The impacts of climate variability on the niche concept and distributions of species

Emilio Berti[a,b,1], Benjamin Rosenbaum[a,b], and Daniel C. Reuman[c]

[a]EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, Leipzig, 04103, Germany

[b]Institute of Biodiversity, Friedrich-Schiller University Jena, Fürstengraben 1, Jena, 07743, Germany

[c]Department of Ecology and Evolutionary Biology and Center for Ecological Research, University of Kansas, Higuchi Hall, Lawrence, KS, 66047, USA

[1]To whom correspondence should be addressed. E-mail: emilio.berti@idiv.de

Contents

1 Abstract **2**

2 Significance statement **2**

3 Keywords **2**

4 Introduction **2**

5 Results **4**

6 Discussion **4**

7 Methods **6**

8 Acknowledgments **9**

1 Abstract

Inter-annual climate variability affects the long-term growth rate and thus the viability of populations. Despite the importance of climate variability, niche models and species distribution models (SDMs) typically do not account for it. This causes systematic biases in the projected distributions of species and can mislead conservation measures. Here, we use ideas from stochastic demography to quantify the effects of inter-annual climate variability on population performance and distributions of species, developing a new SDM framework which we call XSDM. The new framework expands the traditional deterministic notion of the fundamental niche, re-conceptualizing the niche to account for stochasticity. XSDM can be applied widely, requiring only occurrence data, e.g. from GBIF, and it shows superior performance to commonly-used SDMs in simulation studies. Using XSDM, we assessed the impacts of inter-annual climate variability on 10 North-American species chosen as illustrative examples. We found that climate variability reduces the potential distribution of the species on average by 26% and up to 57%. SDMs and niche concepts that do not incorporate variability cannot account for this reduction and can thus be strongly biased. Because climate change is altering not only average conditions, but also the frequency and intensity of extreme events, which are aspects of variability, it is paramount to better understand how climate variability influences the distributions of species in order to help mitigate future biodiversity losses due to climate change. Our new XSDM approach provides a new foundation for such a research program by helping re-orient niche theory to include stochastic effects.

2 Significance statement

Inter-annual climate variability influences populations' long-term viability and, therefore, species' distributional ranges. However, existing niche concepts and species distribution models (SDMs) typically do not account for such variability and therefore cannot accurately predict species' distributions. Here, we developed the new SDM framework "XSDM" that accounts for climate variability when assessing the ecological niche of a species and predicting its distribution. We tested XSDM using simulations, where it performs better than traditional SDMs. By applying XSDM to 10 example species, we found that climate variability impacts their distribution, reducing potential range by up to half. As global change alters climate variability, e.g., through increased frequency and intensity of extreme events, our new paradigm provides better tools for countering future biodiversity losses.

3 Keywords

Ecological niche model, Species distribution model, Climate variability, Stochastic demography, Environmental fluctuations.

4 Introduction

One of the main consequences of climate change is the modification of the distributional ranges of species, as species move to track altered conditions [1]. Redistribution of biodiversity has major conservation consequences, and can furthermore negatively affect ecosystem services, such as productivity and carbon storage, that are essential to human societies [2]. Therefore, effective efforts to determine how species do and will respond to climate change are urgently needed. To assist

with this challenge, a variety of species distribution modelling (SDM) approaches are commonly applied [3]. SDMs relate climatic conditions to the probability of observing a species, and have been used to estimate the current and future distributions of species. However, a major limitation of current SDMs and the niche ideas they are based on is they do not account for inter-annual climate variability, even though variability is known by demographers to play a crucial role in population dynamics and therefore probably also in species distributions [4, 5, 6]. Because climate change is altering climate variability, e.g. by modifying the intensity, frequency, and duration of extreme environmental events such as heat waves and floods [7, 8], addressing the shortcomings of current SDMs with respect to climate variability is crucial for mitigating the impacts of climate change on biodiversity. We here show that ignoring climate variability generates systematic biases in SDM projections of species' distributions that can mislead conservation strategies. And we provide a new SDM approach, based on a stochastic re-conceptualization of the fundamental niche, that effectively accounts for climate variability.

Inter-annual climate variability affects population dynamics by inducing variability in annual net rates of population growth ([9]; see Fig. 1 for an example). Importantly, the effects of climate variability on a population can be quantified using stochastic demography, a field of research which examines how the performance of the population is influenced by fluctuations in population vital rates [10]. A key concept of stochastic demography is the long-term stochastic growth rate (ltsgr), which helps describe the long-term viability of a population [10]. For example, for a population following the simple Lewontin-Cohen model [11],

$$p_{t+1} = \lambda_t p_t, \tag{1}$$

where t is the year, p_t the number of individuals of the population in year t, and λ_t the net growth rate in year t, the ltsgr is, approximately [12],

$$\text{ltsgr} = \log(\overline{\lambda}) - \frac{\text{Var}(\lambda)}{2\overline{\lambda}^2}. \tag{2}$$

Here, $\overline{\lambda}$ is the average growth rate and $\text{Var}(\lambda)$ is the variance of growth rate across the years. We use the natural logarithm here and throughout the paper. Eq. 2 illustrates how inter-annual climate variability can influence long-term population viability: higher climate variability induces elevated inter-annual variance of growth rate, thereby lowering ltsgr.

Though such ideas are elementary in stochastic demography, current SDMs usually rely on long-term climatic averages (also called climatological normals), which neglect inter-annual climate variability. Traditional ideas of the fundamental niche underlying common SDMs have also commonly been based on deterministic growth, e.g., the n-dimensional hypervolume of Hutchinson [13] is commonly operationalized by requiring that *average* environmental conditions be suitable for a *deterministic* population growth rate to be positive. Whereas some SDMs account for intra-annual climate variability, e.g. using measures of seasonality, such variability is quite distinct: annual growth rate may depend on intra-annual variability, but the ltsgr is influenced by inter-annual variability in annual growth.

Here, we show that inter-annual climate variability drastically impacts the distribution of 10 North-American species chosen as examples. We achieve this by developing a novel framework, called XSDM, that integrates concepts of stochastic demography into SDMs to quantify the influence of variability on distributions. XSDM does not require extensive demographic information, is computationally efficient, and relies on easily accessible data. We show that including inter-

annual climate variability is key to more effectively conceptualizing the niche and more accurately estimating the distributions of species.

5 Results

XSDM uses concepts from stochastic demography to infer the fundamental niche of a species from occurrence data and time series of climatic conditions, thereby obtaining the species' potential distribution. Inspired by important previous work [14, 15, 16], XSDM contains two modules (Fig. 2): 1) a demographic response model, where a *growth-environment function* describes how inter-annual variation in climate translates into variation in population net growth rate – this part of XSDM is used to compute the local ltsgr; and 2) an observation model, where a *detection-link function* is assumed to relate the local ltsgr to the probability of detecting the species. Crucially, XSDM directly quantifies the effects of climate variability on a species' distribution through the use of the ltsgr. During model fitting, parameters of both modules are jointly adjusted to maximize agreement between model-predicted and actual species detections. See Materials and Methods for details of how XSDM works.

We performed two extensive simulation studies with virtual species to assess to what extent XSDM could be used to accurately infer parameters, and to compare how XSDM performs relative to existing, commonly used SDMs (Materials and Methods). Model fitting of XSDM accurately recovered model parameters (Fig. S3) and the suitability for virtual species of each simulated habitat patch (Figs 3A, S4), with greater accuracy for larger sample sizes, as expected (Fig. 3B). Moreover, XSDM outperformed other commonly used SDMs (Figs 3C, S5), producing results that were both more accurate and less uncertain.

To highlight how climate variability can affect species' distributions and illustrate the potential applications of XSDM, we modelled the potential distribution of 10 species (1 bird, 1 insect, 3 mammals, 3 plants, and 2 reptiles) chosen from checklists of North America species (Materials and Methods). On average, inter-annual climate variability reduced the potential distribution of species by 26% (median = 23%). The strongest effect was for the reptile *Ophisaurus ventralis*, for which the distribution was reduced by 57% (Fig. 4). Of the species we examined, the grass *Solidago canadensis* was the least affected by climate variability, though its potential distribution was still reduced by 12%. Overall, these results highlight that inter-annual climate variability can substantially influence the geographic distributions of species.

6 Discussion

We showed that inter-annual climate variability strongly influences species' distributional patterns, though this influence has been largely ignored by standard SDMs. We proposed the novel framework XSDM to help resolve this limitation of SDMs and to quantify the current and future influence of climate variability on distributions. Key to these advances was the integration of theory from stochastic demography into niche and distribution modeling. Because XSDM takes into account stochastically fluctuating environments, our framework moves away from the deterministic view of the fundamental niche which has been common in past work, i.e., where the niche has been considered to comprise values of the average environment for which a deterministic growth rate is positive. Instead, our approach focuses on the sets of stochastic environments for which the

long-term stochastic growth rate is positive [14], and the locations in geographic space exhibiting such stochastic environments.

Several important studies have advocated for process-explicit SDMs based on demographic theory, and have helped inspire our work [17, 14, 9, 18, 15, 19, 20]. Keith et al. [21] and Eckhart et al. [22] showed that demographic approaches to SDMs can be constructed, and similar approaches were later used by others [23, 24]. But those models were both limited in their applicability to very extensively studied species and used deterministic demographic approaches that did not account for climate variability. Perez-Navarro et al. [5] included inter-annual variability in their model, showing that it likely plays a role in the distribution of *Pinus halepensis*. But their approach did not model demographic processes. Importantly, Pagel and Schurr [15] and Schurr et al. [16] proposed a research agenda integrating population processes into SDMs. Their framework has been very valuable, but is so data and computationally hungry as to be difficult to apply. Efficiency gains of XSDM relative to the method of [15] are due to the use of tools from stochastic demography, simplifying computations. For instance, the average time needed to fit an XSDM with GBIF data for one of our example species was circa 16 hours (minimum 43 minutes, maximum 3 days, 6 hours; Table S1). Less than 8 Gb of memory were required. It should be straightforward to run XSDM for numerous species on a typical computing cluster.

Karger et al. [25] included inter-annual variances of environmental variables as predictors in traditional SDMs. They showed that model performance was thereby only slightly improved, creating an apparent contrast with the large importance of climate variability we demonstrated. We interpret this contrast as arising because the models of [25] were traditional, non-process-based SDMs. Variance was used by their models as just another predictor which could be used to explain species' suitability. However, the influence of climate variability on population viability is known to be complex, having been quantified through much research in stochastic demography [10, 12]. It may not be possible to adequately account for this influence with the simple phenomenological models of standard SDMs, even when environmental variability data are provided to those models.

Several potential improvements to XSDM seem worth considering in future work, including the following. First, the (st)age-structured demography of a species could be explicitly modelled using stochastic matrix models [10], allowing for different environmental sensitivities for different (st)ages. Second, the "infinitesimal variance" and temporal autocorrelations of population vital rates, both known to demographers to influence population viability [10, 26], could straightforwardly be incorporated. Third, it may be possible to integrate into the XSDM model the potential for the species to exhibit local demographic adaptations. For example, the optimum climate, $\vec{\mu}$, for a species could be modelled to change gradually along a geographic gradient. Fourth, additional factors that do not relate to climate could be allowed to influence the observation model, e.g. habitat type and human land use layers. The simple version of XSDM provided here was sufficient for an initial demographic investigation of the importance of climatic variability to species distributions, but extensions such as those listed above may be necessary for some future applications. Importantly, the XSDM framework allows for future researchers to test whether each extension is statistically warranted.

The fundamental niche, N_F, of a species has been defined [13, 27, 28] as the set of all points in an n-dimensional environment space for which a species growth rate is positive. Specifically, in the language used by Soberón and Peterson [27, 28], this is the Grinnellian fundamental niche and the environmental variables are taken to be scenopoetic [29]. One useful lesson emerging from our results is that the n-dimensional environment space ought to also include axes relating to inter-annual environmental variation through time, as well as the traditional axes representing mean

values of environmental variables; but we think a slightly more abstract conceptualization will be even more useful for guiding future research. Consider, instead, the n-dimensional environment space to be the space of all $p \times T$ matrices representing time series of the p relevant environmental variables over a period of T years; so $n = pT$. Thus, points in environment space are entire temporal trajectories of environmental variables over an appropriate time period for the species (Fig. 2E.2). This viewpoint is similar in some ways to that of [28], though, importantly, their viewpoint is intra-annual and ours is inter-annual. The species growth rate we then use to delineate N_F is the ltsgr (Fig. 2E.5). Our pT-dimensional space projects onto a smaller, $2p$-dimensional space representing the means (the climatological normals commonly used in SDMs) and variances (as used, for example, by Karger et al. [25]) of all p environmental variables, so includes all the information that the smaller space includes. But the larger space also retains information about, for instance, temporal autocorrelations, known to stochastic demographers to be important for population viability (see above). Compressing the environment space from a pT-dimensional space to a smaller $2p$-dimensional space throws away information that may help quantify species performance under actual conditions. This is another viewpoint on the explanation, above, of why the models of Karger et al. [25] only showed slight performance improvements with the inclusion of variance information, whereas our models demonstrated the substantial importance of variability for species' range.

Understanding when and how climate variability influences the distribution of species is important not only for fundamental scientific understanding, but also for helping mitigate the effects of global change. Climate change includes alterations to the frequency and intensity of extreme events [7, 8]; and these are aspects of climate variability. We showed that climate variability can strongly influence species' geographic distributions. Therefore, climate change may alter species distributions not only through its effects on average values of climate variables [1], but also through its effects on their temporal variability. Prior work indicates that changes in climate variability may cause greater changes in species ltsgrs than do changes in climate means [30, 31]. Through XSDM, we here developed the foundations for an improved understanding of these two distinct pathways by which climate change may alter species distributions.

7 Methods

XSDM dynamical model

Populations were modelled in a location by the Lewontin-Cohen model [11],

$$p_{t+1} = \lambda_t p_t, \tag{3}$$

where p_t is the population at time t, and λ_t is the net population growth rate at time t, which depends on aspects of the environment in the location at t. This modelling choice effectively assumes that, for the purposes of determining baseline environmental suitability of a location, density dependence can be neglected; similar to an assumption that a habitat is suitable if a population can reliably increase there from rarity. This is analogous to the invasion criterion used in invasion biology [32]; and assumptions of this kind are common for conservation applications of stochastic demography [10, 33, 34]. See Discussion for future extensions of XSDM that could incorporate population (st)age structure.

The viability of the population is assessed by the long-term stochastic growth rate (ltsgr), which

is

$$\text{ltsgr} = \overline{\log(\lambda)} \tag{4}$$

for eq. 3 [10]. The overbar denotes a mean over time. See introductory texts for background on the ltsgr [10, 33, 34]. The approximation eq. 2 was used to clarify concepts, but the exact expression above was used elsewhere. The "infinitesimal variance," $\text{Var}(\log(\lambda_t))$, could also straightforwardly be incorporated into XSDM, but, for simplicity, was not used here.

XSDM demographic response model

The growth-environment function, describing how λ_t is influenced by environmental factors, will typically depend on several environmental variables (e.g., λ_t may depend on both spring temperature and rainfall). To simplify the presentation of main ideas, the univariate case only is presented here, with the multi-variate case in SI. For our univariate growth-environment function, we used an "asymmetric bell-shaped" curve with niche parameters $\theta_1 = \{\mu, \sigma_L, \sigma_R, \lambda_{\max}\}$, i.e.,

$$\lambda_t = \lambda_t\left(e_t, \theta_1\right) = \lambda_{\max} \exp\left(-\frac{1}{2}\left(\frac{e_t - \mu}{\sigma(e_t, \mu)}\right)^2\right), \tag{5}$$

where μ is the optimal climatic condition for growth and $\sigma(e_t, \mu)$ determines the shape of the curve via $\sigma(e_t, \mu) = \sigma_L$ if $e_t \leq \mu$, and $\sigma(e_t, \mu) = \sigma_R$ if $e_t > \mu$. This function can produce a large variety of shapes, e.g. symmetric ($\sigma_L = \sigma_R$) and asymmetric ($\sigma_L \neq \sigma_R$) bell shapes as well as saturating ($\sigma_R >> 1$) responses (Fig. S1).

XSDM observation model

To relate the ltsgr to the probability of detecting the species, we used a sigmoid detection-link function with parameters $\theta_2 = \{b, c, p_d\}$, i.e.,

$$P(X = 1 | \text{ltsgr}, \theta_2) = \text{logit}^{-1}\big(b(\text{ltsgr} - c)\big) p_d \tag{6}$$

where $\text{logit}^{-1}(x) = 1/(1 + \exp(-x))$, $p_d \in (0, 1)$ controls the maximum possible probability, c controls the location of the center of the sigmoid, and b controls its sensitivity to the ltsgr.

Identifiability

XSDM is "structurally non-identifiable" [35] when parameterized by μ, σ_L, σ_R, $\lambda_{\max}$, b, c, and p_d; i.e., these parameters cannot all simultaneously be determined by fitting. Parameter-space dimension was reduced in a manner that addressed this problem and permitted practical application of the model. The reduced space involved the parameters $\theta_3 = \{\mu, \tilde{\sigma}_L = \sigma_L/\sqrt{b}, \tilde{\sigma}_R = \sigma_R/\sqrt{b}, \tilde{c} = b(c - \log(\lambda_{\max})), p_d\}$. The re-parameterized model was both structurally identifiable and "practically identifiable" [35] for our datasets. Details in SI.

Model fitting

A likelihood function was formulated using the constituents above, and the parameters θ_3 were then jointly estimated using a Bayesian framework implemented using the R and Stan statistical computing platforms. See details in SI, but the basic logic of the likelihood function can be understood,

in its main principles, through these steps: 1) compute the time series λ_t in a location using local climate time series and the growth-environment function, eq. 5 (or its multivariate generalization, SI); 2) use eq. 4 to calculate the ltsgr from the λ_t; and 3) use the ltsgr to compute the probability of detecting the species in the location via eq. 6. The overall likelihood is a product, across all detection locations and (pseudo-)absences for the species, involving these probabilities (SI). It is a function of the parameters θ_3. We used uninformative priors for all parameters (SI).

Habitat suitability and distributions

Outputs of fitting include samples from the posterior distribution of parameters. For the simulations (see below), we used parameter point estimates $\hat{\theta}_3$ together with a combination of eq. 5 (or its multivariate generalization, see SI), eq. 4, and eq. 6 (see SI for details) to quantify modelled climatic suitability for each location for a species. For empirical species, instead, we computed habitat suitability for each location using 300 posterior samples and averaged those values; though results obtained in that way differed very little from simply using $\hat{\theta}_3$. XSDM therefore provides a suitability score for each location in geographic space, incorporating the influence of inter-annual climate variability. Thresholds can be applied to provide potential geographic distributions; we used the threshold that maximized the sum of sensitivity and specificity [36].

Quantifying the influence of climate variability

An important feature of XSDM is that it can directly quantify the influence of inter-annual climate variability on habitat suitability and the species' distribution. This is achieved by comparing the suitability maps or distributions described above with maps or distributions obtained in the same way but starting from artificial environmental time series which are constant at the mean value. The same posterior sample or estimated parameters $\hat{\theta}_3$ are used, and, for the distribution, the same threshold is used. We call this procedure Δ-XSDM.

Simulations

To assess whether XSDM could be used to accurately infer parameter values, including assessing aspects of the bias, variance, and consistency of the parameter estimators provided by XSDM, we simulated data for virtual species using XSDM itself as the data-generating model and then fitted XSDM to these datasets. We simulated climate time series of 40 years, comparable with available climate data, and explored four different scenarios differing in average climate and in its spatial heterogeneity (SI). For each scenario, we ran 1,000 simulations, varying the total number of presence records. XSDM performed similarly in the four scenarios, so we reported only one scenario in the main text. See SI for additional details.

We ran an additional set of simulations to compare the performance of XSDM against traditional SDM approaches, namely: generalized additive models, maximum entropy, generalized linear models, and random forests. For these simulations, we generated presences and absences from the average population density. Specifically, the populations of the virtual species were modelled following:

$$p_{t+1} = \frac{\lambda_t \cdot p_t}{\frac{\lambda_t \cdot p_t}{K} + 1} \tag{7}$$

where p is the number of individuals, K the carrying capacity of the population ($K \sim \mathrm{U}(100, 200)$) and $p_0 \sim \mathrm{U}(5, 15)$. We then calculated the probability of detection using the average population

density across the time period instead of the ltsgr in eq. 6 ($b = 1$, $c = 0$, and $p_d = 1$). The probability of detection was used in a Bernoulli process to generate presences and absences, which were used as input for all SDMs. We compared the predictive performance of SDMs by plotting the predicted suitability against the true suitability. See SI for additional details.

XSDM for 10 species in GBIF

We used XSDM to estimate suitability maps and potential distributions of 10 species (Table S1), chosen as illustrative examples from checklists of North American species (SI for details). GBIF data were filtered to include only occurrences recorded after 1979 and with a spatial uncertainty ≤ 5 km. The remaining occurrence records were additionally filtered using the R package *CoordinateCleaner* [37] to remove spurious records. We sampled pseudo-absences up to 100 km distance from the minimum convex polygon containing all filtered presence records, assumed to be the maximum dispersal range of the species. We kept at most one presence and pseudo-absence record per grid cell. The number of pseudo-absences was set to three times the number of presences, i.e. we fixed the prevalence of all species at 0.25.

For climatic predictors we used detrended annual time series of bioclimatic variables related to temperature and precipitation, derived from CHELSA [38]: average annual temperature (BIO01); mean temperature of the warmest quarter (BIO10); mean temperature of the coldest quarter (BIO11); total annual precipitation (BIO12); precipitation of the wettest quarter (BIO16); and precipitation of the driest quarter (BIO17). For each species, we ran nine competing models using the multivariate version of XSDM and all combination of one temperature and one precipitation variable. We then selected as the best model the one with the highest expected log pointwise predictive density (ELPD) using leave-one-out cross-validation [39]. Posterior samples (see Table S2 for their point-estimates) were extracted from the best model and used to project the distribution of the species in North America, both with and without the influence of climatic variability (see the Δ-XSDM method described above).

Software and data availability

All analyses were performed in the R v4.2.2 and Stan v2.33.0 programming languages [40, 41] at a resolution of $5 \times 5\,\text{km}^2$ using Albers conic equal-area projection (EPSG:5070). Code and data to reproduce our results can be found at `https://zenodo.org/doi/10.5281/zenodo.13378593`.

8 Acknowledgments

The authors thank Jorge Soberón and Town Peterson for helpful discussions. EB and BR acknowledge the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (DFG, FZT 118, 202548816). DCR was partly supported by The Alexander von Humboldt and James S McDonnell Foundations, the California Department of Fish and Wildlife, US National Science Foundation grants DEB-PCE 2414418 and BIO-OCE 2023474, and the University of Kansas.

Author contribution

EB and DCR conceived of the idea and planned the analyses. EB, BR, and DCR performed the analyses. EB and DCR wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript.

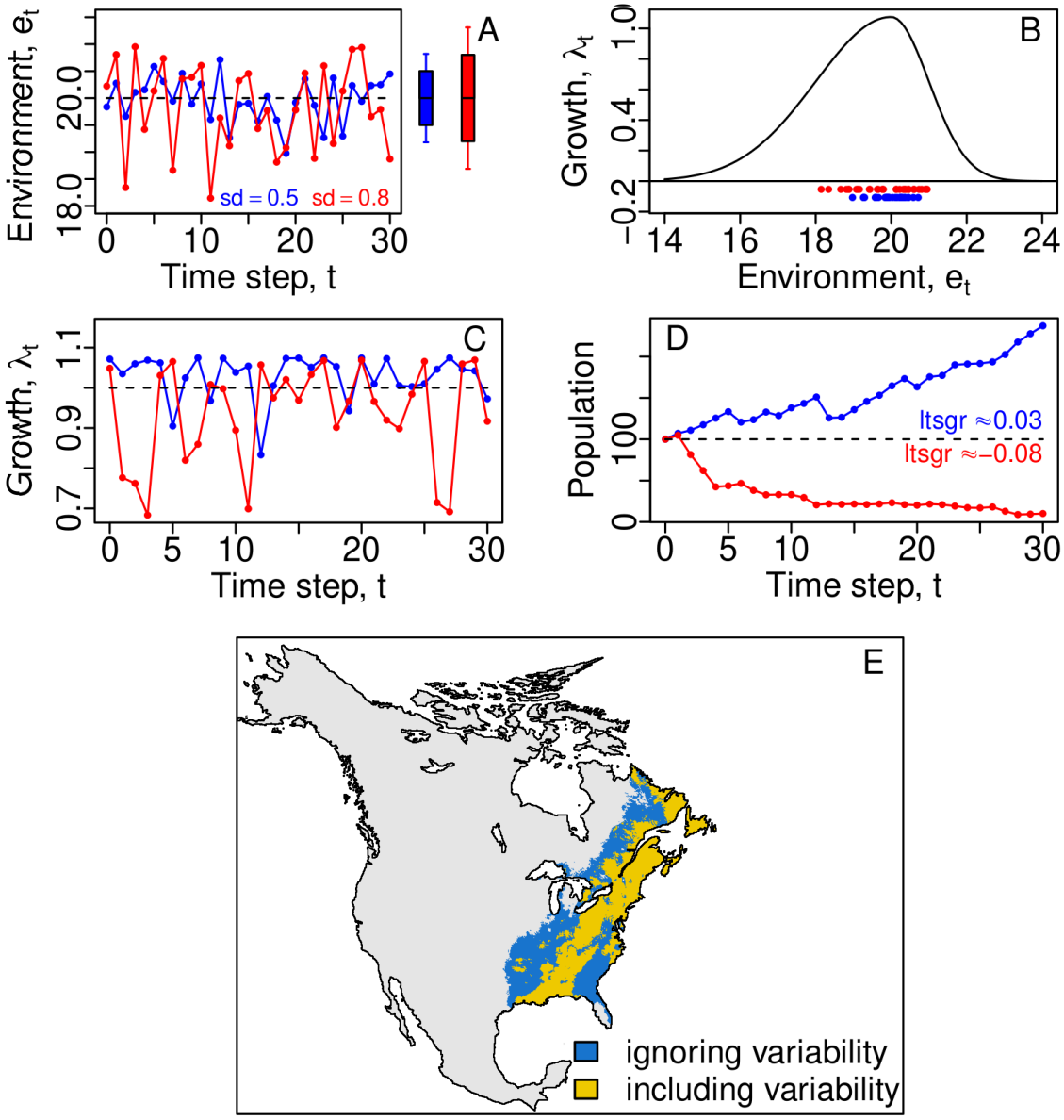

Figure 1: Illustration of how inter-annual environmental variability can alter population viability and how stochastic demography can account for this effect. Two distinct locations (red and blue points/lines in panels A-D) have identical average environmental conditions, $\overline{e_t}$, but different degrees of inter-annual variability (A; sd = standard deviation). If the annual net growth rate, λ_t, of a population is a function of the environment as in panel B, then differences in environmental variance can produce large differences in the time series of growth rates (C), which lead to dramatic differences in survival outcomes of the population (D). The long-term stochastic growth rate (ltsgr), a concept borrowed from stochastic demography, accurately captures population viability in these

two scenarios. The projected environmental suitability can drastically differ when accounting, or not, for inter-annual variability (E). In E, we use a virtual species with dynamics $p_{t+1} = \lambda_t p_t$, with λ_t influenced only by the average precipitation of the driest quarter and with niche parameters (see eq. 5) $\mu = 500$mm, $\sigma_L = 100$mm, $\sigma_R = 2 \cdot 10^7$mm, and $\lambda_{\max} = 1.1$. The species was considered to have occurred (yellow) in cells where ltsgr > 0 (eq. 4); whereas not accounting for variability, $\lambda_t(\overline{e_t}) > 1$, gave dramatically different results (combined blue and yellow).

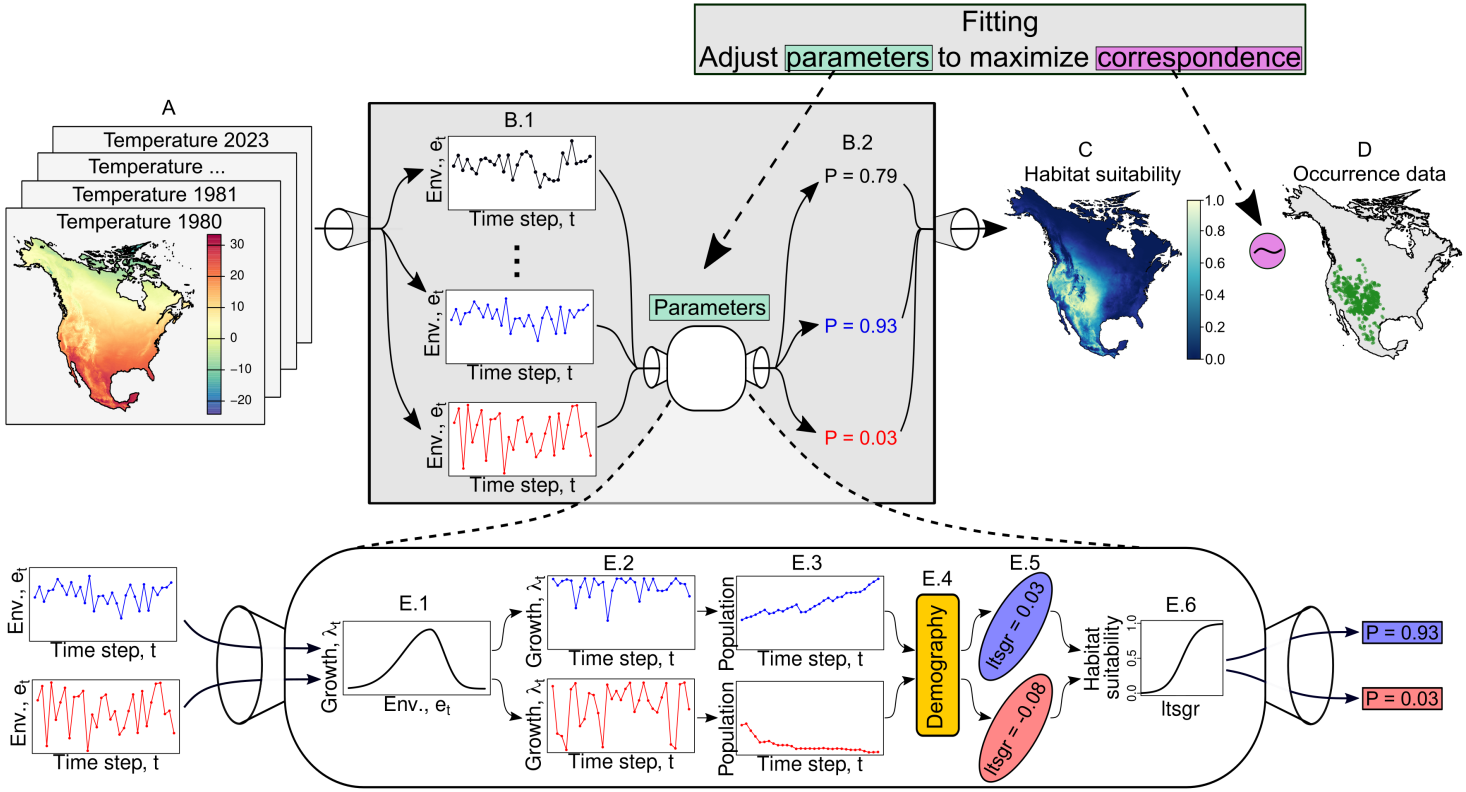

Figure 2: Conceptual illustration of how XSDM works. XSDM takes as input maps of annual values or one or more climate variables (A). It then breaks these into separate time series for each location (B.1) and passes them to the demographic response model, specifically to the growth-environment function (E.1), which describes the influence of environment (e_t) on annual net growth rate (λ_t) and has adjustable parameters. This generates time series of growth rates (E.2), which are related to population growth trajectories (E.3). Demographic theory (E.4) is used to calculate the ltsgr (E.5), which incorporates the influence of climate variability. Larger values of ltsgr correspond to better growth conditions and imply higher habitat suitability, modeled by the observation model through a detection link function with adjustable parameters (E.6). Habitat suitability values (B.2) are aggregated across all locations to produce a suitability map (C). The two demographic and observation models are fitted jointly in XSDM, adjusting the parameters of the growth-environment and the detection link functions (E.1 and E.6) in order to maximize the match between predicted suitability (C) and occurrence data (D). This figure, for pictorial simplicity, assumes throughout that one climate variable only, e_t, controls λ_t; but multiple variables are typically used.

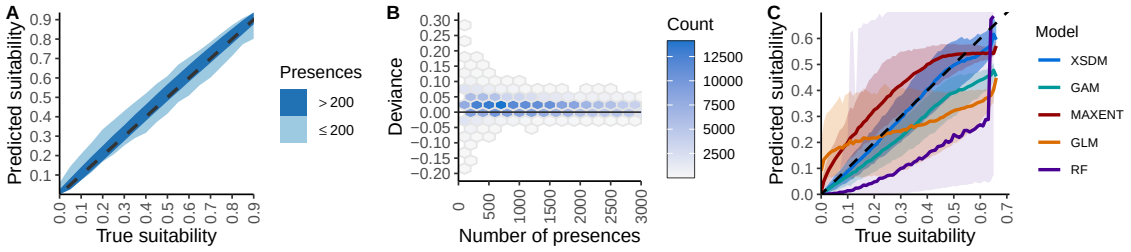

Figure 3: Results of simulations assessing XSDM's ability to infer true habitat suitability (A, B), and its performance compared to other SDMs (C). **A**) XSDM accurately predicts the true climatic suitability of habitat patches for virtual species. Shades show the 95% quantile range of predicted suitability values. The dashed black line is the 1:1 line indicating perfect predictions. Colors show two levels of sample size, highlighting that XSDM performs very well with a number of presences $\geq$ 200 but can also perform well for fewer presences. See Fig. S3 for recovery-accuracy results for particular model parameters. **B** "Deviance" in XSDM predictions, i.e. the difference between predicted and true habitat suitability, decreases with sample size, as expected. The intensity of blue color shows the number of virtual habitat patches from simulations in each hexagon. **C**) XSDM outperforms commonly used SDMs, namely generalized additive models (GAM), Maxent, generalized linear models (GLM), and random forests (RF). See Materials and Methods and SI for details.

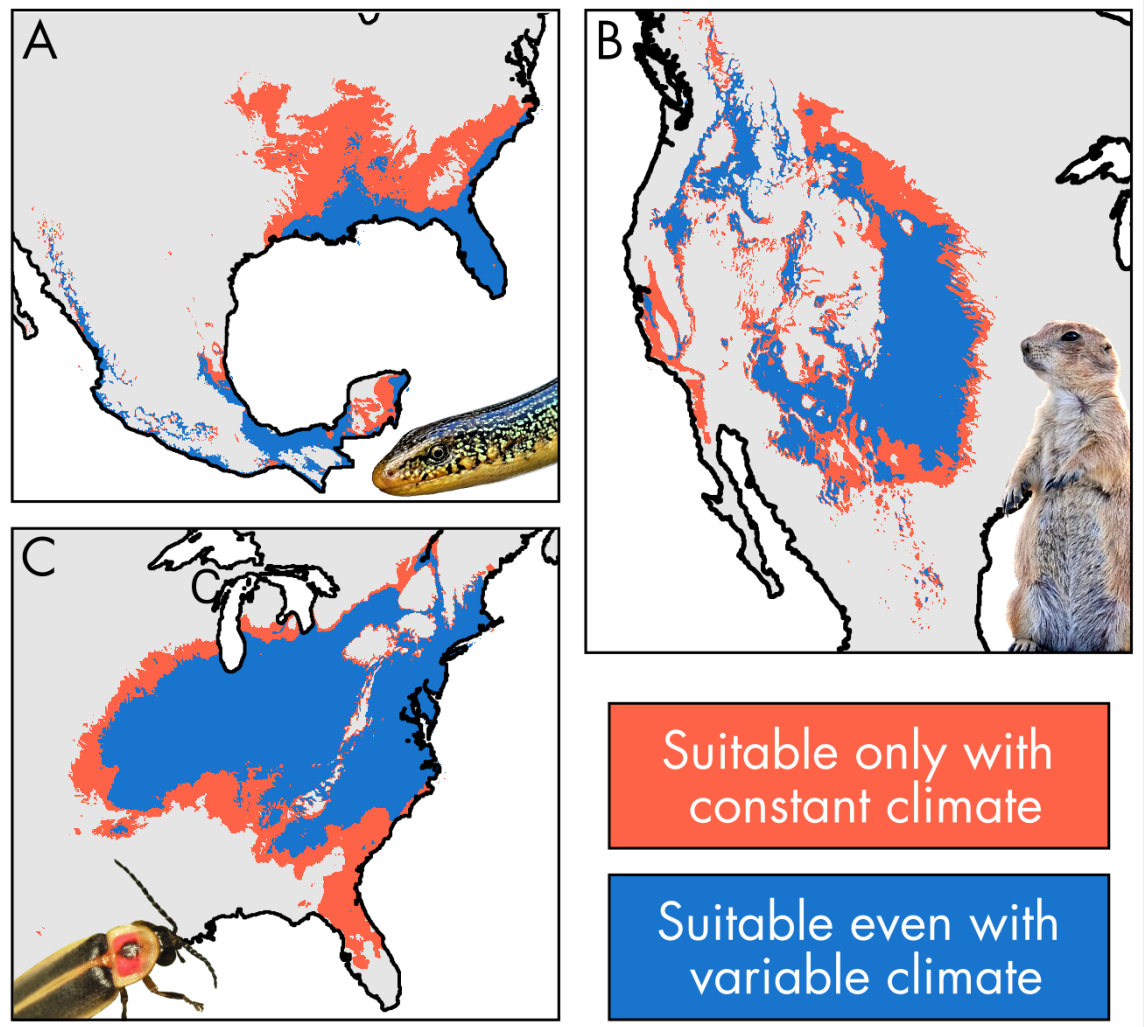

Figure 4: Projected XSDM distributions for the Eastern glass lizard (*Ophisaurus ventralis*; A), the black-tailed praire dog (*Cynomys ludovicianus*; B), and the common Eastern firefly (*Photinus pyralis*; C). Colors show the projected species distribution when accounting for inter-annual climate variability (blue) and when neglecting it (the union of the blue and red, so that red shows the reduction in range from variability). Original animal photos from Wikimedia Commons by Ignioapathy, Cephas, and Katja Schulz (CC BY-SA).

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