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Radically different phylogeographies and patterns of genetic variation in two European brown frogs, genus *Rana*

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ABSTRACT

We reconstruct range-wide phylogeographies of two widespread and largely co-occurring Western Palearctic frogs, *Rana temporaria* and *R. dalmatina*. Based on tissue or saliva samples of over 1000 individuals, we compare a variety of genetic marker systems, including mitochondrial DNA, single-copy protein-coding nuclear genes, microsatellite loci, and single nucleotide polymorphisms (SNPs) of transcriptomes of both species. The two focal species differ radically in their phylogeographic structure, with *R. temporaria* being strongly variable among and within populations, and *R. dalmatina* homogeneous across Europe with a single strongly differentiated population in southern Italy. These differences were observed across the various markers studied, including microsatellites and SNP density, but especially in protein-coding nuclear genes where *R. dalmatina* had extremely low heterozygosity values across its range, including potential refugial areas, whereas *R. temporaria* had comparably high range-wide values, including many areas of probable postglacial colonization. A phylogeny of *R. temporaria* based on various concatenated mtDNA genes revealed that two haplotype clades endemic to Iberia form a paraphyletic group at the base of the cladogram, and all other haplotypes form a monophyletic group, in agreement with an Iberian origin of the species. Demographic analysis suggests that *R. temporaria* and *R. dalmatina* have genealogies of roughly the same time to coalescence (TMRCA ~3.5 mya for both species), but *R. temporaria* might have been characterized by larger ancestral and current effective population sizes than *R. dalmatina*. The unusually high genetic variation in *R. temporaria* can therefore be explained by its early range expansion out of Iberia, with subsequent cycles of differentiation in cryptic glacial refugial areas followed by admixture, while the range expansion of *R. dalmatina* into central Europe is a more recent event.

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1. Introduction

Numerous phylogeographic studies on European animals and plants have contributed to understanding how past climatic changes, with associated regional extinctions and recolonizations, have shaped the distribution and genetic structure of organisms (reviewed in Taberlet et al. (1998), Hewitt (1999, 2004), Waltari et al. (2007) and Weiss and Ferrand (2007)). The origin of most species of animals and plants in this region predates the Pleistocene (e.g., Klicka and Zink, 1997; Avise et al., 1998; Willis and Niklas, 2004), but their major intraspecific phylogeographic units have often diverged in glacial refugial areas (Taberlet et al., 1998; Hewitt, 2004) during the glacial episodes of the Quaternary, about 2 million years ago (mya) to present. Temperate-adapted species are generally thought to have retreated during glaciations into one of the major Mediterranean refugial areas, i.e., the Iberian and Italian peninsulas and the Balkan region, while cold-adapted species retreated to northern refugia during interglacials. Recent work has however revealed a more complex scenario in many species, featuring sporadic refugia in otherwise uninhabitable areas (e.g., Provan and Bennett, 2008; Stewart et al., 2010). In fact, the existence of extra-Mediterranean refugial areas might be the rule and not the exception, and might also apply to many temperate-adapted species (Schmitt and Varga, 2012), possibly favored by specific terrain characteristics (Dobrowski, 2011). As recently argued by Recuero and García-París (2011), geographical refugial areas can be furthermore subdivided into strict-sense refugia (i.e., previously uncolonized areas into which a species retreated during climatic shifts) or sanctuaries (i.e., areas within a species range that remained climatically suitable during glaciations and to which the species was restricted during glacial periods).

The phylogeographic history of a species will also have profound consequences on the genetic variation within species and populations. For markers predominantly shaped by historical and neutral processes, the presence of deep genealogical lineages and divergent haplotypes, often correlated with high values of genetic variation within populations, is suggested to characterize refugial areas. On the other hand, only a few haplotypes and limited genetic variation occur in recently (re)colonized areas because range expansions with associated “allele surfing” lead to changes in allele frequencies and an overall reduction of variation (Excoffier et al., 2009). Hence, in phylogeography, especially in its novel statistical form (Knowles, 2009), assessing variation is paramount to tracing range expansions and to understanding the location of refugial areas. On the other hand, genetic variation of adaptive markers has a plethora of profound consequences for the organisms involved, including population viability (e.g., reviewed by Allentoft and O'Brien (2010) for amphibians) and the success and speed of range expansion (Lockwood et al., 2005; Simberloff, 2009), and in general can influence the ecology of populations, communities and ecosystems (Vellend, 2005; Vellend and Geber, 2005; Hughes et al., 2008). However, variation does not necessarily correlate between neutrally evolving markers and those under selection (e.g., Reed and Frankham, 2001; Bekessy et al., 2003), and mitochondrial and nuclear variation are not necessarily correlated either (e.g., Jorde et al., 2000 vs. Bortoloni et al., 1998).

Cryptic refugial areas have also been found in various European amphibians (e.g., *Rana arvalis*, *R. temporaria*, *Bufo calamita*, *Pelobates fuscus*: Babik et al., 2004; Rowe et al., 2006; Crottini et al., 2007; Stefani et al., 2012). In general, phylogeographic studies of widespread amphibian species, especially at northern latitudes, have shown fast postglacial range expansions inferred from genetic uniformity across large parts of their ranges (e.g., Kuchta and Tan, 2005; Crottini et al., 2007; Babik et al., 2009; Makowsky et al.,

2009). This suggests that some amphibian species are able to disperse over large distances in short time spans, although the phylogeographic pattern encountered in most amphibians consists of deep gene trees with an allopatric distribution of major lineages, and often with private haplotypes in most populations (category I of Avise, 2000).

The genus *Rana*, as currently understood (Frost et al., 2006), is a group of neobatrachian frogs largely restricted to the Palearctic. While the delimitation of the genus is not yet fully clarified with respect to Asian species (e.g., Che et al., 2007), the systematics of Western Palearctic *Rana* is comparatively well understood (Veith et al., 2003). These comprise 10 species of medium to large-bodied (4–8 cm) brown-colored frogs, commonly called brown frogs. While some species have small ranges, e.g. on the southern slope of the central Pyrenees (*R. pyrenaica*) or in Italy (Northern Italy: *R. latastei*; along the Apennine chain: *R. italica*), others are widespread, occupying vast areas of Europe, as illustrated by *R. arvalis*, *R. dalmatina* and *R. temporaria*. Especially the latter, also called the European common frog, is renowned for occupying a diverse set of habitats and maintaining viable populations from sea-level up to 2500–2800 m elevation in the Pyrenees and the Alps, and from subarctic to more temperate regions in northwestern Spain (Grossenbacher, 1997b; Vences et al., 2003; Tiberti and von Hardenberg, 2012). *Rana temporaria* has been intensively studied in many respects; by 2003 there were already more than 4200 scientific publications on this species available (Vences et al., 2003), and its evolution has since then been the focus of many further studies (e.g., Hitchings and Beebee, 1997; Palo et al., 2004; Vieites et al., 2004; Veith et al., 2002, 2012; Schmeller and Merilä, 2007; Lesbarrères et al., 2007; Teacher et al., 2009; Phillimore et al., 2010; Richter-Boix et al., 2010; Zeisset and Beebee, 2010; Lind et al., 2011; Stefani et al., 2012). The European common frog contains deep mitochondrial lineages, which partly are given the rank of subspecies (Veith et al., 2002, 2003, 2012; Palo et al., 2004; Teacher et al., 2009), but the exact geographic distribution of these population lineages is unknown, as a range-wide comprehensive phylogeographic study for this species is missing so far. One recurrent theme in molecular studies of the European common frog has been a relatively high amount of variation found among and within populations of this species. On the contrary, preliminary data suggest low genetic variation in several other European brown frogs, such as the geographically restricted *R. pyrenaica* (Carranza and Arribas, 2008), *R. latastei* (Ficetola et al., 2007), and the northernmost populations of *R. italica* (Canestrelli et al., 2008), but also the widespread agile frog, *R. dalmatina* (e.g., Petraccioli et al., 2010). This latter species co-occurs with *R. temporaria* over much of its range, although its distribution is located more to the south (Grossenbacher, 1997a), and its phylogeography is not well known.

Here, we focus on two European brown frogs that share large parts of their distributions, and compare their range-wide phylogeographic patterns and genetic variation in a wide array of marker systems, ranging from mitochondrial and nuclear single-copy genes to microsatellite loci and sequence reads from the transcriptome. Our target species are the ecologically and morphologically diversified European common frog, *Rana temporaria*, and the more specialized agile frog, *R. dalmatina*. Our goal is to use these species to understand (i) if the previously reported differences in genetic variation among these two species are a range-wide attribute observable across different genetic markers, and (ii) if these species are characterized by different demographic and phylogeographic histories that could explain these patterns.

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