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1 Interannual climate variability data improves niche estimates in species

2 distribution models

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- 4 Dirk Nikolaus Karger^{1*}, Bianca Saladin¹, Rafael O. Wüest-Karpati¹, Catherine H. Graham¹,
- 5 Damaris Zurell^{1,2}, Lidong Mo^{1,3}, Niklaus E. Zimmermann¹
- 6
- ⁷ ¹Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
- 8 ²University of Potsdam, Am Neuen Palais 10, 14469 Potsdam, Germany
- 9 ³Swiss Federal Institute of Technology in Zurich, Department of Environmental Systems
- 10 Science, Universitätstrasse 16, 8092 Zürich, Switzerland
- 11 *corresponding author: <u>dirk.karger@wsl.ch</u>

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.

46 Introduction

47 Climate is known to influence species' distributions (Woodward & Woodward, 1987) across 48 different spatial and temporal scales, thus, detecting the impact of climate on species depends 49 to a large degree on the spatial and temporal scale at which it is assessed (Wiens, 1989; Rahbek, 50 2005). While the effect of spatial variability in climate on species distributions has received 51 heightened attention in recent years due to the ever increasing spatial resolution of freely 52 available climate data (e.g. Hijmans et al., 2005; Fick & Hijmans, 2017; Karger et al., 2017), 53 analyses of the effect of temporal climate variability on species ranges have been much less 54 abundant (Zimmermann et al., 2009). Analytically, an increase in resolution in one dimension 55 often comes at the cost of decreased resolution in the other dimension due to computational 56 limitations (Hourdin et al., 2017; Schär et al., 2019). However, a focus on ever increasing 57 spatial resolution may leave time-dependent phenomena undetected (Wiens, 1989). This is 58 especially of concern since one of the major components of climate change is an increase in 59 climate variability and – in consequence – an increase of extremes (Rahmstorf & Coumou, 60 2011; Seneviratne et al., 2012). Increasing frequencies and severities of extreme events may 61 cause greater physiological stress and may thus result in rapid responses in many species with 62 likely severe consequences for their spatial distribution (Rever et al., 2013; Alexander et al., 63 2015).

64 The spatial ranges of species are commonly estimated using empirical species distribution 65 models (SDMs), sometimes also termed bioclimatic envelope or habitat suitability models (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). SDMs characterize the 66 environmental niche of a species (Hutchinson, 1957) usually with respect to a few key 67 environmental factors, such as temperature and precipitation. It has become common practice 68 69 to use a limited set of climate variables as predictor variables (Araújo & Guisan, 2006) based 70 on long-term means (climatologies) alone (Ashcroft et al., 2011). Such an aggregation of 71 climate variability into long-term climatological means fully removes information on the 72 temporal signal, including inter-annual variability. Species are known to strongly differ in 73 degree to which they can tolerate climatic extremes, and this affects their life cycles, coping 74 strategies through functional adaptations and, ultimately, their spatial distribution. Yet when 75 using long term climatic means, our capacity to distinguish effects from differences in climate variability on species' distributions is basically removed. 76

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.

Based on the potential effects of spatial and temporal climate variability on species discussedbefore, we hypothesize that

i) both the inclusion of spatial and temporal variability positively affect theperformance of SDMs,

ii) the performance of ectotherm SDMs increases more strongly when accounting forspatial 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.

120 Methods

121 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.

132 Climate predictor groups

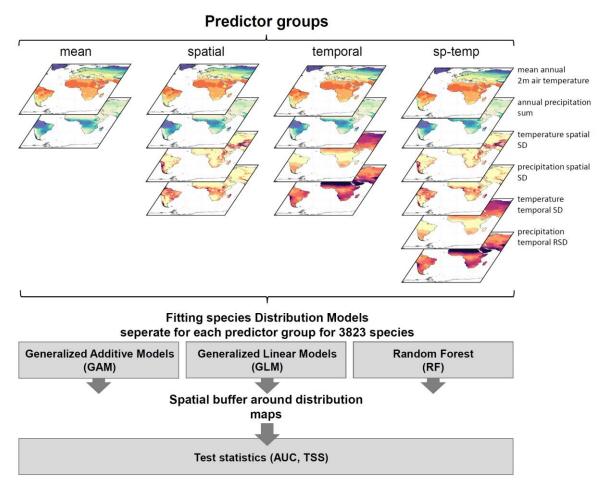
133 We used global climate data from CHELSA V1.2 (Karger et al., 2017a,b) and built several 134 groups of predictors (Fig. 1, Table 1) by aggregating CHELSA to the 0.5° grid of the species data by taking the mean of all 30 arc second grid cells overlapping with a 0.5° grid cell. To 135 136 calculate 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	all 0.0083334° grid cells
	temperature 1979-2013	within a 0.5° grid cell
	standard deviation mean annual precipitation	all 0.0083334° grid cells
	sum 1979-2013	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	all years from 1979-2013
	temperature 1979-2013	
	coefficient of variation mean annual	all years from 1979-2013
	precipitation sum 1979-2013	
sp-temp	mean annual 2m air temperature 1979-2013	-
	mean annual precipitation sum 1979-2013	-
	standard deviation mean annual 2m air	all 0.0083334° grid cells
	temperature 1979-2013	within a 0.5° grid cell
	standard deviation mean annual precipitation	all 0.0083334° grid cells
	sum 1979-2013	within a 0.5° grid cell
	standard deviation mean annual 2m air	all years from 1979-2013
	temperature 1979-2013	
	coefficient of variation mean annual	
	precipitation sum 1979-2013	all years from 1979-2013





150

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.

157

158 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 to166 contain equal numbers of presences and absences.

To assess model performance, we tested SDM predictions only within a buffer around each species' range polygon. By doing so we account for biogeographic history and explicitly test how well a model predicts the actual range of a species rather than how well it also makes predictions far outside a species' range, yet with suitable climate. We applied a buffer of 3000km around each range polygon and fitted and tested SDMs only within this extent.

We evaluated the predictive performance of the SDMs using repeated split-sample tests: we split the data repeatedly into 80% training and 20% test data, fitted the model on the training data, and predicted it to the test data. This procedure was repeated 30 times, while we recorded predictive performance of each repeat. Predictive performance was assessed using a) the true skills statistic (TSS) (Allouche *et al.*, 2006), after thresholding the predictions into presence/absence using a TSS-optimized threshold, and b) the area under the curve (AUC) (Swets, 1988). We provide the full SDM description following the ODMAP protocol (Zurell *et*

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

180 **Performance tests of predictor groups**

We used a linear mixed effects model (Bates et al., 2015) with either TSS or AUC as response 181 182 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).
- 194 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.

199 **Results**

200 Spatial patterns of the predictor groups

While mean annual 2m air temperatures and annual precipitation sums were generally higher in the tropics and decrease towards the poles (Fig. 2, upper), the spatial SD of these two variables is usually highest in mountainous terrain (Fig. 2, middle). Interannual variability (temporal SD) of temperature is generally higher in the northern hemisphere compared to the southern hemisphere, and increases from tropics to continental artic or boreal areas. Variability (temporal RSD) of precipitation is more idiosyncratic, with lowest values estimated in desert areas.

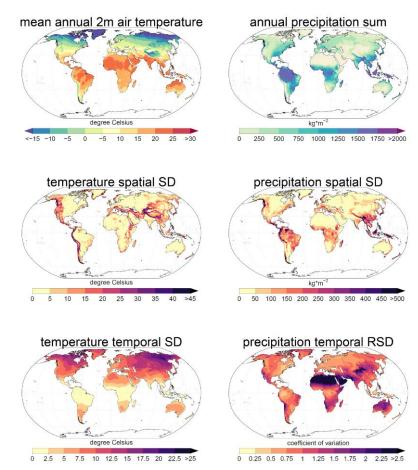




Fig. 2. Spatio-temporal variation in 2m air temperature and precipitation used as predictors in the different SDMs based on CHELSA V1.2. Mean annual values (upper row) show the annual mean for temperature, and the mean annual sum for precipitation averaged over the years 1979-2013 and aggregated to 0.5° 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

- 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
- between 1979-2013, and the relative standard deviation (RSD) calculated as the coefficient of
- 217 variation for precipitation over the same time period.
- 218

219 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
- ranging on from 0.90 to 0.95 between different groups of predictors, SDMs, and climatologies.
- For TSS, values averaged 0.75 with a minimum 0.68 and a maximum of 0.82 for the different 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-
- size plots (below boxplots) for TSS, while results for AUC are equivalent (see Supplemental
- Figure S1).

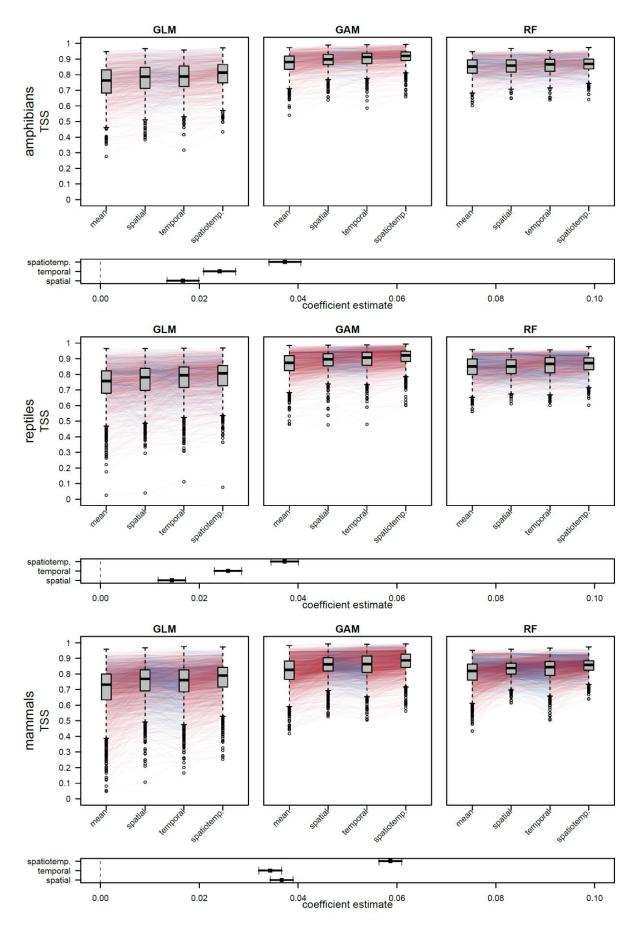


Fig. 3. Comparison of the performance of three different SDM algorithms (GLM = Generalized 243 244 linear model, GAM = Generalized additive model, RF = Random Forests) calculated with four 245 different sets of predictors for amphibians, reptiles, and mammals measured by the True Skill 246 Statistic (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). Including all spatial and temporal predictors resulted in a slight improvement in the spatial 261 model accuracies compared to including the temporal group with the mean predictor group (Fig. 262 263 4: spatio temporal), yet the improvement compared to mean plus temporal SDM were small. 264

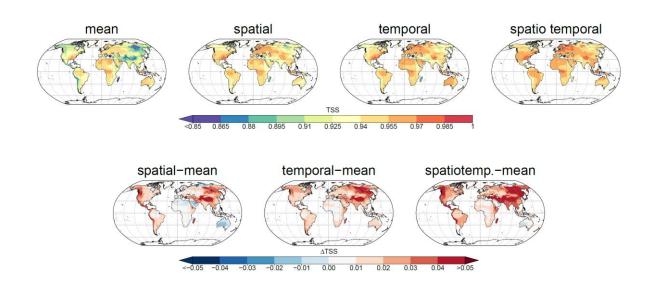


Fig 4. Spatial variation in mean TSS values per grid cell and TSS differences between models using different predictor groups. The upper row illustrates TSS averaged for all mammals, reptiles, and amphibians modeled for the four models using different predictor groups. The lower row illustrates the averaged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

272 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

302

2012).

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

- 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
- 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.

339 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 <u>http://doi.org/YYYYYYY</u>

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353 Author contributions:

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.
implemented the species distribution modelling, B.S. and D.N.K. analyzed the results further,
D.N.K. wrote the first draft of the manuscript, and all authors contributed equally to the
revisions.

358 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

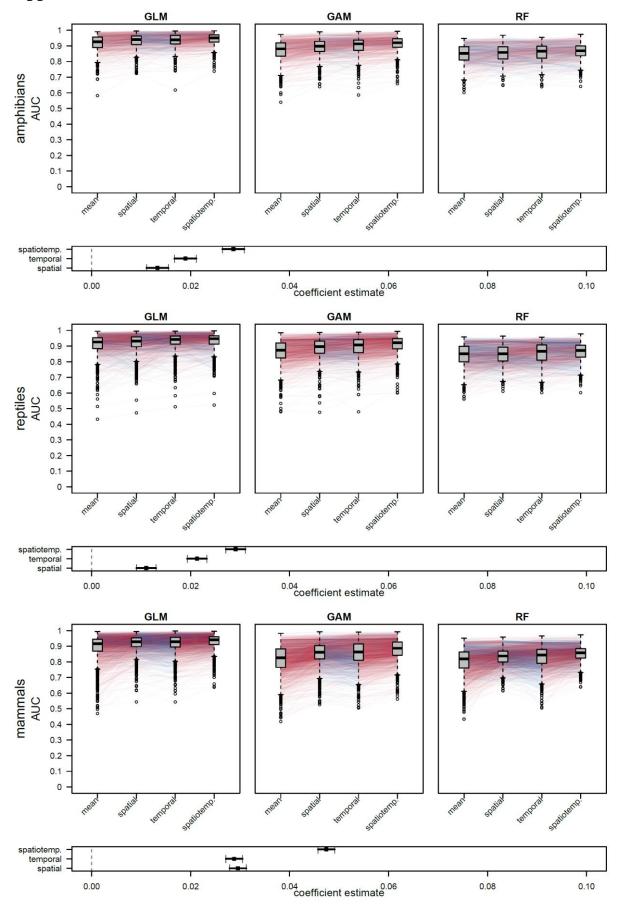


Fig. S1. Comparison of the performance of three different SDM algorithms (GLM = 525 526 Generalized linear model, GAM = Generalized additive model, RF = Random Forests) 527 calculated with four different sets of predictors for amphibians, reptiles, and mammals 528 measured by the Area Under the Curve (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.

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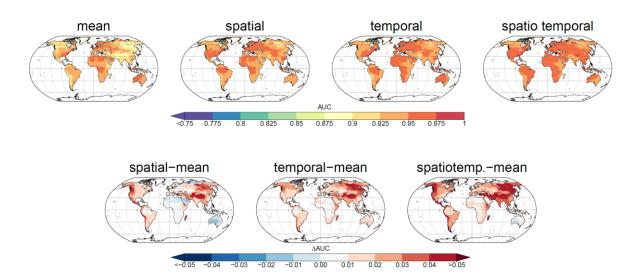


Fig S2. Spatial variation in mean AUC values per grid cell and AUC differences between models using different predictor groups. The upper row illustrates AUC averaged for all mammals, reptiles, and amphibians modeled for the four models using different predictor groups. The lower row illustrates the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

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