

# Explaining declines of newt abundance in northern Italy

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## Abstract

1. Amphibians are an exemplary case of the current biodiversity crisis, being among the vertebrates suffering the fastest decline. Population dynamics of amphibians can result from processes acting at different scales. Both the local characteristics of breeding wetlands and the features of the surrounding landscape can strongly affect the temporal dynamics of amphibian populations. European newts are particularly threatened by land-use change and invasive alien species. While it is known that newts are declining across Europe, few studies have performed broad-scale assessments of their decline, either because abundance dynamics are more complex to analyse than presence/absence data or because they require a high sampling effort and long-term monitoring.
2. In this study, we show that long-term distribution data can be combined with demographic models to quantify the decline in abundance of newt species at the regional scale, and to assess the importance of multiple factors in determining abundance dynamics. We performed multiple surveys between 1996 and 2020 and used *N*-mixture models in a Bayesian framework. We then calculated abundance changes between the first and the last sampling season, which were performed with an average timespan of 13 years across all wetlands.
3. Both Italian crested newts and smooth newts showed large declines, with an average estimated abundance loss between the first and last sampling season of 57% and 63%, respectively. Local characteristics of the wetlands were the main determinants of abundance dynamics: the abundance of both species showed a positive relationship with the area and the permanence of the wetland and a negative relationship with the presence of fish. Additionally, the abundance of Italian crested newts was negatively related to the presence of invasive crayfish. No relationship was detected between abundance and terrestrial habitat availability or connectivity measures.
4. Despite uncertainties in the absolute values of estimated abundance, the striking regional-scale decline of newts is evident. Among the major determinants of

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population dynamics, fish and crayfish presence increased their prevalence in the study area, while other factors remained more stable. Management actions aimed at eradicating or controlling invasive fish and crayfish might halt abundance loss and even revert this declining trend.

5. The application of  $N$ -mixture models to long-term data from representative sites permits the analysis of temporal trends of species at the regional scale even when data come from complex monitoring schemes. We found large declines in abundance of two newt species, suggesting that European newts may be more threatened than previously thought.

#### KEYWORDS

amphibian decline, *Lissotriton vulgaris*,  $N$ -mixture models, *Procambarus clarkii*, *Triturus carnifex*

## 1 | INTRODUCTION

Biodiversity is facing the strongest crisis since the last mass extinction, with extinction rates estimated to be 100 times higher than background rates (Ceballos et al., 2015). The current biodiversity crisis is caused by multiple processes such as habitat modifications, climate change, overexploitation, spread of diseases, anthropogenic nitrogen deposition, and introduction of invasive species (Stuart et al., 2008). However, these drivers do not influence populations independently, but can act together or agonistically at multiple levels, complicating the identification of key processes affecting populations and species survival (Didham et al., 2007; Falaschi et al., 2019).

Amphibians are an exemplary case of the current biodiversity crisis, with >40% of species recognised as threatened by the International Union for Nature Conservation (Hoffmann et al., 2010). Land-use change and alien vertebrates and crustaceans are listed among their main threats (Hof et al., 2011). Habitat loss is the threatening factor affecting the largest number of amphibian species; therefore, we might expect it to be the strongest driver of populations trends. However, the intensity of land-use change can vary through space and time with areas of the world that have suffered strong habitat loss through the past centuries (Falcucci et al., 2007; Goldewijk et al., 2011; Hansen et al., 2013). By contrast, invasive alien species are a growing issue (Falaschi et al., 2020). The number of invasive alien species is exponentially increasing at the global scale, exerting heavy impact even in areas with well-conserved habitat (Denoël et al., 2019; Seebens et al., 2017).

Population dynamics of amphibians can result from processes acting at different scales. Both the local characteristics of breeding sites and the features of the landscape surrounding them can strongly affect the temporal dynamics of amphibian populations (Dalpasso et al., 2022; Falaschi et al., 2021; Lowe & Bolger, 2002). Additionally, amphibians often exploit discrete patches of breeding habitat connected by dispersing individuals, called spatially structured populations (SSP; Revilla & Wiegand, 2008). Hence, factors influencing the connectivity among patches can also be crucial in determining population dynamics (Manenti et al., 2020). Appropriate

management of these features, such as the manipulation of water regime and wetlands density across the landscape, can mitigate the negative impact of other stressors and halt biodiversity loss (Mathwin et al., 2020; Rannap et al., 2009).

Studying population dynamics is the most straightforward way to gather useful information for ecology and biodiversity conservation, and information on abundance changes is pivotal to evaluate the conservation status of species (IUCN, 2001). However, the potential drivers of abundance are often assessed in snapshot correlative studies, in which population abundance at a given time is related to the spatial variation of candidate environmental predictors. Such snapshot studies are often unable to identify the main factors determining temporal dynamics, and similar studies can even yield strongly contrasting results. For instance, Ficetola et al. (2011) found a negative correlation between the abundance of larval amphibians and the presence of alien crayfish, while similar analyses performed in a different area did not detect clear negative relationships (Bélouard et al., 2019). The study of abundance dynamics can be challenging because it requires planning long-term sampling and analysing the collected data with appropriate models. For instance, population growth at a given time can be density-dependent (Cayuela et al., 2019). Additionally, the detection probability of individuals can be low, requiring several surveys at each site within each sampling season to obtain reliable measures of abundance (Falaschi, 2021; Ficetola et al., 2018; Kellner & Swihart, 2014).

These issues strongly limited quantitative assessments of abundance dynamics for species for which exhaustive census data are available. Despite possible challenges, measuring demographic trends, and studying the factors determining temporal changes is essential should we want to assess the conservation status of species, and ensure their long-term persistence (IUCN, 2001; Redford et al., 2013). Recently developed demographic models integrating analyses of detection probability are extremely promising, as they can quantify species trends and identify their drivers (Manenti et al., 2020; Zhao et al., 2019). However, they have been rarely used so far to measure trends at a broad (e.g. regional) scale.

We performed multiple surveys between 1996 and 2020 and used state-space demographic models to assess the importance of multiple factors in determining regional-scale abundance dynamics of a particularly vulnerable group of amphibians: newts, which form complex networks of populations linked to both freshwater and terrestrial environments (Beebee, 2014). We evaluated the effect of candidate drivers at different scales, and we considered: (1) the area, hydroperiod, presence of fish, and the presence of an invasive crayfish as characteristics of breeding sites; (2) terrestrial habitat availability as a landscape feature; and (3) incidence of crayfish and incidence of the focal species in the surrounding landscape as factors acting on the connectivity among wetlands. A previous study assessed the drivers of amphibian occupancy, including newts, in the same study region (Falaschi et al., 2021), but a lack of quantitative estimations of abundance hampered a complete evaluation of demographic changes. Here, we exploit the power of  $N$ -mixture models to estimate trends of abundance at the regional scale and evaluate the drivers of abundance through long-term monitoring of representative sites.

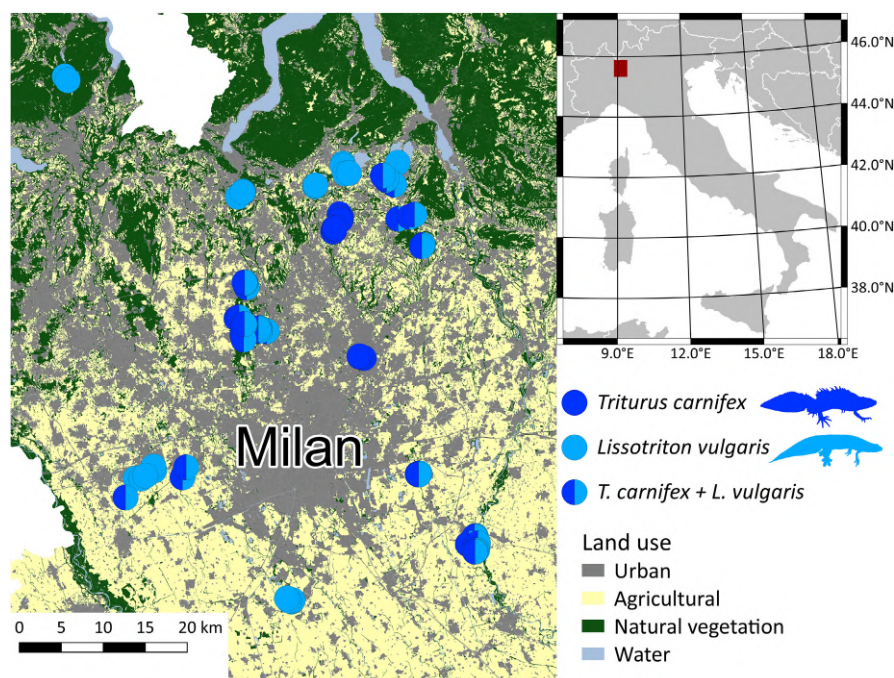
## 2 | MATERIALS AND METHODS

### 2.1 | Study design

The study area (Lombardy region, northern Italy) is a human-dominated region, with prevalence of agricultural and urban landscapes. The southern part of the study area includes suburbs and agricultural landscapes, where wooded areas are small and fragmented. The northern part of the study area, while still dominated by suburbs, is characterised by the presence of several lakes and wooded hilly areas (Figure 1).

We focused on two native amphibians: the Italian crested newt (*Triturus carnifex*) and the smooth newt (*Lissotriton vulgaris*). Newts spend their reproductive period and the larval phase in the aquatic environment, even if in some cases they remain in the water through the year. During the terrestrial phase, they live in small natural or semi-natural microhabitats nearby breeding sites (Denoël & Ficetola, 2008; Joly et al., 2001; Schabetsberger et al., 2004). The Italian crested newt is declining because of landscape anthropisation, climate change, intensive farming, and the introduction of aquatic predators (Falaschi et al., 2021; Ficetola & De Bernardi, 2004; Romano et al., 2009). The smooth newt is more widespread but is still sensitive to aquatic predators and landscape alteration (Denoël, 2012; Falaschi et al., 2021).

Between 1996 and 2020, we performed field monitoring of 125 ponds and ditches (hereafter: wetlands). All the wetlands were monitored at least in two different sampling seasons (i.e. in two different years; average number of sampling seasons per site = 3.4;  $SD = 1.7$ ). The median of first sampling season was 2004 and the median of the last sampling season was 2019. The average time-span between the first and the last sampling season was 13.2 years ( $SD = 5.8$ ). Surveys took place between February and September and, because of the limited detectability of newts, in each sampling season we carried out multiple surveys in each wetland (two to seven field surveys per year; average = 5.0;  $SD = 1.5$ ). Field activities were performed over 25 years, but the number of surveys and the years of sampling differ across sites (Table S1). For this reason, it is not possible to obtain an accurate estimate of total abundance across the whole study area for each year. Nevertheless, since each wetland was surveyed in multiple years, it is possible to evaluate changes in abundance through time, for instance by calculating the ratio of estimated abundance between the last and the first sampling (see below).



**FIGURE 1** Location of the 125 wetlands monitored to study abundance dynamics of the Italian crested newt (*Triturus carnifex*) and smooth newt (*Lissotriton vulgaris*) in northern Italy. The colours of the circles indicate whether the data of a given wetland were used in the analyses of *T. carnifex*, *L. vulgaris*, or both species

During field monitoring, we used visual encounter surveys (Halliday, 2006) to assess the abundance of the two newt species and the detection/non-detection of fish and of the invasive red swamp crayfish (*Procambarus clarkii*), following the protocols described in Falaschi et al. (2021). In each night survey, we searched for adult newts by walking across the entire wadable surface of the wetland using a torch to inspect the water column to count adult newts of the two species. While searching and counting newts, we also reported the detection of fish and red swamp crayfish during the survey. The red swamp crayfish is native to North America and was detected for the first time in some of the monitored wetlands around 2004 (Melotto et al., 2020). Natural and human-driven dispersal events allowed the crayfish to quickly spread, and the crayfish has now invaded many wetlands across the whole study area (Lo Parrino et al., 2020). Most surveys to detect newts, fish, and crayfish were performed at night, to maximise the detectability of target species (Halliday, 2006; Manenti et al., 2019), but at least one survey was carried out at daytime to record characteristics of the breeding sites. To minimise biases due to changes in observer, two of them (G.F.F. and R.M.) performed surveys across the whole study period. Additionally, all the observers participating in surveys were trained by G.F.F. and R.M. and received the same information about survey protocols.

## 2.2 | Site and landscape predictors

In each sampling season, we recorded two microhabitat features of the surveyed wetlands: surface area and hydroperiod (permanent/temporary). Wetland area was measured during daily surveys. We measured the maximum length and width and calculated the area assuming an elliptical shape. For hydroperiod, a site was considered permanent if it retained water throughout the entire sampling season of that given year (maximum range: February/September). The presence/absence of fish and invasive crayfish in the wetlands were considered as additional potential drivers of newt distribution since these groups can have strong negative impacts on amphibian populations (Arribas et al., 2014; Denoël et al., 2019; Ficetola et al., 2011). We extracted a variable representing landscape composition from a land-use map of the Lombardy region (<http://www.cartografia.regione.lombardia.it>; ground resolution: 3 m), to assess the impact of terrestrial habitat availability. The land use map covers the whole study area, is regularly updated by local authorities and is available for 2000, 2005, 2009, 2012, 2015, and 2018. For each sampling season, habitat availability was calculated based on the nearest temporal update of the map. For each wetland and sampling season, we calculated the percentage cover of broadleaved forests, mixed forests, and shrublands, as specified in the land use map (categories 311, 313, and 322), within a radius of 400 m from each wetland, as many amphibians require a buffer zone of c. 400 m of terrestrial habitat (Ficetola et al., 2009; Joly et al., 2001).

## 2.3 | Connectivity measures

Population dynamics at a site can be strongly determined by connectivity to surrounding sites (Falaschi et al., 2021; Manenti et al., 2020; Moilanen & Hanski, 1998). Hence, for each site and year, we calculated two variables describing the processes occurring in surrounding populations: species incidence and crayfish incidence. Species incidence represents the abundance of the focal species in surrounding sites, while crayfish incidence represents the presence of the invasive crayfish in surrounding sites. These measures were weighted with the following incidence functions, following Moilanen and Nieminen (2002):

$$S_{it} = \sum_{j \neq i} \exp(-\alpha d_{ij}) N_{j(t-1)} \quad (1)$$

$$C_{it} = \sum_{j \neq i} \exp(-\alpha d_{ij}) P_{j(t-1)} \quad (2)$$

$S_{it}$  and  $C_{it}$  are, respectively, species incidence and crayfish incidence at site  $i$  and in year  $t$ ;  $d_{ij}$  is the distance between the focal site  $i$  and each other wetland  $j$ ;  $N_{j(t-1)}$  is the highest count of the focal newt species in the  $j$ -th wetland in the previous year;  $P_{j(t-1)}$  is the presence/absence of crayfish in the  $j$ -th wetland in the previous year;  $\alpha$  is the reciprocal of the maximum distance at which single populations of the focal species are known to be connected by dispersing juveniles [ $\alpha = 1/300$  m for the Italian crested newt and  $\alpha = 1/200$  m for the smooth newt (Ficetola & De Bernardi, 2004; Smith & Green, 2005)].

## 2.4 | Data analysis

Analyses were performed on a different set of wetlands for each species since including sites that could not be reached because of dispersal limitations can bias the results (Godsoe, 2010). For instance, relationships between species abundance and environmental characteristics can be masked by the absence of a species from suitable sites due to dispersal but not ecological reasons (Godsoe, 2010). Therefore, we excluded wetlands where the focal species was never detected throughout the whole sampling period and that were too isolated to be reached by dispersing individuals. For each species, we only considered wetlands that were within 1,500 m from wetlands where the target species has been detected at least once during the whole study period. This distance roughly corresponds to the maximum dispersal ability of newts (Glandt, 1986; Haubrock & Altrichter, 2016; Smith & Green, 2005). The two final sets of wetlands included 91 sites for Italian crested newts and 105 sites for smooth newts (Figure 1). The two sets are partially overlapping, and 71 wetlands were included in both sets (Figure 1). This procedure does not influence the outcome of the analysis of changes in abundance, since we excluded wetlands where the species is always absent, while it allows avoiding biases in the estimate of the drivers of abundance during the first sampling season.

Abundance dynamics were analysed using a Ricker logistic model in a Bayesian framework. We used a modified version of the  $N$ -mixture

model used by Manenti et al. (2020), which combines an exponential growth model with density-dependent effect, including also the observational process through the estimation of detection probability, and implemented the model in nimble (de Valpine et al., 2017). A script of the model and the data used to run the analyses are available at figshare (Falaschi et al., 2022). We described the abundance in the first year as following a negative binomial distribution. From the second year, abundance was assumed to follow a Poisson distribution (Dail & Madsen, 2011). Abundance showed a large variability across wetlands, hence a negative binomial distribution was required to take into account such overdispersion. Conversely, a Poisson distribution was appropriate to describe variation of abundance within a site and across years.

N-mixture models are hierarchical models that allow the estimation of individual detection probability from counts, without the need of marking individuals (Ficetola, Barzaghi, et al., 2018). To account for imperfect detection, we included an observational component in the hierarchical model by using a binomial submodel (Royle, 2004). Preliminary models, trying to estimate detection probability on the basis of multiple counts within each year, showed convergence issues and unrealistic detection probabilities (average detection probability <0.01). This probably occurred because newts show complex patterns of seasonal migration between wetlands and nearby terrestrial environments, with some individuals spending the whole spring and summer in water, and others only staying in water at the peak of the breeding season (Fasola & Canova, 1992). This violates the closure assumption of these models along the breeding season and was not successfully modelled by the detection probability component of the model. For this reason, for each site, we used the highest count within each sampling season but we still included a detection component in the models (Falaschi et al., 2022). In this way, while it was not possible to assess the effect of covariates on detectability (e.g., time of the day, date, or temperature), imperfect detection is still taken into account for the estimation of abundance. Using the Hostetler and Chandler (2015) approach, it is still possible to model detection probability considering only a single survey per year because information is retrieved from the deviations from the parametric assumptions of population dynamics. Abundance in the first year was related to habitat availability within 400 m from the wetland, wetland area, permanence, and presence of fish. From the second year, we also included the presence of crayfish, crayfish incidence, and species incidence. Crayfish presence was not considered in the first year because it was rarely found in the first sampling. We calculated crayfish and species incidence on the basis of crayfish or species presence at  $t - 1$  (Equations 1 and 2), hence it is not possible to calculate these variables for the first sampling season. Additionally, to consider stochastic differences between wetlands and years, we added two random effects: site and year. From the second year, we considered two additional fixed effects representing the intrinsic growth rate and the strength of the density-dependence. Hence, abundance at site  $i$  and year  $t$  ( $N_{i,t}$ ) can be represented as follows:

$$\log(E(N_{i,t})) = \log(N_{i,t-1}) + \rho - \eta * N_{i,t-1} + S_i + T_t + \beta_1 * \text{var}_1 + \beta_2 * \text{var}_2 \dots + \beta_n * \text{var}_n$$

where  $N_{i,t-1}$  is the estimated abundance in the previous year of sampling,  $\rho$  represents the intrinsic growth rate,  $\eta$  is the strength of density-dependence,  $S_i$  and  $T_t$  are the two random effects representing the site and the year, and  $\text{var}_1, \text{var}_2 \dots \text{var}_n$  are independent variables related to population dynamics. The density-dependent component  $\eta$  was considered only when population size at time  $t - 1$  was >0, otherwise  $\eta$  was not included and  $\rho$  was substituted by the colonization parameter  $\gamma$ .

For regression coefficients of variables related to abundance, we used a normal prior with mean = 0 and variance = 100. Priors for the two random effects site and year followed a normal distribution with mean = 0 and a standard deviation following a half-Cauchy distribution (Gelman, 2006). Priors for detection probability and for the overdispersion parameter of the negative binomial distribution were uniform, respectively bounded between 0 and 1 and 0 and 50. Before running the models, the percentage cover of available habitat was arcsine-square root transformed, while area, crayfish incidence, and species incidence were log-transformed. All variables were standardised with mean = 0 and standard deviation = 1 to improve convergence and allow the comparison of the effect sizes (Sokal & Rohlf, 2012). For both species, we run three Markov chain Monte Carlo, until reaching convergence (Rhat values for all parameters < 1.1). For *T. carnifex* we ran the chains for 12 million iterations, discarding the first 8 million iterations as a burn-in and sampling with a thinning rate of 3,000. For *L. vulgaris* we ran the chains for 16 million iterations, discarding the first 12 million iterations as a burn-in and sampling with a thinning rate of 4,000. For both species, pairwise correlations among independent variables were always <|0.7|, indicating limited collinearity issues (Tables S2 and S3).

To evaluate the percentage change of abundance between the first and the last sampling, we calculated two derived parameters for each species: total abundance across all sites in the first and in the last year of sampling. By making the ratio between these two derived parameters, we obtained the percentage change in total abundance between the last and the first sampling. Amphibian populations can naturally undergo fluctuations over time (Pechmann et al., 1991). If in the last sampling, season abundance is lower just because of stochastic fluctuations or particularly bad climatic conditions, this could potentially overestimate decline thus biasing our conclusions. To confirm the robustness of results, for all the wetlands sampled in more than two years, we re-calculated the percentage change of abundance by using the second last year of sampling instead of the last one.

## 2.5 | Composition and trends of fish communities

Fish emerged as main drivers of newt population dynamics (results), but we only rarely determined fish species at study sites, and no data is available from other sources, since fish monitoring from regional authorities focuses on the main hydrographic network (i.e. rivers and lakes), while small wetlands are rarely assessed. To identify the most frequent fish species at our study sites, we performed a search on the iNaturalist citizen science platform (<https://www.inaturalist.org/>; accessed on 7 February 2022), selecting all the

research-level observations of fish within 500 m from our study sites. We implemented this list by adding species that were sporadically identified by the authors, reaching a total of 10 species (Table S4). Furthermore, we used the regional-scale assessment of fish communities (Puzzi et al., 2007), reporting data at 45 locations in the study region for the period 1998–2007 (Falaschi et al., 2022), to evaluate how the abundance of these species has changed at the regional scale through time in the last decade. The 45 locations do not exactly match the sites sampled for newts, but were used as indicators of the regional-level trend of fish species. We performed non-metric multidimensional scaling to show changes in fish communities, and used a permutational multivariate analysis of variance (PERMANOVA; 10,000 permutations stratified by site; Oksanen et al., 2020) to test if fish species composition changed through time.

### 3 | RESULTS

Over the whole study period, adult Italian crested newts were detected in 45 wetlands and smooth newts in 49 wetlands. The Italian crested newt showed an average detection probability of individuals of 0.21 (95% credible interval [CI]: 0.06–0.42), while detection probability was lower for individuals of the smooth newt, with an average value of 0.06 (95% CI: 0.03–0.11).

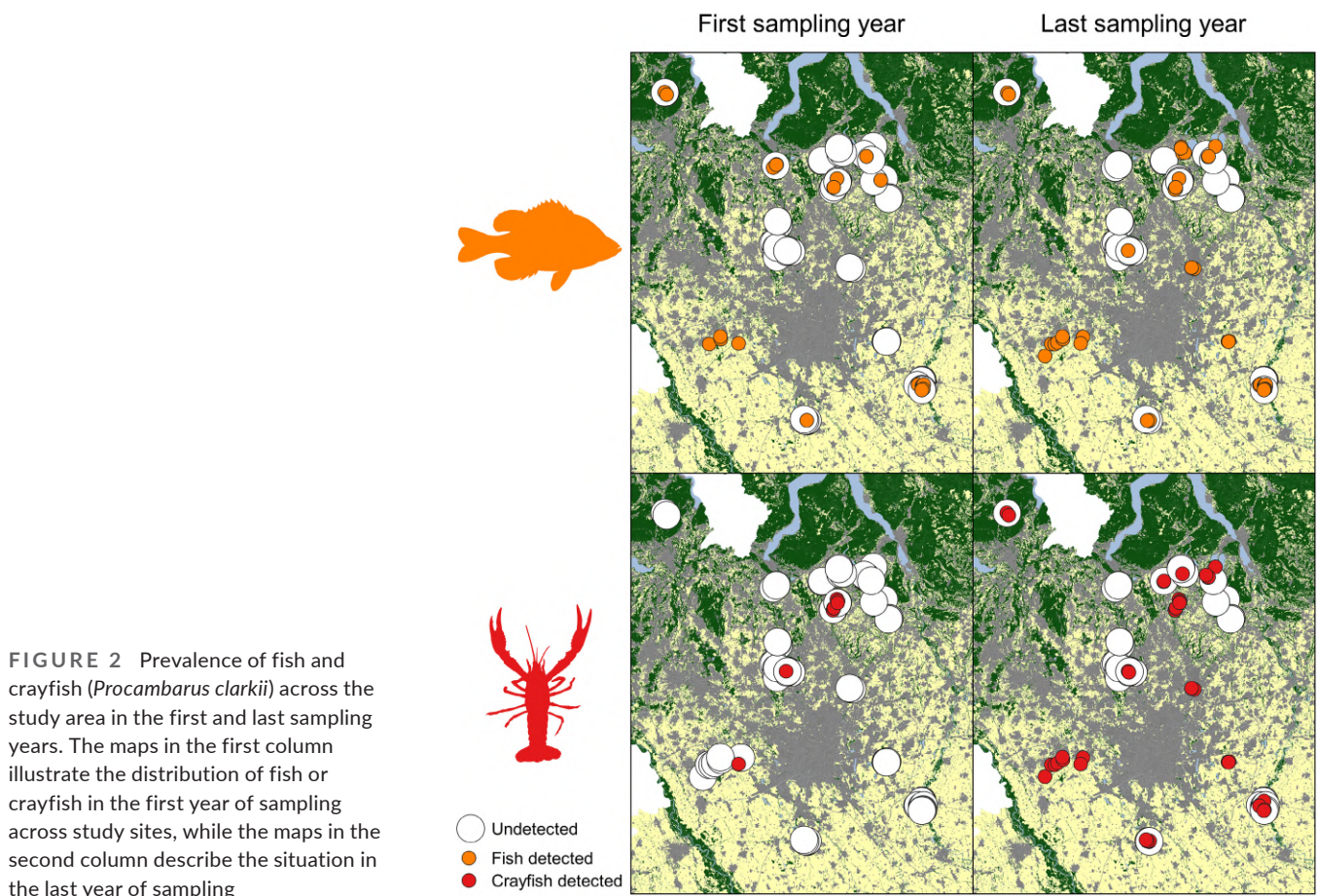
Both fish and crayfish greatly increased their prevalence across the study region (Figure 2). In the first year of sampling, fish were detected

in 27 wetlands, while in the last year we detected them in 51 wetlands. The increase of invasive crayfish was even larger, and it was found in 14 wetlands in the first year of sampling, and in 56 wetlands in the last year.

Ten different fish species were detected at our study sites, among which six can impact newts through predation and four through habitat alteration (Table S4). The composition of fish communities showed a significant change over time in the study region (PERMANOVA:  $p = 0.002$ ; Figure S1), with a clear increase through time of the Italian chub (*Squalius squalus*), which is a large predator.

#### 3.1 | Abundance loss

The estimated total abundance, both in the first and last survey, was higher for smooth newts than for Italian crested newts (Figure 3). Both species showed a strong decrease in the estimated abundance between the first sampling season (median year of sampling = 2004) and the last sampling season (median year of sampling = 2019). The abundance of Italian crested newts was estimated to decrease by 57% (95% CI: 46%–65%; Figure 3a), while the abundance of smooth newts was estimated to decrease by 63% (95% CI: 55%–69%; Figure 3b). Results were strongly consistent when using the second last year of sampling instead of the last year to estimate the decline (Figure S2), with a similar decrease for both species. For the Italian crested newt, the estimated decline from the first to the penultimate



year was 35% (95% CI: 23%–46%); for the smooth newt, the estimated decline from the first to the penultimate year was 57% (95% CI: 50%–64%). This consistency of results points out that, even if there is some uncertainty in the magnitude of the decline, conclusions are not biased due to stochastic fluctuations in a single year.

Newts showed both increase and decrease of abundance over time across different wetlands (Figure 4). Italian crested newts mainly declined in the eastern and northern portion of the study area (Figure 4a); smooth newts showed large declines in northern and eastern wetlands, while abundance increased in some wetlands located in the western portion of the study area (Figure 4b). For both species, most of the wetlands where estimated abundance increased over time showed absence of fish or crayfish (Figure 5).

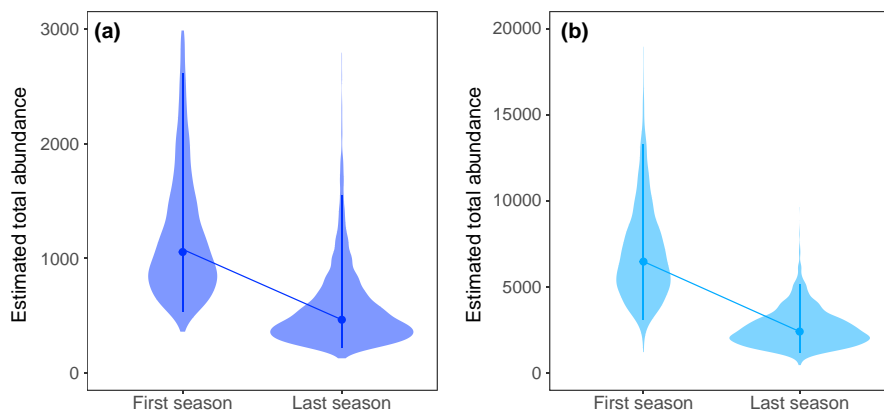
### 3.2 | Determinants of abundance dynamics

The drivers of population abundance dynamics were consistent across species (Figure 6). The abundance of both species showed a positive relationship with the area and the permanence of the wetland and a

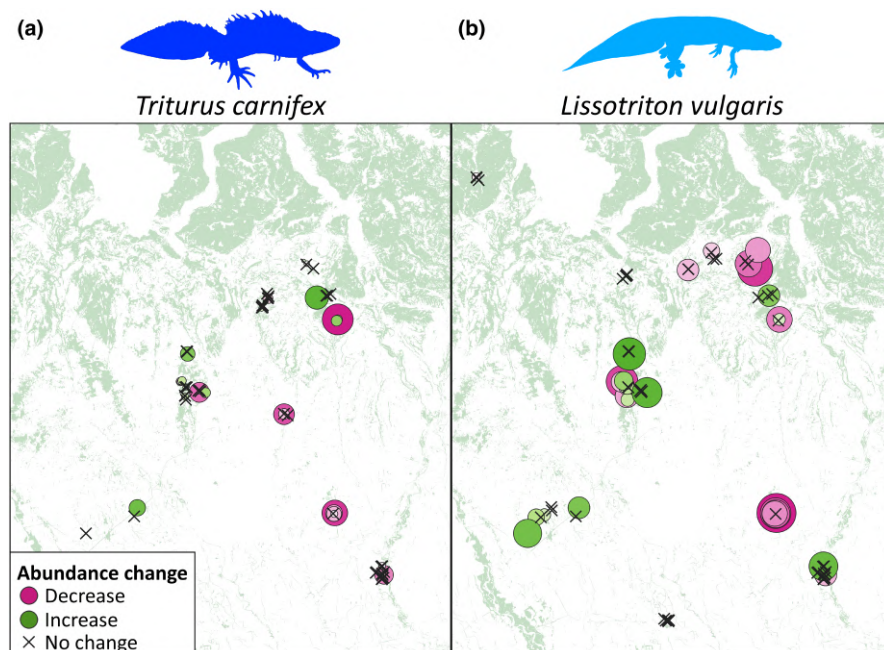
negative relationship with the presence of fish (Figure 6; Table S5). The posterior distributions for habitat availability, crayfish incidence, and species incidence overlapped zero both considering the 95% and the 90% CIs (Figure 6). The only difference between the two newt species was the site-level effect of crayfish. For Italian crested newts, crayfish presence showed some negative effect, with the 90% CI not overlapping zero (Figure 6a), while for smooth newts posteriors widely overlapped zero (Figure 6b). The variation of environmental features between the first and the last sampling is in Figure S3.

## 4 | DISCUSSION

From Spain to Italy, from Finland to Montenegro, European newts are threatened by anthropogenic activities (Denoël et al., 2019; Falaschi et al., 2021; Miró et al., 2018; Vuorio et al., 2015). Studying the variation of newt abundance over 25 years allowed us to assess the extent of abundance loss for two newt species declining at the regional scale, and to evaluate the effects of local, landscape, and SSP drivers of population dynamics.

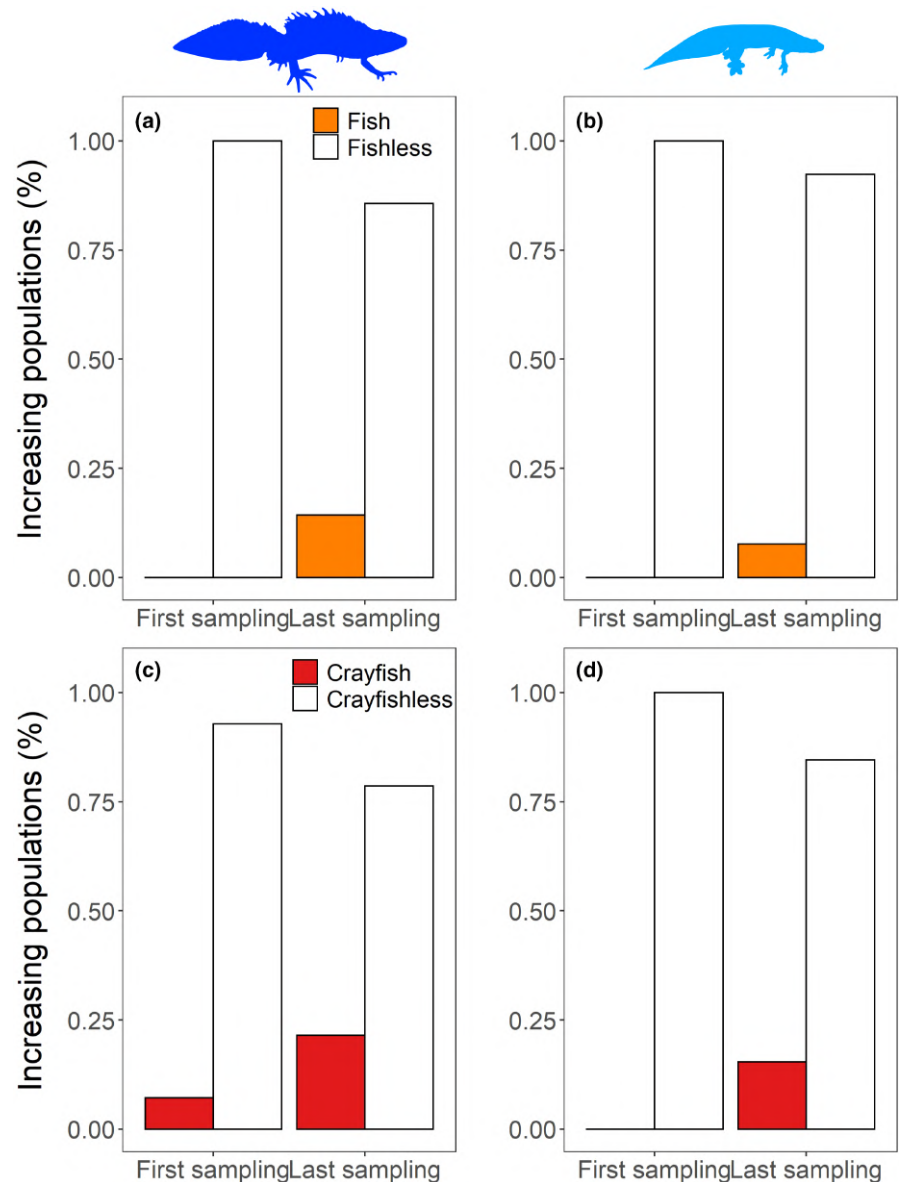


**FIGURE 3** Estimated total abundance at first and last season of sampling for (a) Italian crested newts (*Triturus carnifex*) and (b) smooth newts (*Lissotriton vulgaris*). Violin plots represent the frequency distribution of 3,000 posteriors. Points represent median values and darker bars represent the 95% credible intervals. The vertical axis is different between the two plots for visual representation



**FIGURE 4** Changes in estimated abundance across study sites for (a) Italian crested newts and (b) smooth newts. For each wetland, the value displayed was calculated as the difference between average estimated abundance at last and first sampling. Points size is proportional to the logarithm of abundance change. High-quality terrestrial habitat is shown in light green

**FIGURE 5** Prevalence of fish (a, b) and crayfish (c, d) across wetlands showing an increase in newt abundance between the first and the last sampling, for Italian crested newt (a, c) and smooth newt (b, d). The prevalence of fish and crayfish is shown at both the first and the last sampling. Coloured bars represent the proportion of sites showing population increase and the occurrence of fish (orange) or crayfish (red); white bars represent the proportion of sites showing population increase and the absence of fish or crayfish



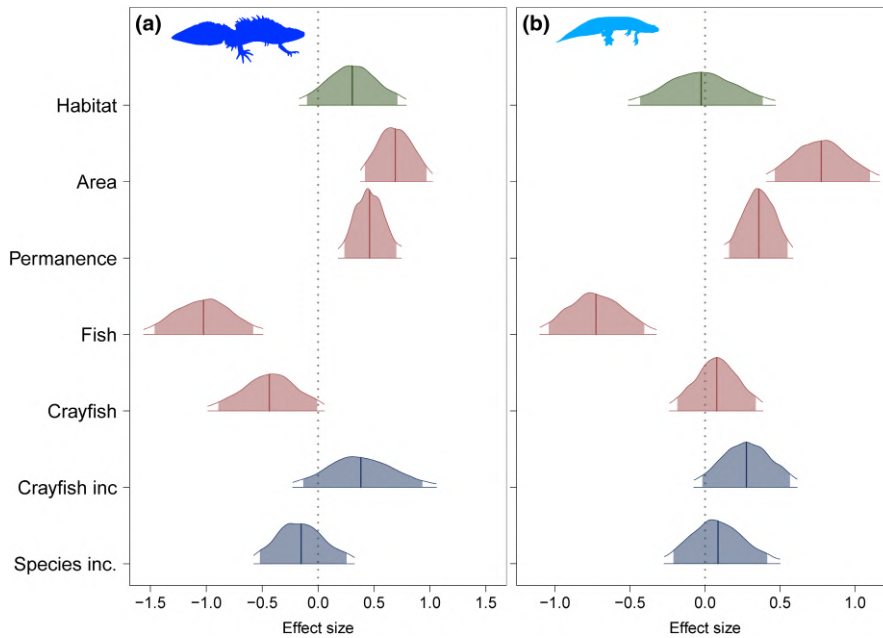
#### 4.1 | Determinants of abundance dynamics

Local characteristics of the breeding sites were the main determinants of abundance dynamics, while terrestrial habitat availability and SSP features did not show strong effects. For both species, abundance dynamics were more positive in fishless wetlands, with a large surface area and permanent throughout the sampling season. A larger breeding site can offer more habitat and resources, consequently sustaining larger carrying capacities and higher vital rates (Hodgson et al., 2009).

Wetland hydroperiod can be a major determinant of population growth for species with water-developing larvae, such as the two newts studied here (Lanza et al., 2007). Newt larvae have a relatively long development time and droughts can cause mass mortality, hampering population growth in the following years. While this negative effect might be mitigated by the ability of larvae to accelerate development in response to droughts, a longer

hydroperiod ensures better survival (Thompson & Popescu, 2021). At the same time, fish occurrence is a well-known factor showing a consistent and strongly negative impact on amphibian populations, with particularly strong impacts of large predators such as chub (Aldrigo & Facoetti, 2006; Denoël et al., 2019; Falaschi et al., 2020; Orizaola & Brana, 2006; Winandy et al., 2017). While fish are mostly associated with wetlands that are permanent over long time scales (Wellborn et al., 1996), anthropogenic introductions in less permanent wetlands are frequent (Gozlan et al., 2010; Rahel & Smith, 2018) and such fish introductions, even if localised, have already caused regional scale declines of newts (Denoël et al., 2005; Denoël et al., 2019). For this reason, limiting fish introductions and removing introduced populations is pivotal to prevent broad-scale biodiversity losses (Rahel & Smith, 2018). Fish can also alter biotic and abiotic conditions of wetlands (Cline et al., 1994; Reynolds & Aldridge, 2021). For instance, carp and other cyprinids can modify both the trophic state and the vegetation of small lakes, determining





**FIGURE 6** Frequency distribution of the posteriors for the relationship between abundance dynamics and environmental predictors for (a) Italian crested newts (*Triturus cristatus*) and (b) smooth newts (*Lissotriton vulgaris*). Curve lines and shaded areas represent respectively the 95% and the 90% credible intervals; vertical lines represent the averages. Colours represent the scale at which a given variable is acting: green, terrestrial landscape; red, breeding site; blue, connectivity

complex effects on the whole communities and also increasing turbidity (Maceda-Veiga et al., 2017; Reynolds & Aldridge, 2021). In principle, increased turbidity could reduce the detectability of individuals of the target species, limiting the accuracy of model estimates of abundance. Nevertheless, there is a non-linear relationship between carp density and water turbidity, and a strong increase of turbidity is only observed when fish density is very high and crosses a threshold (Zambrano & Hinojosa, 1999). While we did not measure fish abundance at our study sites, we never detected very high cyprinid densities comparable to the ones reported by Zambrano and Hinojosa (1999), thus it is more likely that fish presence determined a decline of newt abundance rather than a decrease in detectability. Nevertheless, disentangling the role of environmental factors that can affect both species abundance and detection probability is a major challenge (Kéry, 2010), and more studies are required to evaluate their impact on abundance estimations.

Previous studies showed negative effects of invasive crayfish on amphibian dynamics of patch occupancy, abundance, species richness, and reproductive rates (Arribas et al., 2015; Cruz et al., 2006; Falaschi et al., 2021; Kats et al., 2013). Even if newts seem to be particularly affected by the presence of invasive crayfish (Arribas et al., 2014; Díaz-Paniagua et al., 2014; Ficetola et al., 2011), we are not aware of studies analysing crayfish impacts on the long-term dynamics of newt abundance. We found a negative impact of crayfish on population dynamics of Italian crested newts while we did not detect clear effects on smooth newts. These results confirm that the rarest species is also the one most affected by stressors (Denoël et al., 2013). However, lack of significant effects does not mean that the invasive crayfish does not pose a threat for smooth newts. On one hand, *Procambarus clarkii* and other invasive crayfish seem to exert a very strong predation pressure on larval amphibians (Arribas et al., 2014; Cruz & Rebelo, 2005; Girdner et al., 2017; Muraro et al., 2021; Pérez-Santigosa et al., 2003). On the other hand,

the lower detection probability of adult smooth newts compared to Italian crested newts can make the identification of drivers of population dynamic more complex (Ficetola, Romano, et al., 2018). Invasive crayfish can have complex impacts on freshwater ecosystems; for instance, they can reduce the abundance of both amphibian larval stages and predatory insects (Arribas et al., 2015; Ficetola et al., 2012). Hence the impact of crayfish can be overlooked when focusing only on adult amphibians and unravelling its actual effect requires accurate measures of fitness and the inclusion of other factors such as the composition of mesopredator community.

## 4.2 | Landscape and SSP-level predictors

Characteristics of breeding sites can be major determinants of abundance dynamics of newts; nevertheless, not only local factors but also landscape and SSP features are crucial drivers of population dynamics (Denoël et al., 2013; Falaschi et al., 2021; Joly et al., 2001). In our analyses, however, neither terrestrial habitat availability nor connectivity measures showed clear effects on abundance. We might expect a positive relationship between abundance and the amount of terrestrial habitat available, since wetlands surrounded by more terrestrial habitats might sustain larger populations (Joly et al., 2001). However, habitat availability showed very little variation in the study area over the sampling period and habitat destruction further in the past could already have caused population declines or could be exerting an extinction debt (Dullinger et al., 2013). Historical maps of land cover are increasingly available and could be used to track possible effects of past destruction of terrestrial habitats on current population trends (Goldewijk et al., 2011; Marta et al., 2021; Piha et al., 2007).

Spatial and genetic connections in SSPs are maintained by individuals dispersing through the landscape; hence, factors influencing

the number of dispersers can strongly impact colonisation dynamics (Falaschi et al., 2021; Manenti et al., 2020; Van Buskirk & van Rensburg, 2020; Wright et al., 2020). For this reason, we evaluated two factors acting on the connectivity of the SSP, respectively species incidence and crayfish incidence. A previous study performed in the same area found a strong positive effect of species incidence and a negative effect of crayfish incidence on wetland colonisation probability by Italian crested newts and smooth newts (Falaschi et al., 2021), indicating that higher colonisation of unoccupied patches in wetlands surrounded by many occupied wetlands and with a low incidence of invasive crayfish. However, Falaschi et al. (2021) analysed occupancy dynamics and included all life stages, from adults to larvae. Since invasive crayfish exerts a major predation pressure on newt larvae, the effect of crayfish incidence may vary across life stages. Another possible reason for the lack of effect of the two connectivity measures included here could be the difficulty of obtaining accurate measures of abundance for species with a low detection probability (Rodda et al., 2015). If species incidence is calculated on the basis of biased abundance values, it could be poorly related to the actual number of dispersers. To overcome these issues, it can be possible to increase the number of surveys per wetland within sampling seasons to obtain more accurate measures of abundance (Ficetola, Romano, et al., 2018). Furthermore, it could be useful to distinguish between breeding and non-breeding amphibians in wetlands to assess possible effects of the invasive crayfish at the SSP level on breeding probability or larval density (Cruickshank et al., 2021). Finally, the lack of effect of terrestrial habitat and connectivity might be caused by the strong effect of other factors. For instance, the large impact of fish presence indicates that fish can be the main factor regulating population abundance, hence masking the effect of weaker factors. A more intensive sampling, and a longer time frame, covering a large number of newt generations, could be required to find relationships with terrestrial habitat and connectivity.

### 4.3 | Declines of newt abundance and conservation status

Over the 25 years timespan of this study, both Italian crested newts and smooth newts underwent a decline in abundance of 50%–60%. Despite some uncertainties in the absolute values of estimated abundance, the striking regional-scale decline of newts is evident. In terms of extinction risk as described by the IUCN, this means that both Italian crested newt and smooth newt could be qualified as regionally endangered (EN) since they showed a >50% decline over the last three generations (generation time is about 5 years and the average timespan between first and last sampling was 13.2 years). The consistency of this pattern of decline across Europe (see Denoël, 2012; Denoël et al., 2019) stresses the importance of data from representative sites to ascertain temporal trends of species and should raise awareness about the need for conservation interventions aimed at halting this broad-scale decline, such as management actions aimed

at eradicating or controlling invasive fish and crayfish. Amphibian populations often show large demographic fluctuations, thus detecting declines only from a few samplings along a long time series can be tricky. However, our analyses showed that the integration of data from a large spatial database can detect a net decline at the regional scale, despite some populations registering an apparent increase.

### 4.4 | Study limitations

Our study was able to assess abundance dynamics over a large scale, yet it is not free from some limitations. The first and last surveys were carried out in different years across different sites, hence the described decline is partially asynchronous and is not referred to the entire 1996/2020 period; instead, it can be considered as the average decline of newt populations over 13.2 years, i.e. the average timespan covered across sites. The actual decline from 1996 to 2020 might thus be even larger but, unfortunately, data from the 1990s are scarce.

Amphibians can skip breeding seasons (Cayuela et al., 2014; Díaz-Paniagua, 1998), thus a decline in the number of breeders in one single year might in principle not represent a true decline of the species. However, our conclusions remained robust when we removed the last sampling season, suggesting that they are not biased by adults skipping breeding in one specific year.

Fish were not caught in our study, so we are not able to identify fish species and to tease apart the effects different species can have. However, >70% of study sites are isolated wetlands not connected to the main hydrographic network, hence, when fish are present, they are most likely to be introduced. We generally expect a negative impact of either alien fish or fish species native from the study region but naturally absent from isolated ponds (Denoël et al., 2019). At least 10 fish species were confirmed at our study sites, and all of them can impact newt populations, either directly by predation or indirectly through habitat alteration. The regional-scale assessment confirmed that these fish species are widespread, with some showing a significant increase through time. The Italian chub was the species showing the greatest overall increase. The chub is one of the most angled fish species in Italy, reaches a large size (>50 cm) and is potentially able to prey on many small vertebrates, including amphibians (Aldrigo & Facchetti, 2006; Carosi et al., 2017). An increase of chub in isolated ponds, for instance because of introductions by anglers, could exert strong negative impacts on newt population dynamics, still these data should be interpreted carefully, given that sites used to analyse fish communities do not exactly match our study sites, and fish data only partially cover our study period. The direct sampling of fish can require more intensive techniques compared to amphibians, such as electrofishing or netting (Radinger et al., 2019). Emerging techniques such as environmental DNA metabarcoding can provide reliable information about the composition of fish communities, improving our understanding of how interspecific interaction shape temporal variation of communities, and providing better information for conservation (Kačergytė et al., 2021).

## 5 | CONCLUSIONS

While habitat loss is globally the primary cause of amphibian decline, in our study we observed large declines even with rather stable habitats. Among the major determinants of population dynamics, fish and crayfish incremented their prevalence in the study area, while other factors remained more stable. Newt populations mostly increased in wetlands without fish or crayfish, pointing out the primary role of invasive predators on population dynamics (Figure 5). This does not mean that fish and crayfish are the only drivers of declines: other processes such as extinction lag due to ancient habitat modification can still play a role (Dullinger et al., 2013). Although assessing abundance is more complex and requires more effort compared to just verifying species presence, population size is a key parameter for the long-term persistence of species. Here, we showed that data from representative sites can be combined with *N*-mixture models to successfully ascertain temporal trends of species at the regional scale, even in absence of intensive approaches requiring capture, and even if data come from complex monitoring schemes in which sites are sampled over slightly different periods. This will allow a more generalised assessment of trends in species abundance, and to propose solutions helping the maintenance of large populations or reverting ongoing declines (Redford et al., 2013).

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### AUTHOR CONTRIBUTIONS

M.F., M.M., C.G., and G.F.F. designed the study. M.F., M.M., C.G., E.L.P., F.F., F.B., M.D.N., R.M., and G.F.F. collected the data on the field. M.F., C.G., and D.D.M. performed the analyses. M.F., M.M., R.M., and G.F.F. wrote the first draft of the manuscript. All the authors critically revised the manuscript and approved the final version.

### DATA AVAILABILITY STATEMENT

The dataset and the script used to run the models of population dynamics and data on fish communities are available at figshare: <https://doi.org/10.6084/m9.figshare.19354217.v1>.

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