

Context-dependent dispersal determines relatedness and genetic structure in a patchy amphibian population

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Abstract

Dispersal is a central process in ecology and evolution with far reaching consequences for the dynamics and genetics of spatially structured populations (SSPs). Individuals can adjust their decisions to disperse according to local fitness prospects, resulting in context-dependent dispersal. By determining dispersal rate, distance and direction, these individual-level decisions further modulate the demography, relatedness and genetic structure of SSPs. Here, we examined how context-dependent dispersal influences the dynamics and genetics of a great crested newt (*Triturus cristatus*) SSP. We collected capture–recapture data of 5564 individuals and genetic data of 950 individuals across an SSP in northern Germany. We added genetic data from six sites outside this SSP to assess genetic structure and gene flow at a regional level. Dispersal rates within the SSP were high but dispersal distances were short. Dispersal was context-dependent: individuals preferentially immigrated into high-quality ponds where breeding probabilities were higher. The studied SSP behaved like a patchy population, where subpopulations at each pond were demographically interdependent. High context-dependent dispersal led to weak but significant spatial genetic structure and relatedness within the SSP. At the regional level, a strong hierarchical genetic structure with very few first-generation migrants as well as low effective dispersal rates suggest the presence of independent demographic units. Overall, our study highlights the importance of habitat quality for driving context-dependent dispersal and therefore demography and genetic structure in SSPs. Limited capacity for long-distance dispersal seems to increase genetic structure within a population and leads to demographic isolation in anthropogenic landscapes.

KEYWORDS

gene flow, habitat quality, metapopulation, patchy population, *Triturus cristatus*

Bianca Unglaub and Hugo Cayuela are shared first authorship.

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1 | INTRODUCTION

Dispersal (i.e., all movements of an individual or propagule possibly leading to gene flow; Ronce, 2007) is a central process in ecology and evolution that has far reaching consequences for population dynamics, genetics and conservation (Bailey & Muths, 2019; Bowler & Benton, 2005; Legrand et al., 2017; Ronce, 2007). Dispersal is usually viewed as a three-stage process (Clobert et al., 2009) including emigration from the habitat patch (departure), transience in the landscape matrix and immigration into a new habitat patch (arrival). Phenotypic traits such as morphology, physiology and behaviour influence each stage of the dispersal process, leading to condition-dependent dispersal and dispersal syndromes (Cote et al., 2010; Ronce & Clobert, 2012). Furthermore, individuals use social and environmental cues to adjust their emigration and immigration decisions to maximize their fitness within a patch (i.e., "context-dependent dispersal" or "informed dispersal"; Clobert et al., 2009). In particular, habitat quality and social factors such as inbreeding risk, kin competition and conspecific density may affect the decision of an individual to stay or to move from its patch (Bowler & Benton, 2005; Matthysen, 2012). In addition, the Euclidean distance between patches and the composition of the landscape matrix strongly affect the capacity of individuals to disperse (Baguette et al., 2013). Understanding how the complex interplay between individual phenotypes, patch-specific factors and landscape determines dispersal patterns is a critical step to understand and predict population dynamics and genetic structure.

Dispersal plays a central role in the dynamics of spatially structured populations (SSPs), which are composed of a set of subpopulations occupying discrete breeding patches that are connected by dispersing individuals and regulated by local demographic processes (i.e., mortality and natality; Thomas & Kunin, 1999). By affecting the intensity and direction of individual movement between patches, dispersal strongly influences the structure and growth rate of subpopulations via emigration and immigration, and ultimately the long-term persistence of the whole SSP (Bowler & Benton, 2005; Hanski & Gaggiotti, 2004). For this reason, dispersal has tremendous importance in the classification of the different types of SSP (i.e., Levins-type metapopulation, patchy population and source-sink systems), which can be positioned along a gradient of dispersal intensity (Ovaskainen & Hanski, 2004). At one end of the gradient, an SSP can behave as a patchy population (Harrison, 1991), where individuals disperse frequently among patches and reproduce in several patches during their lifetime. In this type of SSP, dispersal is so high that the system is effectively a single demographic unit which is unlikely to go extinct (Harrison, 1991). At the other end, SSPs show the characteristics of the classic Levins-type metapopulation (Hanski, 1999; Levins, 1969), where most individuals remain in their natal patch, and dispersal events among subpopulations are infrequent, although the dispersal rate is high enough to allow eventual recolonization of patches where a subpopulation has gone extinct. Furthermore, the nonrandomness and asymmetry of dispersal is another essential aspect for SSP classification (Ovaskainen & Hanski, 2004; Thomas

& Kunin, 1999). In source-sink and pseudo-sink systems, individuals from productive high-quality patches move to low-quality patches where local reproductive success fails to balance local mortality, thereby allowing the long-term persistence of subpopulations in low-quality patches (Kawecki, 2004; Pulliam, 1988; Runge et al., 2006). While true sinks would not be viable without immigration from source populations, high immigration rates into pseudo-sinks increase the local population size above the carrying capacity of the patch and consequently depress local reproductive success or increase local mortality as a result of density-dependence. In these systems, the persistence of the SSP depends on the existence of one or more source populations, while extinction-colonization dynamics depend on habitat quality. Although theoretical models describing those population systems were proposed long ago, the empirical testing of their assumptions is still limited to a small number of taxa, mainly due to the scarcity of longitudinal demographic data collected across large SSPs.

Since successful reproduction of dispersing individuals leads to gene flow, dispersal has a strong influence on the genetic structure and connectivity within an SSP (Broquet & Petit, 2009; Cayuela, Rougemont, et al., 2018; Lowe & Allendorf, 2010). As dispersal intensity and nonrandomness strongly determine the classification of SSPs, one might expect contrasting genetic and relatedness structure in Levins-type metapopulations, patchy populations, and source-sink systems (Gaggiotti, 1996; Hastings & Harrison, 1994). In an SSP that behaves like a Levins-type metapopulation, a low dispersal rate should lead to a low effective dispersal rate (or "migration rate"; Broquet & Petit, 2009; Cayuela, Rougemont, et al., 2018) and strong genetic differentiation between patches is evident, expressed as marked isolation-by-distance (IBD) patterns. Low levels of gene flow should also lead to a decrease of genetic variation and a small effective population size (N_e). In addition, individuals in a specific patch should show high levels of relatedness and high inbreeding coefficients. By contrast, an SSP behaving as a patchy population should present the reverse characteristics, due to high dispersal rate and subsequent gene flow. In an SSP following the source-sink model, genetic structure is expected to be weak due to continuous gene flow between source and sink subpopulations driven by habitat quality (Gaggiotti, 1996). In particular, effective dispersal rates are likely to be asymmetric due to nonrandom dispersal; dispersal should mainly occur from source (high-quality patches) to sink (low-quality patches) subpopulations. As a consequence, observed genetic substructure and IBD should be weak, and relatedness and inbreeding coefficients—as well as N_e —should be habitat-dependent.

Pond-breeding amphibians are excellent models to study the influence of dispersal on the dynamics of SSPs and their genetic structure (Cayuela, Valenzuela-Sánchez, et al., 2020; Marsh & Trenham, 2001; Smith & Green, 2005). First, populations of pond-breeding amphibians follow the typical structure of SSPs: breeding subpopulations occupy discrete aquatic patches (e.g., ponds, lakes) connected by dispersing individuals (Cayuela, Valenzuela-Sánchez, et al., 2020). Second, dispersal rates and distances vary strongly both within and between species (Cayuela, Valenzuela-Sánchez, et al., 2020); this

determines the position of an SSP along the gradient from a Levins-type metapopulation to patchy population (Smith & Green, 2005) and strongly influences its long-term viability (Cayuela, Besnard, et al., 2020). Although amphibian SSPs were initially considered to constitute Levins-type metapopulations, increasing evidence suggests that many amphibian SSPs instead behave like patchy populations (Cayuela, Besnard, et al., 2020; Smith & Green, 2005). Furthermore, although simulation models and empirical data suggest that source–sink systems might exist in amphibians (Gill, 1978; Sinsch, 1992; Sjögren Gulve, 1994; Willson & Hopkins, 2013), the assumption of this model has rarely been empirically tested due to the lack of fine-scale demographic data collected in an amphibian SSP. Third, dispersal can be context-dependent in amphibians, suggesting that individuals adjust their emigration and immigration decisions according to conspecific and heterospecific density (Cayuela et al., 2018, 2019), and environmental factors that affect local breeding success (Boualit et al., 2019). Amphibians actively search for breeding ponds using acoustic, magnetic, visual and olfactory cues for both short- and long-distance orientation (Joly, 2019; Sinsch, 2006, 2014). In particular, amphibians use olfaction to orient toward their breeding pond at distances 100–300 m away from it, identify their natal pond and select their oviposition site (Joly, 2019; Jørgensen, 2000; Ogurtsov, 2004; Sinsch, 2006). Such behavioural processes result in nonrandom dispersal rates and distances in SSPs, drastically affecting gene flow (Berven & Grudzien, 1990; Cayuela, Besnard, et al., 2020; Funk et al., 2005), relatedness and inbreeding within breeding patches, as well as N_e (Cayuela, Besnard, et al., 2020).

Here, we examine how dispersal influences the dynamics and genetic structure of an SSP of the great crested newt (*Triturus cristatus*), a pond-breeding amphibian of European conservation concern. Based on an extensive capture–recapture data set of 5564 marked individuals across a large SSP (33 ponds in an area of 7.7 km², of which 27 ponds held breeding subpopulations), we assessed whether the studied SSP behaves like a Levins-type metapopulation, a patchy population or a source–sink system. We quantified the proportion of dispersing individuals and fitted dispersal kernels (these quantify the relationship between dispersal event frequency and Euclidean distance). Furthermore, we empirically tested the assumption of the source–sink model. Under this model, we expected that adult survival and/or breeding probability are positively correlated with habitat quality, and that individuals from high-quality ponds immigrate to low-quality ponds. Alternatively, under the hypothesis of “informed dispersal” (Clobert et al., 2009), we expected that individuals are less likely to emigrate from high-quality ponds and preferentially immigrate to high-quality ponds. In addition, we verified that pond quality was an accurate predictor for the occurrence of reproduction using multistate occupancy models that took pond connectivity within the SSP into account. Furthermore, we examined the genetic structure of the SSP using 1266 individuals genotyped for 17 microsatellite loci. Under a patchy population model with intense gene flow, genetic structure and IBD patterns should be weakly expressed. Furthermore, we expected low relatedness levels within ponds and low variation in inbreeding and relatedness

across ponds. Finally, we assessed genetic structure and gene flow at a regional level within an area of about 350 km². We expected that populations separated by Euclidean distances exceeding the distance covered during long-distance dispersal events should behave like independent demographic units. We investigated this hypothesis by analysing hierarchical genetic structure and quantifying (molecular) migration rates between the different genetic clusters.

2 | MATERIALS AND METHODS

2.1 | Study species and study sites for demographic and genetic analyses

Triturus cristatus is a widely distributed European pond-breeding amphibian. Adult newts can be found in ponds during the breeding season which begins in February/March and ends in June/July (Jehle et al., 2011). Their ventral colour pattern is highly variable and unique, allowing visual individual recognition in capture–mark–recapture studies (Drechsler et al., 2015). Drechsler et al. (2013) characterized 17 polymorphic microsatellite loci for the analysis of genetic population structure. While the maximum dispersal of a single individual within 1 year was recorded as 1290 m in an anthropogenic landscape (Kupfer, 1998), the habitat used during the terrestrial phase is usually close to the breeding pond (less than 150 m away from the pond; Jehle & Arntzen, 2000). More details about the biology and conservation status of the species are given in the extended methods section of the Supporting Information.

We analysed dispersal and gene flow in an SSP encompassing 33 ponds that are located in two adjacent nature reserves called “Höltigbaum” and “Stellmoorer Tunneltal,” covering an area of ~7.7 km². At the regional scale (350 km²), we analysed genetic structure of crested newt populations by adding six additional sampling sites distributed in the surroundings of Hamburg, Germany (Figure 1; see Supporting Information for a detailed description of these sites). The maximum distance between sampling sites at the regional scale is 27 km along the north–south axis, and 13 km along the east–west axis.

2.2 | Demographic analyses within the SSP

2.2.1 | Capture–recapture survey and data

We collected capture–recapture data between 2012 and 2014 across 33 waterbodies within the area of the SSP (Figure 2; site 1 in Figure 1). Newts were captured using Ortman's funnel traps (Drechsler et al., 2010) during two capture sessions (cs) per year, one early (April/May) and one late (June/July) in the breeding season. Every capture session consisted of three consecutive capture events every 2 days (see Supporting Information for more details on collection of data).

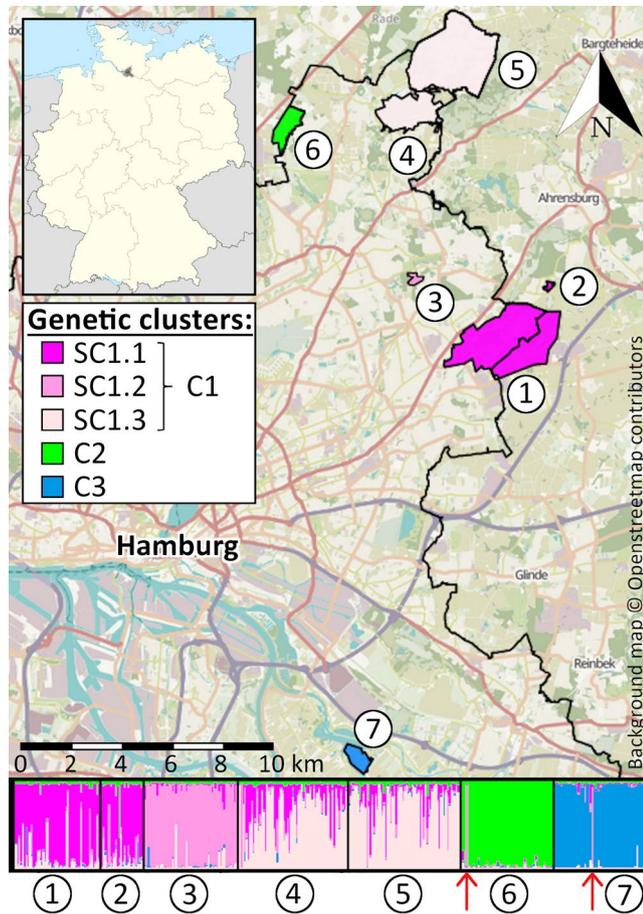


FIGURE 1 Locations of the seven sampling sites in the area of Hamburg, Germany (i.e., the regional level). Genetic clustering analyses of the program *STRUCTURE* resulted in three different clusters (C1, C2 and C3; $k = 3$, indicated by different colours: pink, green and blue) and three different genetic subclusters (SC1.1, SC1.2 and SC1.3) within cluster C1 ($k = 5$, indicated by different pink shades). Red arrows indicate two possible F_0 migrants

2.2.2 | Estimating dispersal distances

We used multistate mark-recapture models (Lebreton et al., 2009) implemented in the program *MARK* (version 6.2; White & Burnham, 1999) to estimate dispersal distances. Model notation follows the standard notation of Lebreton et al. (1992). The model allows estimation of three parameters: apparent survival (ϕ), detection probabilities (p) and dispersal probability (ψ). In this analysis, apparent survival (ϕ) was modelled as constant (.). Detection probabilities (p) were modelled as either constant (.), or as varying among different ponds (Pond), among different years (Y) or the additive effect thereof (Pond + Y). Dispersal probability (ψ) was modelled as constant (.) or as a function of distance between ponds (Dist). This resulted in a set of eight candidate models (see Table 1). Capture events were pooled for early and late capture sessions within each year. We accounted for the unequal time intervals among *cs* (6–8 weeks among *cs* within the same year and 37–40 weeks among *cs* of different years) and estimated weekly survival and dispersal probabilities. Annual apparent

survival was calculated as $(\phi)^{52}$. The corresponding standard error was calculated by applying the delta method (Seber, 1982), and 95% confidence intervals (CI) were obtained using the formula $95\% \text{ CI} = \text{estimate} \pm 1.96 \times \text{SE}$. Model selection was based on the Akaike information criterion adjusted for small sample size (AICc; Burnham & Anderson, 2002). Akaike weights (w) were used as a measure of relative support for each model.

2.2.3 | Estimating the proportion of dispersing individuals

We used the multi-event capture-recapture model described in Denoël et al. (2018) to estimate the proportion of individuals with a dispersing phenotype (i.e., individuals that have dispersed at least once during the study period) within the SSP. In this model, two discrete classes of individuals are considered to accommodate heterogeneity of demographic parameters (Péron et al., 2010; Pradel, 2009). The model includes four main parameters which are estimated from the data: (r) the proportion of individuals with a non-dispersing phenotype, and $(1 - r)$ the proportion of individuals with a dispersing phenotype; (ϕ) the probability of apparent survival; (α) the probability that an individual with a dispersing phenotype remains in the same pond between two sampling sessions (intra-annual: from April/May to June/July; inter-annual: from June/July to April/May), and $(1 - \alpha)$ the probability that it moves to another pond; and (p) recapture probability. For one of the heterogeneity classes, the probability that individuals remained at the same pond is fixed at $\alpha = 1$, which allows for identification of individuals with a non-dispersing phenotype (Cayuela, Boualit, et al., 2019; Denoël et al., 2018). The model was implemented in the program *E-SURGE* (Choquet et al., 2009). All parameters of the model were kept constant, except for recapture probability which differed among years.

2.2.4 | Evaluating the effect of habitat quality on survival, emigration and immigration

Habitat quality was evaluated using the standard habitat suitability index (HSI) developed for *T. cristatus* (Oldham et al., 2000). The HSI ranges from 0 (unsuitable habitat) to 1 (best habitat) and is based on 10 habitat features (e.g., pond area, pond permanence, water quality, fish presence) that can easily be measured in the field or derived from digital maps (see Unglaub et al., 2015). According to the HSI, the optimal habitat for *T. cristatus* would be a temporary, fish-free pond of about 600 m^2 in size, which has good water quality and a diverse macrophyte cover, and which is situated in the centre of the species distribution range, highly connected to other ponds and surrounded by suitable terrestrial habitat where newts can find shelter outside the reproductive season. Newts are more abundant in ponds with a high HSI (Unglaub et al., 2018).

The influence of the HSI on survival, emigration and immigration was examined using the multi-event capture-recapture model

FIGURE 2 Locations of the 33 surveyed ponds within the spatially structured population. Genetic clustering analysis using STRUCTURE resulted in two different genetic population units ($k = 2$): the northeastern (NE; blue) and the southwestern (SW; red) demes. Ponds where no genetic samples were collected (i.e., which were not occupied in 2012) are shown in grey

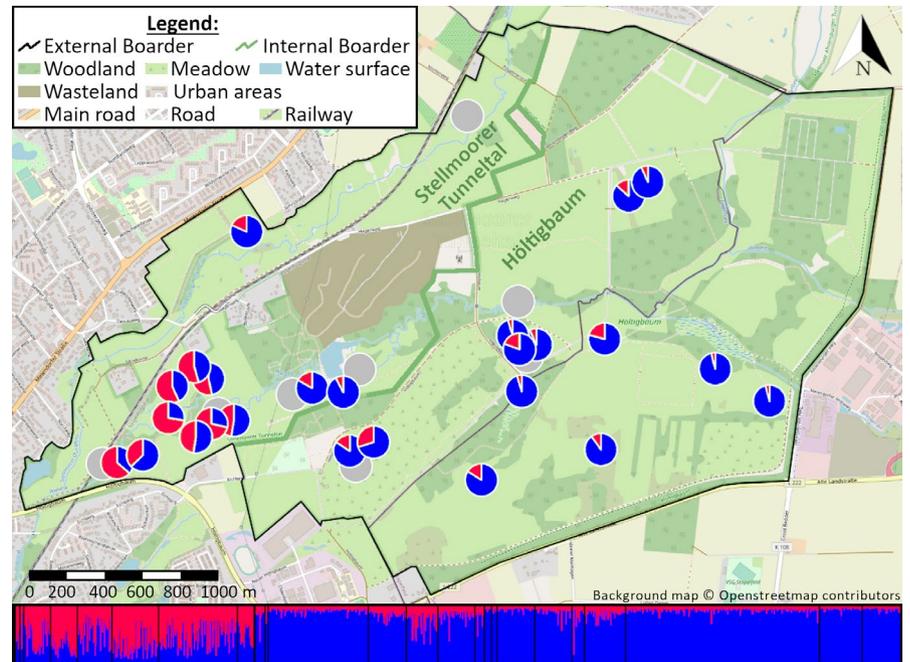


TABLE 1 Selection of multistate mark–recapture models for estimating apparent survival and dispersal probabilities of *Triturus cristatus* within the spatially structured population

Model	ΔAICc	w	k
$\varphi(\cdot), p(\text{Pond}), \Psi(\text{Dist})$	0	0.8080	30
$\varphi(\cdot), p(\text{Pond} + Y), \Psi(\text{Dist})$	2.87	0.1920	32
$\varphi(\cdot), p(Y), \Psi(\text{Dist})$	303.34	0	6
$\varphi(\cdot), p(\cdot), \Psi(\text{Dist})$	304.35	0	4
$\varphi(\cdot), p(\text{Pond}), \Psi(\cdot)$	741.08	0	29
$\varphi(\cdot), p(\text{Pond} + Y), \Psi(\cdot)$	743.54	0	31
$\varphi(\cdot), p(Y), \Psi(\cdot)$	1001.62	0	5
$\varphi(\cdot), p(\cdot), \Psi(\cdot)$	1002.49	0	3

AICc of the best model was 9038.35. Survival probability (Φ) was modelled as constant (\cdot). Capture probability p was modelled as constant (\cdot), and as varying among ponds (Pond), among years (Y) or the additive effect thereof (Pond + Y). Dispersal probability (Ψ) was modelled as constant (\cdot) or as a function of distance between ponds (Dist). AICc: corrected Akaike's information criterion; ΔAICc : difference of the AICc value of the model with the lowest AICc score and the given model; w: Akaike weight; k: number of parameters.

proposed by Tournier et al. (2017), which is an adaptation of the model proposed by Cayuela et al. (2017). The model allows estimation of four parameters of interest: apparent survival probability (φ), emigration probability (ε), immigration probability (α) and recapture probability (p). The model was implemented in the program E-SURGE. Candidate models were ranked through a model-selection procedure using AICc and Akaike weights (w) (Burnham & Anderson, 2002). We performed model-averaging when w of the best-supported model was lower than 0.90. We considered both intra- and inter-annual emigration and immigration probability. To simplify the model structure, intra-annual survival was fixed at $\varphi = 1$, meaning that we only modelled inter-annual survival. Ponds were classified as either high-HSI

ponds when $\text{HSI} \geq 0.78$ or low-HSI ponds when $\text{HSI} < 0.78$; the mean HSI across all ponds was 0.78. In our modelling system, individuals can emigrate from the pond they occupy depending on its HSI status (high-HSI or low-HSI pond). Individuals that have emigrated can then immigrate in a pond with high or low HSI. The effect of HSI on survival, emigration and immigration was examined from the following model: $\{\varphi(\text{HSI}), \varepsilon(\text{HSI}), \alpha(\text{HSI}), p(\text{HSI} + Y)\}$; where Y was the year-specific effect included in recapture probability. We tested all combinations of effects leading to 16 candidate models (see Table 2).

2.2.5 | Evaluating the effect of habitat quality on occurrence of reproduction

We investigated the effect of HSI on adult occurrence and breeding probabilities while taking connectivity among ponds into account. We recorded the presence or absence of newts as well as the occurrence of larvae within 33 ponds of the SSP. Ponds were surveyed during a third capture session in late July/early August in order to detect the presence of larvae. We used the detection/nondetection of larvae as a proxy for successful reproduction (we adjusted for imperfect detection; see below). Adult newts were captured in 27 of 33 surveyed ponds. In the remaining six ponds, no newts were detected in any year of the survey. Larvae were detected in only 19 of 27 occupied ponds. While occupancy states (i.e., whether the species is either present or absent) did not change during the 3 years of sampling (except for one pond which dried up in 2012), the reproduction state (i.e., whether larvae are either present or absent) differed among years. In order to model both the presence/absence of newts and the presence/absence of reproduction (given occurrence), we used a multiseason multistate occupancy model (MacKenzie et al., 2009). This model assumes that the true latent state of the ponds falls into one of three categories: (0) absence of

Model	<i>k</i>	Deviance	AICc	<i>w</i>
φ (.), ε (.), α (HSI), p (Y)	10	13,713.70	13,733.74	0.30
φ (HSI), ε (.), α (HSI), p (Y)	11	13,712.84	13,734.88	0.17
φ (.), ε (HSI), α (HSI), p (Y)	11	13,713.16	13,735.20	0.14
φ (.), ε (.), α (HSI), p (HSI + Y)	11	13,713.68	13,735.72	0.11
φ (HSI), ε (.), α (HSI), p (HSI + Y)	12	13,711.91	13,735.95	0.10
φ (HSI), ε (HSI), α (HSI), p (Y)	12	13,712.22	13,736.26	0.08
φ (.), ε (HSI), α (HSI), p (HSI + Y)	12	13,713.16	13,737.21	0.05
φ (HSI), ε (HSI), α (HSI), p (HSI + Y)	13	13,711.54	13,737.60	0.04
φ (HSI), ε (.), α (HSI), p (HSI)	10	13,799.05	13,819.09	0.00
φ (.), ε (.), α (HSI), p (.)	8	13,803.09	13,819.11	0.00
φ (.), ε (.), α (HSI), p (HSI)	9	13,801.56	13,819.59	0.00
φ (.), ε (HSI), α (HSI), p (HSI)	9	13,802.55	13,820.58	0.00
φ (HSI), ε (.), α (HSI), p (.)	9	13,802.87	13,820.90	0.00
φ (HSI), ε (HSI), α (HSI), p (HSI)	11	13,798.93	13,820.97	0.00
φ (.), ε (HSI), α (HSI), p (.)	10	13,801.34	13,821.37	0.00
φ (HSI), ε (HSI), α (HSI), p (.)	10	13,802.29	13,822.32	0.00

TABLE 2 Testing the effect of pond quality on adult survival, emigration and immigration

Survival probability (φ), emigration probability (ε), immigration probability (α) and recapture probability (p) were modelled as constant (.) or as a function of the habitat suitability index (HSI). Recapture probability was also modelled as varying among years (Y). *k*: number of model parameters; Deviance: residual deviance; AICc: Akaike information criterion adjusted for small sample size; *w*: Akaike weight.

the species, (1) presence without reproduction or (2) presence with reproduction (i.e., presence of larvae). We used only data gathered during the second and third capture session each year for this part of the analyses because larvae were only present during these capture sessions.

We tested whether pond occupancy (ψ) and reproduction probabilities (R) are influenced by HSI, pond surface area and connectivity using the program PRESENCE (version 10.2; Hines, 2006) and used AIC for model selection (Burnham & Anderson, 2002). Connectivity was calculated according to the formula of the incidence function model (Hanski, 1999): $S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j$, where $\alpha = 1/\text{average dispersal distance}$ (the average dispersal distance observed in this study using mark-recapture methods was 137 m), d_{ij} = distance between pond *i* and pond *j*, and A_j = area of pond *j*.

We used a two-step approach to model selection as commonly done in site occupancy analyses (e.g., Groff et al., 2017; Valdez et al., 2015; Weir et al., 2005) and that does not lead to biased parameter estimates in mark-recapture modelling (Doherty et al., 2012). We first modelled the detection process and then the probabilities of site occupancy and reproduction. To identify the best detection model, we held occupancy parameters (ψ and R) constant and evaluated the effect of capture session (*cs*) and sampling year (*Y*), as well as the interaction of both on detection probabilities: (1) the probability of detecting occupancy given that a pond was occupied without reproduction (p^1), (2) the probability of detecting occupancy given that a pond was occupied with successful reproduction (p^2) and (3) the probability of correctly identifying a pond as a breeding site given that successful reproduction did occur (δ). We then analysed the effects of connectivity (*S*), pond

surface area (*Area*) and habitat quality (*HSI*) on pond occupancy (ψ) and reproduction probability (R), while using the best detection model as determined in the first step. Since we observed a single extinction event when a pond dried completely in 2012, we were mainly interested in the influence of these explanatory variables on occupancy and reproduction probabilities rather than in state transition probabilities between years. Variables describing changes over time (i.e., ψ_{t+1}^m and R_{t+1}^m in the transition probability matrix, where *m* = state) were therefore modelled in the same way as the initial variables (i.e., $\psi_{t=1}$ and $R_{t=1}$; see MacKenzie et al., 2009; Unglaub et al., 2015).

2.3 | Genetic analyses

2.3.1 | DNA extraction and microsatellite loci genotyping

In total, 1266 tissue samples were taken from the SSP and the six additional sites (Tables S1a and S1b) by puncturing the tails of newts using micro haematocrit capillary tubes (Carl Roth, \varnothing 1.6 mm). Tissue samples were stored in 80% ethanol. Within the SSP, 950 samples were collected at 25 ponds (Table S1b). To explore structuring at the regional level, we included 316 samples from six additional sites (sites 2–7; 25–66 samples per site). To avoid overrepresentation of individual genotypes from the SSP, we used a standardized sample of 50 representative individual genotypes by random pruning following Chikhi et al. (2010). Taken together, this resulted in a total of 366 genetic samples for the regional scale including samples from

both within and outside the SSP (Table S1a). Each individual sample was genotyped for 17 microsatellite loci (see Drechsler et al., 2013 and Supporting Information for more details).

2.4 | Genetic analyses within the SSP

2.4.1 | Genetic diversity estimates

Across the SSP, 950 individuals could be genotyped for 17 microsatellite loci. Individuals with more than 50% of loci missing (nine individuals) were discarded from further analysis. We computed exact tests (10,000 dememorization steps; 100,000 Markov chain Monte Carlo [MCMC] chain length) for each locus per site to test for significant deviations from Hardy–Weinberg equilibrium (HWE, after Bonferroni correction $p < .002$) and also tested for nonrandom association of alleles at different loci (linkage disequilibrium) using ARLEQUIN 3.5.2.2. Additionally, we checked for the presence of null alleles, scoring errors and large allele dropouts in MICROCHECKER (Van Oosterhout et al., 2004). We calculated genetic diversity parameters (allelic richness [A_r , rarefaction], observed (H_o) and expected (H_e) heterozygosity, inbreeding coefficient [F_{IS}], private alleles [P_A]) for each pond using the R packages *diveRcity* (Keenan et al., 2013) and *PopGenReport* (Adamack & Gruber, 2014).

2.4.2 | Population genetic structure analyses

To analyse the genetic population structure within the SSP, we first calculated pairwise F_{ST} values between the different ponds using the software ARLEQUIN 3.5 (Excoffier & Lischer, 2010). Only ponds with at least 20 genotyped individuals were considered. Then, we used the model-based Bayesian clustering method of the software STRUCTURE (version 2.3.4; Pritchard et al., 2000). Genotyped individuals were assigned to a number of k genetic clusters, using the admixture model with a local prior and a burn-in period of 20,000 MCMC generations, followed by 50,000 iterations for $k = 1$ to $k = 10$ with 10 replicates for each k . We used a local prior to assist genetic clustering at the SSP level because gene flow was presumed to be high. We then used the software STRUCTURE HARVESTER (Earl, 2012) to assess the most likely number of distinct genetic clusters by the estimation of Δk (Evanno et al., 2005) and the evaluation of the logarithm of the probability of the data ($\ln P(D|K)$; Pritchard et al., 2000). The program CLUMPP (Jakobsson & Rosenberg, 2007) was used to align assignment clusters across multiple replicate runs and results were displayed graphically with the program DISTRICT (Rosenberg, 2004).

2.4.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

We performed a spatial autocorrelation analysis with a nondirectional Mantel correlogram (Smouse & Peakall, 1999) using the R-package

ecodist to assess the spatial scale of effective dispersal. Euclidean distance classes were defined every 750 m resulting in seven binary matrices representing the membership of individual pairs to the distance class tested (with “0” for pairs of individuals belonging to the same distance class and “1” otherwise). Each binary matrix was compared to a PhiST matrix (Meirmans, 2006) using a simple Mantel test with 1000 permutations. We then plotted Mantel correlation values over distance classes, with confidence intervals determined by the random removal of 5% of populations (1000 iterations).

2.4.4 | Relatedness structure and IBD analyses

We investigated relatedness structure using the program COANCESTRY version 1.0.1.8 (Wang, 2011) and linear mixed models. We used Wang's estimator (Wang, 2002) that was highly correlated (i.e., correlation coefficient $>.70$; Table S2) with the estimators proposed by Li et al. (1993; *LynchLi* in COANCESTRY), Lynch and Ritland (1999; *LynchRd*), and Queller and Goodnight (1989; *QuellerGt*); the correlation was lower (.40) with the Ritland estimator (Ritland, 1996). We first investigated relatedness structure within the SSP by examining whether mean relatedness among individuals within ponds exceeded relatedness between ponds. We used linear mixed models where individual pairwise relatedness coefficient was included as the response variable (i.e., 450,775 pairwise combinations), individual location was incorporated as explanatory factors with two modalities (i.e., the individuals of the dyad occupy the same pond or two different ponds), and pond was entered as a random effect (i.e., random intercept). The models were implemented in the R package *lme4* (Bates et al., 2015) and the significance of the fixed effect was evaluated with a likelihood ratio (LR) test. We also calculated the marginal R^2 for fixed effects using the *MuMIn* package (Barton, 2009).

In addition, we examined IBD patterns using an individual-based approach relying on pairwise relatedness coefficients (reviewed by Cayuela, Rougemont, et al., 2018). To this end, we built a linear mixed model where pairwise relatedness coefficient (excluding estimates of individuals occupying the same pond, leading to the consideration of 410,348 pairwise combinations) was incorporated as the response variable, Euclidean distance between ponds as the explanatory variable (centered and scaled) and pond as a random effect (i.e., random intercept). We evaluated the significance of the fixed effect with an LR test and calculated the marginal R^2 .

2.4.5 | Effective dispersal rates between genetic clusters and first-generation migrants

Effective dispersal rates (i.e., migration rates) between the two genetic clusters identified by the STRUCTURE analysis within the SSP (see Section 3) were estimated using the programs BIMR (Faubet & Gaggiotti, 2008) and BAYESASS (Wilson & Rannala, 2003).

The program *BIMR* includes a Bayesian assignment test algorithm to estimate the proportion of genes derived from immigrants within the last generation. This multilocus genotype approach can estimate recent gene flow and provide reliable estimates when global F_{ST} values are >0.01 and the number of loci is 10 or more (Faubet & Gaggiotti, 2008). For each analysis, we ran 10 replicates with a total of 2,020,000 iterations. For every replicate, we first ran each MCMC for 20 short pilot runs of 1000 iterations each, in which incremental values were tuned by the program in order to obtain acceptance rates between 25% and 45%. We then used a burn-in period of 10^6 iterations and a sample size of 20,000 with a thinning interval of 50 iterations for each run. Following Faubet et al. (2007), we chose the run with the lowest assignment component of total deviance (D_{assign}) to extract parameter estimates. We examined the 95% highest posterior density interval (HPDI) to assess the significance of asymmetry for pair-wise dispersal rate estimates.

The program *BAYESASS* also uses individual multilocus genotypes to estimate recent effective dispersal rate among populations. This Bayesian approach relies on MCMC techniques to carry out the estimation of posterior probabilities. Following the developer's recommendations, we used the following program settings: the number of iterations for the MCMC was 5,000,000, the thinning interval was 5000 and the length of the burn-in period was 500,000.

To identify possible first-generation (F_0) migrants (i.e., dispersers) among the genetic clusters and to assign them to their source population, we used the Bayesian assignment procedure of Rannala and Mountain (1997), as implemented in the program *GENECLASS 2.0* (Piry et al., 2004). Assignment probabilities were calculated using the Monte Carlo resampling algorithm of Paetkau et al. (2004) with 1000 simulated individuals and a threshold probability of $p = .01$. Since it is possible that some potential source populations were not sampled, we used L_{home} as the likelihood computation instead of $L_{\text{home}}/L_{\text{max}}$ (Paetkau et al., 2004; Piry et al., 2004).

2.5 | Genetic analyses at the regional level

2.5.1 | Genetic diversity estimates

At the regional level, 366 individuals were genotyped for 17 microsatellite loci. The calculation of genetic population diversity estimates at the regional level followed the same workflow as at the local level within the SSP.

2.5.2 | Population genetic structure analyses

We first calculated pairwise F_{ST} values between the seven sites at the regional scale using the software *ARLEQUIN 3.5*. Then, we analysed the population genetic structure using the program *STRUCTURE* following the same approach as described above for SSP analyses.

To assign all genotyped individuals to a number of k clusters, we used the admixture model without local prior (contrary to the SSP analyses) and a burn-in period of 20,000 MCMC generations, followed by 50,000 iterations for $k = 1$ to $k = 7$ with 10 replicates for each k .

2.5.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

We examined the extent of effective dispersal at the regional level using a Mantel autocorrelogram, using the procedure previously described for the SSP analyses (see above) and with distance classes defined every 2 km.

2.5.4 | Effective dispersal rates between genetic clusters and first-generation migrants

Since *STRUCTURE* analyses revealed a hierarchical genetic population structure (see Section 3), we estimated effective dispersal rates among clusters and subclusters over a two-step approach using the programs *BIMR* and *BAYESASS*. First, we estimated effective dispersal rates among three genetic clusters (clusters 1–3; Figure 1) identified at the highest genetic structuring level. Second, at the level of cluster 1, we estimated effective dispersal rates among three distinct subclusters (subcluster 1.1–1.3; Figure 1). We tested all clusters/subclusters for F_0 migrants using the approach previously described for the SSP analyses (see above).

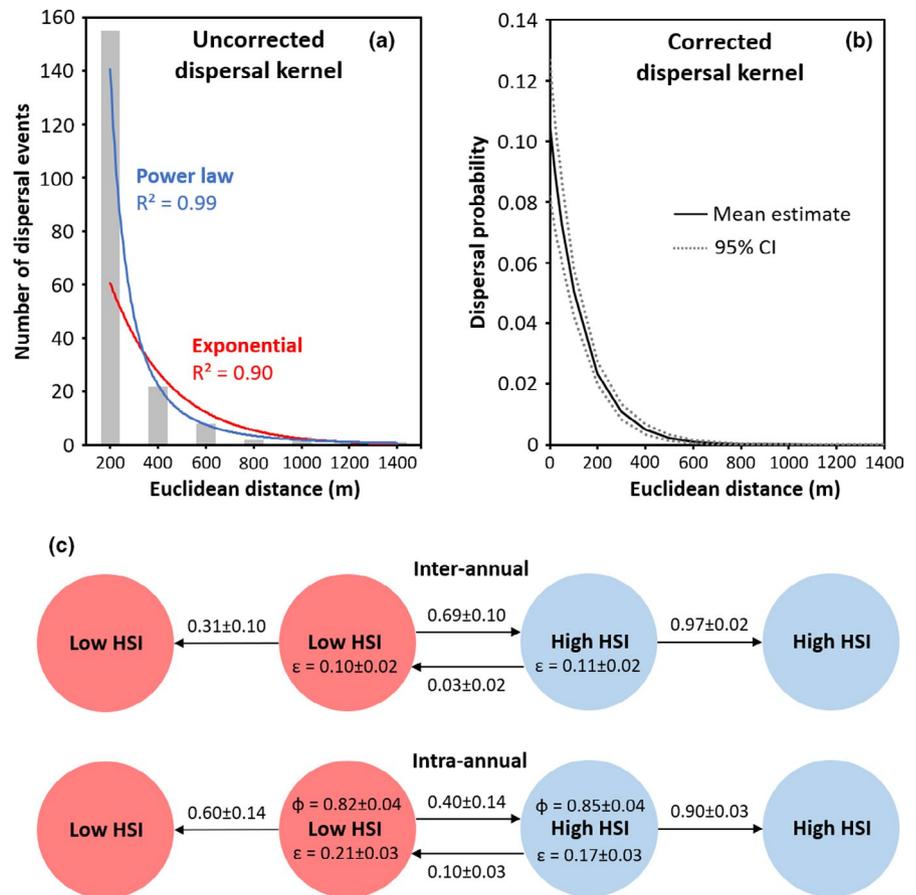
3 | RESULTS

3.1 | Demographic analyses within the SSP

3.1.1 | Dispersal metrics from raw capture–recapture data

In total, 5564 individual capture histories of *Triturus cristatus* (2913 males, 2651 females) were recorded within the SSP. We recaptured 917 individuals at least once, and of these, 189 (20.6%) were found in different ponds during the 3 years of our study. While 66.7% of dispersing newts changed ponds within the SW deme, 32.3% changed ponds within the NE deme, and only two individuals dispersed between demes (for explanation of the two demes, see F_{ST} and *STRUCTURE* analyses below). While 92.1% of dispersing newts moved less than 400 m, 6.9% moved more than 400 m and two individuals more than 1 km (i.e., 1.031 and 1.218 km). Curiously, newts recaptured in different ponds did not move to the nearest pond. The frequency histogram of observed maximum distances moved was better described by a power law ($R^2 = .99$) than by an exponential distribution ($R^2 = .90$), indicating higher proportions of short- and long-distance dispersers (Figure 3a).

FIGURE 3 Dispersal kernels and context-dependent dispersal in a spatially structured population (SSP) of *Triturus cristatus* in Germany. (a) Uncorrected dispersal kernels fitted from raw capture–recapture data using power law and exponential functions. (b) Dispersal kernels corrected for detection issue estimated from a multistate capture–recapture model (mean and 95% CI are shown). (c) Context-dependent dispersal: effect of pond quality (HSI) on adult survival (ϕ), emigration (ϵ), and immigration (α) at inter- and intra-annual levels in the SSP. Immigration probability (α) is given along the arrow that represents the direction of dispersal movements. We provide model-averaged demographic parameters (mean and SE) from the multi-event models presented in Table 2. Circles correspond to low-HSI ponds (in orange; on the left) and high-HSI ponds (in blue; on the right)



3.1.2 | Estimating dispersal distances

The multistate model $\{\phi(\cdot), p(\text{Pond}), \Psi(\text{Dist})\}$ indicating pond-specific recapture probabilities and distance-dependent dispersal probabilities was best supported by the data ($w = 0.8080$; Table 1). Weekly survival probability was constant at 0.995 (95% CI 0.993–0.996). Consequently, annual survival was extrapolated to 0.771 (95% CI 0.770–0.773). Detection probabilities varied among ponds, ranging from 0.004 to 0.210 (though the detection probability of one pond could not be estimated because of a lack of recaptures). Dispersal probability decreased with increasing distance between ponds ($\text{logit}(\Psi) = -2.1509334 - 0.0078935 \times \text{Distance}$; Figure 3b).

3.1.3 | Estimating the proportion of dispersing individuals

Multi-event models (all parameters in Table S3) indicated that the proportion of individuals with a dispersing phenotype (i.e., those that have dispersed at least once during their lifetime) was 0.35 (95% CI 0.22–0.50), while the proportion of fully site-faithful individuals (i.e., the nondispersing phenotype) was 0.65 (95% CI 0.49–0.78). The probability that an individual with a dispersing phenotype changed pond was 0.32 (95% CI 0.19–0.49) and 0.68 (95% CI 0.36–0.89) at the intra- and inter-annual level, respectively.

3.1.4 | Evaluating the effect of habitat quality on survival, emigration and immigration

The best-supported multi-event model was $\{\phi(\cdot), \epsilon(\cdot), \alpha(\text{HSI}), p(\text{Y})\}$ (Table 2). As its Akaike weight was 0.30, the demographic parameters were model-averaged. Our results indicate that survival probability was similar in low-HSI (0.82 ± 0.04) and high-HSI (0.85 ± 0.04) ponds. Emigration probability was higher in low-HSI (0.21 ± 0.03) than in high-HSI (0.17 ± 0.03) ponds at the inter-annual level; by contrast, emigration probability was similar in low-HSI (0.10 ± 0.02) and high-HSI (0.11 ± 0.02) ponds at the intra-annual level. Furthermore, immigration probability was strongly dependent on HSI (Figure 3c). At the inter-annual level, individuals from both low-HSI and high-HSI ponds preferentially immigrated into high-HSI ponds rather than into low-HSI ponds. At the intra-annual level, individuals from high-HSI ponds more frequently immigrated into high-HSI ponds rather than into low-HSI ponds. By contrast, the probability of immigrating into the two types of ponds was more balanced in individuals that emigrated from low-HSI ponds (Figure 3c).

3.1.5 | Evaluating the effect of habitat quality on occurrence of reproduction

We first selected a model that best explained the detection process, while keeping occupancy and reproduction probabilities constant.

Akaike weights (w) suggested that model $\{\psi(\cdot), R(\cdot), \delta(Y^*cs), p^1(cs), p^2(cs)\}$ was best supported by the data ($w = 0.99$; Table S4). This model suggests that the probabilities of detecting newts in ponds occupied with reproduction, as well as in occupied ponds without reproduction, depended on capture session (2nd vs. 3rd cs). However, the probability of correctly identifying ponds as reproduction sites varied among cs and years. We used the top-ranking detection model to determine the effects of connectivity (S), HSI and pond surface area (Area) on occupancy and reproduction probabilities. The model that best explained the data ($w = 0.98$; Table 3) showed that the probabilities of pond occupancy and reproduction increased with increasing habitat quality (Figure 4). In contrast, models assuming that occupancy or reproduction probabilities depend on connectivity or patch size received little support ($w \leq 0.02$; Table 3).

3.2 | Genetic analyses within the SSP

3.2.1 | Genetic diversity estimates

The microsatellite loci analysed for the ponds within the SSP did not significantly deviate from HWE except for locus Tcri46 in pond NE_12 ($p = .001$, homozygote excess). However, the analysis with MICROCHECKER found homozygote excess on this locus in several localities (ponds NE_4, NE_7, NE_11, NE_14, NE_20), and also for

Tcri27 (ponds NE_4, NE_19, NE_20), which was probably caused by high dispersal rates among the ponds of the SSP. Three loci were monomorphic in certain localities: Tcri13 in pond NE_17; Tc58 in ponds NE_7 and NE_15; and Tc85 in ponds NE_1, NE_4, NE_15 and NE_17 (Table S5). As this pattern was not consistent across ponds, the occasionally monomorphic loci were kept for subsequent analyses. Loci Tc50 and Tcri36 were in linkage disequilibrium in 13 of 24 ponds within the SSP, as were loci Tc58 and Tc68b in seven ponds, indicating that alleles on these loci were nonrandomly associated (Table S6).

Genetic diversity was relatively constant between all ponds within the SSP, with pond NE_3 exhibiting the lowest and pond NE_17 the highest diversity (A_r 1.95–2.4, mean 2.41; H_e 0.45–0.65, mean 0.65; Table 4).

3.2.2 | Population genetic structure analyses

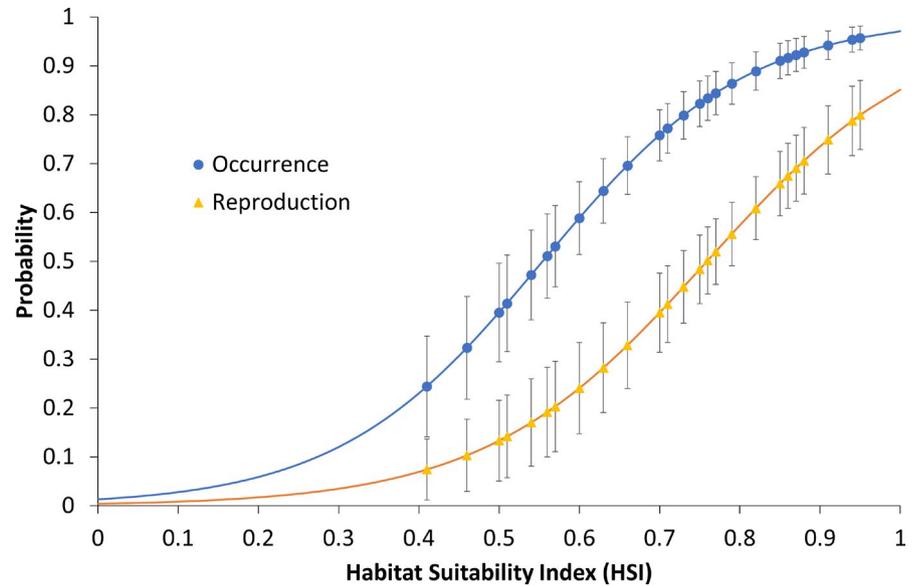
Pairwise F_{ST} values between ponds ranged from 0 to 0.018 and were not always significant, indicating relatively weak population structure within an area of 7.7 km² covered by the SSP (Figure 5a). STRUCTURE analysis indicated the existence of two genetic clusters within the SSP (Figures S1 and S2). One genetic cluster was located in the southwestern part of the nature reserves (SW deme; within the NSG *Stellmoorer Tunneltal*) and the other was in the northeastern

Model	ΔAIC	w	k
ψ (HSI), R (HSI), δ (Y^*cs), p^1 (cs), p^2 (cs)	0.00	0.9810	14
ψ (HSI), R (Area), δ (Y^*cs), p^1 (cs), p^2 (cs)	8.97	0.0111	14
ψ (HSI), R (\cdot), δ (Y^*cs), p^1 (cs), p^2 (cs)	10.28	0.0057	13
ψ (HSI), R (S), δ (Y^*cs), p^1 (cs), p^2 (cs)	12.28	0.0021	14
ψ (\cdot), R (HSI), δ (Y^*cs), p^1 (cs), p^2 (cs)	20.14	0	13
ψ (Area), R (HSI), δ (Y^*cs), p^1 (cs), p^2 (cs)	21.75	0	14
ψ (S), R (HSI), δ (Y^*cs), p^1 (cs), p^2 (cs)	22.00	0	14
ψ (\cdot), R (Area), δ (Y^*cs), p^1 (cs), p^2 (cs)	29.31	0	13
ψ (\cdot), R (\cdot), δ (Y^*cs), p^1 (cs), p^2 (cs)	30.67	0	12
ψ (Area), R (Area), δ (Y^*cs), p^1 (cs), p^2 (cs)	30.92	0	14
ψ (S), R (Area), δ (Y^*cs), p^1 (cs), p^2 (cs)	31.18	0	14
ψ (Area), R (\cdot), δ (Y^*cs), p^1 (cs), p^2 (cs)	32.27	0	13
ψ (S), R (\cdot), δ (Y^*cs), p^1 (cs), p^2 (cs)	32.54	0	13
ψ (\cdot), R (S), δ (Y^*cs), p^1 (cs), p^2 (cs)	32.67	0	13
ψ (Area), R (S), δ (Y^*cs), p^1 (cs), p^2 (cs)	34.27	0	14
ψ (S), R (S), δ (Y^*cs), p^1 (cs), p^2 (cs)	34.54	0	14

TABLE 3 Selection of multiseason multistate models for estimating occupancy and breeding probabilities of *Triturus cristatus* in different ponds within the spatially structured population

AIC of the best model was 565.53. Occupancy probability (ψ) and reproduction probability (R) were modelled either as constant (\cdot) or as a function of habitat suitability (HSI), pond surface area (Area) or connectivity (S), while using the structure of the best detection model $\{\psi(\cdot), R(\cdot), \delta(y^*cs), p^1(cs), p^2(cs)\}$, where the probability of detecting newts in ponds occupied without reproduction (p^1), as well as in ponds with successful reproduction (p^2) depended on cs and the probability of correctly identifying ponds as breeding sites varied among Y and cs. HSI: habitat suitability index; Area: pond surface area; S: connectivity; Y: year; cs: capture session. AIC: Akaike's information criterion; ΔAIC : difference of the AIC value of the model with the lowest AIC score and the given model; w : Akaike weight; k : number of model parameters.

FIGURE 4 The relationship between pond quality (HSI) and occurrence and reproduction probabilities of *Triturus cristatus*. Symbols represent mean estimates and SE. Occurrence and reproduction probabilities were estimated for HSI values observed at 33 ponds within the spatially structured population over 3 years of monitoring



part (NE deme; mainly within the NSG Höltigbaum; see Figure 2). While the occupied ponds in the SW deme all lie within a radius of 300 m and are between 32 and 135 m from the nearest used pond, the ponds in the NE deme spread over almost 3 km and are between 48 and 759 m from the next used pond. The analysis from CLUMPP revealed a high similarity among the 10 replicate runs for $k = 2$ ($H' = 0.964$).

3.2.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

The autocorrelogram based on PhiST indicated a spatial pattern of genetic isolation by distance, with significant positive spatial autocorrelation occurring up to 2 km (Figure 5c). This result suggests that, within the SSP, the spatial extent of effective dispersal is less than 2 km, which is congruent with the maximum noneffective dispersal distance recorded by our mark–recapture data (about 1.2 km).

3.2.4 | Relatedness structure and IBD analyses

Relatedness analyses revealed that the mean relatedness coefficient was close to 0 within each pond (Figure S3). The linear mixed model indicated that mean relatedness was higher within (coefficient: 0.007 ± 0.0008) than between ponds (LR test: $df = 1$, $\chi^2 = 124.25$, $p < 2.2e-16$). However, the proportion of variance explained by the factor WBP (“within vs. between pond”) was very low (marginal $R^2 = .0003$). Furthermore, IBD analyses based on the individual pairwise relatedness coefficient showed that the relatedness level decreased with Euclidean distance (coefficient slope: -0.003 ± 0.0002 ; LR test: $df = 1$, $\chi^2 = 124.25$, $p < 2.2e-16$), but again the proportion of variance explained by the Euclidean distance was negligible (marginal $R^2 = .0005$). Overall, our analyses revealed a weak but still significant relatedness structure and IBD pattern.

3.2.5 | Effective dispersal rates between genetic clusters and first-generation migrants

We calculated effective dispersal rates between the NE and the SW deme. Using BIMR, the run with the lowest Bayesian deviance (D_{assign}) indicated no asymmetric movement between the two demes (95% HPDIs were overlapping): the mean effective dispersal rate was $0.250 (\pm 0.029)$ from the NE to the SW deme and $0.394 (\pm 0.022)$ from the SW to the NE deme. By contrast, BAYESASS indicated asymmetric effective dispersal rates: the mean dispersal rate was $0.286 (\pm 0.007)$ from the NE to the SW deme while it was $0.045 (\pm 0.004)$ from the SW to the NE deme. No F_0 migrants were detected between the two demes.

3.3 | Genetic analyses at the regional scale

3.3.1 | Genetic diversity estimates

The studied ponds were overall in accordance with HWE except for locus Tcr146 (site 3, homozygote excess, $p < .002$) and locus Tc70 (site 4, heterozygote excess, $p < .002$). The analysis with MICROCHECKER additionally showed a homozygote excess for locus Tcr136 at sites 6 and 7. Although these loci did not significantly deviate from HWE, it suggests the presence of null alleles. Locus Tc66 was monomorphic in the sampled individuals from site 7 and locus Tc85 was monomorphic for sites 3 and 7 (Table S5). The data indicated significant linkage: between Tc50 and Tcr136 in six ponds, between Tc58 and Tc68b in five ponds, and between Tcr146 and Tcr135 in four ponds (Table S6). Linkage disequilibrium was also found between other loci, but this was less consistent across ponds.

Genetic diversity varied between sampling sites, with the highest diversity observed each at sites 1, 4 and 5 ($A_r = 6.4$, $H_E = 0.6$), and the lowest observed at site 7 ($A_r = 3.3$, $H_E = 0.4$; Table 4). No significant inbreeding was detected.

TABLE 4 Genetic diversity estimates of the seven regional sampling sites and 19 ponds within the spatially structured population (with $N > 10$ sampled individuals)

Sites	N	A_r	P_A	H_O	H_E	F_{IS}	F_{IS} 95% CI-	F_{IS} 95% CI+
<i>Regional level</i>								
1	50	6.404	5	0.633	0.635	0.005	-0.048	0.04
2	24	5.638	4	0.603	0.594	-0.012	-0.084	0.017
3	54	5.175	4	0.601	0.593	-0.012	-0.065	0.022
4	57	6.454	4	0.664	0.638	-0.049	-0.093	-0.022
5	65	6.447	3	0.627	0.611	-0.026	-0.071	0.004
6	52	4.941	7	0.578	0.575	-0.015	-0.067	0.022
7	39	3.31	4	0.452	0.455	-0.001	-0.074	0.055
<i>Within the SSP</i>								
NE_1	10	2.372	NA	0.612	0.576	-0.066	-0.22	-0.04
NE_4	98	2.496	1	0.642	0.64	-0.008	-0.05	0.023
NE_6	33	2.497	5	0.648	0.649	0.007	-0.07	0.049
NE_7	30	2.48	NA	0.619	0.627	0.012	-0.06	0.049
NE_10	36	2.547	NA	0.684	0.653	-0.056	-0.11	-0.03
NE_11	39	2.469	NA	0.618	0.626	0.011	-0.04	0.036
NE_12	10	2.448	NA	0.659	0.611	-0.05	-0.23	-0.02
NE_17	33	2.565	NA	0.663	0.65	-0.02	-0.09	0.019
NE_18	13	2.47	NA	0.647	0.612	-0.042	-0.18	-0.01
NE_19	39	2.473	NA	0.634	0.625	-0.02	-0.08	0.015
NE_20	188	2.491	4	0.623	0.635	0.023	0	0.045
NE_21	37	2.514	NA	0.657	0.636	-0.034	-0.09	-0.01
NE_22	25	2.423	NA	0.604	0.604	0.007	-0.08	0.056
SW_4	24	2.427	NA	0.596	0.608	0.033	-0.04	0.072
SW_5	25	2.47	NA	0.614	0.626	0.031	-0.06	0.086
SW_6	71	2.47	NA	0.613	0.628	0.03	-0.01	0.059
SW_7	33	2.475	1	0.654	0.632	-0.033	-0.09	0.005
SW_8	46	2.395	1	0.615	0.61	-0.011	-0.07	0.024
SW_9	18	2.379	NA	0.62	0.589	-0.041	-0.13	-0.01

Allelic richness A_r , private alleles P_A , observed and expected heterozygosity (H_O , H_E), inbreeding coefficient (F_{IS}) with confidence intervals (95%). Ponds were named according to the deme they were assigned to (NE, northeastern deme; SW, southwestern deme).

3.3.2 | Population genetic structure analyses

F_{ST} values ranged between sites from 0.1 to 0.17 and were all significant, indicating a relatively strong population structure within this area of 350 km² (Figure 5b). STRUCTURE analysis of all seven sites indicated three distinct genetic clusters at the highest level of genetic structuring (Figures S4 and S5). While sites 6 and 7 represent distinct clusters each, sites 1–5 formed a single cluster, hereafter called cluster 1 (see Figure 1). While CLUMPP analysis revealed a high similarity of clustering solutions across the 10 replicate runs for $k = 3$ ($H' = 0.996$), the mean likelihood L(K) value was highest for $k = 5$ (Figure S5). The structure analysis indicated the presence of three distinct subclusters within cluster 1: subcluster 1.1 (sites 1 and 2), subcluster 1.2 (site 3) and subcluster 1.3 (sites 4 and 5; see Figure 1).

3.3.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

The autocorrelogram based on PhiST indicated a spatial pattern of genetic isolation by distance, with significant positive spatial autocorrelation occurring up to 5 km (Figure 5d). This pattern indicates that, at the regional level, the spatial extent of effective dispersal is less than 5 km.

3.3.4 | Effective dispersal rates between genetic clusters and first-generation migrants

Our results showed that effective dispersal rates among the seven sites were very low. Using BIMR, the run with the lowest Bayesian deviance

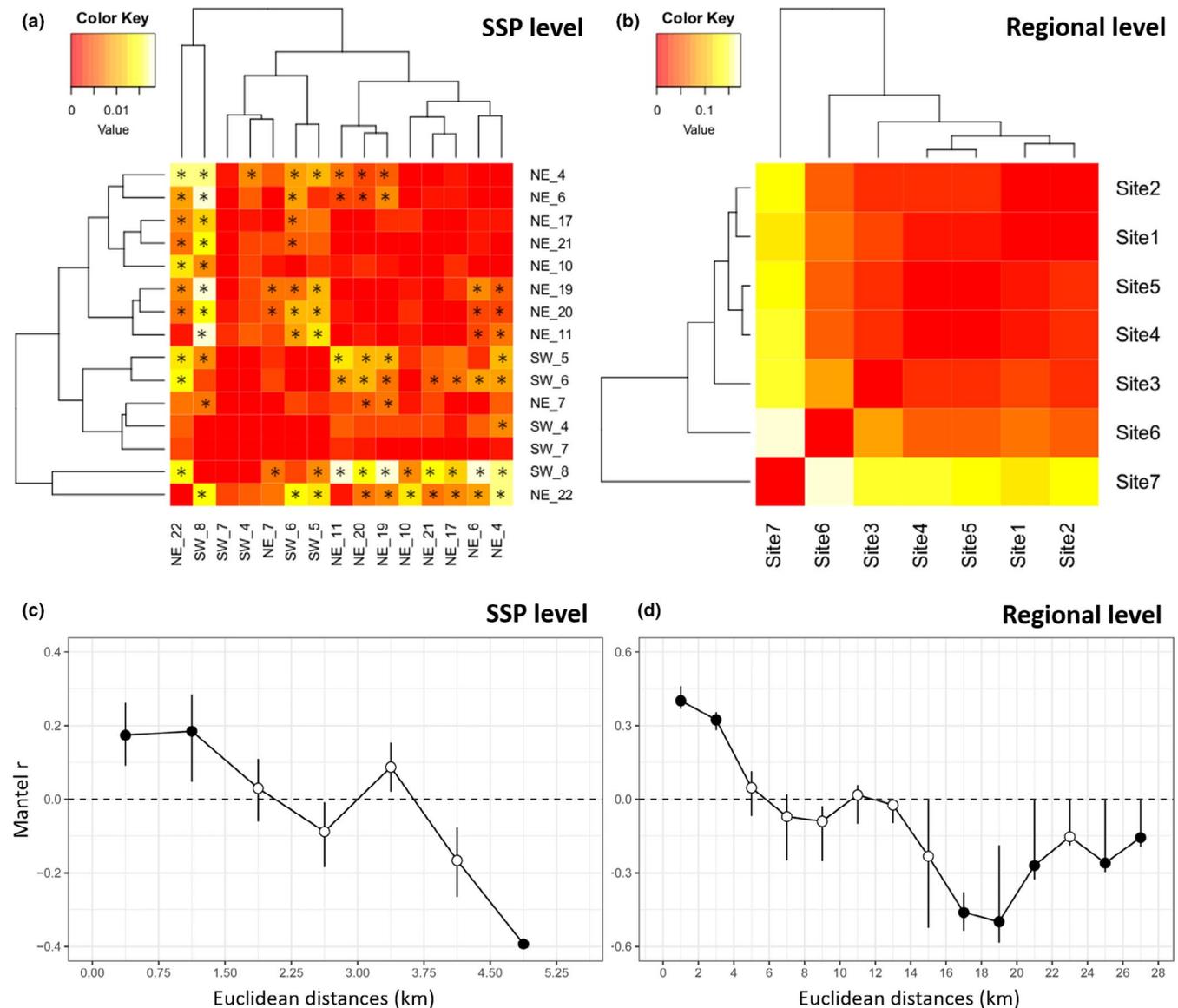


FIGURE 5 Genetic structure at both SSP and regional levels. (a, b) Heatmap and dendrogram of the pairwise F_{ST} distances. (a) Between 15 ponds at the level of the spatially structured population (only populations with $N \geq 20$ individuals were included); ponds were named according to the deme they were assigned to (NE: northeastern deme; SW: southwestern deme); asterisks indicate statistical significance ($p \leq .05$). (b) Between seven sites on the regional level (all values were significant). (c, d) Mantel autocorrelograms showing genetic autocorrelation according to Euclidean distance between ponds (c) and sites (d). The full and empty points show the Euclidean distances where genetic autocorrelation is significant and nonsignificant, respectively

(D_{assign}) indicated low effective dispersal rates (Figure 6a), ranging from 0.002 (± 0.003 , from cluster 3 to cluster 1) to 0.021 (± 0.014 , from cluster 1 to cluster 3). Similarly, BAYESASS indicated very low effective dispersal rates (Figure 6b), ranging from 0.005 (± 0.004 , from cluster 1 to 2) to 0.023 (± 0.011 , from cluster 2 to 3).

Furthermore, we found that effective dispersal rates among the three genetic subclusters within cluster 1 were also generally low. Program BIMR indicated low effective dispersal rates (Figure 6a), ranging from 0.002 (± 0.005 , from subcluster 1.3 to subcluster 1.2) to 0.309 (± 0.054 , from subcluster 1.1 to subcluster 1.3). Similarly, BAYESASS indicated very low effective dispersal rates (Figure 6b), ranging from 0.009 (± 0.009 , from subcluster 1.2 to 1.1) to 0.031 (± 0.018 , from subcluster 1.3 to 1.1).

The analysis of F_0 migrants using the software GENECLASS 2.0 identified two F_0 migrants among clusters. One individual probably dispersed from cluster 1 to cluster 2, which is a distance of around 5 km. The second seems to have dispersed at least 16 km from cluster 1 to cluster 3. No F_0 migrants were detected among the three subclusters within cluster 1.

4 | DISCUSSION

The type of SSP is mainly determined by the dispersal of individuals. Here, we used the analysis of dispersal as a key to characterize the type of SSP of a pond-breeding amphibian, the great crested newt.

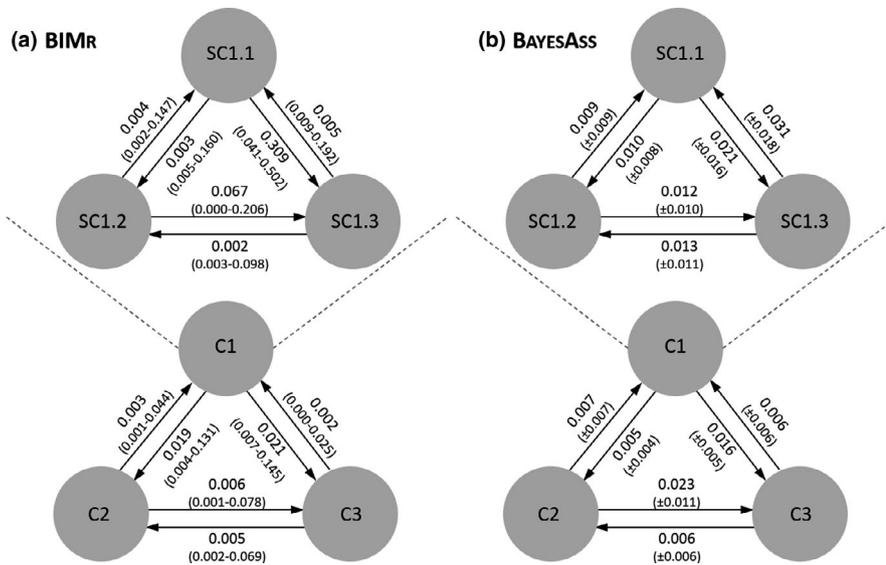


FIGURE 6 Effective dispersal rates at the regional level. We used BIMr and BAYESASS to estimate effective dispersal among the three genetic clusters (C1, C2 and C3) and the three genetic subclusters (SC1.1, SC1.2 and SC1.3) within cluster 1 (C1). Mean and highest posterior density interval are given for BIMr and mean SE are provided for BAYESASS

Within the SSP, we found that dispersal rates were both relatively high and context-dependent. If newts dispersed, individuals preferentially immigrated into high-quality ponds, a move likely to increase their own fitness. Although a few rare events of long-distance dispersal (>1 km) were detected, dispersal mostly comprised short-distance movements of up to 400 m. Overall, these dispersal patterns indicate that the SSP behaves like a patchy population where subpopulations at each pond are demographically interdependent. This demographic system led to a weak genetic structure and low relatedness of individuals within the SSP, although an IBD signal was nevertheless detected. By contrast, at the regional level our analyses revealed a strong hierarchical genetic structure with limited admixture and very few first-generation (F_0) migrants. In addition, effective dispersal rates were also rather low, even between spatially close sites (within 3–6 km), suggesting the presence of several independent demographic units.

4.1 | Context-dependent dispersal as a behaviour to increase reproductive success

Our analyses revealed that in the SSP studied, dispersal was context-dependent (i.e., “informed dispersal” *sensu* Clobert et al., 2009) and depended on HSI, the index of habitat quality. Although habitat quality marginally affected emigration probability, it strongly influenced immigration probability. Individuals preferentially immigrated into high-quality ponds where abundance is generally higher and body condition lower than in low-quality ponds (Unglaub et al., 2018). Overall, our results suggest that adult pond choice does not result from a strategy to maximize their own survival. Annual survival probability was both high and independent of pond habitat quality. It was 0.82 and 0.85 in low- and high-quality ponds respectively, which is similar to survival values estimated in the most long-lived populations of *Triturus cristatus* (Cayuela, Besnard, et al., 2020: 0.83 and 0.87 in populations from southern England and western

France respectively). By contrast, our analyses indicate that context-dependent dispersal is associated with reproductive success in ponds: individuals more frequently immigrate in ponds with a high HSI where the reproduction probability is highest. This result is consistent with previous studies that showed amphibians actively select breeding waterbodies with biotic and abiotic characteristics that increase offspring fitness at premetamorphic stages (Buxton & Sperry, 2017). For example, in the yellow-bellied toad (*Bombina variegata*), adult emigration and immigration probabilities are determined by pond hydroperiod (Tournier et al., 2017) and anthropogenic disturbance (Boualit et al., 2019); both these factors have a strong effect on breeding probability and toadlet production.

Although the proximal mechanisms involved in pond selection during the immigration phase have not been fully deciphered, studies suggest that *T. cristatus* adults could use multiple cues to assess pond quality for reproduction. In particular, individuals could use conspecific and heterospecific density as a “public information” (*sensu* Valone, 1989) to adjust their emigration and immigration decisions (Cayuela, Grolet, et al., 2018; Cayuela, Schmidt, et al., 2019). Moreover, pond odour could also be used to assess pond quality during the immigration phase, since amphibians in general are able to assess the chemical signature of their natal pond (Sinsch, 1991, 2006) as well as the odour of predators (Buxton & Sperry, 2017).

Overall, our study and previous work (Barrile et al., 2021; Boualit et al., 2019; Tournier et al., 2017) suggest that amphibians adjust their dispersal decisions according to environmental and/or social cues reflecting local fitness prospects in the aquatic patches used for reproduction (Cayuela, Valenzuela-Sánchez, et al., 2020). Those results are congruent with the conclusions drawn by a growing number of studies on vertebrates and invertebrates that show dispersal to be a plastic phenotypic trait (Saastamoinen et al., 2018) allowing organisms to respond to the spatiotemporal heterogeneity of their habitat in fragmented landscapes (Baguette et al., 2013; Cote et al., 2017; Hendrix et al., 2017).

4.2 | Demographic consequences of context-dependent dispersal

Our analyses showed that 35% of the individuals dispersed at least once during the 3-year study. Annual survival in the studied SSP is estimated to be 0.77. This means that 77% of the individuals survive 1 year, 59% 2 years and 45% 3 years. Thus, the study period covered half of the lifespan of newts in this SSP. This proportion of dispersing individuals is half that estimated by Denoël et al. (2018; 0.70) using the same modelling approach for a *T. cristatus* SSP in Belgium. In contrast, it is much higher than the proportion of dispersers observed in another SSP in western Germany (Unglaub et al., 2015; 11 dispersing individuals out of 1838 individuals marked). Furthermore, the dispersal kernel estimated in our study shows that most dispersal movements are shorter than 200 m, although rare long-distance dispersal events (>1.2 km) were also detected. These results are congruent with those of Cayuela, Besnard, et al. (2020), indicating that dispersal movements mostly occurred among spatially close ponds (distance between ponds <100 m). Taken together, the studies of Denoël et al. (2018), Cayuela, Besnard, et al. (2020) and the present study suggest that *T. cristatus* SSPs tend to behave as patchy populations when geographical distance between ponds is short (<200 m). In this situation, subpopulations of breeders occupying the different ponds of a network are thus interdependent demographic units connected by high migrant flows (Harrison, 1991).

Our results also showed that despite the asymmetric dispersal rate among ponds, the dispersal pattern in the SSP did not meet the theoretical expectations of the source-sink model even though successful reproduction (i.e., presence of larvae) was observed only in high-quality ponds (Kawecki, 2004; Pulliam, 1988). Instead of mainly immigrating into low-quality ponds, most dispersing individuals from high-quality ponds preferentially immigrated in ponds of similar quality (90% and 97% at the intra- and inter-annual level, respectively). By choosing high-quality ponds, individuals may subsequently maximize their reproductive success. It is nevertheless possible that subsequent marginal disperser inflow from high-quality ponds (10% and 3% at the intra- and inter-annual level respectively) contributes to the long-term persistence of subpopulations occupying low-quality ponds (where there is often no successful reproduction). Further demographic modelling should be performed to evaluate whether this small proportion of immigrants allows effective compensatory immigration, that is an immigrant inflow sufficient to compensate depauperate natality and maintain stable population growth rate ($\lambda \geq 1$) in subpopulations experiencing suboptimal environmental conditions (Kawecki, 2004; Runge et al., 2006).

Overall, our results showed that the studied SSP behaves as a patchy population rather than a Levins-type metapopulation, which supports the idea that SSPs which meet the Levins-type metapopulation assumptions are rare in the wild (Fronhofer et al., 2012), particularly in amphibians (Smith & Green, 2005). Our analyses also revealed that the studied SSP does not present the typical pattern of asymmetric dispersal expected under Pulliam's (1988) source-sink model. However, it is possible that the low dispersal rates observed

between high- and low-quality ponds is sufficient to allow the persistence of populations in low-quality ponds.

4.3 | Genetic consequences of high context-dependent dispersal within the SSP

Our analyses show that high levels of context-dependent dispersal are associated with a weak genetic structure in the patchy population of *T. cristatus*. Although we detected two genetic clusters within the SSP, we found high levels of admixture and high effective dispersal rates between the two demes. In addition, our analyses reveal weak genetic relatedness in the SSP. Relatedness coefficients among individuals within ponds were close to 0, suggesting that subpopulations in ponds are mainly composed of unrelated adults. Furthermore, we show that the relatedness was slightly higher within ponds than between ponds, and that it slightly decreases with Euclidean distance between ponds. An IBD signal was also detected using a Mantel autocorrelogram based on PhiST, which showed that the spatial extent of effective dispersal was up to 2 km. Interestingly, this value was relatively close to the maximum distance of noneffective dispersal recorded using our capture-recapture data (1.2 km).

Together, these findings suggest that relatively high dispersal rates within the SSP lead to intense gene flow that weakens the genetic structure of the SSP and IBD patterns, and decreases the level of relatedness within ponds. This pattern is congruent with previous studies on amphibians showing that natal and reproductive dispersal modulates the strength of the genetic and relatedness structure within the SSP (Berven & Grudzien, 1990; Cayuela, Besnard, et al., 2020; Funk et al., 2005). However, the influence of dispersal on adaptive processes within amphibian SSPs is still poorly understood (Cayuela, Valenzuela-Sánchez, et al., 2020; Pabijan et al., 2020). Further genomic studies could help to investigate how dispersal intensity and context-dependency may erode (i.e., Tigano & Friesen, 2016) or favour (via "habitat matching choice"; Jacob et al., 2017) adaptation to breeding pond characteristics.

4.4 | Long-distance dispersal and genetic structure at the regional scale

At the regional level, we found a hierarchical genetic structure composed of three main clusters, of which one could be further subdivided into three subclusters. Admixture among the main clusters and among subclusters was rather limited and both BIMR and BAYESASS indicated low effective dispersal rates among them. Overall, these results indicate that clusters and subclusters behave like independent demographic/genetic units with limited gene flow between them. They are therefore consistent with previous studies that have highlighted strong genetic differentiation in *T. cristatus* at similar spatial scales (Haugen et al., 2020; Schön et al., 2011). In our study system, limited gene flow between demographic/genetic units separated from each other by relatively short Euclidean distances (from 3

to 27 km) is probably caused by the short distances that *T. cristatus* seem to move; dispersal kernels quantified at the SSP level showed that movements exceeding 1 km are rare events. Furthermore, physical barriers could also limit the movement of newts in the landscape matrix (Haugen et al., 2020), increasing genetic differentiation among clusters and subclusters.

4.5 | Implications for conservation

Identifying the major drivers sustaining the functioning of an SSP is crucial for conservation. Our results confirm previous findings that habitat quality has a strong impact on the demography, dispersal and genetic structure of amphibian populations (Cayuela, Besnard, et al., 2020). In keeping with earlier work (Unglaub et al., 2015, 2018), we find that in *T. cristatus*, higher habitat quality leads to greater abundance and higher reproductive success but is also correlated with a lower body condition of individuals. In contrast, individual survival does not appear to depend on habitat quality. Our finding that newts are more likely to both emigrate from low-quality patches and to immigrate into high-quality patches adds to earlier results which show they are more likely to emigrate from small populations than large populations (Cayuela, Schmidt, et al., 2019). Thus, to preserve *T. cristatus* populations in landscapes where habitat quality is poor, restoration of habitat quality is key to successful conservation. Habitat quality could be restored through the removal of predatory fish, removal of trees which shade the pond, or other actions that mitigate negative anthropogenic influences on habitat quality (Oldham et al., 2000). Enhancing habitat quality will increase the probability that a population produces larvae successfully and therefore recruitment. This will have positive effects on abundance and is likely to increase population viability (Halley et al., 1996; Karlsson et al., 2007). The restoration of habitat quality will also increase connectivity between sites due to increased dispersal rates. However, our study shows that most newts do not disperse farther than 400 m, and we found almost no dispersal between demes at the regional level. Therefore, conservation efforts should focus on sustaining dispersal between networks of ponds on a local scale rather than attempting to set up dispersal corridors between distantly located ponds. We suggest that conservation efforts should focus both on the restoration of habitat quality for existing populations and on the creation of new ponds, preferably on land with marginal value for biodiversity, close to existing ones to function as stepping stones and thus facilitate dispersal over longer distances (Rannap et al., 2009). This will lead to a functional network of populations and a viable patchy population (Griffiths & Williams, 2000; Halley et al., 1996; Karlsson et al., 2007).

5 | CONCLUSION

Our study provides one of the few empirical cases that illustrates the consequences of context-dependent dispersal on the demography, genetic structure and spatial patterns of relatedness of an SSP.

Notably, our results show that a high context-dependent dispersal coupled with short-distance movement leads to the formation of a patchy population. At the regional level, this patchy population behaves like an independent demographic and genetic unit, having limited gene flow with neighbouring populations. Such population systems seem particularly common in amphibians (Smith & Green, 2005), and more generally in organisms with low vagility (e.g., reptiles and some insects, Bowne & Bowers, 2004) that occupy habitat patches in which distribution is spatially heterogeneous due to natural (e.g., variation in soil characteristics, temperature, and hygrometry) and anthropogenic causes (e.g., habitat alteration and habitat fragmentation). However, the long-term viability of many patchy populations is currently threatened by ongoing isolation and habitat loss resulting from anthropogenic changes in land use. Preserving habitat quality of local patches and facilitating dispersal and gene flow between local demographic units—even if limited—within patchy populations is of critical importance to facilitate demographic, genetic and evolutionary functioning, and to rescue these populations in the midst of anthropogenic stressors.

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AUTHOR CONTRIBUTIONS

S.S., B.R.S. and H.C. designed the study. B.U. performed field work. J.G. provided additional expertise and facilities. B.U., B.R.S. and H.C. analysed CMR-data, HSI data and performed demographic analysis. B.U., K.P., S.S. and H.C. analysed microsatellite loci data and performed population genetic analyses. B.U., B.R.S., S.S. and H.C. wrote the manuscript.

CONFLICTS OF INTERESTS

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Individual genotypes of microsatellite data, geographical coordinates of sampling locations of the SSP and at the regional level, capture-mark-recapture data and capture events data (presence/absence data), including HSI values of ponds within the SSP: https://datadryad.org/stash/share/aFMmXrRY9ew9IDAUZrPYbzfKq0cA_tCVJEsBCuleBNQ.

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SUPPORTING INFORMATION

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