

# Determinants and consequences of dispersal in vertebrates with complex life cycles: a review of pond-breeding amphibians

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## ABSTRACT

Dispersal is a central process in ecology and evolution. It strongly influences the dynamics of spatially structured populations, by affecting population growth rate and local colonization-extinction processes. Dispersal can also influence evolutionary processes because it determines rates and patterns of gene flow in spatially structured populations and is closely linked to local adaptation. For these reasons, dispersal has received considerable attention from ecologists and evolutionary biologists. However, although it has been studied extensively in taxa such as birds and mammals, much less is known about dispersal in vertebrates with complex life cycles such as pond-breeding amphibians. Over the past two decades, researchers have taken an interest in amphibian dispersal and initiated both fundamental and applied studies, using a broad range of experimental and observational approaches. This body of research reveals complex dispersal patterns, causations and syndromes, with dramatic consequences for the demography and genetics of amphibian populations. In this review, our goals are to (1) redefine and clarify the concept of amphibian dispersal, (2) review current knowledge about the effects of individual (i.e., condition-dependent dispersal) and environmental (i.e., context-dependent dispersal) factors during the three stages of dispersal (i.e., emigration, immigration, transience), (3) identify the demographic and genetic consequences of dispersal in spatially structured amphibian populations, and (4) propose new research avenues to extend our understanding of amphibian dispersal. In particular, we emphasize the need to (1) quantify dispersal rate and distance rigorously using suitable model systems, (2) investigate the genetic basis and dispersal evolution patterns, and (3) examine dispersal-related eco-evolutionary dynamics. These proposed research avenues tap from the recent advances in quantitative and molecular methods and have the potential to improve our understanding of dispersal in organisms with complex life cycles.

**Keywords:** dispersal syndromes, demography, landscape genetics, movement, emigration, immigration, transience

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# I. INTRODUCTION

Dispersal describes the unidirectional movement of an individual from the natal site to its breeding sites (i.e., natal dispersal) and between breeding sites (i.e., breeding dispersal) (Clobert et al. 2009, Matthysen 2012). Dispersal is a central mechanism in ecology and evolution that has received considerable attention (Gadgil 1971, Johnson & Gaines 1990, Clobert et al. 2001, 2012a; Ronce 2007). It is recognized as being critical to the dynamics of spatially structured populations (Hanski & Gilpin 1991, Thomas & Kunin 1999, Clobert et al. 2009). Dispersal affects demographic interdependence among subpopulations and local population growth (Thomas & Kunin 1999, Lowe & Allendorf 2010, Gilpin 2012). It is also important for the colonization of empty patches, and therefore, plays a central role in colonization-extinction dynamics in heterogeneous landscapes (Hanski & Gilpin 1991, Gilpin 2012). Dispersal also has relevance beyond ecology. Successful reproduction following dispersal results in gene flow between populations (Ronce 2007, Broquet & Petit 2009, Lowe & Allendorf 2010) that can strongly influence adaptive processes (Ronce 2007, Legrand et al. 2017). Through gene flow, dispersal modifies effective population size ( $N_e$ ), regulates the effects of genetic drift and the effectiveness of selection, influencing likelihood and pace of local adaptation (Ronce 2007, Broquet & Petit 2009).

Dispersal can be considered as a three-stage process: emigration (departure), transience (movement in the landscape matrix) and immigration (arrival) (Baguette & Van Dyck 2007, Clobert et al. 2009, Matthysen 2012). The evolution of dispersal is shaped at each of these steps by the balance between the relative costs and benefits associated with going (dispersing) versus staying (not dispersing) (Stamps 2005, Bonte et al. 2012). This cost-benefit balance can be influenced by individual phenotypic variation, resulting in *condition-dependent* dispersal (Clobert et al. 2009). The study of dispersal “syndromes” has revealed complex covariation patterns between dispersal and phenotypic components including morphological, physiological, behavioural and life history traits (Ronce & Clobert 2012, Stevens et al. 2014, Cote et al. 2017a). These associations may lead to multiple dispersal strategies within and between populations and have been reported to have genetic bases (Saastamoinen et al. 2018). The cost-benefit balance of dispersal can be affected by social and environmental variation, resulting in *context-dependent* dispersal (Clobert et al. 2009). Individuals adjust their dispersal “decisions” according to environmental and social cues (i.e., “informed dispersal”, Clobert et al. 2009) that likely reflect an individual’s fitness prospects at a given breeding site. Extrinsic factors such as conspecific and heterospecific density or predation risk can affect emigration and immigration (Bowler & Benton 2005, Matthysen 2012). The reproductive success and body condition of conspecifics can provide “public information” that influences the decision of individuals to disperse or not (Valone & Templeton 2002, Danchin et al. 2004, Blanchet et al. 2010). Furthermore, transience is strongly affected by landscape characteristics such as availability and isolation of breeding sites and permeability to movement (Baguette et al. 2013, Cote et al. 2017).

Dispersal has been studied extensively in vertebrates with relatively simple life cycles, such as viviparous reptiles, birds and mammals (Paradis et al. 1998, Johnson & Gaines 1990, Sutherland et al. 2000, Matthysen 2005, Clutton-Brock & Lukas 2012; Clobert et al. 2012b). In contrast, dispersal has been much less studied in organisms with complex life cycles, such as aquatic invertebrates, fishes and amphibians. Species with complex life cycles are those that exhibit a massive ontogenetic change in morphology, physiology and behaviour (i.e., metamorphosis; Wilbur 1980). In such organisms, dispersal usually occurs after metamorphosis, but conditions before metamorphosis can also affect the costs and benefits of staying versus dispersing. For example, environmental conditions (e.g., water temperature, drought, predation, conspecific density) during larval stages can determine phenotypes at metamorphosis, leading to complex carry-over effects on fitness-related and movement-related traits after metamorphosis (Altwegg & Reyer 2003, Chelgren et al. 2006, Van Allen et al. 2010, Searcy et al. 2014, Ousterhout & Semlitsch 2018), and may therefore have far-reaching consequences for dispersal. This adds complexity to identifying patterns and mechanisms of dispersal compared to taxa with simple life cycles without massive ontogenetic change. Furthermore, predicting dispersal patterns for these organisms based on our knowledge of dispersal in organisms with a simple life cycle is tricky and remains to be tested. Thus, dispersal in animals with complex life-histories offers an intriguing and challenging opportunity to uncover novel aspects of dispersal ecology and evolution in vertebrates.

There are numerous organisms with complex life cycles but pond-breeding amphibians are perhaps the most tractable for the study of dispersal. Most have a biphasic life cycle with aquatic larvae and aquatic and terrestrial juveniles and adults (section II.1). They can be reared easily in the laboratory and used to address questions about dispersal experimentally. In addition, many populations can be surveyed using demographic and genetic tools (Cayuela et al. 2018d), and the genomes of some species are well described (Hellsten et al. 2010, Nowoshilow et al. 2018, Edwards et al. 2018).

Over the two last decades, dispersal in pond-breeding amphibians has received increased attention. Both fundamental and applied studies have been conducted using a broad range of experimental and field approaches. These studies have revealed complex dispersal patterns, causation and syndromes, with important consequences for amphibian population dynamics and genetics. This accumulation of knowledge encouraged us to undertake a general synthesis on the topic, with the following goals: (1) redefine and clarify the concept of amphibian dispersal, (2) review current knowledge about the effects of individual (i.e., condition-dependent dispersal) and environmental (i.e., context-dependent dispersal) factors during the three stages of dispersal (i.e., emigration, immigration, transience), (3) identify the demographic and genetic consequences of dispersal in spatially structured amphibian populations, and (4) identify productive research avenues to extend our understanding of amphibian dispersal based on our updated perspective of the current state of knowledge about dispersal. Finally, we expect that our review will provide a better understanding of dispersal in vertebrates with complex life cycles and will promote additional research on this topic.

## II. DISPERSAL CONCEPT IN POND-BREEDING AMPHIBIANS

### (1) Complex life cycle

The complex life cycle of most amphibians (Wilbur 1980) begins when eggs are laid and fertilized in water – clutch and egg size vary within and among species (Morrison & Hero 2003, Wells 2010). The length of the embryonic and larval stages varies enormously among species, ranging from a few weeks to several years (Wells 2010). There is also variation within species, where speed of development depends on biotic (e.g., density) and abiotic (e.g., temperature) conditions (Section II.4), especially temperature and density. Metamorphosis is a key developmental event that allows the transition from the aquatic to the terrestrial habitat (Wilbur 1980). Size at metamorphosis varies (Werner 1986), depending on environmental conditions experienced as larvae such that age and size at metamorphosis are usually positively correlated (Alford 1999). Typically, the transition is from a fat aquatic tadpole to a spindly terrestrial froglet and involves a trade-off of mass for a change in shape (Alford 1999), and is associated with dramatic physiological changes (Hillman 2009). Importantly, this means that for many species, there is a need for habitat complementation, i.e., they use of non-substitutable resources (water and land) (Dunning et al. 1992, Denoël & Lehmann 2006). After metamorphosis, juveniles grow until they reach sexual maturity. The juvenile stage lasts from one to several years (Wilbur 1980, Werner 1986, Wells 2010). Intraspecifically, the length of the juvenile period depends on age and size at metamorphosis, local density, and environmental factors (Altwegg & Reyer 2003, Schmidt et al. 2012). Adults generally breed each year, but some skip breeding opportunities in one to multiple years (Muths et al. 2006, 2010; Cayuela et al. 2014, Green & Bailey 2015), whereas others may breed twice in a single year (Andreone & Dore 1992). Adult reproductive lifespan varies among species (e.g., 1-2 years in treefrogs and > 10 years in some salamanders, frogs, and toads: Turner 1962).

### (2) Dispersal concept

We define dispersal as the movement of an individual from its natal patch to its first breeding patch (i.e., natal dispersal) or the movement between two successive breeding patches (i.e., breeding dispersal), possibly resulting in gene flow (Ronce 2007, Clobert et al. 2009, Matthysen 2012). By “breeding patches”, we refer specifically to a waterbody (e.g., puddle, pond, swamp or lake) or a group of waterbodies that are physically and functionally dependent (e.g., partially connected with each other during a certain period of the year) and where breeding activity takes place. Therefore, we only consider terrestrial dispersal events. Dispersal is usually thought of as directed movements by juveniles or adults towards new breeding patches (Van Dyck & Baguette 2005). Dispersal movements differ from other movements that satisfy basic requirements for food (i.e., foraging) or shelter (e.g., overwintering sites);

these migratory movements are typically annual, two-way (out and back) movements of individuals between breeding patches and terrestrial habitats where feeding, estivation and/or overwintering take place (Sinsch 1990, Semlitsch 2008). There is a great confusion in the amphibian literature about the meaning of dispersal and migration, with terms used interchangeably (Semlitsch 2008). While as defined, dispersal and migratory are different, there are instances where dispersal events may result from navigational errors during migratory movements (Cote et al. 2017b).

### **(3) Natal and breeding dispersal**

A distinction between natal dispersal (movement between the completion of metamorphosis and first reproduction, Smith & Green 2005, Semlitsch 2008; Pittman et al. 2014) and breeding dispersal (movement after first reproduction) is important because the proximate and ultimate drivers of dispersal differ before and after first reproduction (Bowler & Benton 2005). In most species, juveniles display a fully terrestrial lifestyle in areas that can be either close to the breeding patch, or far - up to kilometers away (Pittman et al. 2014). The juveniles of some species can also occupy nutrient-rich waterbodies where no reproduction is recorded (Cayuela et al. 2017a). After the juvenile stage, first-time breeders can either return to breed at their natal patch (i.e., residents or philopatric individuals) or can breed in a different breeding patch (i.e., dispersers). Breeding dispersal can occur any time after first reproduction. Reproducing year after year in the same breeding patch is sometimes referred as “site fidelity” (Sinsch 2014). In species with a prolonged reproductive season, multiple breeding attempts can take place within a single year, whereas other species breed no more than once per year. Therefore, breeding dispersal can be measured intra-annually and/or inter-annually (e.g., Cayuela et al. 2016a, Denoël et al. 2018).

### **(4) Drivers of dispersal decision and pond selection**

Ponds have abiotic (e.g., hydroperiod, temperature) and biotic (e.g., intra- and interspecific competition, predation) characteristics that affect offspring development and survival before metamorphosis (see section II.5). Furthermore, ponds host groups of breeders whose size and attributes (i.e., relatedness level, inter-individual heterogeneity in reproductive output) vary over space and time (Sánchez-Montes et al. 2017, Cayuela et al. 2017b). The size of the pond, its isolation, and the level of individuals’ philopatry modulate the risks of kin competition and inbreeding (Ronce 2007, Broquet & Petit 2009, Lowe & Allenford 2010). Dispersal framework states that environmental and social factors may affect natal and breeding emigration (Bowler & Benton 2005, Matthysen 2012). Furthermore, it is expected that these determinants should influence habitat selection during immigration (Stamps 2001, Davis & Stamps 2004, Stamps et al. 2009). Pond selection experiments have shown that amphibian breeders select spawning sites according to several factors including predation risk, and intra- and interspecific competition risk (reviewed in Buxton & Sperry 2016). Although these experiments are highly



informative, they do not document the decision making and the costs (time, energy, and mortality) associated with the different steps in the dispersal process. In section III, we report social and environmental factors affecting emigration and immigration.

### **(5) Maternal and environmental carry-over effects on dispersal-related traits**

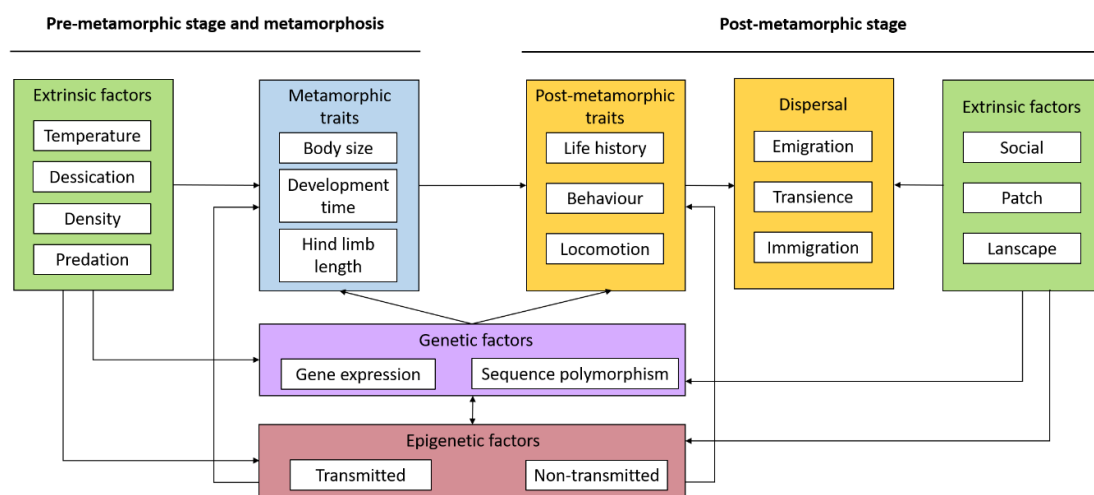
Environmental and maternal effects can affect dispersal by altering individual phenotype (Fig. 1 and Fig. 2). In particular, environmental conditions experienced by embryos and larvae prior to metamorphosis can affect post-metamorphic phenotype, performance, and fitness, which in turn can affect dispersal. Adaptive phenotypic plasticity allows amphibians to accommodate environmental variability during their aquatic stage (Newman 1992, Merilä et al. 2004). Environmental “carry-over” effects can represent a cost of this adaptive plasticity (Richter-Boix et al. 2011a, Ruthsatz et al. 2018). Moreover, maternal effects can also represent a cost to post-metamorphic phenotype and fitness (Laugen et al. 2005, Pruvost et al. 2015). An increasing number of studies show that environmental and maternal carry-over effects may be important drivers of amphibian dispersal evolution.

Larval growth and development rate determine the age and size at metamorphosis (Wilbur 1980, Werner 1986, Alford 1999). Growth and development have heritable bases (Laugen et al. 2005, Lesbarrères et al. 2007), may differ among populations (Laugen et al. 2005, Räsänen et al. 2005), and can be subject to local adaptation (Lind et al. 2008). They are also influenced by maternal effects, especially maternal investment in egg size (Laugen et al. 2005, Räsänen et al. 2005, Dziminski & Roberts 2006, Kaplan & Phillips 2006). Large eggs usually result in higher larval developmental rate and larger size at metamorphosis compared to smaller eggs (Kaplan 1980, Räsänen et al. 2005, Dziminski & Roberts 2006). Additionally, the traits mentioned above are highly sensitive to environmental variation. Hence, genotype–environment ( $G \times E$ ) and maternal effect–environment ( $M \times E$ ) interactions have been observed in multiple species (Laugen et al. 2005, Pruvost et al. 2015, Moore et al. 2015). The environmental factors that affect larval and metamorphic traits include, but are not restricted to, hydroperiod (Márquez-García et al. 2009, Richter-Boix et al. 2011a, Amburgey et al. 2012), water temperature (reviewed in Ruthsatz et al. 2018), conspecific density (Wilbur 1976, Van Buskirk & Smith 1991), parasitism (Goater et al. 1993), and predation (Laurila et al. 2004, Vonesh & Warkentin 2006).

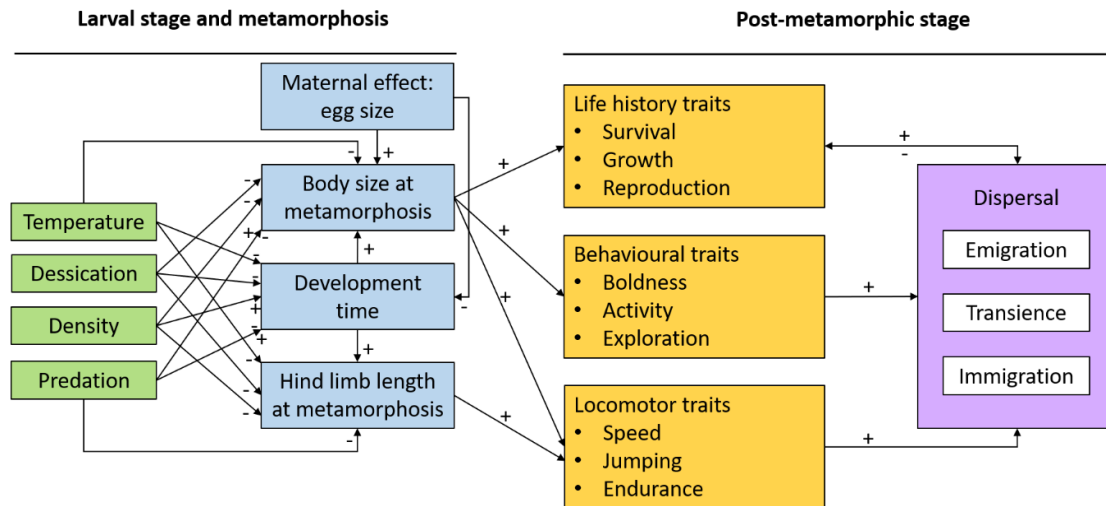
We summarize different factors that are known to affect traits of larval and metamorphic stages and how these effects are carried over to affect dispersal-related processes (Fig. 2). Individual phenotype at metamorphosis has a strong effect on fitness-related traits at the juvenile stage (i.e., survival and growth; Scott 1994, Altwegg & Reyer 2003, Chelgren et al. 2006, Searcy et al. 2014) and on attributes related to natal dispersal (and likely breeding dispersal). Body size at metamorphosis is often positively correlated with dispersal-enhancing behavioural traits (Cote et al. 2010, Ronce & Clobert 2012) such as boldness, activity level and exploration propensity of juveniles (reviewed by Kelleher et al. 2018). In



addition, body size at metamorphosis is positively associated with locomotor traits of juveniles such as jumping distance (Tejedo et al. 2000, Ficetola & De Bernardi 2006, Boes & Benard 2013, Cabrera-Guzmán et al. 2013), speed (Beck & Congdon 2000, Choi et al. 2003), and endurance (Beck & Congdon 2000, Yagi & Green 2017). Independently of body size, parasite load can reduce endurance (Goater et al. 1993). Furthermore, body condition and fat reserve positively influence jumping performance (Drakulić et al. 2016, but see Nicieza et al. 2006). Moreover, longer hindlimbs – corrected for body size – often improve jumping and climbing performances (Choi et al. 2003, Hudson et al. 2016c). Larger body size, longer hindlimb, and higher body condition are therefore expected to enhance emigration propensity and locomotor capacities during transience (see section III).



**Figure 1.** Conceptual framework to show how extrinsic factors (i.e., environmental and social variables) and molecular factors (genetic and epigenetic variation) may affect pre- and post-metamorphic traits and dispersal in pond-breeding amphibians. Extrinsic factors affect larval development and metamorphic traits, which then influence post-metamorphic traits including life history (survival, growth and reproduction), behavioural (boldness, activity, and exploration propensity) and locomotor traits (speed, jumping and endurance). Post-metamorphic traits and extrinsic factors (social context in the breeding patch, abiotic and biotic characteristics of the patch, and landscape variables) may affect the three stages of the dispersal process. Genetic factors including gene expression and sequence polymorphism influence individual phenotype before and after metamorphosis and may therefore affect dispersal (Saastamoinen et al. 2018). Phenotypic plasticity may entail gene expression variation before and after metamorphosis in response to environmental variation (Gilbert et al. 2015). Variation in gene variant frequency may also arise through selection in response to environmental factors. Epigenetic factors (e.g., DNA methylation, micro-RNA profiles, and histone structure) may also affect pre-metamorphic and post-metamorphic phenotype in a way that could affect each stage of the dispersal process (Saastamoinen et al. 2018). Epigenetic factors may affect gene expression (Gibney & Nolan 2010) and sequence polymorphism by affecting mutation rate and transposon reactivation (Fedoroff 2012, Tomkova & Schuster-Böckler 2018). Epigenetic variation may be induced randomly or by environmental factors before and after metamorphosis and can be potentially transmitted to the next generation or not (Verhoeven et al. 2016).



**Figure 2.** Conceptual framework showing carry-over effects (positive ‘+’ or negative ‘-’) of environmental conditions during larval growth on fitness-related traits, behavioural traits and locomotor traits. Breeding site characteristics including water temperature, desiccation risk, conspecific density, and predation negatively or positively affect larval development time, body size at metamorphosis and hind limb length at metamorphosis. Maternal investment in egg size also affects body size at metamorphosis. Body size and hind limb length at metamorphosis are positively correlated with development time. Body size at metamorphosis potentially has positive effects on post-metamorphic fitness related-traits including survival, growth, and reproduction-related traits (age and body size at sexual maturity). Body size at metamorphosis is also has a positive influence on behavioural traits as boldness, activity level, and exploration propensity. In addition, it positively affects locomotor traits including speed, jumping, and endurance. Moreover, hind limb length has a positive influence on speed and jumping. Life history traits may be negatively (trade-off) or positively (mutual reinforcement, pleiotropic effect) correlated with dispersal (e.g., emigration rate, dispersal distance during transience or immigration success). Behavioural traits as boldness, activity level and exploration are expected to facilitate emigration and transience. Locomotor traits as speed, jumping, and endurance should facilitate transience.

### III ECOLOGICAL CORRELATES OF DISPERSAL

#### (1) Emigration and immigration

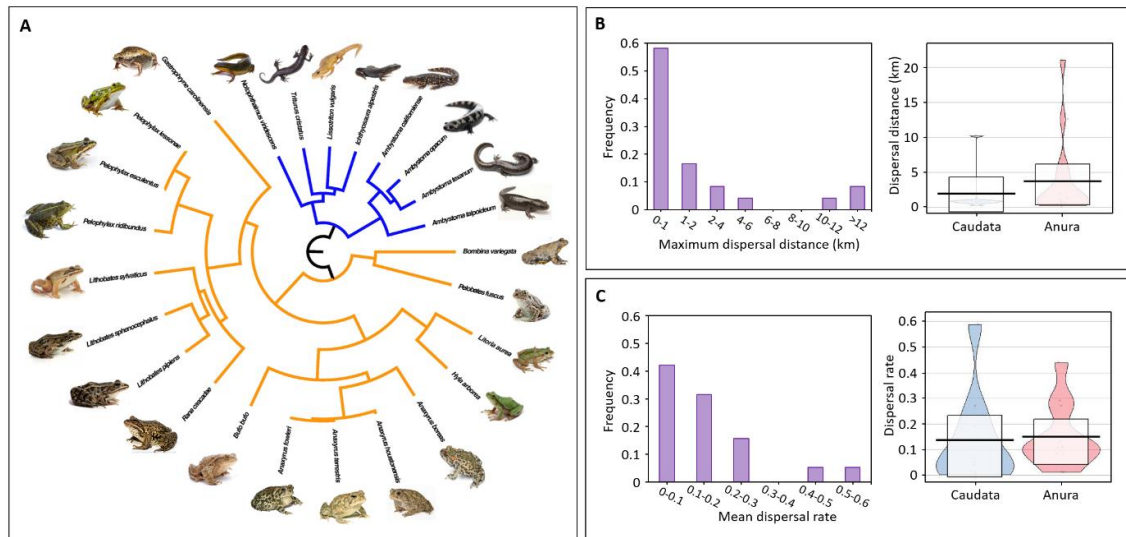
Emigration and immigration are closely associated with breeding habitat selection (Stamps 2001, Davis & Stamps 2004) and depend on a complex interplay among individual phenotype and habitat characteristics. Individuals adjust their emigration and immigration decisions according to local fitness prospects (Clobert et al. 2009). In this section we focus on the intraspecific and interspecific variation in emigration rates (often defined as “dispersal rates”). Additionally, we review correlations among emigration and immigration and phenotypic traits, life history traits, and environmental factors.

### (a) Emigration rates

Emigration rates (usually expressed on an annual scale) can be estimated directly when individuals in a spatially structured population are captured and marked (or recognized using natural marks) and then recaptured on successive occasions at multiple breeding patches. Yet, these data are scarce for amphibians. We found only 22 studies (Appendix A) on 18 species (41% urodeles (*Ambystomatidae* and *Salamandridae*) and 59% anurans (*Bombinatoridae*, *Bufo* spp., *Hylidae*, *Pelobatidae* and *Ranidae*) that reported emigration rates, all published between 1978-2018. Most species (16 of 18) are represented by a single study. Emigration rate (estimates of natal and breeding dispersal were pooled together if available in the species) among the 18 species of pond-breeding amphibians was, on average,  $15 \pm 15\%$ . Anuran and urodele species showed relatively similar dispersal rates (mean =  $16 \pm 14$  and  $13 \pm 16\%$  respectively; Fig.3a). Maximum dispersal distance did not statistically differ between anuran and urodele species (linear models with *F*-test anova,  $F_{1,22} = 2.06$ ,  $p = 0.16$ ; Fig.3b). Twenty seven percent of the studies ( $n = 6$ ) evaluated natal and breeding dispersal rates separately, 4% ( $n = 1$ ) studied only natal dispersal, 54% ( $n = 12$ ) studied only breeding dispersal and 14% ( $n = 3$ ) did not specify if rates correspond to natal or breeding dispersal (Appendix A, Table 1).

*Interspecific variation* – There was a high interspecific variability in emigration rates, ranging from species where it was virtually zero (e.g., Gill 1978) to others where it was as high as 44% (e.g., Hamer et al. 2008). Emigration rates are highly variable among different species, even among species that are closely-related phylogenetically. (Fig.3a). In ambystomatid salamanders, emigration rates were variable, with most <6% (Gamble et al. 2007, Pechmann et al. 2001, Denton et al. 2017) although 26% was reported in *Ambystoma californiense* (Trenham 2001). In Ranid frogs ( $n = 4$ ) emigration was on average 17% but ranged from 9 to 30% (Berven & Grudzzien 1990, Garwood 2009; Fig.3a and Appendix A). There was also a large degree of variation for Hylid frogs (Fig.3a and Appendix A).

*Intraspecific variation* – Similar to the variation reported in emigration rates among species, variation also exists in emigration rates within species. Several examples suggest that variation is not unusual among populations of the same species. Marked differences were reported among populations of *Bombina variegata*, with natal and breeding emigration rates at 10-20% in several populations versus <1% in others (Cayuela et al. 2016a). In *Triturus cristatus*, breeding dispersal rates varied from virtually zero (Kupfer & Kneitz 2000, Unglaub et al. 2015) to 19% in some populations (Cayuela et al. 2018e) compared to rates as high as 59% in other populations (Denoël et al. 2018). Additionally, inter-individual heterogeneity in emigration rates within the same population are common in pond-breeding amphibians (section III.1.c).



**Figure 3.** Dispersal distances and rates in amphibians. (A) Phylogenetic tree showing the 25 species for which we report dispersal distances and rates. (B) Maximum dispersal distance: on the right, distribution of maximum dispersal distances in Caudata and Anura combined; on the left, maximum dispersal distance in Anura and Caudata separately. (C) Mean dispersal rates: on the right, distribution of mean dispersal rates in Anura and Caudata combined; on the left, mean dispersal rates in Anura and Caudata separately.

#### (b) Phenotype-dependent emigration

**Age** – Information on age-dependent emigration in pond-breeding amphibians is limited, mainly because juveniles are difficult to track and to tag (but see Sinsch 1997, Cayuela et al. 2018c). It has been postulated that natal dispersal represents a higher proportion of total dispersal than does breeding dispersal (Semlitsch 2008, Pittman et al. 2014) but empirical evidence suggests that this is not always the case. Although natal dispersal was higher than breeding dispersal in many studies (Schroeder 1976, Berven & Grudzien 1990, Sjögren-Gulve 1998; Garwood 2009), other studies report similar rates of natal and breeding dispersal (Vos et al. 2000, Hohenweg Peter 2001, Reading et al. 1991, Trenham et al. 2001, Smith & Green 2006, Gamble et al. 2007, Cayuela et al. 2018b). This variation in the proportion of overall dispersal represented by different stages of dispersal may be context dependent (Cayuela et al. 2018c). For instance, in several populations of *Bombina variegata* natal dispersal rates were similar to breeding dispersal rates (ranging from 10 to 20%), contrasting with other populations where natal dispersal was virtually zero and breeding dispersal was rare (Cayuela et al. 2018c).

**Body size** – Body size influences both natal and breeding emigration. This is likely underpinned by the effect of body size on behavioural and physiological mechanisms (see below). For instance, body mass and length are positively correlated with dispersal-related behavioural traits such as boldness, activity level, and exploration propensity in both juvenile and adult amphibians (Kelleher et al. 2018).

Additionally, larger individuals are expected to have a higher emigration propensity due to a reduction in the cost of movement due to enhanced locomotor capacity and reduced surface-to-volume ratio decreasing desiccation risk (Newman & Dunham 1994, Child et al. 2008a,b; Hillman 2009, Bartelt et al. 2010). Chelgren et al. (2006) showed that natal emigration rates increased with body size at metamorphosis in *Rana aurora*. A similar pattern was reported in *Ambystoma annulatum* (Ousterhout & Semlitsch 2018). Moreover, Denoël et al. (2018) found that the probability of breeding emigration was comparatively higher in larger *Triturus cristatus* adults. In contrast, Bucciarelli et al. (2016) found that smaller adults of *Taricha torosa* had higher emigration probabilities.

**Body shape** – Dispersal rate may be facilitated by specific morphologies as well as by absolute body size. In the cane toad *Rhinella marina*, individuals from invasion-front populations (where dispersal rates are several-fold higher than in range-core populations) exhibit markedly different morphologies. The highly dispersive phenotype is more gracile, with longer arms and shorter legs, and may disperse by bounding rather than leaping (Hudson et al. 2016a,b,c). Perhaps as a correlated response to shifts in dispersal-related traits, toads from dispersive *versus* sedentary populations also differ in traits such as relative head width as well as other body dimensions (Hudson et al. 2016b, 2018). Some of these interpopulation divergences are heritable whereas others are influenced by developmental conditions (Stuart et al. 2018).

**Sex** – Sex-biased dispersal evolution is related to mating systems in vertebrates (Trochet et al. 2016): polygynic mating systems coupled with active mate searching often result in male-biased dispersal whereas high male territoriality usually leads to female-biased dispersal. In amphibians, sex-biased dispersal has been documented in 18 studies (12 anuran and four urodele species, Table 1) using either demographic or molecular approaches. Note that the latter cannot disentangle the relative contribution of emigration, transience and post-immigration reproductive success to variation in sex-biased dispersal rates. By definition, gene flow results from dispersal events that are followed by a successful reproduction (“effective” dispersal, Broquet & Petit 2009, Lowe & Allendorf 2010, Cayuela et al. 2018d). If we exclude the capture-recapture study that focuses only on transience (Smith and Green 2006, Table 1), 10 studies (59%) report sex-biased dispersal. Among them, three report male-biased dispersal (30%) whereas seven (70%) report female-biased dispersal. Female-biased dispersal seems more common, possibly because lek-like systems with relatively high male territoriality in ponds are widespread, especially in anurans (e.g., many species in the *Hylidae* and *Ranidae* families). Interestingly, seven studies (41%) failed to detect any sex effect. This may arise because environmental and social variation influence emigration decisions of both sexes in a similar way. Indeed, one can expect that both sexes respond similarly to intrinsic factors that dramatically affect offspring phenotype and fitness (e.g., conspecific density and breeding site stochasticity, section III.1.c). Furthermore, sex-bias in emigration rates varies among populations of the same species. For instance, in *Triturus cristatus*, Denoël et al. (2018) reported higher emigration rates in males than females while Cayuela et al. (2018e) found the opposite pattern in another population of the same newts. In this case, habitats differed

significantly (e.g., pond size and width) suggesting that population-specific variation in environmental factors may have facilitated different emigration decisions in these two populations. Other factors such as mating tactics may play a similar role.

**Table 1.** Sex-dependent dispersal in pond-breeding amphibians. We reported the conclusions of 18 studies that have examined sex-biased dispersal in 16 species of pond-breeding amphibians (12 anurans and 4 urodeles) using capture-recapture or genetic methods. For capture-recapture studies, the effect of sex has been assessed on emigration and/or transience (i.e., dispersal distance). For genetic studies, the dispersal step is unknown as genetic differentiation can be affected by sex-specific emigrate rate, sex-specific dispersal distances, and sex-specific dispersal costs (i.e., mortality or reproductive costs paid by the dispersers after immigration).

Species	Dispersal step	Bias	Method	Reference
<i>Physalaemus pustulosus</i>	Unknown	Male-biased	Genetic	Lampert et al. 2013
<i>Triturus cristatus</i>	Emigration	Male-biased	Capture-recapture	Denoël et al. 2018
<i>Triturus cristatus</i>	Emigration	Female-biased	Capture-recapture	Cayuela et al. 2018a
<i>Bombina variegata</i>	Emigration	Female-biased	Capture-recapture	Cayuela et al. 2018e
<i>Rana temporaria</i>	Unknown	Female-biased	Genetic	Palo et al. 2004
<i>Epidalea calamita</i>	Emigration	Female-biased	Capture-recapture	Sinsch 1992
<i>Lithobates catesbeianus</i>	Unknown	Female-biased	Genetic	Austin et al. 2003
<i>Odorrana schmackeri</i>	Unknown	Female-biased	Genetic	Wang et al. 2012
<i>Anaxyrus fowleri</i>	Transience	No	Capture-recapture	Smith & Green 2006
<i>Lithobates sylvaticus</i>	Unknown	No	Genetic	Berven & Grudzien 1990
<i>Amystoma californiense</i>	Emigration and transience	No	Capture-recapture	Trenham et al. 2001
<i>Ambystoma opacum</i>	Emigration and transience	No	Capture-recapture	Gamble et al. 2007
<i>Rana arvalis</i>	Unknown	No	Genetic	Knopp & Merilä 2009
<i>Ichthyosaura alpestris</i>	Emigration	No	Capture-recapture	Kopecký et al. 2010
<i>Ichthyosaura alpestris</i>	Emigration	No	Capture-recapture	Perret et al. 2003
<i>Hyla arborea</i>	Emigration	Male-biased	Capture-recapture	Vos et al. 2000
<i>Rana cascadae</i>	Emigration and transience	Female-biased	Capture-recapture	Garwood 2009
<i>Rana muscosa</i>	Emigration	No	Capture-recapture	Matthews & Preisler 2010

**Behavioural traits** – Although amphibian behavioural syndromes have received significant attention (Kelleher et al. 2018), associations between behavioural traits and emigration rates have been investigated only recently. An unusually well-documented case study is that of the invasive toad *Rhinella marina* in Australia. In this system, range expansion evolves through a combination of spatial sorting and natural selection (Phillips et al. 2008, Phillips et al. 2010, Shine et al. 2011, Pizzatto et al.



2017). Fast-dispersing individuals are found at the colonization front and breed with each other because individuals that disperse slowly and non-directionally have been left behind. This produces offspring with extremely high values for dispersal-enhancing traits (morphology and behaviour), higher than in the parental generation. The co-occurrence of such traits accelerates the evolution of emigration rates (and dispersal distances) through successive generations. Gruber et al. (2017a,c) highlighted a divergence in behavioural phenotypes between range-front and range-core populations. Juveniles from range-front populations reared in the laboratory displayed a higher propensity for exploration and risk-taking than juveniles from range-core populations. In another study, Gruber et al. (2017b) found that range-front juveniles also approached conspecifics more often, and spent more time close to them compared to range-core ones, suggesting that emigration propensity may covary with social behaviour. Antipredator responses differ between dispersive and sedentary populations of cane toads also (Hudson et al. 2017). A second empirical case study focuses on *Bombina variegata*. In this species, the spatially structured populations occur in two environments: (1) river environments where the breeding habitat is predictable, i.e., constant availability of breeding patches in space and time; and (2) forest environments where breeding habitat is unpredictable. Cayuela et al. (2016a) found that natal and breeding emigration rates were 10-20 times higher in populations breeding in unpredictable patches compared to those breeding in predictable patches. This differentiation in emigration rate is associated with divergent behavioural phenotypes in toads reared under controlled laboratory conditions (Cayuela et al. 2018c). Juveniles from populations breeding in unpredictable patches displayed a higher exploration propensity than those from populations breeding in predictable patches.

*Physiological traits* – There is evidence for an association between emigration rates and physiological traits in other vertebrates (Matthysen 2012, Ronce & Clobert 2012) but amphibian studies addressing this association are scarce. Studies of the invasive toad *Rhinella marina* in Australia offer the only empirical data. In the laboratory, Llewellyn et al. (2012) reported reduced investment in energetically costly immune functions in toads from range-front populations (where emigration rates are highest) relative to toads from range-core populations. In a second study Brown et al. (2015) examined differences in physiology between the offspring of range front and range core toads and found that while immune and stress responses did not differ, juveniles of range-front populations had more neutrophils in their blood, and were more effective at phagocytosis (i.e., killing bacteria) than range-core juveniles. Consistent with the penetration of invasive cane toads into thermally severe environments in Australia, the thermal dependency of locomotor ability differs among individuals from dispersive versus sedentary populations and is a heritable trait (Kosmala et al. 2017, 2018).

*Chemical traits* – Amphibians have skin secretions that protect them against pathogenic microorganisms and predators (Rollins-Smith et al. 2005, Xu & Lai 2015). Skin chemical cues also used by amphibians to recognize their kin and select their mates (Blaustein & Waldman 1992, Pfennig 1997). Several newt species as *Taricha torosa* possess a neurotoxin, tetrodotoxin that may act as a feeding stimulant, sexual attractant, or antipredator chemical cue (Bucciarelli et al. 2016). Bucciarelli et al.



(2016) found that adult males of *Taricha torosa* with a lower concentration of tetrodotoxin have a higher emigration probability and explained this pattern through mate selection: non-dispersing males with an increased tetrodotoxin concentration have greater defences, but also greater appeal to mates.

*Life history traits* – Association between emigration rates and life history traits have been assessed in recent studies in both anurans and urodeles. Two studies showed the existence of a dispersal syndrome implicating an association between high emigration rates and faster life histories (Philipps et al. 2009, Cayuela et al. 2016a), while a third study reported opposite patterns (Denoël et al. 2018). Phillips (2009) showed that both tadpole and juvenile *Rhinella marina* from range-front populations grow ~ 30% faster than those from range-core populations. A low conspecific density in the range-front populations results in lower larval competition and drives natural selection to favour increased reproductive rate. In follow-up work, Ducatez et al. (2016) reported that the difference in developmental rates was highly sensitive to conspecific densities; tadpoles from highly dispersive (invasion-front) populations were less capable of dealing with conditions of intense competition. Additional evidence comes from a study of *Bombina variegata*. Cayuela et al. (2016b) showed that the unpredictability of breeding patches affected both emigration propensity and life history strategies. In populations breeding in unpredictable patches, individuals had lower age-dependent post-metamorphic survival rates and higher realized fecundity than did those breeding in predictable patches. This life history shift was associated with higher natal and breeding emigration rates in populations breeding in unpredictable patches (Cayuela et al. 2016a, Cayuela et al. 2018c). A third empirical example reports the coexistence of two alternative dispersal strategies in the same population of a urodele (*Triturus cristatus*) ~ 30% of the population of breeding adults were strictly philopatric whereas 70% emigrated at least once during their lifetime. Dispersing individuals had on average higher survival and a larger body size (Denoël et al. 2018)

### (c) Context-dependent emigration and immigration

*Patch size and conspecific density* – Correlations between emigration and immigration and breeding patch size have been reported in anurans and urodeles. In *Bombina variegata*, Boualit et al. (2018) showed that adults were less likely to emigrate from large patches, where the breeding success was highest, than from small patches where breeding success was lower. Similarly, the probability of immigration was higher at large patches than at small ones. In *Triturus cristatus*, Denoël et al. (2018) found that dispersing adults occurred on average more often in large ponds that were less likely to dry up and that had a larger number of potential sexual partners. Conspecific density also influences emigration and immigration rates. In *Ambystoma opacum*, Gamble et al. (2007) found that emigration probability of all breeders (first-time and experienced) was higher in ponds with small breeding populations. Cayuela et al. (2018e) highlighted a similar pattern in *Triturus cristatus* using an experimental pond network. They showed that breeding emigration rate was lower in ponds with a high density of conspecifics compared to low-density ponds. Similarly, the probability of immigration was

higher at high-density ponds than at low-density ponds. Research on *Litoria aurea* showed experimentally that playback of male advertisement calls attracted additional male frogs to specific breeding sites (James et al. 2015). These studies suggest that breeders avoid ponds with very low conspecific density and that conspecific density plays an underappreciated role in emigration and immigration decisions.

*Predation and interspecific interaction* – Predation and interspecific interactions have a strong influence on breeding pond choice in amphibians (Buxton & Sperry 2016). Experimental studies report that amphibians usually avoid reproducing in waterbodies where predation risk and interspecific competition are high (Buxton & Sperry 2016). Winandy et al. (2017) also showed experimentally that predation risk induced breeding dispersal in *Ichthyosaura alpestris*. In contrast, few studies found similar effects of predation on emigration and immigration probabilities in free-ranging populations. Concerning predation, most evidence is indirect (Gamradt et al. 1997, Pope 2008, Cosentino et al. 2011a). For instance, Pope (2008) found that local adult recruitment – including natality and immigration – in *Rana cascadae* increased immediately after fish were removed from breeding ponds. Concerning interspecific competition, Cayuela et al. (2018f) found that adult *Triturus cristatus* were less likely to emigrate from ponds with high densities of other newts (*Ichthyosaura alpestris* and *Lissotriton vulgaris*) compared to ponds with low densities of those species. Similarly, immigration probability was higher into ponds with high densities of heterospecifics. These studies suggest that heterospecific densities are used by amphibians as public information (Valone & Templeton 2002, Blanchet et al. 2010) to locate, select and/or rank their breeding ponds with high and low habitat suitability. This interpretation is in accordance with three experimental studies showing that newts can use heterospecific cues (e.g., anuran vocalization) to locate and select breeding sites (Diego-Rasilla & Luengo 2004, Pupin et al. 2007, Madden & Jehle 2017).

*Breeding site hydroperiod and interannual persistence* – Hydroperiod and interannual persistence of breeding patches influence emigration rates. In species reproducing in sites with variable hydroperiods (i.e., frequent pond drying), breeders adjust their emigration and immigration decisions according to associated risks and reproductive opportunities (Hamer et al. 2008, Measey 2016, Tournier et al. 2017). For example, breeding *Bombina variegata* are less likely to emigrate from ponds with a long hydroperiod, where reproductive success is high and constant (Tournier et al. 2017); in the extreme case, dispersal is obligatory when a site dries entirely if animals are to breed (Cayuela et al. 2018g). Dispersal plays a critical role in amphibian reproduction in ephemeral breeding patches. Molecular studies suggest that ephemerality of breeding patches results in high emigration rates in desert amphibians, compared to species in temperate environments (Chan & Zamudio 2009, Mims et al. 2015). This effect of pond ephemerality on emigration have been also observed at the intraspecific level. In *B. variegata*, the annual turn-over rate was 20% to 30% in ephemeral breeding patches (a group of tire ruts created by logging activities in forest environments) compared to a zero turn-over rate (no gain and no loss) in permanent breeding patches (groups of rock pools in a riverine environments) (Cayuela et al.

2016a, 2018c). Further, breeding emigration rate in the environments with no turnover in breeding sites was very low (0.01-0.02) and natal emigration was absent (Cayuela et al. 2016a, 2018c). In contrast, both natal and breeding emigration rates were much higher (0.10-0.20) in the environment where turnover occurred. Breeding emigration probability remained high ( $> 0.10$ ) even when the breeding site remained available from one year to another (Cayuela et al. 2018a). Nevertheless, perturbation of breeding patches may not always be detrimental to or encourage emigration. Boualit et al. (2018) found that the presence of log skidders limited natural silting in of ruts so that hydroperiod was longer, breeding success increased, and adults were less likely to emigrate compared to similar habitats without skidder disturbance.

## (2) Transience in the landscape matrix

Transience is considered the costliest step in the dispersal process (Bonte et al. 2012). In homogeneous landscapes, the cost incurred is proportional to the distance travelled, which in turn depends on three parameters: the proportion of time dedicated to dispersing, the rate at which the movement occurs, and the directionality of the movement (Fahrig 2007, Barton et al. 2009). These three parameters are influenced by a combination of morphological, behavioural and physiological factors which all affect both the cost-benefit balance of dispersal and the evolution of dispersal distance (Palmer et al. 2011, Bonte et al. 2012). In heterogeneous landscapes, the cost of transience also depends on the landscape's permeability to movement (Palmer et al. 2011). Physical barriers can impede animal movements across a landscape (Baguette et al. 2013, Cote et al. 2017a). Landscape elements exist along a continuum from mountain ranges and rivers to different substrates or vegetation each with their own level of resistance and related cost to the animal to navigate. Next, we review the effects of individual and landscape factors on dispersal distances in spatially structured populations of amphibians.

### (a) Transience and dispersal distances

We constrained our review to include studies that reported movement distances most likely to represent true dispersal distances and not those associated with foraging or migratory movement. We found 24 published studies (Appendix A) focusing on 25 species (25% urodeles and 75% anurans; Fig.3b). Most studies (21 of 24) reported data for a single species. We found maximum dispersal distance (pooling estimates of natal and breeding dispersal) was, on average,  $3,698 \pm 6,256$  m. The maximum dispersal distance was higher in anurans ( $4,506 \pm 7,269$  m) than urodeles ( $2,212 \pm 3,845$  m). However, maximum dispersal distance did not statistically differ between anuran and urodele species (linear models with  $F$ -test anova,  $F_{1,22} = 0.02$ ,  $p = 0.88$ ; Fig.3b).

*Interspecific variation* – Maximum dispersal distances exhibited high interspecific variability within both anurans and urodeles (and also within families; Fig.3b), a variability that was slightly higher

in anurans than in urodeles (Fig.3b and Fig.3c). Both urodeles (*Ambystoma texanum*) and anurans (*Anaxyrus fowleri* and *Hyla arborea*) can show high vagility, with maximum dispersal distances > 10 km. Extraordinarily large dispersal distances (>30 km in some species) have also been observed in bufonids (Freeland & Martin 1985, Easteal & Floyd 1986, Smith & Green 2005, 2006). Two studies that compared differences between species suggested that dispersal distances increased with body mass (Pabijan et al. 2012, Hillman et al. 2013), likely due to higher locomotor performances of larger species (Choi et al. 2003). Hillman et al. (2013) further proposed that dispersal distance is related to the species' "physiological vagility", a composite metric that incorporates a suite of both anatomic and physiological variables involved in locomotion, including body mass, aerobic capacity, body temperature, and the metabolic cost of transport.

*Intraspecific variation* – Studies have reported among-population variation in amphibian dispersal distances in *Anaxyrus fowleri* (Breden 1987, Smith and Green 2006) and *Notophthalmus viridescens* (Gill 1978, Pechmann et al. 2001). Within spatially structured populations, several studies have also reported that the distribution of natal and breeding dispersal distances (a.k.a. dispersal kernel) is often highly leptokurtic and right-skewed (Breden 1987, Berven & Grudzien 1990, Holenweg Peter 2001, Trenham et al. 2001, Gamble et al. 2007, Hendrix et al. 2017, Cayuela et al. 2018c). This may indicate a polymorphism for dispersal distance, with a small proportion of individuals performing infrequent long-distance dispersal events (Nathan et al. 2012). There is also among-population variation in natal and breeding dispersal distance. In *Bombina variegata*, Cayuela et al. (2018c) showed that populations reproducing in unpredictable habitat displayed dispersal kernels that were more leptokurtic and more right-skewed than populations breeding in predictable habitats. Extensive research on the invasive toad *Rhinella marina* in Australia has revealed large interpopulation variation in rates of dispersal, with concomitant shifts in morphology, physiology, behaviour and life-history traits (reviewed above).

*Dispersal distance variation related to breeding behaviour* – A recent study provides valuable insight about the consequences of pond-breeding behaviour on dispersal distances in a population of *Salamandra salamandra* (Hendrix et al. 2017). This European urodele species can use both permanent streams and temporary ponds for breeding. Interestingly, pond-adapted individuals in this population show a higher vagility than their stream-adapted counterparts, with pond-adapted individuals dispersing further. This evidence suggests that the stability of the breeding habitat may cue an intraspecific differentiation in dispersal distance.

#### (b) Phenotype-dependent transience

*Age* – The age of individuals (that positively covaries with body size) can affect dispersal distances. Several studies report that juveniles disperse further than adults in anurans (*Anaxyrus fowleri*, Breden 1987; *Rana luteiventris*, Funk et al. 2005; *Bombina variegata*, Cayuela et al. 2018b) and urodeles

(*Ambystoma opacum*, Gamble et al. 2007), although other studies did not (*Bufo bufo*, Reading et al. 1991; *Anaxyrus fowleri*, Smith & Green 2006; *Ambystoma californiense*, Trenham et al. 2001; *Bombina variegata*, Cayuela et al. 2018c). In a population of *Bombina variegata*, for instance, a recent study revealed a progressive decrease in kernel leptokurtism over toads' ontogenesis, suggesting a progressive behavioural shift arising over the three years preceding sexual maturity (Cayuela et al. 2018b). This shift might result from a change in the ultimate factors (or benefits) driving dispersal rates and distances (Bitume et al. 2013). Before first reproduction, dispersal might be driven by the avoidance of kin competition and/or inbreeding depression, while after first reproduction it might result from spatiotemporal variability of the breeding habitat (Bowler & Benton 2005). However, the form of the dispersal kernels before and after sexual maturity may also be context-dependent and may vary among populations (e.g., *Anaxyrus fowleri*, Breden 1987 and Smith & Green 2006; *Bombina variegata*, Cayuela et al. 2018c).

**Body size** – A large body size increases absolute locomotor capacities (i.e., absolute jumping performance and endurance; see section II.4) and reduces the mortality risks caused by dehydration and starvation during transience (Hillman 2009). Therefore, one should expect a positive relationship between dispersal distances and body size. In *Rana aurora*, for instance, a larger body size at metamorphosis has been positively associated with natal dispersal distances and survival during transience (Chelgren 2006).

**Hindlimb length** – Hindlimb length has profound implication in amphibian locomotor mode (Enriquez-Urzelai et al. 2015) and is positively correlated with locomotor capacities (see section II.4). Correlation between dispersal distances and size-corrected hindlimb length has been reported in anurans. In *Rhinella marina*, Phillips et al. (2006) demonstrated that long-distance dispersing individuals (juveniles and adults) from range-front populations have longer hindlimbs than those from range-core populations. They also showed that, compared with their shorter-legged conspecifics, individuals with longer hindlimbs move further over a 3-day period. They concluded that this morphological shift is likely involved in the increase of the rate at which the toad invasion has progressed since its first introduction. In a more recent study, Hudson et al. (2016a) suggested that hindlimb length could be under sexual selection favouring longer in males according to mating performance whatever their origin. Moreover, one should also keep in mind that developmental constraints imposed by pond environmental condition such as ephemerality also largely contribute to morphological variations at metamorphosis including leg size (Gomez-Mestre & Buchholz 2006).

**Behavioural traits** – Covariation between dispersal distances and behavioural traits has been reported in two anurans, the invasive *Rhinella marina*, and *Bombina variegata*. In the former species, using common garden experiments, Phillips et al. (2010) showed that toadlets with parents from range-front populations displayed longer daily movement distances than those with parents from range-core populations. This result was confirmed a few years later by Lindström et al. (2013), that found that toads from range-front populations spent longer periods in dispersive mode and displayed longer movements

while they were in dispersive mode than did toads from range-core populations. In addition, the directionality of displacements also differs between populations of *Rhinella marina*. Lindström et al. (2013) showed that individuals from range-front populations displayed more directed movements than individuals from range-core populations. In a second study, Brown et al. (2014) examined movement directionality in field-collected adult toads and common-garden-raised offspring. Their results confirmed Lindström and co-workers' conclusions: individuals at the invasion front moved in straighter paths than did conspecifics radio-tracked at the same site in subsequent years (i.e., when the population was not at the expanding front). In addition, toadlets reared in a common garden setting exhibited straighter paths if their parents came from populations closer to the invasion front. In *Bombina variegata*, Cayuela et al. (2018c) found a covariation pattern between exploration tendency and dispersal distances. They showed that exploration propensity recorded in laboratory trials in toadlets reared in a common garden setting covaried positively with natal and breeding dispersal distances reported in spatially structured populations.

*Physiological traits* – Although estimation of energy costs of dispersal is very challenging (Bonte et al. 2012), amphibian dispersal ability may be positively linked to individual capacity to handle the physiological consequences of long-distance exercise (Llewelyn et al. 2010, Shine et al. 2011). Therefore, physiological determinants of locomotor performances, such as high aerobic capacities (Taigen & Pough 1985), are assumed to be relevant in a context of transience. High endurance capacity could confer greater fatigue resistance. This intrinsic parameter varies widely among anurans. Indeed, depending on the locomotion mode, i.e., walking or jumping, metabolic phenotypes and physiological mechanisms will greatly differ, as do endurance capacities too (Appendix B). Resistance to muscle fatigue may also be influenced by environmental conditions, such as temperature and water balance (Child et al. 2008a). During transience, anurans are exposed to high temperature and/or dehydration for a relatively long time. Many studies have shown that locomotor performance is influenced by temperature and dehydration (Seebacher & Franklin 2011), because of their impact on muscle physiology. Indeed, contractile properties (Bressler 1981, Godt & Lindley 1982, John-Alder et al. 1989), cellular bioenergetics (St-Pierre & Boutilier 2001, Trzcionka et al. 2008) and substrate use (Petersen & Gleeson 2009) all depend on temperature. Dehydration reduces locomotor performances in anurans (Gatten 1987, Gatten & Clark 1989, Tingley et al. 2012, Kosmala et al. 2017). Water loss induces also a decrease of muscle contractile properties (Hillman 1982) in jumping anurans but according to Gatten (1987), dehydration affects aerobic metabolism more than the glycolytic pathways. It is likely due to the increase of blood viscosity, triggering a limited O<sub>2</sub> delivery and an increase of oxidative stress (Hermes-Lima & Storey 1998). Even if ATP production is impacted by dehydration (Gatten 1987), mitochondria bioenergetics seem not to be directly affected (Hillman et al. 1991); the authors hypothesized a limitation of substrate availability – energy/respiratory substrates are molecules which are providing reduced cofactors (NADH or FADH<sub>2</sub>) to the Electron transport system of the mitochondria, for ATP synthesis. Only carbohydrates were tested, which are likely the main substrate for short and intense exercise. No



data are available about lipid utilization, which is the main substrate for endurance exercise (Weber 2011, Navas et al. 2008) and likely critical for amphibians (Fitzpatrick 1976). It is also important to note that temperature and hygrometry could interact, and their synergistic effect on locomotor performance could be important (Navas et al. 2007, Child et al. 2008a, Titon & Gomes 2017, Kosmala et al. 2017).

*Life history traits* – Covariation between dispersal distances and life history traits has been reported in many invertebrates and vertebrates (Stevens et al. 2014). In amphibians, our knowledge about such covariation patterns remains fragmentary. The correlations between dispersal distance and life history traits are similar to those reported between emigration and life history traits in the section III.1.b. In *Rhinella marina*, dispersal distances are correlated to increased growth rates (Phillips 2009; but see Hudson et al. 2015 for the opposite effect on reproductive frequency) in populations at the invasion front; the opposite is found in populations located in the range core. In *Bombina variegata* dispersal distances before and after sexual maturity are associated with an accelerated life history (reduced survival and increased female fecundity) in populations reproducing in unpredictable patches; the opposite is reported in populations breeding in predictable patches (Cayuela et al. 2016b).

#### (c) Context-dependent transience

*Euclidean distances between sites* – The spatial organization of breeding sites (i.e., pond network) affects transience. As dispersal corresponds to between-breeding patches movements, the form of the dispersal kernels is intrinsically linked to the structure of the pond network (i.e., median of the distances between ponds, distance to the nearest and farther pond). As reported in section III.2.a, the frequency of dispersal events decreases in a non-linear fashion with the between-patch Euclidean distances (Breden 1987, Berven & Grudzien 1990, Trenham et al. 2001, Funk et al. 2005, Gamble et al. 2007, Hamer et al. 2008, Hendrix et al. 2017, Cayuela et al. 2018b, Cayuela et al. 2018c).

*Landscape structure* – Both experimental and field studies have found that pond-breeding amphibians are able to detect habitat boundaries (Gibbs 1998, Rittenhouse & Semlitsch 2006, Stevens et al. 2006, Popescu & Hunter 2011, Cline & Hunter 2014) and that they prefer some landscapes over others during their terrestrial movements (see below). In many studies focusing on amphibian movement, the type of movement (i.e., dispersive, migratory or foraging) is not known. If one assumes that landscape structure has similar effects on movements regardless of their function, then amphibian transience would be affected by a number of factors. Landform and slope seem to affect transience, although most evidence comes from molecular studies (section IV.2.a) in which genetic variation between patches cannot be directly interpreted as dispersal (section IV.2). Moreover, studies have shown that waterbodies (not necessarily used for breeding) facilitate movement between breeding patches. Especially, the presence of small streams, canals, agricultural ditches and inundation areas may facilitate amphibian movements (Adams et al. 2005, Mazerolle 2005, Rowley & Alford 2007, Tatariian 2008, Wassens et al. 2008, Bull 2009, Anderson et al. 2015). Long-distance dispersal by invasive cane toads



occurs primarily along corridors of open habitat, especially roads (Brown et al. 2006). Transience also seems to be closely dependent on the canopy cover, especially in forest amphibians that avoid clearcuts and prefer habitats with vegetation cover (DeMaynadier & Hunter 1999, Rothermel & Semlitsch 2002, Patrick et al. 2006, Rittenhouse & Semlitsch 2006, Popescu & Hunter 2011, Cline & Hunter 2014, Cline & Hunter 2016, Ousterhout & Semlitsch 2018). Vegetation cover decreases dehydration rates (Rothermel & Semlitsch 2002, Rothermel 2004, Cosentino et al. 2011b), which reduces mortality risk and increases dispersal distance and success. This sensitivity to vegetation cover seems to differ between species, urodeles being more sensitive than anurans due to their higher susceptibility to body water loss and a lower vagility (Todd et al. 2009). Pond-breeding amphibians occurring in open or semi-arid environments may be less prone to prefer forest surfaces (Stevens 2004, Stevens et al 2006, Youngquist & Boone 2014). Moreover, pond-breeding amphibians often avoid agricultural surfaces including grasslands and crop-fields (Jehle & Arntzen 2000, Rothermel & Semlitsch 2002, Rittenhouse & Semlitsch 2006, Cline & Hunter 2014, Cline & Hunter 2016), although some types of crops seem to be less resistant to movements than others (Cosentino et al. 2011b). Ploughed soils have also been reported to increase dehydration rates and stress hormones levels (i.e., corticosterone concentrations) in several anurans (Mazerolle & Desrochers 2005, Janin et al. 2012). Moreover, transience could also be strongly impacted by transport infrastructure and urban areas, which are usually thought as highly resistant to the movement of these animals (Cushman 2006, Becker et al. 2007). Four mechanisms are usually put forward to explain this detrimental effect: first, roads and urban areas always trigger a loss of aquatic habitats and vegetation cover (Cushman 2006), which increases the mortality risks caused by dehydration and predation. Second, artificial surfaces such as asphalt contain complex mixtures of volatile and nonvolatile chemical compounds may elicit road-avoidance behaviour during transience (Cline & Hunter 2016, Cayuela et al. 2018b). Third, a high mortality due to collision with vehicles may occur when amphibians are forced to cross roads (Hels & Buchwald 2001, Andrews et al. 2008, Beebee 2013). Fourth, vehicle traffic has also been reported to increase hormone stress level in moving amphibians (Tennessen et al. 2014), which could lead to delayed dispersal costs. Nonetheless, we also note the reverse effect, whereby dispersing cane toads actively selected roads as transport routes because the open surface facilitated rapid dispersal (Brown et al. 2006).

#### **IV CONSEQUENCES OF DISPERSAL ON THE DYNAMICS AND THE GENETICS OF SPATIALLY STRUCTURED POPULATIONS**

##### **(1) Consequences of dispersal on population and patch occupancy dynamics**

In this section, we review how dispersal affects demographic connectivity and interdependence, spatial autocorrelation of demographic rates, and colonization-extinction dynamics in amphibians.

(a) Consequences for demographic interdependence and connectivity

Dispersal is a critical parameter for the dynamics of spatially structured populations (Thomas & Kunin 1999, Revilla & Wiegand 2008, Lowe & Allendorf 2010) because the size of a given subpopulation is:

$$N_{t+1} = N_t + \text{births} - \text{deaths} + \text{immigrants} - \text{emigrants}$$

where  $N_{t+1}$  is the subpopulation at time  $t + 1$ , which depends on subpopulation size at  $t$ , gains (births + immigrants) and losses (deaths + emigrants) that occur between  $t$  and  $t + 1$ . As immigration/emigration is part of the dispersal process, dispersal therefore influences, to a lesser or greater degree, the level of demographic interdependency between the units (i.e., subpopulations) forming spatially structured populations (Hastings 1993, Waples & Gaggiotti 2006). The highly variable dispersal rates observed in pond-breeding amphibians (Appendix A) suggest that levels of demographic interdependence might also differ between populations and species. Although several of these populations seem completely independent (dispersal rate = 0), others correspond to metapopulation-like systems with low annual dispersal rates ( $\leq 1\%$ ), or patchy populations with relatively high dispersal rates ( $\geq 10\%$ ). A 10% threshold is often viewed as the point where population dynamics in two patches transition from being independent to behaving as a single demographic entity, with similar population growth rates and, potentially, being synchronized (Hastings 1993, Waples & Gaggiotti 2006).

Simulation models show that the extinction probability in patches decreases with dispersal rates (Stevens & Baguette 2008; but also see Duncan et al. 2015), which indicates that dispersal is a critical parameter involved in demographic connectivity. Following the definition given by Lowe & Allendorf (2010), demographic connectivity is a function of the relative contribution of net local immigration (immigration–emigration) to total recruitment in a subpopulation. Demographic connectivity of amphibian subpopulations has not been studied in detail (Lowe & Allendorf 2010). This is mainly because net local immigration and local recruitment are not easily disentangled using capture-recapture models (Nichols & Pollock 1990), especially if juveniles cannot be identified due to their small size or lack of natural marks (but see Sinsch 1997, Cayuela et al. 2018c). The high dispersal rates reported for several pond-breeding amphibians (section III.1.a) suggest that net immigration is potentially an important contributor to local recruitment in several species. However, high absolute values of dispersal rates should not be directly interpreted as a high level of demographic connectivity or as a proxy for the level of synchronization in local population dynamics. Indeed, net immigration may be high in absolute terms, but represent only a small proportion of total recruitment in rapidly growing subpopulations (Lowe & Allendorf 2010). In contrast, from subpopulations near to extinction to stable ones (i.e., population growth rate  $\leq 1$ ), low net immigration values can represent a large proportion of total recruitment.

(b) Consequences for population synchrony and spatial autocorrelation of demographic rates

Dispersal rates, in combination with spatial autocorrelation of environmental variation, usually increase temporal synchrony and spatial autocorrelation of demographic rates in populations (Ranta et al. 1997). To date, the relative contribution of environmental synchronizers (i.e., the *Moran effect*, Moran 1953, Ranta et al. 1997) and dispersal on the synchronization of spatially structured amphibian populations has not been studied. A study of *Ambystoma californiense* examined the effect of dispersal on spatial autocorrelation of demographic rates (Trenham et al. 2001). These authors highlighted significant weakening in correlation with increasing inter-pond distance for mass and age distributions, but not for local abundance of breeding males. Correlations for both mass and age distributions declined and became more variable for ponds separated by > 1 km. In parallel, they showed that the relationship between inter-pond distance and dispersal probability could be fitted with a negative exponential curve. Dispersal probability decreased from 0.20 to 0.01 with Euclidean distances ranging from 50 to 1500 meters. The authors concluded that in the studied system, ponds separated by less than 1 km commonly exchanged sufficient numbers of dispersers to elevate the levels of spatial autocorrelation for age and body mass distributions.

#### (c) Consequences for colonization/extinction dynamics

Dispersal is a central parameter in metapopulation models because it affects population growth and colonization of empty patches (Hanski & Gilpin 1991, Gilpin 2012). Most metapopulation models describe colonization-extinction dynamics through the area-isolation paradigm (Hanski 1998, Pellet et al. 2007) whereby colonization probability depends on patch size and extinction probability is a function of patch isolation. Patch isolation is usually quantified using distance-based metrics (often called *connectivity metrics*; Calabrese & Fagan 2004), taking into account between-site Euclidean distances and dispersal rates. In amphibians, studies have highlighted a negative relationship between patch occupancy and connectivity (Zanini et al. 2009), extinction probability and connectivity (due to a *rescue effect*; Sjögren-Gulve 1994, Cosentino et al. 2011a) and a positive relationship between colonization probability and connectivity (Cosentino et al. 2011a, Howell et al 2018). In contrast, other studies have not found any effect of connectivity on colonization probability (Pellet et al. 2007). It is interesting to note that the strongest effects were detected in species breeding in permanent waterbodies, with relatively low turn-over rates. In species reproducing in temporary patches, colonization-extinction rates are usually high (sometimes > 0.50) due to frequent drying (e.g., Park et al. 2009, Cayuela et al. 2012, Tournier et al. 2017). In many cases, this is not colonization and extinction in the strict sense, but variation in patch occupancy states caused by water level fluctuation – most of the time researchers do not use multiple season site occupancy models (MacKenzie et al. 2003) providing colonization and extinction probabilities conditional upon site availability (see Miller et al. 2012 for an exception). When a patch is unavailable for breeding during a given year, individuals may disperse towards a flooded patch

or alternatively may remain patch-faithful and skip breeding (Cayuela et al. 2014, 2018g; Green & Bailey 2015). Likewise, recolonization probability depends on the breeding probability of patch-faithful individuals after drying and dispersal from patches that remained flooded during the previous breeding season. The complexity of these processes may explain why studies often fail to detect an effect of connectivity on “colonization-extinction” probabilities in amphibians breeding in temporary patches.

## (2) Consequences for neutral genetic variation and adaptive processes

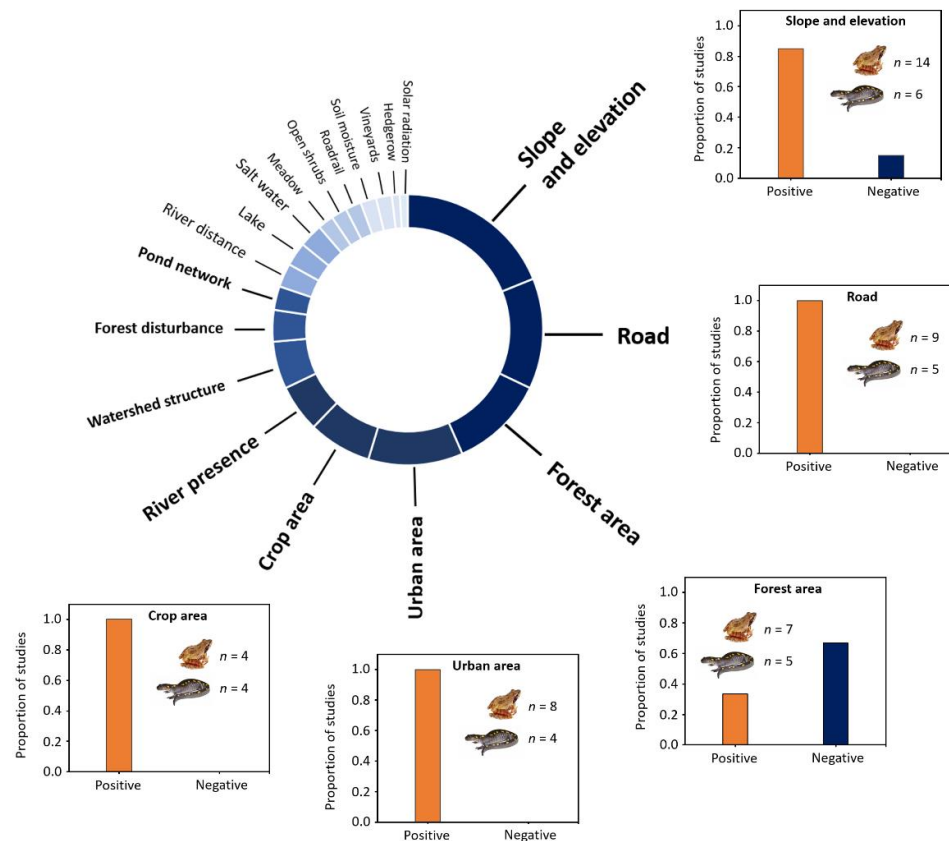
Dispersal-related movements translate into gene flow (i.e., effective dispersal) when they are followed by successful reproduction (Broquet & Petit 2009, Lowe & Allendorf 2010, Cayuela et al. 2018d). As dispersal is a non-random process, it usually results in asymmetric gene flow between patches (Edelaar & Bolnick 2012). In spatially structured populations, neutral genetic variation between patches results from the interplay of two opposing forces: gene flow decreases genetic divergence between patches; by contrast, genetic drift, whose strength is negatively proportional to the effective population size ( $N_e$ ), increases genetic divergence (Slatkin 1985, Hutchison & Templeton 1999). Furthermore, by affecting gene flow, dispersal is also expected to affect local adaptive processes. Indeed, high gene flow increases effective population size within patches, which reduces the effect of genetic drift and the risk of fixation of deleterious allele (Broquet & Petit 2009). However, gene flow into a population can also constrain local adaptation (Lenormand 2002; but also see Jacob et al. 2017).

### (a) Consequences for neutral genetic variation

Evidence indicates that the negative relationship between immigration probability and Euclidean distance between breeding patches (Section III.2.c) translates into genetic Isolation-by-Distance (IBD); i.e., an increased genetic differentiation with increasing Euclidean distance. Indeed, IBD has been reported by 85% of the genetic studies (i.e., 63 of 74; Appendix C) on pond-breeding amphibians (46 species, 15 urodeles and 31 anurans). In addition, several studies combined capture-recapture and genetic analyses to compare dispersal rates and kernels and IBD (Berven & Grudzien, 1990, Funk et al. 2005, Schmidt et al. 2006, Wang & Shaffer 2017, Cayuela et al. 2018c). These studies found that genetic divergence between patches decreased with increasing dispersal rates and distances. Furthermore, Cosentino et al. (2012) found that genetic divergence decreased with increasing wetland connectivity, a metric that included a negative exponential dispersal kernel and accounted for distances to potential source wetlands in *Ambystoma tigrinum*. These authors also showed that genetic divergence was greater among newly colonized patches than among established patches, indicating that founder effects have influenced spatial genetic structuring of the population.

Over the last two decades, landscape genetic studies have extensively examined relationships between genetic divergence and landscape composition and configuration in amphibians. We identified 42 studies (listed in Appendix C) that have detected significant landscape effects (Fig.4) on genetic variation in 41 amphibian species (14 urodeles and 27 anurans). Slope and elevation were the landscape factors most often reported to affect genetic structure of populations. In 47% of the studies, and in 85% of these cases, increases in slope and elevation enhanced genetic divergence among subpopulations. Soil moisture (5% of the studies) and solar radiation (2%) have also been reported to have negative and positive effects respectively on genetic divergence. Regarding the availability and the structure of aquatic habitats, the two most commonly reported effects on population genetic structuring were the watershed structure (15% of the studies) and the presence of rivers (15%). For the former, studies revealed that genetic divergence was lower within than among watersheds (Goldberg & Waits 2010, Murphy et al. 2010). Other research has indicated that the proximity of wetlands and ditches are associated with lower genetic divergence (Sotiropoulos et al. 2013, Coster et al. 2015). For the latter, studies showed that river presence and distance to the river may increase (50% of the studies) or decrease (50%) genetic differentiation, likely depending on river characteristics (depth, width and flow) and species swimming abilities. Other studies revealed that lakes (7% of the studies) and large salt waterbodies (7%) increased genetic divergence. Concerning land use, the two most commonly reported effects were those of forest (28% of the studies) and urban (7%) areas. The influence of forest area varied among species; 66% of the studies found that forest reduces genetic divergence while 33% found the opposite pattern. In 75% the cases, forest disturbance and harvesting increased genetic differentiation. Moreover, all the studies reported that urban area increased genetic divergence. Agricultural areas had varied effects on genetic variation. All the studies that have detected an effect of crops (19% of the studies) and vineyard (5%) found that they increase genetic divergence. By contrast, grassland has been shown to reduce genetic differentiation (5% of the studies). Regarding transport infrastructure, the most frequently reported effect was that of roads (33% of studies), which always increased genetic divergence among subpopulations. Similarly, railways had a positive effect in genetic differentiation (2% of studies).

In the last decade, a few studies have investigated how breeding patch persistence over time affects genetic variation in amphibians (Chan & Zamudio 2009, Mims et al. 2015, Cayuela et al. 2018c). Chan & Zamudio (2009) and Mims et al. (2015) showed that species reproducing in ephemeral waterbodies displayed lower genetic variation between breeding patches compared to those breeding in more stable waterbodies. In *B. variegata*, Cayuela et al. (2018c) showed that spatially structured populations experiencing low-persistence breeding patches displayed lower genetic variation due to higher emigration rates and longer dispersal distances than did populations utilising persistent breeding patches.



**Figure 4.** Environmental associates of genetic divergence in pond-breeding amphibians. At the top left, we show the number of studies that have detected a significant effect of 19 landscape factors on genetic divergence. We focus on the five most reported landscape factors by showing the proportion of studies that have highlighted positive or negative effects on genetic divergence. For each factor, we provide the number of studies (n) that have focused on anurans and urodeles.

#### (b) Consequences for adaptive processes

Gene flow as a consequence of dispersal can have opposing effects on process of local adaptation. On the one hand, it can help spread allelic variants with adaptive value across demes, although this is generally considered a slow process, less efficient than selection acting on local standing genetic variation (Barrett & Schluter 2008). In contrast, gene flow can also counteract or even prevent local adaptation by homogenizing gene pools across demes and disrupting allele combinations favoured by selection in different environmental settings. Studies have provided evidence for local adaptation of amphibian populations to extreme environmental conditions, including low pH (Egea-Serrano et al. 2014), high salinity or water temperature (Hopkins & Brodie 2015, Pastenes et al. 2017; Kosmala et al. 2017, 2018), or high altitude (see below), but few of them have investigated the actual genetic bases of these adaptations, and fewer still have assessed the role of gene flow in this process.



Perhaps the best-studied examples of local adaptation in amphibians involve high altitude populations. Because slope is usually negatively correlated with gene flow in amphibians (see above), altitudinal gradients offer good opportunities for local adaptation to occur. While some studies have focused on comparisons of transcriptomic datasets in low vs high altitude sister taxa (Yang et al. 2012), intraspecific studies can offer valuable insights on the role of dispersal / gene flow on local adaptation. For instance, Bonin et al. (2006) identified eight amplified fragment polymorphisms (AFPLs) associated with high elevation in *Rana temporaria*. Yang et al. (2016, 2017) used a combination of comparative transcriptomics, reciprocal transplant experiments and gene expression analyses to identify genes associated with adaptation to high altitudes in *Bufo gargarizans*. They found both fixed and plastic variations in gene expression, mostly involving genes related with nutrient metabolism, which are generally down-regulated in high altitude populations. In both cases, restricted dispersal and isolation in high altitude populations appear to have led to local adaptation.

Other studies investigating the molecular bases of local adaptation in amphibians have found evidence for local adaptation in the face of gene flow. For instance, Gomez-Mestre & Tejedo (2004) reported strong, heritable differences in tolerance to high salinity in populations of *Epidalea calamita* connected by gene flow. Similarly, Richter-Boix et al. (2011b, 2013) identified a candidate gene (RC08604) that is involved in local adaptation in *Rana arvalis*. Allelic distributions in this gene are correlated with habitat characteristics and differ from patterns observed at neutral loci, which reflect gene flow across populations in different habitats. This gene is part of an up-regulated thyroid hormone receptor coordinating the expression of other genes during metamorphosis and was inferred to be subject to directional selection (Richter-Boix et al. 2011b). RC08604 is linked to variation in larval life history traits like developmental time and growth rate, which are relevant for metapopulation viability and the migration/selection equilibrium (Petranka 2007).

## V. RESEARCH AVENUES

### (1) Quantifying dispersal rates and distances using modelling tools

Relatively few studies ( $n = 28$ , Appendix A) have quantified dispersal rates and distances in pond-breeding amphibians. Importantly, only 14% ( $n = 4$ ) of these studies have used capture-recapture modeling systems that take into account the imperfect detection of individuals (reviewed in Cayuela et al. 2018d). The remaining studies provided only the number of individuals were captured in, at least, two distinct breeding patches during two consecutive or more years. Therefore, dispersal, survival, and recapture rates are confounded and estimates of dispersal rates and distances can thus be biased. Further capture-recapture studies should be undertaken to quantify dispersal rates and distances in more taxa and populations within taxa, using suitable capture-recapture modelling systems.



## (2) Investigating the effect of kin competition and inbreeding risk on dispersal

Our review showed that a set of biotic (e.g., patch size, disturbance, and persistence) and abiotic factors (e.g., density of conspecifics and heterospecifics) affect emigration and immigration. Although the risks of inbreeding and kin competition are usually considered as critical drivers of dispersal in vertebrates (Ronce & Clobert 2012, Matthysen 2012), no studies have examined the effect of social factors on amphibian dispersal. Studies indicate that amphibians have the ability to recognize their kin at both larval and adult stages (Blaustein & Waldman 1992, Pfennig 1997, Hokit & Blaustein 1997). Vocalization (Waldman et al. 1992), chemical cues (Blaustein & Waldman 1992, Houck 2009), and Major Histocompatibility Complex (MHC, Bos et al. 2009) are sophisticated kin recognition systems allowing amphibians to adjust their social behaviors. It is therefore possible that amphibians base their dispersal decisions on social factors, in particular the level of relatedness within the groups of breeders occupying ponds. We encourage further studies to examine this issue using both experimental and field approaches.

## (3) Assessing genetic and epigenetic bases of dispersal

Estimating heritability ( $h^2$ ) is a useful approach to examine the genetic basis of a phenotype (Visscher et al. 2008). In pond-breeding amphibians, heritability of dispersal (propensity or distance) and dispersal-related traits has been quantified in a limited number of species. Brown et al. (2014) quantified heritability of path straightness, a behavioural trait related to dispersal in *Rhinella marina*, and showed that  $h^2$  was 0.18. In the same species, Phillips et al. (2010) found that  $h^2$  of daily dispersal distance was 0.24. Overall, despite relatively low values of  $h^2$ , these studies show that there is additive genetic variation for dispersal traits. This conclusion is congruent with common garden studies showing that behavioural traits related to dispersal may differ among genetically divergent amphibian populations (Maes et al. 2012, Brodin et al. 2013, Cayuela et al. 2018c). Yet, the genetic architecture of dispersal remains largely unknown in amphibians as no quantitative trait loci have been identified. Only one study has investigated how variation in gene expression profile (having genetic bases) correlates with dispersal (and related traits) in *Rhinella marina* (Rollins et al. 2015). In toads from both ends of the invasion-history transect (low emigration propensity and short dispersal distances in core-range populations vs the opposite characteristics in front-range populations), Rollins et al. (2015) found differential substantial upregulation of many genes (not necessary the same at both ends), notably those involved in metabolism and cellular repair. However, beyond this work, no study has examined potential variation in DNA polymorphisms between dispersing and non-dispersing individuals in amphibian populations. Moreover, it is also possible that a part of the phenotypic variation captured by heritability is passed on via epigenetic mechanisms (Saastamoinen et al. 2018), which remain unspecified in amphibians. We

propose a conceptual scheme (**Fig.1**) to show how genetic and epigenetic factors could influence pre-metamorphic and post-metamorphic dispersal in a way that might affect dispersal.

Recent studies in other taxa suggest that dispersal (and related) traits likely evolve through polygenic selection rather than being controlled by a few loci with major effects (Saastamoinen et al. 2018). Therefore, modern whole-genome sequencing approaches could be useful to detect networks of quantitative trait loci involved in dispersal or dispersal-related trait variation. A limitation to such genomic studies in amphibians is their large genomes (Organ et al. 2011, Liedtke et al. 2018), but this technical constraint could be addressed by using exome capture sequencing (Choi et al. 2009) or by focusing on coding regions using RNA-seq methods (Wang et al. 2009). Further studies could examine how variation in dispersal-related traits are related to gene expression using RNA-seq approaches and epigenetic variation as DNA methylation using genome-wide bisulphite sequencing.

#### **(4) Studying dispersal and eco-evolutionary dynamics**

The term “eco-evolutionary dynamics” broadly refers to any unidirectional change in an ecological factor that provokes a heritable change in phenotypic distribution (Pelletier et al. 2009, Schoener 2011). This heritable shift is caused by microevolutionary processes as selection or gene flow, or any heritable change in a trait distribution (mean and shape) that provokes a change in ecological mechanisms. Such eco-evolutionary dynamics have received little attention in the amphibian literature. Yet, complex life cycles should strongly alter the eco-evolutionary dynamics of dispersal in amphibians because dispersal-related traits may be subject to pleiotropic effects resulting from either selective pressure exerted during the larval stage or during the ontogenetic habitat shift. In particular, it is worth noting that pond ephemerality can shape dispersal syndromes in a non-trivial manner. Ephemerality pond is likely to enhance dispersal evolution because it selects for accelerated larval development resulting in lower vagility at metamorphosis (i.e. smaller size). Thus, it appears that amphibians exploiting ephemeral ponds have likely evolved another suit of traits allowing them to compensate for these morphological constraints on locomotion. One may therefore expect some important variations in dispersal syndromes across amphibian species according to the ephemerality of breeding ponds that they use. Such variations are also likely to impede or facilitate adaptation of amphibian species in the context of climate change or other anthropogenic disturbance.

Moreover, because of their ontogenetic habitat shift, pond breeding amphibians have to engage in complementation movements (i.e., nuptial migration and foraging movement; Dunning et al. 1992, Pope et al. 2000) ranging from very short distance to moderate ones according to the specificity of both the aquatic and terrestrial habitat. Since complementation movements are also subject to selection, one may ask whether ecological factors favouring larger scale complementation movements also result in longer dispersal distance. For instance, by splitting apart aquatic and terrestrial habitats, anthropogenic fragmentation could select for efficient movement related traits (locomotion and/or navigation) which

could in turn mitigate the dispersal cost during transition in fragmented landscapes. Work to elucidate this question would be particularly meaningful to unravel the eco-evolutionary dynamics of dispersal in the context of anthropogenic fragmentation.

## VI. CONCLUSIONS

- (1) Amphibian dispersal evolution is affected by immediate and delayed effect of the environment that affect individuals' phenotype and dispersal decisions.
- (2) The dispersal mechanisms at the individual level translate into highly variable emigrate rates and dispersal distances at both intra- and interspecific levels.
- (3) Highly variable emigration rates and dispersal kernels lead to complex gene flow patterns.
- (4) Further studies should be undertaken to investigate the effects of social factors on dispersal, the molecular bases of dispersal, and dispersal-related eco-evolutionary dynamics.

## VII. ACKNOWLEDGMENTS

We warmly thank the Banting Postdoctoral Fellowships program for its financial support. Furthermore, Mathieu Denoël is Research Director at Fonds de la Recherche Scientifique - FNRS. Moreover, any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This manuscript is contribution of the Amphibian Research and Monitoring Initiative (ARMI) of the U.S. Geological Survey.

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