° grid cells within a 0.5° grid cell
temporal	mean annual 2m air temperature 1979-2013	-
	mean annual precipitation sum 1979-2013	-
	standard deviation mean annual 2m air temperature 1979-2013	all years from 1979-2013
	coefficient of variation mean annual precipitation sum 1979-2013	all years from 1979-2013
sp-temp	mean annual 2m air temperature 1979-2013	-
	mean annual precipitation sum 1979-2013	-
	standard deviation mean annual 2m air temperature 1979-2013	all 0.0083334° grid cells within a 0.5° grid cell
	standard deviation mean annual precipitation sum 1979-2013	all 0.0083334° grid cells within a 0.5° grid cell
	standard deviation mean annual 2m air temperature 1979-2013	all years from 1979-2013
	coefficient of variation mean annual precipitation sum 1979-2013	all years from 1979-2013

149

Fig. 1. Schematic representation of the analytical setup. Four predictor groups where formed and three algorithms for species distribution models (SDMs) were fitted from range maps for 3823 species of mammals, amphibians, and reptiles. The different SDMs were predicted spatially and their predictive performance assessed within a buffer of 3000 km around observed ranges, using the area under the curve (AUC) and the true skill statistic (TSS) as performance measures.

Species distribution modelling

We used three algorithms to relate presences and absences with the selected environmental predictor sets: Generalized Linear models (GLM) (Nelder & Wedderburn, 1972), Genearlized Additive Models (GAM) (Hastie & Tibshirani, 1990), and Random Forests (RF) (Breiman, 2001). GLMs were run using linear and quadratic terms, GAMs was run using thin plate splines setting an upper limit of 4 degrees of freedom (k=5). In both cases, we set weights such that the sum of weights of presences equaled the sum of weights of absences (Barbet-Massin *et al.*,

165   2012). A classification RF was fitted using 1500 trees, while sub-sampling was restricted to

166   contain equal numbers of presences and absences.

167   To assess model performance, we tested SDM predictions only within a buffer around each

168   species' range polygon. By doing so we account for biogeographic history and explicitly test

169   how well a model predicts the actual range of a species rather than how well it also makes

170   predictions far outside a species' range, yet with suitable climate. We applied a buffer of

171   3000km around each range polygon and fitted and tested SDMs only within this extent.

172   We evaluated the predictive performance of the SDMs using repeated split-sample tests: we

173   split the data repeatedly into 80% training and 20% test data, fitted the model on the training

174   data, and predicted it to the test data. This procedure was repeated 30 times, while we recorded

175   predictive performance of each repeat. Predictive performance was assessed using a) the true

176   skills statistic (TSS) (Allouche *et al.*, 2006), after thresholding the predictions into

177   presence/absence using a TSS-optimized threshold, and b) the area under the curve (AUC)

178   (Swets, 1988). We provide the full SDM description following the ODMAP protocol (Zurell *et*

179   *al.*, 2020)(Zurell et al. 2020) in Appendix S2.

Performance tests of predictor groups

181   We used a linear mixed effects model (Bates *et al.*, 2015) with either TSS or AUC as response

182   variable and the predictor group as fixed effects together with the SDM algorithm (GLM, GAM,

183   RF) and the species identity as random effects. Adding the type of SDM (GLM, GAM, or RF)

184   as random effect on the intercept considers that algorithms can perform differently well (e.g.

185   have a different mean performance between AUC or TSS, Thuiller *et al.*, 2019). To always

186   compare the same species, but modeled with different sets of predictor groups, we also added

187   the identity of the species as random affect to the intercept. To check if there are differences in

188   SDM performance across climatologies, we ran a paired Wilcoxon test. By this, we tested if

189   one climatology performs better then another.

190   All analyses have been performed using the R language for statistical computing (R Core Team,

191   2015, version 3.6.1), the R packages raster (Hijmans & van Etten, 2014), mgcv (Wood & Wood,

192   2015), and randomForest (randomForest: Breiman and Cutler's Random Forests for

193   Classification and Regression).

Spatial performance of different predictor groups

195   To test if different predictor groups have different performances in different regions, we used

196   the gridded range map at 0.5° resolution from IUCN and assigned the value of the respective

197   test metric (TSS, AUC) to the entire range in which a species is present. All ranges were then

198   stacked and the mean of all TSS and AUC values covering a 0.5° grid cell calculated.

Results

199

Spatial patterns of the predictor groups

200

201   While mean annual 2m air temperatures and annual precipitation sums were generally higher

202   in the tropics and decrease towards the poles (Fig. 2, upper), the spatial SD of these two

203   variables is usually highest in mountainous terrain (Fig. 2, middle). Interannual variability

204   (temporal SD) of temperature is generally higher in the northern hemisphere compared to the

205   southern hemisphere, and increases from tropics to continental artic or boreal areas. Variability

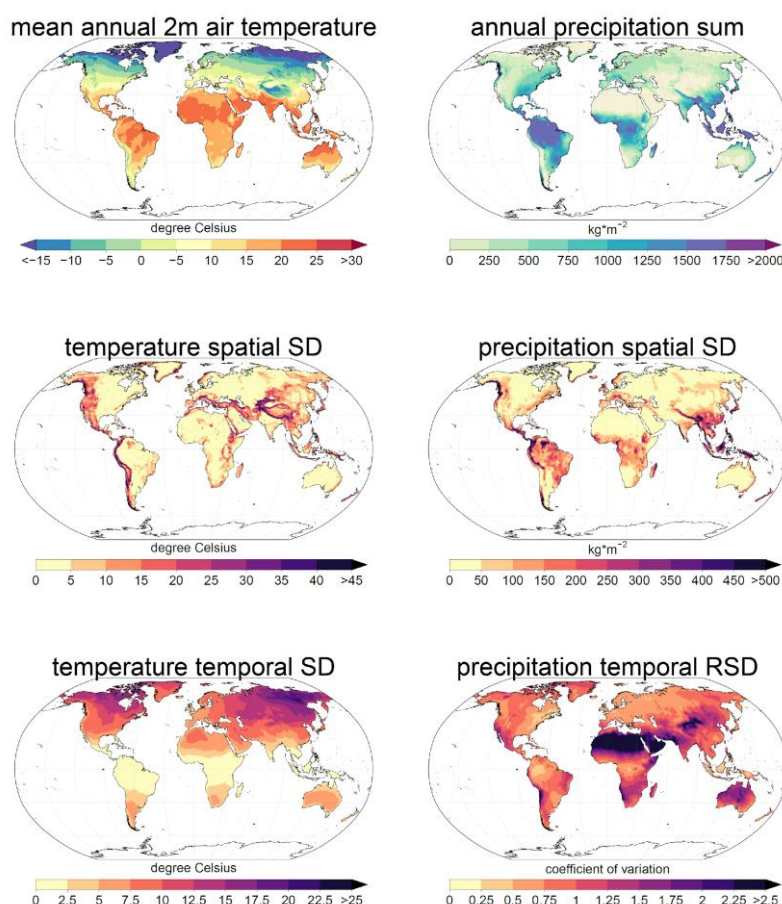206   (temporal RSD) of precipitation is more idiosyncratic, with lowest values estimated in desert

207   areas.

208

Fig. 2. Spatio-temporal variation in 2m air temperature and precipitation used as predictors in

209

210   the different SDMs based on CHELSA V1.2. Mean annual values (upper row) show the annual

211   mean for temperature, and the mean annual sum for precipitation averaged over the years 1979-

212   2013 and aggregated to 0.5° from a 30 arc second spatial grain by taking the mean of a 0.5°

213   grid cell. Spatial variation (middle) indicates the standard deviation (SD) of all temperature

214   values of a 30 arc second grid of temperature or precipitation overlapping with a 0.5° grid cell.

215   Temporal variation (lower row) shows the standard deviation (SD) of temperature over years

216   between 1979-2013, and the relative standard deviation (RSD) calculated as the coefficient of

217   variation for precipitation over the same time period.

218

Performance scores of the SDMs with different predictor groups

220   Overall the predictive performance of the SDMs was high with an average AUC of 0.92 and

221   ranging on from 0.90 to 0.95 between different groups of predictors, SDMs, and climatologies.

222   For TSS, values averaged 0.75 with a minimum 0.68 and a maximum of 0.82 for the different

223   predictor groups.

224   SDMs based on mean climate predictors performed worst among all groups, with average AUC

225   and TSS scores of 0.90 and 0.71, respectively (GAM: 0.91; 0.73, GLM: 0.90; 0.73, RF: 0.90;

226   0.68). SDMs based on mean climate predictors plus spatial predictors performed slightly better,

227   with average AUC and TSS scores of 0.92 and 0.74 (GAM: 0.93; 0.77, GLM: 0.92; 0.76, RF:

228   0.91; 0.70). SDMs based on mean climate predictors plus temporal predictors performed

229   slightly better, with average AUC and TSS scores of 0.94 and 0.80 (GAM: 0.94; 0.81, GLM:

230   0.94; 0.81, RF: 0.94; 0.77). SDMs containing mean climate predictors plus spatial and temporal

231   predictors performed similar as the SDMs with mean and temporal predictors, with average

232   AUC and TSS scores of 0.94 and 0.80 (GAM: 0.95; 0.82, GLM: 0.93; 0.81, RF: 0.94; 0.77).

233   The results of the linear mixed effects model to assess the SDM performance with different

234   predictor groups showed that adding predictors that account for either spatial or temporal

235   variation increased predictive performance of models across all groups of vertebrates. Models

236   based on the temporal predictor group outperformed models based on the spatial predictor

237   group for amphibians and reptiles, but not for mammals (equal performance). Models that

238   included predictors that accounted for both spatial and temporal variation (sp-temp predictor

239   group) performed best across all vertebrate groups. Fig. 3 illustrates these results using effect-

240   size plots (below boxplots) for TSS, while results for AUC are equivalent (see Supplemental
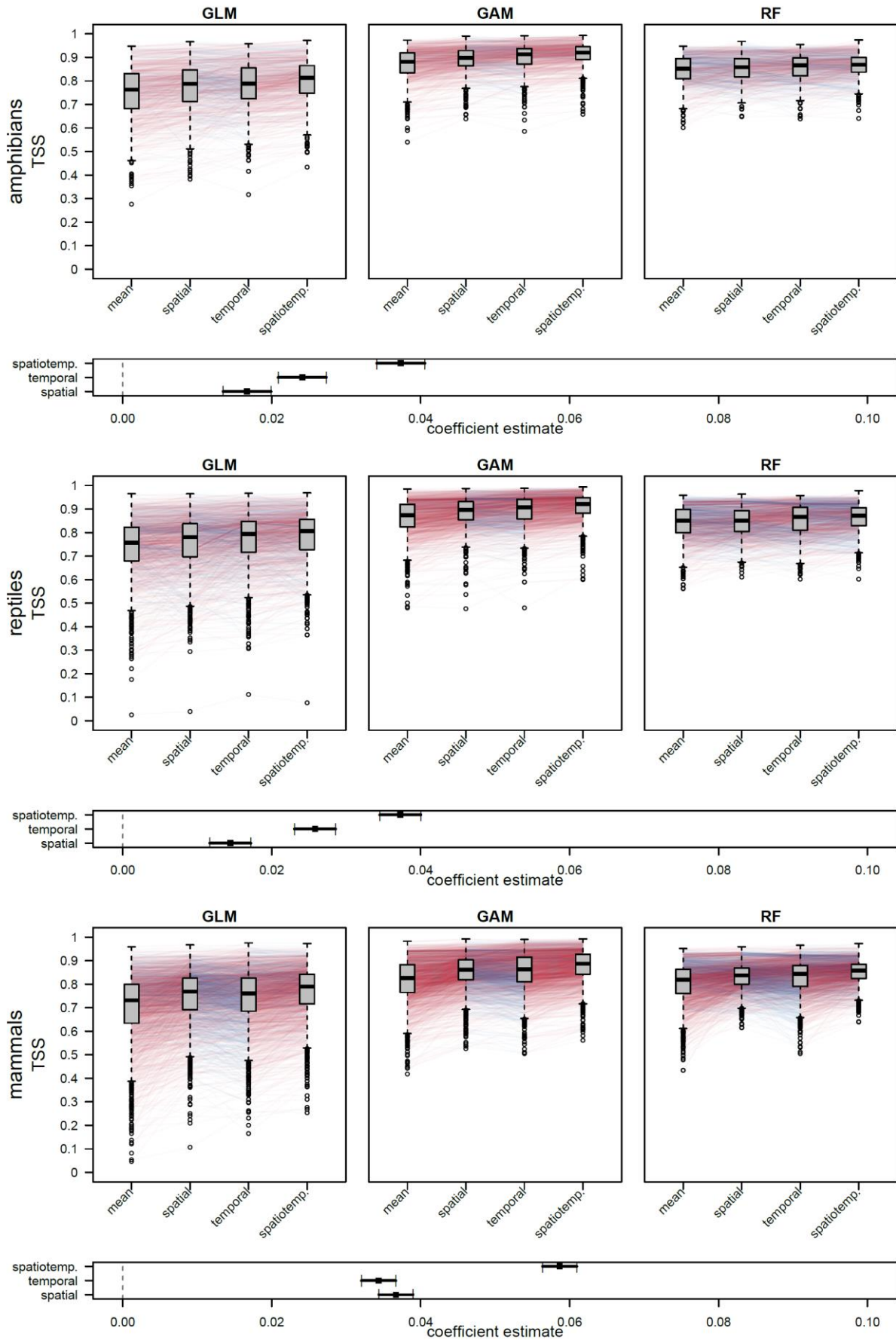
241   Figure S1).

242

243   **Fig. 3.** Comparison of the performance of three different SDM algorithms (GLM = Generalized

244   linear model, GAM = Generalized additive model, RF = Random Forests) calculated with four

245   different sets of predictors for amphibians, reptiles, and mammals measured by the True Skill

246   Statistic (TSS). Colored lines connect pairs of SDMs based on different predictor sets for the

247   same species, with red and blue lines indicating pairs in which TSS values increased and

248   decreased between predictor groups from left to right. Plots below the boxplots shows the

249   coefficient estimates of a linear mixed effects model with TSS as response, the groups (mean,

250   spatial, temporal, sp-temp) as predictor, and the model (GLM, GAM, RF) as well as the species

251   ID as random effects. Coefficients are in relation to the performance of SDMs with the predictor

252   set: mean.

253   **Spatial comparison**

254   The performance of SDMs is highly variable across the globe (Fig. 4). The mean predictor

255   group generally performed worst in mountainous terrain, such as the Andes or the Himalayas,

256   but also Madagascar showed low TSS and AUC scores (Fig. 4, Supplementary Fig. S2 for

257   AUC). Including spatial variability in temperature and precipitation in SDMs improved the

258   models in these areas, but showed a slight decline in performance in desert and arctic areas (Fig.

259   4: TSS differences spatial-mean). Adding temporal variability to the models containing mean

260   predictors resulted in improved SDM performance in almost all areas (Fig. 4: temporal-mean).

261   Including all spatial and temporal predictors resulted in a slight improvement in the spatial

262   model accuracies compared to including the temporal group with the mean predictor group (Fig.

263   4: spatio temporal), yet the improvement compared to mean plus temporal SDM were small.
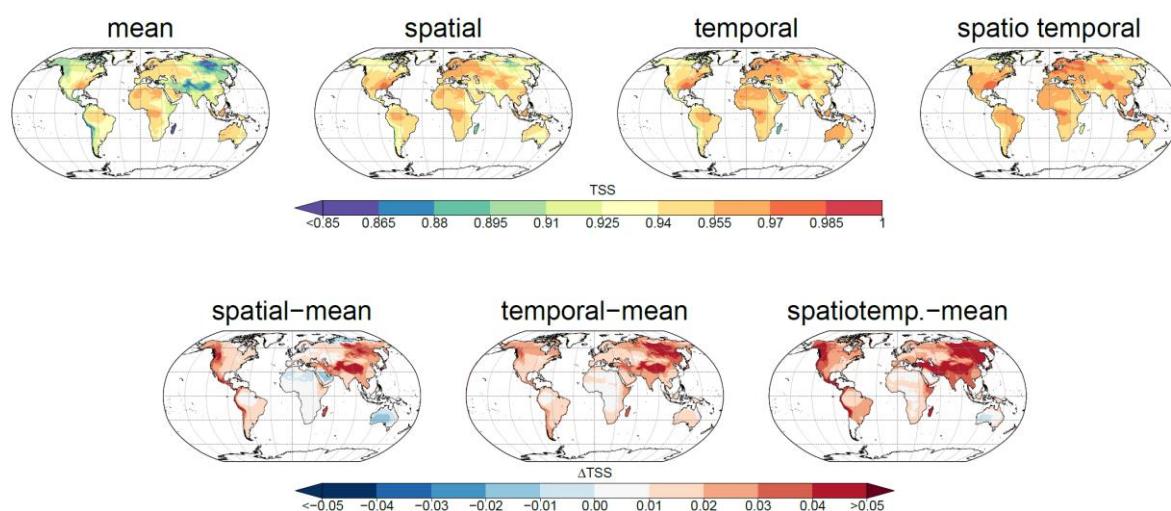
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265

266 **Fig 4.** Spatial variation in mean TSS values per grid cell and TSS differences between models
267 using different predictor groups. The upper row illustrates TSS averaged for all mammals,
268 reptiles, and amphibians modeled for the four models using different predictor groups. The
269 lower row illustrates the averaged TSS difference among all SDMs when adding either spatial,
270 temporal or both spatial and temporal (spatiotemp.) predictors to SDMs based on mean
271 predictors only.

Discussion

273 Including temporal variability of predictors into broad-scale SDMs leads to a greater
274 improvement of model performance than the inclusion of sub-grain spatial variability of these
275 predictors. These findings suggest that especially the inclusion of interannual climate variability
276 has a large potential of improving the estimation of niche characteristics across a large range of
277 taxa. Including temporal predictor variability increased the performance of SDMs in almost all
278 areas across the globe, though to differing degrees. Especially prominent is the increase in areas
279 with marked seasonality such as in tropical monsoon climates, tropical wet and dry climate, or
280 areas that receive very infrequent precipitation such as the Horn of Africa (Beck *et al.*, 2018).
281 Temporal variability does also increase the performance of SDMs in mountainous regions
282 potentially indicating that temporal variability in a climate variable is also capable to capture
283 the niche limitations that are otherwise captured by spatial heterogeneity. One reason for the
284 performance gain when including temporal variability is that it expresses the degree of climatic
285 extremes which can physiologically limit the distribution of species (Zimmermann *et al.*, 2009).
286 Although, the degree to which extremes are represented in such variability predictors certainly
287 depends on the temporal resolution of the climatic input dataset. In the case presented here, we
288 used interannual variation, which means that extreme events are restricted to extremely dry or
289 wet years, or extremely hot or cold years. Using more detailed temporal analyses would allow
290 to refine the representation of climatic extremes further.
291 As expected, the inclusion of the spatial variability improves SDMs mainly in mountainous
292 areas where climate is extremely heterogeneous over short distances. The improvement was
293 specifically strong in tropical mountains where species usually occur in narrow elevational
294 bands with little or no intra-annual variability (Janzen, 1967; Ghalambor *et al.*, 2006). In
295 topographically less heterogenous terrain however, we observed a decline in the predictive
296 power of SDMs. Almost all over Africa, Australia, and the low elevation parts of Eurasia, and
297 North America spatial variability has no effect, or even a negative effect on the performance of
298 SDMs. In these areas spatial heterogeneity is low and inclusion of spatial variability in climate
299 predictors seems biologically unimportant, which leads to a decrease in their performance

300   (Loehle & LeBlanc, 1996; Davis *et al.*, 1998; Vaughan & Ormerod, 2003; Dormann *et al.*,

301   2012).

302

303   The increase in SDM performance is however not equal across the three taxonomic groups

304   analyzed here. While amphibians and reptiles show a significantly higher SDM performance of

305   the temporal predictor group over the spatial predictor group, mammal SDMs do not

306   significantly differ when either spatial or temporal predictors are added to the mean predictor

307   group. This difference might be explained by the differences in physiology between these

308   groups. All three groups have evolved differently in response to their environment, with

309   ectothermic groups being much less adaptable to climatic variations than endothermic groups

310   (Rolland *et al.*, 2018). Such evolved differences in physiology ultimately affect how organisms

311   interact with and are constrained by their environment (Buckley *et al.*, 2012). Ectothermic

312   species for example cannot buffer climate variation as well as endothermic species (Clusella-

313   Trullas *et al.*, 2011; Sunday *et al.*, 2011; Hoffmann *et al.*, 2013; Gunderson & Stillman, 2015)

314   which have evolved the physiological capacity to regulate temperatures to some extent (Pither,

315   2003). When building SDMs from climate means alone, thus neglecting the temporal dimension

316   of predictors, we miss out on important climatic constraint especially for endothermic species

317   distributions, ultimately limiting the accuracy of niche estimations (Zimmermann *et al.*, 2009).

318   Model formulation and parametrization certainly plays a role in the observed differences

319   between predictor groups. More predictors in a model usually lead to a better overall fit of a

320   model (Brun *et al.*, 2019) which can partly explain the increase in predictive power when the

321   predictors based on mean climate are complemented with either spatial or temporal variability.

322   As both, the spatial and the temporal predictor groups have the same number of variables, this

323   effect does not hold when comparing these two. Combining mean with spatial and temporal

324   predictor groups however, lead to an additional improvement. At this point however, the

325   parametrization of has not yet plateaued (Randin *et al.*, 2006; Chala *et al.*, 2016; Brun *et al.*,

326   2019; Gregr *et al.*, 2019) and model performance still increases when using both spatial and

327   temporal variability as predictors. Using different SDM algorithms mainly affects the absolute

328   performance of the SDMs in terms of the specific test metric (AUC, TSS). However, it did not

329   affect the relative difference in model performance between SDMs calculated from different

330   predictor groups.

331   With an increasing need in biodiversity modeling for current, past, and future predictions a

332   better understanding of the climatic predictors that quantify the ecological niche of a species is

333   needed. Here, we show that specifically the inclusion of temporal variability offers a promising

334   improvement in modelling the current distribution of species. Yet, also the inclusion of spatial

335   (sub-grain) variabilities can improve model accuracies, primarily mountains and most clearly

336   in tropical mountains. In summary, we anticipate that a more detailed inclusion of the temporal

337   variability of climate variables offers a highly promising avenue for improving species

338   distribution modelling in the future.

Data Accessibility Statement

340   The data that support the findings of this study are openly available in EnviDat (envidat.ch) at

341   http://doi.org/XXXXXX. Codes related to this study will be available on Zenodo at

342   http://doi.org/YYYYYYYY

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Author contributions:

354   D.N.K. and N.E.Z. developed the idea with input from all co-authors, D.N.K., L.M. and R.O.W.

355   implemented the species distribution modelling, B.S. and D.N.K. analyzed the results further,

356   D.N.K. wrote the first draft of the manuscript, and all authors contributed equally to the

357   revisions.

Biosketch:

359   Dirk Nikolaus Karger is a senior researcher at the Swiss Federal Research Institute WSL and

360   mainly interested in the impact climate has on global ecosystems and species. The author

361   consortium binds a strong interest in species distribution modelling.

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523 **Appendices**
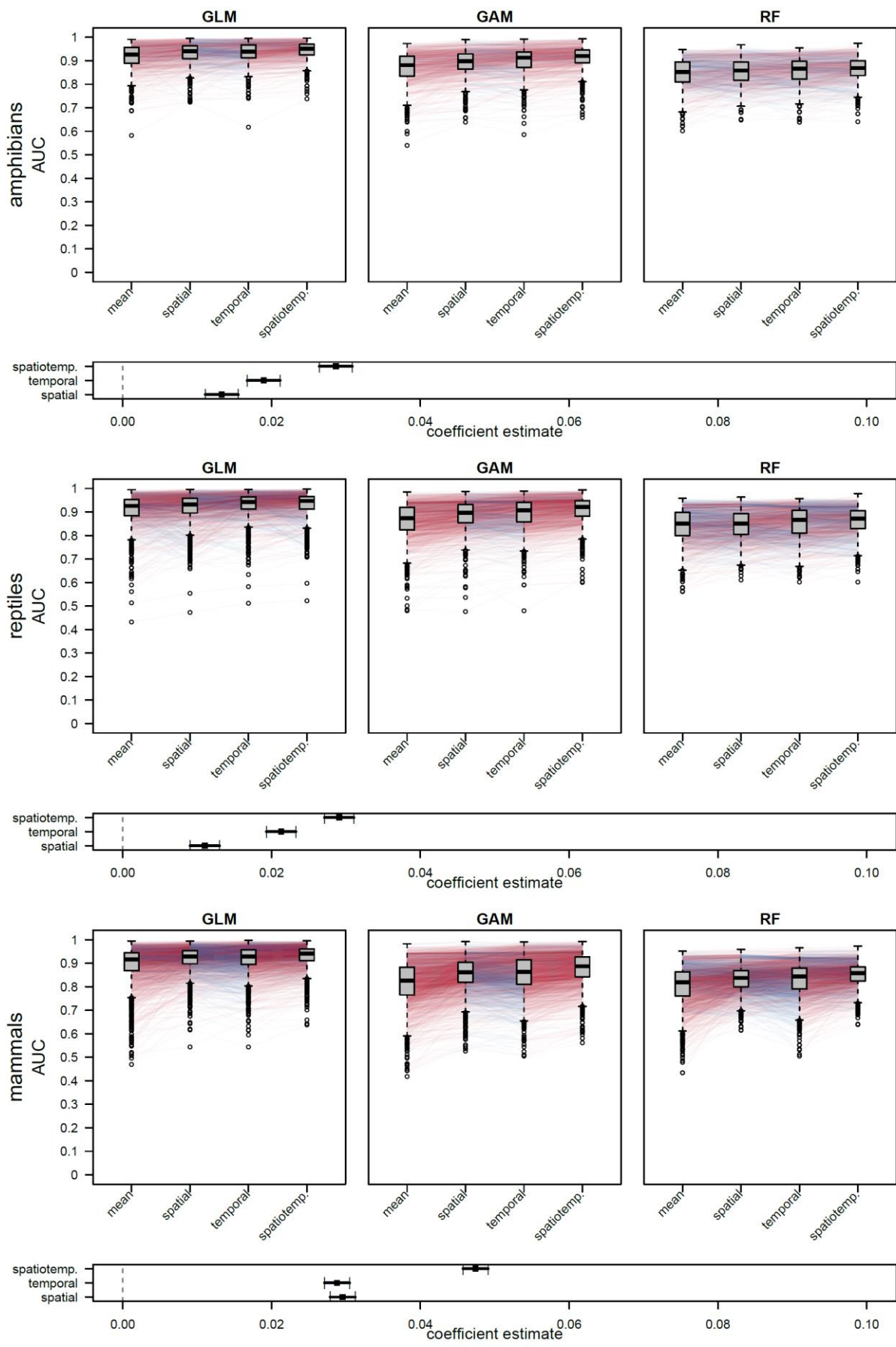

524

525   **Fig. S1.** Comparison of the performance of three different SDM algorithms (GLM =

526   Generalized linear model, GAM = Generalized additive model, RF = Random Forests)

527   calculated with four different sets of predictors for amphibians, reptiles, and mammals

528   measured by the Area Under the Curve (AUV). Colored lines connect pairs of SDMs based on

529   different predictor sets for the same species, with red and blue lines indicating pairs in which

530   AUC values increased and decreased between predictor groups from left to right. Plots below

531   the boxplots shows the coefficient estimates of a linear mixed effects model with AUC as

532   response, the groups (mean, spatial, temporal, spatiotemp.) as predictor, and the model (GLM,

533   GAM, RF) as well as the species ID as random effects. Coefficients are in relation to the

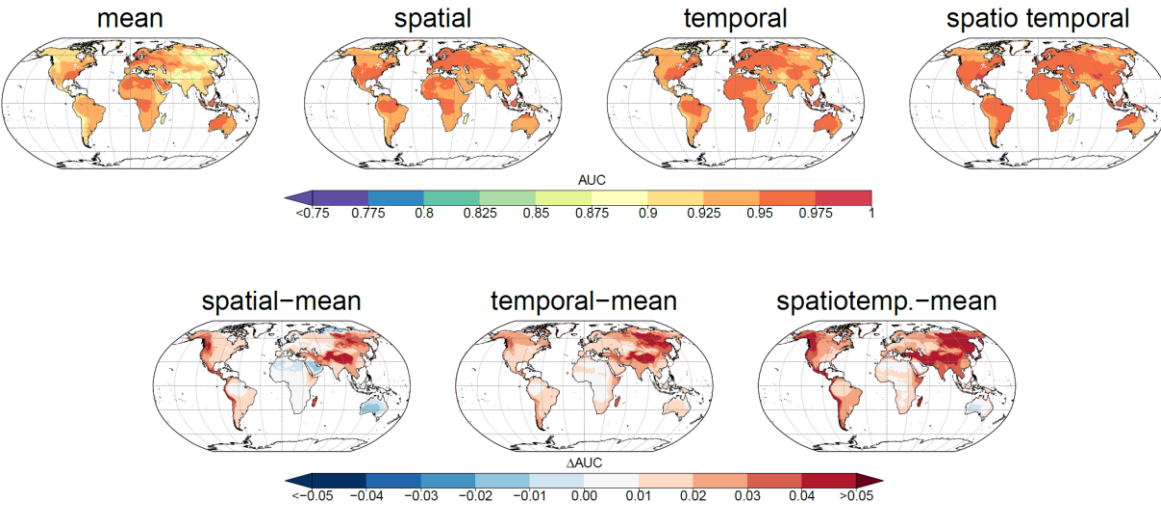534   performance of SDMs with the predictor set: mean.

535

536

537 **Fig S2.** Spatial variation in mean AUC values per grid cell and AUC differences between
538 models using different predictor groups. The upper row illustrates AUC averaged for all
539 mammals, reptiles, and amphibians modeled for the four models using different predictor
540 groups. The lower row illustrates the averaged AUC difference among all SDMs when adding
541 either spatial, temporal or both spatial and temporal (spatiotemp.) predictors to SDMs based on
542 mean predictors only.

543