

Integrating mechanistic and correlative niche models to unravel range-limiting processes in a temperate amphibian

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Abstract

Insights into the causal mechanisms that limit species distributions are likely to improve our ability to anticipate species range shifts in response to climate change. For species with complex life histories, a mechanistic understanding of how climate affects different lifecycle stages may be crucial for making accurate forecasts. Here, we use mechanistic niche modeling (NicheMapR) to derive “proximate” (mechanistic) variables for tadpole, juvenile, and adult *Rana temporaria*. We modeled the hydroperiod, and maximum and minimum temperatures of shallow (30 cm) ponds, as well as activity windows for juveniles and adults. We then used those (“proximate”) variables in correlative ecological niche models (Maxent) to assess their role in limiting the species’ current distribution, and to investigate the potential effects of climate change on *R. temporaria* across Europe. We further compared the results with a model based on commonly used macroclimatic (“distal”) layers (i.e., bioclimatic layers from WorldClim). The maximum temperature of the warmest month (a macroclimatic variable) and maximum pond temperatures (a mechanistic variable) were the most important range-limiting factors, and maximum temperature thresholds were consistent with the observed upper thermal limit of *R. temporaria* tadpoles. We found that range shift forecasts in central Europe are far more pessimistic when using distal macroclimatic variables, compared to projections based on proximate mechanistic variables. However, both approaches predicted extensive decreases in climatic suitability in southern Europe, which harbors a significant fraction of the species’ genetic diversity. We show how mechanistic modeling provides ways to depict gridded layers that directly reflect the microenvironments experienced by organisms at continental scales, and to reconstruct those predictors without extrapolation under novel future conditions. Furthermore, incorporating those predictors in correlative ecological niche models can help shed light on range-limiting processes, and can have substantial impacts on predictions of climate-induced range shifts.

KEYWORDS

activity restrictions, global warming, Maxent, mechanistic niche modeling, microclimate, NicheMapR, thermal limits

1 | INTRODUCTION

Many organisms are shifting their geographic distributions by tracking changes in suitable climatic conditions (Lenoir & Svenning, 2015; Parmesan, 2006; Pecl et al., 2017). Ecological niche models, or ENMs (also known as species distribution models, or SDMs), have become one of the primary tools to explore associations between environmental variables and species' distributions, and to forecast distribution shifts in changing climates (Elith & Leathwick, 2009; Pearson & Dawson, 2003; Sillero, 2011). A plethora of ENM approaches exist, which vary in the degree to which processes are explicitly incorporated. Correlative and mechanistic ENMs can be viewed as two endpoints of that continuum (Dormann et al., 2012; but see Peterson, Papeş, & Soberón, 2016). Correlative ENMs predict distributions by statistically relating current distributions (presences or abundances) to environmental layers (Elith et al., 2006; Guisan & Thuiller, 2005). These models may implicitly capture biotic and abiotic processes that limit species' ranges. Data required to fit correlative models are widely available, and thus correlative models have been extensively applied to climate change forecasting (reviewed in Elith et al., 2006; Elith, Kearney, & Phillips, 2010; Pacifici et al., 2015). In contrast, mechanistic niche models explicitly model range-limiting processes, often from heat and mass balance principles (Kearney & Porter, 2009). Despite the detailed species information required to fit mechanistic niche models, they are progressively becoming more widely applied (Briscoe, Kearney, Taylor, & Wintle, 2016; Carlo, Riddell, Levy, & Sears, 2017; Kearney, 2012; Kearney, Munns, Moore, Malishev, & Bull, 2018; Levy et al., 2015).

Not surprisingly, the extremes of these approaches to model species' distributions have strengths and limitations. Correlative models are a powerful tool to predict current distributions, but may be unreliable when extrapolating (i.e., predicting into novel environments in time or space; Elith & Leathwick, 2009; Elith et al., 2010). Mechanistic models, in contrast, do not require extrapolation, because they directly integrate species' functional traits with available microclimates. Thus, mechanistic models theoretically provide a solid basis with which to predict species' distributions in changing climates (Buckley, Cannistra, & John, 2018; Buckley et al., 2010; Kearney & Porter, 2009; Sears, Raskin, & Angilletta, 2011). Furthermore, mechanistic models can offer invaluable insights into the proximate constraints that underpin species' range limits (Kearney & Porter, 2009). Mechanistic niche models will, however, only be useful if the limiting processes can be unambiguously identified (Elith et al., 2010).

A critical step in modeling species' distributions is to include relevant predictor variables (Araújo & Guisan, 2006; Bucklin et al., 2014). Most attempts to predict species distributions based on correlative ENMs, however, rely on macroclimatic environmental layers which, at best, indirectly capture the microclimatic conditions experienced by animals (Potter, Arthur Woods, & Pincebourde, 2013; Sunday et al., 2014; but see Bennie, Wilson, Maclean, & Suggitt, 2014). Furthermore, most ENMs (both

correlative and mechanistic) focus on a single lifecycle stage (e.g., adults) or combine life stages (Gerick, Munshaw, Palen, Combes, & O'Regan, 2014; Riddell, Apanovitch, Odom, & Sears, 2017). Yet, most species possess complex life histories, which poses a further challenge for predicting the biotic consequences of climate change (Levy, Buckley, Keitt, & Angilletta, 2016; Levy et al., 2015; Maino, Kong, Hoffmann, Barton, & Kearney, 2016). Different lifecycle stages may experience different microclimates (and thus possess different scopes for thermoregulation), and may also have different thermal physiologies. This could result in differential vulnerabilities to climate change among lifecycle stages (Briscoe, Porter, Sunnucks, & Kearney, 2012; Kingsolver et al., 2011; Pincebourde & Casas, 2015; Radchuk, Turlure, & Schtickzelle, 2012; Sinclair et al., 2016).

One way to potentially overcome the limitations presented above is to integrate correlative and mechanistic niche models (Elith et al., 2010; Mathewson et al., 2017; Meineri, Deville, Gremillet, Gauthier-Clerc, & Béchet, 2015). For instance, macroclimatic variables and stage-specific traits could be coupled by using outputs of mechanistic niche models as more proximate "environmental" variables (*mechanistic variables* hereafter) for use as inputs in correlative ENMs. Furthermore, to project ENMs into warming climates, mechanistic variables could be derived using future macroclimatic conditions without extrapolation (Elith et al., 2010; Mathewson et al., 2017). Additionally, variable importance procedures developed for correlative ENMs (Thuiller, Lafourcade, Engler, & Araújo, 2009) allow us to generate hypotheses about which lifecycle stage or modeled processes constrains species' current distributions. Using both approaches can enable robust and useful insights into "why" and "where" species will persist or go extinct under climate change (Briscoe et al., 2016; Kearney, Wintle, & Porter, 2010).

Here, we model the distribution of the European common frog (*Rana temporaria*) under current and future climates using a widely applied correlative modeling method (Maxent; Phillips, Anderson, Dudík, Schapire, & Blair, 2017), and both macroclimatic (WorldClim; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and mechanistic (NicheMapR) variables. In *R. temporaria*—as in most temperate amphibians—embryos and larvae are aquatic, whereas juveniles and adults are terrestrial. Due to the high specific heat and thermal conductivity of water, aquatic stages are confronted with a limited scope for behavioral thermoregulation compared to terrestrial stages (Duarte et al., 2012; Feder & Hofmann, 1999; Kearney et al., 2014; Sears et al., 2011). Moreover, juveniles are diurnal, whereas adults can be diurnal and nocturnal as long as environmental conditions are suitable (Sinsch, 1984; Vences et al., 2000, 2002). Consequently, the different lifecycle stages of *R. temporaria* have unique thermal physiologies (Enriquez-Urzelai, 2018; Enriquez-Urzelai et al., 2019).

To depict stage-specific microclimates and physiologies, we derived proximate mechanistic layers using NicheMapR (Kearney & Porter, 2017), a framework for mechanistic niche modeling consisting of a microclimate model and an energy and mass balance model for ectothermic animals (animal model hereafter; Porter, Mitchell, Beckman, & DeWitt, 1973; Kearney & Porter, 2009). To characterize

the microclimatic conditions experienced by aquatic stages (i.e., eggs and tadpoles), we modeled pond duration and maximum and minimum pond temperatures using the microclimate model alone (Appendix S1). To model activity windows for juveniles and adults, we integrated the microclimate model with the animal model, parameterized with specific traits for each stage (Enriquez-Urzelai, Palacio, Merino, Sacco, & Nicieza, 2018). We employed permutation-based variable importance procedures to generate hypotheses regarding the lifecycle stage(s) or process(es) that limit the distribution of *R. temporaria* across Europe. Finally, to evaluate the consequences of considering stage-specific microclimates and physiologies, we compared current and future predicted distributions of *R. temporaria* using macroclimatic or mechanistic environmental variables.

2 | MATERIALS AND METHODS

2.1 | Presence data

Rana temporaria is a widespread European frog. According to physiological and behavioral studies, it is a cold-adapted species (Ludwig, Sinsch, & Pelster, 2015; Muir, Biek, & Mable, 2014), usually found in marshes, brooks, or near ponds (Vences et al., 2000). We downloaded data on the distribution of *R. temporaria* from the newest available version of the atlas of amphibians and reptiles from Europe (NA2RE; Sillero, Campos, et al., 2014; Sillero, Oliveira, Sousa, Sousa, & Gonçalves-Seco, 2014). The NA2RE dataset aims to accurately depict the entire range occupied by European herptiles at the continental scale at a resolution of 50 km² (Figure S2.1). To that end, NA2RE includes data from multiple sources (e.g., national atlases, websites; Sillero et al., 2018). Additionally, we obtained occurrence records for *R. temporaria* from the GBIF portal (accessed 20/4/2017; <http://www.gbif.org/>; Figure S2.1). Because results are qualitatively equivalent, we only present results obtained with the NA2RE data (see Appendices S2 and S3 for results obtained with GBIF data).

2.2 | Macroclimatic variables

To capture the macroclimatic conditions encountered by *R. temporaria* throughout its distribution, we downloaded six variables from the WorldClim dataset (Hijmans et al., 2005; <http://www.worldclim.org/>) at a spatial resolution of 10 arc-minutes (~19 km²): annual mean temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6), annual mean precipitation (Bio12), precipitation of the wettest month (Bio13), and precipitation of the driest month (Bio14). We chose these variables because they reflect temperature/precipitation averages and extremes expected to limit species' distributions (Carey & Alexander, 2003; Quintero & Wiens, 2013; see Table S2.1 for correlations between variables).

We obtained bioclimatic layers for current conditions as well as for future (2070) climates. To account for uncertainty in future climate predictions (Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009), we considered two global circulation models (GCMs: CCSM4

and GFDL-CM3) and two emission scenarios (low, RCP 4.5, and high, RCP 8.5), representing mild to extreme expected impacts of climate change in Europe: CCSM4 predicts moderate-to-low changes in environmental conditions, while GFDL-CM3 projects larger environmental changes.

2.3 | Mechanistic variables

We developed proximate, mechanistic variables using NicheMapR (Kearney & Porter, 2017; Porter et al., 1973), which includes a microclimate model and an animal model. The microclimate model comprises a set of open-source routines that reconstruct the microclimates available to an animal, given terrain (e.g., slope, aspect, elevation, soil properties, available shade) and climate conditions (i.e., maximum and minimum air temperatures, precipitation, cloud cover, relative humidity, wind speed). We obtained all climatic condition layers from a global dataset of monthly means (1961–1990) at a resolution of 10 arc-minutes (New, Lister, Hulme, & Makin, 2002). We derived slope and aspect layers from a digital elevation model (GTOPO30; <https://lta.cr.usgs.gov/GTOPO30/>), resampled to a resolution of 10 arc-minutes using bilinear interpolation with the *resample()* function of the *raster* R-package (Hijmans & Van Etten, 2013). With these data, the microclimate model provides hourly estimates of solar and infrared radiation, aboveground air temperature, wind velocity, and relative humidity at the animal's height, and soil temperature profiles at 10 user-specified soil nodes (i.e., depths; see Kearney & Porter, 2017; Kearney et al., 2014 for more details). To capture extreme conditions, which could impose distribution constraints, we only modeled microclimates in full sun conditions (0% shade).

The outputs of the microclimate model can be used directly (e.g., as predictor variables in a correlative ENM), or as inputs for the animal model (Kearney & Porter, 2017). We used the microclimate model alone to explore putative limiting factors at the aquatic larval stage (Figure 1). Specifically, based on radiation exchange, convection, conduction, and evaporation, we modeled maximum pond duration and maximum and minimum pond temperatures (Kearney, Porter, Williams, Ritchie, & Hoffmann, 2009) by using the soil moisture functionality of the NicheMapR microclimate model (Kearney & Maino, 2018). To that end, we ran the microclimate model twice. In the first run (*run1*), we modeled a pond with a maximum depth of 30 cm (similar to breeding ponds most often used by the species). We assumed that all 10 arc-minute grid cells contained soil patches with clay substrates which could retain water after reaching saturation (i.e., made primarily of clay; soil composition set to 90% clay in our simulations). We computed the hydraulic properties of the texture-defined soil with the *pedotransfer()* function of NicheMapR. Additionally, to impose water catchment by the pond, we increased the rain multiplier parameter (*rainmult* = 2.8), which increases water pooling, and decreased the proportion of rain that comes in the first rainy day of each month (*rainfrac* = 0.1). In the second run (*run2*), we modeled snowfall and snowpack using the microclimate model with default parameters and the moisture and snow

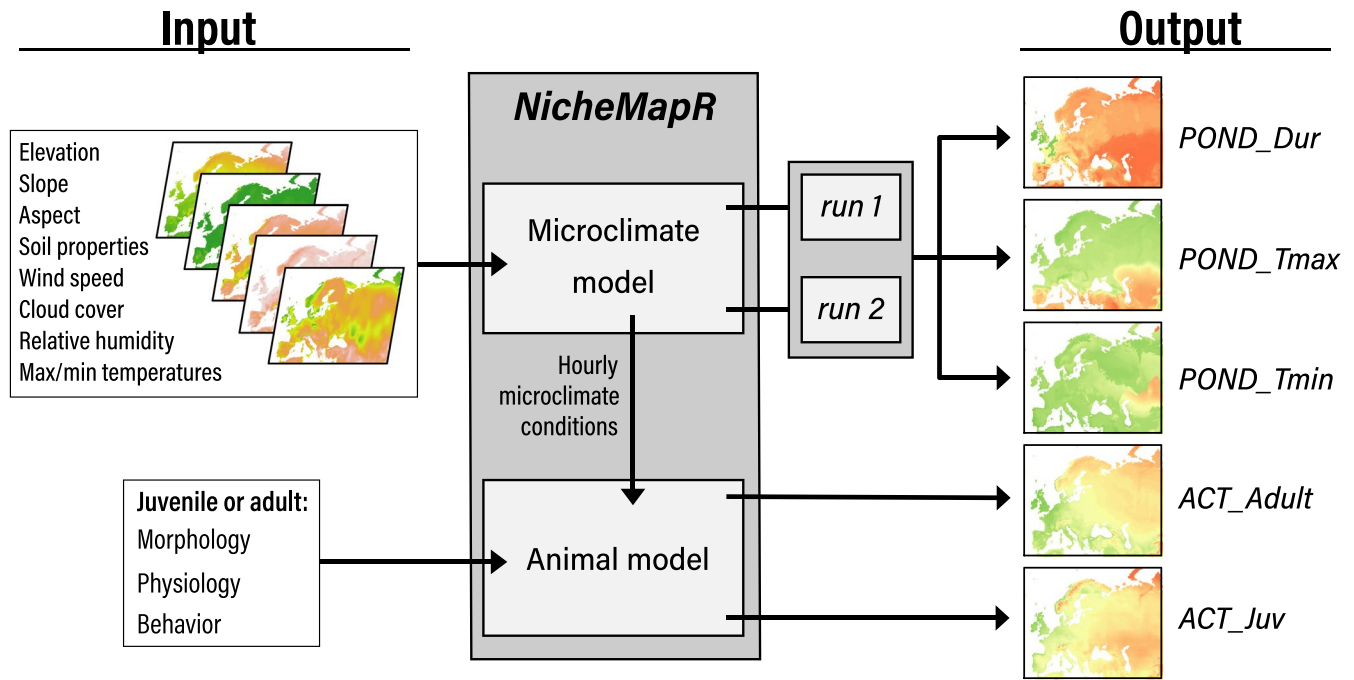


FIGURE 1 Graphical illustration of the framework to generate mechanistic “proximate” variables. We used climate and terrain data as inputs for the microclimate model within NicheMapR (Kearney & Porter, 2017). Using different parameterizations of the model (*run1* and *run2*, see Materials and Methods and Supplementary Material) we computed pond duration (*POND_Dur*), and maximum (*POND_Tmax*) and minimum pond temperatures (*POND_Tmin*) across Europe. Additionally, we generated layers of the activity windows of juvenile and adult *Rana temporaria*, using stage-specific morphology (e.g., size), physiology, and behavior as inputs for the animal model of NicheMapR

subroutines selected, as implemented in the *micro_global()* function of NicheMapR (Kearney & Porter, 2017). With both runs, we computed the maximum duration that the pond remained filled and uncovered by snow (*POND_Dur*, in days; Figure S1.4). Furthermore, we computed maximum (*POND_Tmax*, in °C; Figure S1.5) and minimum water temperatures when uncovered by snow (*POND_Tmin*, in °C; Figure S1.6). We modeled water temperature as the temperature of saturated soil (obtained in *run1*), two nodes above each hourly estimate of pond depth. Using modeled temperature at the estimated pond depth underestimates the amplitude of thermal fluctuations. This parameterization, in contrast, provided estimates that were broadly consistent with pond temperatures recorded by dataloggers deployed 10–15 cm deep in ponds in northern Spain and central Sweden (see Appendix S1).

We coupled the output of the microclimate model with the animal model to explore spatial patterns of potential activity times of early juvenile and adult *R. temporaria* on land (Figure 1). We parameterized the microclimate model with default parameters (as in *run2*), and we supplied the output to the animal model (*ectotherm()* function of NicheMapR). The animal model computes hourly operative temperatures (T_e) iteratively, given available microclimates (output of the microclimate model) and the animal's morphology, behavior, and physiology. We derived layers for activity potential of juveniles (*ACT_Juv*, in hour/year; Figure S1.7) and adults (*ACT_Adult*, in hour/year; Figure S1.8) by modeling a medium-sized early juvenile and adult (0.3 and 30 g, respectively). We set their midpoints at 0.5 and 2 cm respectively, and assumed a shape (and

surface area) equivalent to that of the leopard frog (*Lithobates pipiens*). Likewise, we assumed that 90% of the skin acted as a free water surface when individuals were active (see Kearney et al., 2008 for more information). Since juveniles are predominantly diurnal, we allowed only diurnal activity, bounded within the maximum ($VT_{max} = 18.5^\circ\text{C}$) and minimum ($VT_{min} = 9.5^\circ\text{C}$) temperatures selected in a thermal gradient experiment conducted on juveniles from seven populations from the Iberian Peninsula (Enriquez-Urzelai et al., 2018). For adults, we allowed 24 hr activity. The maximum temperature for activity was set as the maximum temperature ($VT_{max} = 19.4^\circ\text{C}$) selected in thermal gradient experiments with adults (Enriquez-Urzelai et al., 2018), but minimum temperatures were set to 0 ($VT_{min} = 0^\circ\text{C}$), since *R. temporaria* is known to be active at this temperature (Ludwig et al., 2015; À. Richter-Boix, personal communication).

When T_e of juveniles or adults fell outside of these temperatures for activity, animals were simulated to burrow underground to the depth with the closest temperature to their preferred temperature (juveniles: $T_{pref} = 13.1^\circ\text{C}$; adults: $T_{pref} = 16.6^\circ\text{C}$), obtained from thermal gradient experiments (Enriquez-Urzelai et al., 2018). Furthermore, we included the water balance between frogs and soil, with a simplified version of the model developed by Tracy (1976). When frogs were not able to gain water from the substrate—that is, when the microclimate model estimates of soil water potential were below the water potential reported for *L. pipiens*, -72.5 J/kg (Tracy, 1976)—and they lost more than 20% of body mass as water, we forced them to retreat and rehydrate. We allowed frogs to be

active the next hour, assuming individuals could rehydrate in under an hour (Claussen, 1969; Cree, 1988).

We also derived all five mechanistic variables (i.e., *POND_Dur*, *POND_Tmax*, *POND_Tmin*, *ACT_Juv*, and *ACT_Adult*) for 2070 climates. To simulate future climates, we downloaded current and 2070 maximum and minimum temperature and precipitation layers from the WorldClim dataset (Hijmans et al., 2005), and computed predicted monthly differences (i.e., offsets). As for bioclimatic variables, we considered two global circulation models (CCSM4 and GFDL-CM3) and two emission scenarios (RCP 4.5 and RCP 8.5). We added the offsets to the baseline maximum and minimum temperatures and precipitation values (New et al., 2002), and reran the NicheMapR microclimate and animal models (Figure 1). Although mixing climate data from disparate sources might introduce uncertainty into climate change projections, the environmental layers for current climates were almost identical between climate datasets. Furthermore, this approach enabled us to include uncertainty in future predictions and geographic variation in the magnitude and direction of climate change. Due to the high computational demand of generating mechanistic variables—involving six NicheMapR models per grid cell, 81,664 grid cells, and five climate scenarios (2,449,920 models in total; Figure 1)—predictions were generated using a Scientific Modelling Cluster (Xeon 3.60 GHz cores; Cluster de Modelización Científica UNOV05-23-009, Scientific-Technical Services from the University of Oviedo, Mieres, Spain). To match the spatial resolution of occurrence points and predictor variables (both macroclimatic and mechanistic), we aggregated each variable to a resolution of 50 km² with the *aggregate()* function of the *raster* R-package (Hijmans & Van Etten, 2013).

2.4 | Maxent models

We fitted four correlative ENMs using Maxent and different predictor sets for current climates. We fitted models using all macroclimatic (Bio1, Bio5, Bio6, Bio12, Bio13, and Bio14) or all mechanistic predictor variables. Furthermore, we fitted two models using a smaller set of mechanistic variables: one excluding the most influential factor (see Results3) and, because of the extensive support for the animal model of NicheMapR, another only including variables derived using the animal model. We fitted models as implemented in the *maxnet* R-package—an R implementation of the new release of Maxent (v. 3.4.1)—based on point processes (i.e., inhomogeneous Poisson processes; Phillips et al., 2017). Maxent is a presence-background approach, in which environments occupied by a species are contrasted with the available environmental space (i.e., background). Due to the broad geographic distribution of *R. temporaria*, we used all of Europe (all raster cells) as available background. We used hinge features only with the regularization parameter set to 2.5. These settings produce smoother response curves that reduce overfitting, which is especially relevant when projecting to novel conditions (Briscoe et al., 2016; Elith et al., 2010).

To produce maps of current and 2070 climatic suitability, we projected Maxent models onto current and 2070 macroclimatic and

mechanistic layers using the “*cloglog*” transformation, implemented in the *maxnet* R-package. To identify the extent to which Maxent models extrapolated, we built multivariate environmental similarity surfaces (MESS; Elith et al., 2010) as implemented in the *dismo* R-package (Hijmans, Phillips, Leathwick, & Elith, 2016; Figures S2.3 and S2.4). For presentation purposes, we averaged climatic suitability scores across all different GCM and emission scenarios (see Figure 4). Nevertheless, for southern Europe, the area of the distribution range expected to undergo the greatest suitability declines over the next decades, we present the prediction of each GCM and emission scenario combination to assess their influence on predicted future distributions (see Figure 5). To visually compare predictions based on macroclimatic or mechanistic variables, we identified suitable areas (suitability >0.3) predicted using each variable set, and the areas of model congruence, as in Kearney et al. (2010). This threshold provided fairly good predictions for current distributions. Additionally, we identified the areas of congruence using threshold values that maximized different aspects of models (e.g., the sensitivity or the omission rate; Table S2.2; Figures S2.5–S2.8), as calculated with the *threshold()* function of the *dismo* R-package (Hijmans et al., 2016). Since we obtained similar results, we only present areas of congruence obtained with the threshold value of 0.3 (but see Figures S2.5–S2.8).

2.5 | Model evaluation

We assessed the predictive performance of Maxent models with 10-fold cross-validation. In each repetition, we fitted a model using 70% of the data and computed the area under the ROC curve (AUC) with the remaining 30%. We calculated AUCs by comparing the predicted suitability scores of the held-out 30% and the background, using the *dismo* R-package (Hijmans et al., 2016). Finally, we averaged the AUCs of the 10 repetitions. In addition, we employed null models to test the validity of Maxent models. As suggested by Raes and Steege (2007), we fitted a large number of Maxent models similar to empirical models: with the same parameterization and number of occurrences, but with randomly drawn occurrence records. Then, we computed the AUC of those null models and evaluated whether the AUC of empirical models were significantly higher than the “null” distribution of AUC values from null models. One hundred null models sufficed to obtain a robust “null” distribution (see Figure S2.2).

We estimated variable importance to determine the roles of macroclimatic and mechanistic variables in explaining the current distribution of *R. temporaria*. To estimate variable importance, we used the approach proposed by Thuiller et al. (2009), as implemented in the *ecospat.maxentvarimport()* function of the *ecospat* R-package (Broennimann et al., 2015). The method consists of a randomization procedure followed by Pearson's correlations. In each repetition, two models are fitted: one with all environmental variables “untouched” and the other with the variable under investigation randomly permuted. Variable importance is then estimated as $1 - r$, where r is the Pearson's correlation between predictions. High

correlation values mean that predictions do not differ markedly. In such cases, $1 - r$ would be a small number, and the variable would be considered unimportant. We repeated this randomization procedure 10 times and averaged the importance values for each variable. Additionally, to further explore relationships between variables and climatic suitability, we visually inspected response curves using the clog-log transformation for each variable while keeping the rest at their mean value.

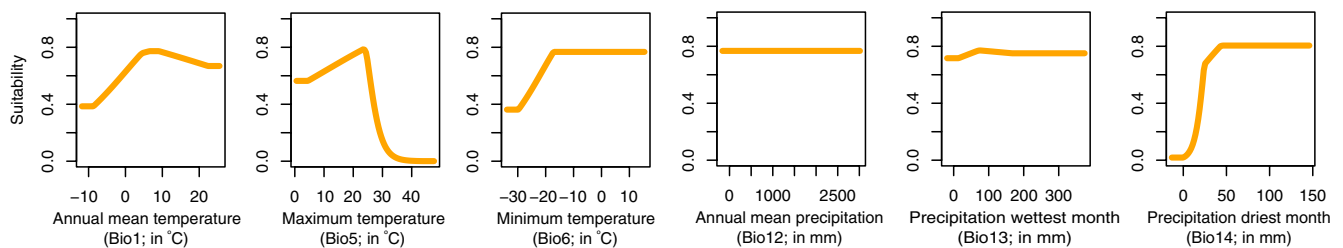
3 | RESULTS

Maxent models performed well regardless of the underlying predictor set. The model with macroclimatic variables showed equivalent AUC values (mean AUC = 0.762, 95% CI = 0.759–0.765) to the model built with all mechanistic variables (mean AUC = 0.762, 95% CI = 0.757–0.767). Due to the pervasive influence of *POND_Tmax* (see below), we also explored a model including all mechanistic variables except *POND_Tmax*, and a model only including *ACT_Juv* and *ACT_Adult*. AUC values decreased slightly compared to the model including all mechanistic variables (excluding *POND_Tmax*: mean AUC = 0.728, 95% CI = 0.724–0.733; activity only: mean AUC = 0.713, 95% CI = 0.708–0.717). AUC values from empirical models statistically outperformed null models, which showed

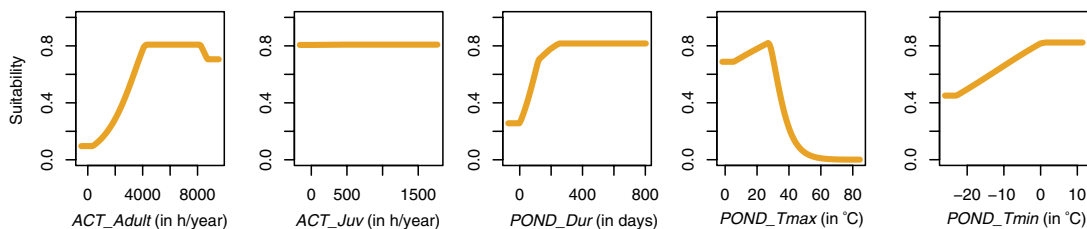
the expected values close to 0.5 (null models with macroclimatic variables: mean = 0.498, 95% CI = 0.496–0.499; with all mechanistic variables: mean = 0.498, 95% CI = 0.496–0.500; mechanistic variables excluding *POND_Tmax*: mean = 0.497, 95% CI = 0.496–0.499; activity only: mean = 0.498, 95% CI = 0.496–0.500; Figure S2.2).

Results from variable importance tests suggest that maximum temperatures constrain the geographic distribution of *R. temporaria*. Among the macroclimatic variables, the maximum temperature of the warmest month (Bio5) and the precipitation of the driest month (Bio14) had the highest variable importance values ($1 - r = 0.328$ and 0.296 , respectively). The rest of the macroclimatic predictors (i.e., annual mean temperature, Bio1; minimum temperatures, Bio6; annual precipitation, Bio12; and the precipitation of the wettest month, Bio13) had almost negligible influence on predictions ($1 - r < 0.005$ in all cases). In the case of the model built with all mechanistic variables, maximum pond temperatures (*POND_Tmax*) was the most influential predictor ($1 - r = 0.777$). Pond duration (*POND_Dur*; $1 - r = 0.055$), followed by activity windows for adults (*ACT_Adult*; $1 - r = 0.020$) had relatively small influences. Minimum pond temperatures (*POND_Tmin*) and activity windows for juveniles (*ACT_Juv*) had negligible impacts ($1 - r < 0.005$ in both cases). When we excluded *POND_Tmax* as a predictor variable, *ACT_Juv* emerged as the most influential predictor ($1 - r = 0.649$), followed by *POND_Dur* ($1 - r = 0.076$),

Macroclimatic variables



Mechanistic variables



Mechanistic variables excluding *POND_Tmax*

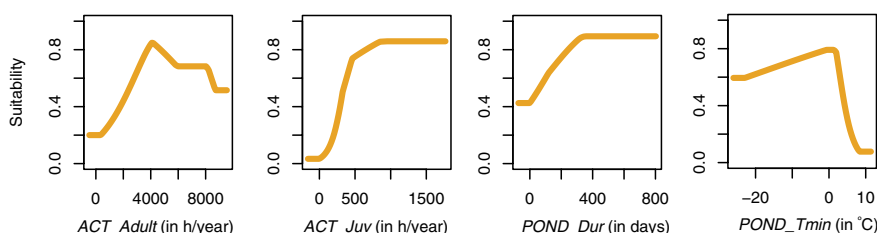


FIGURE 2 Climatic suitability changes across the range of values of each predictor variable (response curves), while keeping the rest of predictors at their mean value. Curves were obtained with the “cloglog” transformation of Maxent output [Colour figure can be viewed at wileyonlinelibrary.com]

POND_Tmin ($1 - r = 0.058$), and *ACT_Adult* ($1 - r = 0.023$). Similarly, the model including only activity-related variables confirmed a higher influence of *ACT_Juv* ($1 - r = 0.961$) compared to *ACT_Adult* ($1 - r = 0.038$).

Climatic suitability decreased sharply at maximum temperatures (Bio5) above $\sim 30^{\circ}\text{C}$ (Figure 2), and in very dry (low precipitation in the driest month; Bio14) or very cold regions (low mean temperatures; Bio1). The model including all mechanistic variables predicted that suitability decreased markedly at maximum pond temperatures (*POND_Tmax*) of $\sim 40^{\circ}\text{C}$ (Figure 2). In contrast, climatic suitability increased with increasing pond duration (*POND_Dur*) or increasing activity windows for adults (*ACT_Adult*). Both the model excluding *POND_Tmax* and the model based on activity-related variables (data not shown) suggested that climatic

suitability increased with increasing activity potential of juveniles (*ACT_Juv* above ~ 500 hr/year).

We found a high congruence between climatic suitability predictions obtained using macroclimatic versus all mechanistic variables for current climates (Table S2.3; Figure 3). The degree of congruence decreased moderately when we excluded *POND_Tmax* from the mechanistic predictor set (Figure 3c,e,g). The model excluding *POND_Tmax* and the model fitted only with activity-related variables—in which *ACT_Juv* was the most influential factor—predicted a higher suitability in southern and northern Europe compared to models based on macroclimatic and all mechanistic variables. The fact that the models based on activity-related variables predicted suitable conditions beyond the species' known range in the south explains the lower AUC of these models.

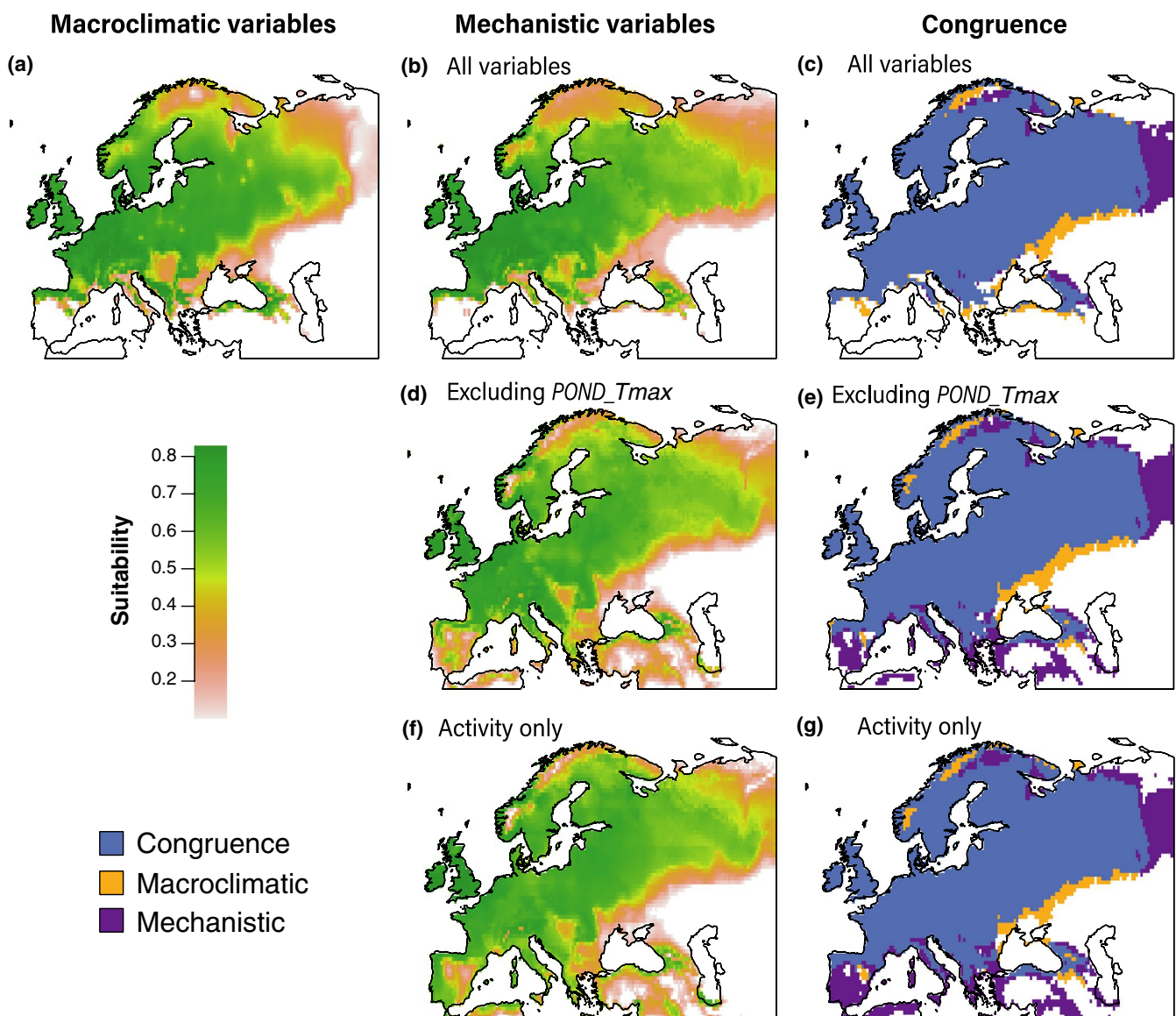


FIGURE 3 Predicted climatic suitability for *Rana temporaria* under current climates. In panel (a), we made projections using the Maxent model built with macroclimatic variables. Alternatively, in (b), (d), and (f) panels (second column), we used Maxent models built with all mechanistic variables (b), all mechanistic variables excluding *POND_Tmax* (d), and only with activity potential variables (f). Panels (c), (e), and (g) show areas of congruence (i.e., agreement; blue), and areas only predicted with macroclimatic (yellow) or mechanistic variables (purple)

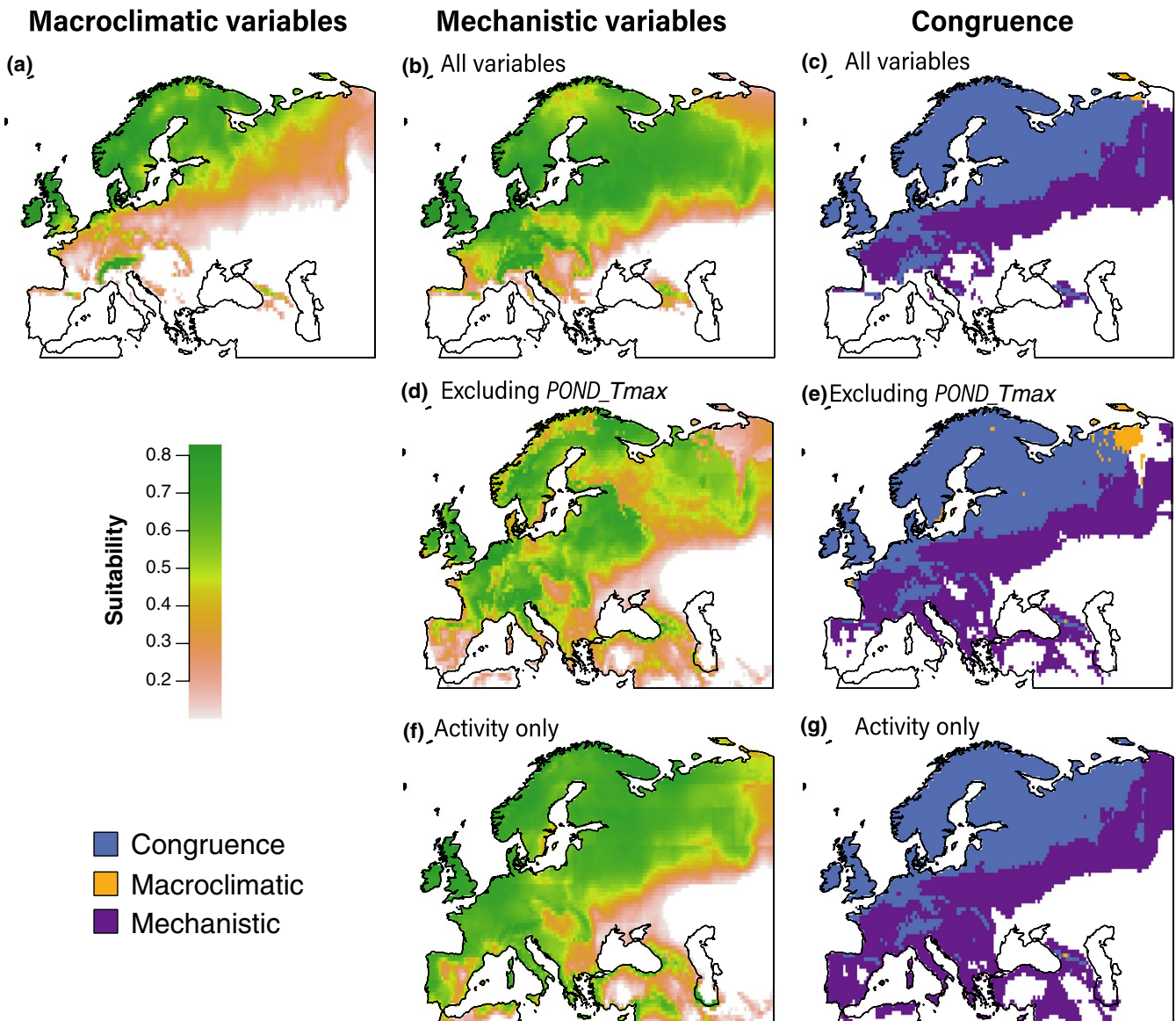


FIGURE 4 Predicted climatic suitability for *Rana temporaria* under future, 2070, climates (averaged across all four climate change scenarios). In panel (a), we made projections using the Maxent model built with macroclimatic variables. Alternatively, in (b), (d), and (f) panels (second column), we used Maxent models built with all mechanistic variables (b), all mechanistic variables excluding *POND_Tmax* (d), and only with activity potential variables (f). Panels (c), (e), and (g) show areas of congruence (i.e., agreement; blue), and areas only predicted with macroclimatic (yellow) or mechanistic variables (purple)

Predictions varied considerably for future (2070) climates depending on the underlying predictor sets. The Maxent model based on macroclimatic variables predicted extensive range contraction in central Europe for 2070 (46.34% of suitable cells lost; Table S2.4; Figure 4a,c and Figure S2.9). In contrast, the model based on all mechanistic variables predicted a less pronounced suitability decrease in central Europe (9.55% of the suitable cells lost; Table S2.4; Figure 4b,c and Figure S2.9). Both models identified the coldest regions as suitable under 2070 climates (i.e., high mountain ranges such as the Alps or the Pyrenees, and northern Europe). Furthermore, both models forecasted a marked decrease in climatic suitability at the current southern range margin of *R. temporaria* (Figure 4c), in particular under a more extreme climate change

scenario (GFDL-CM3 and RCP 8.5; Figure 5g,j,m). The model based on all mechanistic variables, however, predicted slightly lower suitability decreases in southern Europe, especially in the case of the most benign circulation model (CCSM4) and a low emission scenario (RCP 4.5; Figure 5a,d).

Interestingly, Maxent models mostly driven by activity potential for juveniles (i.e., the model excluding *POND_Tmax* and the model fitted with *ACT_Juv* and *ACT_Adult*) predicted moderate-to-low suitability decreases at southernmost latitudes (Figure 4d-g), even in the most extreme scenarios (Figure 5). Although the model excluding *POND_Tmax* predicted an average loss of 9.89% of suitable cells in southern Europe, the model based only on activity potentials predicted an average loss of 3.65% of suitable cells.

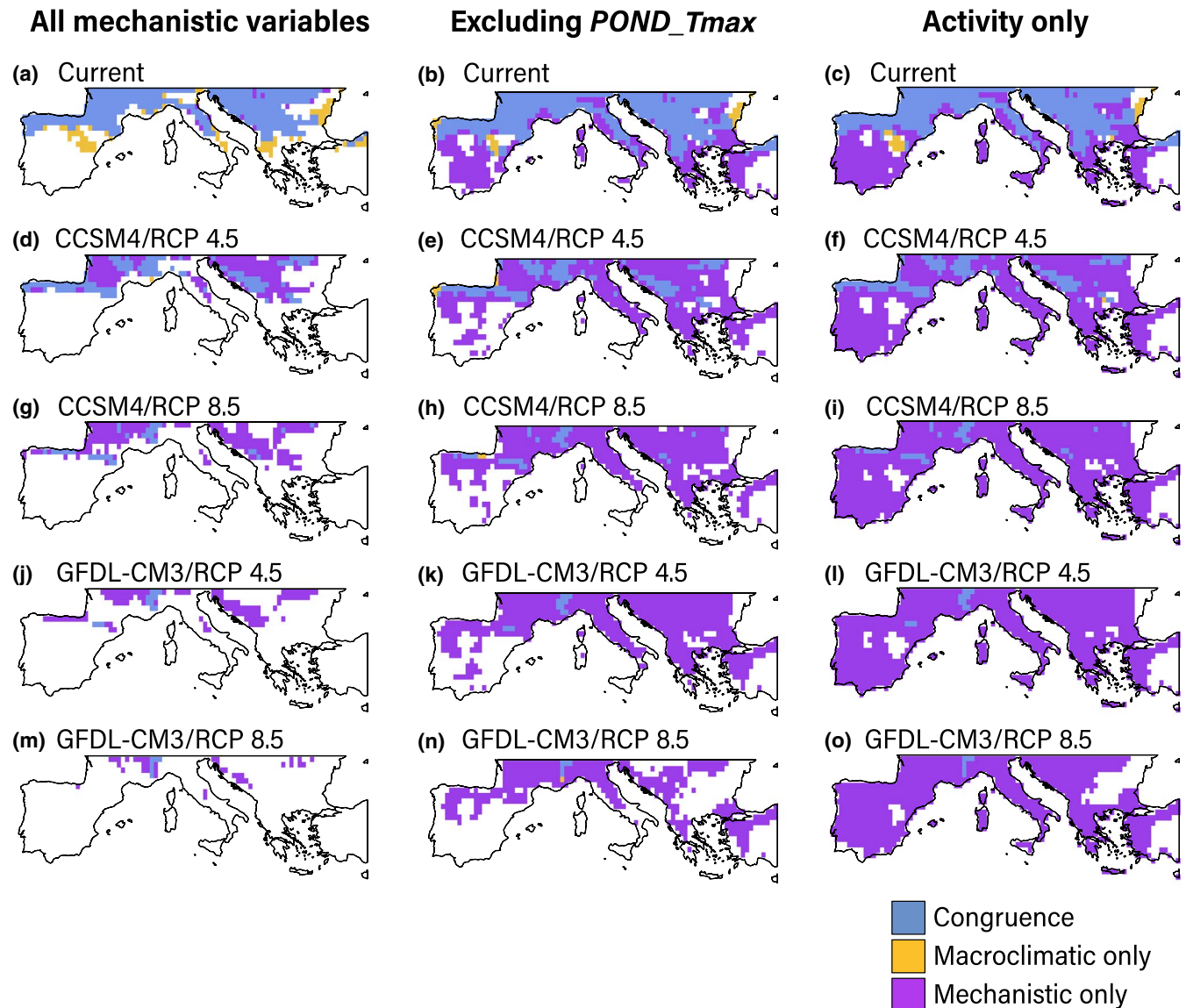


FIGURE 5 Areas of congruence (i.e., agreement; blue) and areas only predicted with macroclimatic (yellow) or mechanistic variables (purple) in southern Europe. In the *first column*, we show results including all mechanistic variables; in the *second column*, we show results excluding *POND_Tmax*; and in the *third column*, we show results including activity-related variables only. Projections are shown for (a–c) current climates, and (d–o) each climate change scenario

Moreover, the latter model predicted that increases in suitability in the north would exceed suitability decreases in the south, resulting in a net gain in range size (Table S2.4). MESS maps suggest that none of the models extrapolated into new environmental condition combinations for current or 2070 climates (Figures S2.3 and S2.4).

4 | DISCUSSION

Disentangling the processes and lifecycle stages that constrain species' distributions may be crucial for improving predictions of contemporary distributions, as well as forecasting range shifts in response to climate change (Evans, Diamond, & Kelly, 2015; Helmuth,

Kingsolver, & Carrington, 2005; Kearney & Porter, 2009; Moritz & Agudo, 2013; Radchuk et al., 2012). Efforts that combine or integrate different approaches (e.g., correlative and mechanistic ENMs) are particularly promising, since they offer robust and independent lines of evidence (Bonebrake et al., 2017; Briscoe et al., 2016; Kearney et al., 2010; Strasburg, Kearney, Moritz, & Templeton, 2007; Tingley, Vallinoto, Sequeira, & Kearney, 2014). Here, we show how mechanistic niche modeling can be used to derive "proximate" process-based variables (Figure 1 and Figure S1.4–S1.8) which, in combination with correlative ENM methods, can help us identify range-limiting factors. Our results suggest that maximum temperatures underpin the contemporary geographic distribution of *R. temporaria*, most likely due to their impact on aquatic tadpoles (Figure 2), which have limited scope to behaviorally avoid maximum pond temperatures.

Furthermore, we show that climate-induced range reductions for *R. temporaria* in central Europe are far more pessimistic based on “distal” macroclimatic variables (i.e., WorldClim), compared to projections based on “proximate” mechanistic variables (Figure 4).

Maxent models built either with mechanistic or macroclimatic variables had “fair” to “good” predictive ability (see Figure S2.2; Reino et al., 2017; Swets, 1988). However, the models built with macroclimatic variables and all mechanistic variables had higher AUC values than models built with a reduce set of mechanistic predictor variables that encapsulate fewer processes. The few studies in which correlative and mechanistic models have been employed jointly have similarly found that process-oriented models showed equivalent (Mathewson et al., 2017) or slightly lower performances than models built with macroclimatic variables (i.e., lower AUCs; Briscoe et al., 2016; Elith et al., 2010). Mechanistic predictors could be expected to perform more poorly because they are derived with a limited set of processes in mind, whereas correlative models are free to find a wider range of possible correlations between climate and distribution.

We found that, among the chosen processes, pond characteristics—mainly maximum pond temperatures—were an important driver of the distribution of *R. temporaria* in Europe. Interestingly, models built with “distal” macroclimatic and all “proximate” mechanistic variables both highlighted the importance of maximum temperature (i.e., Bio5 and POND_Tmax respectively), and, to a much lesser extent, water availability (i.e., Bio14 and POND_Dur). Our results suggest that climatic suitability of *R. temporaria* decreases at locations where water is scarce, or ponds reach temperatures >40°C (Figure 2). This temperature threshold is remarkably close to the critical thermal maxima of *R. temporaria* tadpoles estimated in laboratory experiments (~38°C; Enriquez-Urzelai et al., 2019; Gutiérrez-Pesquera et al., 2016). In the shallow ponds in which *R. temporaria* commonly breeds, thermal conditions are quite homogeneous spatially relative to deeper ponds and terrestrial habitats (Feder & Hofmann, 1999; Livingstone, Lotter, & Walker, 1999), and tadpole temperatures equal water temperatures because of their small body size (Lutterschmidt & Hutchison, 1997). With very limited scope for thermoregulation, tadpoles may be subjected to the actual thermal fluctuations of ponds, and thus extreme pond temperatures may set the limits of the distribution of pond-breeding amphibians (Duarte et al., 2012; Gerick et al., 2014; Gouveia et al., 2013; Gutiérrez-Pesquera et al., 2016). In northern Europe and at high elevations in lower latitudes, *R. temporaria* also uses lakes deeper than 30 cm to breed, which allows tadpoles to thermoregulate to a greater extent than in shallow ponds. Nonetheless, adults lay egg clutches at the shores of these water bodies. Thus, eggs and early tadpoles may be subjected to similar conditions to those encountered in shallower ponds.

Activity windows can also impose strong constraints on species distributions (Gunderson & Leal, 2015; Levy et al., 2016; but see Kearney, 2013). To persist, individuals must remain active long enough to forage sufficiently to fulfill the minimum requirements for growth, storage, and, in the case of adults, breeding (Angilletta,

Niewiarowski, & Navas, 2002; Kearney, 2012; Sinervo et al., 2010). Activity restrictions under climate change may also underpin reported extinction events (Sinervo et al., 2010; Mathewson et al., 2017; but see Kearney, 2013). Our simulations show that activity windows for juvenile and adult frogs vary markedly across Europe, as well as across time (see Figures S1.7 and S1.8). Furthermore, Maxent models in which maximum pond temperature was removed from the mechanistic predictor set revealed that activity windows for juveniles are closely related to the current distribution of the species. Nonetheless, models driven by activity potential predicted suitable areas outside the known current range of *R. temporaria*. It is worth mentioning that the physiological parameters used for mechanistic modeling were derived from southern populations (i.e., from the northern Iberian Peninsula; Enriquez-Urzelai et al., 2018). Thus, activity windows may be underestimated in northern Europe or roughly approximated in other regions. However, activity windows for juveniles in the southern Iberian Peninsula, where the species is absent, are similar to activity windows in the northern Iberian Peninsula, where the species is present, and where the physiological data used to drive the animal model were collected. This result suggests that activity windows may not be the ultimate range-limiting process in *R. temporaria*, as proposed for other ectotherms (Kearney, 2013). In contrast, pond temperatures may exert stronger constraints on the distribution of this frog. As such, they could be informative about potential range shifts associated with climate change.

Increases in air temperatures and more frequent extreme events (e.g., heat waves) due to climate change will impose concurrent changes in pond temperatures. Species could respond in situ by increasing upper thermal limits through genetic adaptation or phenotypic plasticity (Chevin, Lande, & Mace, 2010; Kelly, Pankey, DeBiasse, & Plachetzki, 2016). However, the potential for adaptation and plastic responses to shift thermal tolerances seems limited in ectotherms, relative to predicted environmental changes (Enriquez-Urzelai et al., 2018, 2019; Gunderson & Stillman, 2015; van Heerwaarden, Kellermann, & Sgrò, 2016; Kellermann, Heerwaarden, Sgrò, & Hoffmann, 2009). Thus, species or populations living closer to their maximum thermal tolerance (e.g., southernmost populations of *R. temporaria*) might be especially vulnerable to climate change (Duarte et al., 2012; Gerick et al., 2014; Gutiérrez-Pesquera et al., 2016; Huey et al., 2009).

In line with that expectation, Maxent models built either with “distal” or “proximate” variables predicted a marked northward shift of the southern range limit of *R. temporaria*. However, the magnitude of that shift differed depending on the predictor set used (Figures 3 and 4). While models based on macroclimatic variables predicted that most of continental Europe will become unsuitable for *R. temporaria*, models based on all mechanistic “proximate” variables predicted a more moderate, but nonetheless significant, decline in climatic suitability. Furthermore, models driven by activity windows predicted an even lower decline in climatic suitability across the distribution of the species. Other studies have similarly found that forecasts can disagree considerably between mechanistic and correlative ENMs (Gritti, Duputié, Massol, & Chuine, 2013; Muhling et al., 2017;

Serra-Díaz et al., 2013; but see Briscoe et al., 2016; Kearney et al., 2010). Furthermore, this result concurs with previous studies showing that the magnitude of the decline in environmental suitability decreases when mechanisms are included in models (Mathewson et al., 2017; Morin & Thuiller, 2009). Diamond et al. (2012) showed that thermal tolerances predicted the response of ant species to experimental climate warming better than correlative ENMs at their southern limit. In our study, the Maxent model built with all mechanistic variables, and largely driven by maximum pond temperatures, reflects the limits of the thermal niche of *R. temporaria* tadpoles. Therefore, models fitted with mechanistic “proximate” layers (including maximum pond temperatures) could be more reliable than models based on macroclimatic variables (Martínez, Arenas, Trilla, Viejo, & Carreño, 2014). This would reinforce the idea that good predictions for current distributions are not a guarantee of robust predictions of the impacts of climate change (Araújo, Pearson, Thuiller, & Erhard, 2005; Triviño, Thuiller, Cabeza, Hickler, & Araújo, 2011). Future studies could usefully validate that prediction using empirical data on *R. temporaria* range shifts.

Congruent forecasts of climate change impacts driven by independent lines of evidence are often viewed as more likely than forecasts in which predictions disagree (Briscoe et al., 2016; Gritti et al., 2013; Kearney et al., 2010); here, we found that this was the case for southern Europe. Models based on all proximate and distal variables predicted alarming decreases in climatic suitability for the southernmost populations of *R. temporaria* (Figure 5). Furthermore, both types of models identified similar regions as important climate refugia under climate change. These include the highest latitudes of Europe, as well as mountainous areas, such as the Alps, the Pyrenees, and the Cantabrian Mountains in the northern Iberian Peninsula, which could act as important climate refugia for southern populations. Consistent with previous studies, we found that climate change will improve climatic suitability at the northern range margin of *R. temporaria*, enabling the species to occupy areas that currently might be suboptimal (Blank, Luoto, & Merilä, 2013). However, under the most extreme climate change scenario, most mountain ranges will also become thermally unsuitable by 2070, excluding the Alps (Figure 5c–e). Considering that most of the genetic and phylogenetic diversity of *R. temporaria* is concentrated in the northern Iberian Peninsula (Vences, Sarasola-Puente, Sanchez, Amat, & Hauswaldt, 2017), climate change could cause extensive loss of distinctive genetic diversity (i.e., cryptic biodiversity loss; Bálint et al., 2011; Moritz & Agudo, 2013) and likely the extinction of evolutionary significant units.

Mechanistic niche models, such as NicheMapR, are valuable tools for developing “environmental” gridded layers that directly reflect the microenvironments experienced by organisms at continental scales (Kearney & Maino, 2018; Kearney et al., 2014; Mathewson et al., 2017). Furthermore, by combining microclimate estimates with ectotherm models, it is possible to derive gridded layers of activity windows, required shade levels, or body temperatures, among others (Buckley, Ehrenberger, & Angilletta, 2015; Kearney, 2013; Kearney et al., 2018; Levy et al., 2015). When such indices are re-computed under future climate scenarios, there is a reduced risk of extrapolation because the processes (such as interactions between

air temperature, solar radiation, evaporation rates and pond temperature in the present case) are maintained in the model. Here, we identified maximum pond temperature as an important range-limiting factor for *R. temporaria* and predicted alarming decreases in climatic suitability in genetic “hotspots” of the species (e.g., northern Iberian Peninsula). We acknowledge that our models, like any model, have several limitations, such as neglecting plasticity or evolutionary adaptation in thermal and hydric physiology (Kearney et al., 2009; Riddell, Odom, Damm, & Sears, 2018) or only implicitly capturing biotic interactions (Wisz et al., 2013). In addition, maximum pond temperatures could be mischaracterized in some areas, leading to under- or overprediction. Nonetheless, our models are useful for depicting how the modeled processes vary at continental scales—providing spatial estimates of potential range-limiting factors—and how these might be altered by climate change. Such approaches represent a step forward in identifying range-limiting factors and improving forecasts of the impacts of climate change.

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