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Long-distance dispersal in amphibians

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Abstract

Although the distribution patterns of major amphibian lineages are mainly explained by a Pangean origin with subsequent vicariant diversification, dispersal events have exerted a strong influence on present-day distributions. Long-distance dispersal (LDD) involves movements outside the standard geographic limits and outside the genetic neighbourhood area of individuals. Although considered 'rare', LDD is disproportionately important to amphibian populations, species and communities. To understand the role of LDD in shaping current biogeographic patterns in these tetrapods, we reviewed the cases reported in the literature. A systematic bibliographic search was performed to obtain information on how many studies have dealt with LDD in amphibians, which methods they used, which taxa and distances were involved, and when/where events had apparently occurred. In 41 studies, we recovered at least 90 LDD events (3 active, 87 passive) involving at least 56 extant species and 38 genera. Most events (73) involved the colonization of islands, with rafting being suggested as the most conceivable means of overwater passive dispersal for these vertebrates. In this review, we show that LDD events have played an important role in shaping current amphibian biogeographic patterns, especially the occurrence of disjunct distributions and the colonization of islands.

Highlights

- This is the most complete and up-to-date review of long-distance dispersal (LDD) in amphibians, compiling information from more than 70 articles.
- Although amphibians are considered poor to moderate dispersers, we show that they do perform LDD.
- We propose that 10 km is a reasonable threshold for amphibian movements to be considered LDD.
- The longest active LDD movement recovered in our bibliographic search was 34 km.
- Passive overwater LDD events by means of rafting include movements of around 1,000 km across oceans.

Keywords: Anura, Biogeography, Caudata, Gymnophiona, island colonization, jump dispersal, overwater dispersal, transoceanic movement

Introduction

Some decades ago, there was a fierce debate in biogeography over the most appropriate method for analysing species formation and distributions, i.e., conventional evolutionary taxonomy vs. cladistics (Stoddart 1981). At that time these two methods were seen as opposites, and there was open hostility between the battle lines (Rosen 1981: 3). Discussions were so intense that the two sides accused each other of political motives for their views. Wallace-Darwinian dispersalism was regarded as imperialistic and colonialistic, for it would require colonization, competition and dominance (cf. Nelson 1978, Rosen 1981: 2). Cladistics were regarded as Marxist, for it would reflect the

view that changes occur not gradually but rapidly and abruptly (cf. Halstead 1980).

With the rise of the vicariance school (cf. Croizat, Nelson and Rosen 1974), dispersal was considered by cladistic biogeographers (e.g., Nelson and Platnick 1981) as 'unfalsifiable' and 'untestable' and thus simply not scientific. Over the last decades, however, the advance of molecular techniques and the revision of geological time calibrations have allowed for a refinement of biogeographic studies. This now enables researchers to make accurate predictions of divergence dates and locations of sister lineages, turning dispersal suggestions into subjects of refutation (de Queiroz 2005). Despite the predominance of the vicariance paradigm during the final decades of the last century, recent genetic

studies based on molecular clock calibration have resurrected the debate, strengthening the importance of long-distance movements, such as across oceans and seas (de Queiroz 2005, 2014).

Dispersal

Dispersal definitions vary greatly and are therefore usually confusing, mainly depending on the organism and scale considered. In a broad sense, dispersal can be defined as movement leading to spatial gene flow, whatever the behaviour or movement mode giving rise to it (Ronce 2007, Clobert et al. 2012). Although dispersal is an individual-based process, its consequences frequently scale up to the level of population properties (Jordano 2017). In this sense, rather than being relegated to a distance measurement, dispersal should be seen as a process leading to a distributional outcome of the movement itself (Dingle 1996).

Because dispersal definitions vary so much, it is important to define some concepts that we use in this paper. Normal dispersal is the expected movement of organisms within continuous tracts of suitable habitat or between patches of suitable habitat that are close together (de Queiroz 2014). It is also called short-distance dispersal or diffusion (Pielou 1979) and its result is the (more or less) steady expansion of the species range. Long-distance dispersal (LDD) involves movements outside the standard geographic limits and outside the genetic neighbourhood area of individuals (Jordano 2017), often involving movement across barriers (de Queiroz 2014). We consider jump dispersal as LDD that is performed in a markedly short period of time followed by successful establishment of a population (cf. Pielou 1979). In active dispersal, the organism accomplishes (or contributes to) the dispersal process through control of its own locomotion, whereas in passive dispersal the movement is largely outside the organism's immediate control, depending on external forces such as gravity, wind, water, and carrier organisms (Mattysen 2012).

Long-distance dispersal

LDD events are infrequent and scattered, but given sufficient time, their occurrence over time becomes increasingly probable (Darlington 1938, Stoddart 1981). Although considered rare, LDD is disproportionately important to populations, species, and communities (Nathan 2005, 2006), for it has a strong influence on gene flow and the structure of gene pools (Jordano 2017). Besides enabling the maintenance of genetic connectivity between disparate populations, LDD can also lead to the colonization of vacant habitats and thus range expansions, driving population diversification, including speciation (Jordano 2017). In general, populations founded as a result of LDD (especially jump dispersal) tend to diverge from the source populations. The founder and source populations are genetically isolated from one another because movement between them is hampered *per se* (de Queiroz 2014). The threshold defined for a dispersal event to be considered long-distance vs. normal varies according to the nature of the organisms, and although

it is typically arbitrary, its order of magnitude should reasonably reflect the scale of the process in question (Nathan 2005).

As a rule of thumb, LDD is usually mediated by passive movement (Shigesada and Kawasaki 2002) and is therefore also referred to as occasional dispersal (de Queiroz 2014). Yet, passive LDD should not be seen as 'accidental' or 'random' dispersal because statistical probability can aid in predicting which organisms are more often transported to given places based on knowledge of natural history, direction of currents and winds, etc. (Darlington 1938).

Movement in amphibians

Amphibians are the most basal extant tetrapods. Modern amphibians, comprising three orders, are usually small and possess physiological properties (e.g., their highly permeable skin) that make movements costly so that they only move when necessary (Wells 2007). Smith and Green (2005) compiled information from 166 articles on 90 living amphibian species and found that 44% of them actively moved no farther than 400 m, while just 5% were capable of movements greater than 10 km. They also found differences between orders, with 44% of the anuran and just 6% of the salamander species displaying maximum active dispersal distances greater than 1 km. Based on an inverse power law, Smith and Green (2005) predicted that, for anurans and salamanders, at least one individual is likely to move distances of 11–13 km and 8–9 km, respectively. Considerably less is known about movement patterns in caecilians. The maximum distance found by a mark-recapture study was 4.5 m away from the point of release (Measey et al. 2003), suggesting that caecilians are exceptionally poor dispersers, but further study is needed to characterize the dispersal behaviour of this group with any reliability.

Because amphibians are generally poor to moderate active dispersers and often philopatric, most species formation in this group is vicariant, principally dichopatric, that is, resulting from range subdivision (Vences and Wake 2007). In a large-scale historical biogeographic analysis involving approximately 45% of extant amphibians, Pyron (2014) found that Pangean origin and subsequent Laurasian and Gondwanan fragmentation explain a large proportion of patterns in the distribution of extant species. In line with this, several other phylogenetic studies found similar patterns (i.e., Roelants and Bossuyt 2005, San Mauro et al. 2005, Bossuyt et al. 2006, Feng et al. 2017; for more examples of vicariant species formation in amphibians, see Vences and Wake 2007). Nevertheless, extinction and dispersal have also exerted a strong influence on present-day distributions (Vences and Köhler 2008), including normal dispersal (i.e., terrestrial range expansion and land-bridge colonization) and overwater/stepping-stone events (Pyron 2014).

In fact, some occurrence patterns, such as the presence of amphibians on oceanic islands (i.e., that were never connected with continental landmasses), can only be explained by overwater jump dispersal events. In this regard, it is noteworthy that from

Darwin's time (1859) until recently, it was believed that amphibians could not traverse long distances across oceans because of salt intolerance and the risk of dehydration. Yet, recent reviews have shown that some degree of salt tolerance exists in more amphibian taxa than had previously been assumed (Hopkins and Brodie 2015). Moreover, certain lineages may in fact have dispersed across oceans several times in their evolutionary history (de Queiroz 2005, 2014). In amphibians, this paradigm shift has even led to the revision of previous hypotheses, such as the vicariant origin of eleutherodactyline frogs in the West Indies (Hass and Hedges 1991, Hedges 1996) in favour of overwater dispersal from South America (Heinicke et al. 2007).

Study goals

Recent reviews (e.g., de Queiroz 2005, 2014) have proposed that LDD events involving a variety of amphibian taxa and geographic regions have indeed taken place over geologic time. Our purpose here is to test this hypothesis and to determine the frequency of LDD in amphibians. Because these vertebrates are generally poor to moderate active dispersers, they are usually highly structured genetically over short geographic distances and retain high-resolution signals of historical events that generated current species distributions (Zeisset and Beebee 2008). Moreover, they typically show high levels of geographic variability in molecular markers (Vences and Wake 2007). For these reasons, they tend to be suitable models for the study of different biogeographic hypotheses, including long-distance movements such as jump dispersal across oceans. To understand the role of LDD in shaping current biogeographic patterns in amphibians, we review the cases for these tetrapods reported in the literature. For an introduction to the topic, we first present a general descriptive overview of amphibian passive LDD. Subsequently, based on a systematic review of the literature, we provide definitions of active and passive LDD in amphibians and discuss the principal cases.

Overview of passive LDD in amphibians

Since LDD events are typically 'rare' (Nathan 2005), they are seldom observed (Stoddard 1981). In amphibians, rafting has been suggested as the most conceivable means of overwater jump dispersal (e.g., Hedges 1996, Vences et al. 2003, Measey et al. 2007). In addition, the less-likely cases of storm and bird carriage have been discussed by earlier works (Darlington 1938) as well as more recent analyses (e.g., Measey et al. 2007). All these possible routes of amphibian LDD are discussed in the following sections.

Animals

Thienemann (1950) speculated that amphibian eggs could occasionally be carried in the plumage and on the feet and legs of aquatic birds. He also claimed that experiments conducted by Hesse (1924) revealed that the spawn of some anurans can remain out of the

water for up to four days without losing their capacity for development. Kleyheeg and van Leeuwen (2015) studied the potential of regurgitation by birds as means of seed dispersal and suggested that, if regurgitation occurs only a few hours after ingestion, it could also facilitate dispersal of less resistant organisms, such as – in this case – fish eggs. Fahr (1993) and Measey et al. (2007) discussed bird carriage as a mechanism by which amphibians may have colonized the Gulf of Guinea islands. Although the authors did not rule out this possibility, they considered it unlikely. Despite never having been documented, passive dispersal of amphibians (especially eggs and larvae) by other animals could be possible, although survival of the amphibians may be unlikely.

Humans

Human-mediated introduction of species in new areas, sometimes even on continents other than the species' origin, can result in non-native established populations. Kraus (2009) compiled worldwide information on so-called alien species with regard to amphibians, reporting more than 1,200 introduction events, involving ca. 180 species in ca. 600 localities. Although we recognize the importance of such LDD events, especially the potential of humans to introduce invasive species and spread diseases, in our paper we will not focus on this topic given the already vast literature on it.

Air

Although never proven, there are several published anecdotal reports of frog 'rains' (e.g., McAtee 1917, Elsom 1988), and some scientists have claimed that strong air currents and waterspouts can lift and transport these animals. For instance, Darlington (1938) speculated that amphibians could have reached the Greater Antilles islands via dead palm leaves transported by hurricanes. Nevertheless, such dispersal events of vertebrates are usually considered unimportant, for the animals should be carried for short distances, reach unfavourable environments and often arrive dead (McAtee 1917). Even so, it is important to note that high wind events (i.e., cyclones, typhoons, hurricanes) combined with heavy rains might create favourable conditions for the dispersal of floating rafts over large distances across bodies of water (see below).

Water

Driftwood, rafts, and floating meadows can be carried by river and marine currents over large distances, even crossing oceans and arriving at distant continents (Barber et al. 1959). Schuchert (1935), for instance, reported the occurrence of rafts that originated in the Amazon and Orinoco rivers and have been seen as far as 1,600 km out to ocean. Over the last decades, rafting has been the most invoked means of overwater LDD in amphibians, especially to explain the occurrence of these animals on islands (e.g., Hedges 1996, Vences et al. 2003, Measey et al. 2007). In this context, Kaiser et al. (1994) proposed the occurrence of a natural mechanism, involving the combination of

floating rafts and favourable ocean currents that might facilitate the dispersal of amphibians across oceans. Measey et al. (2007) went further and proposed the existence of 'freshwater paths', a synergy of favourable ocean currents and the reduction of salinity in marine surface waters caused by the discharge of huge amounts of freshwater from the mouths of large river systems. Such a mechanism would enhance chances of amphibian survival in rafts and was invoked to explain the occurrence of seven species (six anurans and one caecilian) native to oceanic islands in the Gulf of Guinea (Measey et al. 2007).

Anurans and even caecilians are commonly found in floating meadow rafts in large river basins (Achaval et al. 1979, Sarli et al. 1992, Schiesari et al. 2003). Small invertebrates can also be found in rafts (Donlan and Nelson 2003) and probably serve as a source of food for the vertebrates that share the flotsam. In journeys across oceans, fresh water could be supplied by rainfall. Additionally, depending on the raft's size and composition, it may even provide shelter from the sun. All things considered, rafting is the most plausible means of amphibian passive LDD, especially for jump dispersal across oceans.

Systematic review of the literature

Methods

We performed a bibliographic search to compile information on how many studies have addressed LDD in amphibians, which methods were used, which taxa were involved, and when and where events had apparently occurred. In October 2018, we conducted a search in Web of Science (all databases/all years since 1980/topic) and Scopus (all subject areas/all years to present/title, abstract, keywords) for scientific papers published in peer-reviewed journals containing the following terms (and their plurals): long-distance *or* jump *or* oversea *or* overwater *or* over-water *or* transoceanic *or* transmarine *and* dispersal *and* amphibia *or* anura *or* gymnophiona *or* caudata *or* urodela *or* frog *or* salamander *or* newt *or* caecilian. Our search retrieved 146 publications. We excluded 29 that dealt with taxa other than amphibians and another 62 that did not address LDD or whose definitions of LDD did not fit ours (see definitions below). We included another 15 published studies of our knowledge that were not listed in the results of these targeted searches. Although most cases of overwater LDD were by ancestral forms of extant amphibian species, in this review we refer to the currently living taxa. Taxonomy follows Frost (2019). Distances involved in past LDD events were estimated in the software GPlates v. 2.2 (Müller et al. 2018) using maps obtained from the PALEOMAP PaleoAtlas (Scotese 2016). To estimate distances, we simply measured the shortest straight line between places of origin and arrival at the geologic time proposed in the studies. We consider this the minimum possible route and acknowledge that true historical scenarios might have been more complex. However, obtaining higher accuracy would require the

use of complex models, which is beyond the scope of this study.

Results

We found 70 articles, all published between 1960 and 2019, mentioning LDD in amphibians (references in Appendix S1). Only 3 studies (4%), published in recent years and all led by W.H. Lowe, have explicitly dealt with amphibian LDD, mainly exploring theoretical questions based on mark-and-recapture studies of salamanders in the field. The majority (68%) of LDD references recovered in our bibliographic search came from molecular studies dealing with varied topics, such as biogeographic, taxonomic, and phylogenetic analyses. In these 48 studies, overwater jump dispersal was invoked as the most plausible explanation for present-day amphibian distributions when times of taxon divergence were not in agreement with geological histories, that is, when a vicariant origin would require much older ages of the lineages than what was in fact observed. Since taxon divergence dates usually go back thousands or even millions of years, LDD events in these studies were inferred instead of observed. The first studies of this kind used allozyme (e.g., Busack 1986, Kaiser et al. 1994, Toda et al. 1997) and albumin immunological data (e.g., Hedges et al. 1992, Hedges 1996). The more recent studies used mainly mitochondrial and/or nuclear DNA markers (e.g., Vences et al. 2003, Heinicke et al. 2007, Zimkus et al. 2017), sometimes coupled with analyses of morphological (e.g. Cannatella 2015) and osteological (e.g., Martínez-Solano et al. 2004) characters. One study (Verneau et al. 2009) performed phylogenetic analyses of parasites instead of their amphibian hosts. Thirty-nine studies (55%) invoked natural overwater passive dispersal by means of rafting (Table 1), most of them to explain the occurrence of amphibian species on islands (see below). Eleven studies (16%) invoked human-mediated overwater events, involving either intentional or accidental introductions. As mentioned before, this kind of LDD is not the focus of our review and will not be discussed.

Amphibian active LDD

Based on LDD definitions and observations in the literature, we consider amphibian active LDD as the movement of individuals (adults, juveniles, or larvae) through the control of their own locomotion at longer distances than those on average involved in regular movements (e.g., reproductive migration). This is regardless of whether the movement leads to the establishment of new populations and, consequently, to a species' geographic range expansion. Although there are many exceptions (Smith and Green 2005), as a group, amphibians are predominantly site-loyal and of low vagility (Vences and Wake 2007). They exhibit a wide range of dispersal strategies, and their dispersal capabilities suggest that occasional active migrants may connect populations separated by tens of kilometres (Smith and Green 2005). It is clear that different groups have different active dispersal

Table 1. Jump dispersal events recovered in a literature review on long-distance dispersal in amphibians.

Extant taxon ¹	From – To	When	Method	Reference
CAUDATA				
Salamandridae				
<i>Lyciasalamandra billae</i>	Turkey → Karpathos archipelago	-	allozymes, mtDNA	Veith et al. 2008
<i>Pleurodeles waltl</i>	Iberian Peninsula → Morocco	~ 0.24 Myr	mtDNA, nuDNA	Gutiérrez-Rodríguez et al. 2017
	Spain – Morocco	-	allozymes	Busack 1986
	Africa → Europe	-	mtDNA	Veith et al. 2004
ANURA				
Alytidae				
<i>Alytes muletensis</i>	Iberian Peninsula → Balearic Islands	~ 3 Myr	mtDNA, osteology	Martínez-Solano et al. 2004
Aromobatidae				
<i>Allobates chalcopis</i>	South America → Martinique	< 11.3 Myr	mtDNA, nuDNA	Fouquet et al. 2013
	South America → Martinique	0 – 45 Myr	albumin immunological data	Hedges 1996
Bufo				
<i>Bufo bufo</i>	Spain – Morocco	-	allozymes	Busack 1986
	between Baltic Sea islands ²	recent, current	allozymes	Seppä and Laurila 1999
<i>Oreophrynella</i>	proto-Andes → Pantepui ³	~ 38 Myr	mtDNA, nuDNA	Kok et al. 2017
<i>Peltophryne guentheri</i>	Mainland ↔ West Indies	~ 51 Myr	albumin	Hedges et al. 1992
	Hispaniola ↔ Cuba	~ 21.6 Myr	albumin	Hedges et al. 1992
	Puerto Rico ↔ Hispaniola	~ 9.6 Myr	albumin	Hedges et al. 1992
<i>Peltophryne lemur</i>	Puerto Rico ↔ Hispaniola	~ 9.6 Myr	albumin	Hedges et al. 1992
<i>Peltophryne peltocéphala</i>	Hispaniola ↔ Cuba	~ 21.6 Myr	albumin	Hedges et al. 1992
	Mainland ↔ West Indies	~ 51 Myr	albumin	Hedges et al. 1992
<i>Peltophryne peltocéphalus</i> Group ⁴	South America → West Indies	51 – 5.3 Myr	albumin immunological data	Hedges 1996
Craugastoridae				
<i>Craugastor</i>	South America → Central America	42 – 31 Myr	mtDNA, nuDNA	Heinicke et al. 2007, Hedges et al. 2008
<i>Pristimantis euphonides</i>	South America → Lesser Antilles	-	allozymes	Kaiser et al. 1994
<i>Pristimantis shrevei</i>	South America → Lesser Antilles	-	allozymes	Kaiser et al. 1994
Cycloramphidae				
<i>Thoropa taophora</i>	Brazil mainland ↔ continental islands	-	nuDNA	Duryea et al. 2015
Dicroglossidae				
<i>Hoplobatrachus tigerinus</i>	Bangladesh (north → south)	recent	mtDNA, nuDNA	Sultana et al. 2016
<i>Limnonectes</i>	Borneo → Philippines	-	mtDNA	Ewans et al. 2003
	Sulawesi → Philippines	-	mtDNA	Ewans et al. 2003
	Philippines → Sulawesi	-	mtDNA	Ewans et al. 2003
	Sulawesi → Moluccas	-	mtDNA	Ewans et al. 2003
	Java/Bali → Lesser Sundas	-	mtDNA	Ewans et al. 2003
	Borneo → Sulawesi	-	mtDNA	Ewans et al. 2003
Hylidae				
<i>Boana heilprini</i>	South America → Greater Antilles (Hispaniola)	30.5 – 20.2 Myr	mtDNA	Duellman et al. 2016
	South America → West Indies	-	albumin immunological data	Hedges 1996

¹Following Frost (2019); ²Possible active movements; ³Not referred to as overwater dispersal in the original publication; ⁴As in the original publication; ⁵*Osteopilus brunneus* in the original publication; ⁶Cited as *Boophis* n. sp. in Vences et al. (2003); ⁷Cited as *Mantidactylus* n. sp. in Vences et al. (2003); ⁸*Xenopus* and *Silurana* in the original publication; ⁹Due to recent taxonomic changes, not possible to determine the species (cited as *Rana limnocharis* in the original publication); ¹⁰Based on Hass and Hedges (1991); ¹¹Based on Maxson and Heyer (1988); ¹²An alternative hypothesis proposed by the author involves normal overland dispersal (with subsequent extinction) across Antarctica.

Table 1. Continued...

Extant taxon ¹	From – To	When	Method	Reference
<i>Dendropsophus ebraccatus</i>	South America → Central America	17.3 – 11.3 Myr	mtDNA	Duellman et al. 2016
<i>Dendropsophus microcephalus</i> Group ⁴	South America → Central America	13.8 – 8.6 Myr	mtDNA	Duellman et al. 2016
<i>Hyla meridionalis</i>	Spain – Morocco	-	allozymes	Busack 1986
<i>Hyla savignyi</i>	Middle East → Cyprus	recent	mtDNA	Poulakakis et al. 2013
<i>Osteopilus</i>	South America → Greater Antilles	26.1 – 17.3 Myr	mtDNA	Duellman et al. 2016
	South America (?) → West Indies	48 – 5 Myr	albumin immunological data	Hedges 1996
<i>Osteopilus dominicensis</i>	Hispaniola ↔ Jamaica	~ 15.6 Myr	albumin	Hedges et al. 1992
	Hispaniola ↔ Cuba	~ 22.2 Myr	albumin	Hedges et al. 1992
<i>Osteopilus ocellatus</i> ⁵	Jamaica ↔ Cuba	~ 25.2 Myr	albumin	Hedges et al. 1992
	Hispaniola ↔ Jamaica	~ 15.6 Myr	albumin	Hedges et al. 1992
<i>Osteopilus septentrionalis</i>	Mainland ↔ West Indies	~ 48 Myr	albumin	Hedges et al. 1992
	Jamaica ↔ Cuba	~ 25.2 Myr	albumin	Hedges et al. 1992
	Hispaniola ↔ Cuba	~ 22.2 Myr	albumin	Hedges et al. 1992
Hyperoliidae				
<i>Heterixalus</i>	Africa → Madagascar	~ 31 Myr	mtDNA, nuDNA	Pyron 2014
	Africa → Madagascar	19 – 30 Myr	mtDNA, nuDNA	Vences et al. 2003
<i>Hyperolius</i>	West-Central Africa → São Tomé	8.9 – 3.4 Myr	mtDNA, nuDNA	Bell et al. 2015a
<i>Hyperolius molleri</i>	São Tomé → Príncipe	1.1 – 0.27 Myr	mtDNA, nuDNA	Bell et al. 2015a
	São Tomé → Príncipe	-	mtDNA, nuDNA	Bell et al. 2015b
<i>Tachycnemis</i>	Africa → Madagascar	~ 31 Myr	mtDNA, nuDNA	Pyron 2014
	Madagascar → Seychelles	11 – 21 Myr	mtDNA, nuDNA	Vences et al. 2003
<i>Tachycnemis seychellensis</i>	Madagascar → Seychelles	11 – 19 Myr	mtDNA, nuDNA	Maddock et al. 2014
	Madagascar → Seychelles	9.79 – 35.34 Myr	nuDNA	Crottini et al. 2012
Eleutherodactylidae				
Eleutherodactylinae	South America → Lesser Antilles	~ 20 Myr	mtDNA, nuDNA	Heinicke et al. 2007
	Hispaniola/Puerto Rico → Lesser Antilles	~ 20 Myr	mtDNA, nuDNA	Heinicke et al. 2007
<i>Eleutherodactylus</i>	South America → West Indies	47 – 29 Myr	mtDNA, nuDNA	Heinicke et al. 2007, Hedges et al. 2008
<i>Eleutherodactylus gossei</i>	Mainland ↔ West Indies	~ 37.2 Myr	albumin	Hedges et al. 1992 ¹⁰
	Jamaica ↔ Cuba	~ 24.6 Myr	albumin	Hedges et al. 1992 ¹⁰
	Hispaniola ↔ Jamaica	~ 22.8 Myr	albumin	Hedges et al. 1992 ¹⁰
<i>Eleutherodactylus nubicola</i>	Mainland ↔ West Indies	~ 37.2 Myr	albumin	Hedges et al. 1992 ¹⁰
	Jamaica ↔ Cuba	~ 24.6 Myr	albumin	Hedges et al. 1992 ¹⁰
<i>Eleutherodactylus pictissimus</i>	Hispaniola ↔ Jamaica	~ 22.8 Myr	albumin	Hedges et al. 1992 ¹⁰
	Hispaniola ↔ Cuba	~ 22.2 Myr	albumin	Hedges et al. 1992 ¹⁰
<i>Eleutherodactylus planirostris</i>	Mainland ↔ West Indies	~ 37.2 Myr	albumin	Hedges et al. 1992 ¹⁰
	Jamaica ↔ Cuba	~ 24.6 Myr	albumin	Hedges et al. 1992 ¹⁰
	Hispaniola ↔ Cuba	~ 22.2 Myr	albumin	Hedges et al. 1992 ¹⁰
<i>Eleutherodactylus (Syrrhophus)</i> ⁴	Cuba → North America	~ 19 Myr	mtDNA, nuDNA	Heinicke et al. 2007, Hedges et al. 2008
<i>Eleutherodactylus (Euhyas) luteolus</i> Species Series ⁴	Cuba → Jamaica	-	mtDNA, nuDNA	Hedges et al. 2008
<i>Eleutherodactylus (Euhyas) ricordii</i> Species Series ⁴	Cuba ↔ Hispaniola	-	mtDNA, nuDNA	Hedges et al. 2008
Leptodactylidae				

¹Following Frost (2019); ²Possible active movements; ³Not referred to as overwater dispersal in the original publication; ⁴As in the original publication; ⁵*Osteopilus brunneus* in the original publication; ⁶Cited as *Boophis* n. sp. in Vences et al. (2003); ⁷Cited as *Mantidactylus* n. sp. in Vences et al. (2003); ⁸*Xenopus* and *Silurana* in the original publication; ⁹Due to recent taxonomic changes, not possible to determine the species (cited as *Rana limnocharis* in the original publication); ¹⁰Based on Hass and Hedges (1991); ¹¹Based on Maxson and Heyer (1988); ¹²An alternative hypothesis proposed by the author involves normal overland dispersal (with subsequent extinction) across Antarctica.

Table 1. Continued...

Extant taxon ¹	From – To	When	Method	Reference
<i>Leptodactylus albilabris</i>	Mainland ↔ West Indies	~ 39.6 Myr	albumin	Hedges et al. 1992 ¹¹
	South America → West Indies	40 – 4.5 Myr	albumin immunological data	Hedges 1996
	South America → West Indies	24 – 58 Myr	mtDNA	Hedges and Heinicke 2007
<i>Leptodactylus fallax</i>	South America → West Indies	23 – 34 Myr	mtDNA	Hedges and Heinicke 2007
	South America → Lesser Antilles	3 – 7 Myr	albumin immunological data	Hedges 1996
<i>Leptodactylus insularum</i>	Central/South America → West Indies	0 – 2 Myr	albumin immunological data	Hedges 1996
	South America → Trinidad	~ 1 Myr	mtDNA	Camargo et al. 2009
<i>Leptodactylus validus</i>	South America → Tobago	~ 220 Ka	mtDNA	Camargo et al. 2009
	Trinidad → Lesser Antilles	400 – 117 Ka	mtDNA	Camargo et al. 2009
	South America → West Indies	0 – 2 Myr	albumin immunological data	Hedges 1996
Mantellidae				
<i>Boophis nauticus</i> ⁶	Madagascar → Mayotte	< 8.7 Myr	mtDNA, nuDNA	Vences et al. 2003
	Madagascar → Mayotte	-	mtDNA, morphology, bioacoustic	Glaw et al. 2019
<i>Blommersia transmarina</i> ⁷	Madagascar → Mayotte	< 8.7 Myr	mtDNA, nuDNA	Vences et al. 2003
	Madagascar → Mayotte	-	mtDNA, morphology, bioacoustic	Glaw et al. 2019
Micrixalidae				
<i>Micrixalus</i>	Africa → South Asia	~ 29 Myr	mtDNA, nuDNA	Pyron 2014
Microhylidae				
Microhylidae	Africa → Madagascar	~ 66 Myr	nuDNA	Feng et al. 2017
	Africa → South America	~ 66 Myr	nuDNA	Feng et al. 2017
<i>Mantophryne</i>	Papuan peninsula → Louisiade archipelago	-	mtDNA, nuDNA	Oliver et al. 2013
	Papuan peninsula → D'Etrecasteaux archipelago	-	mtDNA, nuDNA	Oliver et al. 2013
Pelodyridae				
Pelodyridinae	South America → Australia	61 – 52 Myr	mtDNA, nuDNA	Pyron 2014 ¹²
Phyllomedusidae				
<i>Agalychnis</i>	South America → Central America	12.3 – 7.9 Myr	mtDNA	Duellman et al. 2016
Pipidae				
<i>Xenopus</i> ⁸	South America → Africa	40 – 75 Myr	nuDNA, morphology	Cannatella 2015
Ptychadenidae				
<i>Ptychadena mascareniensis</i>	Africa → Madagascar	-	mtDNA	Vences et al. 2004
	Africa → Madagascar	14.2 – 2.3 Myr	molecular analysis of parasites	Verneau et al. 2009
	East Africa → Madagascar	~ 15.5 Myr	mtDNA, nuDNA	Zimkus et al. 2017
<i>Ptychadena newtoni</i>	East Africa → São Tomé	-	mtDNA	Measey et al. 2007
	Africa → São Tomé	~ 11.4 Myr	mtDNA, nuDNA	Zimkus et al. 2017
Ranidae				
<i>Amnirana</i>	Southeast Asia → Africa	~ 18.7 Myr	mtDNA, nuDNA	Oliver et al. 2015
<i>Papurana kreffti</i>	New Guinea → Solomon and Bismarck Islands	~ 2.98 Myr	mtDNA, nuDNA	Oliver et al. 2015
<i>Pelophylax bedriagae</i>	Middle East → Cyprus	~ 1.65 Myr	mtDNA	Poulakakis et al. 2013

¹Following Frost (2019); ²Possible active movements; ³Not referred to as overwater dispersal in the original publication; ⁴As in the original publication; ⁵*Osteopilus brunneus* in the original publication; ⁶Cited as *Boophis* n. sp. in Vences et al. (2003); ⁷Cited as *Mantidactylus* n. sp. in Vences et al. (2003); ⁸*Xenopus* and *Silurana* in the original publication; ⁹Due to recent taxonomic changes, not possible to determine the species (cited as *Rana limnocharis* in the original publication); ¹⁰Based on Hass and Hedges (1991); ¹¹Based on Maxson and Heyer (1988); ¹²An alternative hypothesis proposed by the author involves normal overland dispersal (with subsequent extinction) across Antarctica.

Table 1. Continued...

Extant taxon ¹	From – To	When	Method	Reference
<i>Fejervarya</i> sp. ⁹	China → Ryukyu archipelago ↔ Japan main islands	-	allozymes	Toda et al. 1997
<i>Rana temporaria</i>	between Baltic Sea islands ²	recent, current	allozymes	Seppä and Laurila 1999
<i>Sanguirana</i>	Luzon → Mindanao	~ 7.3 Myr	mtDNA, nuDNA	Brown et al. 2016
	Luzon → Western Visayas	~ 5.9 Myr	mtDNA, nuDNA	Brown et al. 2016
Rhacophoridae				
<i>Buergeria japonica</i>	Amami → Tokara Archipelago	0.1 – 2.9 Myr	mtDNA	Tominaga et al. 2015
	Amami → Takara	~ 24.8 Ka	mtDNA, nuDNA	Komaki et al. 2017
	Takara → Taira	~ 9.1 Ka	mtDNA, nuDNA	Komaki et al. 2017
	Taira → Naka	~ 4.6 Ka	mtDNA, nuDNA	Komaki et al. 2017
	Naka → Kuchi	~ 1.8 Ka	mtDNA, nuDNA	Komaki et al. 2017

¹Following Frost (2019); ²Possible active movements; ³Not referred to as overwater dispersal in the original publication; ⁴As in the original publication; ⁵*Osteopilus brunneus* in the original publication; ⁶Cited as *Boophis* n. sp. in Vences et al. (2003); ⁷Cited as *Mantidactylus* n. sp. in Vences et al. (2003); ⁸*Xenopus* and *Silurana* in the original publication; ⁹Due to recent taxonomic changes, not possible to determine the species (cited as *Rana limnocharis* in the original publication); ¹⁰Based on Hass and Hedges (1991); ¹¹Based on Maxson and Heyer (1988); ¹²An alternative hypothesis proposed by the author involves normal overland dispersal (with subsequent extinction) across Antarctica.

characteristics and capabilities (larvae vs. juveniles vs. adults; anurans vs. salamanders vs. caecilians; terrestrial vs. aquatic vs. arboreal vs. fossorial; pond-breeding vs. direct development; etc.) and that different features of the landscape can affect the success of such movements. Because of these differences, it is difficult to assign a threshold over which a movement should be considered long-distance. Despite this, the few studies that have compiled information on amphibian movement distances (e.g., Marsh and Trenham 2001, Smith and Green 2005) have shown that, in general, amphibians rarely travel distances greater than 10 km. Smith and Green (2005) found that the average maximum movement recorded for anurans is 2.02 km and suggested that for both salamanders and anurans population differentiation is most likely to occur at scales upward of 10 km. Thus, we here propose that 10 km is a reasonable threshold for an active amphibian movement to be considered LDD.

Amphibian passive LDD

Based on LDD definitions and observations in the literature, we use the following definition for passive LDD in amphibians. Individuals travel passively (movement occurs outside of their own control) over longer distances than those involved in regular active movements, regardless of whether this leads to the establishment of new populations and, consequently, to a species' geographic range expansion. This can apply to individuals at any life stage, from eggs to adults. Jump dispersal, in contrast, requires the successful establishment of a population (cf. Pielou 1979). Following the same criteria we used for active LDD (see above), we propose that 10 km is an appropriate minimum distance for a passive amphibian movement to be considered LDD.

Jump dispersal

Even though only 5 studies explicitly used this term, we consider all of the natural overwater passive

LDD events found in our literature search to be jump dispersal (Table 1, Fig. 1). We recovered at least 87 events involving at least 53 extant species and 36 extant genera reported in 38 studies. The majority of events (84) involved anurans (51 species) and only 3 salamanders (2 species). Although no study reported LDD events for caecilians, the occurrence of an endemic species on a continental island (*Schistometopum thomense* in São Tomé, Gulf of Guinea) was suggested by Measey et al. (2007) to be the result of transoceanic dispersal by means of rafting, that is, jump dispersal.

Even though most cases of jump dispersal reported in the literature (Table 1) involve the colonization of islands (see below), there are also suggestions of movements between continental landmasses separated by oceans and seas, such as between Africa and Europe (*Bufo bufo*, *Hyla meridionalis*, Busack 1986; *Pleurodeles waltl*, Busack 1986, Veith et al. 2004, Gutiérrez-Rodríguez et al. 2017), Africa and South America (*Xenopus* spp., Cannatella 2015; microhylids, Feng et al. 2017), Africa and South Asia (*Micrixalus*, Pyrson 2014) and South America and Central America (*Craugastor*, Heinicke et al. 2007, Hedges et al. 2008; *Agalychnis*, *Dendropsophus ebraccatus*, *D. gr. microcephalus*, Duellman et al. 2016).

Amphibians on islands

Usually, two competing biogeographic views are invoked to explain the presence of amphibians on islands: (i) populations were continuously distributed before island formation and were subsequently isolated following the splitting of land masses and/or the rise of water levels; (ii) populations were introduced by humans or naturally established by dispersal, either normal active dispersal across previous land connections or via jump dispersal.

The Caribbean region has proven to be the ideal natural laboratory to test these alternative hypotheses. Working in this region, based on molecular data, Hedges et al. (1992) were pioneers in providing scientific

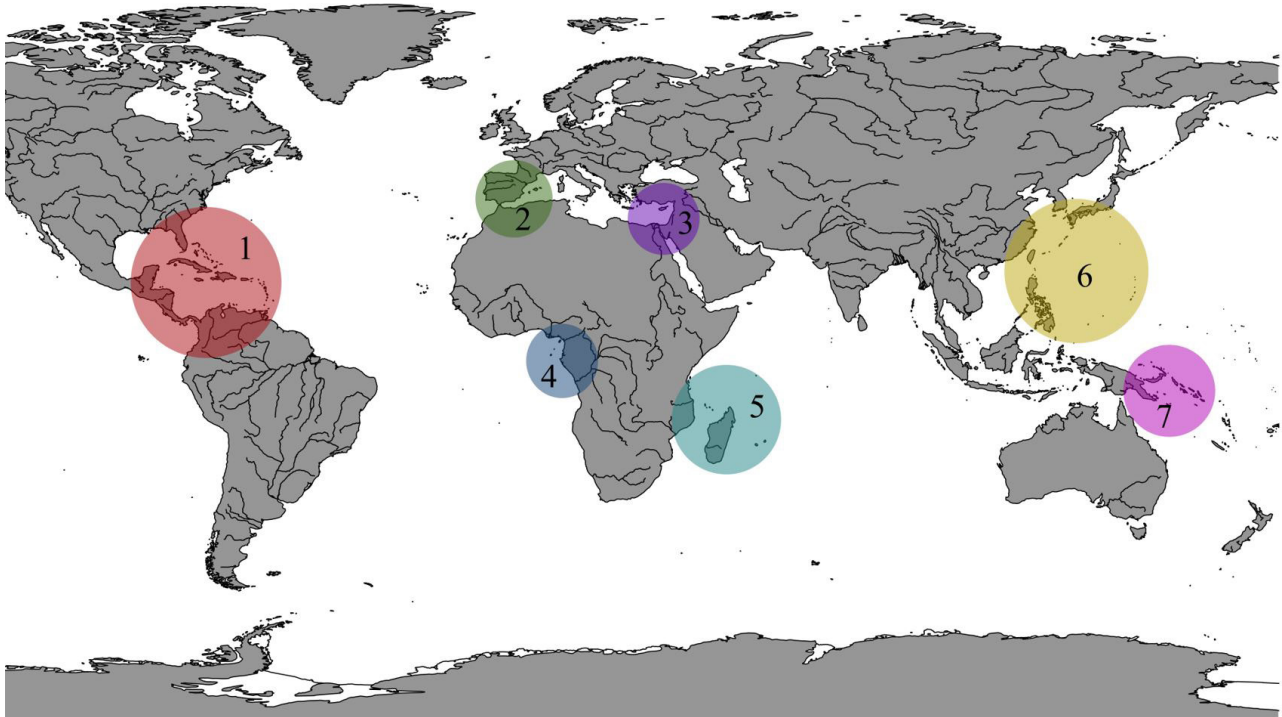


Figure 1. Schematic map showing regions where most long-distance dispersal events of amphibians retrieved in our bibliographic search appear to have occurred. 1 = West Indies and surroundings; 2 = Mediterranean Sea, Iberian Peninsula; 3 = Mediterranean Sea, Middle East; 4 = Gulf of Guinea; 5 = Madagascar, Comoros and Seychelles; 6 = Philippine Sea; 7 = Solomon and Bismarck archipelagos. For detailed information about these events, see Table 1.

evidence that amphibians might have colonized islands via overwater dispersal instead of via ancient land connections. Hedges (1996) went further and, challenging the popular vicariance paradigm, proposed that ancestors of most of the extant Caribbean amphibian fauna arrived on the islands attached to flotsam following water currents originating in South America. Further studies (Hedges and Heinicke 2007, Heinicke et al. 2007, Hedges et al. 2008, Duellman et al. 2016) not only confirmed previous LDD predictions but also included other taxa and refined dates of dispersal events.

Regarding continental islands, sometimes normal dispersal across former land bridges (e.g. O'Connell et al. 2018) and previous occurrence before island formation (e.g., Lourenço et al. 2018, Martínez-Solano and Lawson 2009) were invoked to explain amphibian occurrence. In other cases, such as in Madagascar, transoceanic jump dispersal from Africa, with subsequent species-rich radiations into the rainforests, was invoked to explain the highly endemic amphibian fauna of the island (Vences 2004). With respect to the presence of amphibians on oceanic islands, until recently researchers believed that it was the result of human translocations (Vences et al. 2003). Recent molecular studies have shown, however, that divergence times of island and mainland species are much deeper than the origin of humans, leaving natural jump dispersal as the only possible explanation for amphibian occurrence on these islands.

In our bibliographic search, we found 30 studies reporting at least 73 jump dispersal events that resulted in the colonization of at least 39 islands by at least 42 extant amphibian species and 25 genera (Table 1). The majority of cases (54%) come from the West Indies region. This can be explained both by the high diversity of endemic amphibian species on these islands and the large number of studies conducted in the region. Also worth noting are the studies conducted in Africa (Gulf of Guinea, Comoros, Seychelles and Madagascar), the Pacific Ocean (Tokara, Ryukyu, Philippine, Solomon and Bismarck archipelagos), and the Mediterranean Sea (Cyprus and the Balearic islands) (Table 1, Fig. 1).

Distances

We found only 3 studies that recorded amphibian active movements at distances greater than 10 km, all involving adult bufonid toads, namely *Anaxyrus fowleri* (34 km, Smith and Green 2006), *A. boreas* (13 km, Schmetterling and Young 2008), and *Rhinella marina* (21.8 km, Phillips et al. 2007).

Concerning passive LDD, given the high degree of uncertainty surrounding these events, only a couple of studies have attempted to speculate about the distances travelled. To calculate reliable estimates of these distances, one would have to know – with relatively high accuracy – the timing of the event, the geological conformation of the region at that time (including sea levels, direction of ocean currents, possible existence

of land/ice connections and stepping stone islands, etc.), and the approximate points of origin and arrival. Unfortunately, for most cases, this information is not available or is not accurate enough. In fact, out of 87 jump dispersal events recovered in our bibliographic search (Table 1), only 12 meet these requirements. For the remaining cases, the age estimates of events are not precise enough (or were not estimated at all), the origin and destination points are too generic (e.g., from Africa to South America) or events occurred in places with complicated and still unsolved geological histories, such as the Caribbean region (for a review of the different geological hypotheses for this region, see James et al. 2009). Nevertheless, some cases are worth discussing.

In the Mediterranean Sea, LDD events generally appear to have occurred over shorter distances than in other regions. Gutiérrez-Rodríguez et al. (2017) suggested that the salamander *Pleurodeles waltl* may have rafted from the Iberian Peninsula to Morocco, covering distances between 3.5 and 14.4 km across the Strait of Gibraltar. Poulakakis et al. (2013) proposed that the ranid frog *Pelophylax bedriagae* colonized Cyprus from the Middle East mainland crossing distances of at least 30 km over the sea. Martínez-Solano et al. (2004) argued that the ancestor of the toad *Alytes muletensis* must have reached the Balearic Islands through a transmarine colonization process from the Iberian Peninsula. Our calculations in GPlates estimate distances at 150–250 km for this LDD event.

Distances crossed in the Indian Ocean region were considerably longer. We recovered at least 4 LDD events from the African mainland to Madagascar (*Heterixalus*, Vences et al. 2003, Pyron 2014; *Tachycnemis*, Pyron 2014; *Ptychadena mascareniensis*, Verneau et al. 2009, Zimkus et al. 2017; Microhylidae, Feng et al. 2017). Our calculations in GPlates estimate distances at 350–500 km for these events, depending on the geologic time at which they occurred. Furthermore, Vences et al. (2003) suggested that mantellid frogs (*Boophis nauticus* and *Blommersia transmarina*; cf. Glaw et al. 2019) dispersed from Madagascar to Mayotte in Comoros crossing distances of at least 250 km over the sea.

Still, the most enlightening cases come from the Gulf of Guinea in the Atlantic Ocean. Measey et al. (2007) suggested that the frog *Ptychadena newtoni* reached São Tomé island in rafts leaving the mouth of the Congo River in western Central African mainland, covering distances of around 1,000 km across the ocean. A similar pattern was proposed to explain the presence of hyperoliid frogs (*Hyperolius*) in the Gulf of Guinea. Bell et al. (2015a,b) suggested that these amphibians reached São Tomé via rafts originated either in the mouth of the Congo or the Ogooué rivers (1,000 and 250 km from the island, respectively) and further dispersed over 150 km to its neighbour island Príncipe.

Although our results demonstrate that LDD via rafting can indeed involve long journeys across oceans, it does not necessarily mean that amphibians covered these distances in just one trip. Tectonic processes and past fluctuations in sea levels have constantly increased and decreased land areas, with many potential stepping-stone islands emerging and subsiding over time. Because of that, we cannot rule out that these journeys were in fact completed in multiple shorter steps.

General conclusions

Although the distribution patterns of major amphibian lineages are mainly explained by a Pangean origin with subsequent vicariant diversification following the Laurasian and Gondwanan fragmentation, extinction and dispersal events have also exerted a strong influence on present-day distributions (Vences and Köhler 2008, Pyron 2014). Despite the substantial evidence for dispersal that we have presented in this review, it would still be premature to conclude that dispersal is more important than vicariance in explaining distributions broken up by oceans (de Queiroz 2005). Yet, we have shown that overwater jump dispersal events have played an important role in generating current amphibian biogeographic patterns, especially the occurrence of disjunct distributions and the colonization of islands.

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Author contributions

All authors developed the idea of this study and contributed equally to discussions. LFMF led the bibliographic search and analysis with support of MM. The manuscript was written by LFMF with input from SL.

Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>

Appendix S1. List of 70 studies recovered in the bibliographic search on long-distance dispersal in amphibians.

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