

1 **Long-term drivers of survival and colonization dynamics in spatially-**
2 **structured amphibian populations.**

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15

16 **Abstract**

17

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

41 INTRODUCTION

42

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

58 Understanding the drivers of SSP dynamics is complicated by the fact that the same
59 environmental factor can influence both local extinctions and colonizations. For example, the
60 presence of predators in a breeding patch can increase the rate of local extinctions but can also
61 reduce the chance of subsequent recolonization, as dispersing individuals often select
62 predator-free patches (Trekels & Vanschoenwinkel 2019). When multiple threats are acting
63 on a species or a community, comparing how different factors affect local extinctions and
64 colonizations is essential to plan sound conservation actions and for prioritizing threat
65 mitigation (Tulloch et al. 2016; Cayuela et al. 2018).

66 Amphibians are the group showing the highest rate of decline within vertebrates
67 (Hoffmann et al. 2010). Alien species are among the greatest threat to amphibians and are
68 involved in many declines and extinctions both at the population and at the species level
69 (Stuart et al. 2004; Bellard et al. 2016; Falaschi et al. 2019). Freshwater ecosystems are
70 particularly sensitive to the introduction of alien species, especially when the introduced
71 species is a predator of native members of the invaded community (Cox & Lima 2006), and
72 are suffering a growing number of introductions of alien predators all over the world (Strayer
73 2010).

74 Here we quantified the relative importance of different factors in determining the temporal
75 dynamics of ten amphibian species. We focused on how habitat, landscape, and the presence
76 of alien predators influence persistence and colonization parameters. Many amphibians live in
77 complex networks of breeding patches, where the viability of the entire SSP can be
78 determined by the dispersal of individuals (Cayuela et al. 2020). Thus, factors affecting the
79 connectivity between patches can strongly influence temporal dynamics, and integrating
80 connectivity measures can be critical to unravel the complexity of SSPs (Hanski 1998;
81 Moilanen & Nieminen 2002). Some studies showed that invasive predators can severely
82 impact native populations not only at the local but also at the landscape-level (Resetarits
83 2005; Trekels & Vanschoenwinkel 2019; Manenti et al. 2020), but the interplay between
84 invasive species and the connectivity among local populations has largely been overlooked.
85 Given the importance of connectivity measures in the study of SSPs, in our analyses, we
86 explicitly tested the possibility that alien species can have impacts both at the local and at the
87 landscape scale.

88

89 **MATERIAL AND METHODS**

90

91 **Study system**

92

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

101 Each wetland was monitored in two-seven different years (hereafter: primary periods;
102 $\text{mean} \pm \text{SD} = 3.3 \pm 1.3$). Within each primary period, a wetland was surveyed from one to seven
103 times between February and October (average surveys per wetland per sampling season =
104 4.9 ± 1.5 ; total number of surveys across all the wetlands: 3276; see Fig. S1 for the monthly
105 distribution of surveys). To reduce the amount of missing data and improve model
106 convergence, the number of primary and secondary periods was reduced as much as possible,
107 obtaining seven primary periods, each one with up to seven secondary periods (Appendix S3).
108 During surveys, we assessed the presence of amphibian species by visually searching for
109 adults and egg clutches, by listening to the calls of adult males, and by dip-netting to identify
110 tadpoles and larvae (Dodd 2010). Additional details on sampling and the dataset are available
111 in Appendix S3-S4.

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

116

117 **Habitat and landscape features**

118

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

127 In spatially structured populations, connectivity is a key determinant of the
128 colonization probability of an empty habitat patch (Moilanen & Nieminen 2002; Hanski &
129 Gaggiotti 2004). To consider the processes acting at the landscape-scale, we also included two
130 variables representing the connectivity across wetlands: species incidence in the surrounding
131 landscape, and crayfish incidence in the surrounding landscape. For each amphibian species,
132 species incidence represents the potential influence of the presence of the focal species in
133 other wetlands, while crayfish incidence represents the influence of the presence of the
134 crayfish in other wetlands. Both values were weighted with an incidence function model
135 (Moilanen & Nieminen 2002), and hence show an exponential decay based on distance from
136 the focal wetland. Species/crayfish incidence S in the site i at the time t were determined as
137 follows:

138

$$139 \text{ (eq. 1) } S_{it} = \sum_{j \neq i} \exp(-ad_{ij}) P_{j(t-1)}$$

140

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

149

150 **Statistical analyses**

151

152 *Dynamic occupancy models*

153

154 Species occurring in an area can remain undetected, and this can severely bias
155 estimates of statistical models; therefore, we used dynamic occupancy models to take into
156 account imperfect detection (MacKenzie et al. 2003). We used a Bayesian framework (Royle
157 & Kéry 2007) and implemented dynamic occupancy models in NIMBLE, a highly flexible
158 package to program Bayesian models in R (de Valpine et al. 2017). In our models, we related
159 detection probability to date (expressed as Julian Day) and hour (expressed as minutes after
160 midnight), considering linear and quadratic terms for both variables. We selected date and
161 hour to consider phenology and as a proxy for climatic conditions. Initial occupancy was
162 related to four variables: forest cover, wetland area, permanence, and presence of fish.
163 Persistence probability was related to five variables: forest cover, wetland area, permanence,
164 presence of fish, and presence of crayfish. Colonization probability was related to seven
165 variables: forest cover, wetland area, permanence, presence of fish, presence of crayfish,

166 crayfish incidence, and species incidence. For each species, we fitted a single model,
167 including all the independent variables related to detection and occupancy.

168 Spatial autocorrelation is pervasive in the distribution of amphibians at the landscape
169 scale and can bias the outcome of statistical models (Beale et al. 2010; Băncilă et al. 2017).
170 Therefore, for all three processes (initial occupancy, persistence, colonization), we added a
171 spatial random effect to take into account spatial autocorrelation among wetlands. The
172 random effect was calculated based on an intrinsic Gaussian conditional autoregressive model
173 (ICAR; Banerjee, Carlin, & Gelfand, 2014). ICAR models allow the integration of spatial
174 terms in the error of the model and have excellent performance in the analysis of data with
175 complex spatial structures (Beale et al. 2010). ICAR models used an adjacency matrix with a
176 truncation distance of 25 km, i.e., the minimum distance at which all the wetlands were
177 connected forming a single network. For the prior of the precision of the ICAR model, we
178 used a zero-truncated normal distribution with mean = 0 and precision = 0.1. For regression
179 coefficients of the variables related to detection and initial
180 occupancy/persistence/colonization, we used normal priors, with mean = 0 and precision =
181 0.01 for detection covariates and mean = 0 and precision = 0.1 for initial
182 occupancy/persistence/colonization. Sensitivity analysis showed consistent results with
183 different priors (Table S3).

184 Before running the models, we transformed independent variables to reduce skewness
185 and improve model convergence. Wetland area, crayfish incidence, and species incidence
186 were log-transformed, while forest cover was square-root-arcsine transformed (Sokal & Rohlf
187 2012). Furthermore, all the independent variables were scaled at mean = 0 and standard
188 deviation = 1 to allow the comparison of the estimated effect sizes. Correlations between
189 independent variables were weak ($|r| < 0.48$, Table S4). The models were run for 1,000,000
190 iterations, discarding the first 500,000 iterations as a burn-in and then sampling the posterior

191 distribution with a thinning of 500. For some species these values did not allow convergence,
192 thus we added additional steps of 500,000 iterations until all the parameters attained
193 convergence ($R_{hat} < 1.1$; Table S5).

194

195 *Summarizing the community-level impacts*

196

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

207 All the analyses were performed in the R environment (www.r-project.org), using the
208 packages *rgeos* and *raster* to process maps, *nimble* to run the dynamic occupancy model,
209 *glmmBUGS* and *spdep* to calculate the adjacency matrix for ICAR models, and *MCMCglmm*
210 to run the community meta-analysis. The code used to run the dynamic occupancy models in
211 *nimble* and the meta-analytic model is available in Appendix S4.

212

213 **RESULTS**

214

215 **Amphibian species**

216

217 Overall, we detected 10 taxa of amphibians within the 202 monitored wetlands: the Common
218 Toad (*Bufo bufo*) was detected in 40 wetlands over the study period; the Green Toad (*Bufo*
219 *viridis*; detected in 38 wetlands); the Italian Tree Frog (*Hyla intermedia*; 102 wetlands); the
220 Agile Frog (*Rana dalmatina*; 99 wetlands); the Italian Agile Frog (*Rana latastei*; 110
221 wetlands); the Common Frog (*Rana temporaria*; 9 wetlands only), hybridogenetic Green
222 Frogs (*Pelophylax lessonae* and *Pelophylax klepton esculentus*, considered as a single taxon;
223 173 wetlands); the Fire Salamander (*Salamandra salamandra*; 17 wetlands), the Italian
224 Crested Newt (*Triturus carnifex*; 48 wetlands), and the Smooth Newt (*Lissotriton vulgaris*; 51
225 wetlands). Relationships between initial occupancy of each species and environmental
226 variables are reported in Table S5. For most species the autoregressive terms showed low
227 values, suggesting limited spatial autocorrelation (Table S6).

228

229 **Environmental factors and persistence of populations**

230

231 Among the factors potentially influencing persistence probability (Fig. 2), forest cover showed
232 contrasting effects. For some species (Common Toad and Crested Newt), we detected a strong
233 positive relationship between population persistence and forest cover. In contrast, other
234 species showed less pronounced or even a weak negative relationship. The surface area of the
235 wetland was positively related to population persistence for most of the species, indicating
236 that a population living in a larger wetland had a higher probability of persisting in time. The
237 permanence of the wetland showed a similar but less pronounced pattern, with the persistence
238 of most species being positively correlated to permanence. However, some species showed a
239 negative relationship, and this was particularly evident in Green Toads, which are specialist of
240 ephemeral wetlands (Indermaur et al. 2010). Fish presence in the wetland usually showed a

241 negative relationship with population persistence, with a particularly strong effect on the
242 persistence of Tree Frogs, Agile Frogs and Smooth Newts. Crayfish occurrence in the wetland
243 often showed a negative relationship with persistence probability; however, this effect was
244 usually weak, or even positive for Italian Agile Frogs.

245

246 **Factors influencing colonization probability**

247

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

260 The occurrence of crayfish in the wetland did not show a homogeneous relationship
261 with colonization, with some species showing negative relationships and others positive
262 relationships. While the local-scale impact of crayfish presence was heterogeneous, crayfish
263 incidence consistently showed a negative relationship with colonization probability across
264 species. The negative relationship with colonization probability was particularly strong for
265 Tree Frogs, Green Frogs, and newts. In most cases, species incidence showed a strong

266 positive relationship with colonization probability, indicating that an unoccupied wetland
267 surrounded by many or nearby occupied wetlands has a higher chance of being colonized than
268 a wetland surrounded by fewer or further wetlands.

269

270 **Community-level effects**

271

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

277 Among the variables related to colonization probability (Fig. 3; Table 1), forest cover
278 showed an average positive effect. The surface area of the wetland showed a negative
279 relationship, suggesting that larger wetlands are less likely to be colonized. The permanence
280 of the wetland showed a strong positive relationship with colonization probability, indicating
281 that wetlands where water is available throughout the entire breeding season, are more likely
282 to be colonized. Fish presence showed an overall negative relationship with colonization
283 probability, indicating that wetlands with fish are less likely to be colonized. Crayfish
284 presence in the wetland showed an average effect close to zero. Conversely, crayfish
285 incidence showed a strong negative effect, indicating that wetlands surrounded by many
286 and/or close wetlands invaded by crayfish are less likely to be colonized. Finally, wetlands
287 surrounded by many and/or nearby wetlands occupied by the focal amphibian species are
288 more likely to be colonized (Fig. 3; Table 1).

289

290 **DISCUSSION**

291

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

298

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

300

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

310

311 Pond hydroperiod and predators are often major determinants of freshwater
312 community composition (Wellborn et al. 1996; Van Buskirk 2003). On the one hand,
313 population persistence increased in non-ephemeral wetlands (Fig. 3). All the amphibian
314 species present in the study area have aquatic larvae, and most of them require several months
315 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

316 strongly reduced the persistence of populations (Fig. 3). This is not surprising considering that
317 many alien fish are voracious predators of amphibian eggs and larvae (Falaschi et al. 2020). In
318 this study, we did not capture fish, so species identification was not possible. While fish are
319 usually associated to permanent wetlands, there is a continuum gradient that ranges from
320 small ephemeral wetlands to large permanent lakes (Wellborn et al. 1996), and most of the
321 study wetlands are not connected to the hydrographic network. Thus, fish presence is
322 generally caused by angling-related introductions (See also Appendix S3). Amphibians
323 adapted to an intermediate hydroperiod, where infrequent desiccations do not hinder larval
324 development but prevent the persistence of fish, may be particularly vulnerable to fish
325 introductions (Griffiths 1997; Van Buskirk 2003).

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

334

335 **The landscape-level impact of invasive species**

336

337 The mere occurrence of target species in nearby wetlands is not enough for the
338 colonization of unoccupied sites, as colonization requires nearby populations producing a
339 large number of potential propagules (Hanski & Gaggiotti 2004). Invasive predators are major
340 determinants of amphibian fitness, thus we considered the incidence of a highly invasive

341 crayfish as a measure of the landscape-level impact of invasives on connectivity. Crayfish
342 occurrence in a wetland did not reduce the probability that that wetland is colonized,
343 suggesting that many native amphibians are unable to detect this invasive predator, and
344 continue to attempt breeding in invaded sites (Ficetola et al. 2011). Instead, the impact of the
345 crayfish was particularly evident when measured at the landscape scale. Experimental studies
346 showed that colonization of predator-free patches is lower if closer to patches with predators
347 (Resetarits 2005; Trekels & Vanschoenwinkel 2019), and recent analyses suggested that
348 invasive species affect frog abundance at the SSP level, by reducing the number of
349 immigrants in target wetlands (Manenti et al. 2020). Still, these studies focused on one species
350 only, and information on the generality of this impact is limited. Our community-level
351 analysis shows that crayfish incidence has a general, negative effect on amphibian
352 communities, acting on nearly all the species (Fig. 3). This confirms that the effect of
353 predators at the landscape scale can be a major determinant of colonization dynamics and,
354 even when the patch-level effect is not strong enough to be easily detected, the influence of
355 predators on connectivity can be severe (Bradford et al. 1993). This can be explained by the
356 key role of dispersal on the persistence of amphibian populations (Cayuela et al. 2020). We
357 did not measure the frequency of dispersal events, so it is difficult to assess if our SSPs truly
358 have a source-sink structure (Pulliam 1988). Nevertheless, the primary importance of species
359 and crayfish incidence is in agreement with the source-sink hypothesis, confirming the
360 importance of dispersal for the long-term persistence of SSPs. On the one hand, a wetland
361 invaded by predators can remain occupied by native amphibians if nearby wetlands act as
362 sources (e.g. they are predator-free) and dispersing individuals attempt breeding into the
363 invaded wetland (Fig. 4a). On the other hand, a local population inhabiting an uninvaded
364 wetland can go extinct when the presence of invasive predators in the neighboring wetlands
365 reduces the immigration of individuals (Fig. 4b), particularly if the population is small or if

366 stochasticity causes temporal variation of fitness (Hanski & Gaggiotti 2004). Future studies
367 focusing on the landscape-level effect of alien predators are required to disentangle the
368 mechanism underlying the alteration of colonization dynamics.

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

374

375 **Issues and limitations**

376

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

384 Moreover, we included spatial random effects that allow taking into account the fact that
385 nearby wetlands can be more similar to each other than expected, and limit possible biases in
386 estimates of model parameters (Beale et al. 2010). Finally, with the study methods it was
387 impossible separating alien fish from natives. However, most fish present at study sites are
388 either aliens or introduced (Appendix S3), thus very similar results are expected had we the
389 possibility to focus analyses on introduced-fish only.

390

391 **Conservation implications**

392

393 Assessing the drivers of extinctions and colonizations across >20 years allowed us to
394 identify strategies for amphibian persistence in human-dominated landscapes, and suggested
395 that amphibian communities can greatly benefit from integrated management of hydroperiod,
396 connectivity, and alien species. Ensuring water persistence in wetlands can be a successful
397 strategy for amphibian conservation (Mathwin et al. 2020) but is complicated by the interplay
398 between hydroperiod and the occurrence of predators. In fact, permanent wetlands also suffer
399 the highest presence of introduced fish, with negative impacts on amphibian fitness and
400 survival (Wellborn et al. 1996). Many techniques are available to eradicate invasive fish,
401 including chemicals and physical removal (Rytwinski et al. 2018). Chemical methods are very
402 effective, but in the study area regulations hamper fish removal through chemicals (DL 158
403 20-10-2008). Targeted drying after the end of the breeding season of amphibians can prevent
404 the long-term persistence of fish (Mathwin et al. 2020) and can also reduce the abundance of
405 the invasive crayfish (Ficetola et al. 2012). In the study area, this is achievable by creating
406 new, easily drainable ponds, or by modifying the hydroperiod of existing ponds through dams
407 and other hydraulic infrastructures (Mathwin et al. 2020). For instance, hydraulic structures
408 exist that control the water table level through the year and can influence the hydroperiod also
409 for wetland disconnected to the main hydrographic network (Colombo & Di Palma 1995).
410 The functioning of these structures is currently optimized for agricultural purposes, but better
411 integration of agricultural and biodiversity policies can determine environmental
412 improvements at the regional scale (Williams et al. 2021).

413 Increasing connectivity among habitat patches can be a good strategy to ensure the
414 long-term persistence of SSPs and can be attained by both enhancing the permeability of the
415 landscape for dispersal, or by creating new wetlands near breeding patches or along habitat

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

433

434 In this study, we showed how drivers of population dynamics can act differently
435 across species. Despite the high interspecific variation, we were able to detect some common
436 drivers of change across the entire community, with a strong effect of some classic features
437 commonly used in SSP studies such as patch area and connectivity (Moilanen & Hanski
438 1998). The incidence of an invasive alien species at the landscape scale emerged as one of the
439 strongest drivers of colonization dynamics, suggesting that studies on spatially structured
440 populations should take into account different connectivity variables more often, especially

441 when dealing with biological invasions. Preserving single high-quality wetlands is not enough
442 to ensure the long-term persistence of an SSP, and the maintenance and enhancement of
443 connectivity are necessary (Janin et al. 2009; Rannap et al. 2009).

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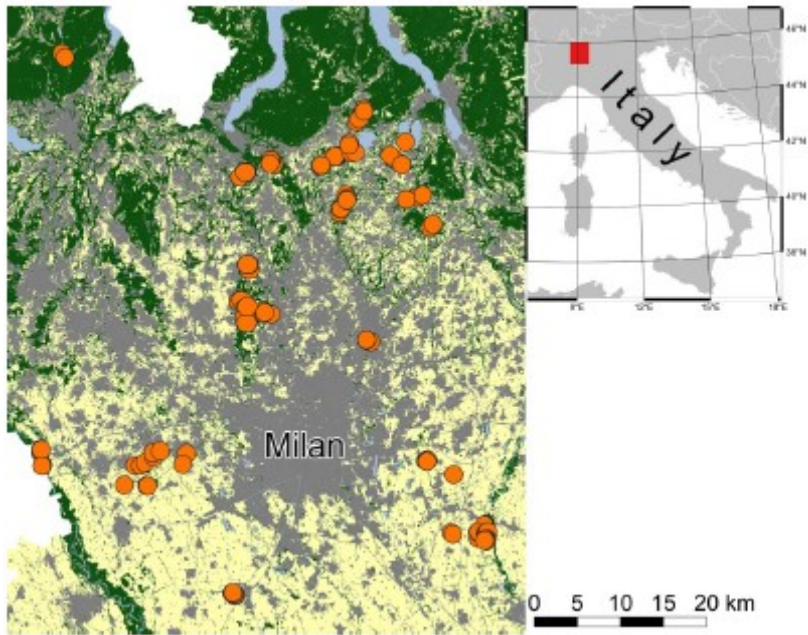
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569 **Table 1.** Summary of the posterior distributions obtained from the meta-analytic model. For
570 each variable related to persistence and colonization probability, we reported the mean, the
571 proportion of positive, and the proportion of negative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

573

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

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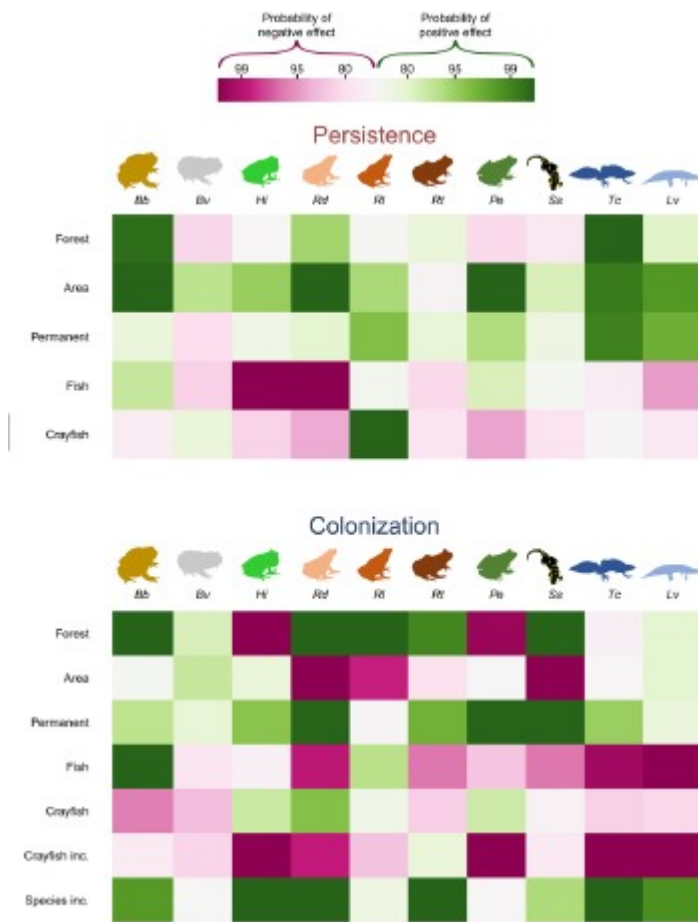


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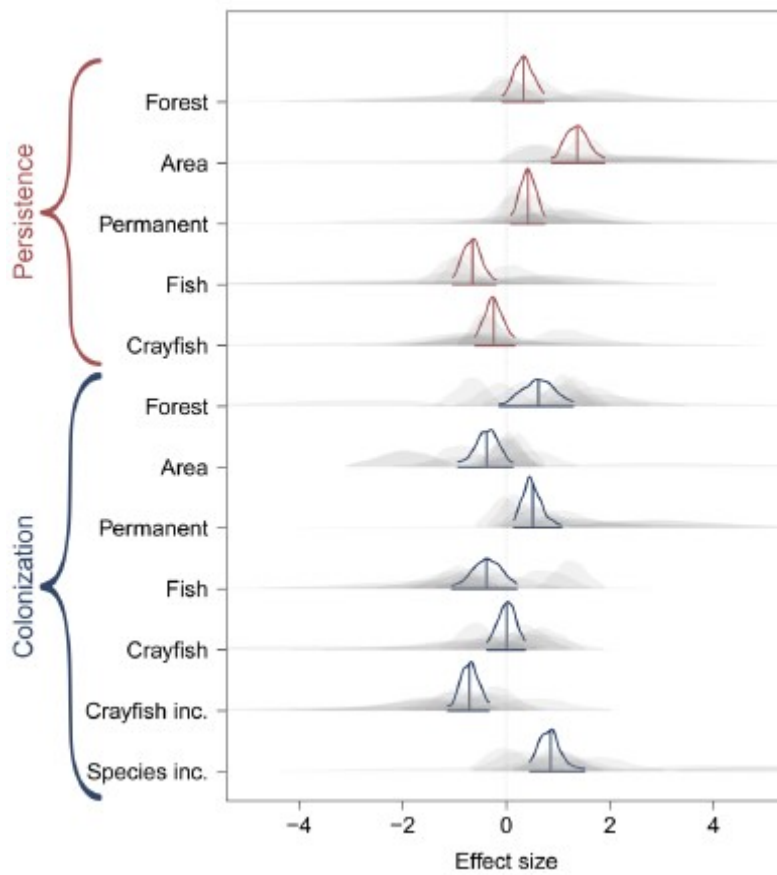
577 **Figure 1.** Location of the 202 wetlands monitored for this study with indication of the extent
578 of the study area in Northern Italy.

579



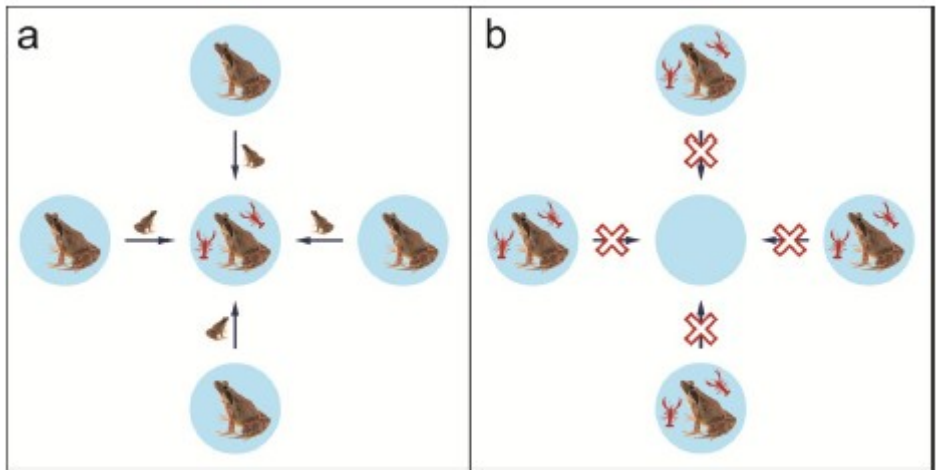
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581 **Figure 2.** Heatmap showing the Bayesian posterior probability of the negative (purple) or
 582 positive (green) effects of environmental factors on persistence and colonization probabilities,
 583 obtained from the dynamic occupancy models,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



587

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



595

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