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## Accounting for flow intermittence in freshwater species distribution modelling

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## Abstract

To forecast species responses to environmental changes, it is crucial to understand drivers of species distribution acting at multiple spatial and temporal scales. While hydrology is acknowledged as a key driver for freshwater species, most studies have been limited to perennial river flow regimes when exploring species distribution in rivers. We developed a method to characterize stream flow to subsequently account for flow intermittence in species distribution models (SDMs). First, we used the hydrological Soil and Water Assessment Tool (SWAT) to simulate flow in the French Pyrenees at fine spatial grain and large spatial extent. Several metrics characterizing flow intermittence were subsequently included in a SDM along with topographic, hydrographic, climatic and land use variables. We applied this methodology to an extensive dataset of the Pyrenean brook newt (*Calotriton asper*) presence in France. This amphibian is highly dependent on aquatic habitats and its distribution could be mainly driven by hydrological and climatic variables. We found that 60% of the stream network of the study area is intermittent. Maximum air temperature and proportion of agricultural areas contribution in explaining species distribution were the most important (26.3 and 21.2%, respectively). Both variables negatively influenced the probability of presence of the Pyrenean brook newt. We also found a negative correlation with the frequency of zero-flow events (13%), emphasizing the role of flow intermittence in driving aquatic species distribution. Our study provides new insights into fine-grained hydrology in the Pyrenees and illustrates intermittence characterization and mapping methods that could be applied elsewhere.

## 1. Introduction

In conservation research, understanding drivers of species distribution acting at multiple spatial and temporal scales is crucial to forecast responses to environmental changes (Beaumont, Pitman, Poulsen, & Hughes, 2007; Williams, Belbin, Austin, Stein, & Ferrier, 2012). Species distribution models (SDMs) that assess statistical relationship between presence or abundance of a species and characteristic of the environment, are the most widely used tools. In the last two decades, plethora of studies have applied SDMs to assess the impact of global change on species range (e.g. Brun et al., 2020), to forecast the risk of invasion by alien species (e.g. Dong et al., 2020), to identify suitable conservation areas (e.g. Mateo et al., 2019), or to explore and identify the environmental factors driving species distribution (Charbonnel et al., 2016). Most studies used variables describing climate, topography or land use. For freshwater taxa, the inclusion of hydrological variables is quite recent (Charbonnel et al., 2015; Kuemmerlen et al., 2014) while they are acknowledged to affect greatly their distribution. The reason is likely that they are difficult to measure finely in the field (i.e. at the subcatchment scale) for studies covering large areas. In addition, they need to be recorded continuously over a long period to get an accurate description of the spatio-temporal hydrological features of a stream. Powerful tools able to model hydrology for large areas but at fine temporal and spatial grain are now available and can be a relevant alternative to *in situ* measurements. The most widely used hydrological model is the Soil and Water Assessment Tool (SWAT) that runs on different time steps (e.g. daily, monthly) and spatial grains (small watershed to river-basin scale), over short or long time periods (Gassman, Reyes, Green, & Arnold, 2007).

When exploring effects of hydrology on species distribution, there is mounting evidence that it is crucial to account for time when no water flows in streambed (hereafter zero-flow event). These zero-flow events can be caused by different mechanisms such as natural drying in headwater streams, karstic geology or excessive water use for human activities. They are forecasted to become more frequent and intense in coming years as a manifestation of warming and reduced precipitation, becoming thus an increasing threat to freshwater ecosystems worldwide (van Dijk et al., 2013; Vander Vorste, Obedzinski, Nossaman Pierce, Carlson, & Grantham, 2020). Streams that recurrently cease to flow or totally dry out are the most abundant (greater than 50% of the global river network; Datry et al., 2014), and their number is increasing with climate change and water demand (Larned, Datry, Arscott, & Tockner, 2010). Recurrent extreme droughts may turn previously suitable habitats into unsuitable habitats, where species highly dependent on the aquatic environment, such as fish

or amphibians, can no longer persist. Although identified as a major concern in hydrology research since the 1980's, accounting for intermittent streams in ecological management is still rare. This lack is even worse in mountainous areas, where low-order streams (i.e. headwater streams) are highly sensitive to flow intermittence (Datry et al., 2014; Lowe & Likens, 2005). As far as we know, flow intermittence has never been included in SDMs to investigate and predict habitat suitability for freshwater species.

Freshwater vertebrate species are considered the most threatened worldwide (Harrison et al., 2018; Reid et al., 2019) among which amphibians that have already suffered a quick and steep decline in recent decades (Reid et al., 2019). Mountain amphibian diversity is particularly threatened by reduction in precipitation and water availability that is forecasted to continue and even intensify in coming years (Auer et al., 2007; Gobiet et al., 2014). In France, among vulnerable amphibian species, the Pyrenean brook newt (*Calotriton asper*), a species endemic to the Pyrenean mountain range, is one with the most incomplete knowledge about distribution, ecology and biology. This species is ectotherm (i.e. its body temperature relies on external sources) and dependent on aquatic habitats, both at juvenile and adult stages. It lives in cold and well-oxygenated mountain freshwater streams (Clergue-Gazeau & Martínez-Rica, 1978). These eco-physiological features make the Pyrenean brook newt sensitive to water temperature (Trochet et al., 2018) and precipitation regime (Colomer, Montori, García, & Fondevilla, 2014), as well as hydrological variations, known to directly affect survival for other mountainous stream salamander species (Lowe, Swartz, Addis, & Likens, 2019). Although direct effect of flow intermittence on the Pyrenean brook newt has not been investigated to date, we expect this species could be negatively affected by this hydrological stream feature given that flow intermittence is known to cause drastic changes in stream macroinvertebrates communities (Piano et al., 2020), that are its main food resource (Montori, 1988). Further, amphibians are sentinels of ecological integrity (Welsh & Ollivier, 1998) due to their sensitivity to environmental perturbations (Corn & Bruce Bury, 1989; Welsh & Hodgson, 2008) induced by agricultural and other human activities. These activities have a negative impact on stream salamander richness and abundance across terrestrial and aquatic habitats (Petranka & Smith, 2005; Surasinghe & Baldwin, 2015). Thus, we expect that the Pyrenean brook newt should be more present in streams that are little or no impacted by human activities.

Local experts and scientists in the French Pyrenees recently achieved an extensive and updated database compiling all the existing observations of the Pyrenean brook newt in France. So far, such a database was the missing piece to investigate and understand

mechanisms driving the Pyrenean brook newt distribution, which is essential to implement appropriate conservation actions.

In this study, a SWAT model was first used to simulate flow in the stream network of the French Pyrenees at fine spatial grain for the period 1990-2011, at monthly step. Second, we called for expert judgement to assess flow regime and identify intermittent streams based on SWAT simulations. Last, these results were used to evaluate the importance of hydrology (including flow intermittence) relative to topography, climate and land use in explaining the distribution of the Pyrenean brook newt in the French Pyrenees streams, by applying the widely used MaxEnt algorithm to the most updated presence-only database for this threatened species.

## **2. Material and methods**

### *2.1 Study area and spatial discretization*

The Pyrenees are high mountains (with Aneto the highest point at 3 404 m, Spain) in southwest Europe, extending along the French-Spanish border for about 430 km from the Bay of Biscay (west) to the Mediterranean Sea (east). In France, the Pyrenees are divided into three main hydrographic regions: (1) the Adour (west part, 16 912 km<sup>2</sup>) and (2) the Garonne (central part, 55 846 km<sup>2</sup>) watersheds that both flow to the Atlantic Ocean, and (3) the Aude and the Mediterranean coastal rivers that flow to the Mediterranean Sea (east part, 5 327 km<sup>2</sup>). These three watersheds are under the influence of an oceanic climate (mean annual rainfall MAR: 1274 ± 241 mm; mean air temperature MAT: 11.3 ± 2.8 °C –SAFRAN © DB), a continental climate (MAR: 1060 ± 224 mm; MAT: 9.9 ± 2.7 °C) and a Mediterranean climate (MAR: 807 ± 175 mm; MAT: 11.7 ± 3.4 °C), respectively. The French Pyrenees are mainly covered by woodland (38%; European Environment Agency, 2012), and agricultural land in foothills (37%). Pastures are mostly located at medium elevations and bare rock dominates in areas of highest elevation.

The study area was delineated using borders of the French Pyrenean brook newt distribution (IUCN, Bosch et al., 2009) (Fig. 1). We divided the study area into 11 distinct watersheds (mean area: 1 220 ± 398 km<sup>2</sup>; min = 477 km<sup>2</sup>; max = 2 014 km<sup>2</sup>) (Fig. 2). To consider the dendritic structure of the hydrographic network, each watershed was subdivided into discrete hydrological units (hereafter called subcatchments, see Fig. 2; mean area: 3.86 ± 6.5 km<sup>2</sup>; min = 1.25.10<sup>-3</sup> km<sup>2</sup>; max = 15.14 km<sup>2</sup>). A unique stream reach is associated to one

subcatchment. A total of 63 119 reaches was delineated (mean length:  $421 \pm 364$  m; min = 25 m; max = 6137 m) using ArcSWAT 2012 (see 2.2.1.1), based on a 25 x 25 m digital elevation model (DEM) and a threshold area (i.e. drainage area) of 10 ha. The spatial delineation was performed at the scale of the Very Small Water Bodies, as defined in the European Water Framework Directive (Directive 2000/60/EC of the European Parliament), to account for headwater streams. Interannual average flow ( $\pm$  standard deviation) of the Adour, the Garonne, and the Aude and Mediterranean coastal rivers, at the outlets of the Pyrenean portion, are  $10.30 \pm 5.39$  m<sup>3</sup>/s (the Adour river at Bagnères-de-Bigorre, 2013-2019),  $53.46 \pm 13.74$  m<sup>3</sup>/s (the Garonne river at Saint-Gaudens, 1990-2019) and  $8.86 \pm 5.49$  m<sup>3</sup>/s (average of interannual average flow of the Tech river at Céret, 2011-2019; the Aude river at Alet-les-Bains, 2014-2019; and the Têt river at Ille-sur-Têt, 2019), respectively.

## 2.2. Environmental variables

A set of 17 uncorrelated environmental variables (Pearson correlation coefficient  $< |0.5|$  according to Fielding & Haworth, 1995) (Tab. 1) was compiled to investigate the Pyrenean brook newt distribution in the French Pyrenees streams. These environmental variables were chosen according to their known eco-physiological effect on the Pyrenean brook newt, on amphibians or on freshwater organisms in general (Charbonnel et al., 2016; Haggerty, Crisman, & Rohr, 2019). Seven of those variables were related to hydrological features, six to land use, two to topography and two to climate. All environmental variables were continuous, except the stream order which was discrete. Environmental data preparation was performed using ArcGIS (Esri) and R (R Core Team 2018).

### 2.2.1 Hydrology

#### 2.2.1.1 Stream flow simulation

SWAT is a hydrological continuous time model that can be used to simulate hydrological cycles, storages, fluxes and river transfers in each compartment of a watershed (see Neitsch, Arnold, Kiniry, & Williams (2013) for details). It requires input data related to topography, climate, soil type and land use to compute water fluxes. We used ArcSWAT 2012 to simulate water flux in each of the 63 119 stream reaches (i.e. subcatchments). SWAT also identifies one or more hydrological response units (HRUs) within each subcatchment that is the

smallest level for water balance computation. In the present study, a single HRU was defined per subcatchment.

We built 11 SWAT projects, corresponding to the 11 watersheds of the study area (Fig. 2).

To improve stream and subcatchment delineation, we used the “Burn-in” algorithm that overlaps an existing digital channel network (here the hydrological network from TOPO © DB –IGN) onto the DEM (Luo, Su, Yuan, Li, & Zhang, 2011). We used a 90 x 90 m resolution land use map (Corine Land Cover (CLC) 2012 © DB) for land use input data, and a 1 x 1 km resolution Digital Soil Map of the World (FAO, 2007) for soil. Climate data were daily precipitation, maximum and minimum air temperature, solar radiation, wind speed and relative humidity, for 1985-2011 (SAFRAN © DB, 8 x 8 km resolution grid).

Monthly stream flow data from 27 gauging stations, extracted from the HYDRO database (<http://www.hydro.eaufrance.fr/>), were used to calibrate and validate the SWAT models. One gauging station located near to the outlet was used for calibration and validation for each of the 11 watersheds and the 16 others were used for additional validation (Fig. 2) (Charbonnel et al., 2015; Qi & Grunwald, 2005).

Sensitive parameters (i.e. parameters that affect model performance) used in SWAT during calibration procedure have been identified by Grusson et al. (2015) and Boithias et al. (2017). We first ran the models with default parameters over the 1996-2000 period and when the Nash–Sutcliffe Efficiency (NSE) metric (i.e. a commonly used metric to assess simulations) was lower than 0.5 after this first run, sensitive parameters (Appendix 1) were modified as recommended by Grusson et al. (2015) and/or Boithias et al. (2017). Each model was calibrated separately and manually over the 1996-2000 period. In addition to the NSE, model performances during calibration procedure were evaluated for the 11 SWAT projects with the following metrics: the percent model bias (Pbias), the coefficient of determination ( $R^2$ ) (Moriassi et al., 2007) and the Kling-Gupta Efficiency (KGE; Gupta, Kling, Yilmaz, & Martinez, 2009). According to Moriassi et al. (2007) and Gupta, Kling, Yilmaz, & Martinez (2009), model is considered accurate when  $R^2 > 0.5$ ,  $Pbias \pm 25\%$ ,  $NSE > 0.5$  and  $KGE > 0$ . Validation was performed with no further adjustment of parameters, over two periods: 1990-1998 and 1998-2011, to evaluate model performances before and after the calibration period (i.e. 1996-2000). For each SWAT project, we performed validation procedure at the gauging station used for calibration and at one or two (if available) additional gauging stations. The same four statistical model performances mentioned above were used. Due to a lack of observed data over the 1996-2000 period at the gauging station used for calibration, the



PA\_center project was calibrated and validated over different time periods, while respecting the partitioning mentioned above (i.e. two periods of validation, before and after the calibration period).

After calibration and validation, we ran the 11 models over the period 1990-2011 at a monthly time step. The following variables derived from simulated stream flow were thus available for each of the 63 119 stream reach and for each month between January 1990 and December 2011: streamflow out ( $\text{m}^3/\text{s}$ ) (FLOW\_OUT), velocity of water ( $\text{m}/\text{s}$ ) (VEL) and water depth ( $\text{m}$ ) (DEP).

#### 2.2.1.2 Zero-flow threshold and flow intermittence

In hydrological modelling, zero-simulated flow values are uncertain (Ivkovic, Croke, & Kelly, 2014; Pilgrim, Chapman, & Doran, 1988). Thus, defining appropriate zero-flow threshold below which it is assumed that no water flows in streams is required. When studying large-scale patterns of flow intermittence, measured data from gauging stations are often used to determine this threshold (Reynolds, Shafroth, & LeRoy Poff, 2015; Snelder et al., 2013). In our study area, there are only two gauging stations in intermittent streams, and they both record low frequency and low duration of zero-flow events (i.e. shorter than one month) (Snelder et al., 2013). We thus developed an alternative methodology using expert judgment to identify reference intermittent stream reaches. Expert judgment is increasingly used in ecological sciences (Martin et al., 2012), and is now recognized as a useful source of information to complement modelling approaches (Aizpurua et al., 2015). The main drawback of using this approach, compared to relying on measured data from gauging stations to characterize flow intermittence (e.g. Snelder et al., 2013), is experts' subjectivity. Without a rigorous monitoring, we acknowledge that it can be difficult to obtain accurate estimations of zero-flow event duration and frequency. However, experts are often consulted for their field experience and knowledge of their study area (Burgman, 2005). We thus expect that their judgment is as relevant as observed data from gauging stations. We questioned 10 local experts (i.e. environmental managers or researchers) distributed along the French Pyrenees to identify and localize known intermittent stream reaches. The stream reaches had to be known to dry out during at least one month during the 1990-2011 period (to have a chance to occur in our monthly simulations). For each intermittent reach identified, we asked them the period of the year at which flow ceases. According to the experts, zero-flow events occur mainly during August and September. Based on these stream reaches known to be

intermittent, we then defined a zero-flow threshold for each of the 11 SWAT projects following two steps (Fig. 3): (1) identification of the minimum value of simulated FLOW\_OUT in August-September during the 1990-2011 period for each known intermittent reach, and (2) computation of the zero-flow threshold as the mean of the minimum values of simulated FLOW\_OUT found for these intermittent reaches. Then, stream reaches for which flow was below the corresponding zero-flow threshold of each SWAT project for at least one month during the period 1990-2011, were assigned to the intermittent category, while the other reaches were considered as perennial streams. To evaluate the accuracy of our intermittent/perennial streams classification, we compared it to an independent database (TOPO © DB - IGN). Due to the way of generating TOPO data (i.e. mainly aerial photography) that is different from our methodology to generate hydrological network, and to a different spatial grain between our study and the TOPO database (1:25000), 14% of the 63 119 stream reaches used for SWAT modelling are not present in the TOPO database, whereas 26 % of the stream reaches of the TOPO database are not present in our dataset. We calculated the percentage of intermittent rivers from the TOPO database that were also assigned to the intermittent category in our classification. To account for the percentage of stream reaches of the TOPO database that are not represented in our database, we considered a shared percentage higher than 70% as satisfactory. For the stream reaches that were not present in the TOPO database, no validation of the classification could be conducted.

### 2.2.1.3 Hydrological metrics

Five hydrological metrics were derived from VEL, DEP and FLOW\_OUT. First, the Froude number was computed from VEL and DEP, as follows:

$$Fr = \frac{VEL}{\sqrt{g * DEP}}$$

where  $g$  is the acceleration due to gravity and  $\sqrt{g * DEP}$  is the wave celerity. This metric provides a measure of hydraulic turbulences, with values  $>1$  for torrential regime (i.e. low water level and high velocity) and values  $<1$  for lentic regime (i.e. high water level and low velocity). Using FLOW\_out monthly data, we computed Q10 ( $m^3/s$ ) that is the flow observed or exceeded 10% of the time (i.e. high-flow) for each stream reach, as well as three metrics describing flow intermittence: (1) the frequency (FREQ) that is the number of zero-flow events (i.e. one month or successive months during which water stops flowing) during the

1990-2011 period, (2) the duration (in months) (DUR) that is the mean duration of zero-flow events over the 1990-2011 period, and (3) the coefficient of variation in duration of zero-flow events (cvDUR). These three metrics are widely used in hydrology to describe flow intermittence (Larned et al., 2010; Snelder et al., 2013). We computed them over the whole 1990-2011 period due to the monthly temporal grain of flow simulations and not on a yearly time step as frequently done (Snelder et al., 2013).

In addition to the five hydrological metrics derived from SWAT simulations, we also used (1) the Strahler stream order (STREAM\_ORDER; Strahler, 1957), indicating the level of branching of a stream, and (2) the density of barriers to flow (e.g. dams, weirs, dykes) within stream reach (DENS\_BAR; number per stream reach meter) using the ROE database (Référentiel des Obstacles à l'Écoulement © - OFB).

### 2.2.2 Land use, topography and climate variables

Land use data were extracted from the third level of the Corine Land Cover database (CLC 2012 © DB). Only the 31 land use classes likely to be found in our study area or that describe a terrestrial habitat expected to be used by the Pyrenean brook newt, were selected. These 31 classes were then aggregated into six land use categories (Tab. 1). From the resulting land use map, we computed the proportion of each of the six land use category within a 100 m buffer around each stream reach.

We computed two variables describing the topography of each stream reach: the slope (%) (SLO) and the minimum elevation of the reach (m) (MIN\_EL). Both were derived from the 25 x 25 m DEM (ALTI © DB).

Climate was described by the mean annual precipitation (mm) (PRECmean) and the mean monthly maximum air temperature (°C) (TMPmax) for the 1990-2011 period. We used air temperature as a surrogate for water temperature (Domisch, Jähnig, & Haase, 2011) because we did not have access to direct measures or estimates of water temperature for the 63 119 stream reaches.

## 2.3 Occurrence records

Occurrence records (i.e. presence-only) of the Pyrenean brook newt in the French Pyrenees were extracted from the database gathered by naturalist associations, environmental consulting companies, environmental agencies and research groups likely to have information about the species. This database includes 1658 geolocalized records collected from 1990 to 2019. Among them, we kept only the oldest record for stream reaches having multiple records. We also removed records in lakes and in hypogean habitats as this study is focused only on stream-dwelling populations of the Pyrenean brook newt, resulting in a dataset of 1035 occurrence records between 1990 and 2019. As the environmental variables were compiled from sources dating back to 2012 (i.e. land use) or were simulated over a pre-2012 period (i.e. climate and hydrology), we only used occurrence records between 1990 and 2011 dataset to build the Pyrenean brook newt distribution model. This data filtering resulted in a final dataset of 654 stream reaches where the Pyrenean brook newt has been observed at least once between 1990 and 2011 (Fig. 1).

#### *2.4 MaxEnt modelling of the distribution of the Pyrenean brook newt*

We fitted a distribution model relating the Pyrenean brook newt occurrence records to the set of environmental variables using the Maximum Entropy species distribution software (MaxEnt; Phillips, Anderson, & Schapire, 2006). MaxEnt estimates the suitability of one place given environmental constraints (i.e. environmental variables) in the covariates space and provides suitability index ranging continuously from 0 (least suitable) to 1 (most suitable) for each place.

##### *2.4.1 Model settings*

Prior to modelling, all environmental variables, except `STREAM_ORDER`, were log-transformed (or  $\log+1$  for variables with zero values) to approximate Gaussian distribution. In addition to species presence data, MaxEnt requires background data to build the model. Background locations, also called pseudo-absences, are locations where presence/absence of the species is unknown, representing the range of environmental conditions in the study area. To account for potential spatial bias in species presence data due to unequal sampling effort, while providing accurate representation of environmental variations in the study area, we followed the recommendations of Barbet-Massin, Jiguet, Albert, & Thuiller (2012) and Phillips & Dudík (2008). We selected a set of 10 000 background stream reaches in the study

area, excluding the stream reaches where the Pyrenean brook newt presence is known. Both background data and species occurrence records were thus biased in the same manner (Phillips & Dudík, 2008). However, the spatial bias in sampling is expected to be low, as Pottier et al. (2021) suggested that the current distribution of the Pyrenean brook newt in France is now relatively well known due to huge sampling efforts since the 1990s. We ran MaxEnt in logistic format to get an estimation of the probability of presence, given the environmental conditions (Phillips & Dudík, 2008), and we used quadratic feature type to approach unimodal species response to environmental variables (Austin, 2007).

#### 2.4.2 Model predictive performances

We followed a 10-fold cross-validation procedure with ten replicates using the Pyrenean brook newt occurrence records from 1990 to 2011. For each replicate, the occurrence dataset ( $N = 654$ ) was randomly partitioned into 10 equal size subsamples: one single subsample was used as testing data and the remaining nine subsamples as training data. Performances of the model were averaged across the 10 repetitions and evaluated using four metrics: (i) AUC of the receiver operating characteristic (ROC) plot, (ii) True Skill Statistics (TSS), (iii) sensitivity (i.e. proportion of occurrence records correctly predicted as suitable), and (iv) specificity (i.e. proportion of pseudo-absences correctly predicted as unsuitable). An AUC value close to one indicates a model accurate in discriminating between presence and pseudo-absences (Pearce and Ferrier 2000). TSS, sensitivity and specificity require binary predictions instead of continuous probabilities to be computed. We used the threshold value maximizing the sum of sensitivity and specificity to transform probabilities (Liu, White, & Newell, 2013). TSS ranges from  $-1$  to  $1$ , where one indicates perfect fitting and values of zero or less indicate a performance no better than random.

#### 2.4.3 Contribution of environmental variables in driving the Pyrenean brook newt distribution

We estimated the relative contribution of each environmental variable to explain the Pyrenean brook newt distribution using the average permutation importance measure (PI) over the 10 replicates (Iannella, Cerasoli, & Biondi, 2017; Phillips, 2017). As there is no commonly accepted guidelines for the interpretation of PI values, we used the scree test method (Cattell, 1966) to decide how many variables should be retained as influential. From the graph showing the descending permutation importance accounted for by the factors

extracted in the MaxEnt analysis, we considered the variables before the first slope break, as influencing the most the distribution of the Pyrenean brook newt. Species response curves, showing the mean response across the 10 replicates to the most contributing environmental variables, were also drawn to explore the way (i.e. direction and magnitude) each variable drives the distribution of the Pyrenean brook newt.

### **3. Results**

#### *3.1 Stream flow simulations*

Overall, stream flow simulations were satisfactory regarding values of evaluation metrics at gauging stations used for calibration over the calibration period (mean across the 11 SWAT projects  $\pm$  SD: NSE =  $0.61 \pm 0.13$ ,  $R^2 = 0.73 \pm 0.11$ , Pbias =  $-8.8 \pm 13.86$ , KGE =  $0.61 \pm 0.24$ ; Tab. 2, Appendix 2). The PA\_east, PA\_west and PA\_center models were accurate according to the four evaluation metrics, while the HP\_east model was inaccurate based on NSE value and the PO\_center model based on the Pbias value (Tab. 2). However, all models had an acceptable  $R^2$  and KGE. When computed for observed data for the first validation period (i.e. 1990-1998) at gauging stations used for calibration, NSE ranges from 0.47 to 0.83,  $R^2$  from 0.6 to 0.89, Pbias from -32.66 to 24.4 and KGE from 0.41 to 0.77. For the second validation period (i.e. 1999-2011), NSE ranges from 0.55 to 0.85,  $R^2$  from 0.56 to 0.88, Pbias from -25.5 to 36.01 and KGE from 0.5 to 0.85. At four gauging stations used only for validation, located in four distinct watersheds (i.e. PA\_center, Ar\_center, Aude, and PO\_center), the NSE value was negative (i.e. the observed mean is a better predictor than the simulated mean) for the three periods tested. These results highlight that hydrographs did not perfectly match in terms of structure of time series. However, mean values of Pbias ( $-14.69 \pm 51.57$ ) and  $R^2$  ( $0.46 \pm 0.3$ ) at these gauging stations for the three periods indicated that simulated data were globally in the same range as the observed data. Negative NSE values likely result from gauging stations located in headwater streams in karstic regions. We suspect that flow in these streams strongly depends on groundwater flux processes, that require higher resolution spatial inputs than those used in this study, to be simulated at the Pyrenees scale (Storey, Howard, & Williams, 2003). In the other gauging stations used only for validation (n=11), the mean NSE for the three periods tested was  $0.41 (\pm 0.26)$ , the mean  $R^2$  was  $0.66 (\pm 0.15)$ , the mean Pbias was  $-1.08 (\pm 30.03)$  and the mean KGE was  $0.45 (\pm 0.2)$  (Tab. 2), indicating acceptable simulations. To assess whether the highlighted discrepancies between observed and simulated flows (Appendix 2) could affect hydrological variables

included in MaxEnt model, we compared observed and simulated Q10. The difference was found not significant (Paired t-test:  $p = 0.09$ ).

### 3.2. Flow intermittence

For three watersheds (i.e. PA-center, PA-west and PO-east), no stream reach was clearly identified by the experts as being intermittent. Consequently, we used the zero-flow threshold defined in the closest watershed as an approximation (Tab. 3). The zero-flow threshold was  $0.022 \pm 0.035 \text{ m}^3/\text{s}$  on average across the 11 watersheds. About 70% of the intermittent stream reaches of the TOPO © DB were classified as intermittent when applying the zero-flow threshold identified from our SWAT simulations (Tab. 3). Three models had nevertheless a lower proportion of intermittent reaches shared with the TOPO © DB: HP-west, PA-center and PA-west. For PA-center and PA-west, this may result from the use of the zero-flow threshold of PA-east combined with poor performances of SWAT simulations. For HP-west, the zero-flow threshold identified from the expert judgement was the highest ( $0.124 \text{ m}^3/\text{s}$ ). Additionally, HP-west was the only model for which the intermittent stream reaches identified by the expert matched with perennial reaches in the TOPO © DB. This result points out the limit of using a subjective judgement rather than an objective method to characterize zero-flow.

Among the 63 119 stream reaches covering the study area, 80.7% (50 980) reaches had at least one month of zero-flow over the 1990-2011 period. Among them, 26.1% (13 330) reaches were simulated to be dry over the whole study period. They are mainly first-order stream reaches (76%). This leads to a proportion of 59.6% of the Pyrenean river network being classified intermittent when excluding these permanently dry streams. Perennial reaches were the large main rivers while the intermittent reaches were mainly located upstream of catchments (Appendix 3). The metric *FREQ* varied between 1 and 60 zero-flow events across the intermittent reaches, with a median of 11 events between 1990 and 2011 (i.e. 0.5 event per year). Duration of zero-flow events (*DUR*) ranged from one to 264 months (i.e. the whole study period) with a median of 6.3 months (i.e. 0.3 month per year). Intermittent reaches with at least one month of flowing water between 1990 and 2011 (i.e. not totally dry during the whole study period) had a median zero-flow duration of 3.5 months (i.e. 0.16 month per year).

Finally, 70.5 % of the 654 occurrence records of the Pyrenean brook newt used in MaxEnt modelling are located in intermittent stream reaches.

### 3.3. MaxEnt modelling

Performances of MaxEnt in predicting the distribution of the Pyrenean brook newt was satisfactory, with a mean  $\pm$  SD AUC of  $0.803 \pm 0.002$  over the 10 replicates and TSS of  $0.483 \pm 0.043$ . Applying the most accurate logistic threshold (mean =  $0.390 \pm 0.016$ ) to transform probabilities in binary predictions, a mean sensitivity of  $0.736 \pm 0.037$  and a mean specificity of  $0.747 \pm 0.013$  were found.

Regarding the importance of variables driving the distribution of the Pyrenean brook newt, all categories of environmental variables were influential, except topography, with a cumulative permutation importance (PI) of only 3% (Fig. 4). Land use and hydrological categories were the most important ones, each contributing to 35.2% in explaining species distribution.

Climate has a cumulative PI of 26.4%, driven almost exclusively by temperature (precipitation mean PI = 0.1%). The scree test suggested that individually, monthly maximum air temperature (26.3%), proportion of agricultural areas (21.2%) and frequency of zero-flow events (13%) were the three variables contributing the most (Fig. 4). For those three variables, the cumulative PI reached 60.5%, indicating that they are strong drivers of the Pyrenean brook newt distribution. Environmental suitability of stream reaches for the Pyrenean brook newt decreased as maximum air temperature, proportion of agricultural areas and frequency of zero-flow events increased (Fig. 5).

### 3.4. *The Pyrenean brook newt prefers cold headwater streams, surrounded by natural areas and with low flow intermittence*

Consistently with accurate predictive performances of the MaxEnt model, the map of predictions (Fig. 6) reveals that presence records overlap mainly with the most suitable predicted stream reaches that are predominantly located in headwaters.

In the most unsuitable intermittent stream reaches (i.e. predictions of habitat suitability between 0 and 0.39), we found a mean of 14.4 no-flow events occurred over the 22-year study period, that is one dry event every 18 months, against a mean of five no-flow events,



that is one dry event every 53 months, in the most suitable intermittent stream reaches (i.e. between 0.8 and 1). We also found a mean monthly maximum temperature of 6.3°C and the absence of agriculture in the most suitable stream reaches, against a mean of 14.8°C and a mean proportion of 29.9% of agricultural areas in the most unsuitable stream reaches.

In addition, our results indicated that 168 of the 654 stream reaches where the Pyrenean brook newt has been recorded between 1990 and 2011 are predicted to be unsuitable (i.e. predictions of habitat suitability between 0 and 0.39), resulting in predicting an absence while the species has been observed (Fig. 6). These predictions are mainly located at low elevation (Fig. 6).

## **4. Discussion**

### *4.1. New insights about flow intermittence in the French Pyrenees*

Flow intermittence is rarely considered in river management, often due to a lack of available data, whereas it is acknowledged to be a key determinant for freshwater biodiversity and ecosystem functioning (Acuña, Hunter, & Ruhí, 2017). In this study, the absence of available data on flow intermittence across the whole French Pyrenees at the stream reach spatial grain, makes us call on expert judgement to get field information about flow conditions during the driest period. This approach is increasingly used for the understanding of flow dynamic as it can provide a low-cost and accurate evaluation of flow variations at fine grain (Turner & Richter, 2011).

In France, Snelder et al. (2009, 2013) conducted a study to understand patterns of flow intermittence at fine spatial grain (i.e. mean length of reaches = 2.5 km), using data from gauging stations. They predicted 39% of the French river network to be intermittent, especially in warm and dry locations. This proportion is driven by the quite rough spatial grain of their analysis and does not highlight intermittent streams in mountains in comparison to our study. Exploring intermittent streams in mountainous areas requires the detection of low-order streams, which can represent more than 70% of the whole river network (Lowe & Likens, 2005), and thus needs high-performance mapping technique. As far as we know, our study is the first one in France to classify fine-grained stream reaches (i.e. mean length = 421 m) of a large mountainous area into intermittent and perennial reaches. We found 60% of the French Pyrenean river network being classified intermittent when excluding streams always dry. This value is much higher than the one predicted by Snelder et al. (2013) but this finding

is not surprising given that headwater streams in mountainous areas are the most expected to dry following snowmelt. Our results thus complement those from Snelder et al. (2013) and support the fact that intermittent rivers are abundant and present in various ecosystems. In addition, when compared with the most recent and exhaustive database including an inventory of stream flow regimes (i.e. TOPO © DB), we found that about 70% of intermittent streams were also classified as intermittent by our methodology.

We acknowledge however that more accurate measures of flow intermittence could be achieved using daily instead of monthly stream flow data. Indeed, water flow can stop for periods shorter than one month (e.g. between two intense rainfalls in summer) with implications for survival of freshwater organisms (e.g. macro-invertebrates) (Crabot, Heino, Launay, & Datry, 2020). Such shorter dry events were unfortunately not detected in our simulations (i.e. fine spatial grain but coarse temporal grain).

#### *4.2. Main drivers of the Pyrenean brook newt distribution*

Among the set of environmental variables tested, we found three variables contributing importantly to the distribution of the Pyrenean brook newt: monthly maximum air temperature, proportion of agricultural areas and frequency of zero-flow events.

The first two variables are well known drivers of aquatic species distribution (Enriquez-Urzelai, Kearney, Nicieza, & Tingley, 2019; Iannella et al., 2017; Surasinghe & Baldwin, 2015), but also of the distribution of other taxa (Redhead, Powney, Woodcock, & Pywell, 2020; Sutton, 2020). Consistently with our expectation, warm monthly maximum air temperature was found to limit the most the presence of the Pyrenean brook newt. Ectotherms such as amphibians are particularly sensitive to temperature because it can affect their physiology through thermoregulation as well as larvae survival. As our mountainous study area presents a strong temperature gradient, this is not surprising that temperature highly influences the distribution of the Pyrenean brook newt. However, Trochet et al. (2018) recently reported a more complex quadratic behavioral response of the Pyrenean brook newt to temperature that seems to be dependent on elevation. They suggested that at high elevation (i.e. >1300 m, with long snow duration), the species can compensate low opportunities of favorable temperature by selecting microhabitat with warmer temperatures for thermoregulation. Conversely, low elevation areas are more covered by forests, with colder temperature under tree canopy. The Pyrenean brook newt could have no opportunities to select microhabitat with warmer temperatures. According to the negative relationship

between temperature and species presence that we highlighted in this study, we hypothesize that forests act as local refuges given air is wetter and temperature is cooler during summer under tree cover, even in warm and dry areas located in lowlands. However, the proportion of forests surrounding stream reaches was not among the major drivers of the Pyrenean brook newt distribution.

Proportion of agricultural areas surrounding stream reaches was the second most important driver of the Pyrenean brook newt distribution in the French Pyrenees. Agricultural practices are acknowledged to have a negative impact on stream salamander richness and abundance (Surasinghe & Baldwin, 2015), and other stream species such as macroinvertebrates and fishes (Horak, Assef, Grech, & Miserendino, 2020), by reducing natural cover (mainly forest) in riparian zones and thus inducing immediate or delayed changes in nutrient cycling, water temperature or sediment transport (Utz, Hilderbrand, & Raesly, 2010; Yates & Bailey, 2010). In our study area, 22.5% of the hydrographic network is partially or totally covered by agriculture in the first 100 m of the riparian zone. These agricultural activities, mainly located in foothills, are dominated by pastures (47%) and complex cultivation patterns (33%). To date, few studies have focused on the effects of water quality on the Pyrenean brook newt (Montori, Llorente, & Nadal, 1982). Yet, chemical and physical perturbations induced by agricultural activities could affect water quality, hence limiting the Pyrenean brook newt presence (Dalibard, Buisson, Riberon, & Laffaille, 2020; Pottier et al., 2021), by affecting larval development for example (Rouse, Bishop, & Struger, 1999). Our results seem to support this hypothesis, as the most suitable stream reaches for the Pyrenean brook newt were predicted to be surrounded by no or small surfaces allocated to agriculture.

As expected, we highlighted the importance of flow intermittence on the Pyrenean brook newt distribution, with a decrease in habitat suitability when frequency of zero-flow events increases. According to our flow regime classification method, intermittent streams are dominant in the French Pyrenees. We predicted that the Pyrenean brook newt can occur in intermittent streams as long as zero-flow events remain occasional (i.e. less than one dry event every 18 months). This is not surprising as 70.5% of the species occurrence record used in MaxEnt modelling are located in intermittent stream reaches and as amphibians live both in aquatic and terrestrial habitats. Early development stages (i.e. eggs and larvae) exclusively occur in water, but adults have functional lungs (reduced for the Pyrenean brook newt; Despax, 1923) allowing them to live out of water. In addition, stream reaches with zero-flow during a time period are generally not continuous along a stream. Dry reaches can be next to

reaches where a thin but sufficient layer of water continues to flow, hence serving as refuges for the Pyrenean brook newt and its prey.

Only a limited number of recent studies have assessed ecological impacts of the frequency and duration of zero-flow events (e.g. Colls, Timoner, Font, Sabater, & Acuña, 2019; Crabot et al., 2020; Vander Vorste et al., 2020). Colls et al. (2019) showed that longer zero-flow events did significantly decrease biomass and gross primary production of biofilms in Mediterranean streams, but that their frequency had no significant impact. Crabot et al. (2020) reported that both frequency and duration of drying events strongly affected temporal dynamic of stream invertebrate communities. These aquatic organisms are the main food resource for many species in freshwater ecosystems, including the Pyrenean brook newt (Montori, 1988). Under climate change, an increase in frequency and duration of zero-flow events could directly affect this resource but also Pyrenean brook newt populations. In regions where intermittent streams are abundant (e.g. arid and semi-arid regions), dramatic climate-driven changes in stream flow are forecasted for coming years, with reduced stream flow continuity and connectivity over time and space, respectively (Jaeger, Olden, & Pelland, 2014; Reynolds et al., 2015). In mountainous regions like the Pyrenees, where we found 60% of the river network to be intermittent, reduction in stream flow is also highly plausible and is probably already occurring. For instance, Blöschl et al. (2019) reported a global trend toward more severe droughts in southern Europe since the 1960's. Thus, long-term viability of species with low dispersal rates (including the Pyrenean brook newt) in intermittent streams is questioned (Montori, Llorente, & Richter-Boix, 2008; Pottier et al., 2021). Like many other amphibian (e.g. Chinese giant salamander, Cow Knob salamander) (Jacobsen, 2019; Zhang et al., 2020) and mountainous semi-aquatic (Charbonnel et al., 2016) species, spatial range of the Pyrenean brook newt is expected to contract or at least to shift in response to both warming and increase of flow intermittence.

Although we achieved quite accurate simulations of water flow, we were not able to simulate possible persistence of water in pools or in ground, even when water stops flowing in surface. These parameters can be accounted for by SWAT during calibration process. In practice, reference data related to these environments are very rare, making difficult their inclusion in fine-grained studies. Yet, such pools or groundwater inputs are known as shelters for aquatic organisms (Clergue-Gazeau & Martínez-Rica, 1978; Finlay, Buhay, & Crandall, 2006). The Pyrenean brook newt is a facultative cave species, completing its life cycle on the surface or within caves, or both, depending likely on water persistence in streams and on water

temperature. As water persistence depends on processes acting at very fine spatio-temporal grains (Snelder et al., 2013), such as meteorology, geology, riverbed structure or land-cover, it seems however difficult to get such data for the whole Pyrenean brook newt range. This critical issue should be addressed for a small number of intermittent streams where the Pyrenean brook newt is present and would require intensive monitoring and precise stream and water flow characterization.

The accuracy of our MaxEnt model was satisfactory in predicting the Pyrenean brook newt distribution in the French Pyrenees. Nevertheless, we also predicted a low occurrence probability in some stream reaches whereas the Pyrenean brook newt was recorded. These predictions can result from different things. The most obvious is that the model could miss important environmental or biotic variables, being thus not accurate in predicting suitable stream reaches for the Pyrenean brook newt. Second, occurrence records sometimes come from observations of single individuals in habitats that could not reflect the habitat of the source population (e.g. individuals in active displacement, adrifted individuals). This point is an acknowledged drawback of using presence data instead of abundances to study species range (Estrada & Arroyo, 2012). Finally, even if the Pyrenean brook newt distribution is considered well described (Pottier et al., 2021) and that sampling bias is probably low over the study period, spatial autocorrelation of data is possible and could result in less precise species distribution model (Miller, 2012). The use of diagnostic tools (e.g. pooling presence-only and presence-absence data for several species) to estimate sampling bias and identify areas in which data are not reliable for statistical inference, would be a first step toward improving predictions.

#### *4.3. Perspectives for freshwater species conservation and management*

There is a growing number of intermittent streams across the world and there is now ample evidence that they have to be considered when managing freshwater ecosystems (Costigan et al., 2017; Datry et al., 2014). In spite of necessary further improvements, our stream classification methodology provides new insights and data about flow intermittence in the French Pyrenees. Such information are particularly relevant as they could help to better understand freshwater biodiversity responses to more frequent zero-flow events in coming decades. They also help to locate intermittent streams and map their distribution, that is a key step towards effective ecological status assessment in intermittent rivers and ephemeral

streams (Stubbington et al., 2018). Including the outputs of hydrological models into SDMs is increasingly used when exploring relationships between freshwater species and environment. This methodology has recently demonstrated its ability to provide more accurate predictions of habitat suitability (Charbonnel et al., 2015; Kuemmerlen et al., 2014). However, a variety of hydrological metrics can be considered, like indicators of flow regime (e.g. frequency and duration of flow and no-flow periods) or flow magnitude (e.g. low- and high-flow), which can influence ecohydrological processes in different ways, as illustrated by Colls et al. (2019). Accounting for flow intermittence is of major concern, given the global coming trend towards more severe droughts (Blöschl et al., 2019; Jaeger et al., 2014). It would likely improve freshwater species distribution modelling provided that fine-grained spatial and temporal flow data are available at the scale of the study. Ecological responses of aquatic or semi-aquatic species to increasingly flow alterations should also be investigated at fine grain to comply with local management opportunities within the context of the European Water Framework Directive.

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### **Data Availability Statement**

Data are available from the authors upon reasonable request.

### **Conflict of Interest Statement**

The authors declare no conflict of interest.

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**Table 1.** Environmental variables computed for each of the 63 119 stream reaches and included in MaxEnt modelling.

Category	Variables	Description	Source
Hydrology	Q10	Monthly stream flow that is observed or exceeded 10% of the time (m <sup>3</sup> /s)	SWAT output
	Fr	Froude number (proxy for hydraulic turbulence)	SWAT output
	FREQ	Number of zero-flow events over the 1990-2011 period	SWAT output
	DUR	Mean duration of zero-flow events over the 1990-2011 period (months)	SWAT output
	cvDUR	Coefficient of variation in duration of zero-flow events (months)	SWAT output
	STREAM_ORDER	Strahler stream order indicating the level of branching of the stream reach	SWAT output
	DENS_BAR	Density of barriers to flow within the stream reach (number per meter)	ROE © DB
Land use	WET	Percentage of inland wetlands	CLC 2012 © DB
	ART	Percentage of artificial surfaces	CLC 2012 © DB
	AGRI	Percentage of agricultural areas	CLC 2012 © DB
	FOREST	Percentage of forest and semi-natural areas	CLC 2012 © DB
	NO_VEG	Percentage of open spaces with little or no vegetation	CLC 2012 © DB
	HERB	Percentage of shrub and/or herbaceous vegetation associations	CLC 2012 © DB
Topography	MIN_EL	Minimum elevation (m)	ALTI © DB
	SLO	Slope (%)	ALTI © DB
Climate	PRECmean	Mean annual precipitation over the 1990-2011 period (mm)	SAFRAN © DB
	TMPmax	Mean monthly maximum air temperature over the 1990-2011 period (°C)	SAFRAN © DB

**Table 2.** Calibration and validation performances for the 11 SWAT projects: NSE, R<sup>2</sup>, PBias and KGE, at gauging stations used for calibration and validation (n°1 for each project) and at gauging stations used for validation only (n°2 and/or n°3 for each project), for three periods (calibration: 1996-2000, validation 1: 1990-1998, validation 2: 1999-2011). PA\_west = Pyrenees-Atlantique-west; PA\_center = Pyrenees-Atlantique-center; PA\_east = Pyrenees-Atlantique-east; HP\_west = Hautes-Pyrenees-west; HP\_east = Hautes-Pyrenees-east; HG = Haute-Garonne; Ar\_west = Ariège-west; Ar\_center = Ariège-center; Aude = Aude; PO\_center = Pyrenees-Orientales-center; PO\_east = Pyrenees-Orientales-east (see Figure 2).

Project ↓	Period →	Calibration				Validation 1				Validation 2			
	Gauging station ↓	NSE	R <sup>2</sup>	PBias (%)	KGE	NSE	R <sup>2</sup>	PBias (%)	KGE	NSE	R <sup>2</sup>	PBias (%)	KGE
PA_west	n°1	0.68	0.76	-15.83	0.68	0.74	0.79	-17.56	0.68	0.69	0.74	-14.21	0.70
	n°2	0.48	0.65	-26.48	0.54	0.46	0.64	-32.40	0.45	0.56	0.68	-24.61	0.58
PA_center*o	n°1	0.73	0.75	0.72	0.64	no observed data				no observed data			
	n°2	0.32	0.77	53.34	0.39	0.39	0.77	56.24	0.39	0.32	0.77	53.34	0.42
	n°3	-0.01	0.52	-40.20	0.16	-0.02	0.43	-32.09	0.13	-0.02	0.52	-40.24	0.16
PA_east	n°1	0.82	0.84	6.50	0.82	0.83	0.85	-5.64	0.77	0.85	0.87	6.42	0.85
	n°2	0.42	0.81	28.09	0.48	0.50	0.83	-31.42	0.49	0.48	0.82	-29.80	0.49
HP_west	n°1	0.57	0.68	-8.02	0.66	0.56	0.63	-8.95	0.62	0.80	0.83	-7.21	0.81
	n°2	0.39	0.66	-18.29	0.60	0.37	0.58	-16.97	0.54	0.74	0.81	-9.23	0.77
HP_east	n°1	0.40	0.66	-9.22	0.55	0.54	0.67	-15.64	0.64	0.62	0.70	-8.64	0.68
	n°2	0.34	0.76	8.99	0.45	0.45	0.75	11.28	0.56	0.45	0.81	11.43	0.51
	n°3	0.62	0.76	-9.48	0.69	0.65	0.70	-12.24	0.67	0.43	0.55	-13.35	0.53
HG	n°1	0.59	0.72	19.48	0.51	0.47	0.74	-32.66	0.41	0.55	0.74	-25.50	0.54
	n°2	0.45	0.52	16.69	0.37	0.52	0.60	-19.77	0.45	0.53	0.63	-19.42	0.45
Ar_west	n°1	0.58	0.59	-1.89	0.57	0.64	0.67	-2.66	0.67	0.66	0.68	6.72	0.66
	n°2	0.71	0.72	7.87	0.69	0.73	0.77	-13.51	0.62	0.72	0.73	-5.04	0.70
	n°3	0.36	0.44	15.69	0.36	0.45	0.55	-18.40	0.48	0.51	0.56	-13.77	0.44
Ar_center	n°1	0.56	0.72	10.36	0.65	0.75	0.76	3.47	0.76	0.81	0.83	6.06	0.81
	n°2	0.01	0.60	-47.04	0.19	0.22	0.66	-43.13	0.26	0.19	0.66	-42.80	0.22
	n°3	-1.60	0.78	66.75	-0.09	-0.65	0.80	55.72	0.11	-1.24	0.82	66.97	0.01
Aude	n°1	0.51	0.57	10.21	0.56	0.56	0.60	3.78	0.59	0.48	0.56	-9.44	0.55

<b>PO_center</b>	<b>n°2</b>	-0.09	0.45	-3.28	-0.10	-0.12	0.78	-75.41	-0.10	-0.22	0.32	-84.05	-0.37
	<b>n°1</b>	0.51	0.87	34.74	0.51	0.58	0.76	24.40	0.63	0.59	0.82	26.68	0.60
	<b>n°2</b>	-0.56	0.07	-24.90	0.03	-0.40	0.08	-32.00	-0.03	-0.74	0.01	-33.56	-0.08
<b>PO_east*</b>	<b>n°3</b>	0.40	0.83	30.87	0.49	-0.20	0.65	36.30	0.31	-0.55	0.53	62.17	0.11
	<b>n°1</b>	0.63	0.89	32.57	0.51	0.78	0.89	4.92	0.71	0.59	0.88	36.01	0.50
	<b>n°2</b>		no observed data				no observed data			-2.91	0.01	18.28	-0.28

\*: projects for which observation data from one gauging station are missing for the calibration and/or validation periods. Simulations were thus assessed based on the performances measured at the other gauging stations of the project.

○: project for which observation data from gauging station n°1 are missing for the calibration period 1996-2000, and for which another calibration period was used (2006-2010). Validation periods at gauging stations used for validation have been adjusted accordingly (validation 1: 1990-2007; validation 2: 2008-2011).

**Table 3.** Comparison between the number of intermittent stream reaches identified from SWAT simulations and expert judgment, and derived from the independent database (TOPO © DB - IGN). N(Reference) is the number of reference intermittent stream reaches identified by the experts, N(Simulations) and N(TOPO) are the number of intermittent reaches derived from the SWAT simulations, and from the TOPO database, respectively. For N(Simulations) and N(TOPO), the percentage of the total number of stream reaches in each model is indicated. N(Simulations+TOPO) is the total number of unique intermittent reaches found both from SWAT simulations and the TOPO database. The shared percentage is the percentage of intermittent reaches from the TOPO database that is also classified as intermittent from SWAT simulations. PA\_west = Pyrenees-Atlantique-west; PA\_center = Pyrenees-Atlantique-center; PA\_east = Pyrenees-Atlantique-east; HP\_west = Hautes-Pyrenees-west; HP\_east = Hautes-Pyrenees-east; HG = Haute-Garonne; Ar\_west = Ariège-west; Ar\_center = Ariège-center; Aude = Aude; PO\_center = Pyrenees-Orientales-center; PO\_east = Pyrenees-Orientales-east (see Figure 2).

Model	N(Reference)	Zero-flow threshold (m <sup>3</sup> /s)	N(Simulations)	N(TOPO)	N(Simulations+TOPO)	Shared percentage (%)
PA_west	0	same as PA_east	2299 (55%)	1448 (35%)	2617	52.76
PA_center	0	same as PA_east	2542 (51%)	2261 (45%)	3673	49.98
PA_east	2	0.029	3249 (55%)	2071 (35%)	3958	65.77
HP_west	12	0.124	1996 (29%)	1968 (29%)	3501	23.53
HP_east	5	0.003	4390 (71%)	2153 (35%)	4644	88.2
HG	4	0.012	2536 (65%)	1666 (43%)	2827	82.53
Ar_west	2	0.001	3830 (58%)	3064 (46%)	4847	66.81
Ar_center	11	0.009	6483 (69%)	3830 (40%)	6949	87.83
Aude	9	0.008	5147 (69%)	3516 (47%)	5652	85.64
PO_center	8	0.001	3516 (66%)	2498 (47%)	4057	78.34
PO_east	0	same as PO_center	1694 (77%)	918 (42%)	1754	93.46

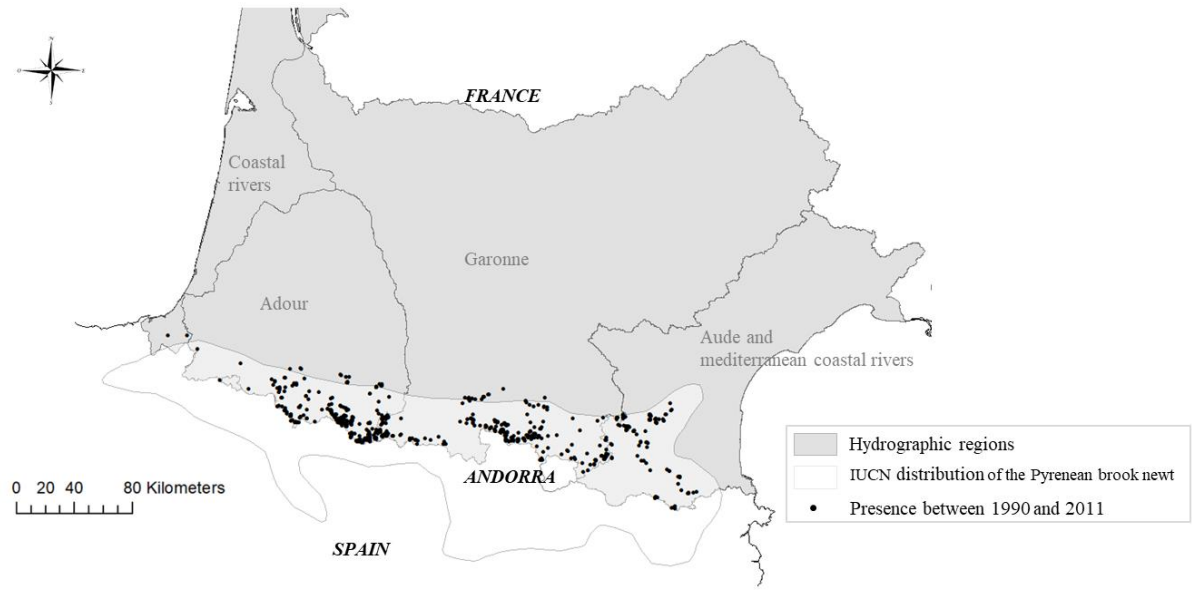


Figure 1. Study area and occurrence records (i.e. presence-only) of the Pyrenean brook newt (1990-2011). The white transparent area shows the distribution of the Pyrenean brook newt according to the IUCN (Bosch et al., 2009).

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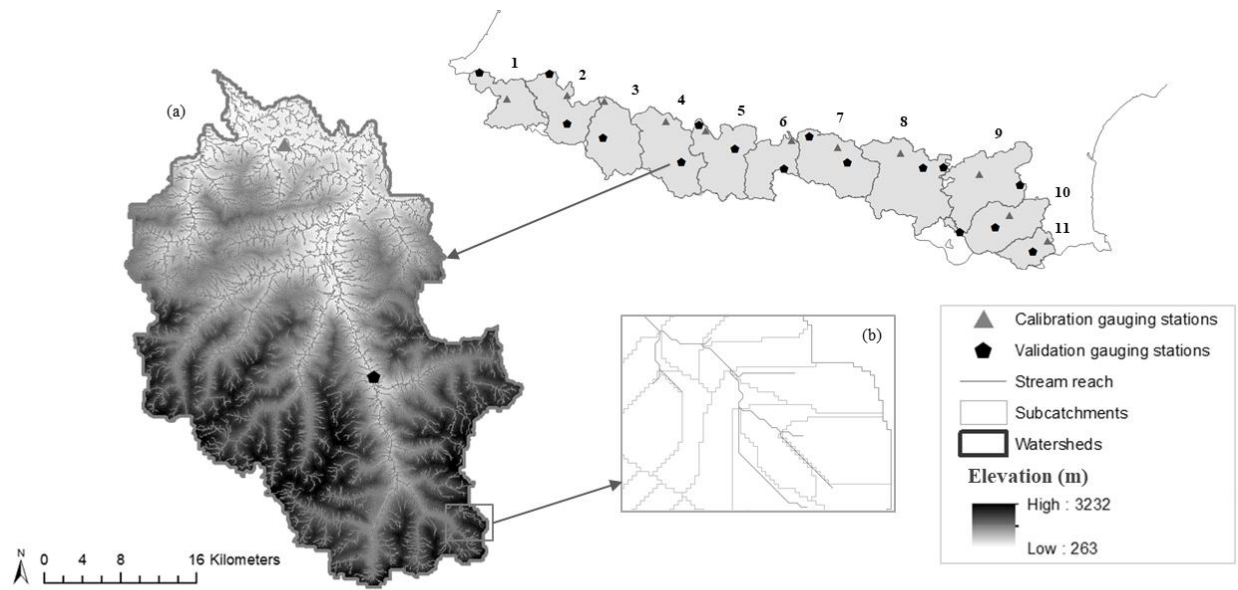


Figure 2. Map of the 11 SWAT projects covering the study area (1: Pyrenees-Atlantique-west, 2: Pyrenees-Atlantique-center, 3: Pyrenees-Atlantique-east, 4: Hautes-Pyrenees-west, 5: Hautes-Pyrenees-east, 6: Haute-Garonne, 7: Ariège-west, 8: Ariège-center, 9: Aude, 10: Pyrenees-Orientales-center, 11: Pyrenees-Orientales-east). Gauging stations used for calibration are displayed by a grey triangle and those for validation by a dark hexagon. Zoom in (a) shows the stream network of the project 4 (grey lines) and inset (b) indicates stream reaches with associated subcatchments (light grey outlines).

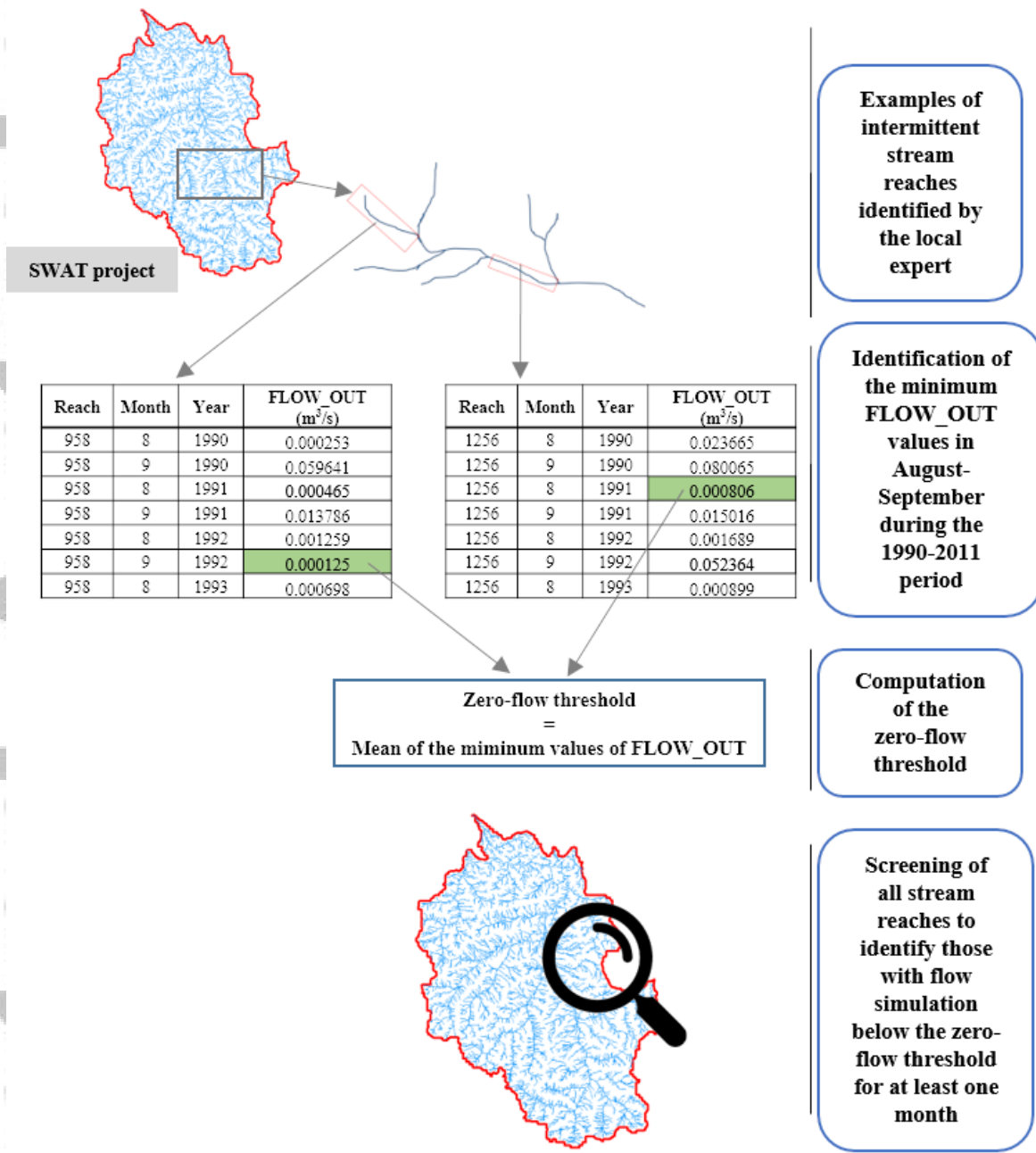


Figure 3. Steps to identify the zero-flow threshold derived from the stream reaches known to be intermittent by local experts. An example is given for the SWAT project 4. Stream reaches in the SWAT project for which monthly flow is below the zero-flow threshold for at least one month during the period 1990-2011 are assigned to the intermittent category, and the remaining to the perennial category.



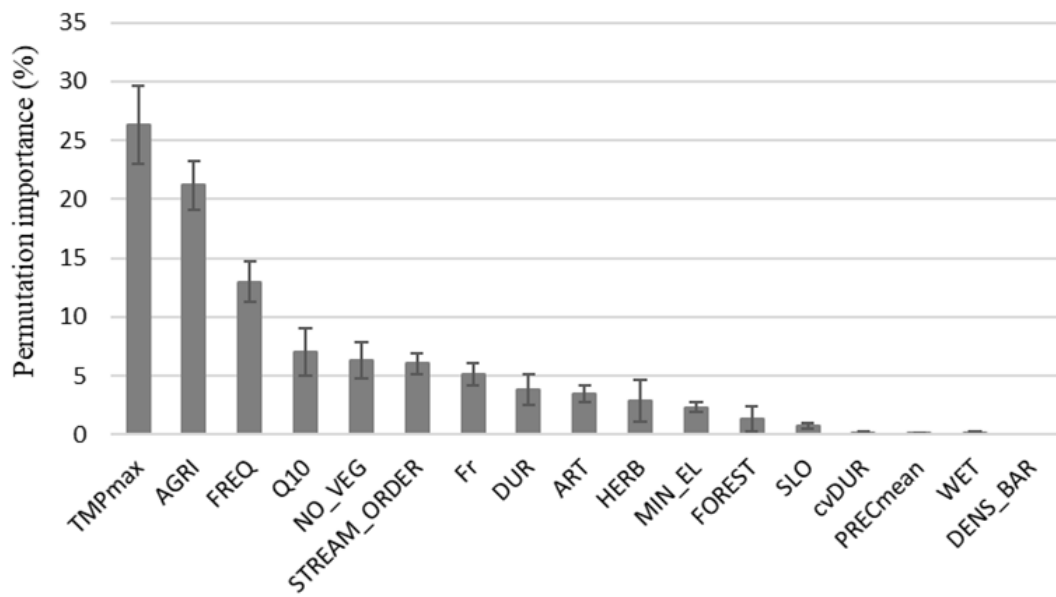


Figure 4. Descending mean and standard deviation permutation importance (PI) of environmental variables in MaxEnt modelling of the Pyrenean brook newt distribution, over 10 replicates.

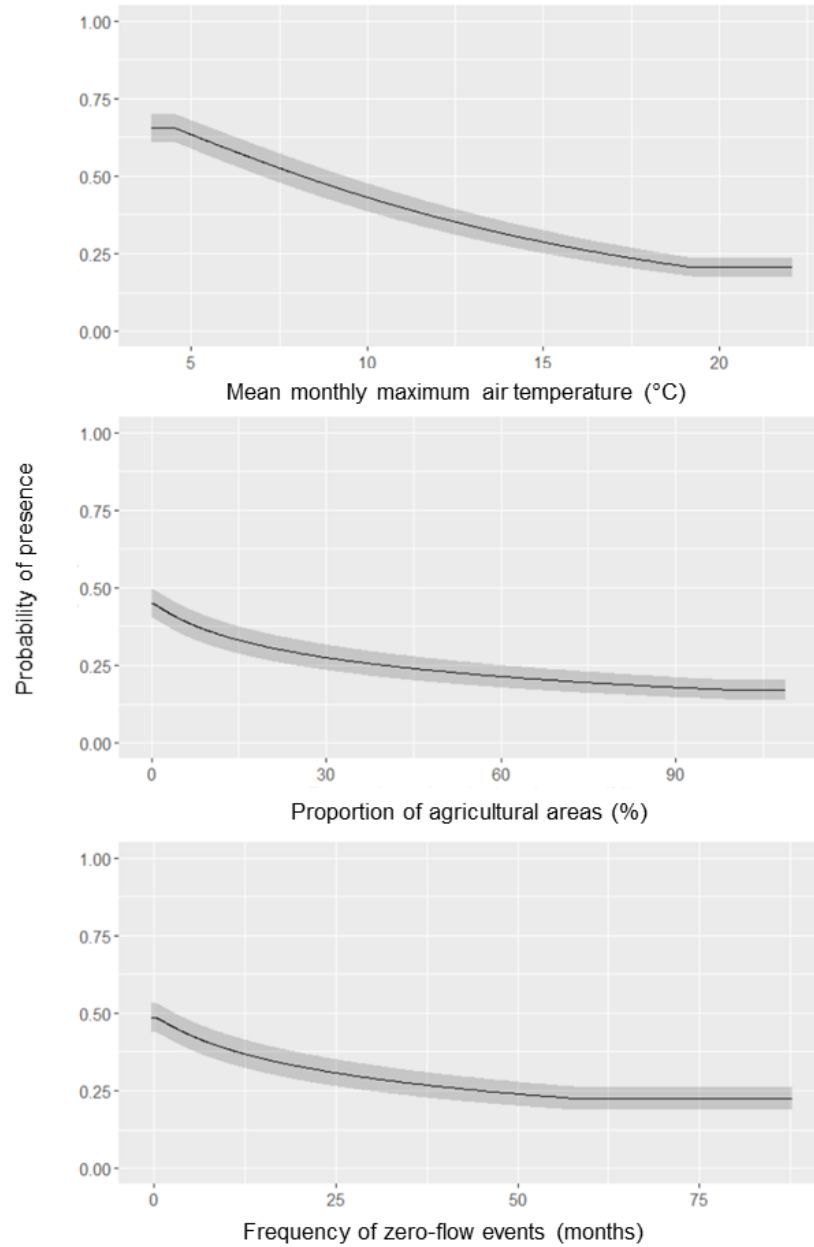


Figure 5. Response curves for the three environmental variables driving the most the Pyrenean brook newt distribution. The curves show how the predicted probability of presence changes according to each variable, keeping all the other variables at their average value. The black line indicates the mean response over 10 replicates and the grey area represents standard deviation.

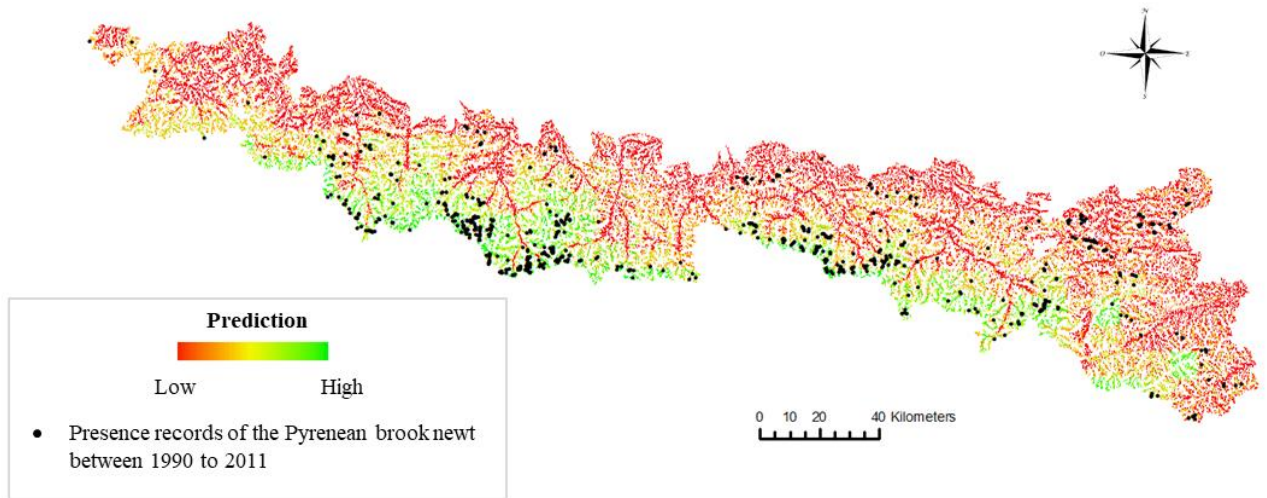
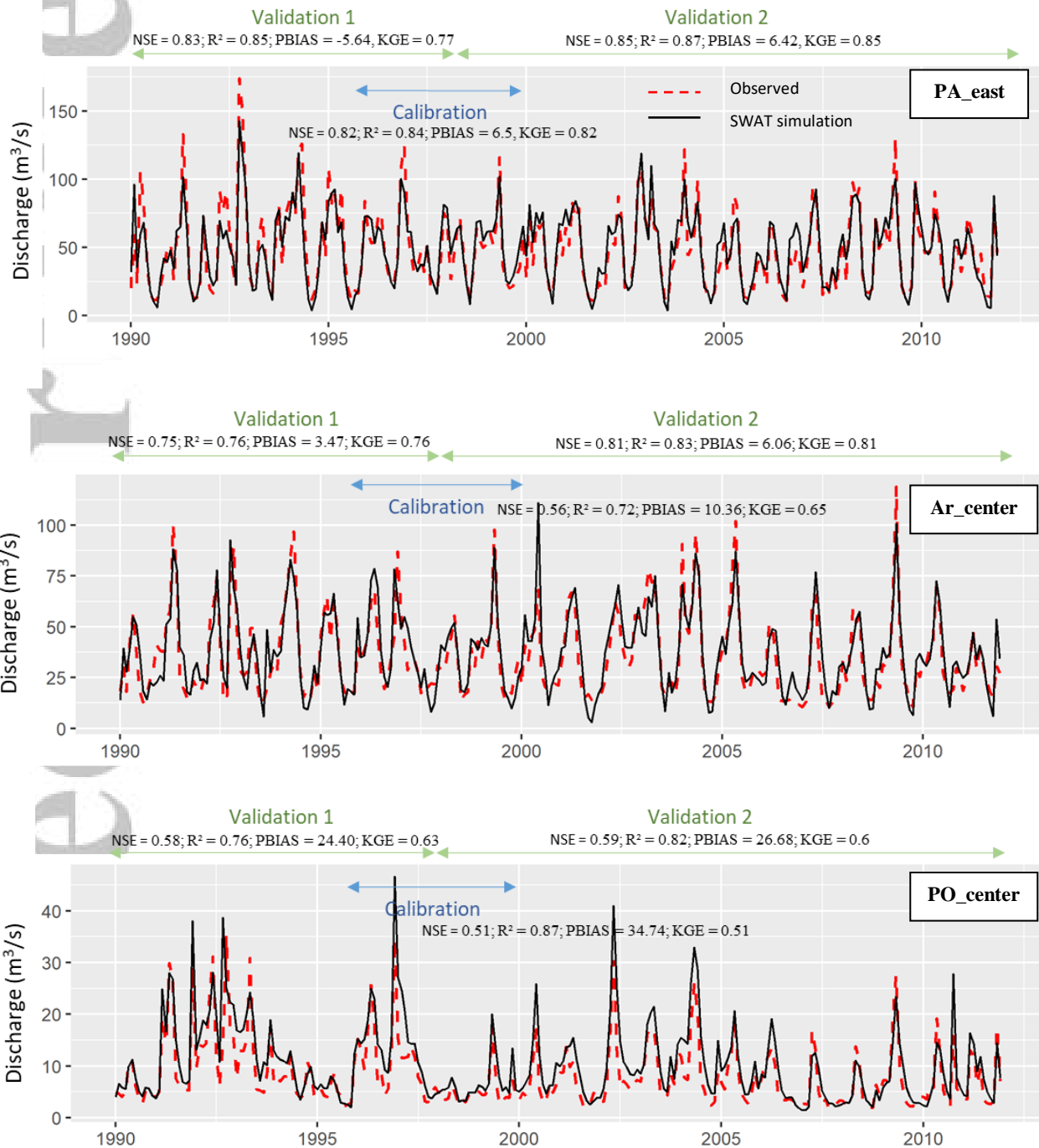


Figure 6. Habitat suitability predicted for the Pyrenean brook newt and presence records (1990-2011).

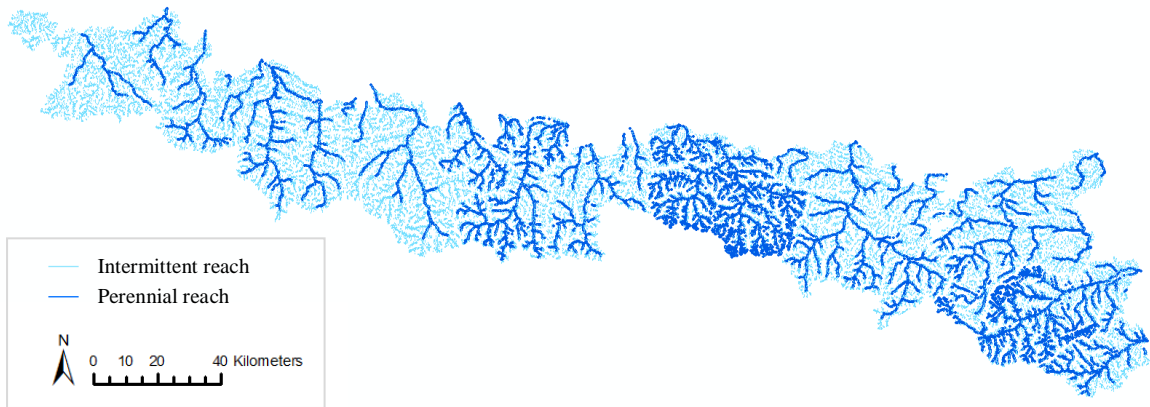
Accepted A

**Appendix 1.** SWAT sensitive parameters, default values and range of values (minimum and maximum) used during calibration process. For CN2 and SOL\_AWC, the default value is given by land cover and soil maps and databases.

Parameters	Description	Range		Default
		Min	Max	
SFTMP	Snowfall temperature (°C)	1	1.3	1
SMTMP	Snowmelt base temperature (°C)	0.5	1.97	0.5
TIMP	Snowpack temperature lag factor	0.14	1	1
SMFMX	Maximum melt rate for snow during year (mm H2O/°C-day)	4.5	4.96	4.5
SMFMN	Minimum melt rate for snow during year (mm H2O/°C-day)	3.16	4.5	4.5
SNOCOVMX	Snow water content that corresponds to 100% snow cover (mm H2O)	1	38.38	1
GW_Delay	Groundwater delay time (days)	4.63	31	31
GW_Revap	Groundwater “revap“ coefficient (-)	0.02	0.1	0.02
GWQMN	Threshold depth of water in the shallow aquifer required for return flow to occur (mm H2O)	1000	1035	1000
ALPHA_BF	Baseflow alpha factor (1/days)	0	0.23	0.01
REVAPMN	Threshold depth of water in the shallow aquifer for “revap” or percolation to the deep aquifer to occur (mm H2O)	1	800	1
RCHRG_DP	Deep aquifer percolation fraction (-)	0.04	0.7	0.05
ESCO	Soil evaporation compensation factor (-)	0.56	0.95	0.95
CN2	Initial Soil Conservation Service (SCS) runoff curve number for moisture condition II (-)	HRU	+10%	HRU
SOL_AWC	Available water capacity of the soil layer (mm H2O/mm soil)	-10%	Soil layer	Soil layer



**Appendix 2.** Hydrographs of observed (dotted red line) and simulated (black line) flow at three gauging stations used for SWAT calibration (one for each of the three hydrographic regions of the Pyrenees: PA\_east = Adour region, Ar\_center = Garonne region, PO\_center = Aude region)



**Appendix 3.** Stream reach intermittence. Perennial streams (FREQ = 0) are shown in dark blue while intermittent streams (FREQ > 0) are in light blue.

## CONFLICT OF INTEREST STATEMENT

Manuscript title: **Flow intermittence and freshwater species distribution modelling**

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