

Long-term drivers of persistence and colonization dynamics in spatially structured amphibian populations

Mattia Falaschi<sup>1,\*</sup>, Simone Giachello<sup>1</sup>, Elia Lo Parrino<sup>1</sup>, Martina Muraro<sup>1</sup>, Raoul Manenti<sup>1</sup>,  
Gentile Francesco Ficetola<sup>1,2</sup>

<sup>1</sup> Department of Environmental Science and Policy, Università degli Studi di Milano, Via  
Celoria 26, 20133 Milan, Italy

<sup>2</sup> Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Écologie  
Alpine, F-38000 Grenoble, France

\* matt\_fala@hotmail.it

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level is pervasive across the entire community of semi-aquatic amphibians.

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## Abstract

Many organisms live in networks of local populations connected by dispersing individuals, called spatially structured populations (SSPs), where the long-term persistence of the entire network is determined by the balance between two processes acting at the scale of local populations: extinction and colonization. When multiple threats act on an SSP, a comparison of the different factors determining local extinctions and colonizations is essential to plan sound conservation actions. Here we assessed the drivers of long-term population dynamics of multiple amphibian species at the regional scale. We used dynamic occupancy models within a Bayesian framework to identify the factors determining persistence and colonization of local populations. Since connectivity among patches is fundamental for SSPs dynamics, we considered two measures of connectivity acting on each focal patch: incidence of the focal species and incidence of invasive crayfish. We used meta-analysis to summarize the effect of different drivers at the community level. Persistence and colonization of local populations were jointly determined by factors acting at different scales. Persistence probability was positively related to the area and the permanence of wetlands, while it showed a negative relationship with the occurrence of fish. Colonization probability was highest in semi-permanent wetlands and in sites with a high incidence of the focal species in nearby sites, while it showed a negative relationship with the incidence of invasive crayfish in the landscape. By analyzing long-term data on amphibian population dynamics, we found a strong effect of some classic features commonly used in SSP studies, such as patch area and focal species incidence. The presence of an invasive alien species at the landscape-scale emerged as one of the strongest drivers of colonization dynamics, suggesting that studies on

SSPs should consider different connectivity measures more frequently, such as the incidence of predators, especially when dealing with biological invasions.

## INTRODUCTION

Studying the factors that influence species distribution is a cornerstone of conservation biology, because it allows assessing how environmental modifications determine population declines and extinctions. Although understanding the processes determining the trends of species and populations is essential to develop management plans and counteract biodiversity loss, many studies do not consider the spatial connections between populations. Many organisms live in networks of local populations that occupy discrete habitats, connected by dispersing individuals (spatially structured populations; SSPs) (Thomas & Kunin 1999; Revilla & Wiegand 2008). The long-term persistence of SSPs is determined by the balance between two processes acting at the scale of local populations: extinction and colonization (Revilla & Wiegand 2008). In a SSP network, stochastic processes can drive local populations to extinction. The risk of local extinction is particularly high for small populations, which are subject to demographic and genetic stochasticity. Spatial connections with nearby populations limit the risk of extinction and can allow the recolonization of unoccupied patches; hence, connectivity among patches is a fundamental process to take into consideration when dealing with SSPs (Hanski 1998; Moilanen & Nieminen 2002).

Understanding the drivers of SSP dynamics is complicated by the fact that the same environmental factor can influence both local extinctions and colonizations. For example, the presence of predators in a breeding patch can increase the rate of local extinctions but can also reduce the chance of subsequent recolonization, as dispersing individuals often select predator-free patches (Trekels & Vanschoenwinkel 2019). When multiple threats are acting

on a species or a community, comparing how different factors affect local extinctions and colonizations is essential to plan sound conservation actions and for prioritizing threat mitigation (Tulloch et al. 2016; Cayuela et al. 2018).

Amphibians are the group showing the highest rate of decline within vertebrates (Hoffmann et al. 2010). Alien species are among the greatest threat to amphibians and are involved in many declines and extinctions both at the population and at the species level (Stuart et al. 2004; Bellard et al. 2016; Falaschi et al. 2019). Freshwater ecosystems are particularly sensitive to the introduction of alien species, especially when the introduced species is a predator of native members of the invaded community (Cox & Lima 2006), and are suffering a growing number of introductions of alien predators all over the world (Strayer 2010).

Here we quantified the relative importance of different factors in determining the temporal dynamics of ten amphibian species. We focused on how habitat, landscape, and the presence of alien predators influence persistence and colonization parameters. Many amphibians live in complex networks of breeding patches, where the viability of the entire SSP can be determined by the dispersal of individuals (Cayuela et al. 2020). Thus, factors affecting the connectivity between patches can strongly influence temporal dynamics, and integrating connectivity measures can be critical to unravel the complexity of SSPs (Hanski 1998; Moilanen & Nieminen 2002). Some studies showed that invasive predators can severely impact native populations not only at the local but also at the landscape-level (Resetarits 2005; Trekels & Vanschoenwinkel 2019; Manenti et al. 2020), but the interplay between invasive species and the connectivity among local populations has largely been overlooked. Given the importance of connectivity measures in the study of SSPs, in our analyses, we explicitly tested the possibility that alien species can have impacts both at the local and at the landscape scale.

## MATERIAL AND METHODS

### Study system

Between 1996 and 2019 we monitored 202 freshwater sites, hereafter wetlands, including ponds, ditches, and lakeshores. These wetlands are located in Lombardy region (North-Western Italy; Fig. 1), a human-dominated region where urban and agricultural landscapes are prevalent. The southern portion of the study area is deeply modified by human activities, and wooded areas are usually small and fragmented. The northern portion of the study area, while still human-dominated, includes less fragmented woodlands and several lakes (Supporting Information, Appendix S1). The wetlands included in the study host 10 species of amphibians (details on species description and nomenclature in Appendix S2).

Each wetland was monitored in two-seven different years (hereafter: primary periods;  $\text{mean} \pm \text{SD} = 3.3 \pm 1.3$ ). Within each primary period, a wetland was surveyed from one to seven times between February and October (average surveys per wetland per sampling season =  $4.9 \pm 1.5$ ; total number of surveys across all the wetlands: 3276; see Fig. S1 for the monthly distribution of surveys). To reduce the amount of missing data and improve model convergence, the number of primary and secondary periods was reduced as much as possible, obtaining seven primary periods, each one with up to seven secondary periods (Appendix S3). During surveys, we assessed the presence of amphibian species by visually searching for adults and egg clutches, by listening to the calls of adult males, and by dip-netting to identify tadpoles and larvae (Dodd 2010). Additional details on sampling and the dataset are available in Appendix S3-S4.

In 2002 the Red Swamp Crayfish *Procambarus clarkii*, a crayfish native to North America, was introduced in the study area (Lo Parrino et al. 2020). Subsequent introductions and natural dispersal events allowed the quick spread of the crayfish, which has now invaded many of the sampled wetlands (Fig. S2).

### **Habitat and landscape features**

Once for each primary period, we recorded four microhabitat characteristics of the surveyed wetlands: surface area of the wetland, presence/absence of fish, presence/absence of crayfish, and if the wetland was permanent (i.e., retained water during the entire sampling season), following the protocols described in Appendix S3. Fish and crayfish were considered present if detected in at least one survey within the sampling season. Additionally, we calculated a landscape variable describing the percentage cover of woodlands within 400m from the wetland by using a land-use map of the Lombardy region (<http://www.cartografia.regione.lombardia.it>; Appendix S3).

In spatially structured populations, connectivity is a key determinant of the colonization probability of an empty habitat patch (Moilanen & Nieminen 2002; Hanski & Gaggiotti 2004). To consider the processes acting at the landscape-scale, we also included two variables representing the connectivity across wetlands: species incidence in the surrounding landscape, and crayfish incidence in the surrounding landscape. For each amphibian species, species incidence represents the potential influence of the presence of the focal species in other wetlands, while crayfish incidence represents the influence of the presence of the crayfish in other wetlands. Both values were weighted with an incidence function model (Moilanen & Nieminen 2002), and hence show an exponential decay based

on distance from the focal wetland. Species/crayfish incidence  $S$  in the site  $i$  at the time  $t$  were determined as follows:

$$(\text{eq. 1}) S_{it} = \sum_{j \neq i} \exp(-\alpha d_{ij}) P_{j(t-1)}$$

where  $d_{ij}$  is the distance between the focal wetland  $i$  and each one of the remaining wetlands  $j$ ;  $\alpha$  is the maximum distance at which populations of the focal amphibian species are known to be spatially connected. The value of  $\alpha$  was different across species and is based on the distance at which populations are known to interact (Table S2). For crayfish incidence,  $P_{j(t-1)}$  was the presence/absence (0/1) of the crayfish in the wetland  $j$  at time  $t-1$ . For species incidence,  $P_{j(t-1)}$  was the occupancy of the focal species in the wetland  $j$  at time  $t-1$ , estimated by running a simplified dynamic occupancy model (see below), including only detection covariates.

## Statistical analyses

### *Dynamic occupancy models*

Species occurring in an area can remain undetected, and this can severely bias estimates of statistical models; therefore, we used dynamic occupancy models to take into account imperfect detection (MacKenzie et al. 2003). We used a Bayesian framework (Royle & Kéry 2007) and implemented dynamic occupancy models in NIMBLE, a highly flexible package to program Bayesian models in R (de Valpine et al. 2017). In our models, we related detection probability to date (expressed as Julian Day) and hour (expressed as minutes after midnight), considering linear and quadratic terms for both variables. We selected date and

hour to consider phenology and as a proxy for climatic conditions. Initial occupancy was related to four variables: forest cover, wetland area, permanence, and presence of fish.

Persistence probability was related to five variables: forest cover, wetland area, permanence, presence of fish, and presence of crayfish. Colonization probability was related to seven variables: forest cover, wetland area, permanence, presence of fish, presence of crayfish, crayfish incidence, and species incidence. For each species, we fitted a single model, including all the independent variables related to detection and occupancy.

Spatial autocorrelation is pervasive in the distribution of amphibians at the landscape scale and can bias the outcome of statistical models (Beale et al. 2010; Băncilă et al. 2017). Therefore, for all three processes (initial occupancy, persistence, colonization), we added a spatial random effect to take into account spatial autocorrelation among wetlands. The random effect was calculated based on an intrinsic Gaussian conditional autoregressive model (ICAR; Banerjee, Carlin, & Gelfand, 2014). ICAR models allow the integration of spatial terms in the error of the model and have excellent performance in the analysis of data with complex spatial structures (Beale et al. 2010). ICAR models used an adjacency matrix with a truncation distance of 25 km, i.e., the minimum distance at which all the wetlands were connected forming a single network. For the prior of the precision of the ICAR model, we used a zero-truncated normal distribution with mean = 0 and precision = 0.1. For regression coefficients of the variables related to detection and initial occupancy/persistence/colonization, we used normal priors, with mean = 0 and precision = 0.01 for detection covariates and mean = 0 and precision = 0.1 for initial occupancy/persistence/colonization. Sensitivity analysis showed consistent results with different priors (Table S3).

Before running the models, we transformed independent variables to reduce skewness and improve model convergence. Wetland area, crayfish incidence, and species incidence



were log-transformed, while forest cover was square-root-arcsine transformed (Sokal & Rohlf 2012). Furthermore, all the independent variables were scaled at mean = 0 and standard deviation = 1 to allow the comparison of the estimated effect sizes. Correlations between independent variables were weak ( $|r| < 0.48$ , Table S4). The models were run for 1,000,000 iterations, discarding the first 500,000 iterations as a burn-in and then sampling the posterior distribution with a thinning of 500. For some species these values did not allow convergence, thus we added additional steps of 500,000 iterations until all the parameters attained convergence ( $R_{hat} < 1.1$ ; Table S5).

#### *Summarizing the community-level impacts*

Given the high variability of environmental responses across species, we conducted a meta-analysis to summarize the general effects on the community. For each variable, we extracted the posteriors of its effect on each species and calculated the mean and the variance of the posterior distributions. The meta-analysis was performed in a Bayesian framework, and for each factor, we calculated the mean value and its credible intervals with a model of the mean (i.e., a model including only the intercept as independent variable; Kéry, 2010). To take into account the uncertainty of estimates, we weighed the contribution of each value by the inverse of the variance of its posterior distribution (Hadfield & Nakagawa 2010). The meta-analytic models were run for 2,000,000 iterations, discarding the first 1,000,000 iterations as a burn-in and then sampling the posterior distribution with a thinning of 1,000.

All the analyses were performed in the R environment ([www.r-project.org](http://www.r-project.org)), using the packages *rgeos* and *raster* to process maps, *nimble* to run the dynamic occupancy model, *glmmBUGS* and *spdep* to calculate the adjacency matrix for ICAR models, and *MCMCglmm*

to run the community meta-analysis. The code used to run the dynamic occupancy models in nimble and the meta-analytic model is available in Appendix S4.

## RESULTS

### Amphibian species

Overall, we detected 10 taxa of amphibians within the 202 monitored wetlands: the Common Toad (*Bufo bufo*) was detected in 40 wetlands over the study period; the Green Toad (*Bufo viridis*; detected in 38 wetlands); the Italian Tree Frog (*Hyla intermedia*; 102 wetlands); the Agile Frog (*Rana dalmatina*; 99 wetlands); the Italian Agile Frog (*Rana latastei*; 110 wetlands); the Common Frog (*Rana temporaria*; 9 wetlands only), hybridogenetic Green Frogs (*Pelophylax lessonae* and *Pelophylax klepton esculentus*, considered as a single taxon; 173 wetlands); the Fire Salamander (*Salamandra salamandra*; 17 wetlands), the Italian Crested Newt (*Triturus carnifex*; 48 wetlands), and the Smooth Newt (*Lissotriton vulgaris*; 51 wetlands). Relationships between initial occupancy of each species and environmental variables are reported in Table S5. For most species the autoregressive terms showed low values, suggesting limited spatial autocorrelation (Table S6).

### Environmental factors and persistence of populations

Among the factors potentially influencing persistence probability (Fig. 2), forest cover showed contrasting effects. For some species (Common Toad and Crested Newt), we detected a strong positive relationship between population persistence and forest cover. In contrast, other species showed less pronounced or even a weak negative relationship. The surface area

of the wetland was positively related to population persistence for most of the species, indicating that a population living in a larger wetland had a higher probability of persisting in time. The permanence of the wetland showed a similar but less pronounced pattern, with the persistence of most species being positively correlated to permanence. However, some species showed a negative relationship, and this was particularly evident in Green Toads, which are specialist of ephemeral wetlands (Indermaur et al. 2010). Fish presence in the wetland usually showed a negative relationship with population persistence, with a particularly strong effect on the persistence of Tree Frogs, Agile Frogs and Smooth Newts. Crayfish occurrence in the wetland often showed a negative relationship with persistence probability; however, this effect was usually weak, or even positive for Italian Agile Frogs.

### **Factors influencing colonization probability**

Among the factors related to colonization probability (Fig. 2), forest cover showed a highly variable effect among species. Forest cover strongly reduced colonization rate for Tree Frogs and Green Frogs, while it increased the colonization of Common Toads, Brown Frogs (*R. dalmatina*, *R. latastei*, and *R. temporaria*), and the Fire Salamander. The surface area of the wetland showed a variable effect on colonization probability. For Agile Frogs, Italian Agile Frogs, and Fire Salamanders, the area of the wetland showed a negative relationship with colonization probability, while for other species the effect was weak. Wetland permanence generally showed a positive relationship with colonization probability, with a particularly strong positive effect for Agile Frogs, Green Frogs, and Fire Salamanders. The presence of fish in the wetland generally showed a negative or a weak effect on colonization probability. However, for Common Toads, we observed a positive relationship between fish presence and colonization probability.

The occurrence of crayfish in the wetland did not show a homogeneous relationship with colonization, with some species showing negative relationships and others positive relationships. While the local-scale impact of crayfish presence was heterogeneous, crayfish incidence consistently showed a negative relationship with colonization probability across species. The negative relationship with colonization probability was particularly strong for Tree Frogs, Green Frogs, and newts. In most cases, species incidence showed a strong positive relationship with colonization probability, indicating that an unoccupied wetland surrounded by many or nearby occupied wetlands has a higher chance of being colonized than a wetland surrounded by fewer or further wetlands.

### **Community-level effects**

The meta-analytic model allowed us to summarize the overall effect of environmental factors across species (Fig. 3; Table 1). Population persistence was generally higher in permanent wetlands with large surface area, while was generally lower in wetlands inhabited by fish. Overall, persistence tended to be positively related to forest cover, and negatively related to crayfish occurrence but with some uncertainty (Fig. 3; Table 1).

Among the variables related to colonization probability (Fig. 3; Table 1), forest cover showed an average positive effect. The surface area of the wetland showed a negative relationship, suggesting that larger wetlands are less likely to be colonized. The permanence of the wetland showed a strong positive relationship with colonization probability, indicating that wetlands where water is available throughout the entire breeding season, are more likely to be colonized. Fish presence showed an overall negative relationship with colonization probability, indicating that wetlands with fish are less likely to be colonized. Crayfish presence in the wetland showed an average effect close to zero. Conversely, crayfish

incidence showed a strong negative effect, indicating that wetlands surrounded by many and/or close wetlands invaded by crayfish are less likely to be colonized. Finally, wetlands surrounded by many and/or nearby wetlands occupied by the focal amphibian species are more likely to be colonized (Fig. 3; Table 1).

## DISCUSSION

Our long-term study allowed us to analyze the complex drivers of amphibian population dynamics at the regional scale and to tease apart the factors related to the persistence and colonization of local populations. Ecological differences among species caused heterogeneous responses to the different environmental drivers; still, the community-level analysis revealed several common patterns, allowing us to identify how management actions can improve the long-term persistence of amphibian communities.

### **The drivers of population persistence and colonization**

Persistence and colonization were jointly determined by drivers acting at different scales. On the one hand, patch-level features (area, water permanence, and fish) strongly affected the persistence of populations. Populations living in larger wetlands were more likely to persist over time, and the surface area of the wetland was the variable showing the strongest effect size on population persistence (Fig. 3). The positive relationship between patch size and persistence is well-established and patch size is one of the fundamental variables considered in SSP studies for over 30 years (Moilanen & Hanski 1998). A large patch usually corresponds to larger carrying capacities and vital rates, lowering the chance of local extinction (Hanski 1998; Hodgson et al. 2009).

Pond hydroperiod and predators are often major determinants of freshwater community composition (Wellborn et al. 1996; Van Buskirk 2003). On the one hand, population persistence increased in non-ephemeral wetlands (Fig. 3). All the amphibian species present in the study area have aquatic larvae, and most of them require several months to attain metamorphosis (Lanza et al. 2007). Hence, for most of the species, a longer hydroperiod reduces the risk of reproductive failure. On the other hand, fish occurrence strongly reduced the persistence of populations (Fig. 3). This is not surprising considering that many alien fish are voracious predators of amphibian eggs and larvae (Falaschi et al. 2020). In this study, we did not capture fish, so species identification was not possible. While fish are usually associated to permanent wetlands, there is a continuum gradient that ranges from small ephemeral wetlands to large permanent lakes (Wellborn et al. 1996), and most of the study wetlands are not connected to the hydrographic network. Thus, fish presence is generally caused by angling-related introductions (See also Appendix S3). Amphibians adapted to an intermediate hydroperiod, where infrequent desiccations do not hinder larval development but prevent the persistence of fish, may be particularly vulnerable to fish introductions (Griffiths 1997; Van Buskirk 2003).

The main determinants of colonization probability were different from the drivers of persistence, as colonization was highest in semi-permanent wetlands, with a high incidence of the target species and a low incidence of invasive crayfish in the surrounding landscape. The incidence of the focal species was the factor showing the strongest and most consistent effect on colonization. Connectivity is often one of the main determinants of colonization probability in SSPs (Hanski 1998; Moilanen & Hanski 1998), and amphibians are particularly sensitive to the negative impact of isolation because an unsuitable landscape matrix can hamper dispersal among habitat patches (Bradford et al. 1993; Cayuela et al. 2020).

## The landscape-level impact of invasive species

The mere occurrence of target species in nearby wetlands is not enough for the colonization of unoccupied sites, as colonization requires nearby populations producing a large number of potential propagules (Hanski & Gaggiotti 2004). Invasive predators are major determinants of amphibian fitness, thus we considered the incidence of a highly invasive crayfish as a measure of the landscape-level impact of invasives on connectivity. Crayfish occurrence in a wetland did not reduce the probability that that wetland is colonized, suggesting that many native amphibians are unable to detect this invasive predator, and continue to attempt breeding in invaded sites (Ficetola et al. 2011). Instead, the impact of the crayfish was particularly evident when measured at the landscape scale. Experimental studies showed that colonization of predator-free patches is lower if closer to patches with predators (Resetarits 2005; Trekels & Vanschoenwinkel 2019), and recent analyses suggested that invasive species affect frog abundance at the SSP level, by reducing the number of immigrants in target wetlands (Manenti et al. 2020). Still, these studies focused on one species only, and information on the generality of this impact is limited. Our community-level analysis shows that crayfish incidence has a general, negative effect on amphibian communities, acting on nearly all the species (Fig. 3). This confirms that the effect of predators at the landscape scale can be a major determinant of colonization dynamics and, even when the patch-level effect is not strong enough to be easily detected, the influence of predators on connectivity can be severe (Bradford et al. 1993). This can be explained by the key role of dispersal on the persistence of amphibian populations (Cayuela et al. 2020). We did not measure the frequency of dispersal events, so it is difficult to assess if our SSPs truly have a source-sink structure (Pulliam 1988). Nevertheless, the primary importance of species and crayfish incidence is in agreement with the source-sink hypothesis, confirming the

importance of dispersal for the long-term persistence of SSPs. On the one hand, a wetland invaded by predators can remain occupied by native amphibians if nearby wetlands act as sources (e.g. they are predator-free) and dispersing individuals attempt breeding into the invaded wetland (Fig. 4a). On the other hand, a local population inhabiting an uninvaded wetland can go extinct when the presence of invasive predators in the neighboring wetlands reduces the immigration of individuals (Fig. 4b), particularly if the population is small or if stochasticity causes temporal variation of fitness (Hanski & Gaggiotti 2004). Future studies focusing on the landscape-level effect of alien predators are required to disentangle the mechanism underlying the alteration of colonization dynamics.

The negative landscape-level effect of invasive species can affect the whole community (Fig. 2). The pervasiveness of this effect suggests that, in the presence of an alien predator, conservation should prioritize networks with high connectivity and a low incidence of invasives. However, more studies are required to understand how frequent the landscape-level effect of alien species is across communities and landscape typologies.

### **Issues and limitations**

Despite the large sample analyzed, this study has some limitations. While study sites cover a large geographic extent, their distribution is clustered. This is due to the natural uneven distribution of wetlands and the impossibility of surveying every existing wetland at the regional scale. To limit possible biases arising from this clustered distribution, we included variables (species and crayfish incidence) representing the effect of nearby wetlands, calculated with an incidence function model (Moilanen & Nieminen 2002). Therefore, nearby sites strongly influence each other, while the effect of distant wetlands is close to zero. Moreover, we included spatial random effects that allow taking into account the fact that



nearby wetlands can be more similar to each other than expected, and limit possible biases in estimates of model parameters (Beale et al. 2010). Finally, with the study methods it was impossible separating alien fish from natives. However, most fish present at study sites are either aliens or introduced (Appendix S3), thus very similar results are expected had we the possibility to focus analyses on introduced-fish only.

### **Conservation implications**

Assessing the drivers of extinctions and colonizations across >20 years allowed us to identify strategies for amphibian persistence in human-dominated landscapes, and suggested that amphibian communities can greatly benefit from integrated management of hydroperiod, connectivity, and alien species. Ensuring water persistence in wetlands can be a successful strategy for amphibian conservation (Mathwin et al. 2020) but is complicated by the interplay between hydroperiod and the occurrence of predators. In fact, permanent wetlands also suffer the highest presence of introduced fish, with negative impacts on amphibian fitness and survival (Wellborn et al. 1996). Many techniques are available to eradicate invasive fish, including chemicals and physical removal (Rytwinski et al. 2018). Chemical methods are very effective, but in the study area regulations hamper fish removal through chemicals (DL 158 20-10-2008). Targeted drying after the end of the breeding season of amphibians can prevent the long-term persistence of fish (Mathwin et al. 2020) and can also reduce the abundance of the invasive crayfish (Ficetola et al. 2012). In the study area, this is achievable by creating new, easily drainable ponds, or by modifying the hydroperiod of existing ponds through dams and other hydraulic infrastructures (Mathwin et al. 2020). For instance, hydraulic structures exist that control the water table level through the year and can influence the hydroperiod also for wetland disconnected to the main hydrographic network (Colombo

& Di Palma 1995). The functioning of these structures is currently optimized for agricultural purposes, but better integration of agricultural and biodiversity policies can determine environmental improvements at the regional scale (Williams et al. 2021).

Increasing connectivity among habitat patches can be a good strategy to ensure the long-term persistence of SSPs and can be attained by both enhancing the permeability of the landscape for dispersal, or by creating new wetlands near breeding patches or along habitat corridors (Janin et al. 2009; Rannap et al. 2009; Kremen & Merenlender 2018). Creating new, suitable wetlands within the extant SSP network can be particularly effective for the long-term persistence of species, since it enhances both the number of populations and the colonization of empty patches (Fig. 4). Selecting the appropriate location for new wetlands is often difficult, but recent technological advancement and new modeling approaches can provide efficient tools to identify the most cost-effective strategies to enhance connectivity and select locations for management actions (Scroggie et al. 2019). The risk of increasing the invasion rate is a possible drawback of enhancing connectivity (e.g., Besacier-Monbertrand et al. 2014). Consequently, new wetlands should be designed to be suitable for amphibians, and simultaneously unreachable or unfavorable for non-native predators. Again, targeted drying can help to maintain fishless ponds in areas where repeated fish introductions might occur. However, this technique would probably be less efficient against invasive crayfish, for which specific barriers can prevent colonization (Falaschi et al. 2020). Finally, targeted communication campaigns are needed to avoid that both fish and non-native species are introduced in ponds by citizens. The practical identification of approaches aimed at enhancing connectivity for natives without favoring invasion is going to be a key challenge for conservationists in the next decades.

In this study, we showed how drivers of population dynamics can act differently across species. Despite the high interspecific variation, we were able to detect some common drivers of change across the entire community, with a strong effect of some classic features commonly used in SSP studies such as patch area and connectivity (Moilanen & Hanski 1998). The incidence of an invasive alien species at the landscape scale emerged as one of the strongest drivers of colonization dynamics, suggesting that studies on spatially structured populations should take into account different connectivity variables more often, especially when dealing with biological invasions. Preserving single high-quality wetlands is not enough to ensure the long-term persistence of an SSP, and the maintenance and enhancement of connectivity are necessary (Janin et al. 2009; Rannap et al. 2009).

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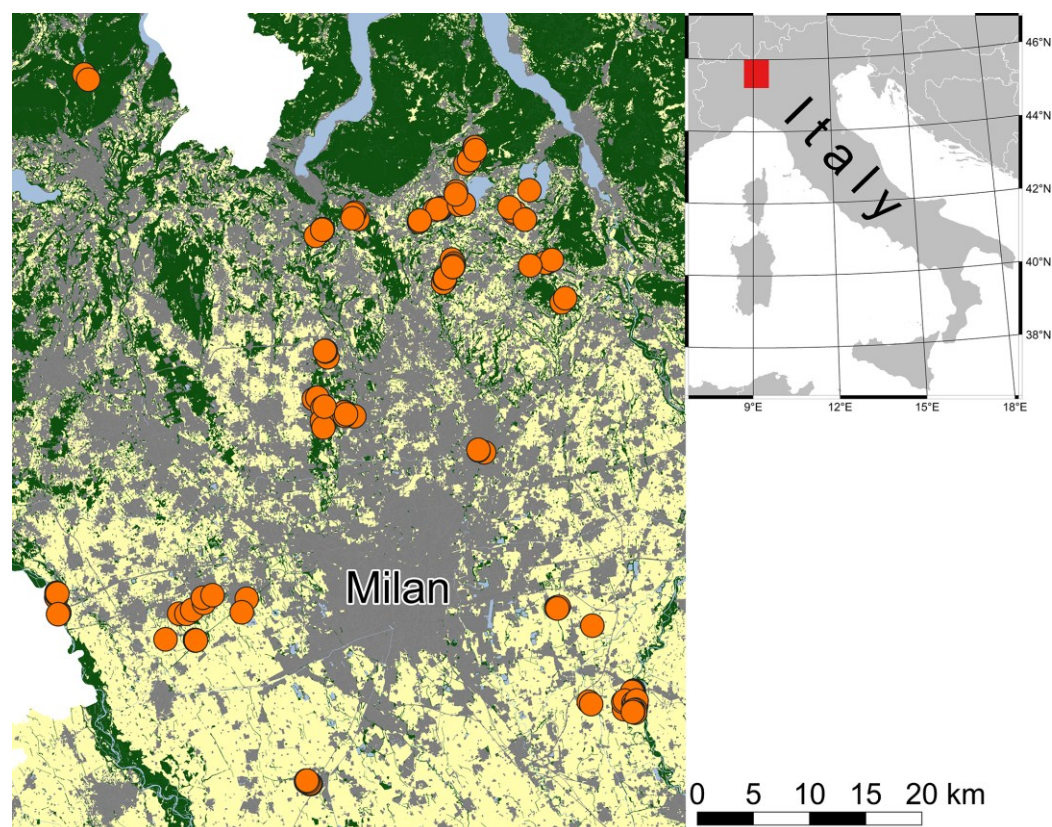


**Table 1.** Summary of the posterior distributions obtained from the meta-analytic model. For each variable related to persistence and colonization probability, we reported the mean, the proportion of positive, and the proportion of negative posteriors of the regression coefficients. Variables for which >95% of posteriors are positive or negative are in bold.

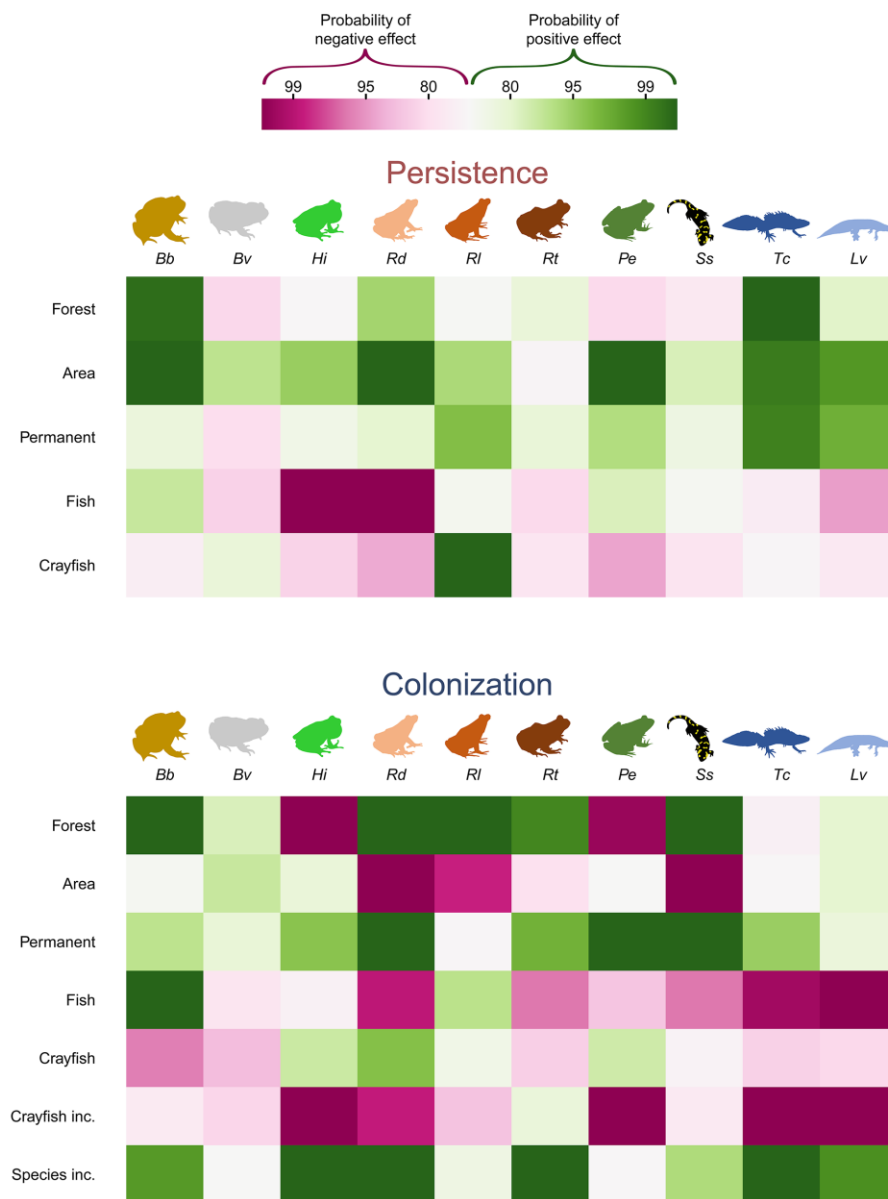
<b>Regression coefficient</b>	<b>Posteriors mean</b>	<b>Proportion of positive posteriors</b>	<b>Proportion of negative posteriors</b>
Persistence			
Forest	0.33	0.95	0.05
<b>Area</b>	<b>1.36</b>	<b>1</b>	<b>0</b>
<b>Permanence</b>	<b>0.42</b>	<b>1</b>	<b>0</b>
<b>Fish</b>	<b>-0.65</b>	<b>0.01</b>	<b>0.99</b>
Crayfish	-0.24	0.12	0.88
Colonization			
<b>Forest</b>	<b>0.62</b>	<b>0.96</b>	<b>0.04</b>
Area	-0.38	0.06	0.94
<b>Permanence</b>	<b>0.51</b>	<b>0.99</b>	<b>0.01</b>
Fish	-0.38	0.11	0.90
Crayfish	0.00	0.53	0.48
<b>Crayfish incidence</b>	<b>-0.71</b>	<b>0</b>	<b>1</b>
<b>Species incidence</b>	<b>0.85</b>	<b>1</b>	<b>0</b>

Figure legends:

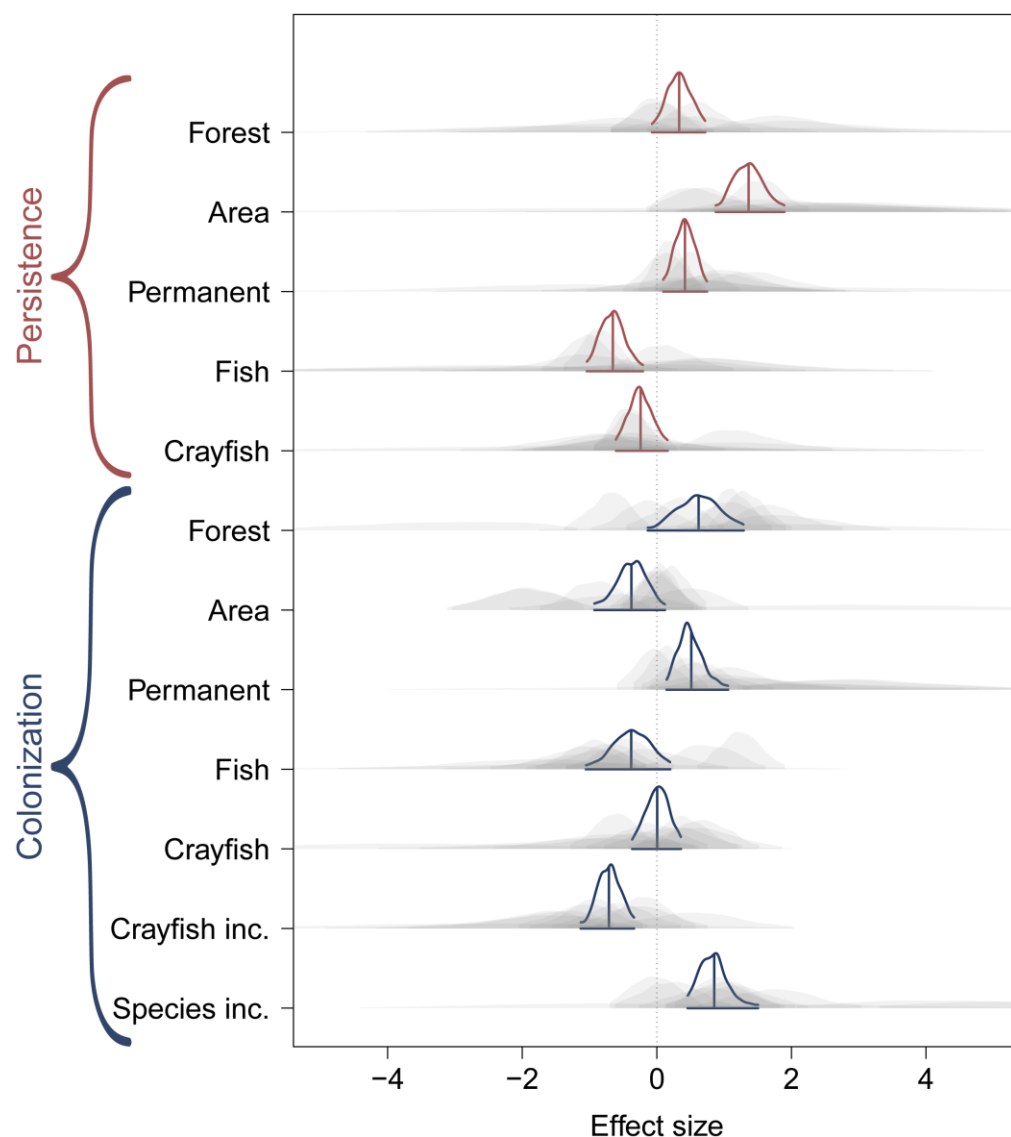
**Figure 1.** Location of the 202 wetlands monitored for this study with indication of the extent of the study area in Northern Italy.



**Figure 2.** Heatmap showing the Bayesian posterior probability of the negative (purple) or positive (green) effects of environmental factors on persistence and colonization probabilities, obtained from the dynamic occupancy models, for the ten species present in the study area. *Bb* = *Bufo bufo*, *Bv* = *Bufotes viridis*, *Hi* = *Hyla intermedia*, *Rd* = *Rana dalmatina*, *Rl* = *Rana latastei*, *Rt* = *Rana temporaria*, *Pe* = *Pelophylax lessonae* and *Pelophylax klepton*, *esculentus*, *Ss* = *Salamandra salamandra*, *Tc* = *Triturus carnifex*, *Lv* = *Lissotriton vulgaris*.



**Figure 3.** Posterior distribution for the community meta-analysis relating environmental factors to persistence and colonization probabilities across all the species of the amphibian community. Colored lines represent the 95% credible interval, and vertical lines represent the mean effect size averaged across all the species. In order to show the variation across species, grey areas represent the 95% credible intervals of the posterior distribution of the effect of the variable for each single species. Red represents parameters related to persistence probability; blue represents parameters related to colonization probability.



**Figure 4.** Possible mechanism underlying the negative effect of crayfish incidence on colonization probability. In the first scenario a) the focal wetland is invaded by crayfish and is surrounded by pods without crayfish. While the crayfish has a negative impact on local recruitment, the viability of the focal population is sustained by immigrants from the surrounding landscape; in the second scenario b) the focal wetland is not invaded but is surrounded by invaded wetlands. In this scenario, the presence of crayfish in the neighboring wetlands reduces the immigration of individuals from surrounding wetlands and, if the focal population is not large enough to sustain autonomously, it will not persist over time.

