

Interactions between species attributes explain population dynamics in stream fishes under changing climate

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Citation: Chevalier, M., L. Comte, P. Laffaille, and G. Grenouillet. 2018. Interactions between species attributes explain population dynamics in stream fishes under changing climate. *Ecosphere* 9(1):e02061. 10.1002/ecs2.2061

Abstract. Species responses to climate change have been shown to vary in both direction and magnitude. Understanding these idiosyncratic responses is crucial if we are to predict extinction risk and set up efficient conservation strategies. The variations observed across species have been related to several species attributes including intrinsic traits such as physiological tolerances or life-history strategies but also to niche characteristics (e.g., niche breadth [NB], niche position [NP]). However, although previous studies have successfully linked species attributes to population dynamics or range shifts, few have considered synergistic effects to explain responses to climate variations. Here, we assessed whether five species attributes (fecundity, thermal safety margin, trophic position [TP], NB, and NP) explained interspecific differences in four parameters influencing population dynamics of 35 stream fish species at the French scale. We used Bayesian N-mixture models to estimate posterior distributions of the growth rate, the strength of density dependence, and the influence of both mean temperature and temperature variability on populations for each species. We then used phylogenetic generalized least squares (PGLS) models to investigate the influence of species attributes and their interactions on interspecific differences in each of the four parameter driving population dynamics. The percentage of variance explained by the PGLS models was relatively high (around 40% on average), indicating that species attributes are good predictors of species population dynamics. Furthermore, we showed that the influence of these single attributes was mediated by other attributes, especially NP and TP. Importantly, we found that models including interaction terms had greater support over simple additive models in explaining interspecific differences in population dynamics. Taken together, these results point to the importance of considering the interplay between species attributes in unraveling the mechanisms involved in population dynamics and understanding the vulnerability of species to global change.

Key words: Bayesian inference; climate mean; climate variability; density dependence; growth rate; N-mixture models; trait-based approach; water temperature.

Received 21 July 2017; revised 13 November 2017; accepted 15 November 2017. Corresponding Editor: Robert R. Parmenter.

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INTRODUCTION

Over the past decades, many studies have investigated the potential risks to biodiversity

posed by climate change (Buckley and Kingsolver 2011). While many studies have investigated range shifts in response to recent climate change (Walther et al. 2002), mounting empirical

evidence also suggests that subtle changes within the distributional ranges of species (i.e., on populations) are likely (Sæther et al. 2008). However, how multiple populations of a given species are affected by climate change throughout its distribution range remains unclear, and large uncertainties still exist about spatial variation in species responses to ongoing and projected climate changes across their range (Moritz and Agudo 2013).

Many attempts have been made to link recent population trends to species attributes (Dalglish et al. 2010, Bowler et al. 2015). Despite the large variability in species responses across taxonomic groups, these studies revealed that specialists, warm-intolerant species, and poor-disperser species have responded most strongly to climate warming (Buckley and Kingsolver 2011). For instance, in common breeding bird species in France, Jiguet et al. (2007) found that populations of habitat specialists and species with a low thermal maximum showed the highest rates of declines. Likewise, there is evidence that dietary requirements are associated with interspecific differences in recent bird population trends (Reif et al. 2010). However, despite the implications of population trends for local extirpation and extinction processes, we still know little about the impact of climate on population dynamics across different species (Bowler et al. 2015).

Several studies have shown that species population dynamics tend to be spread along a slow-fast continuum of life-history variations (Sæther and Bakke 2000, Goodwin et al. 2006, Linnerud et al. 2013). Species characterized by short generation time, early age at maturity, large clutch size, and small body size (i.e., r-selected species) tend to display high growth rate, strong density dependence at low population size, and be more strongly influenced by environmental stochasticity. This contrasts with K-selected species that generally display the opposite characteristics. With respect to environmental drivers, previous comparative studies mainly focused on environmental stochasticity, quantified as the residual variance in population dynamics models. However, climate can also influence populations in a deterministic way (Knape and De Valpine 2011), such that explicitly incorporating climatic variables within statistical models and relating their influence to species attributes may help in

understanding interspecific responses to climate change.

Such responses are likely to depend not only on changes in mean climatic conditions but also on changes in their variability (Morris et al. 2008). For instance, changes in environmental variability can amplify population fluctuations and thus increase extinction risk (Bjørnstad and Grenfell 2001). Life-history traits have been used to explain idiosyncratic responses to changes in environmental variability (Morris et al. 2008, Dalglish et al. 2010). However, the influence of the mean and the variability of climatic variables has generally been studied separately, whereas changes in environmental variability can alter or even reverse the effects of changes in mean conditions (Lawson et al. 2015).

To date, the utility of trait-based approaches for predicting species vulnerability to climate change has been questioned due to their low predictive power (Angert et al. 2011). However, recent research suggests that the relationships previously identified between species vulnerability and species traits might actually be mediated by other species attributes. For instance, Davies et al. (2004) showed that ecological specialization and low population density could act synergistically to elevate extinction risk above that expected from their simple additive effects. Likewise, Pearson et al. (2014) demonstrated that species vulnerability to climate change is likely to depend on the interaction between life-history traits and niche characteristics, such that range-restricted species with long generation times are more vulnerable. This indicates that considering interactions between species attributes may improve the predictive power of trait-based approaches in the context of global changes (Brook et al. 2008).

Here, we used 4976 population time series from 35 stream fish species and built hierarchical N-mixture models to estimate four key parameters of population dynamics. Specifically, we estimated for each species the growth rate, the strength of density dependence, and the influence of both the mean and the variability of water temperature on population abundance. We then used a phylogenetic comparative approach to test whether various species attributes related to life-history strategies, trophic behavior, specialization, and habitat preferences explained

interspecific differences in the four parameters influencing species population dynamics. We chose these five attributes because they have previously been related to population dynamics and responses to climate change (e.g., range shifts) in several taxonomic groups (Voigt et al. 2003, Thuiller et al. 2005, Sunday et al. 2014). Our study aimed to expand previous research by exploring whether considering the interaction between these species attributes provided additional insights regarding the determinants of interspecific differences in population dynamics.

METHODS

Dataset

Population time series.—Our dataset was extracted from the fish database of the French National Agency for Water and Aquatic Environment (Onema; <http://www.image.eaufrance.fr>). These annual data were collected between 1982 and 2012 by electrofishing during periods of low flow. Fish were identified at the species level, counted, and released (for further details, see Poulet et al. 2011). From this database, we selected time series (1) that were composed of at least 10 yr with less than four consecutive missing years and (2) during which the sampling protocol remained the same (mean time series length = 16.41 yr; SD = 3.53 yr). This allowed us to maximize the number of populations and species included in the analyses while ensuring model convergence. This selection process provided us with 4976 time series corresponding to 35 species (the number of population time series ranged from 10 to 392 per species), and located across 583 sites throughout France (Appendix S1: Fig. S1).

Temperature time series.—Daily air temperature data from 1982 to 2012 were provided by Météo France (SAFRAN). This database is a regular 8-km grid, in which the daily air temperature was calculated for each cell by optimal interpolation of climatically homogeneous zones (for further details, see Le Moigne 2002). Daily water temperature data measured from 2009 to 2012 at 135 sites located throughout France (Appendix S1: Fig. S1) were provided by the Onema. To predict daily water temperature at all fish sampling sites, we performed a calibration–evaluation procedure using the 135 sites for

which we had information on both air and water temperatures using a random-forest model (Breiman 2001; see Appendix S2 for details). From the predicted daily water temperature data, we calculated the mean (meanT) and variance (varT) between consecutive sampling occasions at each sampling site. Both variables were subsequently used as covariates in the population dynamics models to determine whether inter-annual changes in the mean and in the variability of water temperatures influenced population abundance.

Species attributes.—1. *Niche breadth (NB) and niche position (NP).*—Niche breadth and NP were estimated using an outlying mean index analysis (Doledec et al. 2000) based on nine habitat and climatic variables (Appendix S3: Fig. S1). Niche breadth represented species realized NB (i.e., the range of their abiotic tolerances) calculated as the standard deviation (SD) of the environmental space used by each species along the main axes of the analysis. Niche position described the position of the species realized niche along the upstream–downstream gradient and was calculated using the coordinates along the first axis of the analysis, with high values indicating upstream species.

2. *Thermal safety margin (TSM).*—Thermal safety margin was calculated as the difference between the lethal temperature measured under laboratory conditions and the mean water temperature experienced by the species during the survey (i.e., how far species lived from their physiological thermal limits; Deutsch et al. 2008).

3. *Trophic position (TP).*—Trophic position was calculated as the average weight of the preys consumed multiplied by the trophic level of each prey and was extracted from Fishbase (Froese and Pauly 2017). Trophic position ranged from 2.70 to 4.42 and was treated as a continuous variable with high values representing top predators.

4. *Fecundity (FE).*—Fecundity (number of oocytes/yr) was extracted from Fishbase and from the literature (Kottelat and Freyhof 2007) and was log-transformed prior to analyses to meet normality assumptions.

Statistical analyses

Population dynamics model.—Population count data are usually affected by observation errors, as

individuals detected during a sampling event are just a fraction of the total number of individuals present. To take these errors into account, we fitted hierarchical N-mixture models to each species dataset (Dail and Madsen 2011, Hostetler and Chandler 2015). These models are a class of state-space models described by two equations: an observation equation that describes how the latent process is observed (in this case imperfect detection) and a state equation that defines the evolution of the process through time. In their original formulation (Royle 2004), N-mixture models require surveys from several different sites and, more importantly, replication of surveys within some subset of sites, while the population at the site is closed to emigration, immigration, death, and birth. This closure assumption strongly restricts the use of N-mixture models because many sampling programs do not use replicated surveys. Recently, Sólymos et al. (2012) relaxed the closure assumption and showed that detection probabilities and expected abundance can be separated based only on count data collected from single visits, provided that detection probabilities and expected abundance can be modeled with covariates, with at least one distinct continuous covariate for each process. The model presented here is based on this framework.

Let the vector $N_t = (N_{1,t}, N_{2,t}, \dots, N_{n,t})$ represent the actual number of individuals, and let the vector $X_t = (X_{1,t}, X_{2,t}, \dots, X_{n,t})$ represent the number of individuals detected at time t and site i . The observation process is described by a binomial distribution:

$$X_{i,t} \sim \text{Bin}(N_{i,t}, p_{i,t})$$

where $p_{i,t}$ is the probability of detection at site i and time t . On the logit scale, $p_{i,t}$ was assumed to vary linearly depending on a set of covariates:

$$p_{i,t} = \varphi + \gamma_1 \times \text{Alt}_i + \gamma_2 \times \text{Day}_{i,t} + \gamma_3 \times S_{i,t}$$

where φ is the intercept, γ is the vector of coefficients related to each covariate, Alt_i is the altitude at site i , $\text{Day}_{i,t}$ is the date of sampling (expressed in Julian day), and $S_{i,t}$ is the sampling area at site i and time t . By doing so, we assumed that the probability to observe any individual of a given species (i.e., the detection probability) varies depending on its habitat requirements (e.g., low vs. high altitude), its period of activity (e.g., early

vs. late in the season), and the sample size. Given that these covariates tend to correlate with river flow, which is known to influence detection probabilities (Schloesser et al. 2012), we are confident about the relevance of our assumptions.

Because abundance is often over-dispersed with respect to the Poisson distribution, we used a negative binomial distribution to model population abundance at site i and time t :

$$N_{i,t} \sim \text{Negbin}(E(N_{i,t}), r)$$

where $E(N_{i,t})$ is the expected value of $N_{i,t}$ under a deterministic stock-recruitment Ricker model (Ricker 1958) and r is the over-dispersion parameter. We chose the Ricker model over alternative models based on a preliminary analysis showing that more than 96% of the time series showed greater support for this model over three alternative models (Appendix S4: Fig. S1). We further assumed that populations are closed to immigration and emigration processes such that $N_{i,t}$ is only dependent on $N_{i,t-1}$, according to a Markovian process. Thus, the population process was expressed as:

$$E(N_{i,t}) = \left[N_{i,t-1} \exp \left(\begin{array}{l} \rho_i - \eta_i \times \frac{N_{i,t-1}}{S_{i,t-1}} + \alpha_i \\ \times \text{mean}T_{i,t} + \beta_i \times \text{var}T_{i,t} \end{array} \right) \right] \times \frac{S_{i,t}}{S_{i,t-1}}$$

where ρ_i corresponds to the expected population growth rate when environmental covariates have no effect on population abundance and $N_{i,t-1}$ equals zero (i.e., no effect of intrinsic and extrinsic factors), η_i is the strength of density dependence per unit area, α_i is the influence of mean water temperature, and β_i is the influence of temperature variability on population abundance, at site i and time t . $S_{i,t}/S_{i,t-1}$ is a correction factor accounting for unequal sampling areas between consecutive years and was treated as an offset in the model. The parameters ρ_i , η_i , α_i , and β_i were all assumed to follow normal distributions with means μ_ρ , μ_η , μ_α , and μ_β and SDs σ_ρ , σ_η , σ_α , and σ_β , respectively. All covariates were standardized to improve model convergence.

Bayesian inference and model fit.—We adopted a Bayesian approach in combination with a Monte Carlo Markov chain (MCMC) algorithm to obtain the joint posterior distribution of model parameters (Clark and Bjørnstad 2004). We chose

independent and uninformative priors for all hyper-parameters. Specifically, we used normal distributions centered on zero with SDs of 100 for the vector of parameters $[\mu, \sigma, \gamma, \phi]$ and a uniform distribution on the range $[0; 100]$ for the parameter r . For the initial abundance at each site, $N_{i,1}$, we used a Poisson distribution with the mean equals to the average number of individuals detected at that site (\bar{X}_i). For each species, we generated three chains of length 70,000 and discarded the first 30,000 iterations as burn-in. For each chain, we chose initial values in different regions of the parameter space and sampled them every 40 iterations. Convergence was visually assessed and confirmed using the Gelman and Rubin statistic with a threshold fixed to 1.1 (Gelman and Rubin 1992).

To evaluate the performance of our model, we used posterior predictive checks (Gelman et al. 1996). Specifically, for each iteration of the MCMC sampling, we computed the posterior predictive distribution of replicated data $X_{i,t}^{\text{rep}}$. These replicated data account for the variability in parameter estimates and may be regarded as the expected data if the model was correct; that is, $X_{i,t}^{\text{rep}}$ is a replication that should be similar to the observed data ($X_{i,t}$) if the model has a good fit. We based the posterior predictive checks on three test quantities (denoted T), computed for both datasets (i.e., observed and replicated). The first test quantity (T_X) was based on the whole dataset and aimed to compare the value of $X_{i,t}$ to the value of $X_{i,t}^{\text{rep}}$ to identify potential outliers. The two other test quantities were summary statistics representing broad features of the data: the average ($T_{\bar{X}}$) and the range ($T_{r(X)}$) of population abundance. We used the range instead of the SD because the latter is sensitive to deviation from normality. For each test quantity, the realized value for the observed data $T(X)$ was compared to the posterior distribution of the values obtained for the replicated data $T(X^{\text{rep}})$ as

$$P = \frac{\sum_{i=1}^S (T(X_i^{\text{rep}}) \geq T(X))}{S}$$

where S is the number of samples in the posterior distribution. The quantity P represents the so-called Bayesian P value and measures how extreme the observed data are relative to the

replicated ones with values close to 0.5, indicating an overall good fit of the model. Here, the different test quantities ($\text{mean}(T_X) = 0.59$, $\text{mean}(T_{\bar{X}}) = 0.51$, $\text{mean}(T_{r(X)}) = 0.38$) confirmed a good performance of the models for all the species (Appendix S4: Table S1).

Relating species attributes to population dynamics.— To test the relationship between the five species attributes and the four parameters influencing population dynamics (i.e., μ_p , μ_{η} , μ_{σ} , and μ_{β}), we used a phylogenetic generalized least squares (PGLS) comparative method (Freckleton et al. 2002). This approach controls for the non-independence among species by adjusting a variance-covariance matrix based on the λ statistic (Pagel 1999), which varies from 0 (i.e., no link with species evolutionary history) to 1 (i.e., evolution under a Brownian model of evolution). Pagel's λ were estimated under a restricted maximum-likelihood approach using a dated, fully resolved phylogeny reconstructed from complete mitochondrial genomes (Comte et al. 2014).

We considered all possible multi-predictor PGLS models that included three terms or fewer ($n = 25$) to avoid over-fitting (Knappe and De Valpine 2011). We considered first-order interactions, in combination with their main effects, only for models including two variables ($n = 10$). After including the null model, we ended up with 36 models (Appendix S5: Table S1 for a full list of the models). The predictors were transformed to z -scores to standardize the slope coefficients (β), and pseudo- R^2 were calculated for each model following Nagelkerke (1991). We evaluated the candidate models using the Akaike information criterion adjusted for small sample size (AICc) and selected all the models that were contained within a ΔAICc of two from the model with the lowest AICc (Burnham and Anderson 2002). From the set of selected models, we calculated model-averaged slope coefficients using the zero method (Burnham and Anderson 2002) that is recommended when the aim is to identify the main factors influencing the response variable (Nakagawa and Freckleton 2011). Thus, for a given predictor, a value of zero was substituted into the models where the predictor was absent and averaging was performed over all selected models with the estimated means weighted by the Akaike weight of the model (w_i ; Johnson and

Omland 2004). Note that this averaging procedure was possible here because all the predictors were standardized prior to analysis, thus providing comparable estimates of slope coefficients, even when interaction terms were present in the model (Grueber et al. 2011). Variance inflation factors revealed no problems of collinearity among the predictors (range = 1.00–1.69; Kutner 2005).

To take into account uncertainties in the estimation of the four parameters influencing species population dynamics, the procedure described above (from model construction to model averaging) was repeated for each sample ($N = 3000$) of the posterior distribution (hereafter called “runs”). As a result, we obtained a posterior distribution of averaged slope coefficients from which we calculated 95% highest posterior density (HPD) intervals. All predictors presenting a 95% HPD interval not overlapping zero were considered to have an effect on the dependent variables.

To evaluate the importance of interactions between species attributes in determining interspecific differences in the four parameters driving species population dynamics, we compared the w_i of the models including or not an interaction term using one-way ANOVAs. We focused on w_i instead of R^2 because the former is sensitive to the number of covariates included in the models, whereas the latter is not. Prior to analyses, w_i

were log-transformed to meet normality assumptions.

The different steps of our approach are summarized in Fig. 1. All analyses were performed within R (R Core Team 2014) using the packages randomForest (Breiman 2001), ade4 (Dray and Dufour 2007), ape (Paradis et al. 2004), nlme (Pinheiro et al. 2015), and MuMIn (Barton 2015). For all MCMC sampling, we used JAGS 3.3.0 (Plummer 2003) run through the program R and the packages R2jags (Su and Yajima 2013) and rjags (Plummer 2014). The JAGS model code is provided in Appendix S4.

RESULTS

Model estimates revealed large interspecific differences in the four parameters influencing fish population dynamics (Fig. 2a), even among closely related species (Fig. 2b). Species-specific estimates of other model parameters are presented in Appendix S4: Fig. S2. Over the 3000 runs, 6922 models were selected to explain interspecific differences in the growth rate (mean $R^2 = 0.45$; SD = 0.09) and 8050 models to explain a variation in the strength of density dependence (mean $R^2 = 0.38$; SD = 0.13). Regarding the influence of climatic variables on population abundance, 6745 models were selected for the mean temperature (mean $R^2 = 0.40$; SD = 0.18) and 6337 models for the temperature variability

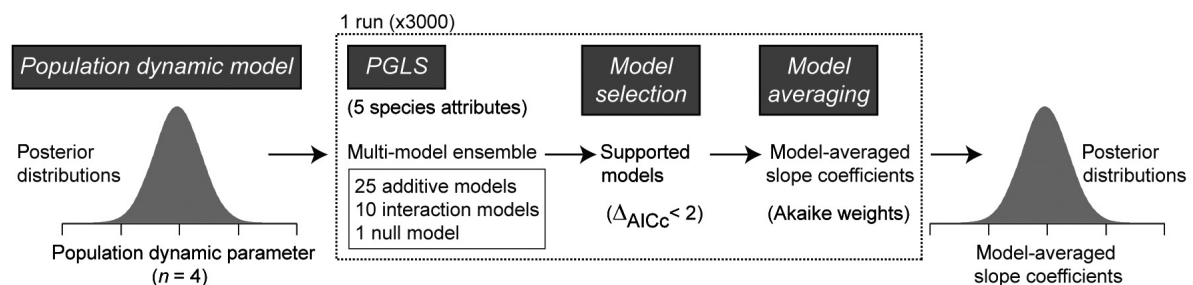


Fig. 1. Description of the procedure used to account for the uncertainty in (1) the estimation of the population dynamic parameters and (2) the model selection procedure used to relate population dynamic parameters to species attributes. Each population dynamic parameter was described by its whole posterior distribution (3000 samples). The model selection procedure was conducted on each sample of the associated posterior distribution, generating a distribution of model-averaged slope coefficients for each parameter. More specifically, we fitted 36 phylogenetic generalized least squares models (25 additive models, 10 models including interaction terms, and the null model), selected all the models that were contained within a ΔAICc of two relative to the best model (models having similar support), and performed model averaging on the selected models.

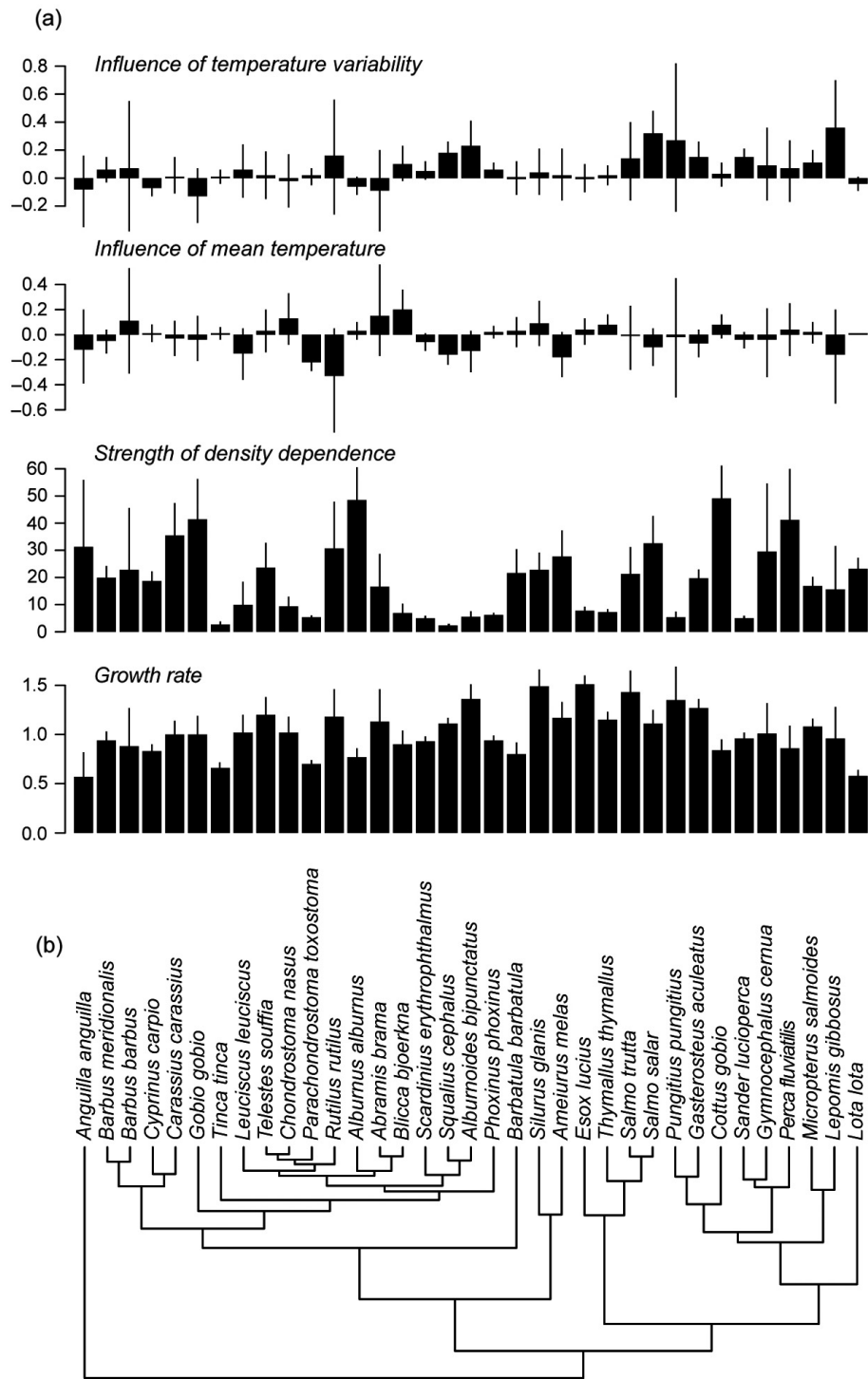


Fig. 2. (a) Posterior summaries (median and 95% highest posterior density intervals) of the four parameters influencing population dynamics of the 35 fish species and (b) phylogeny used to control for the non-independence among species within the phylogenetic generalized least squares models.

(mean $R^2 = 0.44$; $SD = 0.17$; Appendix S5: Table S1).

Single-attribute effects

Trophic position, NP, and FE were included in 53%, 83%, and 76% of the selected models explaining among-species differences in the growth rate, respectively (Appendix S5: Table S1). After averaging model coefficients, these three attributes were all negatively related to the growth rate (Fig. 3a). Fecundity and NP were also important predictors of among-species differences in the strength of density dependence and included in 79% and 29% of the selected models, respectively (Appendix S5: Table S1). After averaging model coefficients, FE was positively related to the strength of density dependence, whereas a negative relationship was found with NP (Fig. 3b). Regarding the influence

of climatic variables on population abundance, we did not find any particular effect of species attributes after averaging model coefficients (Fig. 3c, d). However, some attributes were included in a large percentage of the selected models, thus suggesting that they have the potential to explain among-species differences, although with uncertainty regarding the direction of the effects. For instance, TSM and NP were included in 49% and 54% of the selected models explaining differences in species responses to changes in mean temperature, respectively (Appendix S5: Table S1), with a tendency toward a positive effect of the former and a negative effect of the latter (Fig. 3c). Regarding species responses to temperature variability, TP and TSM were included in 65% and 54% of the selected models, respectively (Appendix S5: Table S1), and were both negatively related to

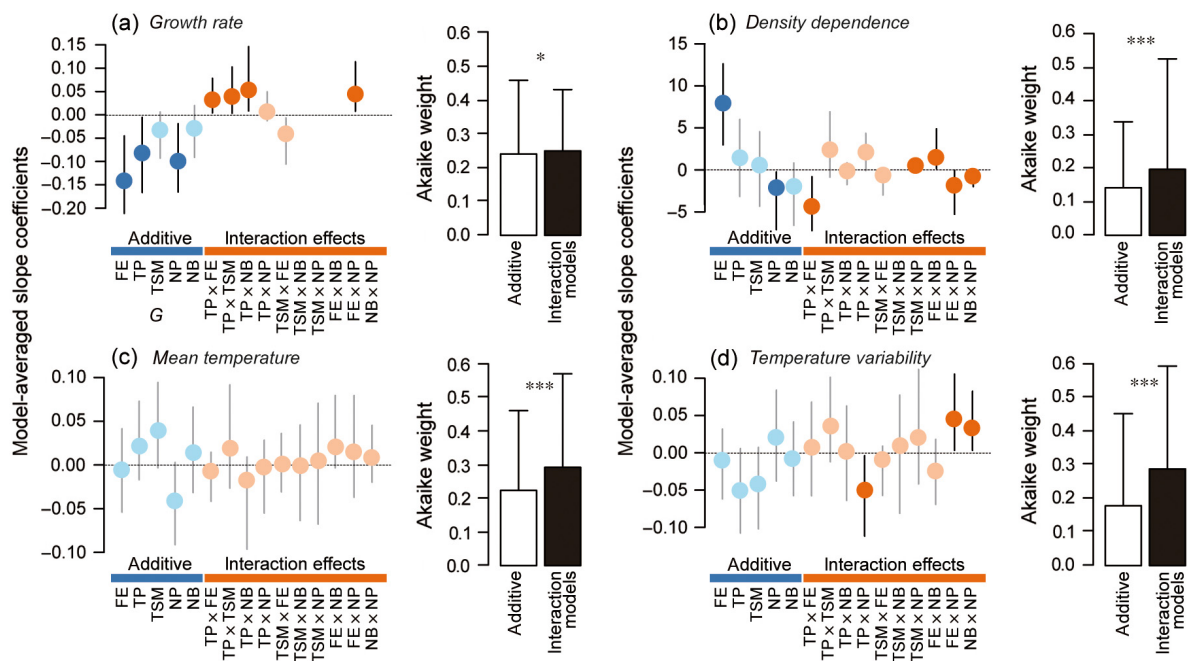


Fig. 3. Posterior summaries of the distributions of model-averaged slope coefficients obtained from the selected phylogenetic generalized least squares models performed on the (a) growth rate, (b) strength of density dependence, (c) influence of mean temperature, and (d) influence of temperature variability. For each coefficient, dots represent the median of the posterior distribution and vertical bars the associated 95% highest posterior density (HPD) intervals. Darker colors indicate coefficients for which 95% HPD intervals do not overlap zero. The right part of each panel corresponds to the mean and standard deviation of the Akaike weights of the models including only single or additive effects (additive) or including interaction terms (interaction models; * $P < 0.05$; *** $P < 0.001$). FE, fecundity; TP, trophic position; TSM, thermal safety margin; NP, niche position; NB, niche breadth.

this parameter, albeit 95% HPD intervals slightly overlapped zero (Fig. 3d).

Synergistic effects

Despite uncertainty in the effect size estimates, synergistic effects appeared important to explain interspecific differences in fish population dynamics (Fig. 3). In particular, models including interaction terms significantly outperformed the other selected models for the growth rate ($P < 0.05$; Fig. 3a), the strength of density dependence ($P < 0.001$; Fig. 3b), and the influence of both mean temperature ($P < 0.001$; Fig. 3c) and temperature variability ($P < 0.001$; Fig. 3d) on population abundance.

For the growth rate, five interaction terms had a 95% HPD interval not overlapping zero and all of them included either TP or FE (Fig. 3a). The interaction between NP and FE was particularly important and was included in more than 24% of the selected models (Appendix S5: Table S1). For the strength of density dependence, five interaction terms had a 95% HPD interval not overlapping zero and three of them included either FE or NP (Fig. 3b). Similar to the growth rate, the interaction between FE and NP was the most represented interaction among the selected models (13% of the selected models; Appendix S5: Table S1). Regarding species sensitivity to changes in mean temperature, none of the selected models clearly outcompeted the others (Appendix S5: Table S1) and none of the interaction terms had a 95% HPD interval that did not overlap zero (Fig. 3c). By contrast, three interaction terms had 95% HPD intervals not overlapping zero regarding the species responses to temperature variability (Fig. 3d). NP was included in all interaction terms and mediated the effect of TP, TSM, and NB. The interaction between TP and TSM also seemed important and was frequently included in the selected models (11%; Appendix S5: Table S1). There was, however, a considerable uncertainty in the direction of the effects after averaging the model coefficients (95% HPD interval overlapping zero; Fig. 3d).

Trophic position was implicated in the strongest interactions identified for the growth rate, the strength of density dependence, and the influence of temperature variability on population abundance (Fig. 4). The strongest interaction was observed between TP and NB for the growth

rate (Fig. 4a), between TP and FE for the strength of density dependence (Fig. 4b), and between TP and NP for the influence of temperature variability on population abundance (Fig. 4c).

DISCUSSION

In this study, we demonstrated the potential of trait-based approaches to explain interspecific differences in the population dynamics of 35 stream fish species over the last 20 yr. Importantly, we found that models considering interactions among species attributes displayed the highest level of support, thus suggesting that accounting for non-additive effects of species attributes may improve our ability to predict population dynamics under climate change.

Single-attribute effects

In accordance with previous findings (Fowler 1981, Blackburn et al. 2009), we found that top predators tend to display a lower growth rate than species occupying lower trophic position, thus strengthening the evidence that those species might be less resilient to environmental changes. Interestingly, we also found a negative relationship between fecundity and population growth rate but a positive relationship between fecundity and the strength of density dependence. This result contrasts with previous studies that considered a linear continuum of life-history strategies (Saether and Engen 2002, Bjørkvoll et al. 2012), and may be explained by the fact that life-history strategies in teleost fishes are best described by a triangular model (Winemiller 1992). According to this model, species with a high fecundity are “periodic” strategists, leaving in periodic, yet predictable environments that favor the establishment of density-dependent processes. Furthermore, because periodic strategists delay maturation to improve adult survival during periods of suboptimal environmental conditions (i.e., bet-hedging strategy), they typically display low population growth rates (Rose et al. 2001, Winemiller 2005).

Our results also indicate that downstream species tend to display a higher growth rate and a stronger density-dependent regulation than upstream species. This finding is consistent with studies conducted at the intra-species level (Carmona-Catot et al. 2011), showing that

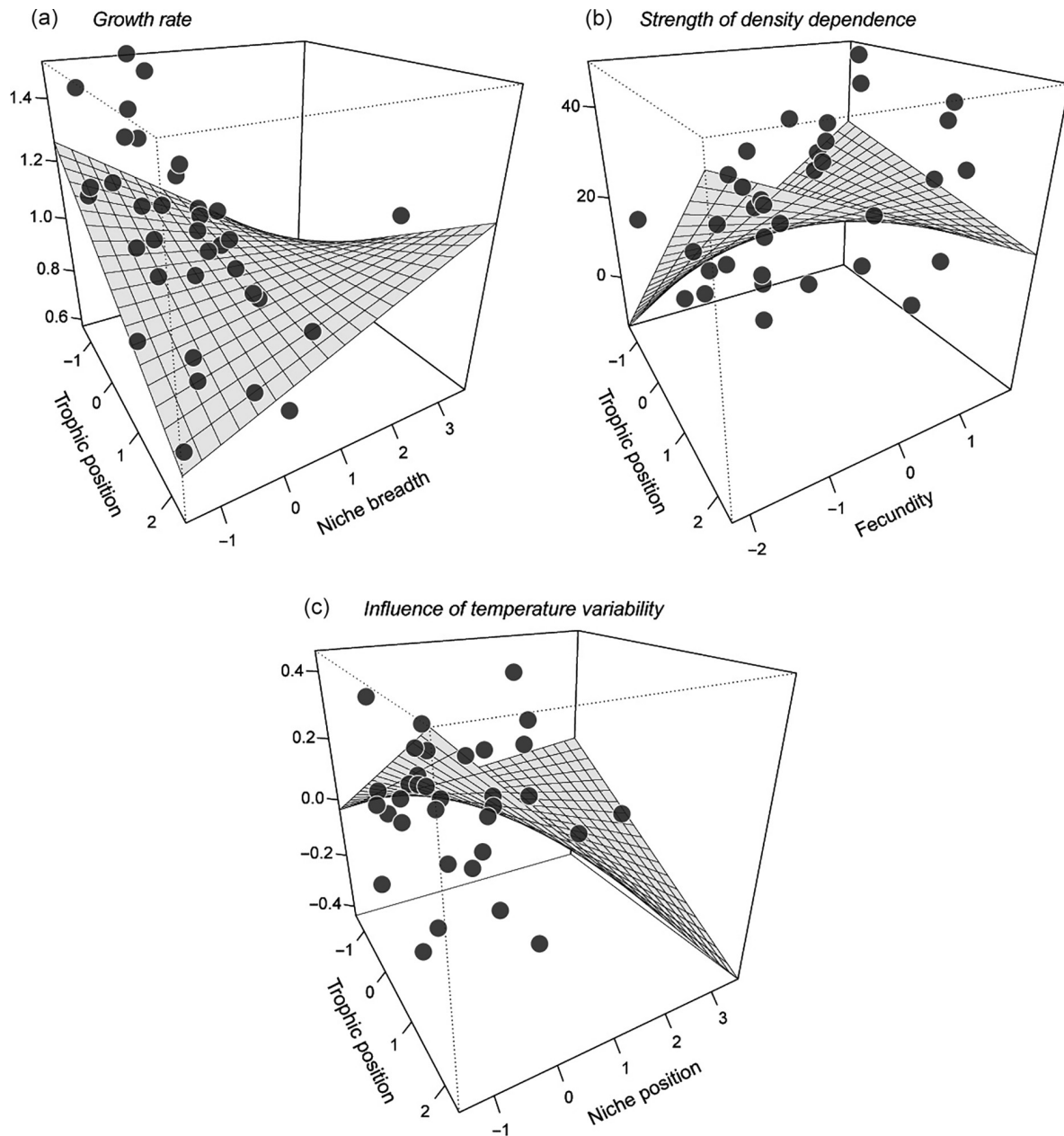


Fig. 4. Illustration of the strongest interactions between species attributes in predicting the (a) growth rate, (b) strength of density dependence, and (c) influence of temperature variability on population abundance. The three-dimensional surfaces were drawn from model-averaged coefficients. The points are the median values of species-specific population dynamic parameters calculated from their posterior distribution.

populations located in lower reaches have higher growth rate relative to upstream populations. This result also parallels the latitudinal gradients found in birds and associated with gradual variations in environmental conditions (Sæther et al.

2008). In riverine environments, species located in downstream areas experience warmer and more stable conditions that favor high reproductive success and stronger competition for resources (Yamahira and Conover 2002).

We found that species attributes could explain a considerable amount of variations in the way species respond to changing climatic conditions, despite some uncertainty regarding the direction of the effects. For instance, we found a tendency for species displaying low thermal safety margins to be negatively influenced by changes in mean temperature but positively influenced by changes in temperature variability. Although the effect of mean temperature has been well described and suggests that species with low thermal safety margins may face an increased extinction risk in the future (Deutsch et al. 2008), the effect of temperature variability is less documented. Environmental variability has been shown to either increase or decrease the growth rate, and theoretical studies suggest that the direction of the effects actually depends on the shape of the relationship (i.e., concave or convex) between the growth rate and the environment (Lawson et al. 2015). Accordingly, when the population growth response is concave, environmental variability is expected to decrease the growth rate. Note, however, that the negative effect of temperature on the population growth rate does not necessarily imply that these species are declining. Indeed, a high population growth rate combined with a positive influence of the mean temperature can compensate the negative effect of temperature variability, ultimately resulting in positive demographic trends (see also van de Pol et al. 2010). This phenomenon called “demographic compensation” has been used to explain complex patterns of range shift in many species (Doak and Morris 2010, Vilellas et al. 2015).

We also found a tendency for upstream species to be negatively influenced by the increase in temperature, thus confirming previous findings showing that cold-water species are more sensitive than warm-water species to global warming (Comte et al. 2013). Finally, we found that top predators tend to be more negatively influenced by increased temperature variability than species displaying a lower trophic position. Given that predator species are at the top of the food-web, this negative effect may be explained by an increase in the variability and availability of resources, propagating through the food-web by bottom-up effects (Soudijn and de Roos 2017). Overall, the patterns reported here suggest that considering several population dynamic

parameters instead of only population trends provides additional insights regarding the response of species to climatic factors.

Synergistic effects

Despite the increasing recognition that synergistic interactions between species attributes could help to understand species responses to climate change, few studies have explicitly considered them (Davies et al. 2004, Davidson et al. 2009). Here, we found that models integrating interaction terms showed greater support (i.e., higher Akaike weights) relative to other models, thus supporting the idea that interactions between species attributes provide additional insights regarding interspecific differences in population dynamics. We also showed that considering these interactions could help to identify the influence of species attributes that may not have been detected otherwise. For instance, although not significant when considered in isolation, NB appeared to mediate the effects of other attributes on species responses to changes in temperature variability. Niche breadth has already been shown to be an important determinant of species range shift (Angert et al. 2011), population trends (Julliard et al. 2004), and extinction risk (Olden et al. 2008, Pearson et al. 2014) as well as to act synergistically with other attributes (Jeppsson and Forslund 2014).

Our results further provide evidence that species position along the upstream–downstream gradient can mediate the effects of species attributes on population dynamics. Similarly, trophic position was involved in a number of important interactions. Previous studies based on experiments (Petchey et al. 1999) or field surveys (Lurgi et al. 2012) provided contrasted results on the role of this particular attribute on range expansion or extinction risks, highlighting the need for further studies to improve our understanding of trophic sensitivity to climate change. Overall, our results strongly suggest that NP and TP are important predictors of interspecific differences in population dynamics and should be incorporated in trait-based studies, when possible.

Future developments

Our hierarchical N-mixture model was based on several simplifying assumptions. First, we

assumed no migration, thus considering extinction and colonization events as simple observation errors. However, if extinction and colonization events have a strong effect on the dynamics of populations, this would result in an underestimation of detection probabilities. In our study, the estimated detection probabilities were quite large for most species (Appendix S4: Fig. S2), thus suggesting that these events were not dominating fish population dynamics. Estimating migration rate in population dynamics has proved challenging and is usually possible only through the use of integrated population models (Abadi et al. 2010), which combine different sources of data (e.g., count data and capture–mark–recapture data) for inference. Recently, Hostetler and Chandler (2015) proposed an extension of the N-mixture model developed by Dail and Madsen (2011) to incorporate a migration parameter to deal with individual gains or losses, not related to local population dynamics. However, in their model, migration was considered constant through space and time, thus implicitly assuming that all populations experience the same migration rate. Given that populations within the distributional range of species are likely to experience source–sink dynamics (Pulliam 1988), this assumption may lead to incorrect estimates of population dynamic parameters. Accounting for migration in population dynamic models is difficult and clearly deserves further attention given its influence on populations through colonization/extinction dynamics (Abadi et al. 2010).

Second, we assumed no age-specific effects because the age structure of the populations was unknown. Age-structured populations can display delayed density dependence, due to competition between age classes, which if ignored, can wrongly be interpreted as direct density dependence (Lande et al. 2006). This can be particularly problematic in comparative analysis including species with varying age structure (Festa-Bianchet et al. 2003). However, we found evidence of delayed density dependence in only 2.5% of the population time series using a Box–Jenkins procedure (Turchin 1990) and found that this proportion did not vary significantly across species ($P = 0.12$). This suggests that our estimation of density dependence may be comparable across species.

Information on age classes would nonetheless be critical if we want to understand the demographic mechanisms through which climate influences populations and should be incorporated in population dynamic models when possible (van de Pol et al. 2010).

Third, we investigated the relationship between population dynamics and species attributes using a PGLS approach based on posterior distributions obtained from Bayesian models. An alternative approach would have been to incorporate all species within the same model and directly relate population dynamics parameters to species attributes. However, beyond the considerable increase in model complexity and computation time, model comparison is also somewhat difficult to accomplish within a Bayesian framework (Dorazio 2016). Nonetheless, future studies specifically interested in the relationship between population dynamics and species attributes could use a single model incorporating all species for inference. Variable selection may then be performed directly into the model, for instance, by using shrinkage priors (Li and Pati 2017).

Fourth, by considering one fixed value of species attribute for each species, we implicitly assumed that interspecific variation was larger than intraspecific variations. Although this assumption might be reasonable for most species (Blanck and Lamouroux 2007), considering intraspecific variations may certainly help to refine the inferences drawn from trait-based models. This is, however, a great challenge because such data are often difficult to obtain at large spatial scales and for many populations (Moran et al. 2016). Similarly, we focused on the average values of population dynamic parameters estimated from several populations, but these parameters are likely to vary spatially within the distributional range of species (Williams et al. 2003, Sæther et al. 2008). Whether populations are positively or negatively affected may depend on both their location (Matías and Jump 2014) and intrinsic species characteristics (Comte et al. 2014). It would therefore be interesting to determine the extent to which differences in population dynamics located at different extremes of species range limits are mediated by different combinations of attributes.

Fifth, the random-forest approach used to predict water temperature at the sampling sites may also represent a non-negligible source of uncertainty. Although the hindcasting procedure revealed a very good performance of the model and no spatial bias in the predictions (Appendix S2), the inherent uncertainty in model predictions might have decreased the statistical power of N-mixture models and bias coefficient estimates (Stoklosa et al. 2015). Although the high predictive performance indicates that this issue is unlikely to have a strong influence on our results, uncertainty in explanatory variables should be considered when possible. This may be easily achieved within our framework by using an appropriate prior distribution (e.g., normal distribution with mean and variance extracted from the random-forest approach).

Other potential areas for future development include the inclusion of non-linear effects as well as non-thermal climate change-related variables. For instance, we assumed a linear and additive influence of the mean and the variability of water temperature on the growth rate. Considering non-linear effects along with interactions between the mean and the variability of environmental variables undoubtedly represents exciting research avenues (Lawson et al. 2015) and clearly deserves further exploration. Similarly, we only considered the influence of water temperature, whereas river flow is also an important driver of fish population dynamics (Lamouroux and Capra 2002). Accounting for hydrological variables may provide additional insights on species sensitivity to climate change, especially regarding the relative contribution of the mean and the variability of flow conditions.

To conclude, our results suggest that although trait-based approaches represent a promising avenue to identify species that will be the most at risk from climate change (Pacifi et al. 2015), species responses should not be studied on a trait-by-trait basis, but instead by addressing the interplay between species attributes. The high R^2 values obtained in this study suggest that trait-based approaches could be used to forecast population dynamics for rare or difficult-to-sample species for which such information is lacking. This is interesting because these species represent most of Earth biodiversity and are often of particular conservation concerns.

ACKNOWLEDGMENTS

We are indebted to the French National Agency for Water and Aquatic Environment (Onema) for providing fish data and Paul Acker for stimulating discussions on Bayesian modeling. We also thank the CALMIP group, in particular Nicolas Renon for computational resources. EDB laboratory was supported by “Investissement d’Avenir” grants (CEBA, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41).

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