

1 **Anthropogenic disturbance drives dispersal syndromes, demography, and gene flow in**  
2 **spatially structured amphibian populations**

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19 **Running head:** Disturbance and dispersal

20

21 **Abstract**

22

23 There is growing evidence that anthropogenic landscapes can strongly influence the evolution of  
24 dispersal, particularly through fragmentation, and may drive organisms into an evolutionary trap by  
25 suppressing dispersal. However, the influence on dispersal evolution of anthropogenic variation in  
26 habitat patch turnover has so far been largely overlooked. In this study, we examined how human-  
27 driven variation in patch persistence affects dispersal rates and distances, determines dispersal-related  
28 phenotypic specialization, and drives neutral genetic structure in spatially structured populations. We  
29 addressed this issue in an amphibian, *Bombina variegata*, using an integrative approach combining  
30 capture–recapture modeling, demographic simulation, common garden experiments, and population  
31 genetics. *B. variegata* reproduces in small ponds that occur either in habitat patches that are persistent  
32 (i.e. several decades or more), located in riverine environments with negligible human activity, or in  
33 patches that are highly temporary (i.e. a few years), created by logging operations in intensively  
34 harvested woodland. Our capture–recapture models revealed that natal and breeding dispersal rates  
35 and distances were drastically higher in spatially structured populations (SSPs) in logging  
36 environments than in riverine SSPs. Population simulations additionally showed that dispersal costs

37 and benefits drive the fate of logging SSPs, which cannot persist without dispersal. The common  
38 garden experiments revealed that toadlets reared in laboratory conditions have morphological and  
39 behavioral specialization that depends on their habitat of origin. Toadlets from logging SSPs were  
40 found to have higher boldness and exploration propensity than those from riverine SSPs, indicating  
41 transgenerationally transmitted dispersal syndromes. We also found contrasting patterns of neutral  
42 genetic diversity and gene flow in riverine and logging SSPs, with genetic diversity and effective  
43 population size considerably higher in logging than in riverine SSPs. In parallel, intra-patch inbreeding  
44 and relatedness levels were lower in logging SSPs. Controlling for the effect of genetic drift and  
45 landscape connectivity, gene flow was found to be higher in logging than in riverine SSPs. Taken  
46 together, these results indicate that anthropogenic variation in habitat patch turnover may have an  
47 effect at least as important as landscape fragmentation on dispersal evolution and the long-term  
48 viability and genetic structure of wild populations.

49 **Keyword:** Dispersal, movement behavior, behavioral syndrome, metapopulation, genetic structure,  
50 amphibian

51 **Introduction**

52 In the age of the Anthropocene, a significant proportion of land cover has been replaced by human-  
53 dominated landscapes (Foley et al. 2005, Pereira et al. 2010, Gibson et al. 2011, Tilman et al. 2017),  
54 with the result that the conditions prevailing in these anthropogenic environments now shape the  
55 evolutionary course of almost all species (Otto 2018, Pelletier & Coltman 2018). Land use changes  
56 usually have the simultaneous effects of habitat loss, alteration, and/or fragmentation into small habitat  
57 patches isolated in a more or less hostile matrix (i.e. unsuitable habitat) (Fahrig 2003, Villard &  
58 Metzger 2014). While it is widely accepted that habitat loss is the main factor involved in local  
59 extinction and biodiversity loss (Sala et al. 2000, Pereira et al. 2010, Newbold et al. 2015, Tilman et  
60 al. 2017), it is also increasingly recognized that habitat alteration and fragmentation are critical  
61 ecological and evolutionary drivers in anthropogenic landscapes (Villard & Metzger 2014, Haddad et  
62 al 2015). Interestingly, the risk of extirpation from anthropogenic landscapes appears to differ between  
63 species (Frishkoff et al. 2014, Edward et al. 2015, Nowakoski et al. 2018) and research is needed to  
64 identify the phenotypic traits that allow some species to cope with and succeed in human-dominated  
65 contexts.

66 Dispersal, i.e. the movement from birth to breeding patch (natal dispersal) or between  
67 successive breeding patches (breeding dispersal), is a key ecological and evolutionary process.  
68 Dispersal provides the demographic supply for population rescuing, habitat (re)colonization (Hanski &  
69 Gaggiotti 2004, Bowler & Benton 2005, Gilpin 2012), and range expansion (Travis et al. 2009,  
70 Kubisch et al. 2014, Ochocki & Miller 2017). Furthermore, it determines the intensity and direction of  
71 gene flow, which has far-reaching consequences for local genetic diversity and adaptive processes  
72 (Lenormand 2002, Ronce 2007, Petit & Broquet 2009, Cayuela et al. 2018a). Dispersal is a complex  
73 phenotype, partially controlled by genetics and relying on a suite of morphological, behavioral and life  
74 history traits that may be subject to joint selection (Saastamoinen et al. 2018). Such associations  
75 between dispersal and individual phenotype are called ‘dispersal syndromes’ and lead to phenotypic  
76 specialization within and between populations (Matthysen 2012, Cote et al. 2010, Ronce & Clobert  
77 2012). Dispersal is also influenced by patch and landscape characteristics: individuals are expected to  
78 adjust their dispersal decisions according to the fitness prospects of a patch (i.e. ‘informed dispersal’,  
79 Clobert et al. 2009), leading to context-dependent dispersal.

80 Over the last two decades, an increasing number of studies have suggested that landscape  
81 anthropization is an important determinant in dispersal evolution as it affects the balance between  
82 fitness benefits and the direct and indirect costs of moving (Bonte et al. 2012) incurred at the different  
83 stages of the dispersal process (i.e. emigration, transience, and immigration) (Kokko & Lopez-  
84 Sepulcre 2006, Cheptou et al. 2017, Cote et al. 2017). The majority of efforts have been devoted to  
85 better understanding the influence of habitat fragmentation on dispersal evolution in anthropogenic  
86 landscapes (Cheptou et al. 2017, Cote et al. 2017, Legrand et al. 2017, Atkin et al. 2019). Overall,  
87 these studies have reported reduced dispersal propensity or capacity in fragmented landscapes, which

88 is usually attributed to prohibitive costs during the transition phase across the matrix (Cheptou et al.  
89 2017, Cote et al 2017). This hypothesis is supported by landscape genetic studies, which often report  
90 increased spatial genetic differentiation depending on the harshness of the matrix that separates demes  
91 (Baguette et al. 2013, Cushman et al. 2015). Nevertheless, habitat fragmentation may have a  
92 contradictory effect on the evolution of dispersal: on one hand, it may make transition across the  
93 matrix costlier, but on the other, it may make dispersal profitable due to the increased local extinction  
94 risk caused by heightened demographic stochasticity within severely fragmented landscapes (Ronce  
95 2007, Hanski & Mononen 2011, Cote et al. 2017). The best empirical support of this hypothesis is  
96 perhaps the well-documented selection for dispersal-specialized phenotypes observed in spatially  
97 structured populations (SSPs, Thomas & Kunin 1999) of the Glanville fritillary butterfly subject to  
98 highly fragmented landscapes (Hanski 2011, Hanski et al. 2017). In this unique example,  
99 environmental stochasticity makes dispersal profitable by creating new patches that can be colonized  
100 by dispersers. The prime importance of spatiotemporal patch variability in promoting dispersal is well  
101 supported by a number of theoretical models (Comins et al. 1980, McPeck & Holt 1992, Armsworth &  
102 Rougharden 2005), and is also advanced as the main driver of wing dimorphism observed in insects in  
103 a gradient of patch temporality (Denno et al. 1996).

104 Habitat alteration in human-dominated landscapes is often associated with shifts in disturbance  
105 regimes (Turner 2010, Newman 2019). For instance, one decade-long worldwide survey revealed a  
106 relatively weak net surface loss of temperate forests, but a high turnover due to forestry practices  
107 (Hansen et al. 2013). Shifts in the disturbance regimes prevailing in habitat remnants could therefore  
108 mitigate or, conversely, magnify the negative effect of habitat fragmentation, depending on their  
109 direction and magnitude. Despite this, apart for aerial dispersal in invertebrates (Denno et al. 1996),  
110 human-induced temporal variation in the spatial distribution of habitat patches has generally been  
111 overlooked when considering dispersal evolution in anthropogenic landscapes. A full appraisal of the  
112 effect of anthropogenic disturbance on dispersal should not only examine whether a dispersal pattern  
113 emerges in a landscape, but whether it gives rise to a genetic footprint throughout successive  
114 generations – and last but not least, to what extent this involves a specialized phenotype. Considering  
115 all the facets of this issue is not a simple task (Kokko & Lopez-Sepulcre 2006, Broquet & Petit 2009,  
116 Ronce & Clobert 2012), and to our knowledge has not yet been investigated in vertebrates.

117 To address this gap, this study examined how human-driven variation in habitat patch turnover  
118 affects dispersal rates and distances, determines dispersal-related phenotypic specialization, and drives  
119 neutral genetic variation in spatially structured populations. We studied this issue in an early  
120 successional amphibian, the yellow-bellied toad (*Bombina variegata*), a species that reproduces in  
121 small waterbodies with a short hydroperiod occurring either in (virtually) undisturbed or  
122 anthropogenic environments (Warren & Büttner 2008; Cayuela et al. 2011, 2015b). In riverine  
123 environments with negligible human activity, the species' habitat patches are groups of rocky pools  
124 that result from long-term geomorphological processes alongside riverbanks (riverine SSPs; Cayuela

125 et al. 2011). This results in a negligible patch turnover rate and makes patches available and  
126 predictable far beyond a toad's lifespan. In contrast, in harvested woodlands, habitat patches consist of  
127 groups of ruts made by logging vehicles that may appear and disappear yearly as a result of the  
128 combined effects of logging operations and rapid natural silting (we refer to these as logging SSPs  
129 hereafter). This leads to a high patch turnover rate and makes patch location and availability more  
130 unpredictable at the scale of a toad's lifespan (Cayuela et al. 2016a, 2016b). Previous studies have  
131 highlighted demographic differences in SSPs from the two environments and found that individuals in  
132 logging SSPs have a faster life history (i.e. a shorter lifespan and higher fecundity; Cayuela et al.  
133 2016a), experience earlier senescence (Cayuela et al. 2019b), and display higher breeding dispersal  
134 probability (Cayuela et al. 2016b) than individuals in riverine habitats. In this study, our first step was  
135 to quantify dispersal probability and distance throughout an individual's lifetime, as natal dispersal  
136 was lacking in previous studies and a review of recent literature suggested that natal and breeding  
137 dispersal patterns can strongly differ in amphibians (Cayuela et al. 2018c). We expected that (1) both  
138 natal and breeding dispersal rates and distances would be higher in logging than in riverine SSPs. In a  
139 second step, we analyzed how patch turnover and related dispersal costs and benefits affected SSP  
140 dynamics and long-term viability using simulations based on published demographic rates. We  
141 hypothesized that (2) dispersal and context-dependent immigration (i.e. depending on patch age)  
142 allows the long-term persistence of logging SSPs. In a third step, we used common garden  
143 experiments to investigate how patch turnover determines dispersal syndromes and may act as a  
144 selective agent on phenotypic specialization in riverine and logging SSPs. We expected (3) toadlets  
145 from logging SSPs to have behavioral traits (i.e. high exploration propensity and boldness) and  
146 morphological traits (i.e. long hind limbs) that generally facilitate dispersal in amphibians (reviewed in  
147 Cayuela et al. 2018c). In a fourth step, we examined how human-driven variation in patch turnover, by  
148 affecting neutral genetic diversity and gene flow, leads to contrasting genetic footprints over the longer  
149 term in riverine and logging SSPs. As genetic differentiation results from the combined effects of  
150 genetic drift and gene flow (Broquet & Petit 2009, Cayuela et al. 2018a), we selected two SSPs per  
151 landscape type in order to determine the relative contribution of each of these drivers. As high  
152 dispersal is expected to increase gene flow and decrease the local effects of genetic drift, we expected  
153 (4) a larger effective population size as well as a lower level of inbreeding and intra-patch relatedness  
154 in logging than in riverine SSPs. We also expected that (5) after controlling for SSP size and landscape  
155 connectivity, higher gene flow would lead to lower genetic structure and weaker genetic Isolation-By-  
156 Distance (IBD) pattern in logging than in riverine SSPs.

157

## 158 **Materials and methods**

159

### 160 *Study area and sampled populations*

161

162 The study was conducted in 8 SSPs in eastern France, three in riverine environments (R1, R2, and R3)  
163 and five in logging environments (L1, L2, L3, L4 and L5). The SSPs were chosen according to  
164 technical constraints or to minimize bias at each stage of the study – our choices are explained below.  
165 The distance separating SSPs from each other varied from 20–500 km (**Fig. S1**).

166

167 **Table 1.** Environmental characteristics of the four SSPs (L1, L2, R1 and R2): patch persistence over  
168 time, environment type (logging vs riverine), patch isolation (mean distance in meters between two  
169 pond networks, and associated variation coefficient) and patch size (mean number of ponds within a  
170 patch and associated variation coefficient).

SSP	Patch persistence	Environment	Patch isolation	Patch size
L1	1 to 10 years	logging activity	2864.50 (57%)	3.70 (70%)
L2	1 to 10 years	logging activity	4424.64 (53%)	5.64 (88%)
R1	>30 years	natural erosion	676.57 (61%)	4.52 (105%)
R2	>30 years	natural erosion	501.62 (61%)	4.71 (93%)

171

172 **Table 2.** Survey design characteristics for the four SSPs (L1, L2, R1 and R2) considered in the study:  
173 study period, survey duration, number of capture sessions performed over the survey period, total  
174 number of captures, total number of individuals identified during the survey and total number of  
175 sampled patches (pond networks).

SSP	Study period	Survey duration	Capture sessions	Number of captures	Number of individuals	Number of sampled patches
L1	2000–2008	9 years	29	953	445	28
L2	2012–2016	5 years	15	16477	12192	189
R1	2010–2014	5 years	13	4747	1003	14
R2	2010–2014	5 years	13	3984	769	8

176

177

178 *Dispersal patterns throughout toad lifespan in riverine and logging environments*

179

180 Studied populations

181

182 We quantified natal and breeding dispersal rates and distances in four SSPs (L1, L2 and R1, R2; see  
183 maps **Fig. S1** and **Fig. S2**) for which breeding rate dispersal had been previously estimated (Cayuela et  
184 al. 2016a, 2016b). The environmental characteristics of the four SSPs and the details regarding the  
185 survey design are presented in **Table 1** and **Table 2** respectively. The number of individuals captured  
186 each year is presented in **Supplementary material, Table S1**. A detailed description of the four SSPs  
187 can also be found in two previous studies (Cayuela et al. 2016a, 2016b). The number of patches  
188 (defined as a group of ruts) occupied by each SSP ranged from 8 to 189. Each SSP was monitored for  
189 a period of at least five years in one to five capture sessions per year that were usually between two  
190 weeks to one month apart. At each capture session, all the patches were sampled in the daytime and

191 toads were captured by hand or dipnet. Based on previous studies (Cayuela et al. 2016a, 2016c), we  
192 considered three life stages: juveniles (i.e. post-wintering metamorphs), subadults (two-year-old  
193 immature animals) and adults (i.e. breeders, three years old or more). This resulted in a total dataset of  
194 12,721 individual capture–recapture (CR) histories.

195

### 196 Naïve dispersal kernels

197

198 We first estimated a dispersal kernel based on distances recorded during sampling using a lognormal  
199 distribution for each population and life stage (juvenile, subadult, and adult). This allowed us to  
200 visualize the form of the kernel from raw data before building complex CR models.

201

### 202 The structure of the multievent model

203

204 For the needs of our study, we extended the CR multi-event model proposed by Lagrange et al. (2014),  
205 which allows estimating survival ( $\phi$ ) and dispersal ( $\psi$ ) in numerous sites. By omitting site identity and  
206 distinguishing between individuals that stay and individuals that move, this model circumvents the  
207 computational issues usually encountered in standard multi-site CR models when the number of sites  
208 is large (Lebreton et al. 2009). Lagrange’s model includes states that incorporate information about  
209 whether an individual is occupying at  $t$  the same site as the one occupied at  $t - 1$  (‘S’ = stayed) or not  
210 (‘M’ = moved). The model also includes information about whether the individual was captured (‘+’)  
211 or not (‘o’) at  $t - 1$  and  $t$ . Recently, Tournier et al. (2017) extended Lagrange’s model by breaking  
212 down dispersal ( $\psi$ ) into distinct parameters of departure ( $\varepsilon$ ) and arrival ( $\alpha$ ). This new parameterization  
213 allows the estimation of the proportion of individuals arriving in sites of different quality or located at  
214 different distances from the source site.

215 We adapted this parameterization for our study to consider states incorporating information  
216 about individual capture (‘+’ and ‘o’) at  $t - 1$  and  $t$  as well as movement status. We also included  
217 states with information about the individual’s age class: juvenile (‘j’), subadult (‘s’) and adult (‘a’).  
218 Additionally, we incorporated information about the Euclidian distance covered by dispersers between  
219 the departure and arrival patch using three distance classes: ‘1’ = 100–800 m, ‘2’ = 800–1500 m, ‘3’ >  
220 1500 m. This led to the consideration of 37 states in the model (**Fig.1** and **Fig.2**). For example, an  
221 individual +jS+ was captured at  $t - 1$  and  $t$ , was a juvenile, and remained in the same patch between  $t -$   
222 1 and  $t$ . An individual +sM1+ was captured at  $t - 1$  and  $t$ , was a subadult, did not occupy the same  
223 patch as at  $t - 1$ , and arrived in a patch located at a distance 100–800 m from the source patch. We  
224 distinguished 16 events, which were coded in an individual’s capture history and reflect the  
225 information available to the observer at the time of capture (**Fig.2**).

226 When captured for the first time, the state of an individual could be ojS+, osS+ or oaS+. We  
227 then considered five modeling steps in which the information of the state descriptor was progressively

228 updated: survival ( $\square$ ), departure ( $\varepsilon$ ), arrival ( $\alpha$ ), age transition ( $\delta$ ) and recapture ( $p$ ). Each step was  
229 conditional on all previous steps. In the first step, we updated information about survival. An  
230 individual could survive with a probability of  $\square$  or die (D) with a probability of  $1 - \square$ . This led to a  
231 matrix with 37 states of departure and 7 intermediate states of arrival (**Fig.1**). Survival probability  
232 could differ between age classes by allowing differing values for  $\square$  in lines 1–12, 13–24 and 25–36 of  
233 the matrix. In the second modeling step, departure was updated. Individuals could move (M) from the  
234 site they occupied with a probability of  $\varepsilon$  or stay (S) with a probability of  $1 - \varepsilon$ . A matrix of 7  
235 departure states and 13 arrival states was considered (**Fig.2**). Departure probability could differ  
236 between age classes by allowing differing values for  $\varepsilon$  in lines 1–2, 3–4 and 5–6 of the matrix. In the  
237 third step, we updated the arrival information. An individual that moved could arrive in a patch located  
238 in the first two distance classes (1 or 2) from the source patch with a probability of  $\alpha$ , or arrive in a site  
239 located in the third distance class (3) with a probability of  $1 - \alpha$ . This resulted in a matrix with 13  
240 departure states and 25 arrival states (**Fig.2**). Arrival probability could differ between age classes by  
241 allowing different values for  $\alpha$  in lines 2–4, 7–8 and 11–12 of the matrix. In the fourth step, the  
242 information about age was updated. An individual could reach the next age class (j, s or a) with a  
243 probability of  $\delta$  or remain in the previous age class with a probability of  $1 - \delta$ , resulting in a transition  
244 matrix with 25 states of departure and 25 states of arrival (**Fig.2**). The adult individuals (a) were forced  
245 to stay in their age class. In the fifth and last step, recapture was updated (**Fig.2**). An individual could  
246 be recaptured with a probability of  $p$  or missed with a probability of  $1 - p$ , resulting in a transition  
247 matrix with 25 states of departure and 37 states of arrival. The recapture probability could differ  
248 between age classes by allowing different values for  $p$  in lines 1–8, 9–16 and 17–24 of the matrix. The  
249 last component of the model linked events to states. In this specific situation, each state corresponded  
250 to only one possible event (**Fig.2**).

251

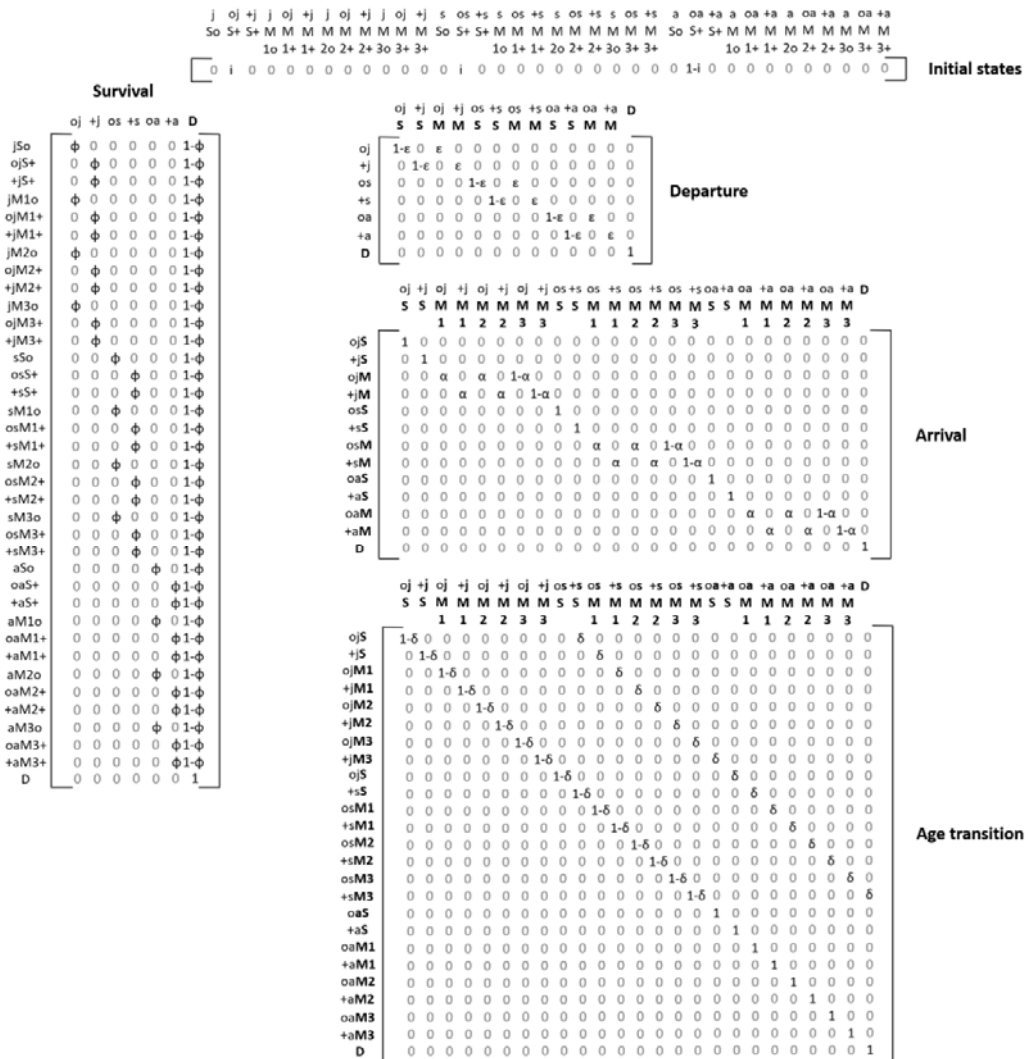
#### 252 Biological scenarios in the E-SURGE program

253

254 The parameterization was implemented in the E-SURGE program (Choquet et al. 2009). The datasets  
255 for the four SSPs considered in our study were analyzed separately, as the number of study years and  
256 capture sessions for these populations varied. Competing models were ranked through a model-  
257 selection procedure using Akaike information criteria adjusted for a small sample size (AICc) and  
258 AICc weights. Following the recommendation of Burnham & Anderson, we performed model  
259 averaging when the AICc weight of the best-supported model was less than 0.90. The models had a  
260 robust design structure (Pollock 1982). As in previous studies of *B. variegata*, the survival probability  
261 was fixed at one between secondary sessions (Cayuela et al. 2016a, 2016c). The robust design  
262 structure allowed both intra-annual and inter-annual dispersal to be considered. Our hypotheses  
263 concerning recapture and state–state transition probabilities were tested using the general model  
264 [ $\square(\text{AGE})$ ,  $\varepsilon(\text{AGE})$ ,  $\alpha(\text{AGE})$ ,  $\delta(\cdot)$ ,  $p(\text{AGE} + Y)$ ], which included two effects: (1) the three age classes



265 (AGE) coded as states in the model, and (2) year-specific variation (Y). The notation (.) indicated that  
 266 the parameter was held constant. We tested whether survival ( $\phi$ ) and departure probabilities ( $\epsilon$ ) varied  
 267 between age class (AGE). Moreover, we hypothesized that the probability of arriving in a patch  
 268 depends on age (AGE), and on the Euclidean distance between patches (the distance classes were  
 269 incorporated as states in the model). Recapture probability was expected to differ between age classes  
 270 (AGE) and years (Y). We tested our expectations about the model parameters in a stepwise fashion.  
 271 From this general model, we tested all the possible combinations of effects and ran 16 competing  
 272 models.  
 273  
 274



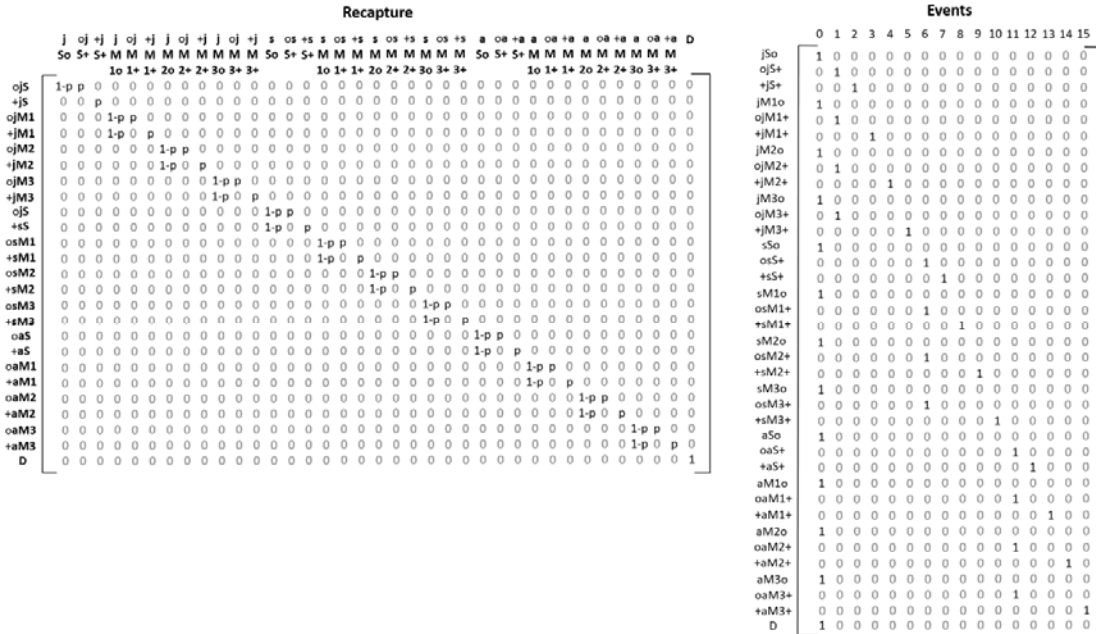
275

276 **Fig.1.** Model structure: matrices of initial states and state transitions (survival, departure, arrival and  
 277 age transition). In the transition matrix, the rows correspond to time  $t - 1$ , the columns to time  $t$ , and

278 whenever a status element is updated to its situation at  $t$ , it becomes bold and stays bold throughout  
 279 the following steps.

280

281



282

283 **Fig.2.** Model structure: state transitions (recapture) and events (field observations). In the transition  
 284 matrix, the rows correspond to time  $t - 1$ , the columns to time  $t$ , and whenever a status element is  
 285 updated to its situation at  $t$ , it becomes bold and stays bold throughout the following steps.

286

287 *Simulating the effect of patch turnover and dispersal on SSP dynamics and long-term persistence in*  
 288 *logging contexts*

289

290 We simulated population trajectories based on different scenarios to investigate the effects of patch  
 291 turnover and dispersal costs on the dynamics and long-term persistence of SSPs in habitats subjected  
 292 to logging. Adopting the most realistic lifecycle for the yellow-bellied toad (see ‘Results’, **Fig.4**)  
 293 determined in previous studies (e.g. Cayuela et al. 2015, 2018), we used a three age-class (juveniles,  
 294 subadults, and adults), female-dominant, prebreeding Leslie matrix (Caswell 2001) (see ‘Results’,  
 295 **Fig.4**). We used the demographic parameters of a riverine SSP (R1; see Cayuela et al. 2016), which  
 296 was considered a reference population whose demographic parameters have not been altered by  
 297 dispersal costs (survival in logging SSPs is lower than in riverine SSPs, likely due to dispersal costs,  
 298 Cayuela et al. 2018b). Both prebreeding survival probability (juvenile survival,  $S_1 = 0.70$ ; subadult  
 299 survival,  $S_2 = 0.77$ ) and adult survival probability ( $S_3 = 0.92$ ) were included in the Leslie matrix.  
 300 Fecundity  $F$  was possible only for adult females and consisted of estimated recruitment: that is, the  
 301 number of recruited juvenile females at  $t$  per breeding female at  $t - 1$  ( $F = 0.52$ , Cayuela et al. 2016).

302 As Boualit et al. (2019) found that juvenile recruitment was higher in newly created and disturbed  
303 patches than in old, undisturbed patches in logging SSPs, we specified that  $F$  decrease linearly (-5%  
304 per year) with the age of the patch. Furthermore, we also considered the possibility that females may  
305 skip breeding opportunities; in the riverine SSP R1, a previous study showed that the probability of  
306 females skipping breeding ( $B$ ) was 0.15 (Cayuela et al. 2016). As in Cayuela et al. (2018, 2019c), we  
307 considered demographic stochasticity for survival, fecundity and skipping breeding. For each year,  
308 demographic parameter values were randomly sampled in a Gaussian distribution centered on mean  
309 parameter estimates, and standard deviation was inferred from two previous studies conducted on this  
310 species (Cayuela et al. 2016a, 2018b). The standard deviation values were: 0.05 for  $S1$ , 0.03 for  $S2$ ,  
311 0.01 for  $S3$ , 0.02 for  $F$ , and 0.02 for  $B$ .

312 Three patch turnover scenarios were considered. In scenario 1 (high turnover), a patch  
313 disappeared three years after its creation, in scenario 2 (medium turnover) a patch disappeared after six  
314 years, and in scenario 3 (low turnover) it disappeared after nine years. These scenarios correspond to  
315 the range of patch turnover in logging SSPs reported by forest managers (Eric Bonnaire, *unpublished*  
316 *data*), variation that depends on local management policies and the frequency of forest harvesting  
317 operations. We also considered three dispersal scenarios. In scenario 1 (no dispersal), individuals were  
318 not able to escape and died when a patch disappeared. In scenario 2 (dispersal with random  
319 immigration), individuals could disperse to escape the disappearance of a patch or could disperse by  
320 choice (i.e. when the patch remained available). The immigration was random between the patches of  
321 the metapopulation and was not influenced by the age of the patch. In scenario 3 (dispersal with  
322 informed immigration), individuals could disperse in response to patch disappearance or by choice.  
323 Based on an assessment of Boualit et al. (2019), we considered that immigration was not random and  
324 that immigration probability linearly decreases with patch age (i.e. a loss of 5% per year). In scenario  
325 2 and 3, in which dispersal was possible, we considered two subsets of scenarios: in subset 1 (non-  
326 costly dispersal), individuals did not incur any survival loss when they dispersed. In subset 2 (costly  
327 dispersal), we considered that survival loss related to dispersal could be low (-5% of survival),  
328 medium (-10%), or high (-15%). As in Cayuela et al. (2018), we made the assumption that survival  
329 loss was similar across life stages (i.e. juvenile, subadult, and adult).

330 Each simulation began with 30 breeding patches over which 1,000 individuals were randomly  
331 scattered. The number of individuals in each age class was obtained through the stable stage  
332 distribution provided by the three age-class Leslie matrix. Then for each time step (a 1-year interval),  
333 we simulated the change in patch availability. We considered that five new patches were created each  
334 year. As the patches disappeared in a deterministic way when they reached the age defined in the  
335 scenario, the number of available patches remained constant over time (except for the few first years).  
336 We simulated the number of individuals in each age class occupying each patch. To do this, we  
337 separately considered patches reaching the age of disappearance versus those that did not disappear. In  
338 the latter, the number of individuals at  $t + 1$  given the number of individuals at  $t$  was predicted by the

339 Leslie matrix using the survival probability of individuals occupying an available patch (reported in  
340 the reference population R1). To be as realistic as possible, we used demographic stochasticity  
341 (fecundity was thus randomly sampled from a Poisson distribution, and survival from a binomial  
342 distribution), as in Cayuela et al. (2018). For patches that disappeared, we applied the same procedure,  
343 but using the survival probability (affected or not by dispersal cost, depending on the scenario) for  
344 individuals occupying patches that subsequently disappeared. Surviving individuals from lost patches  
345 were then randomly spread over the available patches at  $t + 1$  in the ‘dispersal with random  
346 immigration’ scenario, or they were preferentially distributed in new patches in the ‘dispersal with  
347 informed immigration’ scenario. In all dispersal scenarios, we fixed the elective dispersal probability  
348 (dispersal when the patch did not disappear)  $D$  at 0.15, which was consistent with the annual dispersal  
349 rate reported in logging SSPs in the study. We also considered demographic stochasticity in elective  
350 dispersal (the standard deviation value was 0.05). The modeled population was monitored for 100  
351 years. We did not remove the first few years of the simulation, when the number of patches  
352 progressively increased since none were old enough to disappear yet, as these had virtually no impact  
353 on our results (Cayuela et al. 2018). We performed 1,000 simulations for each scenario. At each time  
354 step, we monitored the number of adults in the entire SSP as well as the proportion of simulations in  
355 which the SSP went extinct (the extinction probability).

356

357 *Phenotypic specialization in riverine and logging environments*

358

359 Study populations

360

361 To compare the morphology and behavior of toadlets in riverine SSPs with those of logging SSPs, we  
362 used a common garden experiment. This involved collecting between 8 and 15 egg clutches (hereafter  
363 referred to as ‘family’) in three SSPs in each landscape type (riverine = R1, R2, R3, and logging = L3,  
364 L4, L5; **Fig.S1**). These were selected to minimize spatial proximity between SSPs belonging to the  
365 same landscape type and therefore to avoid potential confounding effects resulting from spatial  
366 autocorrelation in environmental conditions. Five siblings per family were randomly chosen just after  
367 hatching and individually reared under controlled laboratory conditions.

368

369 Rearing protocol

370

371 The egg clutches were carefully transported to the laboratory, where they were individually placed in  
372 aquariums (32×17 cm, height 15 cm) with aged tap water equipped with an oxygen pump. The  
373 aquariums were placed in a climatic room with a light/dark cycle of 18:6, corresponding to the natural  
374 light/dark cycle in the area in the summer, with an ambient temperature varying from 21.5 to 23.5°C.  
375 Embryo development ended 2–5 days after the arrival of the egg clutches at the laboratory. After

376 hatchling, when tadpoles reached Gosner stage 24–25 (active swimming, external gill atrophy)  
377 (Gosner 1960), five siblings per family were randomly chosen and placed individually into plastic  
378 containers (14×8.5 cm, height 13.5 cm) filled with previously aged tap water and aerated in a tank.  
379 The plastic containers were distributed in a predetermined random pattern around the climatically  
380 controlled room. The water was replaced every three days. The tadpoles were fed every day with 150  
381 mg of cooked lettuce, providing ad libitum feeding. At Gosner stage 44–45 (tail atrophy, mouth  
382 posterior to eyes), feeding was terminated, and the water was drained and replaced with a dampened  
383 sponge placed in the bottom of the container. The sponge and the walls were sprayed with aged tap  
384 water every two days. The individuals were kept until their complete metamorphosis (Gosner stage  
385 46) and were then subjected to behavioral assays.

386

### 387 Experimental arenas

388

389 The behavioral assays took place in an arena (70 cm in diameter) made of polyethylene terephthalate,  
390 with a central shelter and a ‘desiccation’ obstacle between this and the 12 possible exits (**Fig. S4**). At  
391 the center of the arena, we placed a removable, cylindrical (9 cm diameter, height 90 cm), opaque,  
392 covered chamber (‘refuge chamber’ hereafter). The cylinder had a circular opening (3 cm diameter)  
393 covered by a lid. Around the interior edge of the arena, we installed a pit (width 10 cm, depth 0.3 cm)  
394 filled with a desiccating mixture of sand and highly active silica gel powder in a weight ratio of 0.8:0.2  
395 (‘desiccant zone’ hereafter). The arena wall included 12 doors placed at regular intervals around the  
396 entire circumference. The arena was confined in an enclosed iron chamber (150×17 cm, height 175  
397 cm) over which a dark opaque sheet was placed to limit potential acoustic and visual interference  
398 during behavioral trials.

399

### 400 Behavioral assays

401

402 At metamorphosis, each toadlet was subjected to a behavioral assay to quantify their neophobia or  
403 exploratory behavior. The behavioral tests were conducted in the circular arena described above.  
404 Before each trial, the toadlet and a dampened sponge (already present in the toadlet’s rearing  
405 container) were gently transferred into an opaque circular release box that was then placed at the  
406 center of the arena. The dampened sponge was considered a known object, making the refuge chamber  
407 more familiar than the rest of the experimental device. Following previous studies on anuran  
408 behavioral syndromes (reviewed in Kelleher et al. 2018), neophobia was quantified as the latency time  
409 to enter a novel environment (i.e. the time delay to leave the familiar refuge chamber: BEHAV1).  
410 Exploration propensity was assessed using two variables: the latency time to enter a novel but harsh  
411 environment (i.e. to reach the desiccant zone after leaving the refuge chamber; BEHAV2), and the

412 latency time to travel the harsh environment and get out of the arena (BEHAV3). The behavior was  
413 recorded for 30 min (1800 s) using a digital camera (Sony DCR-SX34).

414

#### 415 Extraction of behavioral variables from the videos

416

417 The videos were analysed using the BEMOVI R package (Pennekamp et al. 2015) to reconstruct the  
418 movement trajectory of the toadlet in the arena, and to extract a series of behavioral variables from  
419 this. First, the videos were standardized to a length of 29 min (the minimum duration available for all  
420 individuals) removing the initial 60 s and the extra time at the end, if any. Then the videos were  
421 converted to a format suitable for analysis in BEMOVI: rectangular pixels (720 x 576) were converted  
422 into square pixels (1024 x 576), color information was converted into 256 gray levels, frames per s  
423 were decreased from 25 to 5 to limit memory allocation requirements, and the videos were saved as  
424 AVI files. These operations were performed using FFMPEG software (ffmpeg.org).

425 BEMOVI was then run with the following parameters: black and white threshold (40) to  
426 discriminate the toadlet from the background; minimum size (20) and maximum size (150),  
427 corresponding to the size range of the toadlets; link range (7500 frames) to allow any duration of the  
428 ‘disappearance’ of the toadlet from the video (e.g. when it was in the refuge) while still considering it  
429 as a single movement trajectory, and “disp“(100 pixels); in BEMOVI, disp is the maximal distance  
430 covered by the toadlet from one frame to the next, corresponding to 0.2s here. This resulted in a  
431 database with the movement trajectory of each toadlet, i.e. its X–Y position at each time step. This  
432 position was compared to the distance from the center of the arena to determine which zone (refuge  
433 chamber, normal zone or desiccant zone) the toadlet was in at each time step. The results were  
434 checked for errors in toadlet positioning, which were due to varying light conditions, usually at the  
435 beginning of the videos. In a final step, we computed several behavioral variables for each toadlet  
436 from this positioning information.

437

#### 438 Statistical analyses

439

440 We used linear mixed models to test whether morphological traits (body size, body condition and  
441 relative hind limb size) of toadlets differed according to the landscape type of origin (logging vs  
442 riverine). Each morphological trait was treated as a dependent variable, and the landscape type was  
443 introduced as a fixed explanatory term in the model. In the case of body condition and relative leg  
444 size, body size and its interactive effect with the landscape type were also introduced as adjustment  
445 covariates in the fixed part of the model. Both the SSP of origin and the clutch were introduced as  
446 random effects in the model. We also allowed heterogeneity of variance between landscape types by  
447 allowing a separate estimation of the residual variance for each landscape type. The estimation method  
448 was based on restricted maximum likelihood. Variance heterogeneity was first checked using the

449 likelihood ratio test and removed if non-significant. The significance of each explanatory term was  
450 examined with a non-sequential  $F$  test based on the Kenward-Roger method to approximate the  
451 denominator  $df$  (Littel et al. 2006). In the case of covariance analyses (body condition and relative leg  
452 size), the interactive effect was discarded if non-significant to obtain the final model. All  
453 morphological variables were standardized using  $Z$  transformation before the analyses, as  
454 recommended by Schielzeth (2010).

455 We tested whether the behavioral variables BEHAV1 and BEHAV2 varied according to the  
456 landscape type (i.e. logging vs riverine) using a generalized linear mixed model. Each latency time  
457 variable was treated as a dependent variable using a Poisson distribution. The landscape type was  
458 introduced as an explanatory term in the fixed part of the model. We also introduced individual body  
459 size and its interactive effect with the landscape of origin as adjustment covariates in the fixed part of  
460 the model since both locomotion skill and exploratory performance can vary according to individual  
461 size (reviewed in Kelleher et al. 2018). For the analyses of morphological traits, both the SSP of origin  
462 and the clutch were introduced in the model as random effects. Furthermore, a scale parameter was  
463 also introduced to handle data overdispersion and to obtain a corrected statistical test using a quasi-  
464 likelihood approach (McCullagh & Nelder 1989). The estimation method was based on restricted  
465 pseudo-likelihood optimization, and the significance of each explanatory term was examined using the  
466 same methodology as for the morphological analyses. Non-significant terms were successively  
467 removed to obtain the final model, and least square means were used to estimate the difference in  
468 latency time variables according to the landscape of origin.

469 As the third behavioral variable (BEHAV3) was right censored, it was analyzed using a  
470 proportional hazards mixed-effects model (i.e. a frailty model based on a Cox model, PHREG  
471 procedure, SAS Institute Inc. 2012). We tested whether newborn individuals originating from logging  
472 systems were more prone to exit the assay arena than those from riverine systems. It is not possible to  
473 handle multiple random factors in such a model, so we took into account only the family effect since  
474 this was found to be significant for the other behavioral variables but not for the SSP of origin. The  
475 landscape of origin, the body size and their interactive effect were introduced as explanatory terms.  
476 Parameters were estimated using partial likelihood estimation, and the significance of explanatory  
477 terms was assessed using non-sequential chi-square tests.

478

479 *Neutral genetic variation in riverine and logging environments*

480

#### 481 Study populations

482

483 We examined neutral genetic variations within two SSPs in riverine environments (R1 and R2) and  
484 two SSPs in logging environments (L3 and L4) (see map in **Fig. S3**) using 15 polymorphic  
485 microsatellite markers (described and tested in Cayuela et al. 2017a). The four SSPs were selected

486 according to the following criteria: (1) SSPs embedded in a relatively continuous forested matrix to  
487 avoid any confounding effect of matrix composition on gene flow (**Fig. S3**) – woodland is generally  
488 considered highly favorable for the movement of forest amphibians (Cushman 2006a) such as *B.*  
489 *variegata* (Cayuela et al. 2015b); and (2) two small (R1 and L3) and two large SSPs (R2 and L4) to  
490 control for genetic drift. The number of patches and DNA sampled per SSP are given in **Table S2**. We  
491 used the protocol described in Cayuela et al. (2017) for DNA extraction and amplification, individual  
492 genotyping, and allele scoring.

493

#### 494 Estimating basic genetic metrics

495

496 We examined basic assumptions (i.e. detection of null alleles, Hardy–Weinberg equilibrium) and  
497 descriptive statistics (mean number of alleles per locus  $N_a$ ; effective number of alleles per locus  $N_{ef}$ ;  
498 observed heterozygosity  $H_o$ ; and expected heterozygosity  $H_e$ ) of the genetic diversity within each  
499 SSP.  $N_a$ ,  $N_{ef}$ ,  $H_o$  and  $H_e$  were calculated using GENALEX (Peakall & Smouse 2006). The inbreeding  
500 coefficient  $F_{is}$  and the Hardy–Weinberg deviation were assessed with GENEPOP 4.1 (Rousset 2008).  
501 The detection of null alleles was performed using the program MICRO-CHECKER 2.2.3 (Van  
502 Oosterhout et al. 2004). Two microsatellite markers, Bomvar\_Cons470 and bv11.7, were discarded  
503 from the subsequent analyses due to the presence of null alleles in the four SSPs. All descriptive  
504 statistics are provided in **Table S3**.

505

#### 506 Estimating relatedness, inbreeding, and effective population size

507

508 We estimated relatedness and individual inbreeding using COANCESTRY v1.0.1.8 (Wang 2011). We  
509 performed simulations to identify the best relatedness and inbreeding estimator for our combined  
510 datasets; these consisted of 1,000 dyads spread equally across six categories of relatedness: parent–  
511 offspring ( $r_{xy} = 0.5$ ), full siblings ( $r_{xy} = 0.5$ ), half siblings/avuncular/grandparent–grandchild ( $r_{xy} =$   
512  $0.25$ ), first cousins ( $r_{xy} = 0.125$ ), second cousins ( $r_{xy} = 0.03125$ ), and unrelated ( $r_{xy} = 0$ ). According  
513 to our simulations, the best  $r_{xy}$  estimator for relatedness analysis was DyadML, which showed a  
514 strong correlation of 0.74. We used linear mixed models to evaluate how SSP size (small: R1 and L4;  
515 large: R2 and L3) and the type of environment (logging vs riverine) affected individual inbreeding and  
516 intra-patch relatedness. An SSP's size and environment type were coded as fixed effects (we  
517 considered an interaction between the two factors), whereas patch identity was coded as a random  
518 effect. We then estimated the effective population size of the four SSPs using the linkage  
519 disequilibrium method implemented in Ne Estimator v2.1 (Do et al. 2014).

520

#### 521 Clustering approach

522



523 We described the genetic differentiation between patches within each SSP using an assignment  
524 method based on the Bayesian clustering algorithm implemented in the software STRUCTURE  
525 (Pritchard et al. 2000). Specifically, we estimated the most likely number of genetic clusters ( $K$ )  
526 contained in each SSP following the hierarchical approach proposed by Balkenhol et al. (2014) to  
527 detect additional substructures within clusters. The STRUCTURE program was run with the  
528 admixture model, with a burn-in period of 100,000 repetitions, and 100,000 subsequent MCMC  
529 repetitions. The  $K$  values were tested ranging from 1 to 10 and analyses repeated 10 times for each  
530 value. We used STRUCTURE HARVESTER (Earl 2012) to summarize the results, determining the  
531 optimal  $K$  value using both log-likelihood plots and the delta  $K$  statistic (Evanno et al. 2005). We  
532 followed the hierarchical approach proposed by Coulon et al. (2008) to test for additional population  
533 substructures within clusters. Accordingly, these analyses were then repeated for each inferred  
534 population cluster separately until the optimal  $K$  value was 1 (meaning that no additional structure was  
535 found within clusters). To map the spatial distribution of the different clusters, the individual ancestry  
536 values were averaged across the ten STRUCTURE runs using CLUMMP software (Jakobsson &  
537 Rosenberg 2007). The ‘greedy’ algorithm in the CLUMMP program was then used to assign the  
538 individuals to the cluster in which they showed the highest  $Q$ -values.

539

#### 540 Gradient analyses

541

542 We used direct gradient analyses (Prunier et al. 2015) to test whether spatial genetic differentiation  
543 was lower within logging than riverine SSPs while controlling for potential differences in the  
544 functional connectivity prevailing within each SSP. To do this, pairwise genetic distances between all  
545 individuals from each SSP were computed using the Bray-Curtis percentage dissimilarity measures  
546 (Cushman et al. 2006b, Legendre & Legendre 2012), and were then standardized separately for each  
547 SSP. Since by design all SSPs were embedded in a relatively homogeneous forested matrix, we did not  
548 control for the effect of land cover type in these analyses. Rather, we focused on the effect of  
549 topographic roughness (‘slope’ effect) and the hydrological network topology (‘network’ effect) since  
550 both these landscape features have often been reported to affect gene flow in amphibians (Lowe 2003,  
551 Grant et al. 2010).

552 For each SSP, resistance layers were produced using ArcGIS Pro. Minimum geographical  
553 bounding of each SSP was determined and extended to a distance of five kilometres to avoid any edge  
554 effects. The elevation raster and hydrographic network shapefile, available through the French  
555 National Institute for Geographical and Forest Information database (BD ALTI®, and BD TOPO®),  
556 were extracted for SSP surface areas. To determine the percentage of steepness raster maps, the slope  
557 tool was used. Due to the spatial resolution imposed by elevation data, all layers were converted to  
558 raster format and homogenized at a spatial resolution of five meters.

559 Four resistance maps were thus constructed for each SSP. The first map included only the  
560 effect of geographic distance (i.e. isolation by distance, hereafter geographic resistance); it was based  
561 on data extended to include a 5-km buffer and was assigned a uniform resistance of 1 unit for all  
562 pixels. The second map included the topographic roughness (slope), where the resistance of each pixel  
563 was a linear function of the steepness (resistance = 1 + degree of steepness), thus corresponding to  
564 the effect of both geographic distance and topographic roughness. The third map included the  
565 hydrological network topology (network), where the resistance was assigned to 1 unit for all pixels  
566 situated in the hydrological network and to 10 units otherwise. The fourth map included both the slope  
567 effect and the network effect. Pairwise resistance between all patches was then computed from these  
568 four resistance maps using the circuit theory in Circuitscape V4.0 (McRae & Beier 2007).

569 Linear mixed models for pairwise distance matrices were then used to assess the effect of the  
570 geographic distance between patches (i.e. the geographic resistance) on the genetic distance between  
571 toads within each SSP while controlling for the effect of topographic roughness and/or the  
572 hydrological network topology. The non-independence between pairwise distances was taken into  
573 account in the covariance structure of the models. Specifically, we used the method proposed by  
574 Clarke et al. (2002) using a Toeplitz(1) as a covariance structure to specify the non-independence of  
575 pairwise genetic distance according to the patches of origin (see Selkoe et al. 2010, van Strien et al.  
576 2012 for application on pairwise  $F_{st}$  distances). We used the extension presented in Prunier et al.  
577 (2013) for application on individual genetic distance in spatially hierarchized sampling schemes as is  
578 the case in our study. This resulted in two covariance parameters for each SSP, one for the patch  
579 random effect and the other for the individual random effect. Since both slope and network resistance  
580 were highly correlated to geographic resistance and as our main aim was to estimate the effect of  
581 geographic resistance on genetic distance while controlling for the effect of functional connectivity,  
582 we first regressed each of these effective resistances on each geographic resistance using simple linear  
583 regressions to obtain uncorrelated effective resistance respectively related to the slope effect, the  
584 network effect and their combined effect. The relative validity of each alternative landscape  
585 hypothesis (i.e. including the effect of the slope or of the stream network or both or neither on the  
586 genetic distances) was evaluated using weighted AIC (Waic), and the model-averaged estimate of the  
587 beta weight associated with the effect of geographic resistance on genetic distance was computed for  
588 each SSP.

589

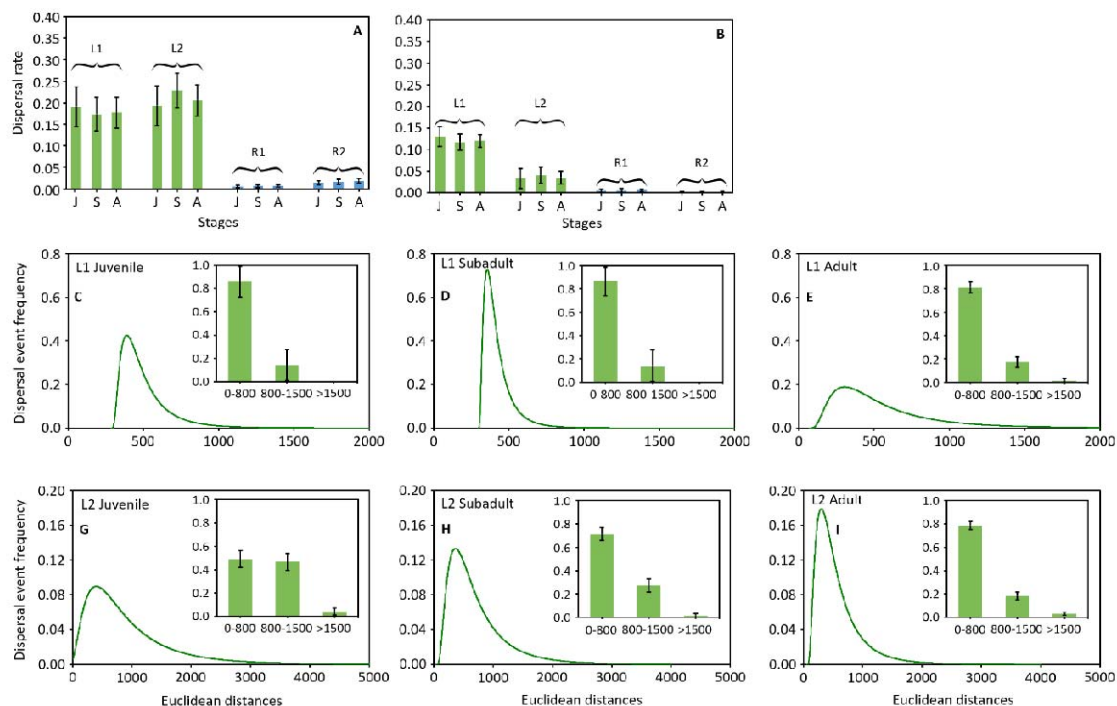
## 590 **Results**

591

592 *Dispersal patterns throughout toad lifespan in riverine and logging environments*

593

594 Model averaging estimates (see **Table S4** for survival and recapture probabilities) indicated that both  
 595 natal and breeding dispersal rates were high in logging environments (around 20% per year, **Fig.3**). In  
 596 contrast, in riverine environments, natal dispersal rates were null and breeding dispersal rates were  
 597 very low (less than 5% per year, **Fig.3**). This higher dispersal propensity in logging than in riverine  
 598 habitats is even more remarkable given that the mean inter-patch distance is three times farther in the  
 599 former than the latter (Table S1). The few adults that did disperse in riverine environments covered  
 600 shorter distances: the median distance was 168 m in R1 and 189 m in R2, while the maximal distance  
 601 was 455 m and 378 m respectively. This result was further confirmed by multi-event CR models  
 602 showing that 100% of dispersal occurred over distances ranging from 100 to 800 m in riverine SSPs.  
 603 In logging environments, dispersers covered substantially longer distances: the median distance was  
 604 431 m in L1 and 568 m in L2, while the maximal distance was 3810 m and 4529 m respectively. This  
 605 result was supported by both the observed dispersal kernel and the multi-event model estimates for  
 606 each life stage (see **Fig.3**). While these results indicate extremely contrasting dispersal regimes  
 607 between logging and riverine landscapes, we also found substantial variations in the dispersal patterns  
 608 in the two logging systems. First, while the inter-annual dispersal rate was similar in both logging  
 609 systems, the intra-annual dispersal rate was substantially higher in L1 than L2 (i.e.  $L1 > 10\%$  and  $L2$   
 610  $< 5\%$ , **Fig.3**; for model selection procedure see **Table 3** and **Table 4**). Second, the dispersal kernels  
 611 show a clear leptokurtic distribution decreasing with age in L2, suggesting a large demographic weight  
 612 of natal dispersal in this SSP. This was not the case in L1, in which leptokurtosis was more reduced in  
 613 juveniles than in adults.  
 614



616

617 **Fig.3.** *Natal and breeding dispersal rates and distances in logging (L1 and L2) and riverine SSPs (R1*  
618 *and R2) (A–B). Inter-annual (A) and intra-annual (B) dispersal probabilities are higher in SSPs in*  
619 *logging landscapes than in riverine SSPs, regardless of the ontogenetic stage (juvenile, J; subadult, S;*  
620 *adult, A). Natal and breeding dispersal distances in logging SSPs (L1 and L2) (C–I). Dispersal event*  
621 *frequency decreases with the Euclidean distance between breeding patches at the ontogenetic stages.*  
622

623 **Table 3.** Multievent models and selection procedure for SSPs L1 and L2.  $r$  = model rank,  $k$  = number  
 624 of parameters, Dev. = residual deviance, AICc = Akaike information criterion adjusted for small  
 625 sample size, wAICc = AICc weight  $\square$  = survival probability,  $\varepsilon$  = departure probability,  $\alpha$  = arrival  
 626 probability,  $p$  = recapture probability,  $A$  = age,  $.$  = constant,  $Y$  = year.

r	Model	k	Dev.	wAICc	AICc
<b>SSP L1</b>					
1	$\square(A), \varepsilon(.), \alpha(A), p(A + Y)$	26	5161.06	0.81	5214.05
2	$\square(A), \varepsilon(A), \alpha(A), p(A + Y)$	28	5160.05	0.17	5217.19
3	$\square(A), \varepsilon(.), \alpha(A), p(Y)$	24	5173.01	0.02	5221.86
4	$\square(A), \varepsilon(A), \alpha(A), p(Y)$	26	5172.00	0.00	5224.99
5	$\square(.), \varepsilon(.), \alpha(A), p(A + Y)$	24	5188.40	0.00	5237.25
6	$\square(.), \varepsilon(A), \alpha(A), p(A + Y)$	26	5187.39	0.00	5240.38
7	$\square(.), \varepsilon(.), \alpha(A), p(Y)$	22	5199.87	0.00	5254.58
8	$\square(.), \varepsilon(A), \alpha(A), p(Y)$	24	5198.86	0.00	5247.70
9	$\square(A), \varepsilon(.), \alpha(A), p(A)$	18	5261.02	0.00	5297.50
10	$\square(A), \varepsilon(A), \alpha(A), p(A)$	20	5260.01	0.00	5300.60
11	$\square(A), \varepsilon(.), \alpha(A), p(.)$	16	5268.73	0.00	5301.11
12	$\square(A), \varepsilon(A), \alpha(A), p(.)$	18	5267.72	0.00	5304.20
13	$\square(.), \varepsilon(.), \alpha(A), p(A)$	16	5289.52	0.00	5321.90
14	$\square(.), \varepsilon(.), \alpha(A), p(A)$	14	5295.71	0.00	5324.01
15	$\square(.), \varepsilon(A), \alpha(A), p(A)$	18	5288.51	0.00	5324.99
16	$\square(.), \varepsilon(A), \alpha(A), p(.)$	16	5294.70	0.00	5327.08
<b>SSP L2</b>					
1	$\square(A), \varepsilon(A), \alpha(A), p(A + Y)$	25	62699.27	0.74	62749.34
2	$\square(A), \varepsilon(.), \alpha(A), p(A + Y)$	23	62705.41	0.23	62751.47
3	$\square(A), \varepsilon(A), \alpha(A), p(Y)$	23	62738.78	0.02	62784.85
4	$\square(A), \varepsilon(.), \alpha(A), p(Y)$	21	62744.92	0.00	62786.98
5	$\square(.), \varepsilon(A), \alpha(A), p(A + Y)$	23	62779.96	0.00	62826.03
6	$\square(.), \varepsilon(.), \alpha(A), p(A + Y)$	21	62786.10	0.00	62828.16
7	$\square(.), \varepsilon(A), \alpha(A), p(Y)$	21	62852.52	0.00	62894.58
8	$\square(.), \varepsilon(.), \alpha(A), p(Y)$	19	62858.66	0.00	62896.71
9	$\square(A), \varepsilon(A), \alpha(A), p(A)$	21	63103.58	0.00	63145.64
10	$\square(A), \varepsilon(.), \alpha(A), p(A)$	19	63109.72	0.00	63147.77
11	$\square(A), \varepsilon(A), \alpha(A), p(.)$	19	63144.67	0.00	63182.72
12	$\square(A), \varepsilon(.), \alpha(A), p(.)$	17	63150.81	0.00	63184.85
13	$\square(.), \varepsilon(A), \alpha(A), p(A)$	19	63185.43	0.00	63223.48
14	$\square(.), \varepsilon(.), \alpha(A), p(A)$	17	63191.57	0.00	63225.61
15	$\square(.), \varepsilon(A), \alpha(A), p(.)$	17	63272.39	0.00	63306.42
16	$\square(.), \varepsilon(.), \alpha(A), p(.)$	15	63278.53	0.00	63308.55

627

628

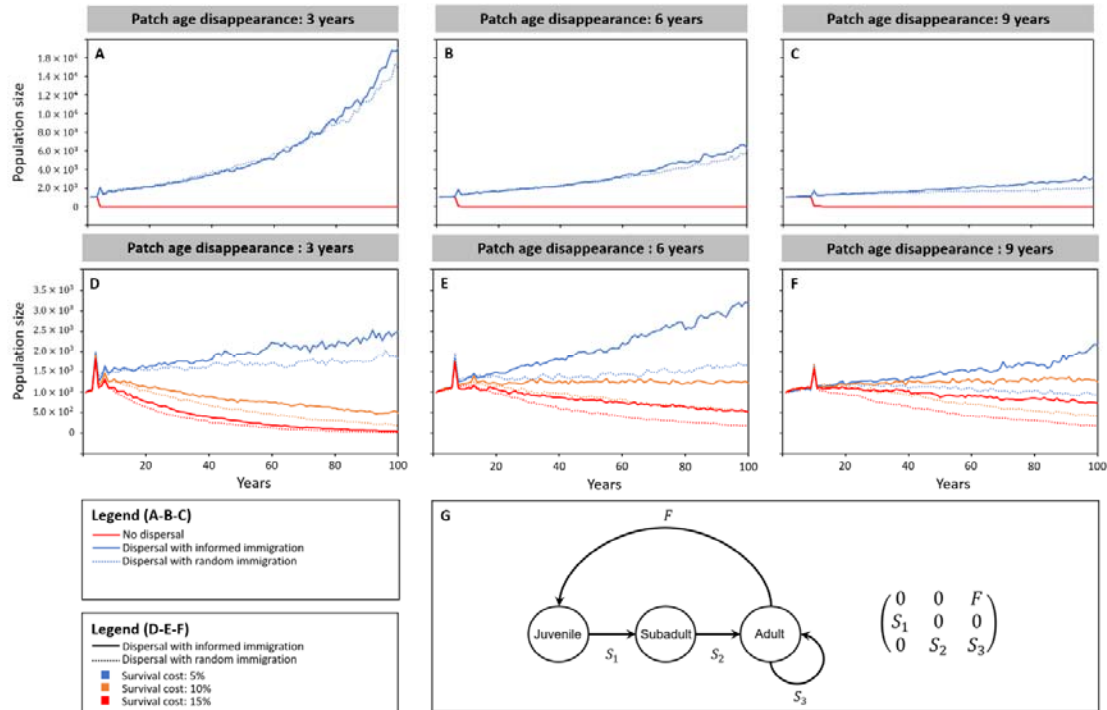
629 **Table 4.** Multievent models and selection procedure for SSPs R1 and R2.  $r$  = model rank,  $k$  = number  
 630 of parameters, Dev. = residual deviance, AICc = Akaike information criterion adjusted for small  
 631 sample size, wAICc = AICc weight  $\square$  = survival probability,  $\varepsilon$  = departure probability,  $\alpha$  = arrival  
 632 probability,  $p$  = recapture probability,  $A$  = age,  $.$  = constant,  $Y$  = year.

r	Model	k	Dev.	wAICc	AICc
<b>SSP R1</b>					
1	$\square(A), \varepsilon(A), \alpha(A), p(Y)$	19	8044.47	0.47	8082.67
2	$\square(A), \varepsilon(A), \alpha(A), p(A + Y)$	21	8041.98	0.22	8084.22
3	$\square(A), \varepsilon(.), \alpha(A), p(Y)$	17	8050.14	0.21	8084.29
4	$\square(A), \varepsilon(.), \alpha(A), p(A + Y)$	19	8047.65	0.10	8085.84
5	$\square(.), \varepsilon(A), \alpha(A), p(Y)$	17	8074.54	0.00	8108.70
6	$\square(.), \varepsilon(.), \alpha(A), p(Y)$	15	8080.20	0.00	8110.32
7	$\square(.), \varepsilon(A), \alpha(A), p(A + Y)$	19	8073.47	0.00	8111.67
8	$\square(.), \varepsilon(.), \alpha(A), p(A + Y)$	17	8079.13	0.00	8113.29
9	$\square(A), \varepsilon(A), \alpha(A), p(.)$	15	8129.11	0.00	8159.23
10	$\square(A), \varepsilon(A), \alpha(A), p(A)$	17	8125.73	0.00	8159.89
11	$\square(A), \varepsilon(.), \alpha(A), p(.)$	13	8134.77	0.00	8160.87
12	$\square(A), \varepsilon(.), \alpha(A), p(A)$	15	8131.39	0.00	8161.52
13	$\square(.), \varepsilon(A), \alpha(A), p(.)$	13	8157.05	0.00	8183.14
14	$\square(.), \varepsilon(.), \alpha(A), p(.)$	11	8162.71	0.00	8184.78
15	$\square(.), \varepsilon(A), \alpha(A), p(A)$	15	8155.63	0.00	8185.75
16	$\square(.), \varepsilon(.), \alpha(A), p(A)$	13	8161.29	0.00	8187.38
<b>SSP R2</b>					
1	$\square(A), \varepsilon(A), \alpha(A), p(A + Y)$	21	11041.21	0.64	11083.41
2	$\square(A), \varepsilon(.), \alpha(A), p(A + Y)$	19	11047.74	0.19	11085.90
3	$\square(A), \varepsilon(A), \alpha(A), p(A)$	17	11052.43	0.13	11086.56
4	$\square(A), \varepsilon(.), \alpha(A), p(A)$	15	11058.96	0.04	11089.06
5	$\square(.), \varepsilon(A), \alpha(A), p(A + Y)$	19	11068.13	0.00	11106.29
6	$\square(.), \varepsilon(.), \alpha(A), p(A + Y)$	17	11074.66	0.00	11108.78
7	$\square(.), \varepsilon(A), \alpha(A), p(A)$	15	11078.84	0.00	11108.94
8	$\square(.), \varepsilon(.), \alpha(A), p(A)$	13	11085.36	0.00	11111.44
9	$\square(A), \varepsilon(A), \alpha(A), p(Y)$	19	11076.17	0.00	11114.33
10	$\square(A), \varepsilon(.), \alpha(A), p(Y)$	17	11082.69	0.00	11116.82
11	$\square(A), \varepsilon(A), \alpha(A), p(.)$	15	11087.00	0.00	11117.10
12	$\square(A), \varepsilon(.), \alpha(A), p(.)$	13	11093.52	0.00	11119.60
13	$\square(.), \varepsilon(A), \alpha(A), p(Y)$	17	11111.72	0.00	11145.85
14	$\square(.), \varepsilon(.), \alpha(A), p(Y)$	15	11118.24	0.00	11148.34
15	$\square(.), \varepsilon(A), \alpha(A), p(.)$	13	11122.54	0.00	11148.62
16	$\square(.), \varepsilon(.), \alpha(A), p(.)$	11	11129.07	0.00	11151.12

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638 **Fig.4.** Effect of patch turnover on SSP size (number of adults) based on simulations. We considered  
639 three turnover rates: high (patch age before disappearance: 3 years, A and D), medium (6 years, B  
640 and E), and low (9 years, C and F). Three dispersal scenarios were also considered: (1) no dispersal  
641 (individuals were not able to escape when a patch disappeared and thus died); (2) dispersal with  
642 random immigration (individuals could disperse to escape the disappearance of a patch or disperse by  
643 choice even if the patch remained available. Immigration was random between the patches in the  
644 metapopulation and was not influenced by the age of the patch); (3) dispersal with informed  
645 immigration (similar to scenario 2, but individuals preferentially immigrated to recently created  
646 patches where fecundity  $F$  was highest). In scenarios 2 and 3, we considered two possible options  
647 regarding dispersal cost: (i) individuals did not incur any survival loss during dispersal (i.e. 'non-  
648 costly dispersal', A, B, and C); (ii) survival loss related to dispersal was either low (5% survival  
649 cost), medium (10%), or high (15%) (i.e. 'costly dispersal', D, E, and F). To investigate the  
650 demographic consequences of these scenarios, we used a female-dominant Leslie matrix ( $G$ ) based on  
651 four demographic parameters:  $F$  = the female achieved fecundity,  $S_1$  = juvenile survival,  $S_2$  =  
652 subadult survival, and  $S_3$  = adult survival with both environmental and demographic stochasticity.

653

654 *Simulating the effect of patch turnover and dispersal on logging SSP dynamics and long-term*  
655 *persistence*

656

657 The results showed that patch turnover rate was a critical driver of logging SSP dynamics. The  
658 absence of dispersal within an SSP experiencing patch turnover necessarily led to the extinction of the  
659 SSP (**Fig.4A, 4B, and 4C**), and the extinction speed increased with patch turnover rate. In contrast,  
660 patch turnover had a positive effect on SSP size (i.e. number of adults) when dispersal was possible

661 and had no survival cost. This was caused by a fecundity-related mechanism: high patch turnover led  
662 to a decrease in the mean patch age within the SSP, resulting in an increase in average fecundity due to  
663 the positive relationship between fecundity and patch age.

664 Our simulations also showed that an SSP's extinction risk increased with the survival cost  
665 related to dispersal and was mitigated by 'informed immigration' (**Fig.4D, 4E, and 4F**). In the  
666 scenarios with a high patch turnover rate (disappearance of patch after 3 years of availability), SSPs  
667 inevitably went extinct when the survival loss was higher than 10%. Random immigration accelerated  
668 the SSP's decline compared to informed immigration directed toward recently created patches (where  
669 female fecundity was highest). In the scenarios with medium patch turnover (disappearance after 6  
670 years of availability), the SSP decreased when the survival loss was 15% with both random and  
671 informed immigration. With a 10% survival loss, informed dispersal mitigated the decline of an SSP,  
672 whereas random dispersal drove the SSP to extinction. In the scenarios with low patch turnover  
673 (disappearance after 9 years of availability), the SSP experienced a marked decline only when  
674 immigration was random and the survival loss was equal to or higher than 10%. In summary, the  
675 simulations showed that patch turnover may result in SSP decline when the survival cost of dispersal  
676 is relatively high (10–15%) and immigration decisions are not adjusted to patch age and related fitness  
677 prospects.

678

#### 679 *Phenotypic specialization in riverine and logging environments*

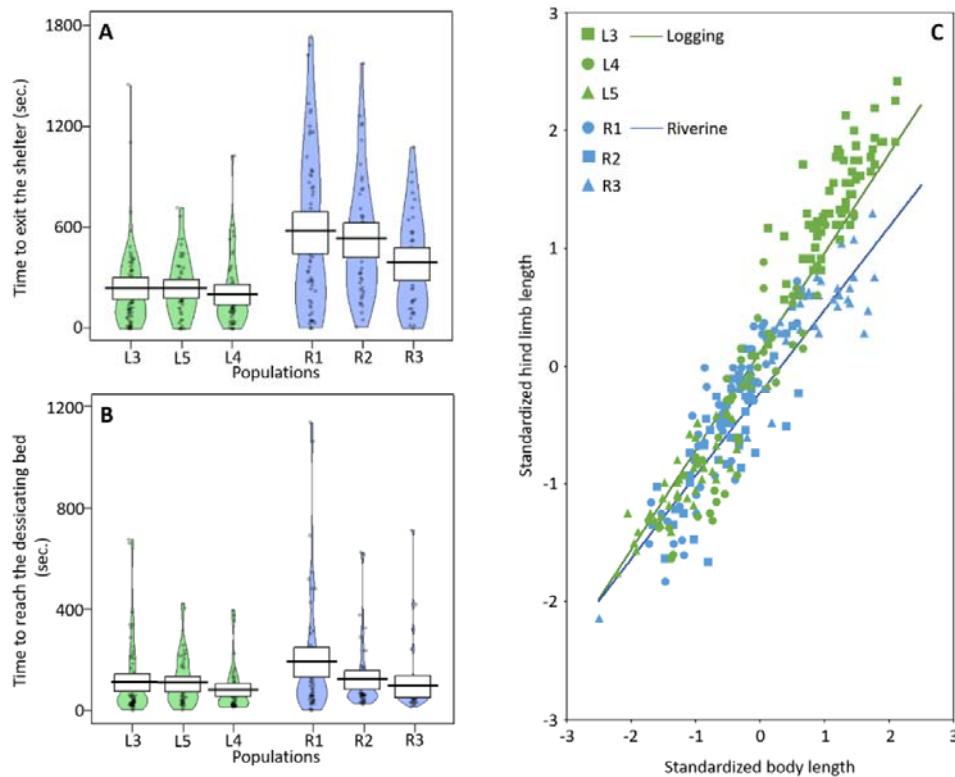
680

681 We focused on three morphological characteristics known to condition movement capacity in  
682 amphibians: body size, body condition and relative leg size (Gomes et al. 2009, Hillman et al. 2014).  
683 Of the 400 tadpoles, 295 survived until metamorphosis, resulting in a relatively high metamorphosis  
684 success rate ( $mean \pm sd = 0.75 \pm 0.08$ ), which did not differ according to the landscape type of  
685 origin ( $n = 400, F_{1,3,8} = 0, P = 0.95$ ). Neither body size nor body condition at metamorphosis varied  
686 according to the landscape type ( $n = 295$ ; body size:  $F_{1,4} = 0, P = 0.99$ ; body condition:  $F_{1,3,3} =$   
687  $1.12, P = 0.36$ ). However, the allometric relationship between leg size and body size varied according  
688 to landscape type ( $n = 295$ ; body size:  $F_{1,227} = 776.91, P < 0.0001$ ; landscape type:  $F_{1,3,4} = 3.74, P =$   
689  $0.13$ ; body size  $\times$  landscape type:  $F_{1,227} = 6.43, P = 0.012$ , Fig. 5). The larger the toadlets, the more  
690 those originating from logging SSPs tended to have longer hind limbs than those originating from  
691 riverine SSPs. Yet this difference was only just significant for large animals, as indicated by sliced  
692 tests (respectively performed at the 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> quartile of the size distribution:  $F_{1,3,8} = 1.64, P =$   
693  $0.27$ ;  $F_{1,3,4} = 3.28, P=0.15$ ;  $F_{1,4,01} = 6.54; P = 0.06$ ).

694 Based on the behavioral trials in the experimental arenas, we measured variables along the  
695 boldness–shyness behavioral axis, a personality trait consistently involved in dispersal syndromes  
696 across different organisms (Cote et al. 2010). Toadlet behavior was characterized using three



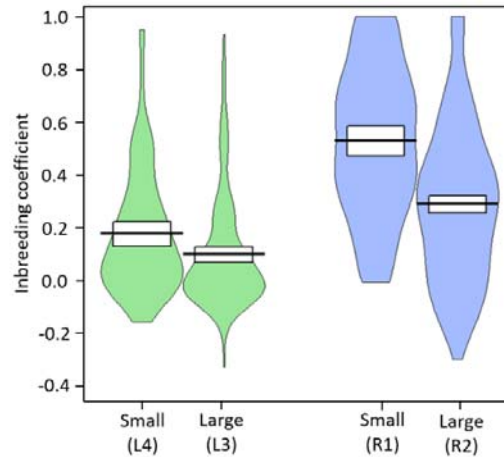
697 measures: one to assess neophobia (BEHAV1 = the time taken to leave the familiar refuge chamber) and  
698 the other two to assess exploration propensity (BEHAV2 = the time taken to reach the desiccant zone  
699 after leaving the refuge chamber; BEHAV3 = the time taken to cross the desiccant zone and get out of  
700 the arena). The findings showed that the neophobia of toadlets significantly varied according to their  
701 landscape of origin (**Fig.5**), but not according to their body size or its interactive effect with landscape  
702 (N=295; landscape type:  $F_{1,3,5}=47.30$ ,  $P=0.004$ ; body size:  $F_{1,13,9}=0.03$ ,  $P=0.86$ ; their interactive effect:  
703  $F_{1,12,1}=0.01$ ,  $P=0.92$ ). Individuals from riverine landscapes were 2.13+0.24 times slower to leave the  
704 refuge chamber than those from logging landscapes (respectively 8.58+0.67 mn and 3.89+0.33 mn,  
705 see **Fig.5**). Once the toadlet left the refuge chamber, the latency time to reach the desiccating zone was  
706 very short (mean 1.83 +- 0.21 mn) and did not vary depending on the landscape of origin, body size,  
707 or their interactive effect (N=295; landscape type:  $F_{1,3,9}=1.84$ ,  $P=0.25$ ; body size:  $F_{1,30}=0.42$ ,  $P=0.52$ ;  
708 their interactive effect  $F_{1,33,4}=0.26$ ,  $P=0.61$ , see **Fig.5**). In contrast, the latency time to get out of the  
709 arena significantly varied depending on the landscape of origin, but not according to body size  
710 (N=295; landscape type:  $\chi^2_{1df}=9.56$ ,  $P=.002$ ; body size:  $\chi^2_{1df}=0.01$ ,  $P=0.91$ ; their interactive effect:  
711  $\chi^2_{1df}=0.28$ ,  $P=0.59$ ). The time taken – and thus the increased hazard – to get out of the arena for  
712 toadlets originating from logging SSPs was 1.93 times greater than for toadlets from riverine SSPs.  
713



714

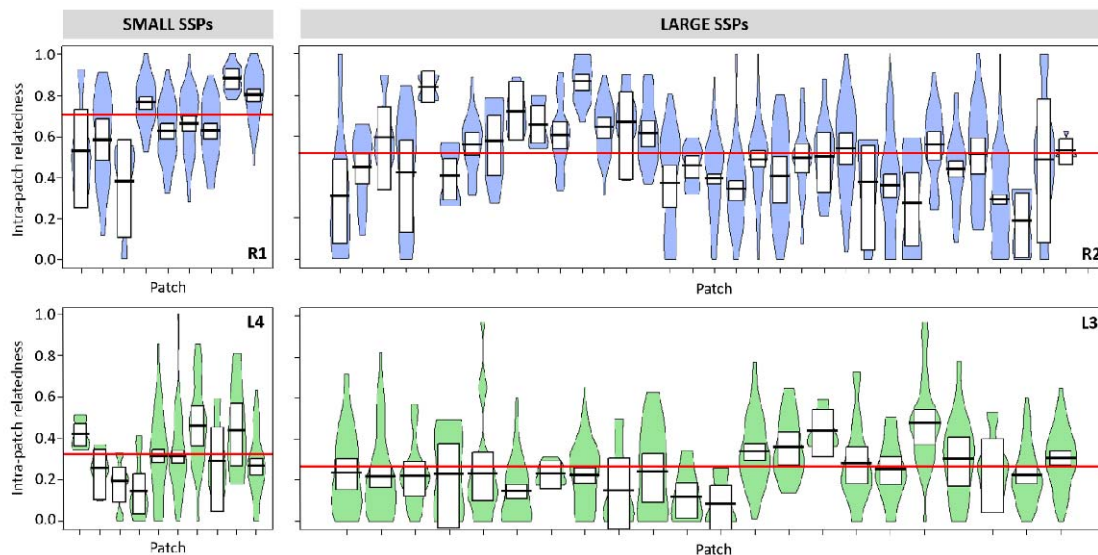
715 **Fig.5.** Behavioral and morphological specialization in six *Bombina variegata* SSPs occurring in  
716 logging environments (L3, L4, and L5) and riverine environments (R1, R2, and R3). We examined how

717 the type of environment affected two behavioral traits: the time to exit the refuge chamber (A), a proxy  
718 for neophobia, and the time to reach the desiccation zone (B), a proxy for exploration propensity. We  
719 also examined how environment type affected hind limb length while considering body length as a  
720 control covariate in the model. These observations were recorded for 295 toadlets at metamorphosis.



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723

**Fig.6.** Inbreeding in the riverine (blue) and logging (green) *Bombina variegata* SSPs.



724  
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726  
727

**Fig.7.** Relatedness within patches in the riverine (blue) and logging (green) *Bombina variegata* SSPs. Patches where less than 6 relatedness values were available were removed from the plot.

### 728 Neutral genetic variation in riverine and logging environments

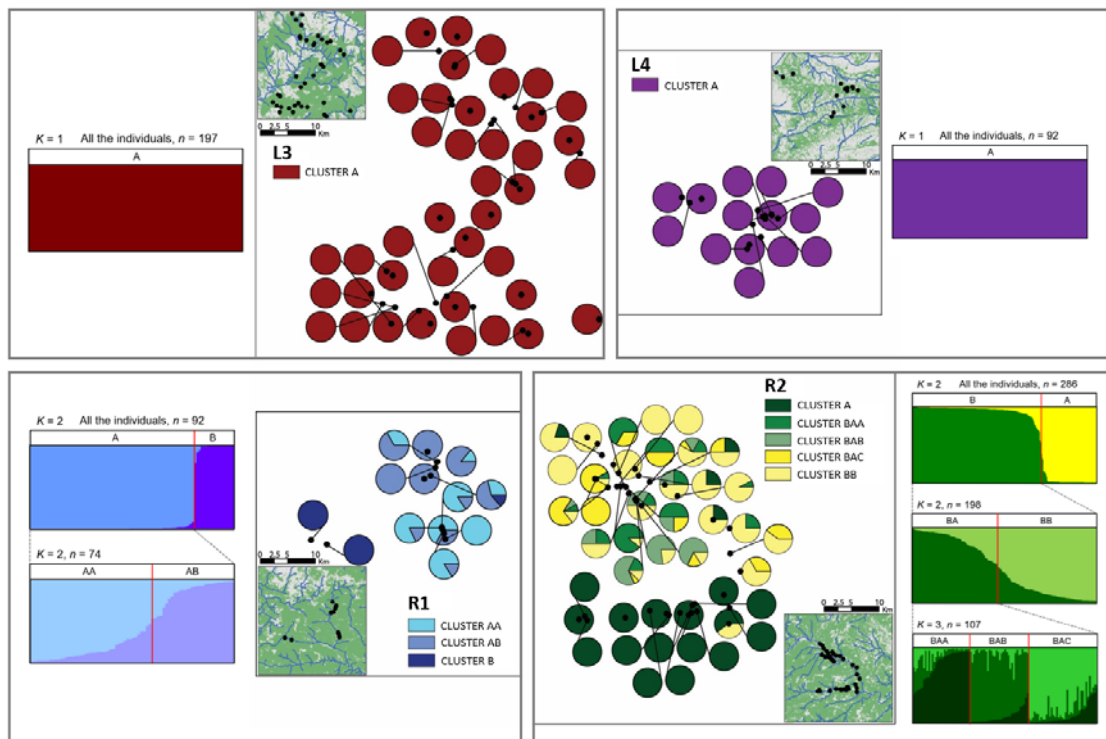
729

730 We investigated the neutral genetic footprint associated with each landscape type using microsatellite  
731 data collected in four SSPs: two from each landscape type (a total of 667 toads genotyped within L3  
732 and L4 logging environments and R1 and R2 riverine environments; **Table S2**). Our analyses  
733 revealed, first, that riverine systems exhibited a higher deviation from the Hardy–Weinberg

734 equilibrium than logging systems. Significant deviation from this equilibrium was detected for 75%  
 735 and 45% of the loci in riverine SSPs R1 and R2 respectively, and 0% and 18% in the logging SSPs L3  
 736 and L4 (**Table S3**). Second, we found lower genetic diversity in riverine SSPs than in logging SSPs:  
 737 both the allelic richness and the expected heterozygosity (uHE) were substantially lower in riverine  
 738 SSPs. In contrast, inbreeding coefficients ( ) were higher in riverine SSPs: 87% of the loci were  
 739 found to have a lower uHE in riverine SSPs compared to logging SSPs (**Table S3**). Similarly, our  
 740 parentage analyses also showed that individual inbreeding (LR test, = 32.55,  $P < 0.0001$ ; **Fig.6**) and  
 741 the relatedness level within patches (LR test, = 43.14,  $P < 0.0001$ , **Fig.7**) were drastically higher in  
 742 riverine SSPs. In addition, riverine SSPs had a much smaller effective population size than logging  
 743 SSPs: the effective population size was 9.7 (95% CI 6.4–13.7) in R1 and 22.6 (95% 19.3–26.3) in R2,  
 744 while it was 138.9 (95% 80.2–353.6) in L4 and 168.6 (95% 129.9–229.3) in L3.

745 Within both types of environment, the size of SSPs (large: R2 and L3; small: R1 and L4) was  
 746 also an important predictor of individual relatedness and inbreeding. The relatedness level within  
 747 patches was higher (**Fig.7**) in small SSPs than in large SSPs (LR test, = 214.38,  $P < 0.0001$ ), and  
 748 this difference was larger in riverine SSPs (LR test, = 6.16,  $P = 0.01$ ). Similarly, inbreeding within  
 749 patches was higher (**Fig.6**) in small SSPs than in large SSPs (LR test, = 76.56,  $P < 0.0001$ ), and the  
 750 interaction between these two factors was also confirmed (LR test, = 8.88,  $P = 0.01$ ).

751



752

753 **Fig.8.** Patterns of neutral genetic variation and spatial distribution of the hierarchical genetic clusters  
 754 in two riverine (R1 and R2) and logging SSPs (L3 and L4). The analyses were conducted using the  
 755 program STRUCTURE. In L3 and L4, no genetic structuring was detected. In contrast, a complex

756 genetic structure was found in R1 and R2. In R1, the hierarchical analysis revealed the existence of  
 757 two initial genetic clusters (A and B), and genetic substructures within cluster A where two nested  
 758 clusters were inferred (AA and AB). In R2, the hierarchical analysis highlighted the presence of two  
 759 initial genetic clusters (A and B), and a substructure was further detected within cluster B (BA and  
 760 BB). Genetic substructures were then identified within the cluster BA, with three additional genetic  
 761 clusters inferred (BAA, BAB, and BAC).

762

763 **Table 5.** Relative support of the mixed models for each of the four SSPs and their related estimates of  
 764 geographic resistance (L3 and L4 = logging SSPs, R1 and R2 = riverine SSPs, see Map S1 for  
 765 details). ‘Model’ indicates the effect introduced in the model in addition to geographic resistance (null  
 766 = the model including only the effect of geographic resistance). ‘Waic’ indicates the weighted AIC of  
 767 the model.  $\hat{\beta}(sd)$  indicates the beta weight associated with the effect of geographic resistance and its  
 768 standard deviation. The variable ‘slope’ corresponds to the effect of both geographic distance and  
 769 topographic roughness. The variable ‘network’ corresponds to the effect of the hydrological network.

770

Model	Waic	$\hat{\beta}(sd)$
<b>SSP L3</b>		
null	0.469	1.4763 (0.1544)
slope	0.245	1.4811 (0.1545)
network	0.191	1.4798 (0.1545)
slope+network	0.095	1.4826 (0.1546)
<b>SSP L4</b>		
null	0.169	0.6783 (0.0415)
slope	0.084	0.679 (0.0415)
network	0.507	0.6764 (0.0415)
slope+network	0.240	0.677 (0.0415)
<b>SSP R1</b>		
null	0.391	2.381 (0.0713)
slope	0.276	2.386 (0.0714)
network	0.226	2.3845 (0.0714)
slope+network	0.107	2.3862 (0.0714)
<b>SSP R2</b>		
null	0.070	2.5459 (0.0251)
slope	0.030	2.5461 (0.0251)
network	0.601	2.5479 (0.0251)
slope+network	0.299	2.5482 (0.0251)

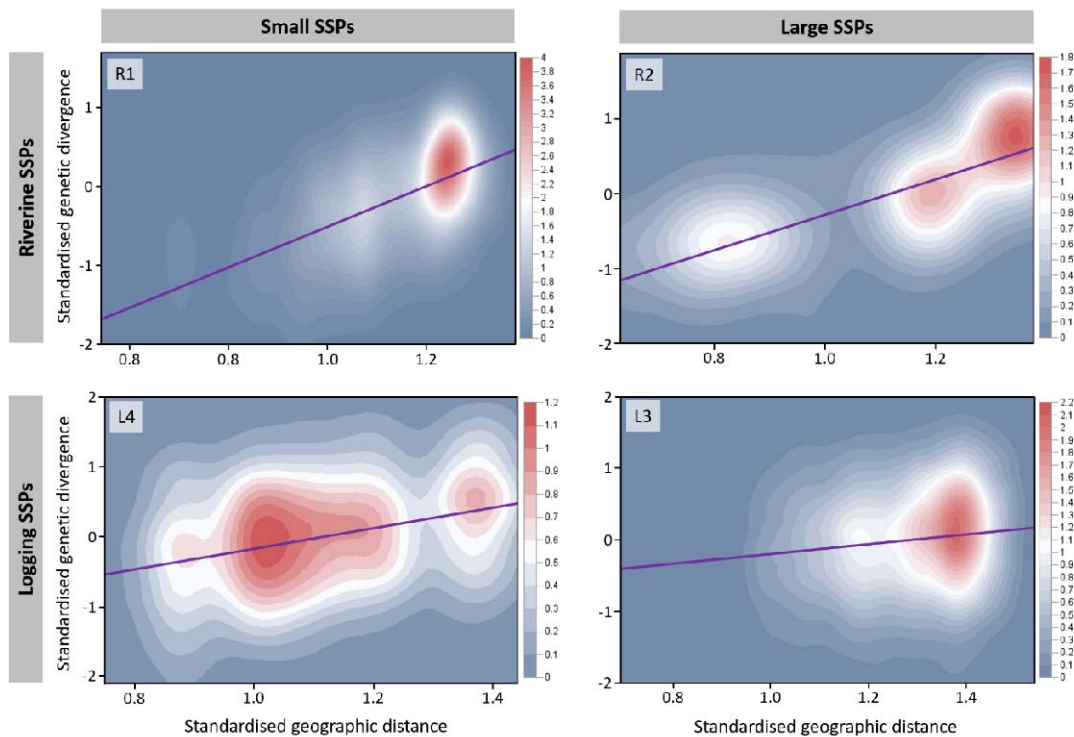
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773

774 We then investigated how patterns of genetic differentiation between patches differed between  
 775 logging and riverine SSPs. First, we used the Bayesian genetic clustering approach to examine  
 776 hierarchical genetic structure in the SSPs. In the two SSPs from logging environments, we failed to  
 777 detect any hierarchical genetic structure ( $K = 1$ ) (**Fig.8**). In contrast, our analyses revealed a strong  
 778 hierarchical genetic structure overlaying the spatial distribution of patches in the two SSPs from  
 779 riverine environments (**Fig.8**). Second, we sought to verify that differences in spatial genetic patterns  
 780 between landscapes were still significant while controlling for the potential difference of functional  
 781 connectivity between SSPs using direct gradient analyses. These revealed that genetic differentiation  
 782 correlated with geographic resistance between individuals whatever the landscape type, indicating  
 783 substantial genetic isolation by distance even in logging systems (**Fig.9**). There was considerable

784 support for the effect of the hydrological network on genetic differentiation in the large SSPs of both  
785 landscape types (SSPs R2 and L3), but not in the small SSPs whatever the landscape type (**Table 5**).  
786 Most importantly, even after correcting for these potential landscape effects, spatial genetic  
787 differentiation remained higher in riverine than in logging SSPs as revealed by the model averaged  
788 slope estimate associated with the geographic resistance effect ( : for R1 and  
789 for R2; for L3 and for L4).  
790



791  
792 **Fig.9.** Genetic divergence according to geographic distance in two riverine (R1 and R2) and two  
793 logging SSPs (L3 and L4). Each figure represents the contour plot of the kernel density bivariate  
794 estimates between the pairwise genetic distance and the pairwise geographic resistance for each SSP.  
795 Kernel densities were estimated using a Gaussian distribution. The graduated color contour  
796 indicating the (smoothed) observation count is presented on the right side of each plot. The line  
797 represents the predicted regression curve between the genetic distance and the geographic resistance  
798 from the linear mixed model estimates.  
799

800

## 801 Discussion

802

803 Taken together, the results of this study provide for the first time an extended picture of the effect of  
804 anthropogenic disturbance on dispersal in a vertebrate, from dispersal-related phenotypic  
805 specialization expressed early in life, through the dispersal pattern emerging in spatially structured  
806 populations, to the genetic footprint arising throughout successive generations. Overall, this analysis  
807 revealed that anthropogenic disturbance not only strongly promotes dispersal throughout a toad's

808 lifetime, but also prenatally enhances a toadlet's risk-proneness and, to a certain extent, favors longer  
809 hind limb length at metamorphosis. Another finding was that gene flow also substantially increased in  
810 anthropogenic landscapes independently of the SSP's size or functional connectivity.

811

812 *Natal and breeding dispersal rates and distances in SSPs depend on patch turnover rate*

813

814 The results revealed contrasting dispersal patterns between riverine and logging SSPs. In the  
815 demographic component of our study, the sampling protocol was weakened by a potential  
816 confounding effect of the population's position along the latitudinal gradient with its status  
817 (logging/riverine). However, we can rule out the possibility of an effect of latitude on the dispersal  
818 patterns drawn in our analyses, as the molecular inferences showed drastically increased gene flow  
819 (resulting from dispersal) in an SSP at a low latitude (L4), which indicates that latitude has a marginal  
820 effect on effective dispersal within SSPs. We are therefore confident in the reliability of our results  
821 regarding the effect of turnover rate on dispersal patterns.

822 In riverine SSPs, we observed a complete suppression of natal dispersal, as well as very low  
823 breeding dispersal, together with a reduced dispersal kernel – the opposite of the dispersal pattern  
824 observed in logging SSPs. In the latter, we nevertheless found some substantial inter-population  
825 variation regarding the contribution of natal dispersal to the overall dispersal process and to seasonal  
826 variation in dispersal rates. Such differences between logging SSPs likely reflect variation in the  
827 anthropogenic disturbance regime resulting from local woodland management practices. Indeed, patch  
828 turnover depends on both the extent and the frequency of the logging activities that create patches, as  
829 well as the post-logging rehabilitation operations that may lead to patch destruction (e.g. filling in of  
830 ruts used as temporary breeding ponds) (Cayuela et al 2018b). This likely results in a continuum of  
831 dispersal strategies along a gradient of patch disturbance, ranging from the near suppression of  
832 dispersal in riverine SSPs to a very high dispersal rate and long dispersal distances in some logging  
833 SSPs (e.g. L1 SSP). This pattern is thus very similar to that observed for wing dimorphism in insects  
834 alongside patch temporality gradients (Denno et al. 1996, Roff & Fairban 2007), in which dispersal is  
835 suppressed (i.e. high rate of wingless forms) in persistent habitats, while it is enhanced (i.e. high rate  
836 of winged forms) in more ephemeral habitats according to the (natural) disturbance regime  
837 experienced at the landscape level.

838

839 *Phenotypic specialization in SSPs depends on patch turnover rate*

840

841 Previous studies on *Bombina variegata* (Cayuela et al. 2018b) have revealed that dispersal events in  
842 logging SSPs are a mixture of departures conditioned by patch disappearance and unconditional  
843 departures that occur well before patch disappearance. The findings from our common garden  
844 experiments highlight that patch turnover rate prenatally mediates dispersal-related phenotypes and

845 leads to phenotypic parallelism in logging and riverine SSPs. In particular, toadlets originating from  
846 logging SSPs exhibited higher risk-proneness than those from riverine SSPs, as revealed by their  
847 swiftness in leaving the refuge chamber and in getting out of the arena after crossing a harsh substrate.  
848 Either neophilia or boldness (see Kelleher et al. 2018 for personality traits in amphibians) could  
849 explain the elevated risk-proneness we observed in logging SSPs. Disentangling these two personality  
850 traits is not straightforward (Greggor et al. 2015, Yuen et al. 2017), and further investigations would  
851 be useful to address this. Regardless of the exact composition of personality traits behind our  
852 identification of risk-prone behavior, our results clearly indicate behavioral specialization early in life  
853 according to the disturbance regime prevailing in the landscape.

854 Concerning morphological traits, we did not find any differences in body size and condition of  
855 toadlets from logging and riverine SSPs. However, the findings showed that toadlets innately have  
856 longer hind limbs in logging than in riverine SSPs. In anurans, hind-limb length is usually positively  
857 associated with locomotor performance (Choi et al. 2003, Philips et al. 2006, Gomes et al 2009,  
858 Hudson et al. 2016), and has also been found to be subject to rapid evolution at the edge of the  
859 invasion front in the introduced species *Rhinella marina* (Philips et al. 2006). Our results thus suggest  
860 that long hind limbs could be a phenotypic trait facilitating dispersal in logging habitats. Yet this  
861 difference in leg length between toadlets from the two environments was only observed in large  
862 individuals and was subject to substantial variation between SSPs. This significant but weak effect of  
863 anthropogenic disturbance on leg length could result from developmental constraints. Limb size  
864 mainly depends on the duration of the larval period in anurans, so species specialized for ephemeral  
865 pools (such as *Bombina variegata*), which are selected for fast larval development, usually exhibit  
866 shorter hind limbs compared to other species (Gomez-Mestre & Buchholz 2006).

867 Overall, dispersal and related behavioral traits are usually highly plastic phenotypes subject to  
868 partial genetic control (reviewed in Saastamoinen et al. 2018), i.e. determined by  $G \times E$  interactions.  
869 Therefore, the phenotypic specialization highlighted in our study may have a genetic basis and/or may  
870 be associated with transgenerational plasticity. In the absence of crossbreed design, we were not able  
871 to disentangle the relative contribution of maternal effect and parental genotypes in the phenotypic  
872 variation observed in logging and riverine SSPs. However, it is possible to rule out the hypothesis of  
873 transgenerational plasticity mediated by toadlet body size at metamorphosis. In amphibians, female  
874 energy investment in breeding influences the size of eggs and the amount of energetic resources  
875 available for the development of embryos and larvae before they become fully heterotrophic (Kaplan  
876 1987, 1992). Studies have reported a positive relationship between egg size and offspring body size at  
877 metamorphosis due to carry-over effects (Laugen et al. 2005, Räsänen et al. 2005, Dziminski et al.  
878 2006), and body size is an important predictor of behavioral traits (e.g. exploration propensity and  
879 risk-taking behavior) related to dispersal (Kelleher et al. 2017, 2018). In our case study, no difference  
880 in body size was detected in toadlets from logging and riverine environments, which indicates that  
881 patch turnover rate is not likely to alter individual behavior due to the morphological state at

882 metamorphosis in SSPs. However, epigenetic factors (e.g. DNA methylation, micro-ARN, and histone  
883 structure) independent from female energy investment strategies may lead to transgenerational  
884 dispersal plasticity and contribute to the expression of phenotypic traits that facilitate or hinder  
885 dispersal over generations (Saastamoinen et al. 2018, Cayuela et al. 2019a). Yet it is very likely that a  
886 genetic basis partially determines phenotypic specialization in logging and riverine environments,  
887 resulting in incomplete genetic parallelism between SSPs (Elmer & Meyer 2011, Conte et al. 2012).  
888 First, transgenerational plasticity in dispersal-related traits is usually subject to genetic control  
889 (Cayuela et al. 2019a), likely due to a strong association between epigenetic variation and genetic  
890 variants in *cis* and *trans* (Dubin et al. 2015, Zaghlool et al. 2016). Second, as predicted by the  
891 dispersal theory and reported in other study systems, dispersal is partly genetically determined, and  
892 behavioral traits related to dispersal often have a polygenic basis (Saastamoinen et al. 2018). Future  
893 studies using Next-Generation Sequencing approaches (Morozova & Marra 2008, Metzker 2010)  
894 could be undertaken to determine the role of genetic, transcriptional, and epigenetic variation in the  
895 disturbance-dependent phenotypic changes and dispersal evolution in *B. variegata*.

896

#### 897 *Patch turnover and related dispersal costs and benefits determine SSP dynamics and persistence*

898

899 Our simulations showed that the absence of dispersal inevitably leads to SSP extinction, and that the  
900 extinction speed increases with patch turnover. When dispersal was possible and had no survival cost,  
901 patch turnover had a positive effect on SSP size. This resulted from an increase in average fecundity  
902 due to the positive relationship between fecundity and patch age reported in logging SSPs (Boualit et  
903 al. 2019) and considered in our models. These results are congruent with field observations reporting  
904 that *Bombina variegata* SSPs may be very large (thousands of adults) in harvested woodlands in  
905 western Europe.

906 The models also showed that the risk of SSP extinction increased with the survival cost related  
907 to dispersal and was mitigated by informed immigration. This result is congruent with theoretical  
908 models and empirical evidence showing that dispersal only evolves if the benefits of moving outweigh  
909 the related costs (Bonte et al. 2012). In logging SSPs, dispersal seems to be favored as its costs are  
910 likely offset by the benefits of colonizing new patches. Survival (at juvenile, subadult, and adult stage)  
911 is lower in logging than in riverine SSPs (Cayuela et al. 2016a), which likely results from mortality  
912 caused by logging operations and dispersal-related mortality (Cayuela et al. 2018b). This survival cost  
913 of dispersal can be direct, i.e. associated with movement in the landscape matrix (Bonte et al. 2012). It  
914 can be also indirect, resulting from the high energy allocation necessary for recurrent dispersal events  
915 over the toad's lifespan, which might lead to earlier and stronger senescence due to trade-offs  
916 (Cayuela et al. 2019b). These direct and indirect costs are obviously offset when animals are forced to  
917 disperse subsequently to patch destruction resulting from logging practices (Cayuela et al. 2018b). It  
918 should be noted that even when patches remain available, dispersal may still be strongly favored since



919 their suitability rapidly declines over time due to the natural silting of ruts if these are not regularly  
920 disturbed by vehicle traffic (Boualit et al. 2019). Furthermore, even if patch suitability is sustained by  
921 regular human disturbance (Boualit et al. 2019), dispersal costs might be mitigated through the  
922 colonisation of recently created patches in which fitness prospects are likely enhanced due to density-  
923 dependent mechanisms. A low density of adults in newly available patches likely reduces the risk of  
924 larval competition, which is an important driver of metamorphosis success (Jasieński 1988) – for this  
925 reason adults preferentially reproduce in tadpole-free waterbodies (Cayuela et al. 2016d, 2017b).

926 These potential benefits likely favor the evolution of dispersal and dispersal-enhancing  
927 morphological and behavioral traits (i.e. ‘dispersal syndromes’) in logging SSPs. They also likely  
928 contribute to context-dependent dispersal (Clobert et al. 2009) and matching habitat choice (Edelaar et  
929 al. 2008), implying that individuals adjust their dispersal decisions according to the local fitness  
930 prospects determined by the biotic and abiotic characteristics of breeding patches. This prediction has  
931 been verified by two studies reporting context-dependent dispersal in logging SSPs (Tournier et al.  
932 2017, Boualit et al. 2019). In particular, these studies showed that adult emigration and immigration  
933 decisions depend on a pond’s hydroperiod and the size and annual disturbance of the patch: three  
934 factors that locally affect juvenile recruitment and very likely individual fitness.

935 In riverine SSPs, the near absence of both natal and breeding dispersal suggests that the  
936 benefits of dispersal do not compensate for its potential costs. First, the absence of patch loss resulting  
937 from anthropogenic or natural processes means individuals are not forced to disperse to survive and  
938 reproduce. In river environments, the local fitness prospects do not deteriorate with patch age, as the  
939 process of natural silting of rocky pools is frequently interrupted by river flooding occurring outside  
940 the breeding period (Cayuela et al. 2011, 2015a). This makes pools available for breeding from one  
941 year to another and limits the risk of larval mortality caused by desiccation. It is also possible that the  
942 near absence of dispersal results from variability in pond characteristics (e.g. hydroperiod and  
943 temperature; Cayuela et al. 2011) within a patch. Indeed, the benefit of dispersing would be low if the  
944 variability in environmental conditions would be similar at intra-patch and inter-patch scales. Overall,  
945 the lack of apparent compensatory benefits should not favor and may even counter-select for dispersal  
946 and dispersal-enhancing traits in riverine SSPs. This is in line with our results, which show that  
947 riverine toadlets innately display low risk-taking behavior and have short hind limbs, two phenotypic  
948 traits hindering dispersal in amphibians (Cayuela et al. 2018c).

949

950 *Genetic variation patterns in SSPs depend on patch turnover rate*

951

952 Our study showed for the first time that the spatiotemporal dynamics of habitat patches in a landscape  
953 may have an effect at least as important as landscape fragmentation on gene flow patterns. The  
954 findings highlighted that low dispersal rates and distances are associated with a weaker genetic

955 structure and lower IBD in riverine than in logging SSPs. Our sampling design allowed us to  
956 disentangle the relative effects of gene flow and genetic drift, which both contribute to genetic  
957 differentiation within SSPs (Slatkin 1977, Broquet & Petit 2009). As well as genetic structure  
958 differences caused by patch turnover, we found higher IBD in the two small SSPs (L4 and R1) than in  
959 the two large SSPs in each environment.

960 Our analysis also took into account the functional connectivity within SSPs by considering  
961 two landscape factors (i.e. topography and hydrological network) that are critically important to the  
962 genetic structure of amphibian populations (reviewed in Cayuela et al. 2018c). As reported in 20  
963 previous studies (Cayuela et al. 2018c), genetic differentiation increases with increasing topographic  
964 slope as this raises the energy cost of dispersal during the transience phase in amphibians. In addition,  
965 our results showed that genetic differentiation was better explained by the distance of the hydrological  
966 network than the Euclidean distance between two patches. This indicates that the hydrological network  
967 improves the functional connectivity between patches by reducing the cost of displacement in the  
968 landscape matrix, which is congruent with the findings of six previous studies (Cayuela et al. 2018c).  
969 Interestingly, genetic differentiation nevertheless remained higher in riverine than in logging SSPs,  
970 despite a denser hydrological network and therefore weaker landscape resistance in riverine SSPs.  
971 This suggests that in our study system, the rate of patch turnover may be a more important driver of  
972 neutral genetic variation than landscape connectivity.

973 Our findings suggest that variation in the turnover rate of SSPs has far-reaching consequences  
974 on the evolutionary forces involved in the migration–selection–drift balance. In riverine SSPs, reduced  
975 gene flow between patches leads to lower genetic diversity and smaller effective population size  
976 compared to logging SSPs. Such low standing genetic variation could limit the adaptive response of  
977 riverine SSPs to novel environmental conditions. The probability of allele fixation increases with the  
978 magnitude of the beneficial effect and the effective population size, and this probability is significantly  
979 higher when the allele has a high initial frequency (Barrett & Schluter 2008, Hedrick 2013). Moreover,  
980 standing genetic variation usually allows faster adaptation as beneficial alleles are already present in  
981 the population (Barrett & Schluter 2008, Hedrick 2013). Overall, our results suggest that riverine SSPs  
982 should suffer from a lower capacity of ‘evolutionary rescue’ (Carlson et al. 2014) than logging SSPs,  
983 which could increase their sensitivity to current global changes.

984 The results also revealed a high level of inbreeding and relatedness within riverine SSPs,  
985 confirming the results of a previous study (Cayuela et al. 2017a). These findings raise important  
986 questions about the mechanisms associated with the repression of inbreeding depression. As  
987 mentioned, the survival rate at all life stages (juvenile, subadult, and adult) is higher in riverine than in  
988 logging SSPs (Cayuela et al. 2016a), suggesting a marginal effect of inbreeding on postmetamorphic  
989 survival and negligible inbreeding depression. A previous study conducted in the R2 SSP indicated  
990 that the absence of disassortative mating does not seem to mitigate inbreeding risk: females even  
991 prefer to reproduce with related males from their own patch (Cayuela et al. 2017a). Although the

992 effect of inbreeding on reproductive performance remains as yet unevaluated, those results suggest a  
993 low genetic load in riverine SSPs. This could be due to high efficiency in purging deleterious alleles  
994 and the genomic architecture of genetic load, especially a low linkage of deleterious recessive alleles  
995 (Bersabé et al. 2016, Hedrick & Garcia-Dorado 2016). Future studies could be carried out to identify  
996 the mechanisms involved in the genetic purging of inbreeding depression resulting from limited  
997 dispersal in riverine SSPs.

998

## 999 **Conclusion**

1000

1001 Our study showed that anthropogenic habitat disturbance is likely an important driver of dispersal  
1002 evolution. The results found that, like landscape fragmentation, human-driven variation in patch  
1003 turnover may promote morphological and behavioral specialization related to dispersal. In particular, it  
1004 may lead to phenotypic parallelism affecting dispersal syndromes and patterns (dispersal rate and  
1005 distance) in SSPs exposed to contrasting levels of patch turnover. This phenotypic parallelism is likely  
1006 underpinned by genetic and/or epigenetic parallelism, for which the molecular basis remains to be  
1007 investigated. Our results also revealed that differences in dispersal patterns are associated with  
1008 variation in the genetic structure of SSPs, which might affect local eco-evolutionary dynamics  
1009 (Legrand et al. 2017). In particular, high gene flow and reduced effects of genetic drift allow higher  
1010 genetic polymorphism to be maintained in SSPs experiencing high patch turnover than in SSPs with  
1011 low patch turnover. In parallel, larger effective population size is expected to increase selection  
1012 effectiveness in SSPs exposed to high patch turnover, giving them higher evolutionary potential and  
1013 increased chances of evolutionary rescue in the case of environmental change (Carlson et al. 2014).  
1014 These results emphasize the central role of anthropogenic disturbance in the spatiotemporal dynamics  
1015 of landscapes and the related ecological and evolutionary processes.

1016 In terms of the implications for conservation, the findings suggest that the approach may need  
1017 to differ depending on the demographic and genetic characteristics of SSPs driven by the level of  
1018 patch turnover. Those SSPs exposed to high patch turnover are likely to be highly sensitive to land use  
1019 changes that result in a loss of functional connectivity between patches. An increase in landscape  
1020 resistance reduces the success of dispersal following the disappearance of a patch and diminishes the  
1021 chance of new patch colonization, which enhances the extinction risk of the whole SSP. In contrast,  
1022 SSPs experiencing a low level of patch turnover suffer a loss of genetic diversity and high inbreeding,  
1023 which may increase their sensitivity to environmental change (e.g. climate change or the emergence of  
1024 new pathogens), potentially speeding up their extinction if they experience a demographic decline (i.e.  
1025 inbreeding depression; Reed & Frankham 2003, Frankham 2010). This underlines the tremendous  
1026 importance of adjusting conservation decisions to the demographic and genetic characteristics of SSPs  
1027 adapted to contrasting regimes of habitat disturbance.

1028

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1030

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1041

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