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Hydroperiod of temporary ponds threats amphibian recruitment in Mediterranean environments

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Abstract. Climate change threatens amphibians because they depend on water availability. The amount of time that a pond is filled with water – the hydroperiod – may play an important role in larval development and recruitment. Nevertheless it is usually not taken into account when predicting future species trends. We evaluated the role of the hydroperiod in the abundance of five amphibian species in temporal ponds of a Moroccan forest during a seven-year period. Particularly, we characterized the ponds and compared the climatic variables affecting our system with the previous eight-year period. We tested the relationship between rainfall and hydroperiod, and we identified the best predictor of amphibian abundance. Our data showed that the last seven years were drier than the previous eight, being three of them so dry that none of the amphibian species bred successfully in those seasons. We demonstrated that hydroperiod was the best predictor of the abundance of amphibian species and affected the amphibian community composition. The rainfall was correlated with the hydroperiod and the number of ponds filled. Species with long larval periods such as the endangered Moroccan spadefoot toad and the sharp ribbed newt might be more vulnerable to climate change since they need longer hydroperiods to develop. However, widespread species with shorter hydroperiods such as the Mauretanian toad or the stripeless tree frog might be favoured. In order to predict accurately amphibian species trend under climate change scenarios and to develop adequate conservation strategies, hydroperiod should be considered in both the models and mitigation actions.

Keywords: amphibians, climate change, hydroperiod, Morocco, rainfall.

Introduction

Climate change presents a particular challenge for amphibians because of their vulnerability to environmental conditions, especially water availability (Thorson, 1955; Bucklet and Jetz, 2007). Rainfall and hydrological regimes have a major impact on amphibian breeding dynamics and influence population trends at long scale (Alford and Richards, 1999; Wellborn et al., 1996), being often used to predict population trends (Rodriguez-Rodriguez et al., 2020). However, the critical factor that affects survival of the larvae of pond-breeding amphibians is the hydroperiod, the duration of water in a pond (Babbitt, 2005; Díaz-Paniagua et al., 2010; Cayuela et al., 2012), which not only depends on the rainfall, but also in the size and depth of the pond, the type of soil, the vegetation and the temperature (Babbit, 2005; Scott and Metts, 2011). Hydroperiod and some associated variables have been postulated to be a major cue in driving metamorphosis (Merila et al., 2000), e.g., the increase of water temperature related to the desiccation of a pond affects the length of the larval period by speeding the develop-

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ment (Harkey and Semlitsch, 1988). In addition, the community structure of pond-breeding amphibians also depends on the hydroperiod, because it constraints the larval period (impeding some species to breed) and affects larval competition (e.g., Semlitsch et al., 1996). Unfortunately, hydroperiod will be altered by climate change since hydrological and seasonal weather patterns will shift (McMenamin et al., 2008; Brooks, 2009; Amburgey et al., 2012). For instance, longer periods of drought and heavy rains are expected in the Mediterranean basin, affecting the temperature of the water and the evaporation rate and, therefore, the speed and timing of pond desiccation (Sanchez et al., 2004).

Mediterranean temporary ponds of natural origin are usually water-filled during the wet season, from autumn to early winter and persist up to late spring, none might persist through summer. In this Mediterranean environment, the risk of reproductive failure depends on environmental factors such as the length of the hydroperiod, the characteristics of the pond, and the annual rainfall (Jacob et al., 2003). In dry years, the lack of autumn-spring precipitations can cause substantial, if not complete, reproductive failure in some amphibians. In particular, the most affected are the ones with long larval periods such as *Pleurodeles* and *Pelobates* species, whose larval periods can last for over four months depending on the conditions (e.g., Buchholz and Hayes, 2002; Flament et al., 2003; Szekely et al., 2010; Hyeun-Ji et al., 2020). However, not only the length of the larval period increases the species risk of becoming extinct, other factors such as the extension of their distribution range also affect. For instance, the temporary ponds of Maamora forest (NW) within Morocco – one of the Mediterranean countries with the highest rates of amphibian endemism (Reques et al., 2013) – harbour a community of seven amphibian species, which raise different concern (Bons and Geniez, 1996). Whereas some species such as the Mauritanian toad, *Sclerophrys mauritanica*, the stripeless tree frog, *Hyla meridionalis*, and the North African green frog, *Pelophylax saharicus*, are abundant and widespread distributed in Morocco (Reques et al., 2013) causing less concern; others, such as the Moroccan spadefoot toad, *Pelobates varaldii* are endangered (IUCN, 2021) and endemic of certain areas of northern Morocco. Indeed, Maamora forest harbours the largest population of Moroccan spadefoot toad and is the core of their distribution (de Pous et al., 2012; Hinckley et al., 2016).

The aim of this study was to evaluate the role of the environmental variables, particularly the hydroperiod, in the recruitment of the pond-breeding amphibian community of a Mediterranean forest during a seven-year period. The specific objectives were i) to characterize the ponds (i.e., hydroperiod, size, and vegetation) and the climatic characteristics (rainfall and temperature) of the studied area during the studied period, ii) to compare these climatic characteristics to the previous eight-year period, iii) to examine the relationship between rainfall and both the number of ponds filled and the hydroperiod of the ponds in the studied period, iv) to identify the best predictor (number of ponds filled, rainfall or hydroperiod) of the abundance of amphibian larvae in the pond during the studied period, and finally v) to identify the differences in pond hydroperiod preference among the pond-breeding amphibian species. This is important to predict the trend of amphibian populations in this area and essential from a conservation point of view, especially for species with small populations and a restricted distribution area such as the threatened Moroccan spadefoot toad.

Methodology

Study site

The study was conducted in an area of low elevation (72-185 m.a.s.l.) sandy soil in Maamora forest (Northwest Morocco; 34°02′54.19″ N, 6°27′19.24″ W, Grou-Bouregreg basin). The climate is Mediterranean, with hot and dry summers, and the annual range of average rainfall is from 300 to 500 mm. Maamora forest is dominated by cork oak trees, *Quercus suber*, with scattered endemic wild pear, *Pyrus mamorensis*, wild olive *Olea europaea*, green olive *Phyllirea latifolia* and mastic *Pistacia lentiscus* and a sparse understory of bush and shrub species such as Mediterranean broom *Genista linifolia*, *Cytisus arboreus*, *Stauracanthus genistoides*, dwarf palm *Chamaerops humilis*, French lavender *Lavandula stoechas*, sage-leaved rockrose *Cistus salviifolius*, *Halimium halimifolium* and *Thymelaea lythroides*. The study itself took place on private land (3000 ha) where amphibians and ponds are preserved.

Environmental characteristics and amphibians

The study was carried out in 35 temporary ponds, for which we recorded data on filling and desiccation during seven consecutive flooding periods since October 2015. From mid-February to mid-May, amphibian larvae were surveyed monthly in each water body (n = 24 ponds in 2017, n = 35 in 2018, n = 18 in 2019, n = 29 in 2021, and n = 0 in 2016, 2020 and 2022; fig. 1). A 55 × 70 cm dip net with a mesh width of 3 mm was used to sample the larvae during the day. The sampling effort was proportional to the pond surface (from 300 to 5080 m^2). Dip net sweeps were done each 10 m while walking the edge pond till 2 m away from the edge (Denton and Richter, 2012). Dip netting is a standard technique (standardized by "number of dip net sweeps" as unit effort) used to sample amphibian assemblages in lentic habitats (Shaffer et al., 1994) and sampling of larvae is the best approach to gather information about the abundance of pond-breeding amphibians such the Moroccan spadefoot toad, which is rare, nocturnal and fossorial (de Pous et al., 2012). Captured larvae were released back to their ponds of origin right after being counted and identified the species. Abundance per year was estimated as the total number of larvae sampled in the three months. The amphibian species studied were: Mauritanian toad, *Sclerophrys mauritanica*, stripeless tree frog, *Hyla meridionalis*, green toad, *Bufotes viridis*, Moroccan spadefoot toad, *Pelobates varaldii*, and sharp-ribbed newt, *Pleurodeles waltl*.

Pond hydroperiod was estimated as the number of months a pond was flooded and classified as: short duration (<4 months), medium duration (4-5 months) and long duration (>5 months). To characterize the ponds (aim one), the vegetation around and within the ponds was surveyed in 2017 and the maximum size of the ponds was measured each year of the study. All plant species (n = 25) were identified and grouped in three categories: i) hygrophytes, ii) submerged macrophytes, in the border of the ponds, and iii) free floating macrophytes in the deeper zones of the ponds (supplementary table S1 for species composition). Therefore vegetation refers to the number of plant species per category. The pond was measured across the longest and shortest axes using an infrared range finder, to afterwards estimate the pond size by multiplying together both values.

In order to have a long-term perspective of the climatic changes in the area (aim one and two), average temperature

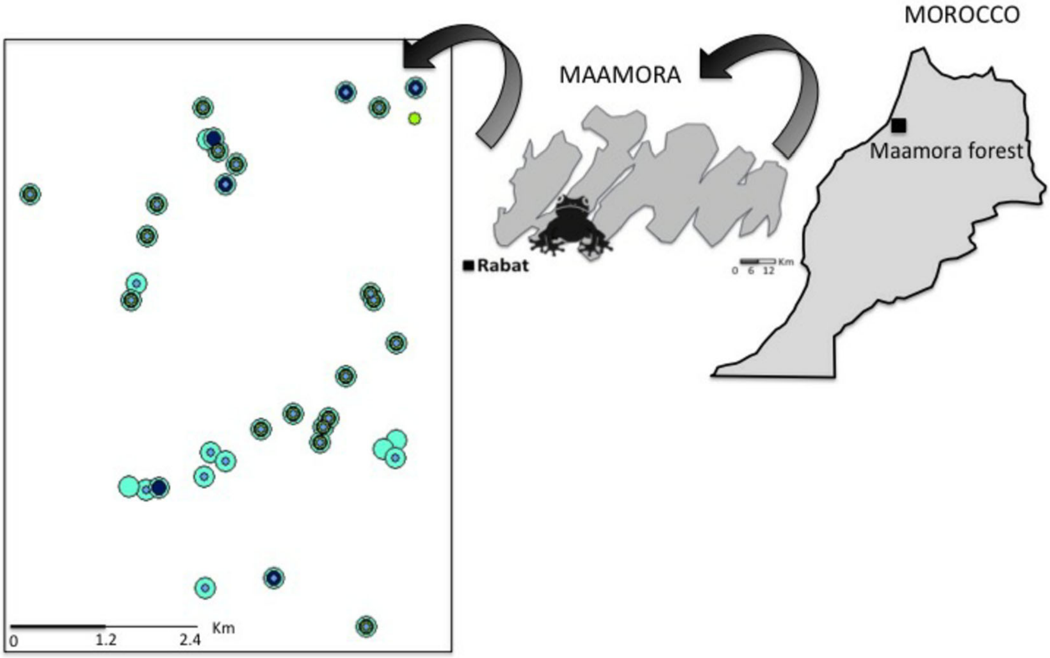

Figure 1. Location of the study area and distribution of the temporary ponds in 2017 (medium bright green dots), in 2018 (bigger light green dots), in 2019 (medium dark blue dots) and in 2021 (smallest light blue dots).

(°C) and rainfall (mm) were recorded monthly since September 2007 to May 2022 from a meteorological station in the study area (near to Tiflet city). The factor rainfall was calculated as the sum of the mm from September of one year to May of the following year.

Statistical analysis

All statistical analyses were performed in R v 4.0.4 (R Core Team, 2019). An ANOVA and a Chi-square test were used to assess whether the ponds with different hydroperiod differ in terms of size and vegetation, respectively (aim one). Furthermore, another segmented modelling via breakpoint regression was performed to compare the annual rainfall and the temperature of the study period and of the previous eight-year period (aim two).

In order to achieve our third aim, a linear regression model was used to test if the number of filled ponds in a year (response variable) was related to the rainfall (explanatory variable), while a zero inflated model (i.e., zero-inflated count data regression, R library *pscl*, command *zeroinfl*) was used to test the relationship between the hydroperiod of a pond in a year (including 0 as an empty pond) and the rainfall. In this zero inflated model there were two parts: the count model with Poisson distribution with log link, and the zero-inflation model with distribution binomial with logit link. To test whether abundance of amphibian larvae was dependent i) on the rainfall – transformed with logarithm to help the model to converge –, ii) the number of ponds or iii) the hydroperiod and since these three variables are correlated, three independent generalized linear mixed models with a Poisson distribution were run (aim four). The first two models considered species and pond as random factors, while the third model included also year. Akaike Information Criterion (AIC) was applied to rank these three models. Furthermore, to identify the preferences of each amphibian species, the abundance of larvae was compared among hydroperiods using generalized linear mixed models with a negative binomial distribution and logit link function. Pond and year were considered random factors (aim five).

Results

Characteristics of environmental variables and hydroperiods

While there was not any significant difference in vegetation among ponds with different hydroperiods ($X^2 = 0.307$, p-value $= 0.98$), there were significant differences between the pond sizes (m^2) according to the hydroperiods, being medium and long hydroperiod ponds significantly bigger (Medium hydroperiod: Est $= 1237$, SE $= 241.6$, $z = 5121$, p-value < 0.05; Long hydroperiod: Est $= 1582.5$, SE $= 357$, $z = 4.433$, p-value < 0.05; table 1; aim one).

Comparing the studied period (i.e., September 2015 to May 2022) with the previous eight years (i.e., September 2007 to May 2015), we identified three different periods 2007/09, 2010/12, and 2013/21 according to the distinct breakpoints. There was a significant difference between the period 2007/09 and 2013/21 (Est $= -348$, SE $= 141.6$, $z = -2.45$, p-value $<$ 0.05) but it was not significant between 2007/09 and 2010/12 (Est $= -123$, SE $= 173.5$, $z = -0.71$, p-value $= 0.489$). Lower annual rainfall and wider variability in annual rainfall by seasons was observed in 2013/21 (fig. 2; aim two). Nevertheless, there were non-significant differences in the average seasonal temperature among the three distinct break points mentioned above (autumn p-value $= 0.61$, p value $= 0.57$, winter: p-value $= 0.09$, p value $= 0.46$, spring p-value $= 0.33$, p value $= 0.57$; supplementary fig. S1).

Table 1. Distribution of the hydroperiod, number of ponds filled (n), and mean size of the ponds per hydrological year.

		Short H		Medium H		Long H	
Year	n	n	Size (m^2)	n	Size (m^2)	n	Size (m^2)
2015/16	0	0		0		0	
2016/17	24	11	959 ± 1023	8	2840 ± 1689	5	2505 ± 891
2017/18	35	14	500 ± 489	17	2438 ± 2164	4	2750 ± 1060
2018/19	18	13	1531 ± 795	2	1971 ± 129	3	2565 ± 1247
2019/20	0	0		0		0	
2020/21	29	15	770 ± 605	11	1932 ± 934	3	2550 ± 841
2021/22	0	0		0		0	

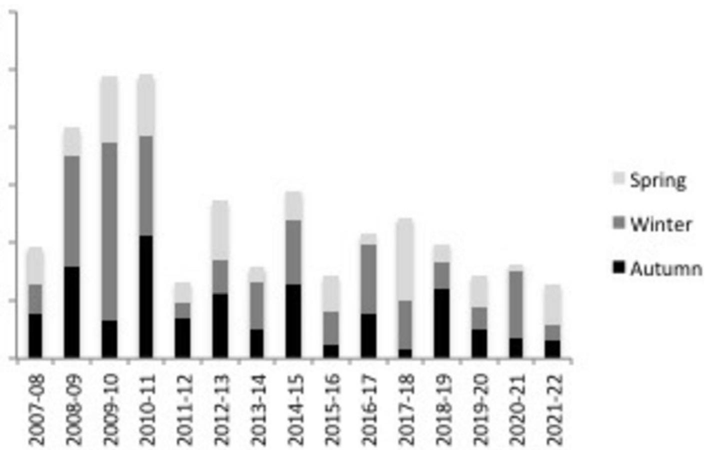

Figure 2. Annual rainfall in Maamora forest from 2008 to 2022. Each hydrological year includes data from September of one year to August of the next year and they are classified in seasonal periods.

Ponds generally filled after the first heavy rains. We have recorded the date of pond filling during the studied seven hydrological years (2015/16-2021/22). It occurred in autumn two years, in winter one year, and in spring one year. In the three very dry years, temporary ponds were not flooded (2015/16, 2019/20, and 2021/22). The linear regression model demonstrated that rainfall explains the number of ponds, hence, the number of filled ponds in spring depended on the precipitation fallen since the previous autumn ($t = 3.511$, p-value < 0.05, fig. 3 and supplementary fig. S2; aim three). The years in which no month reached 100 mm of rainfall, the ponds were not filled. Hydroperiod of the ponds also varied highly during the study: 2017/18 and 2018/19 were mainly represented by medium hydroperiod ponds, while 2018/19 had more ponds with short hydroperiod (table 1). The hydroperiod of a pond was explained by the rainfall but only for the zero-inflation part of the model (Count model: $z = 0.396$, p-value $= 0.692$; zero-inflation model: $z = -8.761$, p-value < 0.0001; supplementary fig. S3; aim three).

Abundance of the larvae of amphibian species

No temporary ponds were filled in 2016/17, 2019/20 and 2021/22 breeding seasons (<200 mm in autumn and winter), therefore, none of the studied amphibian species bred successfully in those seasons. In terms of frequency of larvae in the ponds, the highest presence in all the breeding seasons was associated to the stripeless tree frog and the Mauritanian toad with independence of the hydroperiod (see table 2), which in some cases were in 100% of the ponds sampled. The Moroccan spadefoot toad and the sharp-ribbed newt were more often in ponds with medium hydroperiod although its presence was also frequent in short hydroperiod ponds. Finally, the green toad was more often found in short hydroperiod ponds and never in the long hydroperiod ponds.

The abundance of larvae of the amphibian species was significantly explained by the number of available ponds, the rainfall and the hydroperiod (Nponds: Est $= 0.048600$, SE $= 0.001339$, $z = 36.298$, p-value < 0.0001; Rainfall: Est $= 0.96894$, SE $= 0.04898$, $z = 19.783$, p-value < 0.0001; Hydroperiod: Est $= 0.24869/0.32908$, SE $= 0.04974/0.02832$, $z = 5/11.61$, p-values < 0.0001). However, the best model was the last one ($\text{AIC}_{\text{Nponds}} = 27779$, $\text{AIC}_{\text{Rainf}} = 28732$ and $\text{AIC}_{\text{Hydrop}} = 27614$; aim four). Furthermore, all the species except the sharp-ribbed newt seemed to select ponds

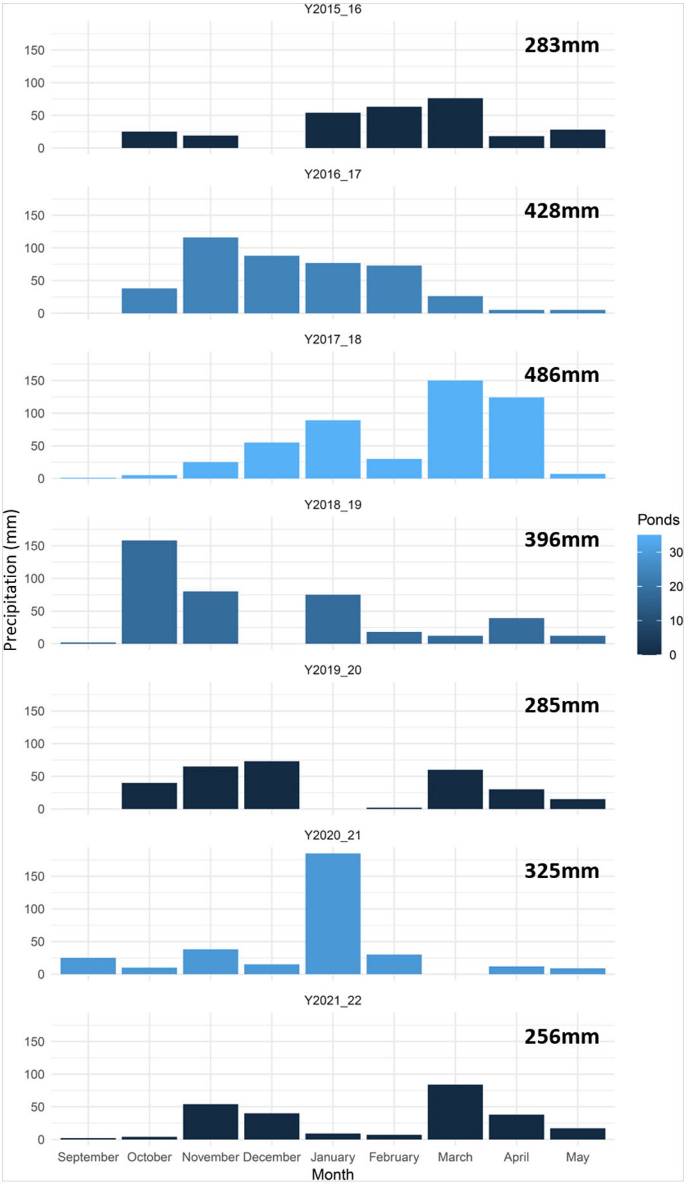

Figure 3. Precipitation fallen per month each hydrological year during the studied period. Colours represent the number of ponds filled at the beginning of the spring. The total amount of precipitation each year is showed in bold.

with a particular hydroperiod (short, medium or long) since their abundance was significantly different depending on the hydroperiod of the pond (supplementary table S2; aim four). While Moroccan spadefoot toad was more abundant in medium hydroperiod ponds (Est = 1.056, SE = 0.456, z = 2.313, p-value = <0.05) as occurred with the stripeless tree frog (Est = 0.589, SE = 0.280, z = 2.1, p-value < 0.05), Mauritanian toad was more abundant in long hydroperiod (Est = 1.589, SE = 0.783, z = 2.069, p-value < 0.05) and contrary green toad was less abundant in long hydroperiods (Est = −1.609, SE = 0.798, z = −2.016, p-value < 0.05).

Table 2. Percentage of ponds in which the species was present from each hydroperiod group (S = short, M = medium, and L = long).

	2017			2018			2019			2021		
	S	M	L	S	M	L	S	M	L	S	M	L
Moroccan spadefoot toad	60	78	60	42	62	0	31	100	0	73	73	0
Sharp-ribbed newt	30	67	20	58	76	0	8	0	0	53	64	0
Mauritanian toad	70	67	100	58	81	100	31	100	100	73	55	100
Stripeless tree frog	80	78	80	92	100	100	77	100	67	87	91	0
Green toad	60	44	0	67	48	0	33	45	3	21	26	0

Discussion

The trend observed in this Mediterranean forest in the last seven years – characterised by low rainfall and a variable seasonal distribution of this rainfall – causes alterations in the hydroperiod of the temporary ponds, which is strongly related to the abundance of larvae of the amphibian species inhabiting this habitat.

Pond-breeding amphibians are especially vulnerable to climate change since they depend on the availability of water bodies to reproduce (Duarte et al., 2012; Rodriguez-Rodriguez et al., 2020). In the Mediterranean region, the number and hydroperiod of ponds will be affected by the reduction in seasonal precipitation and the increase of temperature, both associated to climate change (Lionello and Scarascia, 2018; Grillas et al., 2021). Our data demonstrated that the last seven years were drier and there was wider variability in annual rainfall by seasons than in the previous eight-year period. The rainfall was correlated with the available number of ponds and their hydroperiod. However, the correlation between hydroperiod and rainfall was driven by the dry years because rainfall was significant only in the zero inflated part of the model (i.e., with empty ponds). Therefore, rainfall is important to fill the ponds but other factors seem to affect the hydroperiod in our system when there is no drought. Although the availability and variability of the ponds depends mainly on the timing and amount of rainfall (Serrano and Zunzunegui, 2008; Díaz-Paniagua et al., 2009; Cayuela et al., 2012), the hydroperiod might also be conditioned by the physical and biotic characteristics of the pond (Babbit, 2005; Scott and Metts, 2011). In our study, the vegetation composition among the ponds with different hydroperiods was similar (although see Grillas et al., 2021), which might indicate related spatial pattern. Nevertheless the size of the pond showed differences; short hydroperiod ponds were smaller than medium and long hydroperiod ponds. This is related to the amount of water contained in the pond and speed of drying, which might play a role in the hydroperiod variability. Further studies of the depth, soil and temperature of the pond will allow distinguishing if there is an influence of a spatial pattern, which might be linked to the observed lack of differences in the vegetation, in addition to the temporal variations. Regarding abundance of pond-breeding amphibian species, hydroperiod was a better predictor than rainfall when the ponds were filled. This was expected because hydroperiod is directly influencing the amphibian abundance while rainfall is indirectly affecting it (through hydroperiod). Therefore, hydroperiod, instead of rainfall, should be included in the projections of habitat suitability of Mediterranean amphibian species under climatic scenarios allowing more realistic predictions. For instance, using rainfall among other climatic variables, Moroccan spadefoot toad has been predicted to increase its climatic range under different climatic scenarios (Rodriguez-Rodriguez et al., 2020). However, our results showed a constraint in their frequency and abundance in the last seven years. Their larvae have reduced their frequency in the ponds from 95-71% in the previous period (i.e., 2008/15; De Pous et al., 2012; Hinckley et al., 2016) to 67-33% in the studied period (i.e., 2016/22 excluding very dry years). This threatened species might be more vulnerable to climate change due to a relatively lower capacity to adapt to new conditions (Rodriguez-Rodriguez et al., 2020). Improving our predictions under climate change, especially for this kind of species, is essential to identify the vulnerable populations and focus the conservation efforts (Hannah et al., 2002; Hagerman et al., 2010; Hansen et al., 2010; Cayuela et al., 2012).

Hydroperiod of Mediterranean temporary ponds not only affects the abundance of breeding amphibians, but also influences the number of species in a pond (Díaz-Paniagua, 1992; Snodgrass et al., 2000; Diaz-Paniagua et al., 2010). A pond changes over time, being optimal for different species in different months and years (Semlitsch, 2003). In our study, we found a relationship between hydroperiod and the abundance of pond-breeding amphibian species, as well as a replacement of species along the breeding season, e.g., Moroccan spadefoot toad and sharp ribbed newt were early colonizers, while stripeless tree frog, green toad, and Mauritanian toad appeared later in all the breeding seasons (pers. obs.). This is probably related to the length of their larval periods (e.g., Flament et al., 2003; Bekhet et al., 2014; Hyeun-Ji et al., 2020). Similar facts were recorded in other Mediterranean areas from Portugal (Beja and Alcazar, 2003; Fonseca et al., 2008). Furthermore, shorter periods of flooded ponds starting in winter, instead of late autumn, might give no option to amphibian species with long larval periods such as the Moroccan spadefoot toad and the sharp-ribbed newt (>100 days; e.g., Flament et al., 2003; Hyeun-Ji et al., 2020). Their phylopatric nature drives them to breed in shorter hydroperiod ponds causing lack of a successful recruitment. The lack of recruitment, especially due to pond drying, has been demonstrated to cause an increase on the risk of extinction (Gibbons et al., 2000; Stevens and Baguette, 2008; Di Minin and Griffiths, 2011). This fact might also benefit other widespread species such as stripeless tree frog and Mauritanian toad, which have fewer requirements when it comes to hydroperiod. Therefore, the changes in the hydroperiod suffered in the Maamora forest in the last seven years might have caused alterations in the amphibian community.

Our study highlights the reduction and seasonal change of rainfall in the last seven years, and how this affects the hydroperiod of the ponds, especially in dry years. Since pond-breeding amphibian abundance and community composition are closely related to the hydroperiod, they might suffer serious modifications, which could even result in the extirpation of endangered species such as the Moroccan spadefoot toad. Mitigation strategies manipulating pond hydroperiod by including irrigation, filling drainage ditches and managing evapotranspiration through vegetation manipulation (Shoo et al., 2011) had showed encouraging results in other regions (Mathwin et al., 2020). However, long term monitoring, to identify which ponds would maintain water longer and could function as ecohydrologic refugia from droughts (Cartwright and Wolfe, 2021), as well as forecasts of amphibian responses to changes in climatic conditions based on models including hydroperiod (Grillas et al., 2021), are needed in order to decide where to implement these mitigation strategies.

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