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keywords
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abstract
Dispersal is a central process in ecology and evolution. It strongly influences the dynamics of spatially structured populations and affects evolutionary processes by shaping patterns of gene flow. For these reasons, dispersal has received considerable attention from ecologists, evolutionary biologists, and conservationists. 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 ever-increasing interest in amphibian dispersal and initiated both basic 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: redefine and clarify the concept of amphibian dispersal; 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, transience, and immigration); identify the demographic and genetic consequences of dispersal in spatially structured amphibian populations; and propose new research avenues to extend our understanding of amphibian dispersal.

Introduction

DISPERSAL describes the unidirectional movement of an individual from its natal site to its breeding site (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 and Gaines 1990; Clobert et al. 2001, 2012a; Ronce 2007). It is recognized as being critical to the dynamics of spatially structured populations (Hanski and Gilpin 1991; Thomas and Kunin 1999; Clobert et al. 2009). Dispersal affects demographic interdependence among populations and local population growth (Thomas and Kunin 1999; Lowe and 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 heterogenous landscapes (Hanski and Gilpin 1991; Gilpin 2012). Dispersal also has relevance beyond ecology. Successful reproduction following dispersal results in gene flow between populations (Ronce 2007; Broquet and Petit 2009; Lowe and Allenford 2010) that can strongly influence adaptive processes (Ronce 2007; Legrand et al. 2017). Through gene flow, dispersal modifies effective population size (N_e) and regulates the effects of genetic drift and the effectiveness of selection, influencing the likelihood and pace of local adaptation (Ronce 2007; Broquet and Petit 2009) and even speciation (Marques et al. 2019).

Dispersal can be considered as a three-stage process: emigration (departure), transience (movement in the landscape matrix), and immigration (arrival; Baguette and Van Dyck 2007; Clobert et al. 2009; Matthysen

2012). The evolution of dispersal is shaped by the balance between the relative costs and benefits associated with leaving (dispersing) versus staying (not dispersing; Stamps et al. 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, behavioral, and life-history traits (Ronce and 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 also be affected by social and environmental variation, resulting in c*ontext-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 prospect at a given breeding site. Extrinsic factors such as conspecific and heterospecific density or predation risk can affect emigration and immigration (Bowler and 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 and 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. 2017a).

Although dispersal has been extensively studied in vertebrates with simple life cycles, such as viviparous reptiles, birds, and mammals (Johnson and Gaines 1990; Paradis et al. 1998; Sutherland et al. 2000; Matthysen 2005; Clobert et al. 2012b; Clutton-Brock and Lukas 2012), it remains much less understood in organisms with complex life cycles, such as many aquatic invertebrates and amphibians (Comte and Olden 2018). Species with complex life cycles are those that exhibit an ontogenetic change in morphology, physiology, and behavior (i.e., metamorphosis; Wilbur 1980) and an ontogenetic niche shift (Werner and Gilliam 1984). In such organisms, conditions during early ontogenetic stages can dramatically influence the dispersal process taking place after metamorphosis; indeed, environmental conditions (e.g., water temperature, rates of pond drying, predation rates, and conspecific density) during egg and larval stages shape phenotypes at metamorphosis and later in life. This leads to complex carryover effects on fitness-related and movement-related traits, which have far-reaching consequences for dispersal (Altwegg and Reyer 2003; Chelgren et al. 2006; Van Allen et al. 2010; Searcy et al. 2014; Ousterhout and Semlitsch 2018). Additionally, multiple life stages with complex carryover effects add complexity to identifying patterns and mechanisms of dispersal compared to taxa with simple life cycles. Therefore, the study of dispersal in animals with complex life cycles offers an intriguing and challenging opportunity to uncover novel aspects of dispersal ecology and evolution. It also provides an unparalleled chance to better inform the conservation of some of the most threatened taxa around the world (e.g., freshwater biodiversity; Dudgeon et al. 2006).

There are numerous organisms with complex life cycles but pond-breeding amphibians are perhaps the most tractable for the study of dispersal. Pond-breeding amphibians have a biphasic life cycle with aquatic larvae and aquatic and terrestrial juveniles and adults (see the section titled Complex Life Cycle). 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. 2018b), and the genomes of some species are well described (Hellsten et al. 2010; Edwards et al. 2018; Nowoshilow et al. 2018). Additionally, a comprehensive understanding of dispersal in this group is key in supporting evidence-based conservation, a pressing global issue since amphibians are the most threatened class of vertebrates (Catenazzi 2015).

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 our understanding of amphibian population dynamics and genetics. This accumulation of knowledge encouraged us to undertake a general synthesis on the topic, with the following goals: redefine and clarify the concept of amphibian dispersal; 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, and transience); identify the demographic and genetic consequences of dispersal in spatially structured amphibian populations; and identify productive research avenues to extend our understanding of amphibian dispersal. We do not discuss the importance of dispersal for the conservation of amphibians because two recent reviews have already covered this topic (Bailey and Muths 2019; Joly 2019).

Dispersal Concept in Pond-Breeding Amphibians

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 and 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 the speed of development depends on biotic (e.g., density) and abiotic (e.g., temperature) conditions (see the section titled Drivers of Dispersal Decision and Pond Selection). Metamorphosis is a key developmental event that allows the transition from the aquatic to the terrestrial habitat (Wilbur 1980). Size at metamorphosis varies both within and among species (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 tradeoff of mass for a change in shape (Alford 1999), and is associated with dramatic physiological changes (Hillman et al. 2009). Importantly, this means that for many species, there is a need for habitat complementation, i.e., the use of nonsubstitutable resources (water and land; Dunning et al. 1992; Denoël and Lehmann 2006). After metamorphosis, juveniles grow until they reach sexual maturity. The juvenile stage lasts from one to several years (Wilbur 1980; Werner 1986). Intraspecifically, the length of the juvenile period depends on age and size at metamorphosis, local density, and environmental factors (Altwegg and 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 and Bailey 2015), whereas others may breed twice in a single year (Andreone and Dore 1992). Adult reproductive life span varies among species (e.g., 1–2 years in treefrogs and more than 15 years in some salamanders, frogs, and toads; Turner 1962).

dispersal concept

We define dispersal (Figure 1) 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 to a waterbody (e.g., puddle, pond, wetland, 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 toward new breeding patches (Van Dyck and 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

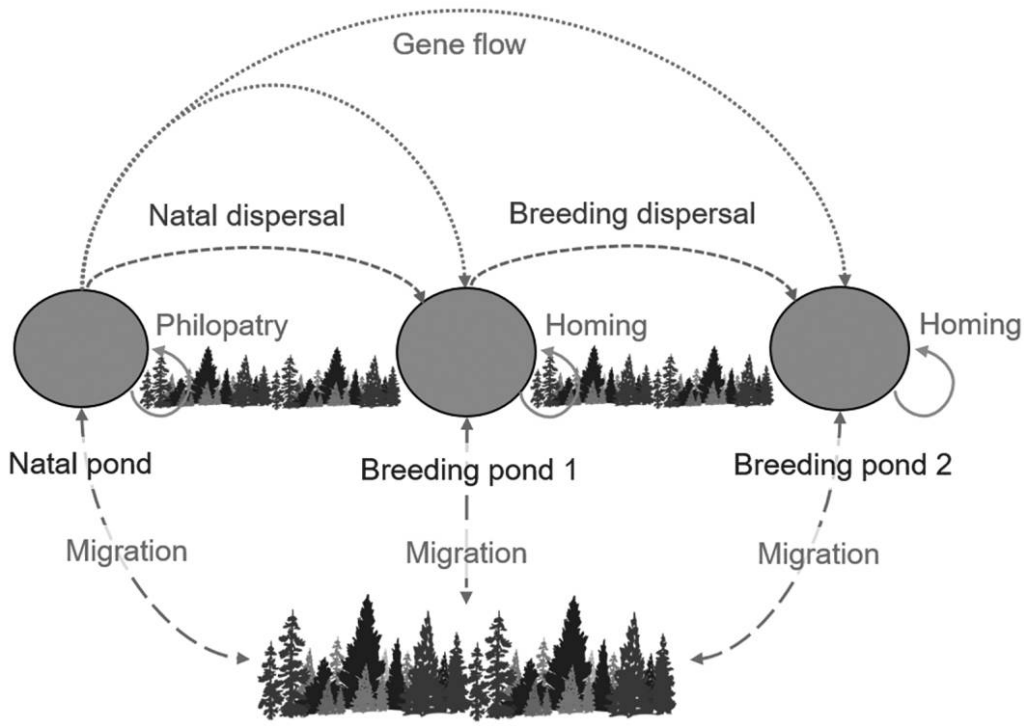

FIGURE 1. CONCEPTUAL SCHEME OF DISPERSAL AND MIGRATION IN POND-BREEDING AMPHIBIANS

Newly metamorphosed individuals can return to their natal pond to breed (i.e., philopatry) or may disperse to another pond (i.e., natal dispersal). Individuals may also disperse after their first reproduction between successive breeding ponds (i.e., breeding dispersal) or may remain faithful to their breeding site (i.e., homing behavior). Both natal and breeding dispersal result in gene flow if dispersers successfully reproduce after immigrating into their new pond. Note that dispersal differs from migration, which comprises all complementation movements between pond and terrestrial habitat and does not lead to gene flow. See the online edition for a color version of this figure.

about the meaning of dispersal and migration, with terms used interchangeably (Semlitsch 2008). The definitions show that dispersal and migration are different processes, but there are instances where dispersal events may result from navigational errors during migratory movements (Cote et al. 2017b).

NATAL AND BREEDING DISPERSAL

A distinction between natal dispersal (movement between the completion of metamorphosis and first reproduction; Smith and 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 and 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 to 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 interannually (e.g., Cayuela et al. 2016a; Denoël et al. 2018).

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 the section titled Maternal and Environmental Carryover Effects in Dispersal-Related Traits). Furthermore, ponds host groups of breeders whose size and attributes (i.e., relatedness level, interindividual heterogeneity in reproductive output) vary over space and time (Cayuela et al. 2017b; Sánchez-Montes et al. 2017). The size of the pond, its isolation, and the level of philopatry of individuals modulate the risks of kin competition and inbreeding (Ronce 2007; Broquet and Petit 2009; Lowe and Allenford 2010). The dispersal framework states that environmental and social factors may affect natal and breeding emigration (Bowler and Benton 2005; Matthysen 2012). Furthermore, it is expected that these determinants should influence habitat selection during immigration (Stamps 2001; Davis and Stamps 2004; Stamps et al. 2005). 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 and Sperry 2017). 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 the section titled Ecological Correlates of Dispersal, we report social and environmental factors affecting emigration and immigration.

maternal and environmental carryover effects on dispersal-related traits

Environmental and maternal effects can affect dispersal by altering individual phenotypes (Figures 2 and 3). In particular, environmental conditions experienced by embryos and larvae prior to metamorphosis can affect postmetamorphic 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 "carryover" effects can represent a cost of this adaptive plasticity (Richter-Boix et al. 2011; Ruthsatz et al. 2018). Moreover, maternal effects can also influence postmetamorphic phenotype and fitness (Laugen et al. 2005; Pruvost et al. 2013). An increasing number of studies show that environmental and maternal carryover effects may be important drivers of amphibian dispersal evolution.

Larval growth and development rate determine 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 and Roberts 2006; Kaplan and 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 and Roberts 2006). Additionally, the traits mentioned above are highly sensitive to environmental variation. Hence, genotype–environment (G × E) and maternal effect–environment (M × E) interactions have been observed in multiple species (Laugen et al. 2005; Pruvost et al. 2013; 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. 2011; Amburgey et al. 2012), water temperature (Ruthsatz et al. 2018), conspecific density (Wilbur 1976; Van Buskirk and Smith 1991), parasitism (Goater et al. 1993), and predation (Laurila et al. 2004; Vonesh and 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

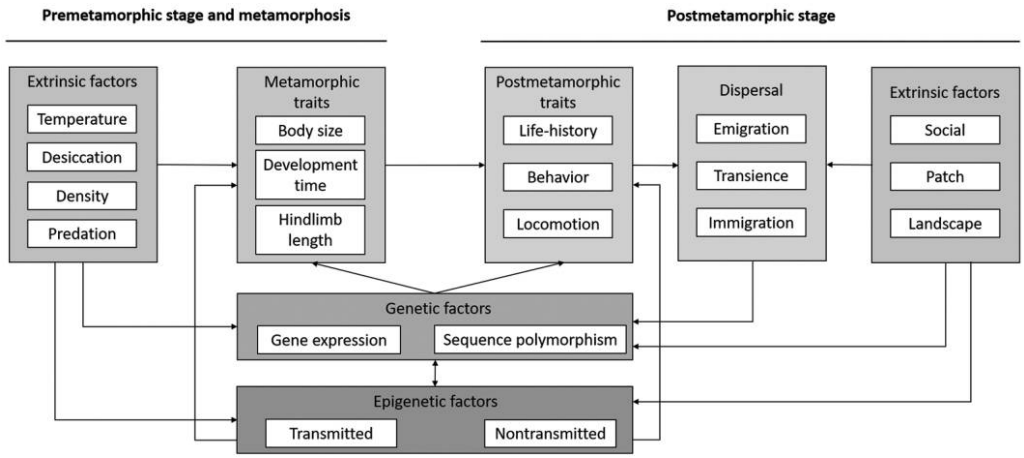

FIGURE 2. CONCEPTUAL FRAMEWORK TO SHOW HOW EXTRINSIC FACTORS (I.E., ENVIRONMENTAL AND SOCIAL VARIABLES) AND MOLECULAR FACTORS (GENETIC AND EPIGENETIC VARIATION) MAY AFFECT PRE- AND POSTMETAMORPHIC TRAITS AND DISPERSAL IN POND-BREEDING AMPHIBIANS

Extrinsic factors affect larval development and metamorphic traits, which then influence postmetamorphic traits, including life history (survival, growth, and reproduction), behavioral (boldness, activity, and exploration propensity), and locomotor traits (speed, jumping, and endurance). Postmetamorphic 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 variation (e.g., DNA methylation, microRNA profiles, and histone structure), transmitted to the next generation or not (Verhoeven et al. 2016), may also affect premetamorphic and postmetamorphic phenotype in a way that could affect each stage of the dispersal process (Saastamoinen et al. 2018). Epigenetic factors may affect gene expression (Gibney and Nolan 2010) and sequence polymorphism by affecting mutation rate and transposon reactivation (Fedoroff 2012; Tomkova and Schuster-Böckler 2018). See the online edition for a color version of this figure.

(Figure 3). Individual phenotype at metamorphosis has a strong effect on fitness-related traits at the juvenile stage (i.e., survival and growth; Scott 1994; Altwegg and 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 behavioral traits (Cote et al. 2010; Ronce and Clobert 2012) such as boldness, activity level, and exploration propensity of juveniles (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 and De Bernardi 2006; Boes and Benard 2013; Cabrera-Guzmán et al. 2013), speed (Beck and Congdon 2000; Choi et al. 2003), and endurance (Beck and Congdon 2000; Yagi and Green 2017). Independent of body size, parasite load can reduce endurance (Goater et al. 1993). Furthermore, body condition and fat reserves 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 hindlimbs, and higher body condition are therefore expected to enhance emigration propensity and locomotor capacities during transience (see the following section).

ECOLOGICAL CORRELATES OF DISPERSAL

EMIGRATION AND IMMIGRATION

Emigration and immigration are closely associated with breeding habitat selection

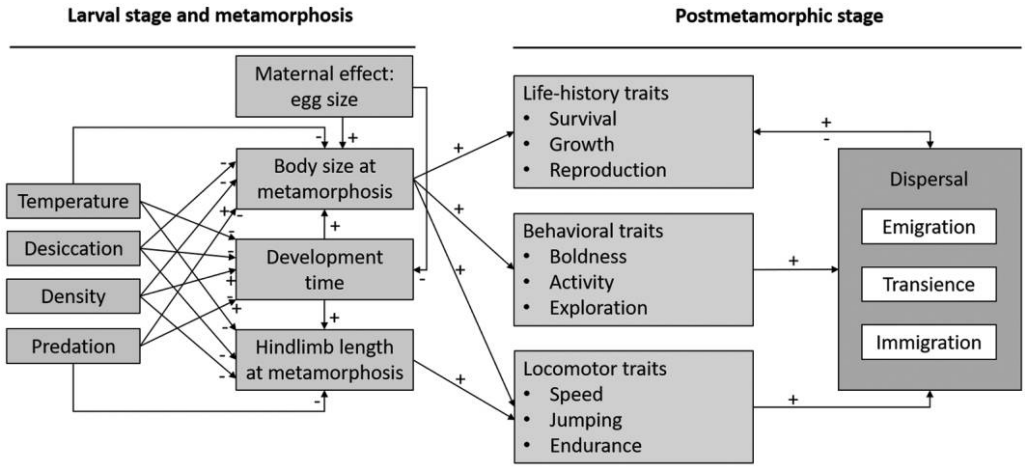

Figure 3. Conceptual Framework Showing Carryover Effects (Positive "+" or Negative "–") of Environmental Conditions During Larval Growth on Fitness-Related Traits, Behavioral Traits, and Locomotor Traits

Breeding site characteristics, including water temperature, desiccation risk, conspecific density, and predation, negatively or positively affect larval development time, body size at metamorphosis, and hindlimb length at metamorphosis. Maternal investment in egg size also affects body size at metamorphosis. Body size and hindlimb length at metamorphosis are positively correlated with development time. Body size at metamorphosis potentially has positive effects on postmetamorphic fitness-related traits, including survival, growth, and reproduction-related traits (age and body size at sexual maturity). Body size at metamorphosis also has a positive influence on behavioral traits such as boldness, activity level, and exploration propensity. In addition, it positively affects locomotor traits, including speed, jumping, and endurance. Moreover, hindlimb length has a positive influence on speed and jumping. Life-history traits may be negatively (tradeoff) or positively (mutual reinforcement, pleiotropic effect) correlated with dispersal (e.g., emigration rate, dispersal distance during transience or immigration success). Behavioral traits such as boldness, activity level, and exploration are expected to facilitate emigration and transience. Locomotor traits such as speed, jumping, and endurance should facilitate transience. See the online edition for a color version of this figure.

(Stamps 2001; Davis and 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 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.

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, available at https://doi.org/10.1086/707862) on 18 species—41% urodeles (Ambystomatidae and Salamandridae) and 59% anurans (Bombinatoridae, Bufonidae, 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) was, on average, 15±15% (sd). Anuran and urodele species showed similar dispersal rates (mean = 16±14 and 13±16%, respectively; Figure 4C). Mean dispersal rate did not differ between anuran and urodele species: $F_{1,16} = 0.22$, $p = 0.64$; test based on a linear model where breeding dispersal rate (one value per species)

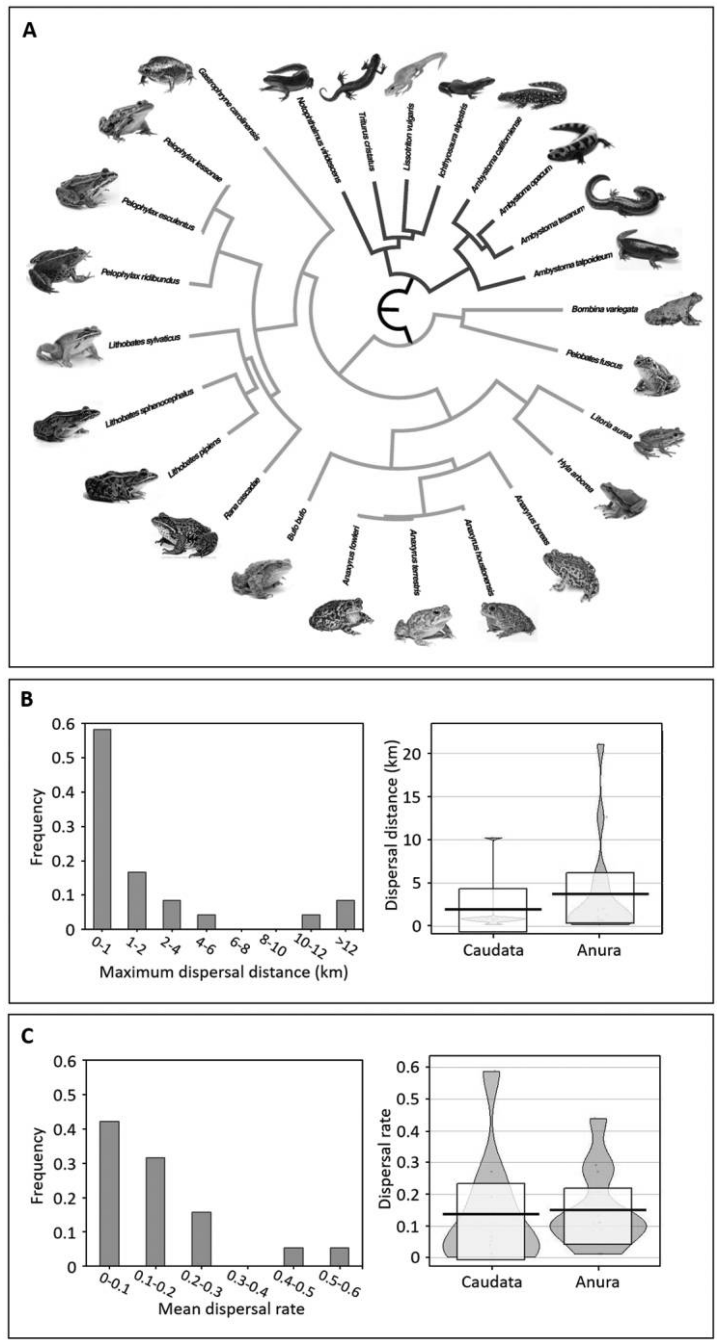

FIGURE 4. DISPERSAL DISTANCES AND RATES IN AMPHIBIANS

(A) Phylogenetic tree showing the 25 species for which we report dispersal distances and rates. (B) Maximum dispersal distance: on the left, distribution of maximum dispersal distances in Caudata and Anura combined; on the right, maximum dispersal distance in Caudata and Anura separately. (C) Mean dispersal rates: on the left, distribution of mean dispersal rates in Caudata and Anura combined; on the right, mean dispersal rates in Caudata and Anura separately. See the online edition for a color version of this figure.

TABLE 1
Sex-dependent dispersal in pond-breeding amphibians

Species	Dispersal step	Bias	Method	Reference
Physalaemus pustulosus	Unknown	Male-biased	Genetic	Lampert et al. (2003)
Triturus cristatus	Emigration	Male-biased	Capture-recapture	Denoël et al. (2018)
Triturus cristatus	Emigration	Female-biased	Capture-recapture	Cayuela et al. (2018a)
Bombina variegata	Emigration	Female-biased	Capture-recapture	Cayuela et al. (2019c)
Rana temporaria	Unknown	Female-biased	Genetic	Palo et al. (2004)
Epidalea calamita	Emigration	Female-biased	Capture-recapture	Sinsch (1992)
Lithobates catesbeianus	Unknown	Female-biased	Genetic	Austin et al. (2003)
Odorrana schmackeri	Unknown	Female-biased	Genetic	Wang et al. (2012)
Anaxyrus fowleri	Transience	No	Capture-recapture	Smith and Green (2006)
Lithobates sylvaticus	Unknown	No	Genetic	Berven and Grudzien (1990)
Ambystoma californiense	Emigration and transience	No	Capture-recapture	Trenham et al. (2001)
Ambystoma opacum	Emigration and transience	No	Capture-recapture	Gamble et al. (2007)
Rana arvalis	Unknown	No	Genetic	Knopp and Merilä (2009)
Ichthyosaura alpestris	Emigration	No	Capture-recapture	Kopecký et al. (2010)
Ichthyosaura alpestris	Emigration	No	Capture-recapture	Perret et al. (2003)
Hyla arborea	Emigration	Male-biased	Capture-recapture	Vos et al. (2000)
Rana cascadae	Emigration and transience	Female-biased	Capture-recapture	Garwood (2009)
Rana muscosa	Emigration	No	Capture-recapture	Matthews and Preisler (2010)

We reported the conclusions of 18 studies that have examined sex-biased dispersal in 16 species of pond-breeding amphibians (12 anurans and four 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).

was included as the response variable and the order as a discrete explanatory variable with two modalities (anuran versus urodele). 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 high interspecific variability in emigration rates, ranging from species where it was virtually zero (e.g., Gill 1978a) 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 (Figure 4A). In ambystomatid salamanders, emigration rates were variable, with most that were less than 6% (Pechmann et al. 2001; Gamble et al. 2007; 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 and Grudzien 1990; Garwood 2009; Figure 4A; Appendix A). There was also a large degree of variation for hylid frogs (Figure 4A; 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 some populations versus less than 1% in others (Cayuela et al. 2016a). In *Triturus cristatus*, breeding dispersal rates varied from virtually zero (Kupfer and Kneitz 2000; Unglaub et al. 2015) to 59% in other populations (Denoël et al. 2018). Additionally, interindividual heterogeneity in emigration rates within the same population is common in pond-breeding amphibians (see the section

titled Context-Dependent Emigration and Immigration).

Phenotype-Dependent Emigration

Age

Information on age-dependent emigration in pond-breeding amphibians is limited, mainly because juveniles are difficult to track and tag (but see Sinsch 1997; Cayuela et al. 2019b). It has been postulated that natal dispersal represents a higher proportion of total dispersal than does breeding dispersal (Gill 1978a,b; 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 and Grudzien 1990; Sjögren-Gulve 1998; Garwood 2009), others report similar rates of natal and breeding dispersal (Reading et al. 1991; Vos et al. 2000; Holenweg Peter 2001; Trenham et al. 2001; Smith and Green 2006; Gamble et al. 2007; Cayuela et al. 2019a). This variation in the proportion of overall dispersal represented by different stages of dispersal may be context dependent (Cayuela et al. 2019b). For instance, in several populations of *B. 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. 2019b).

Body Size

Body size influences both natal and breeding emigration. This is likely underpinned by the effect of body size on behavioral and physiological mechanisms (see below). For instance, body mass and length are positively correlated with dispersal-related behavioral 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 and Dunham 1994; Child et al. 2008a,b; Hillman et al. 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 and Semlitsch 2018). Moreover, Denoël et al. (2018) found that the probability of breeding emigration was higher in larger *T. 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 severalfold 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. 2019).

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 (including 11 studies containing emigration estimates, six genetic studies, and one study with transience only) in 12 anuran and four urodele species using either demographic or molecular approaches (Table 1). Note that the latter cannot disentangle the relative contribution of emigration, transience,

and postimmigration reproductive success to variation in sex-biased dispersal rates. By definition, gene flow results from dispersal events that are followed by successful reproduction ("effective" dispersal; Broquet and Petit 2009; Lowe and Allendorf 2010; Cayuela et al. 2018b). When only capture-recapture studies are considered, six studies out of 11 (i.e., 54%) report sex-biased emigration. When we consider both genetic and capture-recapture studies (17 if we exclude the study focusing on transience only), sex-biased dispersal is found in 10 studies (i.e., 59%). Among them, three report male-biased dispersal (30%) whereas seven (70%) report female-biased dispersal. Female-biased dispersal thus 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 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 affect offspring phenotype and fitness (e.g., conspecific density and breeding site stochasticity; see the section titled Context-Dependent Emigration and Immigration). Furthermore, sex-bias in emigration rates varies among populations of the same species. For instance, in *T. cristatus*, Denoël et al. (2018) reported higher emigration rates in males than females while Cayuela et al. (2019c) found the opposite pattern in another population of the same species. In this case, habitats differed significantly (e.g., pond size) suggesting that variation in environmental factors may have facilitated different emigration decisions in these two populations.

Behavioral Traits

Although amphibian behavioral syndromes have received significant attention (Kelleher et al. 2018), associations between behavioral traits and emigration rates have been investigated only recently. A well-documented case study is that of the invasive toad *R. marina* in Australia. In this system, range expansion evolves through a spatial sorting process (or spatial selection; Phillips et al. 2008, 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 nondirectionally have been left behind. This produces offspring with extremely high values for dispersal-enhancing traits (morphology and behavior), 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 behavioral 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 behavior. A second empirical study focuses on *B. variegata*. In this species, the spatially structured populations occur in two environments: river environments where the breeding habitat is predictable, i.e., constant availability of breeding patches in space and time; and forest environments where breeding habitat is unpredictable. Cayuela et al. (2016a) found that natal and breeding emigration rates were 10 to 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 behavioral phenotypes in toads reared under controlled laboratory conditions (Cayuela et al. 2019b). 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 and Clobert 2012), but amphibian studies addressing this association are scarce. Studies of the invasive toad *R. 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 juveniles of range-front populations had more neutrophils in their blood, and were more effective at phagocytosis 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 and Lai 2015). Skin chemical cues are also used by amphibians to recognize their kin and select their mates (Blaustein and Waldman 1992; Pfennig 1997). Several newt species such as *T. 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 *T. torosa* with a lower concentration of tetrodotoxin have a higher emigration probability and explained this pattern through mate selection: nondispersing males with an increased tetrodotoxin concentration have greater defenses, and 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 2009; Cayuela et al. 2016a), while a third study reported opposite patterns (Denoël et al. 2018). Phillips (2009) showed that both tadpole and juvenile *R. marina* from range-front populations grow approximately 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 favor increased reproductive rate. In a 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 *B. 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 postmetamorphic 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, 2019b). A third empirical example reports the coexistence of two alternative dispersal strategies in the same population of a urodele (*T. cristatus*) where approximately 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).

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 *B. 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 rate of immigration was higher at large patches than at small ones. In *T. 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. (2019c) highlighted a similar pattern in *T. cristatus* using an experimental pond network. They showed that breeding emigration rate was lower in ponds with a high density of conspecifics. Similarly, the probability of immigration was higher in high-density ponds than in 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 and Sperry 2017). Experimental studies report that amphibians usually avoid reproducing in waterbodies where predation risk and interspecific competition are high (Buxton and Sperry 2017). Winandy et al. (2017) 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. (2018c) found that adult *T. cristatus* were less likely to emigrate from ponds with high densities of other newts (*I. 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 and Templeton 2002; Blanchet et al. 2010) to locate, select, and/or rank the suitability of their breeding ponds as high or low. 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 and Luengo 2004; Pupin et al. 2007; Madden and 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 *B. 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 pond dries entirely if animals are to breed (Cayuela et al. 2018d). Molecular studies suggest that ephemerality of breeding patches results in high emigration rates in desert amphibians, compared to species in temperate environments (Chan and Zamudio 2009; Mims et al. 2015). This effect of pond ephemerality on emigration has been also observed at the intraspecific level. In *B. variegata*, the annual turnover rate was 20% to 30% in ephemeral breeding patches (a group of wheel ruts created by logging

activities in forest environments) compared to a zero turnover rate (no gain and no loss) in permanent breeding patches (groups of rock pools in a riverine environments; Cayuela et al. 2016a, 2019b). 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, 2019b). 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 (greater than 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 local fitness prospect, which may lead to lower emigration rate in highly disturbed patches. 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.

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 traveled, 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, behavioral, and physiological factors that 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.

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; Figure 4B). Most studies (21 of 24) reported data for a single species. The maximum dispersal distance (pooling estimates of natal and breeding dispersal) was, on average, 3698 ± 6256 m. The maximum dispersal distance was higher in anurans (4506 ± 7269 m) than urodeles (2212 ± 3845 m). However, maximum dispersal distance did not differ between anuran and urodele species ($F_{1,21} = 0.25$, $p = 0.70$; Figure 4B) when tested using linear models where dispersal distance (one value per species) was included as the response variable and the Order as a discrete explanatory variable.

Interspecific Variation

Maximum dispersal distances exhibited high interspecific variability within both anurans and urodeles (and also within families; Figure 4B), a variability that was slightly higher in anurans than in urodeles (Figure 4B). Both urodeles (*Ambystoma texanum*) and anurans (*Anaxyrus fowleri* and *Hyla arborea*) can show high vagility, with maximum dispersal distances of greater than 10 km. Extraordinarily large dispersal distances (greater than 30 km in some species) have also been observed in bufonids (Freeland and Martin 1985; Easteal and Floyd 1986; Smith and Green 2005, 2006). Two studies that compared dispersal across species suggested that dispersal distances increased with body mass (Pabijan et al. 2012; Hillman et al. 2014), likely due to higher locomotor performances of larger species (Choi et al. 2003). Hillman

et al. (2014) 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 *A. fowleri* (Breden 1987; Smith and Green 2006) and *Notophthalmus viridescens* (Gill 1978a; Pechmann et al. 2001). Within spatially structured populations, several studies have also reported that the distribution of natal and breeding dispersal distances (also known as dispersal kernel) is often highly leptokurtic and right-skewed (Breden 1987; Berven and Grudzien 1990; Holenweg Peter 2001; Trenham et al. 2001; Gamble et al. 2007; Hendrix et al. 2017; Cayuela et al. 2019b). 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 *B. variegata*, Cayuela et al. (2019b) showed that populations reproducing in unpredictable habitats displayed dispersal kernels that were more leptokurtic and more right-skewed than populations breeding in predictable habitats.

Dispersal Distance Variation Related to Breeding Behavior

A recent study provides valuable insight about the consequences of pond-breeding behavior on dispersal distances in a population of *Salamandra salamandra* (Hendrix et al. 2017). This species can use both permanent streams and temporary ponds for breeding. 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.

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 (*A. fowleri*, Breden 1987; *Rana luteiventris*, Funk et al. 2005; *B. variegata*, Cayuela et al. 2019a) and urodeles (*A. opacum*, Gamble et al. 2007), although other studies do not (*Bufo bufo*, Reading et al. 1991; *A. fowleri*, Smith and Green 2006; *A. californiense*, Trenham et al. 2001; *B. variegata*, Cayuela et al. 2019b). In a population of *B. variegata*, for instance, a recent study revealed a progressive decrease in kernel leptokurtism over toads' ontogenesis, suggesting a progressive behavioral shift over the lifetime of individuals (Cayuela et al. 2019a). 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 and Benton 2005).

Body Size

A large body size increases absolute locomotor capacities (e.g., absolute jumping performance and endurance; see the section titled Drivers of Dispersal Decision and Pond Selection) and reduces mortality risks caused by dehydration and starvation during transience (Hillman et al. 2009). Therefore, one should expect a positive relationship between dispersal distances and body size. In *R. aurora*, for instance, a larger body size at metamorphosis has been positively associated with natal dispersal distances and survival during transience (Chelgren et al. 2006).

Hindlimb Length

Hindlimb length has profound implications in anuran locomotor mode (Enriquez-Urzelai et al. 2015) and is positively correlated with locomotor capacities (see the section titled Drivers of Dispersal Decision and Pond

Selection). Correlation between dispersal distances and size-corrected hindlimb length has been reported in *R. 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 three-day period. They concluded that this morphological shift is likely involved in the increased rate at which the toad invasion has progressed since its first introduction. In a more recent study, Hudson et al. (2016a) suggested that leg length could be under sexual selection favoring longer hindlimbs in males according to mating performance whatever their origin. Moreover, one should also keep in mind that developmental constraints imposed by pond environmental conditions such as ephemerality also largely contribute to morphological variations at metamorphosis including leg size (Gomez-Mestre and Buchholz 2006).

Behavioral Traits

Covariation between dispersal distances and behavioral traits has been reported in two anurans, the invasive *R. marina*, and *B. 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), who 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 *R. 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 et al.'s conclusions: individuals at the invasion front moved in straighter paths than did conspecifics radiotracked 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 exhibited straighter paths if their parents came from populations closer to the invasion front.

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 titled Phenotype-Dependent Emigration. In *R. 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 *B. 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).

Context-Dependent Transience

Euclidean Distances Between Sites

The spatial organization of breeding sites (i.e., pond network) affects transience. As dispersal corresponds to movement between breeding patches, 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 farthest pond). As reported in the section titled Transience and Dispersal Distances, the frequency of dispersal events decreases in a nonlinear fashion with the

between-patch Euclidean distances (Breden 1987; Berven and Grudzien 1990; Trenham et al. 2001; Funk et al. 2005; Gamble et al. 2007; Hamer et al. 2008; Hendrix et al. 2017; Muths et al. 2018; Cayuela et al. 2019a,b).

Landscape Structure

Both experimental and field studies have found that pond-breeding amphibians are able to detect habitat boundaries (Gibbs 1998; Rittenhouse and Semlitsch 2006; Stevens et al. 2006; Popescu and Hunter 2011; Cline and 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., dispersal, migration, 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 (see the section titled Consequences For Neutral Genetic Variation) in which genetic variation between patches cannot be directly interpreted as dispersal (see the section titled Consequences For Neutral Genetic Variation and Adaptive Processes). 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 and Desrochers 2005; Rowley and Alford 2007; Tatarian 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 and Hunter 1999; Rothermel and Semlitsch 2002; Patrick et al. 2006; Rittenhouse and Semlitsch 2006; Popescu and Hunter 2011; Cline and Hunter 2014, 2016; Ousterhout and Semlitsch 2018). Vegetation cover decreases dehydration rates (Rothermel and 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 semiarid environments may be less prone to prefer forest surfaces (Stevens et al. 2005, 2006; Youngquist and Boone 2014). Moreover, pond-breeding amphibians often avoid agricultural surfaces such as grasslands and crop fields (Jehle and Arntzen 2000; Rothermel and Semlitsch 2002; Rittenhouse and Semlitsch 2006; Cline and Hunter 2014, 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 and 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 cause 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 that may elicit road-avoidance behavior during transience (Cline and Hunter 2016; Cayuela et al. 2019a). Third, high mortality due to collisions with vehicles may occur when amphibians are forced to cross roads (Hels and Buchwald 2001; Andrews et al. 2008; Beebee 2013). Fourth, vehicle traffic has also been reported to increase hormone stress levels 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).

Consequences of Dispersal on the Dynamics and the Genetics of Spatially Structured Populations

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.

Consequences For Demographic Interdependence and Connectivity

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

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

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 the level of demographic interdependency between the units (i.e., subpopulations) forming spatially structured populations (Hastings 1993; Waples and 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 and Gaggiotti 2006).

Following the definition given by Lowe and 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 and Allendorf 2010). This is mainly because net local immigration and local recruitment are not easily disentangled using capture-recapture models (Nichols and 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. 2019b). The high dispersal rates reported for several pond-breeding amphibians (see the section titled Emigration Rates) 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 and Allendorf 2010). In contrast, for subpopulations experiencing decline (i.e., population growth rate of less than 1), low net immigration values can represent a large proportion of total recruitment.

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 *A. 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 interpond 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 greater than 1 km. In parallel, they showed that the relationship between interpond 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.

Consequences For Colonization/ Extinction Dynamics

Dispersal is a central parameter in metapopulation models because it affects population growth and colonization of unoccupied patches (Hanski and Gilpin 1991; Gilpin 2012). Most metapopulation models describe colonization-extinction dynamics through the area-isolation paradigm (Hanski 1998; Pellet et al. 2007) whereby extinction probability depends on patch size and colonization probability is a function of patch isolation. Patch isolation is usually quantified using distance-based metrics (often called *connectivity metrics*; Calabrese and Fagan 2004), taking into account between-site Euclidean distances and dispersal rates. In amphibians, studies have highlighted a negative relationship between extinction probability and connectivity (due to a *rescue effect*; Sjögren-Gulve 1994; Cosentino et al. 2011a) and a positive relationship between patch occupancy and connectivity (Zanini et al. 2009), and 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 turnover rates. In species reproducing in temporary patches, colonization-extinction rates are usually high (sometimes greater than 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. When a patch is unavailable for breeding during a given year, individuals may disperse toward a flooded patch or alternatively may remain patch-faithful and skip breeding (Cayuela et al. 2014, 2018d; Green and Bailey 2015). Likewise, recolonization probability depends on the breeding probability of patch-faithful individuals after pond refilling 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 ponds.

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 and Petit 2009; Lowe and Allendorf 2010; Cayuela et al. 2018b). As dispersal is a nonrandom process, it usually results in asymmetric gene flow between patches (Edelaar and 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 and 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 alleles (Broquet and Petit 2009). However, gene flow into a population can also constrain local adaptation (Lenormand 2002; but also see Jacob et al. 2017).

Consequences For Neutral Genetic Variation

Evidence indicates that the negative relationship between immigration probability and Euclidean distance between breeding patches (see the section titled Context-Dependent Transience) 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 B, available at https://doi.org/10.1086/707862) 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 and Grudzien 1990; Funk et al. 2005; Schmidt et al. 2006; Cayuela et al. 2019b). These studies found that genetic differentiation between patches decreased with increased dispersal rates and dispersal 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*. Cosentino et al. (2012) 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 populations.

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 B) that have detected significant landscape effects (Figure 5) 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. Those two variables were considered in 47% of the studies and 85% of these papers found that increases in slope and elevation enhanced genetic divergence among subpopulations. Soil moisture (5% of the studies) reduces genetic differentiation whereas solar radiation (2%) increases genetic differentiation. 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 differentiation was lower within than among watersheds (Goldberg and Waits 2010; Murphy et al. 2010). Other research has indicated that the proximity of wetlands and ditches are associated with lower genetic differentiation (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 the swimming abilities of species. Other studies revealed that lakes (7% of the studies) and large salt waterbodies (7%) increased genetic differentiation. 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 differentiation while 33% found the opposite pattern. In 75% of the cases, forest disturbance and harvesting increased genetic variation. Moreover, all of the studies reported that urban areas increased genetic differentiation. Agricultural areas had varied effects on genetic variation. All of the studies that have detected an effect of crops (19% of the studies) and vineyards (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 on genetic differentiation (2% of studies).

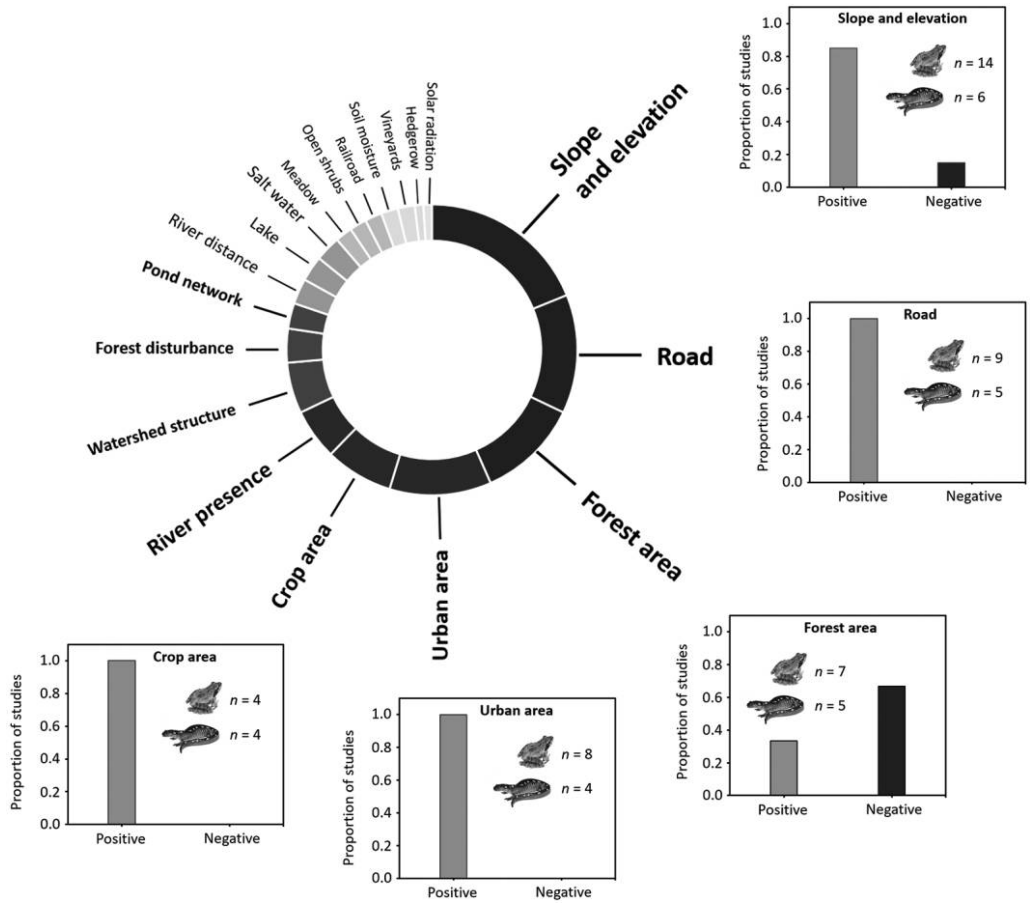

Figure 5. Environmental Associates of Genetic Divergence in Pond-Breeding Amphibians

At the top left, we show the proportion 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. See the online edition for a color version of this figure.

In the last decade, a few studies have investigated how breeding patch persistence over time affects genetic variation in amphibians (Chan and Zamudio 2009; Mims et al. 2015; Cayuela et al. 2019b). Chan and 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. (2019b) showed that spatially structured populations experiencing low-persistence breeding patches had lower genetic variation due to higher emigration rates and longer dispersal distances than did populations utilizing persistent breeding patches.

Consequences For Adaptive Processes

Gene flow as a consequence of dispersal can have opposing effects on the process of local adaptation. On 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 and Schluter 2008; but see

Marques et al. 2019). In contrast, gene flow can also counteract or even prevent local adaptation by homogenizing gene pools across demes and disrupting allele combinations favored 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 and Brodie 2015; Kosmala et al. 2017, 2018; Pastenes et al. 2017), 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. For instance, Bonin et al. (2006) identified eight amplified fragment length polymorphisms (AFLPs) 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 variation in gene expression, mostly involving genes related to nutrient metabolism, which are generally downregulated in high-altitude populations. In both cases, restricted dispersal and isolation in high-altitude populations appear to have led to local adaptation.

Research Avenues

quantifying dispersal rates and distances using modeling 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 to deal with imperfect detection of individuals (reviewed in Cayuela et al. 2018b). The remaining studies provided only the number of individuals that were captured in, at least, two distinct breeding patches during two or more consecutive years. Therefore, dispersal, survival, and recapture rates are confounded and estimates of dispersal rates and distances can be biased. Further capture-recapture studies should be undertaken to quantify dispersal rates and distances in more taxa and populations within taxa.

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 (Matthysen 2012; Ronce and Clobert 2012), no studies have examined the effect of social factors on amphibian dispersal. Studies indicate that both larval and adult amphibians have the ability to recognize their kin (Blaustein and Waldman 1992; Hokit and Blaustein 1997; Pfennig 1997). Vocalization (Waldman et al. 1992), chemical cues (Blaustein and 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.

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 behavioral trait

related to dispersal in *R. 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 behavioral traits related to dispersal may differ among genetically divergent amphibian populations (Brodin et al. 2013; Maes et al. 2013; Cayuela et al. 2019b). 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 *R. marina* (Rollins et al. 2015). In toads from both ends of the invasion-history gradient (low emigration propensity and short dispersal distances in core-range populations versus the opposite characteristics in front-range populations), Rollins et al. (2015) found differential upregulation of many genes, notably those involved in metabolism and cellular repair. However, beyond this work, no study has examined potential DNA polymorphism between dispersing and nondispersing 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 unstudied in amphibians. We propose a conceptual scheme (Figure 2) to show how genetic and epigenetic factors could influence premetamorphic and postmetamorphic 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 bisulfite sequencing.

Studying Dispersal and Eco-evolutionary Dynamics

An eco-evolutionary feedback occurs when external (biotic and abiotic) factors experienced by a population reciprocally influences fitness variation, selection pressures, and/or evolutionary responses (Pelletier et al. 2009; Schoener 2011). Feedback loops may emerge from the effects of individuals on population-, community-, and ecosystem-level processes. Eco-evolutionary dynamics have received little attention in the amphibian literature. For instance, Cayuela et al. (2019b) showed that anthropogenic variation in patch turnover in the spatially structured populations of *B. variegata* strongly affects dispersal patterns, which has far-reaching consequences on the evolutionary forces involved in migration-selection-genetic drift balance. In populations experiencing high patch turnover, increased dispersal and gene flow lead to higher neutral genetic diversity and larger effective population size (N_e) than in populations with low patch turnover. Large N_e usually increases the rate of evolution in populations (Gillespie 1999; Lanfear et al. 2014) and high standing genetic variation facilitates local adaptation (Barrett and Schluter 2008). Therefore, in populations with high patch turnover, larger N_e and higher genetic polymorphism should increase the evolutionary potential and the capacity of adaptive response to environmental changes (e.g., climate change, pollution). Furthermore, enhanced gene flow within these populations should increase the probability of evolutionary rescue (Vander Wal et al. 2013; Carlson et al. 2014) via the inflow of beneficial alleles under novel environmental conditions. Overall, this study suggests that humans, by affecting habitat persistence and dispersal, could select for toads that are more likely to persist through further additional anthropogenic stresses. Beyond the study case

presented by Cayuela et al. (2019b), dispersal-related eco-evolutionary dynamics remain poorly studied and we encourage further studies to examine this issue in amphibians.

Because of their ontogenetic habitat shift, pond-breeding amphibians have to engage in cyclical movements (i.e., nuptial migration and foraging movement; Dunning et al. 1992; Pope et al. 2000) ranging from very short distances to moderate ones according to the specificity of both the aquatic and terrestrial habitats. Since complementation movements are also subject to selection, one may ask whether ecological factors favoring 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) that 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.

Conclusions

Our review emphasized that the ecology and evolution of amphibian dispersal is influenced by immediate and delayed effects of the environment that affect the phenotype of individuals and dispersal decisions. The dispersal mechanisms at the individual level translate into highly variable emigration rates and dispersal distances at both intra- and interspecific levels. Highly variable emigration rates and dispersal kernels lead to complex patterns of gene flow, which likely have far-reaching consequences for eco-evolutionary processes. Overall, our synthesis complements the studies on dispersal of other organisms with complex life cycles, especially insects (e.g., Odonata, Trichoptera, Diptera, and Ephemeroptera). It shows that a larval stage in highly variable aquatic environments may have dramatic consequences for ecological and evolutionary processes in semi-aquatic organisms, which is particularly relevant in the context of current global change. Furthermore, our review provides new insights into the diversity and complexity of dispersal syndromes and patterns in vertebrates and highlights the suitability of amphibians as biological models to investigate the ecology and evolution of dispersal.

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